HOMING, POPULATION STRUCTURE AND MANAGEMENT OF ATLANTIC COD (Gadus morhua), WITH EMPHASIS ON SPAWNING AT BAR HAVEN IN PLACENTIA BAY, NEWFOUNDLAND

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Homing, population structure and management of Atlantic cod (*Gadus morhua*), with emphasis on spawning at Bar Haven in Placentia Bay, Newfoundland

by

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Abstract

I have assessed the potential for small-scale population structure within a cod stock on the south cost of Newfoundland, since decreases in productivity can occur if managers fail to match the scale of the management unit to that of the population. A group of cod (*Gadus morhua*) that spawns at the Bar Haven ground (Placentia Bay, Newfoundland) were studied in detail. I examined the homing of adults, and the retention of spawning products. Over three consecutive spawning seasons, all relocations of spawning cod, tagged acoustically at Bar Haven, were within 10 km of the tagging site, the majority within a few hundred meters. No tagged fish were relocated at other known spawning grounds or elsewhere in the bay. Navigation while homing was most likely towards an omnidirectional "attractor" at the spawning ground that dissipates with distance, such as a characteristic sound or geophysical signature. Movements during spawning seasons were sex-specific, and suggested that females move in and out of male-dominated spawning aggregations. Local retention of eggs and larvae was observed, but was greater in warmer water, in which eggs and larvae develop faster, thus settling before drifting with currents out of the bay. Given exacting homing, and local retention, there is a strong possibility that population sub-structure exists within Placentia Bay. However, a review of the literature shows that cod migratory behaviour ranges from sedentary to highly migratory, and no behaviour is limited to inshore or offshore environments, or to any part of the North Atlantic range.

Although management of cod at Bar Haven may benefit from recruitment predictions resulting from simple age 0 cod surveys, predictions more quantitative than a ranking of year-class strengths were complicated by density-dependent site-use. However, important, temporally stable nursery grounds were recognisable within the bay. Acoustic assessment of Bar Haven spawners was complicated by high rates of turnover of individuals within a spawning season. Thus, acoustically determined abundance estimates from serial surveys must be adjusted to account for the proportion of individuals present during more than one survey.

Overall, I review the diversity of cod migratory behaviours, and illustrate the potential for small-scale population structure, specifically where cod perform precise homing migrations and eggs are retained near spawning areas. I discuss how managers can use information about population structure to hinder local depletions and to help avoid overall reductions in productivity.

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1 General introduction and overview

1.1 Introduction

After the great fisheries in the western North Atlantic collapsed in the early nineties, several authors (e.g., Lear and Parsons, 1993; Roughgarden and Smith, 1996; Myers et al., 1997) predicted rates of recovery that were far more rapid than those that have since been observed. According to Myers et al. (1997), many erroneous estimates were the result of poor approximations of population growth rate. However, despite using a robust estimate of population growth rate, Myers et al. (1997) wrongly predicted a biomass doubling in four years, a tripling after seven years and recovery to "desired" levels after about a decade of minimal fishing mortality. Unfortunately, after four to five years of fishing moratoria followed by four to five years of modest fishing, most stocks of Atlantic cod (*Gadus morhua*) have not increased in biomass at predicted rates, none have returned to pre-collapse levels, and some continued to decline during moratoria (Lilly et al., 1999; Hutchings, 2000). Hutchings (1999) suggested that the population growth rate can be influenced by stochastic variation in life history variables, and even be negative when conditions result in poor post-reproductive survival. Another possible explanation for the overly optimistic recovery predictions is a failure to account for possible depensatory responses of populations at low biomass levels. Although Myers et al. (1995) concluded that depensation is not a common characteristic of marine fish stocks, the failure of western Atlantic cod stocks to recover at rates predicted from nondepensatory models must be considered.

Depensation may be caused by lowered recruitment, reduced growth, or increased natural mortality rates (or some combination of these) at low population size. Frank and

Brickman (2000) pointed out that small-scale population structure may make stocks more vulnerable to recruitment overfishing and depensatory processes than would be the case under a panmictic stock structure. Using a model in which management units were comprised of multiple spawning groups, they demonstrated that a failure to treat each spawning group separately can lead to extinctions and a concomitant reduction in the productivity of the management unit. Thus, productivity decreases at low levels of abundance within the management unit (i.e., depensation). Moreover, they showed that regional (management unit) depensation can occur despite normal compensatory dynamics within spawning groups. Given the present results, that small-scale population structure can exist within cod management units, I suggest that depensatory processes such as those described in (Frank and Brickman, 2000) may be important in Placentia Bay. Given its importance to fishery management, I focus on population structure in this thesis, especially the mechanisms which could generate and maintain small-scale populations of Atlantic cod.

The development and maintenance of population structure depends on the segregation of spawning groups during reproduction (Templeman, 1979), and on spawning products being retained in such a way that allows maturing individuals to eventually join their parent population. For many marine fishes, eggs are broadcast into the water column, and develop while drifting passively with local currents. Although Atlantic cod is a broadcast spawner (Jónsson, 1982; Bergstad et al., 1987; Jákupsstovu and Reinert, 1994) there is growing but controversial evidence from genetic studies for the existence of local cod populations within management units throughout its range (Ruzzante et al., 1998, 1999; Beacham et al., 2000), particularly in coastal areas. For small-scale population structure of this kind to exist, two biological processes must be limited: 1) dispersal of eggs and larvae; and 2) straying of adults among spawning grounds.

Dispersal of eggs and larvae can be limited if spawning occurs in areas where oceanographic conditions favour retention of eggs. Retention is a common feature at oceanographic fronts, and can result where bottom topography creates complex current patterns (e.g., Mullineaux and Mills, 1997). Spawning in retention areas has been documented for many marine species, and explains population richness of several species (Sinclair, 1989). Alternately, effective dispersal can be limited if young fish home to natal areas subsequent to their departure from distant nursery grounds. Natal homing has been documented for diadromous species (Hasler, 1971; Gross et al., 1988) and for estuarine spawners (Thorrold et al., 2001). Depending on the species, salmonids are thought to use some combination of celestial cues (Quinn and Brannon, 1982) and magnetic fields (Quinn et al., 1981) to navigate in the open ocean, and spawning sites are recognised by olfactory identification of stream characteristics (Hasler, 1966). However, for marine broadcast spawners a mechanism whereby widely dispersed juveniles home to their natal ground (where they may have only existed as undeveloped eggs) has not been demonstrated (Rätz, 1994), and remains largely speculative (Harden-Jones, 1968; Godø, 1984c; Netzel, 1990; Hovgård and Riget, 1991).

Straying may be limited among migrating populations if individuals repeatedly and precisely return to the same location each time they spawn (homing) or if the home range of individuals is small relative to the distance among spawning grounds (site fidelity). Homing is well recognised in diverse animal taxa (see Papi, 1992), including many fishes (Quinn and Dittman, 1992), but is largely speculative for Atlantic cod (Harden-Jones, 1968; Godø, 1984c; Netzel, 1990; Hovgård and Riget, 1991). How individual cod might locate their oceanic spawning ground remains largely unknown. Nonetheless, other fishes navigate using a variety of methods including chemoreception (the use of chemical gradients to orient toward a signature destination), magneto-reception (sensing of the magnetic field of the earth), the use of spatial memory (to follow underwater landmarks) or solar/celestial cues (Hasler, 1971; Wootton, 1992). (e.g., Rose, 1993) suggested that knowledge of migratory routes is transmitted socially from older to younger cod.

Homing of cod has traditionally been assessed by catching and releasing fish at a given location, after tagging them. When tagged individuals are recaptured (usually by sport or commercial fishers) their location is sometimes noted, and reported to the resource managers (e.g., Taggart et al., 1995). These data are limited because only two observations of location are made for any given individual (mark, and then recapture). For example, if fish must pass one spawning ground en route to another ground, a portion of these fish may be recaptured at a location that is not their final destination. Without the ability to make multiple observations of individuals, I cannot determine if fish are spawning at a certain ground, or simply passing through. Conventional tagging studies also cannot determine the portion of fish which use the same ground over several years, and cannot address questions regarding the behaviour of fish on the spawning ground, the turnover of spawners on the ground, or the amount of time each individual spends there. However, advancements in underwater telemetric techniques now allow tagged individuals to be observed and tracked for extended periods, sometimes for several years. In this thesis, I take advantage of this new technology to assess multi-year homing of cod, and to determine their ability to return to a capture site after being transplanted. Underwater telemetry was also used to examine individual differences in behaviour, including the effects of sex and age on movements around the spawning ground.

In this thesis, I also developed a telemetric management tool to assess the independence of a set of abundance estimates from serial surveys. Since surveys of abundance are sometimes repeated during a season, it is important to determine whether or not these discrete "snapshots" are counting the same fish. When the time of residence of individual fish on the spawning ground is short relative to the interval between surveys, abundance estimates from each survey should be summed to estimate total abundance. If the residence time is protracted, the estimates should be averaged. Since intermediate cases are likely, I suggested the use of telemetry to assess the average residence times of individual fish.

I explored another potential management tool in this thesis, namely the use of proxy variables to forecast recruitment to the Bar Haven spawning group. Proxy variables are indices that can reliably predict the value of a variable of interest. In this case, I explored whether depth, temperature and salinity, and a number of biotic factors could predict recruitment, measured as the relative abundance of demersal juveniles in Placentia Bay. Demersal juvenile distribution was also used to identify important nursery grounds for the cod in Placentia Bay.

1.2 Overview

In order to ascertain the potential for population structure at the Bar Haven spawning grounds, I needed to examine the factors which, in combination, can allow for the development of structure. These are: 1) the potential for retention of eggs and larvae in the vicinity of spawning; and 2) the degree of homing and/or site fidelity of adult cod to their spawning ground. I examined the first factor in Chapter 3, and the second factor in Chapters 4 through 6. Specifically, in Chapter 3, I examined evidence for local retention around the Bar Haven spawning ground by looking at the distribution of the successive life-history stages from spawning events to settlement over a three-year period. In Chapter 4, the pervasiveness of homing and site-fidelity of cod to spawning grounds was reviewed using published tagging studies from throughout the North Atlantic. In Chapter

5, I narrowed the scale of focus from the entire North Atlantic to that of one single spawning ground in Placentia Bay, and studied the homing of acoustically tagged cod over three consecutive spawning seasons. In Chapter 6, I examined the ability of Bar Haven cod to home after being transplanted to locations throughout the bay.

The remaining chapters have management of cod in Placentia Bay as their common theme. In Chapter 7, I explore individual differences in the behaviour of cod around the spawning grounds in order to determine if fishing on the spawning grounds could result in differential catch rates of a given sex or size of cod. In Chapter 8, I developed a method for stock assessment in which telemetric data allowed estimates of spawner abundance to be adjusted to account for turnover of individuals on the spawning ground. In Chapter 9, I attempted to determine if a simple set of proxy variables could be used to forecast recruitment, and examined whether important nursery areas in Placentia Bay could be determined from the distribution of demersal juveniles.

Overall, I present in this thesis my attempt to quantify the homing capabilities of Bar Haven cod and the degree of local retention of their spawning products in order to assess the potential for small-scale population structure. The result will be of interest within the fishery because management over inappropriate spatial scales can result in local depletions and overall reductions in productivity (Hilborn and Walters, 1992; Frank and Brickman, 2000). The results presented here for Bar Haven cod are likely to apply to other groups of cod, especially those in coastal regions and retention areas in the North Atlantic. Similar arguments could potentially apply to other broadcast spawning species with wide-spread distribution and localised spawning grounds.

1.3 Terminology

For this thesis it was necessary to define and distinguish between the terms "population", "management unit" and "stock". "Population" refers to a biological grouping of individuals that were relatively isolated from individuals in other populations during spawning. Spawning isolation could result from geographic distance, differences in timing, or from assortative mating at a common site. A "management unit" is a geographic area, the boundaries of which delimited individuals into artificial groupings for the purposes of assessment and management. Under ideal circumstances, the boundaries of a management unit should match those of the population it purports to manage. "Stock" refers to the individuals within a management unit. The stock of an ideal management unit should be a population.

2 Co-authorship statement

2.1 General

With the exception of that noted below, all major intellectual and practical contributions to this work were my own. Except where noted, I designed the research proposal, and carried out all aspects of the research, data analysis and manuscript preparation. I am principal author on all manuscripts included in this thesis. My supervisor, Dr. George A. Rose is junior author on all manuscripts. He was responsible for funding the research included here, as well as for valuable insights and editorial comments. At the end of each chapter, I acknowledge all those who provided advice, equipment and field assistance.

2.2 Chapter 3 Co-authorship

This chapter was the result of a major collaborative effort among the members of the Fisheries Conservation Chair. The overall concept was to explore relationships among the different life-history stages of cod in Placentia Bay. All those named contributed data and ideas, for which I am grateful. However, after many long and fruitful discussions, it was left to me to decide the direction and scope of the synthesis of these data for my thesis. The data on ichthyoplankton came from research by Ian A. Bradbury, whose thesis supervisor was Dr. Paul V. R. Snelgrove. The spawner data came from research by Gareth L. Lawson, whose thesis supervisor was Dr. George A. Rose. All data collected by Bradbury and Lawson have been published elsewhere, in a different form, and have been referenced in the text of the chapter. I take full responsibility for the analyses and interpretation of these data, and discussion and wording of the results. Daily otolith rings were counted by Cynthia Mercer.

3 On local retention, population structure and spawning timing in a marine broadcast spawner, Atlantic cod

Co-authors: Ian R. Bradbury, Gareth L. Lawson, George A. Rose, and Paul V. R. Snelgrove

3.1 Abstract

To determine the degree to which Atlantic cod (*Gadus morhua*) eggs and larvae were retained locally from spawning at Bar Haven, Placentia Bay, Newfoundland, the timing, magnitude and distribution of the various life-stages from spawning through to juvenile recruitment were monitored for three consecutive years. In 1997, spawning rate declined after that observed in April in 0 °C waters, and early stage eggs were plentiful, but late stage eggs and larvae were few. Poor recruitment of demersal juveniles followed. In comparison, peak spawning in 1998 was at least one month later, and occurred in 11 °C water. Although fewer early stage eggs were produced in 1998, larger numbers of late stage eggs and larvae were observed within the bay, and stronger local recruitment of demersal juveniles resulted. Transport of eggs and larvae into the bay was not observed, suggesting that recently settled juveniles within the bay were of local origin. In all years, demersal juveniles were distributed in the head of the bay and on the western side (downcurrent from Bar Haven), suggesting retention of Bar Haven spawning products within the bay. The similarity in distribution of early and late stage eggs within a given year was further evidence of local retention. The extent of local retention was related to the timing (or temperature) of spawning. Later spawning in warmer water led to faster egg development and larval growth, and enhanced local retention. Smaller-scale population structure, associated with local retention, implies that the scales of present

fishery management may be too large, that local sub-stock decimation may lead to depensatory dynamics and overly optimistic predictions of population growth rates on vacant grounds.

3.2 Introduction

The development and maintenance of population structure in marine fishes depends on segregation during reproduction (Templeman, 1979). Eggs produced must be distributed in such a way to allow survivors to eventually join their parent population. However, many marine fishes are broadcast spawners whose eggs are released into the water column and develop while drifting passively with local currents. Widespread dispersal is considered typical of these species because in the unpredictable marine environment dispersal maximises the probability that some products will experience conditions favourable for survival (Sinclair, 1989). However, a mechanism whereby widely dispersed juveniles of these species are able home to their natal ground (where they existed only as undeveloped eggs) has not been demonstrated (Rätz, 1994). As a result, stocks are typically considered to have expansive distributions with elastic edges, potentially encompassing multiple neighbouring spawning grounds, and management has been practised over large (1000's of km) spatial scales.

Despite being a widespread open ocean and coastal broadcast spawner (Jónsson, 1982; Bergstad et al., 1987; Jákupsstovu and Reinert, 1994) Atlantic cod show evidence of small-scale stock structure. Cod can show a high degree of homing (Tåning, 1940; Godø, 1984c; Lear, 1986b), and there is growing but controversial evidence from genetic studies for the existence of local cod populations within management units in Newfoundland (Ruzzante et al., 1998, 1999; Beacham et al., 2000), Norway (Fevolden and Pogson, 1997) and Iceland (Jónsdóttir et al., 1999), particularly in coastal areas (but see Pepin and

Carr, 1993). If there is indeed small-scale stock structure, what is the mechanism by which young cod eventually recruit to their parental stock? Is there a complex long-distance homing behaviour, or are the majority of eggs that survive and recruit retained locally? These and related questions are difficult to answer with traditional single life-stage studies using tagging or genetics. Few studies have attempted to sequentially monitor all stages of the process from spawning to recruitment in marine fishes, and none that I am aware of have done this with Atlantic cod.

The south coast of Newfoundland and adjacent banks (Fig. 3-1) currently hold the largest cod biomass in the Northwest Atlantic. In order to determine the degree of local egg and larval retention in Placentia Bay, I follow the stages of the cod life cycle from spawning through to recruitment for three consecutive years by combining demersal juvenile catch data with recently published accounts of spawner (Lawson and Rose, 2000b, a) and ichthyoplankton (Bradbury et al., 2000) distributions from concurrent periods. These accounts suggest that eggs and larvae may be retained locally. In this paper, I examine the distribution and relative abundance of the demersal juvenile life stage to explore the hypothesis that local spawning and egg and larval retention leads to local recruitment of juveniles. I also investigate the oceanographic and biological conditions under which local retention may occur. Finally, I discuss the scale at which management measures are applied in this region and a depensatory mechanism to account for the failure of Atlantic cod stocks to recover at predicted rates.

3.3 Methods

3.3.1 Survey Area

Placentia Bay (Fig. 3-1) is the largest embayment in Newfoundland. Its dominant currents enter on the east and exit on the west side of the bay (mean north-south current speeds are 10.56 ± 8.70 cm s-1 into the bay and 3.29 ± 2.93 cm s-1 out of the bay, Hart et al., 2000). Currents in the head of the bay are more variable, and weaken from spring to summer (Schillinger et al., 2000). Sea surface temperatures, determined from AVHRR (Advanced Very High Resolution Radar) satellite imagery (http://dfomr.mar.dfo-mpo.gc.ca/science/ocean/ias/seawifs/seawifs_3.html), and from CTD casts, cycle between -0.5 °C in spring and 18 °C in summer (Fig. 3-2). Phytoplankton blooms occur early in spring and autumn. At other times elevated phytoplankton productivity is observed primarily in upwelling areas in the northern and western portions of the bay (a difference of approximately 2.40 μg l-1 between the inner and outer parts of the bay, Bradbury et al., 2000).

3.3.2 Spawner Surveys

Information on timing and distribution of spawning activity came from Lawson and Rose (2000b; 2000a). Spawners were surveyed during daylight hours (Lawson and Rose, 1999) over 12 transects spaced 4 nautical miles apart (Fig. 3-1) using two standard sphere-calibrated BioSonics single beam DT4000 echosounders (38 and 120 kHz, 6 ° half-power beam widths, pulse duration 0.4 ms, 42 kHz digital sampling rates, pulse rates 2 pings s^{-1}). Additional adaptive surveys were conducted over identified grounds and aggregations (Lawson and Rose, 2000a). Acoustically located cod aggregations were sampled using handlines. Only cod were ever captured, and previous acoustic and submersible surveys in this area indicated that species acoustically-similar to cod (e.g., haddock, pollock) are rare (Lawson and Rose, 2000b). Acoustic backscatter was scaled to areal density (cod m^{-2}) using an empirically determined (Rose and Porter, 1996) relationship between target strength and fish length: $TS_{(dB)} = 20 \log_{10} Length_{(cm)} - 66$ (at 38 kHz). Acoustic surveys were conducted throughout the pre-spawning and spawning period (April to July) of 1997 and 1998. No adult data was available for 1999.

Acoustically located cod aggregations were sampled to assess maturity state which, for females, was categorised as "immature" (ovaries small, undeveloped), "ripening" (eggs present in ovaries, but none hydrated), "spawning" (hydrated eggs present in ovaries), or "spent" (ovaries fully developed, but largely empty and stretched to indicate the recent presence of eggs) as per Morrison (1990).

The distribution of spawning activity was determined by plotting the global position of all cod aggregations greater than 0.005 fish m^{-2}. These densities were determined from acoustic integration (MacLennan and Simmonds, 1992). The cut off of 0.005 fish m^{-2} was chosen because it is characteristic of spawning aggregations. Fishing on these aggregations revealed cod in spawning condition (Lawson and Rose, 2000a).

The timing of spawning activity was determined using maturity data collected from cod aggregations that were located during acoustic surveys. The percent of sampled cod that were female and in spawning condition (hydrated cod eggs will usually be spawned within three days, Kjesbu et al., 1990) was coupled with the density of cod from acoustic surveys at the Bar Haven spawning ground (which were representative of patterns throughout the bay, (Lawson and Rose, 2000b) to calculate the density of spawning females. Then, this value was used to calculate "predicted egg density" using a fecundity function (Pinhorn, 1984) based on the length distribution of sampled cod. This egg density was then plotted for each survey of the bay and plotted against the survey mid-date.

3.3.3 Ichthyoplankton Surveys

Information on ichthyoplankton distributions came from Bradbury et al. (2000). Planktonic eggs and larvae were sampled over a grid of 48 stations, spaced four nautical miles apart along six parallel transects spaced eight nautical miles apart (Fig. 3-1). Sampling was conducted near-monthly throughout the spawning and post-spawning periods from April to August, 1997, from April to September, 1998, and from April to August, 1999. Ichthyoplankton samples were collected using a 4 m^2 Tucker trawl with double oblique tows to 40 m depth. No samples were taken from the eastern side of the bay in 1999.

Cod eggs and larvae were counted and concentrations computed using the volume of water sampled, which was estimated from flow-meters at the mouth of the net. All cod eggs were staged I-IV (Markle and Frost, 1985). Although stage I cod eggs cannot be distinguished from those of haddock and witch flounder, late stage eggs and larvae of the latter two species were rare (<1%) thus all stage I eggs were assumed to be cod. Predictions of egg development time were made in relation to temperature (Pepin et al., 1997).

Concentrations of cod larvae and the various stages of eggs were plotted and contoured for each of the years under study. Temporal trends were examined by plotting the mean concentration for each survey of the western side of the bay against survey mid-date. Only western stations were included in the plot in order to facilitate comparison to 1999 when no eastern samples were collected. In 1997 and 1998, western concentrations far exceeded those of the eastern side of the bay (Bradbury et al., 2000).

3.3.4 Demersal Juvenile Surveys

Demersal juveniles were sampled with a 25 m bottom seine, fished from shore at 18 sites around the bay from September to December, 1997-1999 (Fig. 3-1). The seine fished a standardised area of 880 m^2 on each tow (16 m along shore x 55 m offshore). Deployment of the seine is described in Schneider et al. (1997). Specific sites were chosen based on the presence of eelgrass habitat and accessibility by small craft.

All sites were sampled in as short a period as possible at the start of every month, in an order that was largely determined by weather. Sampling at any site was not confined to a particular tide level or time of day, although all sampling was done during daylight hours. At each site, two sets approximately 30-100 m apart were made in immediate succession. Within a metre, the same sets were made each month. The sum of the two sets is used in all analyses.

The standard length of cod caught in each tow was recorded, and whenever possible, fish were returned alive to the sea. Hatch dates were calculated from an age-length relationship developed using standard lapillus daily-otolith-ring counts ($Age_{(days)} = 26.97 + 1.414\ SL_{(mm)}$; $r^2 = 0.71$; cod of standard length between 15 and 65 mm were aged; 73.1% of the young-of-the year cod caught were in that size range), and spawn dates were calculated from the development-temperature relation described in Pepin et al. (1997).

3.4 Results

3.4.1 Spawners

The distribution of spawning varied among years. Spawning females in 1997 and 1998 were concentrated at three shoal areas of Placentia Bay: Cape St. Mary's, Oderin Bank, and Bar Haven (Fig. 3-3a-b). Spawning ground usage varied between years. Cape St.

Mary's and Oderin Bank were used most heavily in 1997 and 1998, respectively. The Bar Haven shoal was used more consistently during all years. Timing of spawning also varied among years. In 1997, highest adult spawner densities were observed in April (mean surface temperature 0.0 °C). In 1998, peak spawning was delayed until June when surface temperatures were 11.0 °C.

3.4.2 *Ichthyoplankton*

Early stage egg concentrations were highest in the inner bay near the Bar Haven ground in all three years (Fig. 3-3c-e). In all three years, egg concentrations were highest during the earliest surveys, and declined thereafter, most rapidly in 1997 (Fig. 3-2). During the three-year period, the egg concentrations were greatest early in the 1997 spawning season; lowest overall concentrations were seen later that same year. Late stage eggs (Fig. 3-3f-h) and planktonic larvae (Fig. 3-3i-k) were concentrated in the inner and western parts of the bay 'downstream' of the spawning grounds. The larval concentrations were very low in 1997 and 1999; only in 1998 was there significant larval presence in the bay, with peak values observed during the August 7 survey (Fig. 3-2).

3.4.3 *Demersal Juveniles*

Post-settlement juveniles were concentrated disproportionately in the inner bay and on the western side in all three years (Fig. 3-3l-n; 1997: $\chi^2_2 = 63.6$, $p < 0.001$; in 1998: $\chi^2_2 = 108.3$, $p < 0.001$; in 2000: $\chi^2_2 = 6.64$, $p < 0.05$). They were caught in very low numbers in both 1997 and 1999. Catches were 5 fold higher in 1998 (Fig. 3-2), the only year in which catches were comparable to those of other Newfoundland bays (Smedbol et al., 1998). Back-calculated spawn dates (Fig. 3-2) show that the majority of juveniles caught were the result of spawning later in the season. In all three years, greater than 50% of the juveniles caught were the result of spawning that occurred after August 8. Moreover, only a small minority resulted from pre-June spawning (7%, 20% and <1% for the three years respectively).

3.5 Discussion

3.5.1 Local Retention

The presence of demersal juvenile cod near the spawning grounds at Bar Haven could be taken as evidence of local retention of spawning products. Given the counter-clockwise circulation in the bay, and the scarcity of eggs and larvae on the eastern side, it is unlikely that these juveniles are products of spawning events at Cape St. Mary's or further offshore. Although the import of spawning products is possible, localised retention is a more parsimonious explanation for the disproportionately large numbers of demersal juveniles caught in the head of the bay in all years, and the considerable catches of late stage eggs found at the same stations where early stage eggs were concentrated previously in the season. Drifters released at Bar Haven during the spawning season were most often recovered among the islands in the head of the bay, along the west coast of Merasheen Island (Bradbury et al., 2000). These drifter relocation sites are similar to those where young of the year juveniles were found each autumn. Retention of propagules in the head of the bay is consistent with the variable and relatively weak currents (Schillinger et al., 2000), complex bottom topography, and presence of many small islands, particularly on the west side of the bay.

The data suggest that retention of demersal juveniles may be a function of the timing of spawning in addition to the location and amount of eggs produced. The peak in overall egg production (stages I - IV) occurred in April of 1997, concurrent with the peak in spawning activity in the head of the bay. This spawning resulted in poor local recruitment, with negligible numbers of larvae and few settled juveniles within the bay. In 1998, peak spawning was delayed until late June and evidence of spawning existed as late as September. In that year, the greatest numbers of late stage eggs, larvae, and demersal juveniles were observed in the bay despite fewer eggs (Stages I - IV) being produced. Although water temperatures were similar among years, the one month delay in spawning was accompanied by an 11 °C difference in water temperature during peak activity. Warmer waters result in shorter egg and larval development times and a computed 73% decrease in egg stage duration as a consequence of faster development rates (Pepin et al., 1997). Larvae were therefore more likely to develop swimming behaviour and settle to the bottom before being swept out of the bay, and the overall time spent in the vulnerable pelagic stage was decreased. Furthermore, in all years, back calculations of spawning dates using otolith ages and expected egg stage durations indicated that locally settled juveniles resulted mainly from spawning that occurred from June onward (Fig. 3-2). Larvae and demersal juveniles that were spawned before June were rarely observed despite an abundance of pre-June spawning, presumably because eggs that developed in colder springtime waters were less likely to hatch within the bay. It can be concluded that the degree of successful local recruitment is a function of the amount of spawning which occurs in warm water.

It is important to note that the fate of eggs and larvae that drift out of the bay is unknown. They could be swept southwestward and settle successfully on St. Pierre Bank, or inshore, further west along the southern coast of Newfoundland. At least in recent years, nearshore environments have been identified as the most important nursery grounds for cod, with relatively few young-of-the-year found on Newfoundland offshore banks compared to nearshore areas on the Northeast coast (Dalley and Anderson, 1997). Although offshore sampling from south of Placentia Bay was limited both temporally and spatially, Bradbury et al. (2000) showed very low concentrations of early egg stages and an absence of late stage eggs.

3.5.2 Population Structure and Depensation

Recent microsatellite evidence (Ruzzante et al., 1998) has suggested that fish caught in the head of Placentia Bay can be distinguished genetically from those caught near Cape St. Mary's. Moreover, a recent telemetric tagging study has demonstrated that cod spawning at Bar Haven can exhibit exacting homing over multiple spawning seasons, with no evidence of straying to other spawning grounds in Placentia Bay (Chapter 5). Both genetic and tagging studies are suggestive of small-scale population structure. The present study documents evidence of one mechanism (i.e., local retention near the Bar Haven grounds) by which structure could be sustained.

Several studies (e.g., Lear and Parsons, 1993; Roughgarden and Smith, 1996) predicted rates of recovery in Northwest Atlantic cod stocks far greater than those observed. According to Myers et al. (1997), the erroneous estimates were the result of poor approximations of population growth rate (r). More conservative estimates of r used by Myers et al. (1997) predicted a biomass doubling in four years, a tripling after seven years and recovery to "desired" levels after about a decade of minimal fishing mortality. Unfortunately, after years of moratoria (with limited fishing allowed in only a few regions over the past four to five years), most stocks of Atlantic cod have not increased at predicted rates, none have returned to pre-collapse levels, and some continued to decline despite fishing moratoria (Lilly et al., 1999; Hutchings, 2000). One explanation for the overly optimistic predictions is a failure to account for depensatory responses of populations at low biomass levels

Small-scale population structure, with concomitant local retention of early life stages, and homing of adults may make stocks more vulnerable to recruitment overfishing and depensatory processes than would be the case under a panmictic stock structure. Frank and Brickman (2000) made this explicit with a model in which management units were comprised of multiple spawning groups. They demonstrated that a failure to treat each spawning group separately can lead to extinctions (which go "unnoticed" by the manager), and a concomitant reduction in the productivity of the management unit. Thus, productivity decreases at low levels of abundance within the management unit (i.e., depensation). Moreover, they showed that regional (management unit) depensation can occur despite normal compensatory dynamics within spawning groups. Given the present results, that small-scale population structure can exist within cod management units, I suggest that depensatory processes such as those described in Frank and Brickman (2000) could be responsible for the failure of cod to recover at predicted rates.

3.6 Acknowledgements

I thank all members of the Fisheries Conservation Chair, especially Ian Bradbury, Gareth Lawson, George Rose and Paul Snelgrove. I also thank the crews of the R.V. Mares, R.V. Innovation, C.C.G.S. Shamook and C.C.G.S. Teleost, P. Pepin, B. deYoung, C. Mercer, D. Sencial, and personnel of the Atlantic Reference Centre at the Huntsman Marine Lab.

Figure 3-1: Map of Placentia Bay. Acoustic transects are shown as dashed lines. Ichthyoplankton stations are shown as dots. Open dots were not sampled in 1999. Stars indicate the sampling sites for demersal juveniles. Inset: The Island of Newfoundland with box showing location of Placentia Bay.

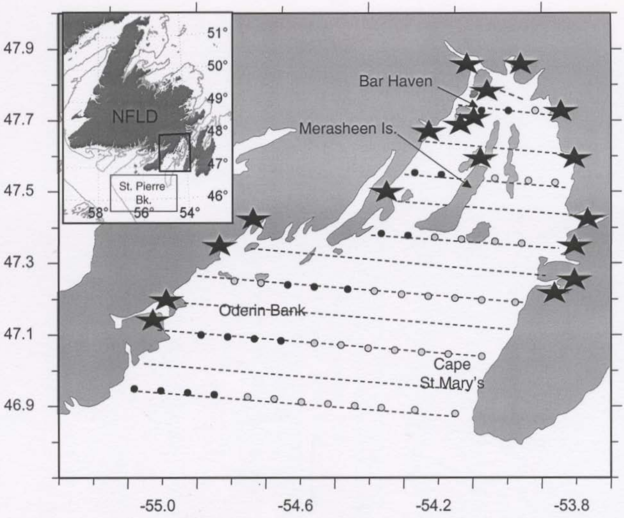

NFLD
51°
50°
49°
48°
47°
46°
58°
56°
54°
St. Pierre Bk.
Bar Haven
Merasheen Is.
Oderin Bank
Cape St Mary's
47.9
47.7
47.5
47.3
47.1
46.9
-55.0
-54.6
-54.2
-53.8

Figure 3-2: Temporal trends in temperature (°C), egg density (number per m^{2}; calculated from spawning female densities), egg and larval concentration (number per m^{3}; from Tucker trawl surveys), and demersal juvenile catch (number caught in monthly beach seine surveys) for Atlantic cod in Placentia Bay from 1997-1999. Note log scales for egg density and concentration. In the bottom panel, the three rightmost lines represent catch of demersal juveniles (see the right vertical axis). Also shown, with lines lacking symbols, are spawn dates back-calculated from the length distribution of the demersal juveniles (leftmost lines, see the left vertical axis).

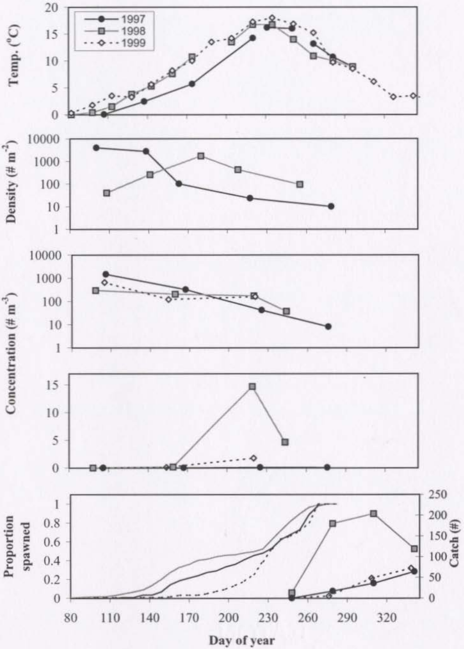
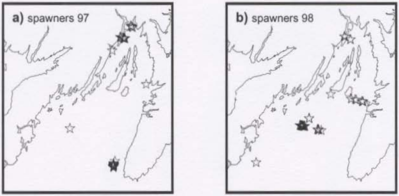
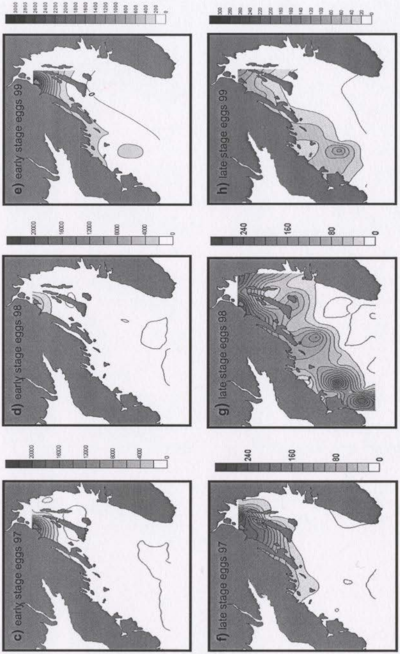
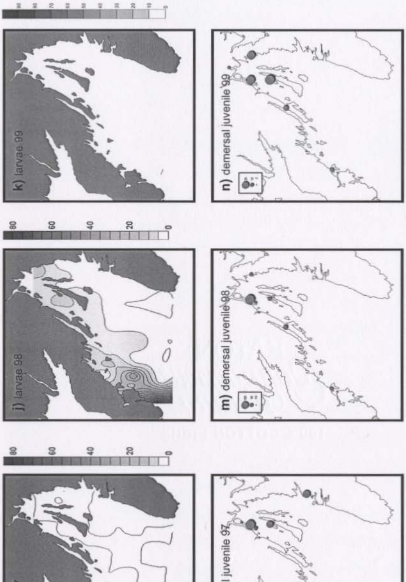

1997
1998
1999
Temp. (°C)
20
15
10
5
0
Density (# m-2)
10000
1000
100
10
1
Concentration (# m-3)
10000
1000
100
10
1
15
10
5
0
Proportion spawned
1
0.8
0.6
0.4
0.2
0
Catch (#)
250
200
150
100
50
0
80
110
140
170
200
230
260
290
320
Day of year

Figure 3-3 - Maps showing the distribution of the various Atlantic cod life history stages in Placentia Bay from 1997 to 1999. Note variable scales. 1997 data are shown in panels a, c, f, i and l. 1998 data are shown in panels b, d, g, j and m. 1999 data are shown in panels e, h, k, and n. **(a-b)** Spawners: stars indicate the position of spawner densities > 0.005 fish m^{-2} (adapted from Lawson and Rose, 2000b; 2000a) during the spring and summer of each year; **(c-k)** Ichthyoplankton: The concentration at each station is averaged over spring and summer of each year. Contours are lines of equal ichthyoplankton concentration (# m^{-3}). Early stage eggs (Stages I and II) are shown in panels c-e. Late stage eggs (Stages III and IV) are shown in panels f-h. Larval concentrations are shown in panels i-k). All ichthyoplankton panels are adapted from Bradbury et al. (2000). **(l-n)** Demersal juveniles: Expanding circles represent the number of age 0 cod caught at each site during the autumn of each year




c) early stage eggs 97
20000
16000
12000
8000
4000
0
d) early stage eggs 98
20000
16000
12000
8000
4000
0
e) early stage eggs 99
3000
2800
2600
2400
2200
2000
1800
1600
1400
1200
1000
800
600
400
200
0
f) late stage eggs 97
240
160
80
0
g) late stage eggs 98
240
160
80
0
h) late stage eggs 99
300
280
260
240
220
200
180
160
140
120
100
80
60
40
20
0


i) larvae 97
j) larvae 98
k) larvae 99
l) demersal juvenile 97
m) demersal juvenile 98
n) demersal juvenile 99
80
60
40
20
0
80
60
40
20
0
90
80
70
60
50
40
30
20
10
0

4 Site fidelity, homing and population structure of cod throughout the North Atlantic

Co-author: George A. Rose

4.1 Abstract

Behaviours such as homing and site fidelity can result in the development of population structure within stocks, making effective management more difficult. To assess the pervasiveness of these behaviours, and determine the areas within which population structure can be expected, I reviewed tagging studies for all major stocks of Atlantic cod (*Gadus morhua*) in the North Atlantic. Cod populations can be classified into four categories based on their migratory behaviour: First, populations that perform long-distance migrations and accurately home to spawning grounds; Second those that home less accurately; Third, those that exhibit strong site fidelity, and can be found year-round within a relatively small geographic range; Fourth, populations that disperse or tend to move within large geographic areas. Although the relative proportion of these behavioural categories across the range of the species could not be accurately determined (because of the limitations of conventional tagging studies under review, and the subjectivity with which behaviours are assigned to a category), cod migratory behaviour was highly variable throughout all parts of its range, and no category was limited to inshore or offshore environments, or to any part of the North Atlantic range. Cod sometimes also show more than one type of behaviour within a limited geographic area. This suggests that the spatial scale of population structure may be variable throughout the range of cod, and cannot be predicted using simple rules of thumb. Failure of fisheries management to acknowledge the potential importance of such variations in behaviour when considering

small-scale population structure and productivity may lead to incorrect estimates of population growth rates, and reduce effectiveness of cod management.

4.2 Introduction

Population differences within a species (i.e., population structure) is important within marine fishes not only because of the perceived benefits of genetic diversity (Hunter, 1996) but because spatial and temporal diversity in spawning distribution is thought to enhance the probability of regional recruitment success (Sinclair, 1989; Cushing, 1995). Population structure can develop and be sustained if exchange of spawners and spawning products is limited among populations.

Frank and Brickman (2000) showed that failure to recognise population structure within a management unit can lead to inadvertent sub-structure overfishing, local extinctions and reductions in potential productivity. For example, overfishing can result if populations within a management unit are not equally productive or if fishing effort is not divided proportionally among them (Frank and Brickman, 2000). Fishery managers should therefore strive to treat each spawning population separately, by matching the boundaries of management units to the distributions of the populations in question.

Atlantic cod (*Gadus morhua*) is an open ocean and coastal broadcast spawner (Jónsson, 1982; Bergstad et al., 1987; Jákupsstovu and Reinert, 1994) distributed throughout inshore and continental shelf areas of the North Atlantic. Throughout its range, cod management units are large (1000's of square km, e.g., Jakobsen, 1987; Daan et al., 1990; Halliday and Pinhorn, 1990). However, there is growing but controversial evidence from genetic studies for the existence of local cod populations within management units in Newfoundland (Ruzzante et al., 1998, 1999; Beacham et al., 2000), Norway (Fevolden and Pogson, 1997) and Iceland (Jónsdóttir et al., 1999), particularly in coastal areas. For small-scale population structure of this kind to exist, two biological processes must be limited: 1) dispersal of surviving eggs and larvae; and 2) straying among spawning grounds. A third condition, that juvenile life history stages must be adapted to local conditions, is not considered in this paper.

Dispersal of eggs and larvae can be limited if spawning occurs in areas where oceanographic conditions favour local retention. Retention is a common feature at oceanographic fronts, and can result where bottom topography creates complex current patterns (e.g., Mullineaux and Mills, 1997). Spawning in retention areas explains population richness in several marine species (Sinclair, 1989). Alternatively, effective dispersal can be limited if young fish home to natal areas subsequent to their departure from distant nursery grounds. Natal homing has been documented for diadromous species (Hasler, 1971; Gross et al., 1988) and for estuarine spawners (Thorrold et al., 2001). Depending on the species, salmonids are thought to use some combination of celestial cues (Quinn and Brannon, 1982) and magnetic fields (Quinn et al., 1981) to navigate in the open ocean, and spawning sites are recognised by olfactory identification of stream characteristics (Hasler, 1966). However, for marine broadcast spawners a mechanism whereby widely dispersed juveniles home to their natal ground (where they may have only existed as undeveloped eggs) has not been demonstrated (Rätz, 1994), and remains largely speculative (Harden-Jones, 1968; Godø, 1984c; Netzel, 1990; Hovgård and Riget, 1991).

Straying may be limited among migrating populations if individuals return repeatedly to the same location each time they spawn. The tendency to return to a location in subsequent years is defined in this review as 'homing'. Natal homing (philopatry) is a special case in which the return is to the natal site. Non-migratory populations can also show limited straying when the home range of individuals is small relative to the distance among spawning grounds. Home ranges, in the cases where small-scale population structure develops, will be concomitantly small. In this review, animals which spend the majority of their lifetime within the spawning area are said to show 'site fidelity'.

In Taggart et al.'s (Taggart et al., 1998) review of evidence for localised stock-structure in the Northwest Atlantic, he concluded, based on genetic data and 2 tagging studies that genetically distinguishable populations will be seen on scales between 60 and 100 nautical miles. This implies that the factors affecting the geographic scale of population structure act in a way to consistently compartmentalise cod into units 60-100 nm in size. As such, the accuracy in homing, and the degree of site fidelity of cod would have to be constant throughout its range.

The purpose of this review is to describe the extent of site fidelity, homing and substock structure in Atlantic cod throughout the North Atlantic. The paper is divided into major regions, reviewing studies from the Baltic, North and Irish Seas, the Faroe Islands, Iceland, Greenland, Norway, and North American waters.

4.3 Terminology and Methods

In this review, it is necessary to define and distinguish between the terms "population", "management unit" and "stock". "Population" refers to a biological grouping of individuals that are relatively isolated from other populations during spawning. Spawning isolation could result from geographic distance, differences in timing, or from assortative mating at a common site. A "management unit" is the spatial unit of fisheries management. It refers to a geographic area, the boundaries of which delimit individuals into artificial groupings for the purposes of assessment and management. Management units are typically divided into "statistical areas," geographic areas (usually defined based on latitude/longitude gridlines) from which fisheries statistics (e.g., catch rate, etc.) are gathered. "Stock" refers to the individuals within a management unit. Ideally, the stock of a management unit should be a population. Finally, cod tagged together, or at a common location are called "groups", where it was necessary to avoid making assumptions about their population structure or management. The interim time between spawning seasons is the 'feeding season'.

Throughout this review, I've summarised much of the tagging data in terms of the percent of recaptures that exhibited site fidelity and homing. Site fidelity was calculated as the percent of recaptures caught 'near' the release location over the duration of the tagging study (see below for definition of 'near'). Homing was calculated as the percent of recaptures that were caught 'near' the release location only during the time of year when tagging was done (e.g., during each of the spawning seasons over the course of the study). Given the variable spatial resolution with which the tagging data were presented in the literature reviewed, the distance at which a recaptured individual was considered to be 'near the release location' could not be held constant across experiments. For example, McKenzie (1956) considered recaptures within 12 nm to be 'near' the tagging location, while Taggart et al. (1998) drew the line at 30 nm, and many others were more liberal still (e.g., Lear, 1984a). For studies in which recaptures were divided into statistical areas, recaptures made within the statistical area where tagged were considered 'near'. When recaptures were presented graphically, the area considered to be 'near' would generally correspond to the bank or bay where tagging occurred. Similarly, the variable temporal resolution with which the tagging data were presented in the literature made it impossible to always exclude recaptures made immediately after tagging. Given these considerations, percentages in Table 4-1 should be compared with caution.

Using the site fidelity and homing metrics (shown in Table 4-1), cod were classified into one of four behaviour types, those which are "sedentary" (S = behaviour type 1), those that home, accurately (AH = behaviour type 2) and inaccurately (IH = behaviour type 3), and those which "disperse" (D = behaviour type 4). Cod groups were considered to show behaviour type 1 (S) if > 60% of recaptures showed site fidelity (Table 4-1). Note that as the terms are defined here, cod that show 'site fidelity', (i.e., are found in the same location year-round) will also show 'homing' (i.e., are found in the same location when only a subset of each year, that which corresponds to the season when tagging was performed, is considered). Therefore, only cod groups that showed strong (> 60%) homing and poor (< 60%) year-round site fidelity were considered to show behaviour type 2 (AH). Cod that showed poor site fidelity and poor homing were categorised as behaviour type 3 (IH) or 4 (D) based on qualitative descriptions of the migratory behaviour extracted from the text of the tagging study reports. On the occasions that percentages for both homing and site fidelity could not be obtained from a tagging study report, the qualitative information in the text of the tagging study reports were again used to help assign a behaviour type to the group in question. When insufficient information disallowed the assignment of a behavioural category to a cod group, all possible categories are listed in Table 4-1. Also noted in Table 4-1 are unidirectional movements, usually associated with ontogenetic shifts in range. Populations exhibiting each of these behavioural patterns are discussed below, followed by a more general treatment of homing, site fidelity and population structure.

Migratory behaviour of individuals is likely to be fairly uniform within a population, and is often an important attribute used to define the boundaries of management units (e.g., Templeman, 1979; Lear, 1984a; Godø and Totland, 1995). In this review, I discuss the migratory behaviour of 'populations', rather than that of the 'individuals within a population'.

4.4 The Baltic Sea

The Baltic Sea (Fig. 4-1) is a large shallow estuary with an average depth of 34 m, but with several distinct basins reaching 459 m in depth (Bagge and Thurow, 1994). It is characterised by low salinity, and a strong year-round halocline, which prevents mixing of the upper and lower water layers (Thurow, 1974; Bagge and Thurow, 1994). In the bottom layer, oxygen constantly declines as a result of the decomposition of settled organic particles. Replenishment of the oxygen supply can only result from inflows of water from the Kattegat (Thurow, 1974). These inflows are rare, sometimes at several year intervals, because the water must pass over 2 shallow sills (6 and 18 m) to enter the Baltic, and only occur under extreme weather conditions in which strong, westerly winds prevail (Bagge and Thurow, 1994). Good year-classes in the Baltic are in general the result of these inflows (Otterlind, 1974, 1984). The northern and easternmost areas (the Gulfs of Bothnia and Finland) are less affected by these inflows. Both have low salinities year-round (around 5 ppt) and no sharp halocline, thus no oxygen deficiency (Modin, 1987).

The low salinity in the Baltic poses problems to cod reproduction (Westin and Nissling, 1981; Rohlf, 1997). When the salinity drops below 11 ppt, eggs will sink to the bottom where presumably they do not survive (Uzars et al., 1991 cites Glowinska and Voznjak, 1980, and Grauman, 1961). As a result, effective spawning is restricted to the deep saline basins in the southern parts of the Sea (Rutkowicz, 1959). This results in a patchy distribution of spawning which could allow for the existence of several small populations in the area. Despite considerable effort, no early stage eggs have been found in less saline areas (Otterlind, 1959; Modin, 1987).

Cod in the eastern and western Baltic do not appear to mix extensively. Studies of the morphometric, meristic (Schmidt, 1930; Poulsen, 1931; Ziecik, 1938; Birjukov, 1969; Bagge and Knudsen, 1974; Kändler 1944, as cited in Bagge and Steffensen, 1989; Berner and Müller, 1989) and biological characters, such as spawning time (Bleil and Oeberst, 1997) or egg size (Kändler, 1944, as cited in Otterlind, 1966), reveal that the boundary between the range of the two groups of cod lies near Bornholm. One form, called the "Baltic cod", *Gadus morhua callarias* (Svetovidov, 1963), inhabits the areas east of Bornholm, and northwards into the Gulf of Bothnia to about 63 °N. The other form, *Gadus morhua morhua*, inhabits the areas west of Bornholm, the Belt Seas and Kattegat, and resembles a transition between eastern Baltic cod and North Sea cod. Berner and Vaske (1985) confirmed the differences between forms, but found more extensive mixing in the Arkona and Bornholm areas than was previously known.

4.4.1 Western Baltic Cod

The cod in the western Baltic spawn in the deeps of Mecklenburg and Kiel Bays, the Belt Sea and in Arkona Basin (Hinrichsen et al., 1999 cites Kändler, 1949 and Berner, 1960). Some fish travel to the southern Kattegat to spawn (Berner, 1967; Bagge, 1969b; Aro, 1989) but no reverse migration has been observed (Bagge, 1981; Otterlind, 1985). Most fish undertake only short migrations from shallow-water feeding grounds to the spawning deeps and back (Berner, 1967, 1974; Bagge, 1981; Berner, 1981), however migrations may reach the Bornholm area, the Slupsk Furruw, and even Gdansk Bay (Berner, 1967, 1974; Tiews and Lamp, 1974; Berner, 1981).

Netzel (1963; 1990) believed that western Baltic cod were capable of natal homing. In years of strong westerly winds, when inflows into the Baltic occur, western Baltic cod eggs, which can be discriminated from eastern Baltic cod eggs by size (Kändler, 1944, as cited in Otterlind, 1966), and spawn date (Hinrichsen et al., 1999), have been found in the areas around Bornholm (Otterlind, 1966; Aro, 1989; Hinrichsen et al., 1999). Netzel's observed movement of tagged fish from the southern Baltic into Arkona might have represented a return migration of these cod to their natal grounds, but there is no real evidence for this conclusion.

4.4.2 Eastern Baltic Cod

The cod in the eastern Baltic spawn in four main grounds: Bornholm Deep, Slupsk Furrow, Gdansk Deep and Gotland Deep (Wieland and Horbowa, 1996 cites Strodtman, 1906 and Kändler, 1944, 1949). Fish spawning at each of these grounds could not be distinguished biologically (e.g., age structure Tiews, 1974; or fecundity Kraus et al., 1999) or morphometrically (Birjukov, 1969). Since the 1950's, almost 60000 cod have been tagged by all countries bordering the Baltic (Bagge et al., 1994). Reviews of these experiments are given in Bagge and Steffensen (1989) and in Aro (1989). These taggings show that there is extensive mixing of fish among the spawning grounds. Cod tagged at each of the four grounds during spawning have been recaptured at all other grounds in subsequent years (Netzel, 1958; Rutkowicz, 1959; Otterlind, 1961; Netzel, 1963; Biriukov and Shirokova, 1964; Otterlind, 1966; Netzel, 1968; Bagge, 1969a; Birjukov, 1969; Netzel, 1969; Otterlind, 1969; Bagge et al., 1974; Netzel, 1974; Tiews and Lamp, 1974; Thurow, 1985; Bagge and Steffensen, 1989; Netzel, 1989). The relative importance of the four spawning grounds, and degree of spawning-ground-switching is probably a result of varying hydrographical conditions (Netzel, 1963; Baranova, 1995). Netzel (1989) found a highly significant negative correlation between the frequency of westward migration from Gdansk and the salinity of near-bottom waters there.

Young cod in the brackish juvenile nursery areas of the northern Baltic Sea (off Sweden and Finland) typically show unidirectional ontogenetic movements. As young cod mature, they become less tolerant of low salinities, and move to more southerly parts of the Baltic to feed and spawn. Site fidelity for cod tagged off Åland and Finland ranged from 0 to 77%, and from 0 to 23%, respectively. Experiments in which larger proportions of the tagged cod were younger than the age of outmigration account for the higher site fidelity observations (Otterlind, 1961, 1962; Sjöblom and Aro, 1977; Sjöblom et al., 1980; Aro and Sjöblom, 1983).

4.4.3 Baltic Cod in General

There have been several studies of the homing abilities of cod in the Baltic Sea (Table 4-2). Of 90 cod transplanted from the Slupsk Furrow to Bornholm, 27 were recaptured including 25 at the release site; none returned to the original capture location. Of 92 cod transplanted from the Arkona Basin to the Belt Sea, 24 were recaptured including 19 at the release location and 1 at the site of original capture. Some homing was observed when 91 cod were transplanted from the Bornholm Basin to Arkona. Of the 16 recaptures, 12 had returned to the original capture area, and only 2 were caught at the release site (Tiews and Lamp, 1974). These experiments seem to imply that cod home between some sites, but not others. Otterlind (1985) provided an explanation for this result. He described 16 transplantation experiments that were coupled simultaneously with a series of control experiments in which fish were tagged and released without transplantation. These experiments showed that the movement pattern of the transplanted fish was the same as that of the local fish that they met upon release. Only in a few cases did fish show any tendency to home above and beyond the movements of the local fish. In all, only 12.5% of the fish transplanted by Bagge (1973; 1983) from the eastern Baltic to the Kattegat returned to the eastern Baltic, and only 18.5% of the cod transplanted by Otterlind (1985) from the Kattegat to the Sound moved back towards the Kattegat. Successful homing appeared to be limited to cases where cod could follow a strong salinity gradient. In none of these experiments did a fish return to the original capture location. In short, the ability to home is not well developed in cod of the Baltic Sea. The lack of strong hydrological gradients throughout most of the Baltic may be a factor in the lack of homing evident in most experiments.

4.5 The Faroe Islands

The Faroe Islands (Fig. 4-2) are surrounded by the Faroe Plateau that extends to the 200 m isobath. The Faroe Bank lies 150 km to the south-west of the islands and is separated from the Plateau by a channel 830 m deep at its shallowest point. The Bank is 100 to 200 m deep and is one fifth the size of the Plateau. There is one spawning ground on the Bank, and two on the Plateau: one to the west of the islands, and one to the north of the islands (see Fig. 4-2, from Hansen et al., 1990).

The cod inhabiting the Bank are believed to be a separate population from those on the Plateau. Bank fish are lighter in colour (Jamieson and Jones, 1967), grow faster (Jones, 1966), are in better condition (Fjallstein and Magnussen, 1996) and have more vertebrae than Plateau cod (Schmidt, 1930). Differences between these two groups have also been detected at the genetic level (Jamieson and Jones, 1967). The two populations can remain separate despite their proximity, because persistent, separate, anticyclonic flows occur in shallow waters over both the Bank (Hansen et al., 1986) and the Plateau (Hansen, 1979) resulting in local retention of the pelagic eggs and larvae produced in each area (Hansen et al., 1990).

Spawning-site fidelity has been demonstrated for the Bank cod. Tagging studies have shown that exchange of individuals between the Bank and the Plateau is very rare. Up to and including the 1960's, 11212 fish were tagged in Faroese waters, and only 35 of the 3346 (1%) recaptured fish had crossed the channel. Since there is only one spawning ground on the Bank, a 99% spawning site fidelity for Faroe Bank cod is implied. Furthermore, since it is likely that these fish are self-recruiting (Jones, 1966), they must also be spawning on their natal grounds.

Evidence that cod on the Faroe Plateau repeatedly use only one of the two spawning grounds is unclear. Firstly, although the great majority of the spawning activity occurs at the two grounds described above, it also occurs at low levels all over the Plateau (Hansen et al., 1994). Secondly, the location of the main spawning activities varies from year to year: usually it occurs in approximately 100 m depth (6-8 nautical miles offshore), but it can sometimes be as deep as 140-180 m (10-15 nautical miles offshore) (Joensen, 1954; Jákupsstovu and Reinert, 1994). Thirdly, Joensen (1954) found that older, larger cod were caught mainly on the northern ground, while smaller, younger fish were predominantly caught on the western ground. These results suggest that Plateau cod may switch spawning grounds with size or age.

Tåning (1940) provided the best evidence for homing in Plateau cod in his review of the tagging experiments on large (spawning) cod at the northern spawning ground during spawning season. The trend for all experiments was the same: (1) Immediately after release, some fish were recaptured in the tagging area, while others had moved south, and were caught on both the east and west sides of the islands; (2) From June to December, the fish were dispersed to the west, east, and south of the islands, with no recaptures on the northern spawning grounds; (3) At the end of the calendar year, recaptures again occurred near the northern part of the island; (4) From January to May of the next calendar year (i.e., the subsequent spawning season), 70% of recaptures came from the tagging location. This number increased to 87.5% if only March-June recaptures were considered; and (5) There were also first quarter recaptures from the tagging location three to five years after release. These data demonstrate that mature cod tend to return to the same or nearly the same locality to spawn in successive years. Similar trends have been observed for the few spawning cod tagged in the experiments described by Strubberg (1916; 1933).

Straying between spawning grounds can be inferred from the proportion of fish tagged on the northern ground and recaptured in spawning condition on the western ground (approximately 17% of recaptures). Tåning treated these as being "on their way" to the northern spawning ground because the fish were large (and in his view, the western spawning ground is used only by small fish) and were caught early in the spawning season. I cannot, however, discount the possibility that some degree of straying between spawning grounds was occurring.

Overall, I conclude that there is strong evidence for homing and site fidelity in Faroese cod populations. A very low amount of exchange occurs between the Bank and Plateau populations. The Bank cod exhibit strong site fidelity, and likely spawn at their natal ground. The Plateau cod, once a certain size, tend to home to the northern spawn grounds year after year, although there is evidence of a small proportion straying.

4.6 Greenland

There are several groups of cod inhabiting the waters off Greenland. The fjord fish are thought to be separate from the cod inhabiting the deeper waters around offshore banks (Hovgård and Christensen, 1988).

4.6.1 Fjord Cod

There are differences between the fjord and bank cod in otolith form (Hansen, 1949), and parasite infestation (Boje, 1987). Also, the fjord fish move much less than the bank cod (Hovgård and Christensen, 1988). Hansen (1949) described experiments in which cod were tagged in these fjords, the majority of which (75-76%) were recaptured in the fjord in which they were tagged. Very few fish tagged in fjords are recaptured outside the fjords, and a negligible number leave Greenland waters. Since spawning occurs in the fjords along the west coast (Harden-Jones, 1968), and the fish in some of these fjords show a high degree of site fidelity, they are thought to be separate, local populations (Hansen, 1949).

4.6.2 Bank Cod

The bank cod spawn on the offshore banks on both the west and east coasts of Greenland (Jónsson, 1959). They are more mobile than the fjord cod (Hovgård and Christensen, 1988), and many emigrate to Iceland at maturity (Schmidt, 1931; Hansen, 1949; Meyer, 1962; Biester, 1972; Jones, 1978; Hovgård et al., 1989; Hovgård and Riget, 1991; Riget and Hovgård, 1991). The bank cod can be divided at Cape Farewell (Fig. 4-3) into West and East Greenland cod. The western component can be further divided into northern and southern bank cod, at approximately 62 °N.

4.6.2.1 Northern Bank Cod

The northern bank cod extend along the west coast of Greenland from Disko Bay to Godthaab Fjord. Quite a low proportion of fish tagged in northern districts of West Greenland are caught in Iceland (6.3% of recaptures, Rasmussen, 1957).

Evidence that northern bank cod home between feeding and spawning grounds each year was reported by Rasmussen (1957) and Biester (1972). Cod were tagged in summer while feeding in the northern parts of their range. Recaptures showed that in winter, the cod moved over the shallow parts of the bank in a southward direction to spawning grounds south of 62 °N (including Frederikshåb, Dana, Fiskenaes, and Fylla Banks). Later in the season, the fish returned north, taking a course with the currents along the slopes of the Banks (Harden-Jones, 1968). The recaptures of spent fish in May and June (and sometimes July) were made on the southern Banks, but farther north later in the season. By the summer, recaptures came largely from the area in which they were tagged. Similar migratory patterns were found for taggings throughout the northern banks (Hovgård and Christensen, 1988). A plot of the midpoints of bi-monthly recapture-distributions shows, regardless of the latitude at which cod spent their feeding season (i.e., regardless of where tagged), an annual movement between northern feeding grounds and the spawning grounds in southwest Greenland near 62 °N. Thus, the distance over which cod migrated was greater for cod that were tagged at (and which return to) northerly feeding grounds compared to those that homed to more southerly locations. Regardless of tagging location, these fish show a high degree of homing to the feeding grounds, and return to a general spawning area year-after-year.

4.6.2.2 Southern Bank Cod

The southern bank cod can be found offshore of Frederikshaab and Julianehaab districts (Harden-Jones, 1968) on the southwest coast of Greenland. These fish have a different otolith form and growth rate from the northern bank cod (Biester, 1972).

Quite a high proportion of the southern bank cod have been reported on the spawning grounds at Iceland (Harden-Jones, 1968). As much as 70% of the recaptured fish tagged in SW Greenland were caught in Iceland (i.e., they are 10 times more likely to emigrate to Iceland than the northern bank cod, Rasmussen, 1957).

There is speculation that at least part of the southern bank cod are of Icelandic origin (Harden-Jones, 1968). In many years, there was negligible spawning at the southern bank, yet young cod were caught around the adjacent coast in considerable numbers. In several cases, large abundances of young haddock were also found in southern Greenland despite a total absence of spawning adults (Hovgård and Messtorff, 1987). Accordingly, fry of both cod and haddock have been detected drifting between Iceland and Greenland (Tåning, 1934; Vilhjálmsson and Magnússon, 1984, 1985) in the Irminger current (Jones, 1978).

4.6.2.3 East Greenland Cod

The fish found on the offshore banks along the east coast of Greenland are not well studied, and there have been few tagging studies on these fish (Rätz, 1994). Of 772 cod tagged in east Greenland, 90% of the recaptures were made in Iceland (Hansen, 1949). There is no evidence that east Greenland fish migrate to the west into south or west Greenland waters (Rätz, 1994).

Based on protein polymorphism, east Greenland fish were found to be genetically distinct from northern bank cod from west Greenland (Jamieson and Jónsson, 1971). The southern bank cod were more similar to east Greenland cod. No genetic differences are found between east Greenland fish and those from Iceland (Jamieson and Jónsson, 1971).

4.6.3 Emigration to Iceland

There is no evidence from tagging or genetic studies that Greenland fjord cod emigrate to Iceland. Greenland northern bank cod typically perform closed migrations between feeding and spawning grounds and are only slightly more likely to migrate to Iceland. However, a significant portion of south bank and east Greenland cod may at times migrate to Icelandic waters.

Because of the limitations of conventional tagging techniques, it is not clear whether the emigrants ever return to Greenland. For example, cod tagged and recaptured in Greenland may have made a round-trip migration to Iceland, or may not have moved at all.

Determining the rate of movement from Iceland to Greenland is difficult. Hansen (1949) described a series of experiments in which 8424 adult spawning cod were tagged on the spawning grounds in Iceland. Of 1015 cod that were recaptured, only 19 (1.9%) were caught in Greenland. Of these, 13 were from one single marking bout. Since it is not known how many of the tagged fish were of Greenland origin, the proportion of Greenland fish that returned home after spawning in Iceland cannot be determined. Results are further complicated by differences in fishing effort between locations.

There are two lines of indirect evidence that Greenland fish return to Greenland waters after spawning in Iceland. Firstly, no fish tagged while immature in Iceland has ever been recaptured at Greenland. Hence, all known migrants from Iceland to Greenland <u>may</u> have grown up in Greenland waters. Secondly, fish tagged while immature in Greenland are frequently recaptured at Iceland. That cod tagged in Greenland before maturity are only recaptured in Icelandic waters once mature, mostly on the spawning grounds, and rarely outside of spawning season (Tåning, 1934; Hansen, 1949) implies that cod from Greenland vacate Icelandic waters after the spawning season. Nevertheless, the evidence for a return migration is at best weak, and Jones (1978) believed the vast majority of the emigrants to Iceland never return to Greenland.

It is possible that the fish that emigrate to Iceland are the same individuals which, as juveniles, drifted across the Denmark Strait from Iceland to Greenland; that they are making the reverse migration to return to their natal grounds. This would imply that year-classes with a high proportion emigrating to Iceland correspond to years when more larvae drifted across the Denmark Strait. Hovgård and Riget (1991) examined the 1984 year class, which was the first year-class "known" to be of Icelandic origin (larvae were observed drifting across the Denmark Strait in 1984) and found an unprecedented proportion of recoveries from Iceland. However, in a subsequent analysis, Riget and Hovgård (1991) concluded that in general year-classes "considered" to be of Icelandic origin were no more likely to emigrate than any other. Interpretation of the results of these analyses is difficult because differences in fishing effort among years or between countries have not been considered. In conclusion, the extent to which southern bank and East Greenland cod exhibit natal homing to Iceland must still be regarded as an open question.

4.7 Iceland

In the spring, fish from around Iceland (Fig. 4-4) perform annual migrations to spawning grounds in the warm waters off the southwest coast and near Faxa Bay (Schmidt, 1931;

Jónsson, 1965; Marteinsdóttir and Petursdóttir, 1995; Jónsson, 1996), where the majority of the spawning in Icelandic waters takes place (Schmidt, 1931; Jónsson, 1982). There are non-migratory groups inhabiting the fjords on the north and probably east coasts of the island, but the spawning activity there is minor in extent relative to that of the migratory fish (Jónsson, 1982).

The currents at the main spawning ground carry eggs northward along the west coast. There, the current splits, and most eggs drift along the north coast in an easterly direction, but some veer west and drift towards Greenland (Schmidt, 1931; Harden-Jones, 1968). Age 0 cod can be found all along the west and north coasts, in greatest concentrations off the northwest coast. Few age 0 cod are found on the east and south coasts (Vilhjálmsson and Magnússon, 1984, 1985; Begg and Marteinsdóttir, 2000).

4.7.1 Tagging on the Main Spawning Grounds

Jónsson (1986; 1996) described 69 experiments made between 1949 and 1968 in which 7772 fish were tagged on the spawning grounds during spawning season. Recapture data show that most fish leave the spawning grounds when spent. The majority of non-spawning season recaptures came from the northwest coast, though a few recaptures were reported from all parts of the island. During subsequent spawning seasons (end of March to beginning of May), the fish showed a strong tendency to return to the spawning grounds, as more than 97.8% of the spawning-season recaptures were caught there (as calculated from Figures 5.1 - 5.4 in Jónsson, 1996). Schmidt (1931) reported similar results from earlier tagging. The presence of a local non-migratory group, separate from those that return to northwest coast between spawning seasons was inferred from a number of recaptures (approximately 27.5% of feeding season recaptures, calculated from

Figures 5.1 - 5.4 in Jónsson, 1996) made at the spawning ground outside the spawning season (Jónsson, 1965).

Small-scale population structure in Icelandic cod has recently been deduced from differences in protein sequences found among fish at different spawning grounds within the main spawning area along the southwest shore of Iceland (Jónsdóttir et al., 1999). Data from storage tags attached to mature cod showed that the depth and temperature profiles experienced by cod during consecutive spawning seasons were characteristic of the inshore spawning areas near the southwest coast (Thorsteinsson and Eggertsson, 1998; Thorsteinsson and Marteinsdóttir, 1998). However, spawning depths sometimes varied among years (Pers. comm., V. Thorsteinsson). Variation in spawning depth was also found by Marteinsdóttir et al. (2000). They showed that older, larger fish spawned predominantly in shallower waters, while smaller fish were more frequently found in adjacent deeper bank waters. Their data suggests a shift in spawning site use with age, but doesn't rule out fidelity within a size-group.

4.7.2 Tagging Outside the Main Spawning Grounds

Tagging studies made outside the main spawning grounds show generally that in areas around the island there may be both migratory and resident groups (Jónsson, 1965, 1996), distinguishable by size (Pers. comm., V. Thorsteinsson). Spawning-season recaptures of cod at locations throughout Icelandic waters may indicate local spawning (Jónsson, 1996).

The relative proportions of migrants and residents vary among tagging locations. Starting at the southwest spawning grounds, and moving in the direction of the current (clockwise) around the island, there is a decrease in the proportion of migrants (Jónsson, 1996). A far greater proportion of fish tagged along the north coast are recaptured on the main spawning grounds, compared to those from the east coast. The proportion of migrants around the island may be related to the prevalence of natal homing. Begg and Marteinsdóttir (2000) aged juvenile cod caught from all around the island, and back-calculated spawn-date in order to determine the proportion that were spawned significantly before or after the spawning activity at the main grounds. The proportion that could have come from the main spawning grounds decreased with distance from the spawning ground in the direction of the current. The proportion peaked at 97% on the northwest coast, immediately downcurrent of the spawning grounds. The proportion decreased along the north and east coasts to a minimal value of 63% on the southeast coast. Since fewer eggs spawned on the southwest coast reach remote areas, one would predict, assuming natal homing, that fewer adults in remote areas would be migrants.

There is still debate about which areas are host to local populations. Jónsson (1982) believed there to be a local population at Nordfjardfloi since spawning occurs there every year and resident spawners are smaller than migrants. He also believed that local populations exist on the east coast, because so few fish tagged there have been recaptured on the southwest spawning grounds (Jónsson, 1996). There is likely no local population on the southwest coast, since so few cod remain there year-round (Jónsson, 1965).

4.7.3 Icelandic Cod in General

In general, there are indications that most coastal zones of Iceland hold localised populations. In most there may be both a residential and a migratory group. It is not clear to what extent migratory fish mix with local spawners. The balance of the evidence suggests that homing or fidelity to spawning grounds is practised by the majority of Icelandic cod.

4.8 North Sea

The International Council for the Exploration of the Sea (ICES) treats the North Sea (Fig. 4-5) as a single management unit (Daan et al., 1990). Adult cod are most abundant in the northern parts although they can be found in low numbers throughout most of the North Sea. (Heessen, 1993). Spawning at most known grounds results in eggs and larval drift to the Danish or Norwegian coasts, or into the German Bight (Graham, 1924). The 0 and 1 year old cod are found in cold, shallow water, mostly in the German Bight, along the Dutch coast, and along the northeast coast of England (Daan, 1978; Heessen, 1991, 1993).

The spawning grounds of cod in the North Sea can be divided into three main areas: the central North Sea (54° to 58° 30' N; west of 5 °E); the Dutch and Belgian coasts; and the Scottish east and north coasts (ICES, 1971). The classic grounds, described in Graham (1924), include Ling Bank, Fisher Bank, Forties and Flamborough. More recently, spawning has been observed at Silver Pit, Clay Deep, Dogger Bank and in the Southern Bight (ICES, 1970, 1971; Daan, 1978). Outside the North Sea, spawning occurs in the English Channel and in shallow waters around Scotland (ICES, 1971). Spawning times vary with location between late January to late March (Brander, 1994a).

Tagging studies done throughout the North Sea have shown consistent results: 1) Tagged fish have been mostly recaptured near the tagging location (rarely more than 30-70 miles) and cod appear not to roam over the entire North Sea (ICES, 1971; Daan et al., 1990); 2) Recaptures have been more dispersed in summer than in winter; and 3) Fish tend to occupy the same range year-after-year. North Sea cod can therefore be divided into regional groups inhabiting non-overlapping areas: the Skagerrak; the east coast of the UK from Flamborough to the north coast of Scotland; the Southern Bight; the English

Channel; and the central North Sea (ICES, 1971). Other than the Skagerrak, each of these regions contains one or more of the known North Sea spawning grounds listed above.

The Skagerrak - The cod on the Norwegian side of the Skagerrak could split into a few small groups, each independent of the North Sea and of the Danish side. (Danielssen, 1969 as cited in ICES, 1971). Likewise, fish tagged on the Danish Skagerrak coast were not recaptured on the Norwegian side, rather they were caught where tagged (81%), in the North Sea (14%) or in the Kattegat (5%, Danielssen, 1969 as cited in ICES, 1971).

The Scottish Coast - Spawning has been reported throughout Scottish waters, but concentrated inshore in waters less that 100 m depth (Raitt, 1967). Small-scale (mostly < 20 miles) movements of tagged cod occurred along the coast (ICES, 1971; Easey, 1987). There appears to be little exchange of cod between the coast and offshore areas of the northern North Sea. Only 9% of recaptures of cod tagged offshore occurred inshore. Generally, between 0.2% and 1.8% of recaptures of cod tagged inshore were caught offshore (Symonds and Raitt, 1966; LeFranc, 1973). However, limited (9%) movement into the central North Sea was observed for cod tagged at the Shetland Islands (Easey, 1987).

The Moray Firth was considered to be an important spawning and nursery ground, into which large cod made annual spawning migrations (Bowman, 1928 as cited in Symonds and Raitt, 1966). However no eggs or larvae were detected there during surveys from 1959 to 1964 (Raitt, 1967), and despite heavy tagging efforts between 1962 and 1964, few recaptures were reported from outside the Firth (< 20%, Symonds and Raitt, 1966). Perhaps cod spawning locations have changed locations over time.

The English Coast - The main spawning area on the English coast has been at Flamborough. Cod tagged at Flamborough appear to comprise several groups, all of which move up and down the coast throughout the year, but only 38% to 65% return to Flamborough in winter (Bedford, 1966). Dispersal is greater in summer (Graham, 1924; Bedford, 1966), when some fish have been recaptured as far north as the Orkneys. In summer, some fish have been reported to move east into the central North Sea (Bedford, 1966), but are rarely recaptured more than 30 miles from shore (ICES, 1971).

The Southern Bight - Fish tagged in the Southern Bight spawn in the southern parts of the Bight, and near the Strait of Dover. During the summer, some tagged fish have been recaptured in the English Channel (deClerck, 1973). Most disperse northwards in summer throughout the Southern Bight and into the central North Sea (Bedford, 1966; Daan, 1969), but are never recaptured north of Dogger Bank (Lamp, 1973). Depending on the area, homing in subsequent seasons has ranged from 14% (for tagging at North Foreland, Bedford, 1966) to 100% (for one of several experiments in the German Bight, LeFranc, 1967; Daan, 1969; deClerck, 1973).

The English Channel - Fish tagged off the south coast of England, in the western parts of the English Channel, have been recaptured there throughout the year (31% to 57% of recaptures were within 60 km of the tagging area). However, some English Channel fish disperse in summer into the Southern Bight and the southern North Sea (always South of 55 °30'N, Bedford, 1966; LeFranc, 1968). Cod tagged in the western English Channel and eastern Channel near the Strait of Dover show similar patterns of dispersal. However, Strait of Dover fish are never recaptured in the western part of the Channel at any time of year. As a result, the eastern and western Channel fish have been considered to be separate groups. Bedford (1966) considered the eastern Channel fish to be part of the Southern Bight group. Homing for English Channel taggings has ranged between 33% and 81%.

The Central North Sea - Fish tagged in the central North Sea show no tendency to winter south of Dogger Bank, and are therefore likely to be separate from the Southern Bight group (ICES, 1971). They are also likely to be separate from the English coast group, since they have not been recaptured near shore (Bedford, 1966; LeFranc, 1967). Central North Sea cod disperse to the northwest during summer, usually between 30-70 miles, although some venture as far north as the Shetland Islands (Easey, 1987). In winter, these fish return to the various central North Sea spawning grounds. There is evidence that for many of the known spawning grounds, there was a resident group of spawners, each showing fidelity to their ground. For example, fish tagged on the Farn Deep showed no significant movement (LeFranc, 1967). LeFranc (1967; 1969; 1970) found that fish tagged on Dogger Bank didn't mix with fish from surrounding areas, and were recaptured year-round (60% to 85%) within about 60 km of the tagging locale. Although Bedford (1966) found much greater dispersion for Dogger Bank cod (only 16% of recaptures near the tagging location), there was little evidence of exchange with other areas of the North Sea. Bedford (1966) found similar results for cod tagged on Cleaver Bank and the North West Roughs, concluding that they were separate groups, with little overlap during the spawning season. The exact boundaries between these groups are not well defined (ICES, 1971).

4.8.1 North Sea Cod in General

Whether the groups in and around the North Sea can be considered to be separate populations is uncertain. The many spawning sites are fairly close together. There have been no published genetic studies or reports of population differences. Some of the groups appear to be relatively isolated, while others show some degree of intermingling, and there are some larger-scale movements. ICES (1971) concluded that the fish could be coarsely grouped into several units: a) one off the Norwegian Skagerrak coast; b) one or more along the eastern UK coast from Flamborough to north Scotland; and c) several within the English Channel, the Southern Bight, the Danish Skagerrak, and the central North Sea. The lines between these units could not be clearly defined. Results from spawning site fidelity studies have varied widely from site to site, and also among experiments at the same site.

The existence of small-scale population structure is not likely in the North Sea, even though tagging studies show that there is little range overlap between some groups. Whether any of these groups recruit separately from others is not well known, because of a dearth of data on the circulation and mixing of eggs and larvae (ICES, 1971). Some differences in year-class strength have been reported (specifically, between the Scottish coast and the southern North Sea in 1963), indicating that perhaps some groups may at times be independent of a pooled supply of recruits (ICES, 1971). However, given the proximity and that eggs drift from many spawning grounds into a few common nursery areas, it is unlikely that observed groups represent self-sustaining populations (Daan, 1978). Groupings could be maintained if fish show fidelity to the spawning group that is adopted at maturity.

4.9 Irish Sea

Very little has been published about site fidelity or homing of Irish Sea (Fig 4-5) cod. Brander (1994a) identified two spawning grounds in the Irish Sea, one in the Celtic Sea and one in the Bristol Channel that were consistent over time, although their relative importance varied among years.

Agnew (1988) reported that resident and larger at age migrants use a single spawning ground in the Irish Sea. He argued that the two populations are vertically segregated in the water column, resulting in non-random mating. However, the difference in growth rate could be the result of the migratory strategy, and is not conclusive evidence of a difference between the groups. Agnew (1988) suggests that the local group of fish uses the same spawning grounds year-after-year, but a lack of tagging data means that the site-fidelity of the migrants cannot be ascertained.

4.10 Norway and the Barents Sea

The cod off Norway and in the Barents Sea (Fig. 4-6) are managed as two units, the coastal cod, and the Northeast Arctic cod (Jakobsen, 1987). The coastal cod are relatively stationary and are caught in and around the fjords and along the Norwegian coast year-round and may be comprised of several separate populations (Jakobsen, 1987; Godø, 1995). In contrast, the Northeast Arctic cod perform long-distance migrations throughout the Norwegian and Barents Sea, but return annually to areas along the Norwegian coast between March and April to spawn (Ponomarenko, 1963; Harden-Jones, 1968; Berger, 1969; Maslov, 1972; Lebed et al., 1983; Godø, 1984c; Warnes, 1989). During the feeding season, the geographic ranges of the two groups have limited overlap, and in the more southern coastal areas they are totally separated (Godø, 1984a).

Coastal Norwegian and Northeast Arctic cod have been shown to differ in several ways. Otolith form differs between these groups (Rollefsen, 1934), and has been used by scientists and fishery managers for racial identification (Reisegg and Jørstad, 1983). Coastal cod, on average, grow faster, reach maturity earlier and have fewer vertebrae than the Northeast Arctic cod (Rollefsen, 1934). Genetic differences in haemoglobin polymorphism (Møller, 1966, 1968; Reisegg and Jørstad, 1983; Jørstad, 1984; Jørstad and Nævdal, 1989) and synaptophysin-coding DNA sequences (Fevolden and Pogson, 1997) have been reported between the groups. However, Mork (1985) found limited variation throughout the range of Atlantic cod.

Coastal and Northeast Arctic cod appear to spawn at similar locations and times (Møller, 1968; Godø, 1984a; Bergstad et al., 1987). The mechanisms that lead to reproductive isolation are as unknown. Møller (1968) speculated that fish from the different groups might identify themselves by distinctive grunting sounds. Recently, cod spawning vocalisations have been documented (Nordeide and Kjellsby, 1999), but there is no evidence that its function is for group discrimination.

The evidence that Norwegian coastal and Northeast Arctic cod comprise different populations is not entirely satisfactory. The different environments experienced by the individuals of each group could result in their distinct morphometric characteristics (Karpov and Novikov, 1980; Borisov et al., 1998), and the many intermediate otolith forms are found which cannot be assigned to either coastal or Northeast Arctic cod (Reisegg and Jørstad, 1983; Fevolden and Pogson, 1997). There is also evidence that the genetic units in which group differences have been observed are influenced by selective forces and are therefore not good indicators of race (Mork et al., 1984; Mork et al., 1985; Mork and Sundnes, 1985; Bergstad et al., 1987; Borisov et al., 1998). Furthermore, the majority of polymorphic loci examined fail to distinguish the two groups; haemoglobin being the rare exception (Fevolden and Pogson, 1997). Finally, coastal and Northeast Arctic cod, when reared under similar conditions show no difference in their tendency to migrate or be stationary (Godø and Totland, 1995).

4.10.1 Northeast Arctic Cod

There is some evidence for homing in the Northeast Arctic cod. Various tagging programs in the Barents Sea have shown consistent recapture patterns, which indicated that the shoals of cod follow a similar path year after year (Berger, 1969; Maslov, 1972). There are some indications, however, that the migration path changes with age, either showing more extensive migration with size (Lebed et al., 1983), or a shift away from nursery areas at maturity (Trout, 1957). The annual migration includes spawning at one of two main locations on the Norwegian coast (Lofoten and Møre) in March to April, followed by a dispersal to feeding areas throughout the Barents Sea (Godø, 1984c; Warnes, 1989).

Godø (1984c) studied the homing of Northeast Arctic cod by tagging 14855 ripe fish at Lofoten and Møre during the peak spawning season. Of the fish tagged at Lofoten, 82% of the recaptures during subsequent spawning seasons homed, and only 1% strayed to Møre. Of the fish tagged at Møre, 77% of the recaptures homed, while only 9% were recaptured at Lofoten. Some of the Lofoten recaptures may have been "on the way" to Møre, since Lofoten is located between the feeding grounds and Møre. These results demonstrate that cod can exhibit accurate return to spawning grounds and very strong homing. Lebed et al. (1983) found a different result. They reported that larger fish were more likely to use the Møre ground, possibly because they were better able to migrate to the more distant ground. Their results implied that cod can shift spawning grounds with size, and that homing was not as strong as suggested by Godø (1984c). However, Godø's data are inconsistent with this hypothesis as his recaptures showed that the more frequent shift in spawning ground is to the less distant site.

Despite evidence of a high degree of homing to spawning grounds, two transplantation experiments have shown little evidence that fish could home to their original capture location (Table 4-2). Hylen (1963) transplanted 66 fish from Finnmark to the Møre area. Over the next four years ten were recaptured. Five were recaptured near the release site, three at Lofoten, and one at Iceland. Only one fish was recaptured on the Finnmark coast and hence showed signs of a return to the original capture location. In a more recent study, Godø (1995) tagged 40 cod with conventional tags and nine with acoustic tags off the north coast of Norway. The fish were subsequently released in a fjord about 120 miles from Møre. All acoustically tagged fish left the fjord soon after release, so it is assumed that the conventionally tagged fish left as well. Four of the latter group were recaptured in the fishery: one in the Skagerrak, two in the North Sea and one on the coast just north of the release site. None showed any tendency to return to the north coast of Norway.

Whether Lofoten and Møre cod represent separate populations is unclear. Fish tagged at Møre and Lofoten have been reported to differ in the location of feeding-season recaptures (Godø, 1984c). Fish tagged at Møre had a slightly more southerly and westerly recapture distribution than did those tagged at Lofoten, although there was considerable overlap in range in the central areas of the Barents Sea (Godø, 1984c). Differences in migratory behaviour and segregation during the spawning season lend support to Møre and Lofoten fish being different populations. Moreover, there are differences in otolith form, which distinguish fish caught in the eastern versus western Barents Sea (Trout, 1953, 1957). On the contrary, Warnes (1989) described a tagging study in which 2% of the fish tagged in the eastern Barents Sea and 2% of those tagged in the western Barents Sea were recaptured at Møre during the spawning season. In the Warnes (1989) study, fish spawning at Møre do not appear to be segregated into one part of the Barents Sea during the feeding season. Furthermore, the lack of genetic differences between the spawning groups (Reisegg and Jørstad, 1983) supports the idea that Lofoten and Møre cod are not separate populations.

4.10.2 Coastal Cod

There is strong evidence for site fidelity in the coastal cod. Most tagging studies show that the majority of coastal cod are sedentary, showing little tendency to migrate (Godø, 1986; Godø et al., 1986). Godø (1984a) found between 83 and 93% of the tagged coastal cod were recaptured in the area of tagging (although it dropped to 68% for more offshore tagging locations).

Jakobsen (1987) tagged 7272 fish in fjords of Finnmark, 94-100% of which were coastal cod. During Jan-June (a period including spawning season) an average of 80% of the recaptures came from the fjord in which the fish was tagged, 12% from just outside that fjord, and the remaining 8% from neighbouring fjords. Since no spawning locations are known outside the fjords, Jakobsen (1987) suggests that 90% of the coastal cod spawn in the same fjord year after year.

In Jakobsen's study, the proportion of fish exhibiting site fidelity varied among fjords, ranging from 93% in Porsangerfjord to 54% in Tanafjord. This variability implies that some fjords are more likely to be host to a separate, local population than others. Genetic differences between fjord fish and the surrounding coastal cod have been reported in Porsangerfjord (Jørstad, 1984), Smøla (Reisegg and Jørstad, 1983) and Malangen (Jørstad and Nævdal, 1989; Fevolden and Pogson, 1997).

These local populations may not be exhibiting "site fidelity" in the sense that there is something about a particular location that keeps them near it, rather, they may simply lack a drive to migrate. When coastal cod were transplanted from the Northwest coast of

Norway to a fjord on the southwest coast, they showed no tendency to leave the fjord. Instead, they established home ranges, and remained in the new fjord at least until the end of the study (Godø, 1995).

Although most studies have found coastal cod to be stationary, Nordeide and Salvanes (1988) reported that 54% of tagged mature cod were recaptured outside of the tagging area, with the largest fish travelling the farthest and intermingling with cod in the other fjords. More significantly, three fish were recaptured ripe at other spawning grounds during the same spawning season in which they were tagged and released.

4.10.3 Norwegian Cod in General

Overall, there is impressive evidence that cod can both accurately home to a spawning ground, and show very strong site fidelity. Coastal populations are largely sedentary. In the much larger Northeast Arctic cod, little exchange occurs between Lofoten and Møre, but perhaps enough to ensure genetic homogeneity. Some exchange may occur between coastal and migratory groups since they share spawning grounds; evidence that they are different populations is for the moment speculative.

4.11 North America

Cod in North American waters range from North Carolina to Northern Labrador (Fig. 4-7), spanning a broader range of latitude than in the Northeast Atlantic. Deep channels that cut across the broad continental shelf may act as barriers to cod movement (McKenzie, 1956; Templeman, 1962; Wise, 1963; Martin and Jean, 1964; Gascon et al., 1990; Rollet et al., 1994; Campana et al., 1999), and coarsely divide the cod's range into four areas: 1) south of the Fundian Channel; 2) the area between the Fundian and Laurentian Channels; 3) north of the Laurentian Channel; and 4) the Flemish Cap.

4.11.1 South of the Fundian Channel

Cod in the area south of the Fundian Channel can be divided into several groups based on tagging studies (Smith, 1902; Schroeder, 1930; Wise, 1963), interviews with fishers (Ames, 1998) and investigations of spawning time (Colton et al., 1979), growth rate (Penttila and Grifford, 1976), otolith features (Penttila, 1988), vertebral counts (Templeman, 1962) and parasite infestation (Sherman and Wise, 1961). There is at least one group in the inshore areas of the Gulf of Maine, one in the Georges Bank-Southern Channel area, and one or two in waters off southern New England-Middle Atlantic Bight (Templeman, 1962; Serchuk and Wigley, 1992; Serchuk et al., 1994).

Evidence for homing comes from a report of interviews with retired Gulf of Maine fishers. The fishers identified almost 200 distinct spawning grounds within coastal Gulf of Maine, most of which are no longer in use (Bigelow and Schroeder, 1953; Ames, 1998; Langton, 1998). The bay-by-bay "abandonment" of cod from of these grounds (Ames, 1998) is consistent with extinctions of small-scale populations. Interviewed fishers recalled how cod could be found in the vicinity of abandoned spawning grounds, but did not use them for reproduction, indicating a low tendency to stray among spawning grounds. Ames believes that homing coupled with a limited influx of eggs from offshore regions (Pettigrew, 1996 as cited in Ames, 1998) resulted in many spawning grounds remaining empty once the resident population disappeared. Consistent with this, Wise (1958) reported on tagging studies near Cape Cod in which the majority of recaptures (83.5% and 91.2%) occurred in the vicinity of the tagging site. Wise (1963) concluded from literature reports (see references therein) that coastal Gulf of Maine cod were likely comprised of many subgroups. In contrast, Bowen's (1987) report on the outcome of a stock structure workshop suggested that there could be mixing among these inshore groups. Tagging by Perkins et al. (1997) in Sheepscot Bay showed evidence of dispersal with only 48% of recaptures within a 3300 square km area around the tagging site.

Georges and Browns Bank cod appear to show a high degree of site fidelity. Wise (1963) reported results of three tagging experiments on Georges Bank spawners, only one of which yielded recaptures beyond the first season. In this experiment, 66.6% of the recaptures with greater than six months at liberty were from the tagging area. All of the strays from this experiment crossed the Fundian Channel, 90.1% of which were recaptured around Browns Bank. Hunt et al. (1999) tagged 7205 cod on the eastern tip of Georges Bank, and recaptured only 55.8% on Georges Bank. Most of the remaining fish were caught on Browns Bank and areas off Digby and Yarmouth. Timing of recaptures is not provided, so spawning site fidelity and homing cannot be assessed. However, Georges and Browns Bank cod have been shown to be genetically distinguishable using microsatellite techniques (Ruzzante et al., 1999), so gene flow between the areas may be low. The recruitment dynamics of Georges and Browns Bank cod are likely independent given that they have different peak spawning times (Colton et al., 1979; Hurley and Campana, 1989) and that both feature gyre-like circulation (Bowen, 1987; Lough et al., 1994) with long residence times (Bolz and Lough, 1984; Werner et al., 1993) that minimise the potential for mixing of spawning products among banks (O'Boyle et al., 1984; Sherman et al., 1984; Lough and Bolz, 1989; Suthers and Frank, 1989; Page et al., 1999).

Homing of cod in the southernmost part of their range was difficult to assess. Fish were tagged in winter off New Jersey, moved north where they were recaptured off Cape Cod in summer, and returned to the tagging area the following winter, following a migratory pathway along Long Island (Schroeder, 1930; Wise, 1958). For the two published experiments combined, 70% of winter recaptures came from the New Jersey area, the other 30% coming from Long Island, possibly caught en route to a New Jersey wintering destination. Homing could not be assessed from these publications because the first season recaptures were not distinguished from subsequent ones. However, the lack of recaptures off Cape Cod in the winter was evidence for a strong return migration.

In general, cod homing and site fidelity in this region are difficult to assess from the available literature. In one study, tags were shed in less than a year (Smith, 1902). In most others, recaptures were grouped in space or time in a manner that precluded this assessment (Wise, 1958, 1963; Hunt et al., 1999).

4.11.2 Between the Fundian and Laurentian Channels

The cod in the area between the Fundian and Laurentian Channels are managed as two groups. The "Scotian Shelf" group ranges from the Bay of Fundy to Cape Breton, including several inshore and offshore spawning locations (McKenzie, 1956; Templeman, 1962). The "Southern Gulf" cod spawn in June (Powles, 1958) throughout the area between Cape Breton and Gaspé (Powles, 1958; Lett, 1980). In winter they move out of the Gulf of St. Lawrence onto the Laurentian Channel slope where they mix with Scotian Shelf cod on Misaine Bank and, to a lesser extent, Banquereau (Jean, 1964; Clay, 1991).

4.11.2.1 Scotian Shelf Cod

The Scotian Shelf group is considered to include up to eight inshore populations and at least three offshore (Templeman, 1962). In general, westernmost groups, both inshore and offshore, have lowest vertebral numbers (McKenzie and Smith, 1955), highest growth rates (Shackell et al., 1997b) and earliest spawning times (O'Boyle et al., 1984; Brander and Hurley, 1992).

4.11.2.1.1 Inshore

McKenzie's (1956) summary of cod taggings off the southern Canadian mainland suggests that inshore cod show strong site fidelity and homing. Mixing among inshore populations is very limited, and occurs only among immediately adjacent groups. McKenzie identified at least five populations along the Nova Scotian coast. Cod tagged at Seal Island were mostly (80%) recaptured within 50 miles of the tag site. Cod tagged at Shelburne showed a moderate offshore movement in winter, and a summer return. Over a four year period, 85-90% were recaptured near the tagging region. Cod tagged along the coast between Lunenburg and Halifax showed no real migration, with 75% of recaptures within 12 miles of tagging area, regardless of season. Halifax taggings showed a distinct offshore dispersal in winter, but 80% of summer recaptures were within 12 miles of Halifax. Cod tagged during summer between Egg Island and Jeddore Rock spread during winter throughout the coastal Nova Scotia and went offshore to Sable Island Bank and Banquereau. In subsequent summers, 83% of recaptures were within 12 miles of the tagging site. McCracken (1956) tagged 1804 cod off Lockeport, which showed no pronounced seasonal movements, except to move 100 m deeper in winter, and about 93% of recaptures came from the tagging area throughout the year. Gagné et al. (1983) reported similar results from their later taggings in Sandy Cove and Lockeport. For both experiments, cod showed no tendency to migrate, and over 95% of recaptures came from the area of tagging.

An inshore population with unusually low vertebral numbers that spawned annually near Halifax Harbour in autumn was identified by McKenzie (1940). Autumn spawning was anomalous given that typical Scotian Shelf cod spawning occurs in winter and spring. Temporary residence at Halifax was inferred from the annual sudden drop in October and subsequent rise in April of the average vertebral counts of cod caught in the area. Tagging results were unconvincing because of low recapture numbers (see McKenzie, 1956), but the distinct, repeated trend in vertebral averages off Halifax showed that these fish might home year after year, possibly to their natal grounds.

Homing and site fidelity of Bay of Fundy cod cannot be examined from the accounts of tagging studies in the published literature, however there is evidence of considerable exchange between the two sides of the bay (Hunt and Neilson, 1993). Campana and Simon (1984) published results from spring tagging on the western side, which showed that 50% of recaptures in the subsequent spring were from the western side of the bay. Bay of Fundy cod are genetically distinguishable from those on Browns Bank (Ruzzante et al., 1998).

In general, inshore Scotian Shelf region cod populations showed very strong site fidelity, mostly being recaptured within 12 miles of the release areas. The inshore populations that did migrate tended to spread offshore in winter, and, with the exception of Bay of Fundy cod, showed strong and exacting homing in subsequent summers.

4.11.2.1.2 Offshore

Cod inhabiting the Scotian Shelf offshore banks move off the banks into deeper water in winter, and show less accurate homing than inshore populations. In McKenzie's (1956) summary of cod taggings off the southern Canadian mainland, few fish were recaptured at the tagging site, but many returned to the bank where they were tagged, and most returned to the offshore banks in general. Cod tagged on northeastern Banquereau and western and eastern Sable Island Bank showed the strongest homing, with 79%, 76% and 65% of recaptures on the bank where they were tagged. Cod tagged north of Sable Island, and northwest of the Sable Island Bank showed weaker homing, with 56% and 54% returning to the same offshore bank where they were tagged. For taggings on Emerald Bank, and on southern, eastern and central Banquereau, 57%, 56%, 46.5% and 29%, respectively, of recaptures were made on the bank where tagged.

Martin and Jean (1964) described winter taggings on Western Bank and Banquereau. Western Bank cod moved about the area, but showed strong site fidelity, and little migratory tendency. Over the next four years, recaptures by seasonal quarter were 93%, 88%, 86% and 100% from the tagging area. Banquereau cod migrated into the southern Gulf of Saint Lawrence in summer, but 84% of winter recaptures were on the bank where tagged.

Tagging on Browns Bank in 1957 (Wise, 1963) showed significant exchange with inshore Nova Scotia and Georges Bank. Only 57% of recaptures after the first six months were on Browns Bank. In 1969, taggings in the same area yielded different results (Halliday, 1973). Over four years, 95% of recaptures were on Browns Bank; only 5% were from Georges Bank. Tagging in the 1980's and 1990's (Hunt et al., 1999) show movement throughout the Scotia Shelf area, only 32.5% of recaptures on Browns Bank, and 6.5% on Georges. Shackell et al. (1997b) report that Browns Bank cod are most likely of any Scotian Shelf cod to move long distances. None of these studies provide information about temporal distribution of recaptures.

In general, movements of fish tagged off central and western Nova Scotia tend to be inshore-offshore (McKenzie, 1956), with substantial evidence of large scale homing to the bank where tagged. It is conceivable that neighbouring banks have independent recruitment dynamics related to the gyre-like circulation patterns in waters around the

Scotian Shelf banks (Gagné and O'Boyle, 1984; O'Boyle et al., 1984). Larval transport in the region is thought to be somewhat limited (Campana et al., 1989; Shackell et al., 1997a; Ruzzante et al., 1999). Movement from the Scotian Shelf and into the southern Gulf of Saint Lawrence was most pronounced for fish tagged on the more easterly banks. There may well have been Southern Gulf cod on a return migration (McKenzie, 1956; Martin and Jean, 1964). Summer tagging would be required to assess the homing tendencies of cod resident on Banquereau and Misaine Banks. In general, the scale of population structure on the Scotian Shelf is likely to be larger on the offshore banks than inshore because homing and fidelity appear to function at larger scales (1000's of km) on the banks compared to inshore (15 to 60 km).

4.11.2.2 Southern Gulf Cod

The Southern Gulf cod are more migratory than those of the Scotian Shelf, most likely because of differences between the areas in availability of suitable winter temperatures (Jean, 1964). Most commercial sized cod move out of the Gulf to areas along the Laurentian Channel slope (Jean, 1964; Paloheimo and Kohler, 1968; Hanson, 1996; Campana et al., 1999) beginning in November (Lambert, 1993; Sinclair and Currie, 1994), some venturing as far as Banquereau. These fish return to the shallow areas of the Gulf areas in May (Sinclair and Currie, 1994), perhaps tracking the abatement of ice (Frechet, 1990).

The Southern Gulf cod can be divided by vertebral averages into four distinct populations: Gaspé, Chaleur Bay, Prince Edward Island (PEI), and western Cape Breton (McKenzie and Smith, 1955; Templeman, 1962). Four distinct spawning aggregations have been observed, corresponding to these divisions: just west of western PEI, off the tip of Chaleur Bay, just west of the Magdalene Islands, and on the Laurentian Channel just off the Sydney Bight (Lett, 1980).

Cod tagged in 1938-39 off the Gaspé Peninsula (McKenzie, 1956) were recaptured mostly (95%) near the tagging area. If there was a substantial winter migration out of the Gulf (as is the case for other Gulf of St. Lawrence populations), many more recaptures would be expected outside the Gulf. The few distant recaptures were made on the Scotian Shelf, around Cape Breton Island, and near the Magdalene Islands, but never far from the Laurentian Channel. A more substantial overwintering migration was apparent from cod taggings in summer at Gaspé between 1955 and 1981 (Lambert, 1993). In these studies, 13.75% were recaptured on the overwintering grounds above Cape Breton. Discounting recaptures from the overwintering grounds, 84% of the remaining recaptures came from the tagging area and 9.4% from the migration route between the overwintering and summering grounds (Lambert, 1993).

Cod tagged in summer off Chaleur Bay (McCracken, 1959) showed cyclical seasonal migrations. In winter, 76.2% of recaptures came from the southern side of the Laurentian Channel off eastern Nova Scotia, only about 10% coming from the tagging area. By summer, cod had homed successfully, with 80.6% of recaptures coming from the tagging region. A few recaptures came from the areas between summering and overwintering areas (West coast of Cape Breton, Magdalene Islands), either showing the migration route, or a small degree of straying. Tagging reported by McKenzie (1956) showed similar results: 75% of summer recaptures came from the tagging area, the remaining from PEI and the Magdalene Islands.

Cod tagged in summer off the Magdalene Islands showed similar seasonal movements. In winter 82.6% of recaptures came from the southern side of the Laurentian Channel, some from as far as Banquereau. Only about 16% came from the tagging area. In spring, returns came primarily from the tagging area, but later were spread throughout the southwestern Gulf. Between June and November, 98.3% of the recaptures were in the southern Gulf, but only 45% were caught near the Magdalene Islands. If the Magdalene Island cod are not part of the Chaleur Bay group, then straying is significant (Powles, 1959).

Cod tagged at PEI exhibit less marked migrations. In three tagging experiments, recaptures at PEI were 4 of 6 (66%), 8 of 12 (66%), and 18 of 46 (39%). Most winter recaptures (4 of 6) occurred in the southern Gulf, and none east of Sydney Bight (McKenzie, 1956).

Cod tagged on the west coast of Cape Breton Island in summer exhibit only a moderate degree of homing. In winter, these cod move into the Sydney Bight and to the Scotian Shelf. McKenzie (1956) reported that only 16% of recaptures occurred in the tagging area. In summer, most (74%) occurred in the tagging area, the remainder were recaptured off northern Cape Breton, and in Gulf areas adjacent to the Laurentian Channel. Of cod tagged in summer off western Cape Breton between 1955 and 1981 (Lambert, 1993) 38% of recaptures occurred on the overwintering grounds above Cape Breton. The remaining recaptures were distributed throughout the southern Gulf, with only 35.4% caught within the tagging area.

Sydney Bight cod appear to exhibit more exact homing. Cod tagged in summer at Sydney Bight moved onto the Scotian Shelf in winter, with only 20% remaining in the tagging area (McKenzie, 1956). In summer, 71% of recaptures came from the tagging area, although a few were caught in areas adjacent to the Laurentian Channel (McKenzie, 1956). Cod tagged in winter moved into the southern Gulf of Saint Lawrence in summer, and homed back to the general area of tagging in subsequent winters. Most (86%) winter recaptures came from the southern parts of the Laurentian Channel between the northern tip of Cape Breton Island and Misaine Bank (Martin and Jean, 1964).

In general, homing appears to be quite strong in the southern Gulf, but straying throughout the area is also not uncommon. The group off Sydney Bight appear to be a discrete population, a large part of which winters outside the Gulf. Both the PEI and Gaspé populations show strong site fidelity. The cod off PEI appear to reside predominantly in the Gulf, with only a few strays to waters out of the Gulf. Cod in the Gaspé area were also mainly resident. Populations located near the Laurentian Channel appeared to use the Channel for directed seasonal migrations, whereas those farther away, such as PEI, showed less directed dispersion (McKenzie, 1956).

4.11.3 North of the Laurentian Channel

Cod north of the Laurentian Channel are managed as several units. These cod can be divided coarsely into several populations based on range, despite considerable intermingling at various times of year (see review in Templeman, 1979). Cod from the Labrador and Northeast Newfoundland Shelves are managed as one unit called "Northern cod" (Lear, 1986a). Fish in the Northern Gulf and on the westernmost part of the south coast of Newfoundland are considered one management unit. Cod which inhabit the southern coast of Newfoundland are managed as a single unit despite recognition of up to five groups moving in and out of the area at various times of year (Templeman, 1979; Brattey, 1996). Cod found in areas around the Avalon Peninsula are a complex mix of spawning groups, most of which move across boarders of management units regularly. Cod on the Grand Bank are also managed separately (Templeman, 1979).

4.11.3.1 Labrador and Northeast Newfoundland Shelves

"Northern cod" inhabit Labrador and Northeast Newfoundland Shelf. They spawn during late winter - early spring (Fitzpatrick and Miller, 1979) in bays and shallow nearshore waters (Wroblewski et al., 1996; Smedbol and Wroblewski, 1997; Rose, 2000), and various sites on the shelf (Hutchings et al., 1993; Rose, 1993), along the slopes of banks and near the shelf break (Serebryakov, 1965). Spawning extended for more than 700 nautical miles from north to south (Templeman, 1979). The majority of spawning likely occurred at three main sites on the shelf: 1) Hamilton Bank-Hawke Channel-Belle Isle Bank; 2) Funk Island Bank; and 3) Bonavista corridor-North Cape-Grand Bank (Rose, 1993; Kulka et al., 1995). Spawning products drifted southwards in local currents, and portions are thought to have settled in shallow nearshore embayments (Lear and Green, 1982; Lear and Wells, 1984) although most settled offshore or were swept off the shelf (Helbig et al., 1992; Anderson et al., 1995; Anderson and Dalley, 1997).

A number of localised populations have been postulated to exist within the range of Northern cod (Templeman, 1979; Lear, 1984a; deYoung and Rose, 1993; Taggart, 1997). Individuals have been shown to vary among the offshore banks in meristic characters, parasite infestation, spawning time, growth rate and length at maturity (for review see Lear, 1986a). However, each of these characters can be influenced by environmental differences. Genetic differences are reported to exist between cod collected around the Grand Banks and those from off Labrador (Ruzzante et al., 1998). Northern cod are managed as a single unit likely because of the great intermingling of local groups during the feeding season (Templeman, 1979).

The large subpopulations of Northern cod are long distance migrants. Cod tagged while overwintering on offshore banks move inshore in spring-summer where they disperse to feed along the southern Labrador and northeast Newfoundland coasts and often into the Strait of Belle Isle. The summering range differs slightly among the cod tagged on the various offshore banks from north to south, however overlap is considerable (Postolakii, 1967; Templeman, 1979; Lear, 1982, 1984a, 1986a). In fall, these fish undertake a return migration, and during subsequent spawning seasons are found offshore, most often around the bank where originally tagged (Lear, 1986a; Taggart, 1997).

Homing to the vast offshore banks (to a few hundred square km around the tagging area) appears to be common in the Northern cod. For cod tagged on Belle Isle Bank, between 70% and 85% homed to a >77000 km^2 area, however only between 2% and 35% showed more accurate (to within a <49000 km^2 area) homing (Templeman, 1979; Lear, 1982, 1986b). Homing of cod tagged on the eastern and southeastern portions of Hamilton Bank ranged from 64% to 85% (Lear, 1982, 1986b). On the other hand, cod tagged on western and northeastern parts of Hamilton bank showed only 6% to 22% homing (Templeman, 1979; Lear, 1982). Homing appeared to be rare to more narrowly defined grounds within an area of 75 x 57 km (a statistical unit) around the tagging site. For taggings on western, northeastern, eastern and southeastern Hamilton Bank, such accurate homing rates were 0%, 1.7%, 17.5%, and 8.3%, respectively (Templeman, 1979; Lear, 1982, 1986b). Similar results were found for taggings on Funk Island Bank. Cod tagged on the northern portions of Funk Island Bank showed homing rates to the bank of origin of between 57% and 73%. Cod tagged on the southern part of the bank exhibit a 50% homing rate (Lear, 1982, 1986b). However, cod tagged on other parts of the bank showed lower levels (0% to 41%) of homing (Templeman, 1979; Lear, 1982). Furthermore, when homing was more narrowly defined to within one or two statistical areas, homing rates were lower. Of cod tagged on northern portions of Funk Island Bank, only 28% could be considered to have homed to within an 8600 km^2 area. Cod tagged elsewhere on the bank had low homing rates of 4% to 18% (Lear, 1982, 1986b).

To investigate homing to coastal areas, cod have been tagged inshore during summer. It may be important to keep in mind that recent (1990's) and historical results may not be fairly compared because current and historical distribution patterns bear little resemblance (Rose et al., 2000a). Historical data show no trend for cod from certain inshore areas to be recaptured on certain offshore banks except on very coarse scales (Templeman, 1974, 1979; Lear, 1982). Cod tagged in coastal Labrador dispersed along the coast to a greater extent than those from coastal Newfoundland, and homing was weaker in general (Templeman and Fleming, 1962; Templeman, 1974, 1979). Strays were recaptured in neighbouring areas and throughout offshore banks (Templeman and Fleming, 1962; Templeman, 1974, 1979; Lear, 1982, 1984b). More recent recapture data suggest that in most parts of the northeast Newfoundland coast, two groups of cod are present: one local resident group and another that overwintered on the south coast (Brattey, 1999, 2000). Cod tagged around the Bay Verte Peninsula, Fogo Islands, and in Bonavista and Trinity Bays showed strong site fidelity (55%, 78-92%, 77% and 55-70% respectively) and were caught year-round in the bay where tagged, reinforcing the possibility of local bay populations (Taggart et al., 1998). Most strays were recaptured in closely neighbouring bays (Brattey, 1999, 2000). Cod tagged in other areas of coastal Newfoundland showed poor homing to specific tagging locations, but relatively strong homing (Table 4-1) to the general stretch of coast where tagged. Strays were recaptured in neighbouring areas, and in wintering locations, including the south coast (Brattey, 1999, 2000). A notable exception was the Gilbert's Bay cod that remained in the bay year-round despite an unimpeded (although narrow) opening to the ocean (Green and Wroblewski, 2000).

There are several lines of evidence for the existence of localised bay populations. First, cod are known to overwinter at specific locations in southerly inlets of the northeast Newfoundland coast (Wroblewski et al., 1994; Anderson, 2000; Rose, 2000). Second, cod have been observed spawning repeatedly at the same sites in inshore waters (Wroblewski et al., 1996; Smedbol and Wroblewski, 1997; Rose, 2000). Third, genetic studies of cod from a variety of inshore locales showed population structure. Cod collected in Trinity Bay could be differentiated from those in Conception Bay. However, there was not evidence for bay populations in all areas examined. For example, cod from Notre Dame, Bonavista and Trinity Bays could not be distinguished (Beacham et al., 2000). Large genetic distances show that cod from Gilbert's Bay, a small Labrador inlet, are more reproductively isolated than other identified components around the Northeast Newfoundland coast (Ruzzante et al., 2000). Gilbert's bay cod spawn later than cod in adjacent offshore waters, which likely creates temporal barriers to gene flow. Furthermore, several thousand Gilbert's Bay cod have been tagged since 1997, and none have been recaptured outside the bay to date (J. M. Green, pers. comm.).

There is convincing evidence of population differences among the coastal and shelf Northern cod. Temporally stable differences in microsatellite signatures allowed cod that overwinter in Trinity Bay to be distinguished from those offshore (Ruzzante et al., 1996; Ruzzante et al., 1997). Ruzzante et al. (1998) found that cod sampled from the Saint Anthony and Notre Dame Bay areas could be distinguished from samples taken from offshore banks.

Population structure within the offshore areas occupied by Northern cod was postulated by Templeman (1962). He reasoned that each shelf region (e.g., Bonavista, Fogo, St. Anthony) projecting seawards with deep water on each side could have a population of its own. This notion was supported by the retention of large portions of tagged fish within the area of tagging for many years after tagging (see references in Lear, 1986a). Further evidence from genetic studies suggests that cod from the northern offshore banks (Hamilton Bank, Funk Island Bank and Hawke Channel) differ from those of more southerly areas (North Cape, Grand Bank and the Nose of the Bank, Bentzen et al., 1996; Ruzzante et al., 1998). Although these studies show evidence for population structure within Northern cod, differences were on a scale coarser than that hypothesised by Templeman (1962), and in general conform to those hypothesised by deYoung and Rose (1993) based on oceanographic circulation patterns in the region.

4.11.3.2 The Northern Gulf of St. Lawrence

The Northern Gulf cod feed and spawn during summers in the Gulf of St. Lawrence, north of the Laurentian Channel (Templeman, 1979) to the Strait of Belle Isle (Thompson, 1943). These cod make annual overwintering migrations through the Cabot Strait to the southwest coast of Newfoundland (Gascon et al., 1990; Castonguay et al., 1999). Many move onto Burgeo Bank (Chouinard and Fréchet, 1994) where they share grounds with cod from the Avalon-Burin populations, although the extent of intermingling is thought to be low (Campana et al., 1999). Northern Gulf fish seldom cross the deep Hermitage Channel onto St. Pierre Bank (Rollet et al., 1994) and only the rarely stray farther east.

The return into the Gulf of St. Lawrence from the overwintering grounds is accomplished by the end of April (Frechet, 1990; Gascon et al., 1990) and most spawning occurs between May and early June at the entrance of the Esquiman Channel, off St. George's Bay before the cod disperse to the feeding areas along the Quebec North Coast (Ouellet et al., 1997). Spawning may occur to the northern extent of the Esquiman Channel in which the migration occurs (G. A. Rose, unpublished data). Ichthyoplankton surveys have shown that each year several simultaneous spawning events take place in different sectors of the Northern Gulf, although their location has not been consistent among years. These likely represented different spawning groups (Ouellet et al., 1994). The relative amounts of spawning in the various locales are not known, and knowledge of spawning group fidelity is lacking (Templeman, 1979). For now, Northern Gulf cod are managed as a single unit.

The northern Gulf evidently retains sufficient eggs and larvae in current eddies to maintain the population (Templeman, 1979). Vertebral averages and otolith microchemistry can distinguish Northern Gulf cod from neighbouring populations, such as the Southern Gulf cod, or Northern cod caught outside the Strait of Belle Isle (Templeman, 1962; Campana et al., 1999).

There is evidence of considerable homing of the local populations of the Northern Gulf to their summer-autumn feeding areas (Templeman, 1979; Gascon et al., 1990). For taggings at Flowers Cove, Lark Harbour, Bonne Esperance and Seven Islands, between 52% and 74% of subsequent recaptures occur within a 4300 square km area around the tagging site (Templeman, 1974, 1979). However, homing to other areas was less accurate. Of cod tagged at St. George's Bay, Forteau and Baie Johan Beetz only 5% to 16% homed with any accuracy (Templeman, 1974, 1979). Homing to a general area was common and most (60-80%) cod homed to within 40000 square km. There was no evidence of homing to Cape Whittle Bank, Gros Morne, or to the Central Northern Gulf, but in these areas cod may were likely tagged while migrating between areas (Templeman, 1979).

4.11.3.3 South Coast – Avalon Cod

The cod fisheries on the south coast of Newfoundland and around the Avalon Peninsula are thought to exploit a complex assemblage of populations that move in and out of the area over the course of the year (Davis et al., 1994; Brattey, 1996). Cod spawning groups have been regularly observed on the St. Pierre Bank (including the Halibut Channel and the Haddock Channel), Burgeo Bank, in Placentia and St. Mary's Bays and on the west and on the northwest slopes of the Grand Bank (Templeman, 1979). In summer, most groups that spawn offshore move shoreward and disperse along south coast of Newfoundland and around the Avalon Peninsula. While inshore, they intermingle with feeding schools from Labrador and the Northeast Newfoundland Shelves and eastward-displaced members of the Northern Gulf populations (Templeman, 1979).

Results of tagging studies have shown that cod spawning in the Avalon and south coast areas exhibit strong homing to the general tagging area, and suggest that the scale of population structure is small relative to that of the management units. Cod tagged around the Avalon Peninsula (Baccalieu Island, Cape Spear, Fermuse, and Cape Pine) overwintered throughout the offshore banks from Hamilton Bank to St. Pierre Bank, and in coastal areas of the south coast of Newfoundland (Templeman, 1974, 1979; Brattey, 2000). Winter recaptures from the more northerly banks tended to be from more northerly tag locations, while recaptures on the Grand Bank and St. Pierre Bank were more common for tagging near St. Mary's Bay (Templeman, 1974, 1979). During subsequent summers, homing to tagging locations was poor (from 26% to 65%) but quite strong to within the general area (62% to 82%, Templeman, 1974, 1979).

Cod tagged in Placentia Bay were commonly recaptured in the bay. Cod tagged at the spawning grounds in the head of the bay showed 87% fidelity to the bay in subsequent years (Brattey et al., 1999; Lawson and Rose, 2000a), although those tagged at other known spawning grounds showed less fidelity. Specifically, cod tagged at Cape St. Mary's and Oderin Bank showed 38% and 63% fidelity, respectively (Templeman, 1974; Brattey et al., 1999). Of cod tagged at Burin, 70% homed to within 60 km (Templeman and Fleming, 1962). Little Paradise cod moved little from the tagging area (50% recaptured within 10 km), as did Little Harbour cod (33% within 35 km, Lawson et al., 1998). Similarly, cod tagged in the inner parts of Fortune Bay were largely (53%) recaptured within the bay (Lawson et al., 1998).

Cod inhabiting banks off the south coast exhibited strong homing to the general tagging area, but accurate homing to tagging locations was weak. Cod tagged around the St. Pierre Bank, Mortier Bank, Burgeo Bank, and Penguin Islands disperse in summer. During subsequent years, cod homed poorly to tagging locations (from 8% to 25%) but strongly to within the general area of the bank on which they were tagged (54% to 86%, Templeman, 1974, 1979; Lear, 1984c).

Genetic studies have shown that there is significant differentiation between Fortune and Placentia Bay cod (Beacham et al., 2000). Furthermore, there is a suggestion that population structure may be resolved at even finer scales. For example, cod from the northern reaches of Placentia Bay were distinguishable from those caught in the outer parts of the bay (Ruzzante et al., 1998). The size of the management unit on the south coast of Newfoundland is approximately 91200 km^2, very large relative to a 100 km range within which 89% of recaptures from taggings at the head of Placentia Bay were located.

4.11.3.4 Grand Banks

Few studies have focused on the migrations and population structure of cod on the Grand Banks. Based on vertebral counts, these fish have been reported to overwinter on the southern Grand Banks, and a small portion migrate north in the feeding season to the southeastern coast of Newfoundland where they intermingle with Avalon populations (Templeman, 1974). Spawning occurs between April and June (Fitzpatrick and Miller, 1979). Eggs are larvae drift south around the bank and move slowly over the bank in the eastern branch of the Labrador Current. In favourable years, cod larvae may be more strongly retained on the Bank (Templeman, 1979).

Grand Bank cod are genetically distinguishable from Northern cod inhabiting the Hamilton, Belle Isle and Funk Island Banks (Bentzen et al., 1996). However, no genetic differences were found among cod taken within the Grand Banks, including the North Cape, the north slope, and the nose of the Bank.

Accurate homing of Grand Banks cod has not been reported, although there is evidence of homing to the more general vicinity of release. Homing to within a 4300 km^2 statistical area around the tagging site was 13% for Halibut Channel, 20% for cod tagged on the North Cape, between 0 and 60% for Virgin Rocks cod, 10% on the central bank, 8% on the western part of the bank, and 29% for cod tagged on the Southeast Shoal. Homing could be described as moderate if recaptures in neighbouring statistical areas were included. Homing to within a >38000 km^2 area around the tagging site was 37% for Halibut Channel, between 0 and 52% for cod tagged on the North Cape, 63% for Virgin Rocks cod, between 20 and 52% for cod tagged on the northeast part of the bank, 63% on the central bank, 46% on the western part of the bank, and 48% for cod tagged on the Southeast Shoal. Straying to other tagging areas was commonplace, indicating a substantial amount of mixing throughout the Grand Bank (Templeman, 1974, 1979; Lear, 1982, 1986b).

4.11.4 The Flemish Cap

Cod from the Flemish Cap were believed to form a population separate from the neighbouring Grand Bank cod. Evidence of separation includes an earlier spawning time (Fitzpatrick and Miller, 1979; Myers et al., 1993b), lower vertebral average (Templeman, 1962), and lacked infestation by *Lernaeocera branchialis* (Templeman, 1962) and the nematode *Terranova decipiens* (Templeman, 1979).

Flemish Cap cod spawned in deep water on the southwest part of the bank in March-May (Fitzpatrick and Miller, 1979; Myers et al., 1993b). When water and current conditions were favourable, clockwise eddies circled the bank, and retained eggs and larvae near the central part (Serebryakov, 1965; Templeman, 1981). However, in certain years, cold Labrador Current water reached the Cap and must have carried with it some cod larvae from the northern Grand Bank (Templeman, 1979).

Tagging studies have shown that Flemish Cap cod exhibit strong site fidelity and have little exchange of adults with neighbouring banks. For tagging on the Cap between 1962 and 1964, only 15% of the recaptures were caught west of the Flemish Channel (excluding first year recaptures, Templeman, 1979). For taggings in the early 1990's, 93% of recaptures were on the Cap (deCárdenas et al., 1993). Of cod tagged on the Grand Banks, and in areas west of the Flemish Channel, only 4 of 15350 recaptures were caught on the Flemish Cap (Templeman, 1979). And from 35293 cod tagged by the USSR between 1960 and 1966, none of 971 recaptured cod had migrated to or from the Flemish Cap (Templeman, 1979).

Consistent with low stray rates, and local egg and larval retention, cod on either side of the Flemish Channel were distinguished genetically using microsatellite frequencies (Cross and Payne, 1978; Bentzen et al., 1996; Ruzzante et al., 1998, 1999; Beacham et al., 2000). Evidence for a separate population is very strong for the Flemish Cap cod.

4.12 Discussion

The cod reviewed were classified into one of four migratory categories (Fig. 4-8). For a given study in which cod are tagged while spawning, and recaptured in subsequent spawning seasons, the behaviours ascribed to the fish in question will depend on their migratory restlessness, and the size of the spawning ground. When the spawning ground is small, long-distance migrants will appear to home with great accuracy. Other migrants, that move between vast feeding and spawning areas will not necessarily return accurately to the tagging site in subsequent years. Non-migratory cod (i.e., those that do not use different grounds for spawning and feeding) appear highly sedentary when their home range is small, but when it is large relative to the area of tagging, they appear to disperse away from the tagging area in subsequent years.

When straying is significant, cod will either appear to disperse or show inaccurate homing. In such cases, exchange of individuals among spawning groups is usually large enough to eliminate population structure among groups. Thus, the 'population' (i.e., all groups with significant exchange of spawners) can be considered to have a large spawning area (i.e., all the individual spawning grounds combined) relative to the size of a tagging locale. In effect, 'straying' and 'inaccurate homing' become synonymous when the inaccuracy rate matches that required to eliminate population structure.

Of the 145 groups examined in this review for which a behavioural type could be assigned, 25 showed accurate homing to spawning grounds (16 inshore, 9 offshore), and 65 were sedentary (50 inshore, 15 offshore), not moving much over the course of a year (Table 4-1). Inaccurate homing was seen in 28 groups (21 inshore, 7 offshore), and dispersal in 27 groups (17 inshore, 10 offshore). Compared to frequencies expected under a null (random) model, inshore groups were slightly more likely to be sedentary than offshore groups, and correspondingly, offshore groups were slightly more likely than those inshore to show accurate homing and to disperse. (Fig. 4-9). These differences were not significant ($\chi_3^2 = 2.7$, $p = 0.43$.). Although the abundance of inshore groups (104) compared to offshore (41) may reflect a bias towards inshore tagging, it is also consistent with a hypothesis that population structure is more complex inshore compared to offshore. Examination of the distances considered to be 'near' the tagging location (Table 4-1) shows that inshore groups generally move shorter distances that offshore ones. However, the important result is that in both inshore and offshore environments all behavioural categories were frequently observed. Populations showing each of the four behavioural patterns are discussed below.

4.12.1 Long-distance Migrants

Several cod populations perform long-distance movements between feeding, overwintering, and spawning locations, and home accurately to the same locations year-after-year. Perhaps the most convincing evidence of homing comes from Northeast Arctic cod. After travelling as many as 1000 km from feeding areas throughout the Barents Sea (Trout, 1957; Godø, 1984c, b, 1986, 1989) between 71% and 92% have been shown to return in subsequent years to the spawning ground at which they were tagged. Only small numbers (< 9%) strayed to the other ground (Godø, 1984c). Long distance migrants that show strong homing to a spawning ground are found throughout the North Atlantic (e.g., western Greenland, Halifax autumn spawners, German Bight) and are not limited to either inshore or offshore areas.

Other cod populations show obvious long-distance migrations among a number of vast geographic areas, but do not appear to home with much accuracy. Because the general area to which they home is large (relative to a tagging locale), homing to the tagging location can be weak, even if that to the spawning ground is strong. For example, many cod that summer in the southern Gulf of St. Lawrence migrate out of the Gulf in winter. Although they don't home accurately to one area, few individuals fail to return to the southern Gulf in the subsequent summers. Long distance migrants that do not accurately return to tagging locations in subsequent years are found throughout the North Atlantic (e.g., "northern" cod on the Northeast Newfoundland and Labrador Shelves, cod wintering on Banquereau, cod throughout the North Sea) and are not limited to either inshore or offshore tagging areas.

It is important to note that exact percentages for homing cannot be determined from the tagging studies reviewed here. This is a result of the limitations of conventional tagging studies, for which only two locations can be known for any individual. In the case where individuals are recaptured away from the ground where they were tagged in previous years, it cannot be determined whether they strayed, or were simply caught while en route to the location where they were originally captured (e.g., Tåning, 1940; Godø, 1984c). Similarly, individuals recaptured at the tagging location could have been transients.

4.12.2 Non-migrant Cod

Non-migratory cod do not perform long distance movements but remain within a small geographic range for spawning, feeding and overwintering. These cod appear highly sedentary when their home range is small relative to the area of tagging). When the home range of these fish is small, intermingling with cod in neighbouring areas will be limited (e.g., some inshore Nova Scotia cod rarely travel more than 12 nm from the tagging location), a requirement for small-scale population structure to develop. In some cases, however, migratory groups move in and share spawning grounds with more sedentary cod (as is the case in the Norwegian and Irish Seas).

Cod in Gilbert's Bay show no evidence of moving outside their small inlet in the Labrador coast. Although cod from surrounding areas enter into parts of Gilbert's Bay, and intermingle with resident cod, no tagged resident has ever been recaptured outside of the bay. Coupled with their late spawning time, this group's relatively sedentary behaviour likely explains their strong genetic differentiation from neighbouring cod, smaller size and distinguishable colour. Other non-migratory cod with relatively small home ranges are found throughout the North Atlantic (e.g., Faroe Bank, Flemish Cap, cod inhabiting the Greenland and Norwegian Fjords, coastal Nova Scotia, coastal Scotland, Bornholm, etc.), and are not limited to either offshore or inshore groups.

When home range is large relative to the area of tagging, non-migratory cod appear to disperse away from the tagging area in subsequent years. When widely dispersed, tagging recaptures are equally likely from any point within the home range, thus, if a tagging area is small relative to the home range, evidence for homing or site fidelity will be weak despite the pattern of the movements. For example, coastal Labrador, Northeast Newfoundland coast and Avalon Peninsula cod disperse throughout neighbouring stretches of coastline (although evidence for more sedentary bay populations are also found). Cod that dispersal throughout a large range, and thus show no evidence of homing or site fidelity can be found throughout the North Atlantic (English coast, the

Central North Sea, the Southern Bight and English Channel area, Scotian Shelf, Gulf of Maine, Bay of Fundy, etc.) and are not limited to either inshore or offshore locations.

Aside from the four behavioural patterns described above, another form of movement was observed in the literature. Some cod movements appear to be unidirectional (thus, non-migratory), and often associated with ontogenetic shifts in range (e.g., a shift from nursery areas to adult range, Otterlind, 1985). Unidirectional ontogenetic movement were typical of young cod in the brackish juvenile nursery areas of the northern Baltic Sea (off Sweden and Finland) as they matured and moved to more southerly parts of the Baltic to feed and spawn.

It is important to note that as they are defined here (see Fig. 4-8), 'sedentary' cod are simply unique cases of 'homing' cod for which migratory distance approaches zero. Similarly, 'accurate' and 'inaccurate' homing are functions of the size of the tagging area relative to the size of the spawning ground. Although for discussion purposes, I divided the possible values of migratory distance into "short' and 'long', and the values of spawning ground size into 'small' and 'large' (Fig. 4-8), both variables are actually continuous, and any combination of them is possible. As such, the distinction between sedentary and homing, for example, is based entirely on a subjective decision of where to split the range of possible values. Percentages in Table 4-1 should thus be interpreted with caution.

4.12.3 Maintenance of Population Structure

One of the requirements for development and maintenance of small-scale population structure is isolation of the group during spawning. This can be achieved by homing or showing strong site fidelity to a spawning ground. Overall, about 62% of the groups (sedentary and accurately homing groups combined) considered in this review could potentially show small-scale population structure. Although these percentages are approximate given the constraints of the data, and interpretation should be with caution, I can conclude that no part of the range of behaviours was not limited to any part of the North Atlantic, and all were equally likely in both inshore and offshore environments (Fig. 4-9). This suggests that the spatial scale of population structure may be variable throughout the range of cod, and cannot be predicted using simple rules of thumb. This is interesting in light of the speculation of Taggart et al. (Taggart et al., 1998) who suggested that genetically distinguishable populations would be seen on scales between 60 and 100 nautical miles.

Another factor that could enhance relatively small-scale population structure is limited dispersal of eggs and larvae. Dispersal can be limited if spawning occurs in areas where oceanographic conditions favour retention of eggs (e.g., Sinclair, 1989). Retention is a common feature at oceanographic fronts, and can also result where bottom topography creates complex current patterns (e.g., Mullineaux and Mills, 1997). In the literature reviewed here, spawning in retention areas was frequently cited as a mechanism whereby adjacent populations could be potentially distinct. Perhaps the best example is the gyre-like circulations of the Faroe Bank and Plateau at which cod remain separate despite their proximity (Hansen et al., 1990). Another example occurs at the Flemish cap where eggs and larvae are caught in circular eddies and retained (Serebryakov, 1965; Templeman, 1981). Similarly, eggs and larvae spawned in areas of gyre-like circulation by cod on Georges (O'Boyle et al., 1984; Sherman et al., 1984; Lough and Bolz, 1989; Suthers and Frank, 1989; Page et al., 1999) on Browns Bank cod (Campana et al., 1989), and perhaps on other Scotian Shelf Banks (Gagné and O'Boyle, 1984; O'Boyle et al., 1984) showed limited dispersal.

Another strategy thought to retain eggs within the home range of the population is migration upcurrent before spawning. This strategy may reduce the necessity for exact homing and site fidelity except at very large scales. This pattern of migration is evident for southern Greenland cod, which move against the Irminger Current to spawn in Iceland (Harden-Jones, 1968; Vilhjálmsson and Magnússon, 1984, 1985). Similarly, cod from northwest Greenland move south against the West Greenland current to spawn (Hovgård and Christensen, 1988) in areas where their eggs drift north to adult summering and feeding areas (Harden-Jones, 1968). Northern Gulf of St. Lawrence cod spawned in the mid-Gulf where currents carry eggs to the adults' summer feeding range along the coast of Quebec (Ouellet, 1997). Northern cod spawn primarily to the north where the dominant Labrador Current carries their eggs and larvae southward to the coasts of Labrador and Newfoundland (Helbig et al., 1992; deYoung and Rose, 1993).

Effective dispersal can also be limited if fish home to natal areas to spawn. Although no mechanism has been found whereby widely dispersed juveniles could home to a natal ground last occupied as undeveloped eggs (Rätz, 1994), some data reviewed here are consistent with natal homing. Southern Greenland cod, which are thought to be seeded by eggs that drift in the Irminger Current from Iceland (Hansen, 1949), make reverse spawning migrations to Iceland (Hovgård and Messtorff, 1987). It is noteworthy that both spawning in retention areas and upcurrent from the juvenile home range can be considered natal homing. This form of natal homing doesn't require imprinting during early life, a condition considered unrealistic for most broadcast spawners (Rätz, 1994). It only requires an ability on the part of adults to gauge current speed and direction and a predisposition to migrate against them to a spawning ground. Cod, like many species of fish have been shown to be capable of recognition of current direction (Rose et al., 1995; Wroblewski et al., 2000).

Strong, 'accurate' homing was observed in 17% of the groups considered in this review, yet it is interesting to note that only in rare instances would transplanted cod return to the place of original capture. Many animals renowned for their homing abilities are capable of finding their way back to their home area even when transplanted into unfamiliar areas (for review see Papi, 1992). Many animals, including some fishes, are known to orient using a solar compass, celestial cues or magnetic geopositioning (Hasler, 1971; Quinn and Brannon, 1982) for larger-scale navigation, and using chemoreception and underwater landmarks for more localised orientation. Under the assumption that cod benefit from homing, and that they try to home, their lack of success in the transplantation studies suggests either that cod are not capable of navigating using celestial or geomagnetic cues, or that transplantation distances were not great enough for these cues to be useful. Matthews (1955) found that transplantation distances more that 55 to 80 km were required for pigeons to use celestial cues. These distances were much less than those over which cod were transplanted in the studies reviewed here (majority between 125 and 1000 km). There were two studies that found 50% or greater homing to the area of original capture (Tiews and Lamp, 1974; Green and Wroblewski, 2000), and in both transplantation distances were small (between 15 and 75 km). These results suggest that cod are better at orienting using more localised cues, for example odours or underwater landmarks (Hasler, 1966). This raises the question of how cod that successfully home year after year in the wild navigate over long distances. Rose (1993) suggested that cod navigate long distances underwater along learned migration pathways. In the end, the critical experiments to determine which cues cod use during navigation have not been done, so this discussion remains speculative.

Another interesting feature observed in a number of cod populations was an ontogenetic shift in spawning site use. Differences among spawning grounds in the size distribution of cod was observed in Iceland (Marteinsdóttir et al., 2000), Norway (Lebed et al., 1983) and the Faroes (Tåning, 1940). In Iceland, young cod spawned more frequently at grounds located near the shelf break, whereas larger individuals were more often found near shore. In Norway, spawners at Møre were smaller than those at Lofoten (but see Godø, 1984c). Similarly, spawners on the western Faroese ground were smaller than those that used the more northerly location. However, no documented case was found in which a small cod was tagged at one ground and recaptured at the other when significantly larger, likely because most tagging studies target larger fish.

Several questions about cod migrations and homing were raised while reviewing this literature that could not be addressed because of the limitations of conventional tagging techniques. However, the recent miniaturisation of long-life acoustic transmitter tags make feasible repeated, non-intrusive observations of the same individual over a period of several years. Such technology could help resolve the many controversies about cod homing and site fidelity, such as the proportion of Iceland-spawning Greenland cod that subsequently return to Greenland, the rate at which cod which stray to Bornholm from the various Eastern Baltic spawning grounds return to their 'home' ground in years of improved water quality, or the scale of the sub-components of the Northern cod. Finally, telemetry can determine more accurately the homing rates among spawning grounds in locations where authors have regarded potential strays as being "on their way" to the 'appropriate' tagging ground (e.g., Tåning, 1940; Godø, 1984c).

The migratory behaviour of Atlantic cod is highly variable. Although in this paper I describe cod behaviour as sedentary, dispersive, or showing accurate or inaccurate homing, these descriptors simply categorise a wide range of behaviours into a few simple groups. Behavioural patterns are thus variable within each category. Large variability in cod behaviour was observed on both sides of the North Atlantic and in both inshore or offshore areas. The spatial-scale over which one can expect reproductive isolation (and thus population structure) will therefore vary throughout its range without a simple rule of thumb, even within a relatively limited geographic range. Failure of fisheries management to acknowledge the potential importance of such variations in behaviour when considering population structure and productivity may lead to incorrect estimates of population growth rates, and reduce effectiveness of cod management. In conclusion, I speculate that the variability in behaviour has been adaptive, and may have been key to cod's success as a species.

4.13 Acknowledgements

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Table 4-1: Homing and site fidelity of groups of tagged Atlantic cod. Observed behaviours were categorised as sedentary (S), dispersive (D), accurate homing (AH), and inaccurate homing (IH). When the behavioural pattern could not be determined from the data or the text of a tagging study, all possible behaviours were listed. Unidirectional movements (U), often associated with ontogenetic range shifts are also noted.

Experiment location	Homing†	Site Fidelity¥	behaviour	Comment	Reference
Baltic Sea					
Western Baltic, offshore					
Skagerrak, danish side		81%	S	on Danish side	Danielssen, 1969 as cited in ICES, 1971
Western Baltic		92.3%	S	*1st yr excluded; within 45 km	Strubberg, 1922
Western Baltic, inshore					
Kiel Bay		79.0%	S	within area	Thurow, 1985
Mecklenburg Bay		38.9%	D	within area	Berner 1971 as cited in Bagge and Steffensen, 1989
Mecklenburg Bay		49.1%		within area	Thurow, 1985
Mecklenburg Bay		33% to 80%		within area	Berner, 1974
Mecklenburg Bay		81%		within area	Berner, 1981
Mecklenburg Bay	44%			within area	Berner, 1967
Middle and Eastern Baltic					
Arkona		57%	S	* within area	Bagge et al., 1974
Arkona		51% to 60%		within area	Berner, 1967
Arkona		43% to 85%		within area	Berner, 1974
Arkona		62%		within area	Berner, 1981
Arkona		94.3%		within area	Otterlind, 1962
Arkona		64.6%		within area	Otterlind, 1969
Arkona		70.3% to 73.1%		within 60 km	Thurow, 1985
Arkona		44.7% to 58.5%		* within area	Tiews and Lamp, 1974
Borhnolm		60.9% to 71.6%	S	* within area	Tiews and Lamp, 1974
Bornholm		66% to 95%		* within area	Bagge et al., 1974
Bornholm		77% to 100%		within area	Berner, 1974
Bornholm		92%		within area	Berner, 1981
Bornholm		33.3%		within area	Birjukov, 1969
Bornholm		81.6% to 85.6%		within 50 n mi	Netzel, 1969; 1974
Bornholm		81.8% to 92.3%		* within 50 n mi	Otterlind, 1962
Bornholm		90.9% to 95.7%		within area	Otterlind, 1962
Bornholm		93.5%		within 60 km	Thurow, 1985
Slupsk Furrow		32%	D	* within area	Bagge et al., 1974
Slupsk Furrow	22.7%			within area	Netzel, 1968
Slupsk Furrow		70.3%		within 60 km	Thurow, 1985
Slupsk Furrow		31.8% to 37.5%		* within area	Tiews and Lamp, 1974
Gdànsk		53.6% to 58.3%	D	* within area	Tiews and Lamp, 1974
Gdànsk		60%		within area	Birjukov, 1969
Gdànsk		55.1%		within area	Netzel, 1963
Gdànsk		35.2% to 45.1%		within 50 n mi	Netzel, 1969; 1974
Klaipeda		18.6%	D	within area	Birjukov, 1969
Gotland		52.2%	AH/IH/D	within area	Otterlind, 1969

Experiment location	Homing†	Site Fidelity¥	behaviour	Comment	Reference
Gotland		9.5% to 32.8%		* within area	Tiews and Lamp, 1974
Gotland		34.2%		within area	Birjukov, 1969
Northern Baltic					
Åland		0% to 16%	AH/IH/D	* within subdivision	Aro and Sjöblom, 1983
Åland		48.4% to 77.1%		in tagging area	Otterlind, 1961
Åland		49.4%		* within 50 n mi	Otterlind, 1962
Åland		34.5%		*1st yr excluded	Sjöblom et al., 1980
Finland		23.3%	U	* within area	Sjöblom and Aro, 1977
Finland		0%		*1st yr excluded	Sjöblom et al., 1980
The Faroe Islands					
Faroe Bank	99%	99%	S	only one spawning ground	Jones, 1966
Faroe Plateau	70% to 87.5%	low	AH	*	Tåning, 1940
Greenland					
Fjords					
Kangia		42.9%	S	within fjord; 100% within 35 mi	Hansen, 1949
Godthaab Fjord		76.3%	S	within fjord	Hansen, 1949
Godthaab Fjord		82.4%		within fjord	Hovgård and Christensen, 1990
Ikertok Fjord		75.3%	S	within fjord	Hansen, 1949
Offshore Banks					
Northern offshore banks (1A - 1D)	strong		AH	from oscilation of recap. distrib'n	Rasmussen, 1957; Hovgård and Christensen, 1990
SW offshore banks (1E - 1F)		82.4%	S	* 13% in Iceland	Hovgård and Riget, 1991
SW offshore banks (1E - 1F)		>30%		up to 70% caught in Iceland	Harden-Jones, 1968
SW offshore banks (1E)		62%		* recaps in Iceland ignored	Hovgård and Christensen, 1990
SW offshore banks (1F)		81%		* recaps in Iceland ignored	Hovgård and Christensen, 1990
East Greenland		10%	D/IH/U	90% in Iceland	Hansen, 1949
Iceland					
SW spawning grounds (Subareas 1&9)	79.0%	48.3%	AH	* within subarea	Jónsson, 1996
Faxafloi (Subarea 2)	72%	82%	S	* within subarea	Jónsson, 1996
Subarea 3	20.7%	56.9%	S+H	* within subarea	Jónsson, 1996
Subarea 4	50.0%	55.0%	S+H	* within subarea	Jónsson, 1996
Subarea 5	43.4%	45.6%	S+H	* within subarea	Jónsson, 1996
Subarea 6	54.5%	40.0%	S+H	* within subarea	Jónsson, 1996
Subarea 7	66.7%	59.1%	AH	* within subarea	Jónsson, 1996
Subarea 8	50.0%	11.1%	IH	* within subarea	Jónsson, 1996
Subareas 3&9	high		AH	inferred from DSTs	Thorsteinsson and Eggertsson, 1998
North America					
Middle Atlantic Bight					
New Jersey	70%		S		Wise, 1958
Southern New England					
Chatham, MA		83.5%	S	*	Wise, 1958
Highland Ground, MA		91.2%	S	*	Wise, 1958
Georges Bank					
Georges Bank		66.6%	S	*	Wise, 1963
Gulf of Maine, inshore					
Gulf of Maine inshore	very strong		S	inferred from interviews	Ames, 1998
Sheepscot Bay, ME	60%	>70%	S	* within 30 nm of area	Taggart, 1998

Experiment location	Homing†	Site Fidelity#	behaviour	Comment	Reference
Bay of Fundy					
New Brunswick side	50%		D,H	* within management SubDiv	Campana and Simon 1984
Nova Scotia inshore					
Seal Island NS		80%	S	within 50 mi	McKenzie 1956
Shelburne NS		65% to 90%	S	within 25 mi	McKenzie 1956
Lunenburg-Halifax NS		75%	S	within 12 mi	McKenzie 1956
Halifax NS	80%		AH	within 12 mi	McKenzie 1956
Halifax autumn spawners	strong		AH	inferred from vertebrae	McKenzie 1940
Egg Island-Jeddore Rock NS	83%		AH	within 12 mi	McKenzie 1956
Lockeport NS		93%	S	within 40 mi	McCracken 1956
Lockeport NS		>95%		within management SubDiv	Gagné et al 1983
Sandy Cove NS		>95%	S	within management SubDiv	Gagné et al 1983
Scotian Shelf					
Browns Bk		57%	S	* on the bank	Wise 1963
Browns Bk		95%		on the bank	Halliday 1973
Browns Bk		33%		on the bank	Hunt et al 1999
Emerald Bk	57%		D	on the bank	McKenzie 1956
Western Bk		86 to 100%	S	* on the bank	Martin and Jean 1964
Sable Island Bk western	76%		AH	on the bank	McKenzie 1956
Sable Island north of	56%			on the bank	McKenzie 1956
Sable Island Bk northwestern	54%			on the bank	McKenzie 1956
Sable Island Bk eastern	65%			on the bank	McKenzie 1956
Banquereau	84%		H	on the bank	Martin and Jean 1964
Banquereau central	29%			on the bank	McKenzie 1956
Banquereau southern	56%			on the bank	McKenzie 1956
Banquereau northern	79%			on the bank	McKenzie 1956
Banquereau eastern	46.5%			on the bank	McKenzie 1956
Southern Gulf of St Lawrence					
Sydney Bight Cape Breton	71%		AH		McKenzie 1956
Sydney Bight Cape Breton	86%			in southern Laurentian Ch	Martin and Jean 1964
Cheticamp Cape Breton	74%		H		McKenzie 1956
Cheticamp Cape Breton	35.4%				Lambert 1993
Magdalen Islands	45%		H		Powles 1959
PEI		39% to 66%	D		McKenzie 1956
Chaleur Bay NB	80.6%		AH	*	McCracken 1959
Chaleur Bay NB	75%				McKenzie 1956
Gaspe QC		95%	S		McKenzie 1956
Gaspé QC	64%	72.5%			Lambert 1993
Baffin Area					
Ogac Lake		31.6%	S	within about 500 m 100% within a few km	Patriquin 1967
Labrador					
Nain Hopedale	13.1%		D	* within a 8600 sq km statistical area	Templeman 1979
Nain Hopedale	34.4%			* within a 77400 sq km statistical area	Templeman 1979
Saglek Bay	0.0%		D	* within a 38700 sq km statistical area	Templeman 1979
Cape Harrison	25.8%		D	* within a 8600 sq km statistical area	Templeman 1979
Cape Harrison	45.5%			* within a 51600 sq km statistical area	Templeman 1979

Experiment location	Homing†	Site Fidelity‡	behaviour	Comment	Reference
Domino Labrador	60.0%		D	* within 100 km	Templeman and Fleming 1962
Domino Labrador	20.0%			* within a 4300 sq km statistical area	Templeman 1979
Domino Labrador	41.0%			* within a 38700 sq km statistical area	Templeman 1979
Gilbert's Bay		100%	S	* within Gilbert's Bay	Green and Wroblewski 2000
Hawke Channel S side	0.0%		D	* within a 8600 sq km statistical area	Templeman 1979
Hawke Channel S side	13.9%			* within a 51600 sq km statistical area	Templeman 1979
Hamilton Bank W	0.0%		IH	* within a 4300 sq km statistical area	Templeman 1979
Hamilton Bank W	22.2%			* within a 38700 sq km statistical area	Templeman 1979
Hamilton Bank E	17.5%			* within a 6600 sq km statistical area	Templeman 1979
Hamilton Bank E	64.0%			* within a 68800 sq km statistical area	Templeman 1979
Hamilton Bank NE	1.7%			* within a 8600 sq km statistical area	Lear 1982
Hamilton Bank NE	6.8%			* within a 51600 sq km statistical area	Lear 1982
Hamilton Bank SE	8.3%			* within a 4300 sq km statistical area	Lear 1982
Hamilton Bank SE	83.3%			* within a 38700 sq km statistical area	Lear 1982
Hamilton Bank SE	49.1%			* within a 43000 sq km statistical area	Lear 1986
Hamilton Bank SE	85.3%			* within a 175900 sq km statistical area	Lear 1986
Northeast Newfoundland Shelf					
Cape St. Anthony	23.0%		IH	* within a 4300 sq km statistical area	Templeman 1974
Cape St. Anthony	68.5%			* within a 38700 sq km statistical area	Templeman 1974
Englee, Northern Penin	33.3%		D	* within 60 km	Templeman and Fleming 1962
Quirpon	21.5%		IH	* within a 4300 sq km statistical area	Templeman 1979
Quirpon	62.2%			* within a 38700 sq km statistical area	Templeman 1979
Grey Island	0.0%		IH	* within a 8600 sq km statistical area	Templeman 1979
Grey Island	79.3%			* within a 51600 sq km statistical area	Templeman 1979
La Scie	3.7%		D	* within a 4300 sq km statistical area	Templeman 1974
La Scie	55.6%			* within a 38700 sq km statistical area	Templeman 1974
Bay Verte Peninsula		55.6%	AH+IH(D)	* within 55 km	Bratley 1999
Exploits, Notre Dame Bay	60.0%		AH	* within a 19800 sq km statistical area	Lear 1982, 1984b
Exploits, Notre Dame Bay	80.0%			* within a 33100 sq km statistical area	Lear 1984b
Fogo-Twillingate		76.3%	S	* within 80 km	Bratley 1999
Fogo Island		92.3%		* within 125 km	Bratley 1999
Cape Fogo	9.5%		IH	* within a 4300 sq km statistical area	Templeman 1979
Cape Fogo	52.4%			* within a 38700 sq km statistical area	Templeman 1979
Cape Bonavista	31.7%		IH	* within a 4300 sq km statistical area	Templeman 1974
Cape Bonavista	61.0%			* within a 38700 sq km statistical area	Templeman 1974
Cape Bonavista	50.0%			* within a 8600 sq km statistical area	Templeman 1979
Cape Bonavista	70.5%			* within a 51600 sq km statistical area	Templeman 1979
Bonavista Bay		77.8%	S	* within Bonavista Bay (45 km)	Bratley 1999
Bonavista Bay		76.2%		* within 70 km	Bratley 1999
Trinity Bay		56.0%	S	* within Trinity Bay (75 km)	Bratley 2000
Trinity Bay		>70%		* within 60 km	Taggart et al. 1998
Smith Sound		55.0%	AH+IH(D)	* within Trinity Bay (60 km)	Bratley 1999
Conception Bay	37.3%		IH	* within a 5300 sq km statistical area	Lear 1982, 1984b
Conception Bay	50.6%			* within a 12900 sq km statistical area	Lear 1982
Conception Bay	70.6%			* within a 15800 sq km statistical area	Lear 1982, 1984b
Conception Bay	42.1%			* within a 5300 sq km statistical area	Lear 1982, 1984b

Experiment location	Homing†	Site Fidelity‡	behaviour	Comment	Reference
Conception Bay	58.2%			* within a 12900 sq km statistical area	Lear 1982
Conception Bay	81.2%			* within a 19800 sq km statistical area	Lear 1982 1984b
Conception Bay	78.9%			* within a 5300 sq km statistical area	Lear 1984b
Belle Isle Bank	2.1%		Ht	* within a 4300 sq km statistical area	Templeman 1979
Belle Isle Bank	24.7%			* within a 38700 sq km statistical area	Templeman 1979
Belle Isle Bank	8.2%			* within a 49800 sq km statistical area	Lear 1986
Belle Isle Bank	70.0%			* within a 276400 sq km statistical area	Lear 1986
Belle Isle Bank	34.5%			* within a 17200 sq km statistical area	Lear 1982
Belle Isle Bank	85.1%			* within a 77400 sq km statistical area	Lear 1982
Funk Island Bank	0.0%		D	* within a 51600 sq km statistical area	Templeman 1979
Funk Island Bank N	25.5%			* within a 49800 sq km statistical area	Lear 1986
Funk Island Bank N	43.2%			* within a 49800 sq km statistical area	Lear 1986
Funk Island Bank N	73.2%			* within a 227500 sq km statistical area	Lear 1986
Funk Island Bank N	12.5%			* within a 49800 sq km statistical area	Lear 1986
Funk Island Bank N	57.1%			* within a 227500 sq km statistical area	Lear 1986
Funk Island Bank N	27.8%			* within a 8600 sq km statistical area	Lear 1982
Funk Island Bank N	59.3%			* within a 51600 sq km statistical area	Lear 1982
Funk Island Bank NE	4.5%			* within a 8600 sq km statistical area	Lear 1982
Funk Island Bank NE	0.0%			* within a 51600 sq km statistical area	Lear 1982
Funk Island Bank NE	18.6%			* within a 4300 sq km statistical area	Lear 1982
Funk Island Bank NE	41.4%			* within a 38700 sq km statistical area	Lear 1982
Funk Island Bank E	8.5%			* within a 8600 sq km statistical area	Lear 1982
Funk Island Bank E	19.1%			* within a 51600 sq km statistical area	Lear 1982
Funk Island Bank SE	18.2%			* within a 79400 sq km statistical area	Lear 1986
Funk Island Bank S	50.0%			* within a 12900 sq km statistical area	Lear 1982
Funk Island Bank SW	16.7%			* within a 8600 sq km statistical area	Lear 1982
Funk Island Bank SW	33.3%			* within a 51600 sq km statistical area	Lear 1982
Funk Island Bank SW	22.6%			* within a 52900 sq km statistical area	Lear 1986
Northern Gulf of St. Lawrence					
Rose Blanche	21.9%		D-Ht	* within NAFO Subdiv. 3Pn (4800 sq km)	Muguelet 1994
Port Au Basques	51.3%		Ht	* within a 8600 sq km statistical area	Templeman 1979
Port Au Basques	85.6%			* within a 51600 sq km statistical area	Templeman 1979
Strait of Belle Isle	71.2%	46.4%	An	* within NAFO 3Pn4RS (179100 sq km)	Gascon et al. 1990
Newfoundland West Coast	63.3%		S	* within NAFO Div. 4R (66300 sq km)	Muguelet 1994
Newfoundland West Coast	90.1%	84.0%		* within NAFO 3Pn4RS (179100 sq km)	Gascon et al. 1990
Flowers Cove	63.2%		S-An	* within a 4300 sq km statistical area	Templeman 1974
Flowers Cove	78.9%			* within a 38700 sq km statistical area	Templeman 1974
Port Au Choix	71.7%		Ht	* within a 38700 sq km statistical area	Templeman 1974
Port Au Choix	47.7%			* within a 4300 sq km statistical area	Templeman 1979
Port Au Choix	83.2%			* within a 38700 sq km statistical area	Templeman 1979
Port Au Choix	41.4%			* within a 4300 sq km statistical area	Templeman 1974
Lark Harbour	81.0%		An	* within 60 km, 42% in feeding season	Templeman and Fleming 1962
Lark Harbour	73.8%			* within a 4300 sq km statistical area	Templeman 1979
Gros Morne	5.1%		D	* within a 51600 sq km statistical area	Templeman 1979
Central North Gulf	5.0%		D	* within a 38700 sq km statistical area	Templeman 1979
Newfoundland SW Coast	94.1%	89.7%	S	* within NAFO 3Pn4RS (179100 sq km)	Gascon et al. 1990

Experiment location	Homing†	Site Fidelity#	behaviour	Comment	Reference
St George's Bay	5.4%		D	* within a 4300 sq km statistical area	Templeman 1979
St George's Bay	35.1%			* within a 38700 sq km statistical area	Templeman 1979
E Quebec North Coast	98.1%	94.6%	S	* within NAFO 3Pn4RS (179100 sq km)	Gascon et al 1990
Forteau	77.2%		IH	* within a 38700 sq km statistical area	Templeman 1974
Forteau	9.9%			* within a 4300 sq km statistical area	Templeman 1974
Bonne Esperance	58.6%		IH	* within a 4300 sq km statistical area	Templeman 1979
Bonne Esperance	81.8%			* within a 38700 sq km statistical area	Templeman 1979
La Tabatiere	14.4%		IH	* within a 4300 sq km statistical area	Templeman 1979
La Tabatiere	59.3%			* within a 38700 sq km statistical area	Templeman 1979
W Quebec North Coast	95.3%	93.9%	S	* within NAFO 3Pn4RS (179100 sq km)	Gascon et al 1990
Cape Whittle Bank	12.5%		D	* within a 38700 sq km statistical area	Templeman 1979
Above Anticosti	84.5%	84.6%	S	* within NAFO 3Pn4RS (179100 sq km)	Gascon et al 1990
Baie Johan Beetz	16.4%		D	* within a 4300 sq km statistical area	Templeman 1979
Baie Johan Beetz	49.3%			* within a 51600 sq km statistical area	Templeman 1979
Seven Islands	52.4%		IH	* within a 4300 sq km statistical area	Templeman 1979
Seven Islands	61.9%			* within a 38700 sq km statistical area	Templeman 1979
Avalon					
Eastern Avalon		26.3%	A/IH/D	* within Eastern Avalon (35 km)	Brattey 2000
St John's	80.0%		S	* within 60 km 61% in feeding season	Templeman and Fleming 1962
Baccalieu Island	40.7%		IH	* within a 8600 sq km statistical area	Templeman 1979
Baccalieu Island	70.4%			* within a 51600 sq km statistical area	Templeman 1979
Cape Spear	26.5%		IH	* within a 4300 sq km statistical area	Templeman 1979
Cape Spear	73.5%			* within a 38700 sq km statistical area	Templeman 1979
Fermuse	27.7%		IH	* within a 4300 sq km statistical area	Templeman 1974
Fermuse	62.4%			* within a 38700 sq km statistical area	Templeman 1974
Fermuse	33.8%			* within a 4300 sq km statistical area	Templeman 1979
Fermuse	69.2%			* within a 38700 sq km statistical area	Templeman 1979
Cape Pine	0.0%		IH	* within a 4300 sq km statistical area	Templeman 1974
Cape Pine	59.3%			* within a 38700 sq km statistical area	Templeman 1974
Cape Pine	65.3%			* within a 8600 sq km statistical area	Templeman 1979
Cape Pine	82.9%			* within a 51600 sq km statistical area	Templeman 1979
St Mary's Bay		12.1%	D/IH	* within St Mary's Bay (45 km)	Brattey 1999
Southwest Coast					
Cape St Mary's	28.6%		D	* within a 4300 sq km statistical area	Templeman 1974
Cape St Mary's	39.3%			* within a 38700 sq km statistical area	Templeman 1974
St Brides Placentia Bay		38.5%	A/IH/D	* at Cape St Mary's (within 20 km)	Brattey et al 1999
Little Hr Placentia Bay		33.3%	A/IH/D	* in inner eastern Pbay (max 35 km)	Lawson et al 1998
Head of Placentia Bay		89.4%	S	* in Placentia Bay (110 km)	Brattey et al 1999
Gal Haven Placentia Bay		87.0%	S	in Placentia Bay (110 km)	Lawson and Rose 2000
Little Paradise Placentia Bay		50.0%	A/IH/D	* within tagging area (10 km)	Lawson et al 1998
Oderin Bank Placentia Bay		62.7%	S	* in Placentia Bay (100 km)	Brattey et al 1999
Mortier Bank	8.0%		IH	* within a 8600 sq km statistical area	Templeman 1979
Mortier Bank	75.4%			* within a 51600 sq km statistical area	Templeman 1979
Burin Pbay	70.6%		S	* within 60 km 25% in feeding season	Templeman and Fleming 1962
Lord's Cove Burin Penin		15.2%	IH	* in Lord's Cove area (30 km)	Brattey et al 1999
Inner Fortune Bay		53.3%	A/IH/D	* in Fortune Bay (50 km)	Lawson et al 1998

Experiment location	Homing†	Site Fidelity¥	behaviour	Comment	Reference
Forty Mile Ground	57%	55%	D/IH	within 30 mi	LeFranc, 1973
Scottish East Coast		86.2%	S	within apr 100 x 125 km area	Symonds and Raitt, 1966
East Orkney		48.2%	AH/IH/D	within apr 50 x 300 km area	Symonds and Raitt, 1966
Scottish North Coast		76.2%	S	within apr 100 x 80 km area	Symonds and Raitt, 1966
Moray Firth	57% to 94%		S	* within apr 125 x 80 km area	Symonds and Raitt, 1966
Moray Firth		80.7% to 94.9%		within apr 125 x 80 km area	Symonds and Raitt, 1966
Papa Bk		34.7%	AH/IH/D	* within tagging area	Easey, 1987
North Shetlands		55.6%	AH/IH/D	* within tagging area	Easey, 1987
South Shetlands		25.4%	AH/IH/D	* within tagging area	Easey, 1987
Hebrides		24.5%	AH/IH/D	* within tagging area	Easey, 1987
English Coast					
Flamborough, English Coast	38% to 65%	25% to 58%	D/IH	* within 60 x 60 km area	Bedford, 1966
Central North Sea					
Flamborough Spawning grounds	14.8%	16.1%	D	* within 60 x 60 km area	Bedford, 1966
Cleaver Bk, Central North Sea	0% to 33%	26% to 27%	D/IH	* within 60 x 60 km area	Bedford, 1966
Fisher Bk	8.4%	8.0%	D/IH	* within 60 x 60 km area	Bedford, 1966
NW Rough, Central North Sea	20%	17%	D/IH	* within 60 x 60 km area	Bedford, 1966
NE Dogger Bank & Clay Deep	23.4%	16.0%	S	* within 60 x120 km area	Bedford, 1966
Dogger Bank	61.9%	60.2%		* on southern Dogger Bk	LeFranc, 1969
Dogger Bank		74.2%		on southern Dogger Bk	LeFranc, 1970
Dogger Bank		84.2%		within 60 km	LeFranc, 1967
Farns Deep		75%	S	within 60 km	LeFranc, 1967
Clay Deep		45.5%	AH/IH/D	* within 60 km	deClerck, 1973
Southern Bight					
North Foreland, Southern Bight	14.3%	13.6%	D	* within 60 x 60 km area	Bedford, 1966
Sizewell Bk, Southern Bight	47.8%	33.3%	D/IH	* within 60 x 60 km area	Bedford, 1966
German Bight	21% to 100%		AH	* within 100km	Lamp, 1973
Dutch Coast		44.2%	D/IH	* within 60 km	Daan, 1969
Dutch Coast	33.3%	67.6%		* within 60 km	deClerck, 1973
Belgian Coast	33.3%	16.7%	D/IH	* within 60 km	deClerck, 1973
Belgian Coast	28.6%	36.0%		* within 60 km	deClerck, 1973
Belgian Coast	75.0%	44.4%		* within 60 km	deClerck, 1973
English Channel					
Pas de Calais	81.3%	53.5%	AH	* within 60 km	LeFranc, 1968
Beachy Head, English Channel	33% to 60%	31% to 57%	D/IH	* within 60 x 60 km area	Bedford, 1966
Eastern English Channel	63.6%	53.3%	AH	* within 60 x 60 km area	Bedford, 1966
Norway and the Barents Sea					
Coastal Cod					
Flødevigen		93%	S	in tagging area	Moksness and Øiestad, 1984
Sørlandet		93%	S	within 5km	Løversen, 1946 cited in Moksness and Øiestad, 1984
Area 3, fjords		97%	S	in statistical area	Godø, 1986
Area 4, fjords		92%		in statistical area	Godø, 1986
Area 5, fjords		99%		in statistical area	Godø, 1986
Area 7, fjords		100%		in statistical area	Godø, 1986
Sørfjord		100%	S	within 30 n.mi	Godø et al., 1986
Sotra		100%	S	within 30 n.mi	Godø et al., 1986

Experiment location	Homing†	Site Fidelity¥	behaviour	Comment	Reference
Forty Mile Ground	57%	55%	D/IH	within 30 mi	LeFranc, 1973
Scottish East Coast		86.2%	S	within apr 100 x 125 km area	Symonds and Raitt, 1966
East Orkney		48.2%	AH/IH/D	within apr 50 x 300 km area	Symonds and Raitt, 1966
Scottish North Coast		76.2%	S	within apr 100 x 80 km area	Symonds and Raitt, 1966
Moray Firth	57% to 94%		S	* within apr 125 x 80 km area	Symonds and Raitt, 1966
Moray Firth		80.7% to 94.9%		within apr 125 x 80 km area	Symonds and Raitt, 1966
Papa Bk		34.7%	AH/IH/D	* within tagging area	Easey, 1987
North Shetlands		55.6%	AH/IH/D	* within tagging area	Easey, 1987
South Shetlands		25.4%	AH/IH/D	* within tagging area	Easey, 1987
Hebrides		24.5%	AH/IH/D	* within tagging area	Easey, 1987
English Coast					
Flamborough, English Coast	38% to 65%	25% to 58%	D/IH	* within 60 x 60 km area	Bedford, 1966
Central North Sea					
Flamborough Spawning grounds	14.8%	16.1%	D	* within 60 x 60 km area	Bedford, 1966
Cleaver Bk, Central North Sea	0% to 33%	26% to 27%	D/IH	* within 60 x 60 km area	Bedford, 1966
Fisher Bk	8.4%	8.0%	D/IH	* within 60 x 60 km area	Bedford, 1966
NW Rough, Central North Sea	20%	17%	D/IH	* within 60 x 60 km area	Bedford, 1966
NE Dogger Bank & Clay Deep	23.4%	16.0%	S	* within 60 x120 km area	Bedford, 1966
Dogger Bank	61.9%	60.2%		* on southern Dogger Bk	LeFranc, 1969
Dogger Bank		74.2%		on southern Dogger Bk	LeFranc, 1970
Dogger Bank		84.2%		within 60 km	LeFranc, 1967
Farns Deep		75%	S	within 60 km	LeFranc, 1967
Clay Deep		45.5%	AH/IH/D	* within 60 km	deClerck, 1973
Southern Bight					
North Foreland, Southern Bight	14.3%	13.6%	D	* within 60 x 60 km area	Bedford, 1966
Sizewell Bk, Southern Bight	47.8%	33.3%	D/IH	* within 60 x 60 km area	Bedford, 1966
German Bight	21% to 100%		AH	* within 100km	Lamp, 1973
Dutch Coast		44.2%	D/IH	* within 60 km	Daan, 1969
Dutch Coast	33.3%	67.6%		* within 60 km	deClerck, 1973
Belgian Coast	33.3%	16.7%	D/IH	* within 60 km	deClerck, 1973
Belgian Coast	28.6%	36.0%		* within 60 km	deClerck, 1973
Belgian Coast	75.0%	44.4%		* within 60 km	deClerck, 1973
English Channel					
Pas de Calais	81.3%	53.5%	AH	* within 60 km	LeFranc, 1968
Beachy Head, English Channel	33% to 60%	31% to 57%	D/IH	* within 60 x 60 km area	Bedford, 1966
Eastern English Channel	63.6%	53.3%	AH	* within 60 x 60 km area	Bedford, 1966
Norway and the Barents Sea					
Coastal Cod					
Flødevigen		93%	S	in tagging area	Moksness and Øiestad, 1984
Sørlandet		93%	S	within 5km	Løversen, 1946 cited in Moksness and Øiestad, 1984
Area 3, fjords		97%	S	in statistical area	Godø, 1986
Area 4, fjords		92%		in statistical area	Godø, 1986
Area 5, fjords		99%		in statistical area	Godø, 1986
Area 7, fjords		100%		in statistical area	Godø, 1986
Sørfjord		100%	S	within 30 n.mi	Godø et al., 1986
Sotra		100%	S	within 30 n.mi	Godø et al., 1986

Experiment location	Homing†	Site Fidelity‡	behaviour	Comment	Reference
Altafjord	61.6%	55.3%	AH	* in fjord where tagged	Jakobsen 1987
Revsbotn	83.2%	78.7%	S	* in fjord where tagged	Jakobsen 1987
Porsangerfjord	94.3%	92.7%	S	* in fjord where tagged	Jakobsen 1987
Laksefjord	80.3%	75.5%	S	* in fjord where tagged	Jakobsen 1987
Tanafjord	60.5%	54.2%	AH	* in fjord where tagged	Jakobsen 1987
Masfjorden		46.0%	AH/IH/D	within fjord (within 5 km)	Nordeide and Salvanes 1988
Area 3 coast		57%	S	in statistical area	Godø 1986
Area 4 coast		78%		in statistical area	Godø 1986
Area 5 coast		84%		in statistical area	Godø 1986
Area 7 coast		98%		in statistical area	Godø 1986
Møre seine grounds		90.8%	S	at tagging location	Godø 1984b
Møre trap grounds		84.1%		at tagging location	Godø 1984b
Møre trawl grounds		67.8%		at tagging location	Godø 1984b
Northeast Arctic cod					
Lofoten	75% to 88%		AH	* at spawning ground where tagged	Godø 1984a
Lofoten	77.6%			* at tagging location	Godø 1989
Møre	71% to 92%		AH	* at spawning ground where tagged	Godø 1984a
Møre	76.8%			* at tagging location	Godø 1984c
Area 7 offshore (Møre)		93%		in statistical area	Godø 1986
Area 2 offshore		26%	D/IH	in statistical area	Godø 1986
Area 3 offshore		45%		in statistical area	Godø 1986
Area 4 offshore		28%		in statistical area	Godø 1986
Area 10 offshore		10%		in statistical area	Godø 1986
Area 11 offshore		8%		in statistical area	Godø 1986
Area 12 offshore		3%		in statistical area	Godø 1986
Area 13 offshore		1%		in statistical area	Godø 1986
Area 15 offshore		1%		in statistical area	Godø 1986
Area 20 offshore		26%		in statistical area	Godø 1986
Area 21 offshore		25%		in statistical area	Godø 1986
SE Barents Sea		65.2%	S	in the half of Barents Sea where tagged	Lebed et al. 1983
Spitsbergen area (NW Barents Sea)		55.1%	AH/IH/D	in the half of Barents Sea where tagged	Lebed et al. 1983

† % of recaptures caught near the tagging area during the time of year in which tagging was conducted

‡ % of recaptures caught near the tagging area throughout the study

* recaptures from 1st season are excluded

Table 4-2. Transplantaion experiments. Presentation as in Table 4-1.

Stock	Homing†	Comment	Reference
North Sea			
Monkey Bk --> Kattegat	0%	moved back to North Sea	Bagge, 1973; 1983
Fladen Ground --> Kattegat, Sound	0%	moved back to North Sea	Bagge, 1973; 1983
German Bight --> Kiel Bight	0%	moved back to North Sea	Lamp, 1978; 1990
Baltic Sea			
Kattegat --> the Sound	18.5%	moved in correct direction	Otterlind, 1985
17 transplant experiments	0%	moved different from local fish	Otterlind, 1985
Klaipeda --> Sound	27%	moved in correct direction	Bagge, 1983
Bornholm --> Sound	38%	moved in correct direction	Bagge, 1983
Slupsk Furrow --> Bornholm	0%	moved in correct direction	Tiews and Lamp, 1974
Bornholm --> Arkona	75%	returned to tagging area	Tiews and Lamp, 1974
Arkona --> Belt Sea	21%	returned to middle Baltic	Tiews and Lamp, 1974
Norway and Barents Sea			
Northeast Arctic cod --> Fanafjord	0%	returned to tagging location	Godø, 1995
northern fjord --> Fanafjord	0%	returned to tagging location	Godø, 1995
Finnmark Coast --> Stadhavet	40%	moved in proper direction	Hylen, 1963
Gilbert's Bay			
Inside --> outside Long Arm	50.0%	over sill into Long Arm	Green and Wroblewski, 2000

† % of recaptures caught near the tagging area during the time of year in which tagging was conducted.

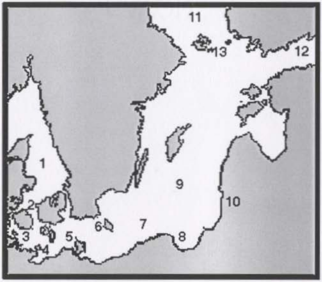


Figure 4-1: Map of the Baltic Sea with place names indicated as: 1. Kattegat; 2. Belt Seas; 3. Kiel Bay; 4. Mecklenburg Bay; 5. Arkona; 6. Bornholm; 7. Slupsk Furrow; 8. Gdansk Bay; 9. Gotland Basin; 10. Klaipeda; 11. Gulf of Bothnia; 12. Gulf of Finland; 13. Åland.

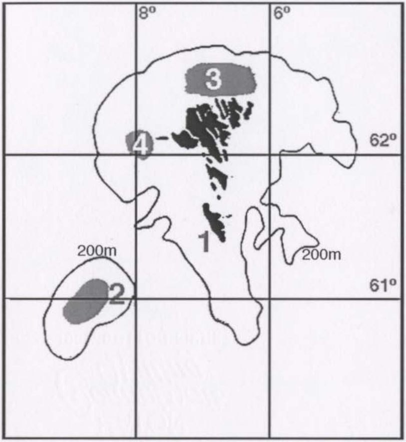


Figure 4-2: Map of the Faroe Islands with place names indicated as: 1. Faroe Plateau; 2. Faroe Bank; 3. Northern spawning ground; 4. Western spawning ground.

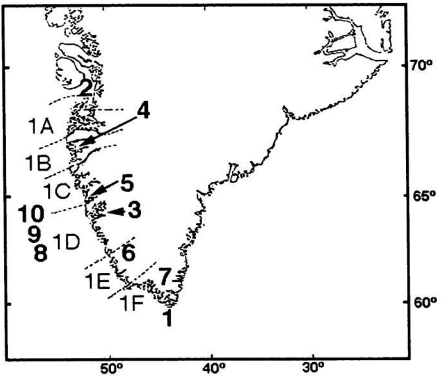


Figure 4-3: Map of Greenland showing the management divisions 1A-1F. Place names are indicated as: 1. Cape Farewell; 2. Disko Bay; 3. Godthaab Fjord; 4. Ikertok Fjord; 5. Kangia; 6. Frederikshaab district; 7. Julianehaab district; 8. Dana Bank; 9. Fiskenaes Bank; 10. Fylla Bank.

Figure 4-4: Map of Iceland showing the statistical Sub-areas 1-9.

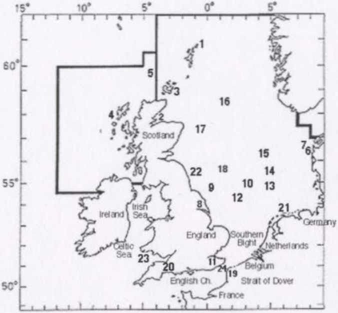


Figure 4-5: Map of the North and Irish Seas, and surrounding areas. Place names are indicated as: 1. Shetland Islands; 2. Moray Firth; 3. Orkneys; 4. Hebrides; 5. Papa Bank; 6. Thorsminde; 7. Monkey Bank; 8. Flamborough; 9. Flamborough spawning ground; 10. Cleaver Bank; 11. North Foreland; 12. Silver Pit; 13. Clay Deep; 14. Dogger Bank; 15. Fisher Bank; 16. Ling Bank; 17. Forties; 18. North West Roughs; 19. Pas de Calais; 20. Beachy Head; 21. German Bight; 22. Farn Deep; 23. Bristol Channel; 24. Straits of Dover.

Figure 4-6: Map of Norway and the Barents Sea with place names indicated as: 1. Masfjorden; 2. Finnmark (includes Altafjord; Revsbotn; Porsangerfjord; Laksefjord; Tanafjord, Varangerfjord); 3.Sorlandet (includes Flødevigen); 4. Spitsbergen; 5. Lofoten; 6. Møre (includes Smøla); 7. Bergen (includes Sotra and Sørfjord); 8. Malangen.

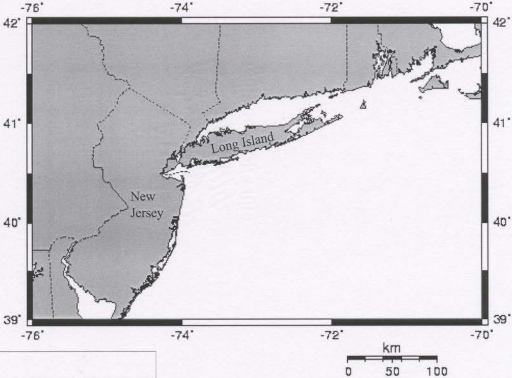
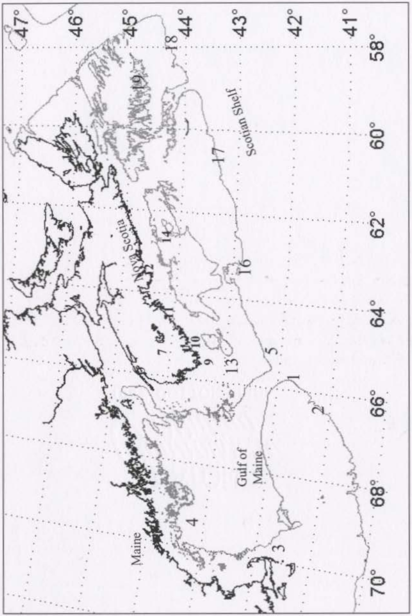


Figure 4-7a: Map showing southern New England and the Middle Atlantic Bight regions.

Figure 4-7b: Map of the Gulf of Maine and the Scotian Shelf. Place names are indicated as: 1. Fundian Channel; 2. Georges Bank; 3. Cape Cod (Includes Chatham, Highland Ground); 4. Sheepscot Bay; 5. Browns Bank; 6. Bay of Fundy; 7. Sandy Cove; 8. Digby; 9. Yarmouth; 10. Lockeport-Shelburne; 11. Lunenburg; 12. Halifax; 13. Seal Island; 14. Egg Island -Jeddore Rock; 15. Cape Breton; 16. Western and Emerald Banks; 17. Sable Island Bank; 18. Banquereau; 19. Misaine Bank.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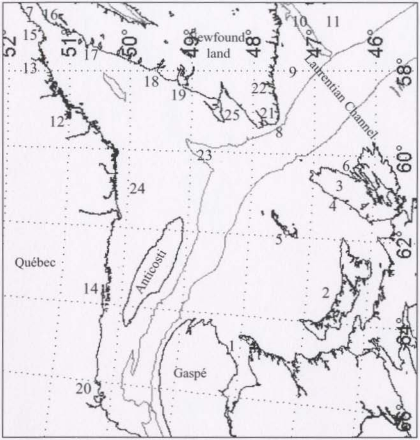


Figure 4-7c: Map of the Gulf of St. Lawrence with place names indicated as: 1. Chaleur Bay; 2. Prince Edward Island (PEI); 3. Cape Breton; 4. Cheticamp; 5. Magdalene Islands; 6. Sydney Bight; 7. Strait of Belle Isle; 8. Cabot Strait; 9. Burgeo Bank; 10. Hermitage Channel; 11. St. Pierre Bank; 12. La Tabatiere; 13. Bonne Esperance; 14. Baie Johan Beetz; 15. Forteau; 16. Flowers Cove; 17. Port Au Choix; 18. Gros Morne; 19. Lark Harbour; 20. Seven Islands; 21. Port Au Basques; 22. Rose Blanche; 23. Esquiman Channel; 24. Cape Whittle Bank; 25. St. George's Bay.

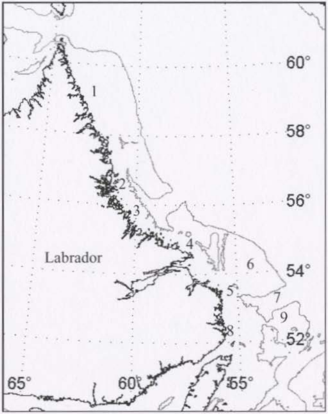
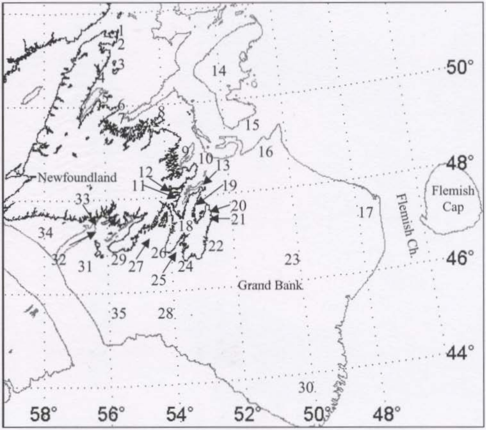


Figure 4-7d: Map of Labrador with place names indicated as: 1. Saglek Bay; 2. Nain; 3. Hopedale; 4. Cape Harrison; 5. Domino; 6. Hamilton Bank; 7. Hawke Channel; 8. Gilbert's Bay; 9. Belle Isle Bank.

Figure 4-7e: Map of Newfoundland with place names indicated as: 1. Quirpon; 2. Saint Anthony; 3. Grey Island; 4. Englee; 6. La Scie; 5. Bay Verte Peninsula; 7. Notre Dame Bay; 8. Fogo Islands; 9. Bonavista Bay; 10. Cape Bonavista; 11. Trinity Bays; 12. Smith Sound; 13. Baccalieu Island; 14. Funk Island Bank; 15. Bonavista corridor; 16. North Cape; 17. Nose of the Bank; 18. Avalon Peninsula; 19. Conception Bay; 20. St. John's; 21. Cape Spear; 22. Fermuse; 23. Virgin Rocks; 24. Cape Pine; 25. St. Mary's Bay; 26. St. Brides; 27. Placentia Bay (see Fig 4-6f); 28. Haddock Channel; 29. Lord's Cove; 30. Southeast Shoal; 31. St. Pierre Bank; 32. Fortune Bay; 33. Penguin Islands; 34. Burgeo Bank; 35. Halibut Channel.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Flemish Ch.
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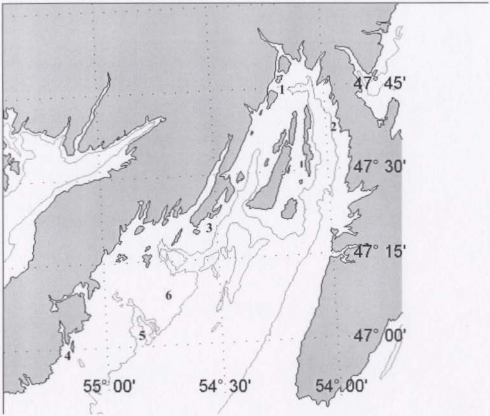
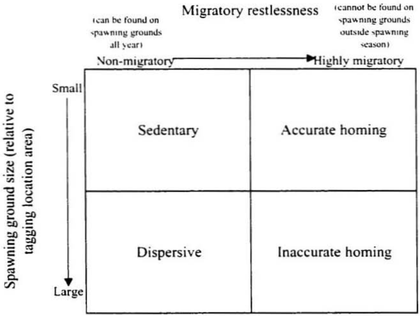


Figure 4-7f: Map of Placentia Bay with place names indicated as: 1. Bar Haven; 2. Little Harbour; 3. Little Paradise; 4. Burin; 5. Mortier Bank; 6. Oderin Bk.

Figure 4-8: Schematic diagram showing the range of possible migratory behaviours that can be observed in cod tagging studies where cod are tagged while on the spawning ground and recaptured during subsequent spawning seasons. Every combination of migratory restlessness and spawning ground size is possible, in theory. These have been divided into four categories. When spawning grounds are small relative to the size of the tagging area, migratory fish will appear to home accurately, and non-migratory fish will seem sedentary. When the size of spawning home range is large relative to the tagging area, migratory species will appear to home with little accuracy, and non-migratory species will appear to have dispersed away from the tagging area.



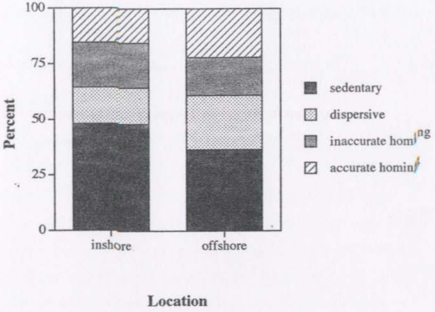


Figure 4-9: The relative proportion of inshore and offshore cod groups that can be classified as "sedentary", "dispersive", "accurate homing", and "inaccurate homing" based on migratory behaviour inferred from tagging studies.

5 Evidence from acoustic telemetry for multiyear homing of Atlantic cod to a spawning ground

Co-author: George A. Rose

5.1 Abstract

In order to assess the degree of multi-year homing of cod (*Gadus morhua*) spawning at Bar Haven (Placentia Bay, Newfoundland), long-term sonar transmitting tags were implanted in 27 females and 21 males in April 1998. Two-thirds of the tagged fish were relocated during the study. All fish relocated during the spawning seasons of 1999 and 2000 were within ten km of the tagging site, the majority within a few hundred meters. No tagged fish were relocated at other known spawning grounds or elsewhere in the bay during spawning season. Outside the spawning season, several tagged fish were relocated at other parts of the bay, the fishery returned 13 tags from throughout the bay, and two from long-distances outside the bay. Homing rates to the Bar Haven ground in the two years after release were 39% and 53%, after adjustments for tag loss, mortality, misreporting and relocation efficiency based on returns from a beacon tag left permanently at Bar Haven. Multi-year homing was observed in 26% of cod tagged. This study provides the first direct evidence that cod undertaking long-distance feeding migrations may home to a specific spawning ground in consecutive years, and implies a potential for fine-scale stock structure unaccounted for in fisheries management.

5.2 Introduction

Stock structure underpins the spatial and biological rationale for assessment and management of most commercial fisheries. A rich stock structure is thought to enhance genetic diversity (Hunter, 1996) as well as diversity in spawning times and locations, which, in turn, enhances the likelihood of egg and larval survival (Cushing, 1995) and regional recruitment success (Sinclair, 1989). Stock structure implies that spawners achieve some degree of segregation from other stocks during spawning. Segregation can occur among natal groups (philopatry) or among spawning groups adopted or formed at first maturity (Alverson and Chatwin, 1957). In diadromous fishes, philopatry is well known (Hasler, 1971; Gross et al., 1988) although adoption of new spawning grounds at first maturity has also been reported (Kwain, 1982). Site fidelity and homing have also been found in freshwater and coral reef fishes (e.g., Gerking, 1959; Munro, 1983; Chapman, 1997; Marnane, 2000). Despite the fact that stock structure has long been recognised in marine broadcast spawners, philopatry and homing to spawning grounds remain largely speculative (Harden-Jones, 1968; Godø, 1984c), and mechanisms by which homing may occur are poorly understood (Rätz, 1994).

Atlantic cod (*Gadus morhua*) is an open ocean and coastal broadcast spawner that for the most part spawns in large aggregations (Jónsson, 1982; Bergstad et al., 1987; Jákupsstovu and Reinert, 1994) at specific locations throughout its range (Brander, 1994b). Tagging studies have led to speculation that cod may home to the same spawning area over long distances year-after-year (Tåning, 1940; Rasmussen, 1957; Templeman, 1979; Godø, 1984c; Jónsson, 1996). However, these studies have remained largely inconclusive because only single release and capture points could be determined.

Recent developments in the miniaturisation of long-life acoustic transmitters enable fish to be tracked for periods of years and to be repeatedly relocated. My goal was to determine the degree of multi-year fidelity of cod to a major spawning ground in Newfoundland waters. I used tags designed to transmit for > 2 years (3 spawning seasons), and monitored the spawning ground during the spawning seasons of 1998, 1999 and 2000.

5.3 Methods

5.3.1 Study Site

The Bar Haven spawning ground (Fig. 5-1) is located in Placentia Bay, Newfoundland (NAFO Subdivision 3Ps). This site was selected because the cod there have not suffered the recent massive declines typical of many other Newfoundland areas (DFO, 2000). As a result, Bar Haven is one of the most important spawning grounds for the largest contemporary stock in Newfoundland waters (Lawson and Rose, 2000b, a). Furthermore, local knowledge and recent surveys both indicate that Bar Haven is consistently used as a spawning location each spring (Davis et al., 1994; Lawson and Rose, 2000b).

5.3.2 Tagging

In April 1998, aggregations of spawning cod were located acoustically near Bar Haven, in an area consistently used by cod for spawning during spring (Lawson and Rose, 2000b, a). Fish were taken from these aggregations using feather hooks. Larger individuals (> 60 cm) thought to be in spawning condition were held in flow-through tanks and sexed by cannulation. For each fish, an individually-coded ultrasonic transmitter was surgically implanted (see Appendix A) into the peritoneal cavity, and an external spaghetti tag was anchored on the left side, adjacent to the first dorsal fin. Tagged fish were held for up to 10 hours, and those that appeared to be robust and in good condition were released at the location where they were caught. In total, 48 cod, including 27 females (lengths 64 to 87 cm) and 21 males (lengths 67 to 88 cm) were released. To avoid observing a period of abnormal behaviour that may follow surgery (Godø and Michalsen, 2000). I waited 15 days after tagging before beginning the first telemetric survey of Placentia Bay.

5.3.3 Telemetry Surveys

Fish were monitored during three consecutive spawning seasons using an acoustic receiver (Lotek Model SRX-400) and omnidirectional hydrophone (Lotek Model LHP-1). Each transmitter emitted a unique coded signal, allowing individual discrimination. Signals were emitted every 5 seconds for the duration (> 2 years) of the transmitters' battery life.

Relocation efficiency, i.e., the probability of relocating a tag when it is present in the survey area, was measured as the proportion of surveys in which a "beacon tag" (a transmitter left on the bottom throughout the study) was detected. Over the three years of the study, the relocation efficiency was 80%.

Effective range of the telemetry equipment was measured as the minimum distance from the beacon tag at which its signal could not be detected. Preliminary tests determined the range of the telemetry gear to be approximately 0.5 nm (0.96 km). As such, a survey grid was established with 0.5 nm intervals between monitoring stations. Distance between monitoring stations was reduced to 0.3 nautical miles (0.58 km) in 2000 to account for the observed decay of transmitter power.

The survey areas included all known spawning grounds in Placentia Bay (Fig. 1, Lawson and Rose, 2000b). Deep areas of the bay in which cod were rarely located during these years (Lawson and Rose, 2000a) were not surveyed. During each survey, the research vessel stopped at a series of monitoring stations, spaced throughout the bay at half a nautical mile (0.96 km) intervals, corresponding to the range of the gear. In 2000, only the head of the bay was surveyed because of vessel constraints, but in prior years no fish were relocated in other areas. Surveys of the bay took approximately 2 weeks. Surveys of the Bar Haven spawning ground were repeated (the timing and number depending on the weather and ship availability) over the 2-3 month spawning season, and in all years were terminated when no tagged cod could be located for a period of several days. The presence of fish thus determined the number of surveys in each year.

5.3.4 Transmitter Returns

A fishery was conducted each year of this study and there was an expectation that some tagged fish would be caught. Hence a reward of $100 CDN was offered for the return of transmitters with information on date and location of capture. Fishers were interviewed subsequent to transmitter return. All fish were reported to have been in good condition, indicating complete recovery from the surgery. All but one of the 15 tags returned over the course of the study were still transmitting.

5.3.5 Homing Rate Calculation

Homing was calculated as the proportion of tagged fish that returned to Bar Haven during the spawning season:

$$\frac{(\#\,observed)e^{-1}(1-f)^{-1}}{(\#\,tagged)(1-M-F-Z_{tag})}.$$

In the numerator, the number of tagged individuals observed at Bar Haven each spawning season was adjusted to account for a relocation efficiency (e) of 80% and a transmitter failure rate (f) of 6%. The denominator (i.e., the number of tagged fish at large during each survey) was calculated as the number of fish originally tagged, less natural mortality (M was set to 0.2, Hilborn and Walters, 1992), tagging-induced mortality (Z_{tag} = 6%, based on conventional tagging data for Placentia Bay during the same years as this study; N. Cadigan and J. Brattey, unpublished data), and fishing mortality (F). The fishing mortality was calculated as the proportion of tagged fish for which transmitters were returned, adjusted for a tag underreporting rate (u) of 35% (based on conventional tagging data; N. Cadigan and J. Brattey, unpublished data):

$$F = \frac{(\#returned)(1+u)}{48}.$$

5.3.6 Randomization tests

Given the larger sampling effort at Bar Haven relative to other parts of the bay, it was necessary to evaluate whether the proportion of tagged fish that was relocated at Bar Haven was a result of chance. The dataset consisted of one record for every time our hydrophone went into the water, including observations on the location, time and fish (if any) relocated. I performed 1000 tests in which the fish-relocation column was randomly redistributed relative to the date and location columns. As such, there was a greater chance that fish would be "relocated" in areas where sampling effort was concentrated. For each of the 1000 different random configurations, I recorded the number of fish "located" at Bar Haven. Given the distribution of those values, it was possible to calculate the probability that the observed value occurred by chance if tagged cod were randomly distributed.

5.4 Results and Discussion

The data indicate that the cod studied here showed a marked degree of homing. A full 67% of tagged fish were accounted for over the course of the study either being relocated using telemetry, or recaptured in the fishery. All fish relocated in subsequent spawning seasons were within 10 km of the Bar Haven spawning grounds, where the fish were originally tagged (Fig. 5-1). The majority was relocated within a few 100 meters of the tagging site. The fate of the non-relocated fish remains uncertain. However, none were observed during the spawning season at other known spawning grounds in Placentia Bay. The probability of relocating no fish at the other known spawning grounds, given my sampling effort is < 0.02 (compared to a null distribution generated under the hypothesis of a random assortment of tagged fish among the spawning grounds). Moreover, in no cod aggregation, located during spawning season acoustic surveys throughout the bay, was a tagged fish ever relocated, except at Bar Haven. The probability of not relocating a single fish outside the Bar Haven area during the spawning period, given my sampling effort is < 0.00003 (given a null hypothesis that tagged fish were randomly distributed throughout the entire bay). At other times of year, tagged cod were relocated at other sites.

Fifteen transmitters were returned by fishers until June 2000. Fishery recaptures (Fig. 5-2) occurred in every month except during the peak spawning season (March to May) when the fishery was restricted. All but two recaptures were made in Placentia Bay along known migration pathways to and from Bar Haven (Lawson and Rose, 2000a). These two recaptures were made in September 1998 in Conception Bay on the northeast coast, and in February 2000 about 100 nautical miles off the south coast of Newfoundland (Fig. 5-2), and both were typical of Placentia Bay cod migrations (Brattey, 1996; Lawson et al., 1998; Brattey, 1999). Fishery recaptures are not used here as measures of homing or straying because single recaptures provide uncertain information about the spawning destination of the fish.

What proportion of tagged fish successfully homed? During the two surveyed spawning seasons subsequent to that of tagging (i.e., 1999 and 2000), eight and six tagged fish were relocated using telemetry. Three fish were relocated at Bar Haven in all three years. To compare annual returns, these raw relocation data were adjusted to account for mortality, tag under-reporting, and tag failure (see Methods). The adjusted homing rates for the 1999 and 2000 spawning seasons were 39% and 53% (Table 5-1). Multi-year homing was observed in 26% of cod tagged (Table 5-1). Although these estimates are somewhat sensitive to the rates of tagging-induced mortality and fishery under-reporting, when either parameter was set at 0, homing was never less than 39% in 2000. In reality, the values of these parameters were likely underestimates, given that they were derived from externally attached tagging studies, and we consider the homing estimates presented in Table 1 to be conservative. In at least one known case a transmitter (of unknown identity) was thrown overboard because the fisher did not want to possess such a tracking device. Moreover, homing percentages are limited somewhat by survey effort, especially in 1999, when spawning occurred early and surveys missed a portion of the spawning.

This study demonstrates for the first time that cod can home long-distances to a spawning ground over multiple years. The results suggest that spawning cod leave the grounds during early summer and migrate long distances during the feeding season, and prior to the next spawning season. Bar Haven cod are known to perform long distance migrations (several hundred km) and to leave the bay between spawning periods (Brattey, 1996; Lawson and Rose, 2000a). In a similar but smaller scale study, Green and Wroblewski (2000) reported that in Gilbert's Bay, a small inlet on the southern Labrador coast, tagged cod tended to stay in or return to specific locations in the bay, where they overwintered and spawned. No cod showed any tendency to leave the bay, despite unimpeded access to the open ocean. Homing was shown for a single year, but the battery life of the transmitters used by Green and Wroblewski (2000) was only 10 months, hence no individual could be tracked over multiple spawning seasons. The homing rates inferred from conventional tagging data were between 71 and 92% for Northeast Arctic cod tagged at Møre and Lofoten, Norway (Godø, 1984c) and between 72 and 79% for cod tagged at the spawning grounds off southwest Iceland (Jónsson, 1996). However, the scale of these studies was very large, and fish were considered to have homed if they returned to any part of a vast portion of coastline (10s - 100s of km). The scale over which I measured homing is much finer (a few km), and included only one spawning site within a large bay contained within a larger management unit. Compared to the studies of Godø (1984c) and Jónsson (1996), cod in this study required a far greater degree of accuracy for their behaviour to be considered as "homing".

Although there have been few studies on homing in marine broadcast spawners, diadromous and estuarine fishes are better studies. Homing rates for Pacific salmonids ranged between 75-90% (Quinn, 1984), and a recent studied showed that homing for Atlantic weakfish (*Cynoscion regalis*) was between 60-81% (Thorrold et al., 2001). These rates are higher than that observed for cod in this study of accurate homing, but are similar to those found in the coarse-scale studies of Godø (1984c) and Jónsson (1996).

For marine fishes, assumptions of broad stock structure and little evidence of homing, laid the foundation for management being conducted over very large oceanic regions (100 000's square km) encompassing multiple spawning grounds. For example, Newfoundland cod fisheries are managed over spatial scales greatly exceeding those of the stock structure suggested by my results and by recent genetic studies (e.g., Ruzzante et al., 1998). Such management could inadvertently cause differential sub-structure overfishing, local extinctions, and reductions in productivity (Frank and Brickman, 2000).

It should be noted that a recent study reported that cod at the head of Placentia Bay might be distinguished genetically from those caught in the outer parts of the bay (Ruzzante et al., 1998). Such small-scale genetic structure implies a higher degree of homing than observed in this study. However, Ruzzante et al. (1998) did not state whether samples from the different parts of the bay were collected concurrently, thus limiting the usefulness of their observations because, at certain times, Placentia Bay is likely to contain fish from adjacent areas (Brattey, 1996).

Although straying to neighbouring spawning grounds was not observed in this study, the number of unaccounted for fish implies that straying occurred, perhaps to areas outside Placentia Bay. The straying rates inferred from my results suggest a degree of genetic exchange among adjacent populations. Very low rates of straying are considered to be disadvantageous in variable or unpredictable environments (Quinn et al., 1991) such as Newfoundland waters. As with salmonids, my data suggest that cod straying rates are ample for recolonization of adjacent or new grounds (Kwain, 1982). The balance between homing and straying will affect the rate of recolonization and recovery of depleted populations (Smedbol and Wroblewski, 2000). The relatively strong homing evidenced in this study suggests relatively slow range expansion and recolonization, even when spawning populations are large, as they have been at Bar Haven and in 3Ps in general (Brattey, 2000). These results may provide a possible (or partial) explanation for the slow rate of recovery of many depopulated spawning grounds in Newfoundland waters, relative to rates predicted from historical data (Hutchings, 2000), and the relatively quick rebuilding of others (Rose, 2000) despite equivalent protection from fishing since the 1992 moratorium.

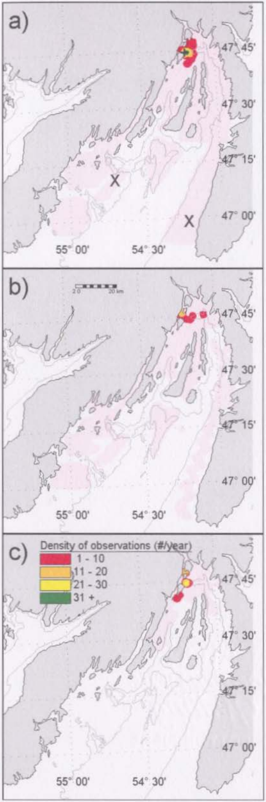
5.5 Acknowledgements

I thank G. Rose, W. Hiscock, L. Mello, B. Nolan, R. Jamieson, and D. Methven for field assistance, R. Wilson and J. Wroblewski for technical assistance, and the crews of the C.C.G.S. Shamook, M.V. Mares and M.V. Innovation.

Table 5-1: Homing rates for Bar Haven (BH) cod in 1999 and 2000, and the parameters used in their calculation. Formulas use alphabetic column headings as shorthand. Mortality is abbreviated as "mort".

A	B	C	D	E	F	G	H	I	J	K	L
year	# of cod relocated at BH during spawning season	efficiency of telemetry gear	cumulative number of transmitters returned from the fishery	fishing mort.	natural mort.	tagging induced mort.	rate of tag under-reporting in the fishery	rate of trans-mitter failure	# alive at spawning time	# alive with functioning tags	Homing
				D/48					48(1-E-F-G)-HD	J-IJ	(B/K)/C
1999	8	0.8	6	0.13	0.2	0.06	0.35	0.0667	27	26	0.39
2000	6	0.8	15	0.31	0.2	0.06	0.35	0.0667	15	14	0.53
both	3	0.8	15	0.31	0.2	0.06	0.35	0.0667	15	14	0.26

Figure 5-1: Density of fish observations (# of relocations over the year) in Placentia Bay during three consecutive spawning seasons: a) 1998; b) 1999; c) 2000. Pink areas are the locations monitored during telemetric surveys. Shadings indicate the density of observations (note that the "density of observations " increases with the number of fish relocated in the same place). In Panel a, "+" marks the spawning ground where the fish were tagged, and "X" marks the other known spawning grounds in Placentia Bay.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47° 00'
55° 00'
54° 30'
c)
Density of observations (#/year)
1 - 10
11 - 20
21 - 30
31 +
47° 45'
47° 30'
47° 15'
47° 00'
55° 00'
54° 30'

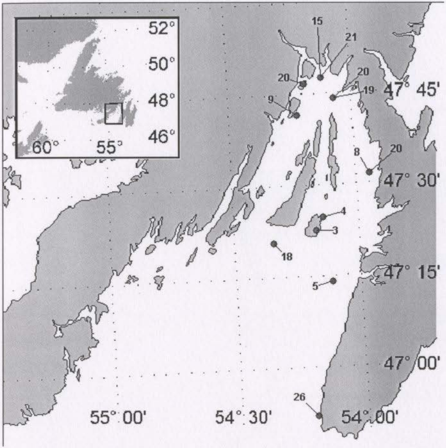

Figure 5-2: Distribution of fishery-returned transmitter catch locations. Numbers indicate months at liberty. The distribution agrees with the known migration pathway of Bar Haven cod into and out of Placentia Bay (Lawson and Rose, 2000b). No fishery recaptures occurred during spawning season (March to May) when the fishery was restricted. Not shown: one recapture in Conception Bay (47°40'N 53°00'W September 1998), and one on St. Pierre Bank (45°05'N 55°10'W February 2000). Inset: The Island of Newfoundland with a box around the Placentia Bay study area.

6 Homing mechanisms in transplanted cod

Co-author: George A. Rose

6.1 Abstract

To investigate navigation mechanisms used by cod to locate their spawning ground, I conducted a biotelemetric study in which 23 large spawners were displaced in small groups up to 35 km from their coastal Newfoundland spawning ground. Overall, approximately 60% of the fish homed to the grounds. Homing success was negatively related to distance of the release sites from the spawning ground, irrespective of current directions or known spawning routes. Transplanted groups did not stay together. Females and males homed at approximately equal rates, although more females homed successfully from distant sites. I conclude that underwater landmarks and celestial clues were unlikely to be important homing mechanisms in Placentia Bay. Of the mechanisms considered here, the data is most consistent with homing towards an omnidirectional "attractor" at the spawning ground that dissipates with distance, such as a characteristic sound or geophysical signature.

6.2 Introduction

Homing to natal spawning grounds is well documented in salmonids (Hasler, 1971) and Atlantic eels (Gross et al., 1988), but is largely speculative for marine broadcast spawners (Harden-Jones, 1968; Godø, 1984c; Netzel, 1990; Hovgård and Riget, 1991). Homing to a spawning site, philopatric or otherwise, has been hypothesised to occur in some marine fishes (Sinclair, 1989), including Atlantic cod, *Gadus morhua* (e.g., Tåning, 1940; Rasmussen, 1957; Templeman, 1979; Godø, 1984c; Jónsson, 1996), but evidence of such behaviour in cod has been sparse. However, a recent long-term acoustic tagging study has shown that cod can return year-after-year to the same spawning ground (Chapter 5).

How individuals might relocate an oceanic spawning ground remains largely unknown. Several navigatory methods have been proposed in fishes, including using spatial memory to follow underwater landmarks, navigating along gradients in chemical concentrations (chemoreception, Hasler, 1966) or water-current velocities (rheotropism, Harden-Jones, 1968), using solar or celestial cues (Hasler, 1971; Wootton, 1992), sensing the magnetic field of the earth (Quinn et al., 1981), and social transmission of routes from older to younger fish (e.g., Rose, 1993). The mechanisms of relocation are best studied in salmonids, in which homing from an oceanic to a riverine environment involves a series of large to smaller scale navigation methods (Quinn and Brannon, 1982). At large scales, during open ocean migration, salmon are thought to utilise celestial cues (Quinn and Brannon, 1982) and the Earth's magnetic field (Quinn et al., 1981) to navigate, but at smaller scales the spawning site is recognised by olfactory identification of stream characteristics (Hasler et al., 1983).

The cod stock off the south coast of Newfoundland (NAFO subdivision 3Ps) is currently one of the largest in the Northwest Atlantic. Repeated acoustic surveys and conventional tagging studies have demonstrated the existence of three major spawning grounds in Placentia Bay (Lawson and Rose, 2000b), the largest embayment in 3Ps and indeed in all Newfoundland waters. A biotelemetric study at one of these grounds, Bar Haven (Fig 6-1), showed that cod exhibit homing, and have little tendency to stray to the other grounds (Chapter 5). Homing cod almost certainly pass other major spawning grounds during migrations into the bay toward Bar Haven (Lawson and Rose, 2000a). However, the mechanisms that cod use to home to specific spawning grounds remain unknown.

In this study I used biotelemetric techniques to examine the homing ability of Bar Haven cod that were transplanted from their spawning ground to various locations throughout Placentia Bay. As a preliminary examination of several hypotheses on homing mechanisms, fish were released in small groups at various distances both upcurrent and downcurrent of the spawning grounds. I hypothesised that cod would migrate in groups, and that homing rate would be related to current direction, distance of the release site from the spawning ground, and familiarity with the route. If individuals used larger scale navigation mechanism like the earth's magnetic field or celestial clues, homing success should not be negatively affected by distance or direction of the release site from the spawning ground (if anything, these mechanisms become more accurate at larger distances, Hasier, 1966). If olfactory clues were important, individuals should home more successfully when released downcurrent of the spawning ground, and success should decline with distance. If individuals relied heavily on spatial memory, cod released along a familiar migration pathway should have a higher homing rate relative to those released in a less known area.

In this paper I am primarily interested in factors affecting Bar Haven cod's ability to home to their spawning ground after being transplanted. Secondarily, I hope to shed light on which navigatory mechanisms are potentially being used by cod during homing migrations.

6.3 Methods

In April 2000, spawning cod aggregations were located acoustically in the inner part of Placentia Bay, Newfoundland, near Bar Haven, an area consistently used by cod for spawning during spring (Lawson and Rose, 2000b, a). On April 3 and 4, approximately 85 cod (total lengths 45 - 89 cm) were taken from these aggregations using feather hooks.

The fish were in water near 0 °C temperature, at depths between 30-50 m. Larger individuals (> 70 cm) thought to be in spawning condition were held in flow-through tanks and sexed by cannulation. Maturity state of females was evaluated based on the proportion of hydrated eggs in the cannula. For each fish, an individually coded ultrasonic transmitter was surgically implanted into the peritoneal cavity (see Appendix A), and an external spaghetti tag was anchored on the left side, near the first dorsal fin. After tagging, the fish were observed for between 2 and 30 hours, and only cod that appeared to be robust and in excellent condition were released. In total, 23 cod, including 12 females (lengths 70 to 98 cm) and 11 males (lengths 75 to 95 cm), were tagged and released in small groups of even sex ratio (see Table 6-1 for details of release groups) at various locations throughout the bay.

The locations of the release sites are shown in Fig. 6-1, and details of the releases are outlined in Table 6-1. A control group was released at the Bar Haven spawning ground (47° 45.22' N 54° 13.37' W) where they were caught. Two groups were released on the western side of the bay, downcurrent of the spawning site. Of these, one group was released in Clattice Harbour (47° 29.77' N 54° 27.55' W), into an aggregation of small (mean TL = 56.45 cm), largely immature cod, and another was released on the northern tip of Isle Valen (47° 31.14' N 54° 23.21' W). Three groups were released on the eastern side of the bay, upcurrent of the spawning site, at, in order of increasing distance, Cheese Island (47° 42.41' N 54° 05.16' W), Southern Head (47° 47.58' N 54° 04.20' W), and Haystack Bank (47° 37.07' N 54° 00.94' W). Hold times were independent of distance of release site from the spawning ground ($F_{1,5} = 1.93$; $p = 0.22$).

To determine whether the tagging procedure reduced the level of activity of the fish (as per Arnold et al., 1994), I returned to the Cheese Island release site 15.5 hours after the fish were released. No fish were relocated at the release site, indicating some level of activity. The biotelemetric surveying for fish was therefore started as soon as possible, on April 8.

A survey grid comprising approximately 130 stations was established in the Bar Haven area (Fig. 6-1). On most days between April 4 and April 13, 2000 the grid was surveyed using an acoustic receiver (Lotek Model SRX-400) with an omnidirectional hydrophone (Lotek Model LHP-1) designed to detect the signal emanating from the implanted transmitters at a maximum range of approximately 0.5 nm (0.96 km). Each transmitter emitted a unique signal, allowing the receiver (Lotek Model SRX-400) to discriminate between all individual fish. Monitoring stations were 0.3 nautical miles (0.58 km) apart. One minute was spent at each station, allowing ample time to detect and identify the transmitters, which emit signal every 5 seconds. Simultaneously, another larger vessel surveyed the deeper, more exposed areas adjacent to the spawning area. Between April 20 and June 28, the same grid was run approximately weekly.

On April 8 and 12, the survey vessels monitored other parts of the bay, including the release sites. The stations surveyed on these days are shown in Fig. 6-1.

Survey coverage, even with 2 vessels is never synoptic, hence not all tagged fish present on the grounds can be expected to be relocated during every survey. The movement of fish within the survey grid, and to areas immediately outside that surveyed would reduce the probability of relocating all fish that are in the general area during all surveys. I therefore assumed individuals to be "residents" of the general Bar Haven area from the first time they are relocated until the last. Since cod gradually left the spawning grounds over the course of the season, the number of residents declined with time. As such, I assumed that the probability that a transplanted cod would home to the spawning ground would also decline with time. I therefore used the relocation rate of the control group as a basis on which to evaluate the relocation rate of transplanted fish. The relocation rate for each survey was defined as the proportion of fish released which were resident at the Bar Haven spawning grounds. I also examined the miss rate, i.e., the proportion of surveys during which an individual was deemed to be resident but was not relocated.

I explored how homing success and timing was affected by the distance of the release site from Bar Haven. The effect on time at large was tested using a standard least squares regression, with ln transformed homing times. The effect on homing success was tested with a logit regression fitted using maximum likelihood and assuming a binomial error structure (confidence limits were solved iteratively).

6.4 Results

Of the 23 fish released, 13 (56.5%) were relocated on the Bar Haven spawning grounds during the study, ten within one week of release. On April 9, during my first survey of the Bar Haven area (4-6 days after release) six of the 19 transplanted individuals had already returned to the spawning ground. Another three subsequently returned (Table 6-2).

All of the four "control" fish caught and released at the Bar Haven spawning ground were relocated there at least once (Table 6-2). One control individual was relocated only once on the day after release, April 4. Two others were relocated the day after release, and subsequently relocated repeatedly; one until May 14 and the other until May 30. The remaining individual was not relocated until April 10, but was subsequently relocated until April 13. The relocation rate of cod released at Bar Haven peaked between April 10 and 13, then declined gradually over the next 2 months, reaching zero on June 6 (Fig. 6-2).

Of the 11 fish released upcurrent of the spawning site, one was relocated consistently at the same location about 0.5 nautical miles from the release site, in the direction of Bar Haven (and is presumed to have either died or expelled its transmitter shortly after release). Of the other ten, seven (70%) were relocated on the spawning ground. Six of these had returned by April 9 (less than a week after release), the other by April 20 (less than 3 weeks after release). The remaining three fish were never relocated.

Only two of the eight fish released downcurrent of the spawning grounds were relocated at Bar Haven. All of the fish released in Clattice Harbour were relocated near the release site on both April 8 and 12 near an aggregation of largely immature cod. Two of the tagged adults subsequently returned to Bar Haven, one relocated on April 20, the other on May 30. One of the four fish released at Isle Valen was relocated near the release site on April 12, but was never relocated at Bar Haven. The other three were never relocated.

The relocation rate of transplanted fish peaked on April 20, then gradually declined to zero by June 6 (Fig. 6-2). The ratio of the relocation rate for transplanted fish to that of control fish peaked at 0.8 on April 20, decreased to less than 0.2 after mid May. The time required to home to the spawning ground was related to transplantation distance (Fig. 6-3; $\ln \text{time} = 0.51 + 0.15 \cdot \text{distance}$; ANOVA: $F_{1,11} = 27.67$; $p < 0.001$). Homing success was independent of the time that fish were held prior to release (ANOVA: $F_{1,5} = 1.56$; $p = 0.27$; $\beta = 0.82$).

The proportion of individuals that homed to Bar Haven was greater for eastern release sites than for western sites (East = 0.72; West = 0.25). However, the proportion that homed was related to the distance of the release site from the spawning ground (Fig. 6-4; slope parameter significantly negative, $\chi_1^2 = 5.23$; $p = 0.022$; $n = 6$). The easterly and westerly release site data do not appear to differ when distance is accounted for, although samples sizes are too low for a meaningful statistical comparison.

The dominant currents in Placentia Bay flow counter-clockwise, entering on the east and exiting on the west side of the bay. North-south mean current speeds were 10.56 ± 8.70 cm s^{-1} into the bay and 3.29 ± 2.93 cm s^{-1} out of the bay in 1997 and 1998 (Bradbury et al., 2000).

6.5 Discussion

The results indicate that many cod homed rapidly to the capture site spawning ground after being transplanted to several locations in the bay. Six of nine (66%) transplanted fish that homed to Bar Haven had done so before my first survey of the spawning grounds, 4-6 days after release. Moreover, the relocation rate for transplanted fish reached 78% of the control fish, which are a proxy for full homing. The high proportion and rapid rate of homing observed in this study contrasts with other cod transplantation studies. In most previous transplantation experiments (Bagge, 1973; Lamp, 1978; Bagge, 1983; Otterlind, 1985; Lamp, 1990; Godø, 1995) cod have shown few signs of homing. However, it is important to note that all transplantations in these studies were of distances greater than mine (125 to 1000's of km), which may have impeded homing and involved different mechanisms more appropriate for large scale and coarser navigation. Moreover, there are two published transplantation experiments which report 50% or greater homing to the area of original capture (Tiews and Lamp, 1974; Green and Wroblewski, 2000), and in both transplantation distances were small (between 15 and 75 km). These results suggest that cod are better at orienting using more localised cues, for example odours or underwater landmarks (Hasler, 1966). In this study, time at large was a power function of distance of the release site from the spawning ground, indicating that successful homing took disproportionately longer when fish were transplanted greater distances. Nevertheless, the mechanisms by which cod home short distances may differ from those used for larger-scale navigation.

The data indicate a strong negative relationship between homing success and transplantation distance. This finding suggests that an omnidirectional point source rather than a broadly based navigation system is used by cod at the relatively small scales measured here (tens of km from the spawning ground). For example, if broad scale celestial or solar clues were important, homing success should not have declined with increasing release site distance. Such clues should have been equally observable throughout the bay, and their use is likely to result in more accurate homing when transplantation distances are greater (Matthews, 1955). However, it should be noted that transplantation distances in this study were short relative to those in which celestial clue use has been demonstrated (e.g., Matthews, 1955). Alternatively, if cod were navigating along a directional gradient, such as that which might be produced if there were a chemical signature around the spawning ground, then individuals should have homed more successfully when released downcurrent of the spawning ground, and success should have declined as the chemical would become increasingly diluted with distance of the release site from the spawning ground. Although homing success did decline with distance, fish released upcurrent and downcurrent of Bar Haven homed at similar rates after release site distance was taken into account. Hence, the data provide little support for the hypothesis that Bar Haven cod used chemical clues to home in Placentia Bay. In contrast, Otterlind (1985) showed that transplanted Skagerrak cod homed to the vicinity of the original capture site only when there was a strong chemical gradient to follow. Several authors have demonstrated that fishes navigate towards non-chemical attractors, which are not affected by current direction, but which dissipate with distance. Godø

(1995) found evidence that cod use sound to navigate after being transplanted, and Klimley (1993) argued that fish can navigate towards recognisable magnetic patterns in the seabed. The use of this sort of omnidirectional attractor is consistent with the data.

The hypothesis that spatial memory was used is more difficult to resolve. However, if Bar Haven cod used spatial memory and underwater landmarks to navigate to the spawning ground, then individuals released on the eastern side of Placentia Bay along a familiar migration pathway (Lawson and Rose, 2000a) should have homed more successfully than those released on the less-used western side of the bay. Although cod released on the eastern side did show a higher percentage of homing, the direction effect was negligible when distance was taken into account. It should be noted that all tagged fish were large spawners that could have been equally familiar with all parts of the bay. However, the strong effect of release site distance on homing success is inconsistent with spatial memory being the key factor in homing observed here, as there is little reason to postulate that memory should decline in linear fashion over the scales studied here. Furthermore, there are species across many taxa, capable of precise navigation and homing for which spatial memory is not of major importance (for review, see Papi, 1992).

The data indicate that only when fairly close to the spawning ground do individuals home at high rates, yet year after year large populations are thought to return to spawning grounds over 100's of kilometres (Harden-Jones, 1968). I speculate that there could be a social component to cod homing that I cannot account for in this study. The cod tagged in this study appeared to navigate individually. The proportion of individuals from each release group that homed successfully took all possible values between 0 and 100%, indicating that the released individuals didn't stay together after transplantation. Successful homing was not strongly related to size, sex or maturity state. Perhaps individuals that homed successfully were simply better at navigating or more determined to do so than those that did not. Such traits could account for the "scouts" that led the migratory cod shoals described by Rose (1993) and DeBlois and Rose (1996). It is noteworthy that in the present study all tagged individuals were larger and presumably older fish, suggesting that homing ability is not solely a function of age. In any event, individuals with strong navigation and homing abilities could be essential for the maintenance of stock structure. Previous experiments have shown wide dispersal of transplanted individuals (Godø, 1995), while others showed that transplanted cod adopt the migratory patterns of the schools they meet upon release (Otterlind, 1985). I observed that Clattice Harbour transplants released near a large aggregation of cod did stay in that area for some time. But two of the four fish subsequently homed to Bar Haven.

It is important to note that animals likely have redundant sensory modalities for navigation. For example, fish that use celestial cues are not necessarily lost under heavy cloud cover. Redundancy is an important consideration when attempting to demonstrate that particular navigatory mechanisms are in use. For example, a blinded fish that can still home should not be used as evidence that vision is not otherwise important for navigation. However, if blinded fish cannot home there is no need to consider redundant sensory modalities. In this study, I am not trying to demonstrate that any mechanism is used. For example, the data are consistent with the navigation towards sound or magnetic attractors, but could be biased by redundant sensory modalities that I have not considered. As such, this discussion of navigation mechanisms is a speculative one. I simply tested some predictions that were based on the theoretical means by which animals might navigate. Clearly I have in no way performed the critical (physiological) experiments required to rule out any of the mechanisms considered here. Furthermore, I point out that cod may use other unknown navigatory mechanisms. However, on the basis of the results, I do advocate further experimentation on cod's ability to use sound and magnetism to navigate at sea.

In this study, the relocation rate for transplanted fish declined with time at a faster rate than for control fish. Although sample sizes are too small for strong conclusions, one interpretation of the results is that transplanted fish were more likely to leave the Bar Haven spawning grounds after returning than non-transplanted individuals. However, another interpretation is that transplanted cod were subject to higher miss rates. It is noteworthy that during all surveys, the sex ratio of the transplanted fish that homed was nearly even, but that of the control group was skewed in favour of males (Table 6-2). In a longer term study at Bar Haven, male cod had higher relocation rates than their female counterparts (see Chapter 7). The differences in relocation rates between control and transplanted groups are consistent with differences in sex composition and behaviour, and are the most likely explanation for the differences in relocation rate between control and successfully homing transplanted cod.

In conclusion, none of the navigation mechanisms investigated were entirely consistent with the homing observed in this study. The most parsimonious conclusion from the data is that Bar Haven cod tracked an omnidirectional source that dissipates with distance (e.g., a characteristic sound or geophysical signature), perhaps in combination with spatial memory.

6.6 Acknowledgements

I thank G. Rose, W. Hiscock, R. Jamieson, and D. Methven and the crew of the C.C.G.S. Shamook for field assistance.

Table 6-1: Details of release sites, and the total lengths (TL) of the fish released

Release Site	Latitude	Longitude	Dist. from catch site (km)	brg	TL of females released	TL of males released	Site notes
Bar Haven	47° 45.22'N	54° 13.37'W	0	-	74, 87	84, 95	Spawning site
Cheese Is.	47° 42.41'N	54° 05.16'W	11.92	139°	70, 98	78, 84	Upcurrent of spawning site
Haystack Bk	47° 37.07'N	54° 00.94'W	22.46	156°	83, 85	75, 80	Upcurrent of spawning site
Clattice Hr.	47° 29.77'N	54° 27.55'W	34.94	234°	79, 80	80, 82	Downcurrent of spawning site
Isle Valen	47° 31.14'N	54° 23.21'W	29.95	227°	95, 95	80, 80	Downcurrent of spawning site
Southern Hd.	47° 47.58'N	54° 04.20'W	12.69	91°	74, 79	82	Upcurrent of spawning site

Table 6-2: Date and vicinity of fish relocations. Shaded area indicates residency. Abbreviations are: BH = Bar Haven, CH = Cheese Island, CL = Clattice Harbour, HB = Haystack Bank, IV = Isle Valen, and SH = Southern Head.

Release location	Fish	Apr 4	Apr 8	Apr 9	Apr 10	Apr 11	Apr 12	Apr 13	Apr 20	Apr 27	May 4	May 14	May 20	May 30	Jun 6	Jun 13	Jun 20	Jun 28
BH	f137				BH	BH		BH										
BH	f161	BH																
BH	m104	BH		BH	BH	BH		BH	BH	BH	BH	BH						
BH	m109	BH		BH	BH	BH		BH	BH			BH	BH	BH				
SH	f167			BH	BH	BH		BH	BH	BH	BH							
SH	f79			BH	BH	BH		BH	BH	BH								
SH	m61			BH	BH	BH		BH	BH	BH	BH							
CH	f150																	
CH	f162 †		CH	CH		CH		CH										
CH	m62			BH	BH	BH												
CH	m91			BH	BH	BH		BH	BH	BH	BH	BH						
HB	f154		CH	BH	BH			BH	BH	BH	BH							
HB	f168																	
HB	m59																	
HB	m60								BH									
IV	f138						IV											
IV	f153																	
IV	m110																	
IV	m98																	
CL	f142		CL				CL							BH				
CL	f168		CL				CL		BH									
CL	m92		CL				CL											
CL	m97		CL				CL											

† presumed dead

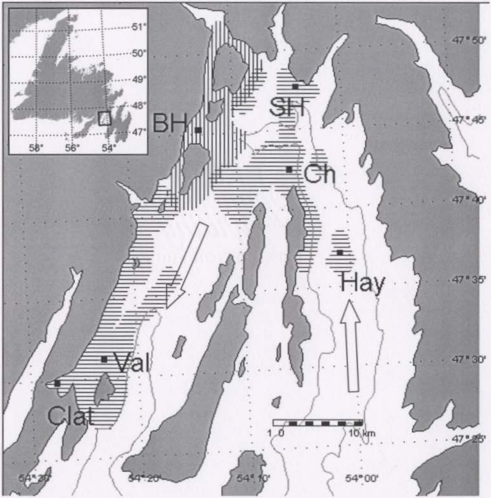

Figure 6-1: Map of the head of Placentia Bay. Arrows indicate current direction. Vertically shaded areas were surveyed as part of the Bar Haven grid. Horizontally shaded areas are extra-grid survey stations. The six release sites are shown (black squares), and are abbreviated as: Clat - Clattice Harbour, Val - Isle Valen, BH - Bar Haven, SH - Southern Head, Ch - Cheese Island, Hay - Haystack Bank. The 150 m depth contour is shown in grey. Inset: Newfoundland with box indicating the location of study area.

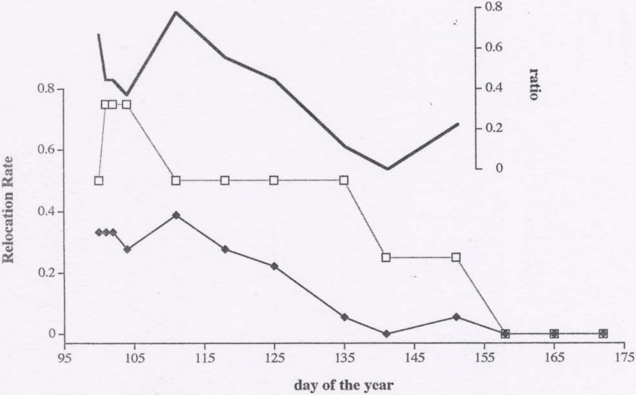

Figure 6-2: The relocation rate (lower panel) declines over the course of the spawning season (in Julian days) for transplanted fish (diamonds) and control fish (squares). The ratio of the relocation rates of transplanted to control fish (upper panel) also declines with time.

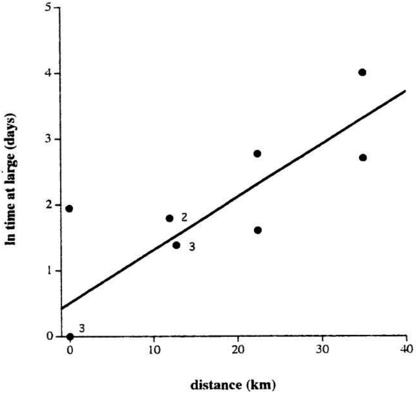

Figure 6-3: Time required to home increases with the distance of the release site from the spawning ground (ln time = .51 - 0.15•distance). Each point represents a successfully homed individual. Numbers indicate when several data points occupy the same space.

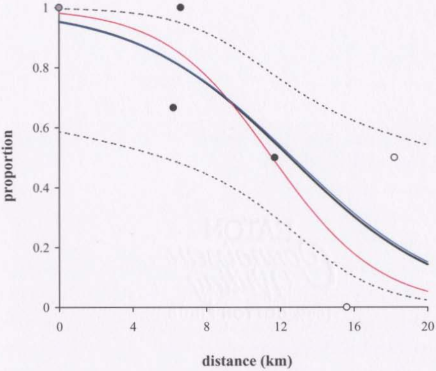

Figure 6-4: The negative effect of distance of the release site from the spawning ground on the proportion of fish that successfully home. The fitted curve, when all data are included, is shown in black (solid line) with 95% confidence limits (dotted lines). The trends for eastern (filled dots) and western (open dots) release sites (i.e., upcurrent and downcurrent) are shown in red and blue, respectively. Bar Haven (grey dot) is included in both eastern and western regressions.

7 Sex differences in cod behaviour on a spawning ground

Co-author: George A. Rose

7.1 Abstract

In order to assess whether the sexes of Atlantic cod (*Gadus morhua*) behave differently on a coastal Newfoundland spawning ground, 21 males and 27 females were tagged and released in April 1998 at Bar Haven in Placentia Bay. Telemetric tags were used, and the distribution of individuals was monitored over a grid of listening stations for three consecutive spawning seasons (1998-2000). Of the 48 tagged fish, 30 were relocated acoustically and fifteen caught in the fishery (including seven previously relocated) during this study. Only eight were never relocated. On average, males stayed on the spawning ground at least 12 days, and females 22 days. The rate of departure from the spawning grounds varied among years. There was no effect of body length on the timing of departure from the spawning ground, for either males or females. Males departed from the grounds earlier than females. The relocation rates for males were greater than for females in all years, suggesting that females move in and out of male-dominated spawning aggregations. Mobile and intercept fisheries on cod spawning grounds could disrupt the movements of spawning females or lead to sex biased harvest rates.

7.2 Introduction

Reproductive behaviours and courtship rituals are key to reproductive productivity in many animals (e.g., Barlow, 1991; Lank and Smith, 1992; Bourne, 1993; Höglund and Alatalo, 1995; Miller et al., 1998), but are poorly understood in marine fishes because direct observation is difficult. Nevertheless, it is possible that courtship and spawning behaviour in marine fishes is sufficiently complex to be impacted by fisheries. For example, Morgan et al. (1997) found that a single trawl towed through a spawning aggregation of Atlantic cod (*Gadus morhua*) affected their distribution across an 800 m swath for up to 77 minutes. Disruptions caused by repeated trawling could adversely impact reproductive success.

Atlantic cod is a demersal broadcast spawner whose reproductive behaviour has been reported to include complex rituals, movements and vocalizations. At sea, Sund (1935) reported elaborate pelagic behaviours in spawning cod, and Rose (1993) and Lawson and Rose (2000b) have observed that during the spawning season, cod aggregate in dense columns above the seafloor. In the lab, cod undergo intricate courtship rituals involving displays (Brawn, 1961; Hutchings et al., 1999) and vocalizations (Nordeide and Kjellsby, 1999) as do other gadids (Hawkins, 1990).

The timing of cod spawning events is likely to be variable, and may be influenced by age, size, feeding history, and temperatures experienced during gonadal development (Hutchings and Myers, 1993; Kjesbu, 1994). Several authors have reported that larger individuals may start spawning earlier, and continue for longer than smaller ones (Hutchings and Myers, 1993; Thorsteinsson and Marteinsdóttir, 1998).

Previous experiments at sea on spawning cod have addressed group rather than individual behaviour. Hydroacoustic surveys have suggested that the behaviour of male and female cod may differ in terms of residence time and activity on spawning grounds (e.g., Lawson and Rose, 2000b). Morgan and Trippel (1996), using bottom trawl survey data, reported that unequal sex ratios existed in areas occupied by cod during the spawning season, and that a higher proportion of both males and females were in spawning condition in male dominated areas. Based on these observations, Morgan and Trippel (1996) hypothesised that males might arrive at the spawning area first, and that females would move onto the ground periodically during the spawning season to release batches of eggs. Telemetric methods have the potential to enable tracking of individual fish for extended periods up to several years.

In this paper, I use acoustic telemetry of individually tagged males and females to examine sex-specific behaviour of cod on one of the most important spawning grounds in coastal Newfoundland. I examine predictions of 2 hypotheses. The hypothesis of Morgan and Trippel (1996) predicts that males would be found more consistently on the grounds than would females. The oft stated hypothesis that size affects residence time on the spawning grounds predicts that larger cod spawn earlier and spend a longer time on the grounds (at least for females). Finally, I discuss my findings with respect to previous sea and laboratory observations of cod spawning behaviour and their importance to fisheries management.

7.3 Materials and Methods

7.3.1 Tagging

In April 1998, aggregations of spawning cod were located acoustically from the C.C.G.S. Shamook (25 m research trawler) in the inner part of Placentia Bay, Newfoundland, near Bar Haven, in an area consistently used by cod for spawning during spring (Lawson and Rose, 2000b, a).

On April 19 and 20, 1998, approximately 215 cod (total length 34 - 102 cm) were taken from these aggregations using feather hooks. The fish were in water of near 0 °C temperature, at depths between 30-50 m. Larger individuals (> 60 cm) were held in flow-through tanks and were cannulated to assess sex and maturity stage (adapted from Morrison, 1990). As I was interested in sex-related behaviours of spawners, only mature and ripening or near-spawning individuals were tagged.

For each fish, an individually-coded ultrasonic transmitter was surgically implanted into the peritoneal cavity (see Appendix A), and an external spaghetti tag was anchored on the left side, adjacent to the first dorsal fin. Tagged fish were held for up to ten hours, and those that appeared to be robust and in excellent condition were released at the location where they were caught. In total 48 cod, including 27 females (lengths 64 to 87 cm) and 21 males (lengths 67 to 88 cm) were released (Table 7-1). All procedures were approved by the Memorial University animal research committee.

7.3.2 Telemetric Surveys

To avoid observing a period of abnormal behaviour that may follow surgery (Godø and Michalsen, 2000), I waited 15 days after tagging before beginning a biotelemetric survey of the Bar Haven spawning ground. The survey area included mostly shallow waters (35-70 m) off and between Bar Haven and Woody Islands, and extended eastward to just beyond the 150 m isobath. Fish were monitored between May 5 and June 24 using an acoustic receiver (Lotek Model SRX-400) with an omnidirectional hydrophone (Lotek Model LHP-1) to pick up the signal emanating from the implanted transmitters. Each transmitter emitted a unique signal, allowing the receiver to discriminate between the individual fish. The transmitters repeated their signal every five seconds, which allowed multiple observations of the individual, required for confirmation of identity. One minute was spent at each monitoring station, except when transmitters were detected, in which case extra time was spent attempting to confirm identification, and to triangulate their location. Surveys of the spawning ground were repeated during the two subsequent spawning seasons (April 8 to May 26, 1999; and April 4 to June 26, 2000). Surveys in all years were terminated in July, or when no tagged cod could be located for several consecutive surveys.

A beacon tag was left on the seafloor within the survey area for the duration of the study. Preliminary tests with the beacon tag determined the range of the telemetry gear to be approximately 0.5 nm (0.96 km). As such, a survey grid was established with 0.5 nm intervals between monitoring stations. Distance between monitoring stations was reduced to 0.3 nautical miles (0.58 km) in 2000 to account for the observed decay of transmitter power. Mean detection efficiency, measured as the proportion of spawning ground surveys in which the beacon tag was detected, was 0.8.

Most surveys took one day to complete. However, on several occasions, because of bad weather and time constraints, all stations of the complete Bar Haven grid could not be monitored in one day. As such, the data from all days required to monitor the entire grid of stations were pooled together as a single survey, and the survey "mid-point" was calculated as the average of the contributing dates. In total, Bar Haven was surveyed 11 times in 1998, three times in 1999, and 14 times in 2000.

7.3.3 Data Treatment

Individuals were often relocated in several non-consecutive surveys. The whereabouts of these individuals between surveys in which they were relocated is not known. The possibility of a fish being present but undetected within the Bar Haven survey grid was assumed to be low (the relocation efficiency of the beacon tag was 80%), although it is likely that some fish eluded detection during a survey (especially multiple-day surveys). For these analyses, all undetected individuals were treated as being outside of the Bar Haven survey grid, given that they returned and were subsequently relocated within the grid. These fish were considered to be "resident" in the general area (i.e., the Bar Haven survey grid plus the surrounding, unsurveyed waters), but to have "wandered" from the Bar Haven survey grid. As such, an individual was considered to be a "resident" of the general area from the first until the last time it was relocated, and the period of time between these relocations was referred to as "residency time" (note that fish tagged in 1998 were considered resident from the time of tagging until the last relocation that year). Furthermore, a "wander rate" was calculated as the proportion of surveys during which an individual was a resident of the general area but not relocated in the Bar Haven grid. Individuals that were only relocated once during the survey year were not included in wander-rate analyses.

Bar Haven relocation rates for each of the three years were calculated as the proportion of tagged fish that were relocated at Bar Haven as:

$$\frac{(\#\,observed)e^{-1}(1-f)^{-1}}{(\#\,tagged)(1-M-F-Z_{tag})}.$$

In the numerator, the number of tagged individuals observed at Bar Haven was adjusted to account for a relocation efficiency (e) of 80% and a transmitter failure rate (f) of 6.7% (see Chapter 5). The denominator (i.e., the number of tagged fish at large during each survey) was calculated as the number of fish originally tagged, less natural mortality (as per standard fisheries practices, M was set to 0.2 Hilborn and Walters, 1992), tagging-induced mortality (Z_{tag} = 6%, based on conventional tagging data for Placentia Bay during the years of this study; N. Cadigan and J. Brattey, unpublished data), and fishing mortality (F). The fishing mortality was calculated as the proportion of tagged fish for which transmitters were returned, adjusted for a tag underreporting rate (u) of 35% (based on conventional tagging data; N. Cadigan and J. Brattey, unpublished data):

$$F = \frac{(\#returned)(1+u)}{48}$$

Evacuation rates were calculated for 1998 and 2000 (there were only three surveys in 1999) by plotting the number of resident fish during each survey of Bar Haven against the survey's mid-date. Proportions of the total number of residents observed each year were used in order to allow comparison among years. In 2000, the first two surveys (before the proportion reached unity) were excluded because they described the shape of the arrival part of the residency curve (rather than the departure). Sigmoid decay was chosen as the functional form for curve fitting because the proportion of fish could not drop below zero, or go above 100%. The dose-response equation was:

$$Y_i = \frac{1}{1 + e^{(\beta_0 (\beta_1 - X_i))}}$$

where β_0 was the slope, β_1 was the day of the inflection point, X_i was the date of the *i*th survey (or mid-date if the survey took multiple days to complete), and Y_i was the number or residents during the *i*th survey (as a proportion of the total number of individuals that were relocated that year). The data were linearized as:

$$Z_i = m X_i + b$$

(where Z_i is $\log(Y_i / (1 - Y_i))$, m is β_0, and b is $-\beta_0\beta_1$) and fitted, assuming a binomial error structure. The two parameters, m and b, and their confidence limits were estimated iteratively, using maximum likelihood. As such, the confidence limits of the slope (β_0) were estimated directly (since $m = \beta_0$), but the estimation of the error around the inflection date (β_1) was complicated by its interdependence on the slope (since $\beta_1 = -b/\beta_0$). Any sex-related differences in inflection date were therefore described only in terms of the sample sizes required to achieve statistical significance. Confidence limits were calculated for the original data set, then for three newly generated data sets in which the proportions were held constant and the sample sizes were adjusted by factors of two, five and ten (e.g., if 7 of 21 fish were recorded as present in the original data, then, after a doubling of the sample size, there would be 14 of 42 recorded as present in the new data). The level of sampling effort required for confidence limits to be non-overlapping gives an indication of the effect size relative to the power of the test.

In cases when analyses were of borderline significance, data were randomised. Data sets of n observations were resampled n times with replacement, generating 1000 new data sets each with n observations. The significance level of each of the 1000 data sets were computed and compared to that of the original data set.

7.3.4 Fishery Recaptures

Throughout the study, fishers were offered rewards ($100 CDN) for the return of transmitters with information on date and location of capture. All fishers were interviewed subsequent to transmitter return. All reported the fish to be in good condition, showing complete recovery from the surgery.

7.4 Results

Of the 48 tagged fish, 30 were relocated acoustically at least once during the study. Fifteen tagged fish were recaptured in the fishery, including seven that had previously been relocated during the spring telemetry surveys. A further two fish were relocated in December as part of another research programme. In all, only eight tagged fish were never relocated.

Fishery recaptures (see Chapter 5, Fig. 5-2) occurred in every month except during peak spawning season (March to May) when the fishery was restricted. All but two recaptures were made in Placentia Bay along known migration pathways (Davis et al., 1994; Lawson and Rose, 2000a). The exceptional recaptures were made in September 1998 in Conception Bay on the Northeast coast, and in February 2000 about 100 nautical miles off the south coast of Newfoundland. In this study, fishery recaptures are only used to determine the number of tagged fish available to be relocated at Bar Haven.

The relocation dates and residency times for individual fish are shown in Table 7-1(a-c) for the 1998 through 2000 spawning seasons. In 1998, 24 tagged fish (50% of the total releases) were relocated (Table 7-1a), including 11 females (40.7%) and 13 males (61.9%). Fish that were relocated and those that were not did not differ significantly in length (relocated: 74.9 cm; not relocated: 77.2 cm; $F_{1,47} = 1.96$; $p = 0.17$) maturity stage (relocated: 87.5% early stage; not relocated: 79.2% early stage; $\chi^2_1 = 0.60$; $p = 0.44$) or sex (relocated: 45.8% female; not relocated: 66.6% female; $\chi^2_1 = 2.11$; $p = 0.15$). During the spring 1999 survey, eight tagged fish (two females, six males) were relocated in the Bar Haven area, four of which (one female, three males) had not been relocated during 1998 (Table 7-1b). During the 2000 survey, six tagged fish (three females, three males) were relocated in the Bar Haven area, three of which had been present in all three years (Table 7-1c). On average, males stayed on the spawning ground at least 12.5 days, and females 22.3 days.

For tagged cod in 1998, 1999 and 2000, 71%, 39% and 53%, respectively, were relocated at Bar Haven (Table 7-2). These relocation rates were skewed towards males in all years. Wander rate (proportion of surveys during which an individual was resident but not relocated) was higher for females (0.40) than for males (0.23; $t_{21} = 1.45$; $p = 0.16$) and was independent of fish length ($F_{1,21} = 0.087$; $p = 0.77$). When the data for the effect of sex on wander-rate were randomised, keeping sample size for males and females fixed, 555 of 1000 F-values were significant at the $\alpha=0.05$ level, and 765 were greater than the original (unrandomised) F value. Females wandered more than males in 982 of the randomised data sets.

The dose response curves fit the 1998 and 2000 data well (Fig. 7-1; 1998: $r^2 = 0.98$; 2000: $r^2 = 0.89$). The rate at which resident fish left the spawning ground differed between 1998 and 2000 (data from 1999 are not included in this analysis because there were only three surveys that year). In 1998, most fish left early and over a relatively short period of time (date of inflection = 142.3 and slope = -0.15; 95%CI: $-0.195 < \text{slope} < -0.117$). In 2000, evacuation occurred later (date of inflection = 151.6) and was more significantly more gradual (slope = -0.04; 95%CI: $-0.064 < \text{slope} < -0.019$), with several individuals remaining on the spawning grounds until late June.

On average, males departed the spawning grounds earlier than females (Fig. 7-2a). In 1998, males had an earlier inflection date than did females (Male = 140.3; Female = 144.4), although differences were not large. Modelling of the effects of sampling effort on confidence intervals (Fig. 7-2b) revealed that sex-differences in time of departure from the spawning ground would have been significant if more than 96 fish had been tagged in this experiment. There were no significant sex-differences in rate of departure from the spawning ground (Males: 95%CI: $-0.206 < \text{slope} < -0.099$; Females: 95%CI: $-0.210 < \text{slope} < -0.099$). In 2000, the slope and inflection dates could not be calculated reliably because only three males and three females were relocated. However, the data are consistent with the trend observed in 1998. For example, when the last survey was conducted on 28 June 2000 (day 180), two of three females remained on the spawning ground, whereas the last male had departed by 13 June (day 165). Furthermore, the male:female sex ratio declined with time in both 1998 and 2000 (Fig. 7-3; ratio_{1998} =

$2.78 - 0.013 \cdot day_{1998}$; $ratio_{2000} = 4.06 - 0.024 \cdot day_{2000}$). Although these sex ratios are based on sample sizes that are too small to make rigorous statistical generalisations, the results do indicate that the trend for earlier male departure was observed in 2000 as well as in 1998.

Although preliminary analysis showed that larger males left the spawning grounds earlier than smaller males (Fig. 7-4; departure date = 241.24 - 1.43•TL; $F_{1,20} = 4.74$; $p = 0.042$; $r^2 = 0.19$), the trend was weak and explained only a small portion of the variance. However, spawning and departure dates were earlier in 1999 compared the other two years ($F_{2,19} = 4.97$; $p = 0.018$) and may have influenced the relationship. As such, I plotted the residuals of the departure date vs. year ANOVA against total length, and found no significant relationship ($F_{1,20} = 0.89$; $p = 0.36$). Apparently, the preliminary trend was driven by a few large fish (that left early) in 1999. Length also did not affect the departure date of females (Fig. 7-4; exit date = 173.84 - 0.44•TL; $F_{1,14} = 0.20$ $p = 0.66$).

7.5 Discussion

The data tentatively show that individual Atlantic cod exhibited sex differences in residency on the Bar Haven spawning ground in Placentia Bay. Females had higher wander rates then males in 98% of data randomizations (the difference between sexes was only statistically significant in 56% of cases due to the low sampling power of the study); and females had correspondingly lower observed relocation rates in all years (Table 7-2). Females left the grounds an average of four days later than males. Although the difference between sexes was not statistically significant using only 48 tagged fish, the trend was supported by declining male:female sex ratios within each spawning season. Since I do not know when these fish arrived on the grounds, I cannot address whether or not females spawned over a more protracted period. These findings suggest that during the spawning season, females were less likely to stay within the observation area (the spawning grounds) than were males. Males were more likely to be within the Bar Haven spawning grounds (i.e., the survey grid) while resident in the general area than were females. The sex ratio of cod in this area does not differ from 1:1 overall (G. A. Rose, unpublished data).

The data are consistent with the hypothesis that females move in and out of male dominated spawning aggregations when ready to release an egg batch (Morgan and Trippel, 1996). The precise location of females when not observed within the Bar Haven grid is unknown. However, Morgan and Trippel (1996) reported that female dominated aggregations were distributed in deeper waters, and suggested they might use the warmer water to increase their rate of egg development. In this study, in is unlikely that wanderers ventured very far, as many would come and go within a day or two. Moreover, the deeper waters adjacent to the spawning ground were not surveyed, and are most the likely destination of the wanderers. It is important to note that the geographic scale of the present study is small (one spawning ground; a few kilometres) compared to that of Morgan and Trippel's study, which spanned the entire Grand Banks, and areas to the north (1000's of kilometres). These differences must dictate temporal differences in the scale of movements of the female fish. For energetic reasons, females are unlikely to travel back and forth 100s of km between spawning batches. Nevertheless, the findings of these studies conducted over very different scales both suggest that males hold the spawning ground while more mobile females come and go when ready to spawn.

The data did not indicate any size-related differences in the timing of spawning. The literature contains several conflicting reports on this issue. Thorsteinsson and Marteinsdóttir (1998) found that in Icelandic waters, larger males arrived at and departed from the spawning grounds earlier than smaller males, and that residence time was not size related. For Newfoundland waters, Hutchings and Myers (1993) drew the opposite conclusion, that larger cod spawned over longer periods of time and finished spawning later than smaller cod. Marteinsdóttir and Petursdóttir (1995) found that both small and large cod finished spawning at about the same time in Icelandic waters, which is similar to the present observations. Marteinsdóttir and Petursdóttir also found that larger fish started spawning earlier, which is consistent with previous reports (Hutchings and Myers, 1993; Kjesbu et al., 1996; Lawson and Rose, 2000b) that larger females spawn over a longer period of time.

The data further show that the date and rate of departure from the Bar Haven spawning ground differed between years. However, in all years the majority of the fish had evacuated the spawning ground by the end of June. This agrees well with Brander's (1993) report that cod in the area of Placentia Bay spawn from May to June. However, there is evidence that spawning occurs later (July and August) in some years at Bar Haven (Lawson and Rose, 2000b). Differences in departure rate and timing between years may result from differential temperature or food availability experienced by the fish during gonadal development, or from differences among years in the length/age-structure of the spawners (Hutchings and Myers, 1993; Kjesbu, 1994). I have inadequate data on the temperatures experienced by the fish during gonadal development. However, interannual changes in the size and age structure coincide with observed timing differences in spawning (G. A. Rose, unpublished data).

In conclusion, the results show that the residence characteristics and movements of cod on and around the spawning ground investigated here are complex and sex specific. Males appear to hold the grounds. Females are more transient, moving onto the grounds, presumably to batch spawn, then departing. It is possible that females venture into warmer "incubating" waters during their departure. These results have important fishery management implications. Fisheries on spawning grounds may capture a greater proportion of one sex, and it is feasible that mobile and intercept gear types (e.g., trawls or gillnets) could sufficiently disrupt fish movements and behaviour, especially of batch spawning females, to compromise stock productivity.

7.6 Acknowledgements

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Table 7-1: Observations and residency of tagged fish at Bar Haven during spawning season. "Residents" are fish that are distributed either within the Bar Haven survey grid (positive relocations at Bar Haven are indicated with dots), or in the surrounding, unsurveyed waters (shaded cells, with no dot). Residence times for individuals are from the first relocation within the Bar Haven grid until the last. **(a)** 1998 surveys; **(b)** 1999 surveys; **(c)** 2000 surveys.

(a)

	Julian date										
Fish	128	138	139	141	145	148	152	155	156	160	164
f031	•										
f037	•	▨	•								
f038	•	•	•								
f047	•										
f048	•	▨	•	▨	•	•	•				
f054	•	▨	▨	▨	•						
f057				•	▨	•					
f066	•	▨	▨	•	▨	•	•	▨	•	•	
f068				•							
f114	•										
f126					•	▨	▨	▨	•		
m031			•	•	▨	•	•				
m032	•										
m036	•	▨	•								
m037	•										
m038	•										
m042	•										
m047	•	▨	•	•							
m054	•	▨	•								
m057										•	•
m078	•	▨	▨	•	•	•					
m114	•										
m126	•	•	•	•	•	•					
m160	•										
# of residents	19	10	11	9	8	7	4	2	2	2	1
# Male residents	11	5	6	4	3	3	1	0	0	1	1
# Female residents	8	5	5	5	5	4	3	2	2	1	0
Resident sex ratio	1.38	1.00	1.20	0.80	0.60	0.75	0.33	0.00	0.00	1.00	inf

Table 7-1 continued.

(b)

Fish	Julian date 116	133.5	146
f048	•	•	
f050	•		
m090	•		
m031	•	•	
m050	•		
m068	•		
m114		•	
m160	•		
# of residents	7	3	0
# Male residents	5	2	0
# Female residents	2	1	0
Resident sex ratio	2.50	2.00	inf

(c)

Fish	Julian date 100	101	102	104	111	118	125	135	141	151	158	165	172	180
f033			•		•									
f050	•	•	•	•	•	•	•	•	•	•	•	•	•	•
f114			•	•				•	•					•
m031	•	•	•	•	•	•								
m049		•	•	•	•	•	•	•	•	•	•			
m050	•	•	•	•	•	•	•							
# of residents	3	4	6	6	6	5	4	3	3	3	3	2	2	2
# Male residents	2	3	3	3	3	3	2	1	1	1	1	0	0	0
# Female residents	1	1	3	3	3	2	2	2	2	2	2	2	2	2
Resident sex ratio	2.00	3.00	1.00	1.00	1.00	1.50	1.00	0.50	0.50	0.50	0.50	0.00	0.00	0.00

Table 7-2: Relocation rates for male and female Bar Haven (BH) cod between 1998 and 2000, and the parameters used in their calculation. Formulas use alphabetic column headings as shorthand. Mortality is abbreviated as "mort".

	A	B	C	D	E	F	G	H	I	J	K	L
YEAR sex	number tagged	# of cod relocated at BH during spawning season	efficiency of telemetry gear	cumulative number of transmitters returned from the fishery	fishing mort.	natural mort.	tagging induced mort.	rate of tag under-reporting in the fishery	rate of trans-mitter failure	# alive at spawning time	# alive with functioning tags	Homing
					D/A					A(1-E-F-G) -HD	J-IJ	(B/K)/C
1998												
M	21	13	0.8	0	0.00	0	0.06	0.35	0.0667	19.7	18.4	0.88
F	27	11	0.8	0	0.00	0	0.06	0.35	0.0667	25.4	23.7	0.58
total	48	24	0.8	0	0.00	0	0.06	0.35	0.0667	45.1	42.1	0.71
1999												
M	21	6	0.8	2	0.10	0.2	0.06	0.35	0.0667	12.8	12.0	0.63
F	27	2	0.8	4	0.15	0.2	0.06	0.35	0.0667	14.6	13.6	0.18
total	48	8	0.8	6	0.13	0.2	0.06	0.35	0.0667	27.4	25.6	0.39
2000												
M	21	3	0.8	6	0.29	0.2	0.06	0.35	0.0667	7.4	6.9	0.54
F	27	3	0.8	9	0.33	0.2	0.06	0.35	0.0667	7.8	7.3	0.51
total	48	6	0.8	15	0.31	0.2	0.06	0.35	0.0667	15.3	14.3	0.53

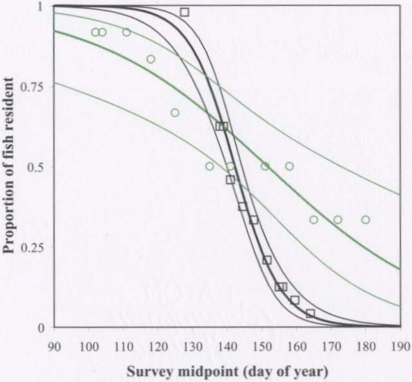

Figure 7-1: The decline in number of Bar Haven residents over time in 1998 (squares, black lines) and 2000 (circles, green lines). For comparison between years, the number of residents is shown as a proportion of the maximum number of residents for that survey year. Fitted curves and 95% confidence bounds are shown as bold and light lines, respectively.

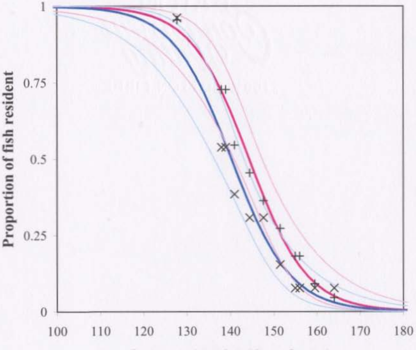

Figure 7-2a: The decline in number of male (Xs, blue lines) and female (+s, pink lines) residents at Bar Haven over time in 1998. For comparison between sexes, the number of residents is shown as a proportion of the maximum number of residents of that sex. Fitted curves and 95% confidence bounds are shown as bold and light lines, respectively.

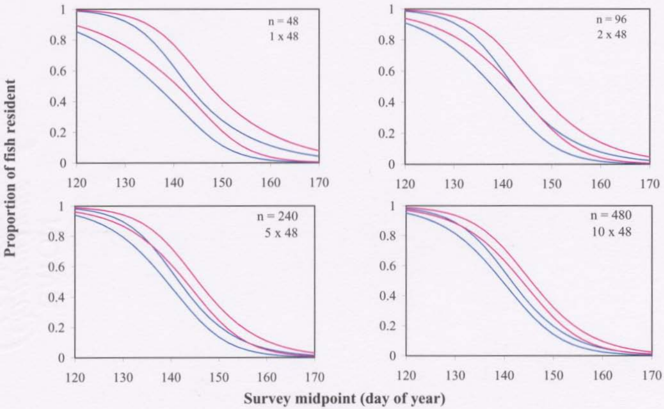

Figure 7-2b: The confidence bounds for male (blue) and female (pink) evacuation models at Bar Haven, 1998. Progressive panels show how the bounds shrink with increased tagging effort (shown in top right). The model estimates the proportion of fish resident (vertical axis) for any given day (horizontal axis).

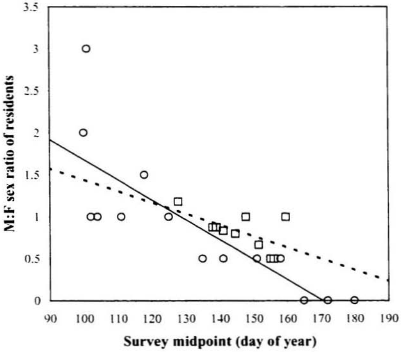

Figure 7-3: The decline in male:female sex ratio over the spawning season at Bar Haven in 1998 (squares, dotted line) and 2000 (circles, solid line).

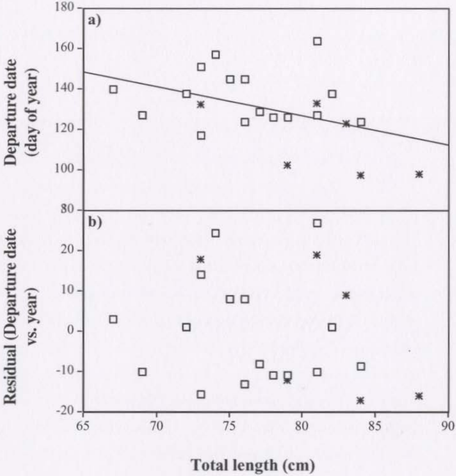

Figure 7-4: **(a)** Date of departure from the spawning ground of Bar Haven males by total length. **(b)** Residuals of an ANOVA (departure date vs. year) against total length. Individuals observed in multiple years are represented by more than one point. The 1999 data are shown as stars

8 Assessing evacuation rates and spawning abundance of marine fishes using coupled telemetric and acoustic surveys

Co-author: George A. Rose

8.1 Abstract

Assessing the spawning abundance of marine fishes is difficult if spawning periods exceed the residency of individual fish on the spawning grounds. For Atlantic cod (*Gadus morhua*), which has a protracted spawning period, I use biotelemetric surveys to estimate the rate at which individual fish vacate the spawning ground and develop a method to adjust multiple acoustic survey results to account for spawner turnover. Two acoustic surveys conducted one month apart (May and June 1998) on a cod spawning ground in Placentia Bay, Newfoundland, yielded abundance estimates of 220 000 and 210 000 fish of mean length 63 cm. Rates of evacuation from the spawning ground, observed over two separate spawning seasons, were modelled as logistic decay functions with good fit (r^2 = 0.98 in 1998; r^2 = 0.89 in 2000). My method estimated that only 8.0% of the fish counted during the second survey were present during the first, and that between 398 292 and 423 096 fish were actually present over the full spawning season. Coupled telemetric and acoustic surveys could be used to estimate spawning abundance in many marine fishes.

8.2 Introduction

Marine fish populations are often surveyed during spawning periods when distributions are concentrated and species mixing is minimal (Godø, 1989; Coombs and Cordue, 1995; Kloser et al., 1996; Williamson and Traynor, 1996; Lawson and Rose, 2000b). Such surveys are sometimes repeated during a season in an attempt to estimate error around abundance estimates. However, the potential for movement of fish into and out of the spawning area calls into question the likelihood that multiple surveys are true replicates. Surveys conducted as discrete "snapshots" of the spawning abundance may or may not be measuring the same fish. In the extreme case, if the time of residence of individual fish on the spawning ground is short relative to the interval between surveys, abundance estimates from each survey should be summed to estimate total abundance. If the residence time is protracted, the estimates should be averaged. Intermediate cases are likely, and typically, the average residence times of individual fish are unknown.

Atlantic cod (*Gadus morhua*) spawn in large aggregations and are surveyed acoustically in several areas of the north Atlantic (Godø, 1989; Ouellet et al., 1997; Rose et al., 2000a; Anderson and Rose, 2001). Spawning is often protracted over many weeks (Brander, 1993; Hutchings and Myers, 1994; Lawson and Rose, 2000b). The residence time of cod on their spawning grounds is thought to vary among sex and age groups (Marteinsdóttir and Petursdóttir, 1995; Kjesbu et al., 1996; Thorsteinsson and Marteinsdóttir, 1998). However, the impact of variation in mean residence time of cod on the spawning ground on survey estimates of abundance is unknown.

In this study, I use biotelemetric techniques to estimate the rate at which individual cod evacuate a spawning ground in Placentia Bay, Newfoundland. Empirical evacuation curves are applied to a set of acoustic surveys to demonstrate how multiple survey data can be adjusted to account for spawner turnover and to more accurately estimate total spawner abundance.

8.3 Methods

8.3.1 Telemetry

In April 1998, aggregations of spawning cod were located acoustically from the CCGS "Shamook" (25 m research trawler) near Bar Haven Island in the inner part of Placentia Bay, Newfoundland. This area is consistently used by cod for spawning during spring (Lawson and Rose, 2000b, a).

On 19 and 20 April 1998, approximately 215 cod (total length 34 - 102 cm) were taken from these aggregations using feather hooks. The fish were in water of near 0 °C temperature, at depths between 30-50 m. Larger individuals (> 60 cm) observed to be in spawning condition were held in flow-through tanks and sexed by cannulation. For each fish, an individually-coded ultrasonic transmitter tag was surgically implanted into the peritoneal cavity (see Appendix A) and an external spaghetti tag was anchored on the left side, near the first dorsal fin. Tagged fish were held for up to 10 hours, and those that appeared to be robust and in excellent condition were released at the location where they were caught. In total, 48 cod, including 27 females (lengths 64 to 87 cm) and 21 males (lengths 67 to 88 cm) were released (Table 8-1).

To avoid observing a period of abnormal behaviour that may follow surgery (Godø and Michalsen, 2000), I waited 15 days after tagging before beginning a biotelemetric survey of the Bar Haven spawning ground. Fish were monitored between 5 May and 24 June using a decoding acoustic receiver (Lotek Model SRX-400) and omnidirectional hydrophone (Lotek Model LHP-1). The spawning area was surveyed using a grid of monitoring stations spaced 0.5 nautical miles (0.96 km) apart to correspond with the average effective range of the telemetry equipment, tested on a control tag left on the bottom throughout the study. Surveys of the spawning ground were repeated during the two subsequent spawning seasons (8 April to 26 May 1999; and 4 April to 26 June 2000). Distance between monitoring stations was reduced to 0.3 nautical miles (0.58 km) in 2000 to account for the observed decay in transmit power of the control tag. Surveys in all years were terminated when no tagged cod could be located for a period of several days.

Coverage of the survey grid at Bar Haven was not synoptic, and all stations could not be surveyed in a single day. This condition, and the probability that fish were moving about the ground during a survey, indicated that not all fish on the ground could be expected to be relocated each survey. It was therefore assumed that an individual fish remained within the survey area from the first time it was relocated until the last, regardless of whether or not it was relocated in the days between. The period between first and last relocation is referred to as "residency time". Fish on the spawning grounds are referred to as "residents" (note that fish tagged in 1998 were considered resident from the time of tagging until the last relocation that year). In total, Bar Haven was surveyed 11 times in 1998, three times in 1999, and 14 times in 2000. There were too few surveys in 1999 to estimate residence and these data are not included in this study.

Evacuation rates were calculated for 1998 and 2000 by plotting the number of resident fish during each survey of Bar Haven against the survey midpoint. Proportions of the total number of residents observed each year are used to allow comparison among years. The data were fitted with sigmoid (dose response) curves by estimating two parameters, b and m as:

$$Y = \frac{e^{(b+mX)}}{1+e^{(b+mX)}} \qquad \text{(eq. 8-1)}$$

where Y is the proportion of residents observed in a given survey, and X is the survey date (or midpoint, when surveys took multiple days). A sigmoid decay curve was chosen as the functional form because the proportion of fish could not drop below zero, or go above 100%.

The data were adjusted as per Neter et al. (1985), and the parameters were estimated using maximum likelihood, where a logit link ($\ln(Y(1-Y)^{-1})$) and a binomial error structure were assumed. The confidence limits around the fitted curve were calculated (iteratively) such that for any given day, I could predict the proportion of tagged fish resident with 95% confidence.

Confidence limits calculated under binomial error are sensitive to number of tagged fish. To examine the error behaviour, eight new data sets were generated in which the proportions were held constant and the sample sizes were adjusted by factors of two through nine (e.g., if 5 of 10 fish were recorded as present in the original data, then, after a doubling of the sample size, there would be 10 of 20 recorded as present in the new data). For each new data set, the model was fitted, and the confidence limits around the fitted curve were estimated.

8.3.2 Acoustics

A portion of the spawning ground was surveyed acoustically on 9 May and 7 June 1998 using a BioSonics single beam digital DT4000 echosounder (120 kHz, 6 ° half-power beam-width, pulse duration 0.4 ms, 42 kHz sampling rate, pulse rate 5 $\text{pings}\cdot\text{s}^{-1}$). The transducer was mounted on a dead weight body towed at 4 knots (7.4 $\text{km}\cdot\text{h}^{-1}$) at a depth of 1.5 m alongside either the RV Innovation or the RV Mares (<14 m) over the grid of survey stations used for the telemetry. For comparison, only acoustic data from the part of the ground covered on both surveys is used to estimate densities and numbers.

The transect data were partitioned horizontally into 50 m bins. Based on signal patterns (e.g., LeFeuvre et al., 2000), and the fact that cod was the only species caught while fishing on areas of identified signal, all backscatter was attributed to cod. The density of cod in each bin was calculated from areal backscatter (S_A) as

$$\mathrm{Density}_{\mathrm{bin}} = S_{A\ \mathrm{bin}} \left(4\pi\left(10^{TS/10}\right)\right)^{-1} \qquad \text{(eq. 8-2)}$$

using the empirically determined target strength (TS) model (Rose and Porter, 1996):

$$TS_{(dB)} = 20\log L_{(cm)} - 66 \qquad \text{(eq. 8-3)}$$

where $L_{(cm)}$ is the mean length of cod in the area (in cm). Abundance was extrapolated to the surveyed portion of the spawning ground of 5 nm^2 (18.4 km^2).

8.3.3 Estimate of Spawning Abundance

For k acoustic surveys, let abundance be $\{\mathbf{N_1} \ldots \mathbf{N_k}\}$ and the proportion of tagged fish resident on the spawning ground be $\{\mathbf{p_1} \ldots \mathbf{p_k}\}$. To estimate total spawning abundance, $\mathbf{N_2}$ through $\mathbf{N_k}$ must be adjusted to account for fish already counted in previous acoustic surveys. For example, if 50% of the fish present during acoustic survey 1 are present during acoustic survey 2, then half of the fish in the second survey must be ignored:

$$N_{\mathrm{total}} = N_1 + (N_2)\left(1 - \frac{p_2}{p_1}\right) . \qquad \text{(eq. 8-4)}$$

Similarly, if three acoustic surveys are conducted, then the fish in second survey must be adjusted to account fish already counted in the first survey, and the fish in the third survey must be adjusted to account for those already counted in the second survey. For example, if $\mathbf{p_1}$, $\mathbf{p_2}$ and $\mathbf{p_3}$ were 1, 0.5 and 0.1, respectively, then 50% of $\mathbf{N_2}$ will have been previously counted during acoustic survey 1, and 20% of $\mathbf{N_3}$ will have been previously counted during acoustic survey 2:

$$N_{total} = N_1 + (N_2)\left(1 - \frac{p_2}{p_1}\right) + (N_3)\left(1 - \frac{p_3}{p_2}\right). \qquad \text{(eq. 8-5)}$$

Note that although 10% of $\mathbf{N_3}$ will have been counted in survey 1 *and* 2, there should be no fish counted in survey 1 *and* 3 that *was not* counted in survey 2 (since fish were resident from tagging until the last detection). As such, each of the $\mathbf{N_k}$ terms need only be adjusted to account for fish counted in the immediately preceding survey. The general equation can be written as:

$$N_{total} = N_1 + \sum_{i=2}^{k} (N_i)\left(1 - \frac{p_i}{p_{i-1}}\right). \qquad \text{(eq. 8-6)}$$

8.4 Results

8.4.1 Telemetry

In 1998, 24 tagged fish (50% of the total releases) were relocated on the spawning ground. The greatest number of residents at any time was 19 fish, observed in the first survey (midpoint 7 May; day 127). During the 2000 survey, six tagged fish (three females, three males) were relocated. The greatest number of residents was six fish, observed early in the season on 11 April (day 102).

The proportion of relocated fish resident on the spawning ground was well described by a decay curve in both 1998 and 2000 ($r^2 = 0.98$ and 0.89 for 1998 and 2000, respectively; Fig. 8-1). The rate at which resident fish left the spawning ground differed between 1998 and 2000. In 1998, most fish left early and over a relatively short period of time (date of inflection = 142.3 and slope = -0.15; 95%CI: $-0.195 < \text{slope} < -0.117$). In 2000, evacuation occurred later (date of inflection = 151.6) and was more significantly more gradual (slope = -0.04; 95%CI: $-0.064 < \text{slope} < -0.019$), with several individuals remaining on the spawning grounds until late June.

8.4.2 Acoustics

The areal backscatter for the 50 m bins was autocorrelated with lags up to and including 3 ($r_3 = 0.14$, $p = 0.0002$). Bins pooled over 200m were independent ($r_4 = 0.07$; $p > 0.05$) and used in all analyses. The mean lengths of cod caught in association with the acoustic surveys were 62.4 cm in May and 63.9 cm in June and did not differ significantly ($t_{37} = 0.471$; $p = 0.6$). The mean densities of cod distributions in May and June were 0.0119 and 0.0115 fish per m^{-2}, respectively (Fig. 8-2). Estimated abundance within the surveyed area was 220 000 fish in May and 212 000 fish in June.

8.4.3 Abundance Estimate

The proportion of tagged fish resident on the spawning ground was calculated from eq. 8-1 to decline from 0.88 during the acoustic survey on 9 May to 0.07 for that on 7 June (Fig. 8-3). As such, approximately 16 960 ($p_2/p_1 = .080$) of the 212 000 fish counted in June were previously counted in May. Hence the estimated total number present within the surveyed area over the spawning season was:

$$N_{total} = N_1 + (N_2)(1 - p_2 \cdot p_1^{-1}) = 220\,000 + (212\,000)(1 - 0.080) = 415\,040.$$

The 95% confidence intervals for the predicted proportions given above were {0.79 to 0.94} for May and {0.04 to 0.13} for June. Using these limits, I obtain a range of estimates of 398 292 to 423 096 spawning fish. These confidence limits were sensitive to sampling effort, and varied within and among years. For example, on the sampling date with lowest confidence (day 139, Fig 8-4) the estimate of the proportion of fish resident was precise to ± 0.88, whereas that on day 164 was precise to ± 0.029. For the days of the acoustic surveys (days 129 and 159), estimates of the proportion of fish resident could be precise to within 5% if sampling effort was doubled (about 100 tagged fish).

8.5 Discussion

In this study, I demonstrated a method to determine the degree of independence of sequential fisheries surveys and estimate total spawner numbers. My method is applied to acoustic surveys of Atlantic cod but could be used with other species that are surveyed acoustically when they aggregate to spawn. My surveys at Bar Haven were conducted approximately one month apart and yielded similar abundance estimates, specifically 220 000 and 212 000 fish. However, I estimated that only 8.0% of the fish counted during the second survey were present during the first survey. Hence, an average of the two values would have underestimated the number of spawning fish at Bar Haven in 1998 by between 51.1% and 54.2%, based on the upper and lower confidence limits of total abundance. On the other hand, summing the two survey estimates would have over-estimated spawner abundance. The data illustrate the importance of spawner turnover during a spawning season. My method has the advantage over standard survey techniques by taking spawner turnover into account in assessments of population density and hence biomass.

Many fish stocks are surveyed during the spawning season (Doubleday and Rivard, 1981; MacLennan and Simmonds, 1992). Typically only one survey is undertaken, although in some cases replicates are run. Such methods require an accurate knowledge of the timing of spawning since for many stocks spawning timing varies interannually (e.g., Jónsson, 1982; Wieland and Horbowa, 1996). In the present study, spawning timing was coarsely similar among years, yet turnover rates varied considerably (Fig. 8-1). As such, single-survey abundance estimates would have been affected by survey timing, and would have been gross underestimates. Single or replicate survey designs should in most cases be regarded as minimal estimates of the number of fish using the grounds over a spawning season.

The probability of spawner turnover during protracted spawning periods has been recognized in some fisheries. In a few cases attempts have been made to undertake sequential surveys throughout the spawning period. For example, in surveys of spawning hoki (*Macruronus novaezelandiae*) in the Cook Strait in New Zealand, which have been conducted since 1987, the likelihood of turnover on the grounds has been specifically recognized in the survey design, and attempts have been made to adjust survey results to represent an average mid-season level of biomass (e.g., Livingston, 1990; Cordue, 1994). However, this methodology depends on the temporal patterns of spawning and spawner turnover being somewhat more constant between years than I observed with Atlantic cod, and furthermore limits interpretations of biomass to a relative index rather than an absolute estimate.

To the best of my knowledge, this work is the first to incorporate telemetry into an acoustic biomass survey of spawning fish. In the present study, ship costs were relatively high because the telemetric and acoustic surveys were not conducted simultaneously. However, one vessel could conduct both surveys by sounding while steaming between telemetry survey stations. If this were done, not only would the costs be reduced, but actual values of the proportion of fish on the grounds might be used instead of estimates computed from decay-rate evacuation models.

The necessity for the concurrent telemetry during each acoustic survey will depend on the level of variability in the turnover rate. Stocks that exhibit static turnover rates and spawning times (as implied for Northeast Arctic cod in Brander, 1994a) could have evacuation rates modelled so that telemetry would not be required during each spawning survey. For other stocks (including that studied here) in which evacuation rates appear to vary considerably among years, a single model may be inappropriate. However, it is important to note that the error introduced by using even an average curve is unlikely to be as great as from calculations based on averaging or summing survey estimates. In addition, I speculate that variations in the slope and inflection point of the evacuation curve might be related to factors such as temperature or spawner age structure (Jónsson, 1982; Hutchings and Myers, 1994; Marteinsdóttir and Björnsson, 1999). If so, then improved knowledge of fish behaviour could be incorporated into a multivariate approach to define model parameters.

The confidence intervals about the abundance estimate calculated here do not include a full treatment of the uncertainty of either the tagging proportions or the acoustic estimates. It is not my intent here to conduct a full error analysis, but rather to demonstrate how telemetric tagging and acoustic surveys can be used together to estimate overall spawning numbers. A fuller treatment dealing with all errors in acoustic methods (Rose et al., 2000b), and telemetric surveys (e.g., Samuel and Kenow, 1992; Smith et al., 1998) are considered elsewhere. Estimates of these uncertainties could be incorporated into the present methods. It is important to note however, that telemetry-related estimates will be sensitive to the number of fish tagged, and in future studies under similar conditions, I recommend that at least 100 fish be tagged.

An important requirement for the present method to yield meaningful results is that a representative part of the spawning population be tagged. For standard fishery surveys, the areas and times surveyed are based on assumptions about the behaviour of the stock (Rose, 2000). These same assumptions are made when choosing the areas for telemetric tagging. Care should be taken that a range of sizes and a sex ratio reflecting the spawning population be tagged. In the present study, fish were sexed before tagging, but only large individuals were tagged as a consequence of the relatively large size of the transmitter tags. However, miniaturised sonar tags are coming to market soon and will allow safe tagging of most all sizes of spawning marine fish.

In conclusion, survey estimates of total spawner numbers for populations having protracted spawning periods and relatively short spawner residence times can be gross underestimates if residency time is not considered. It is evident that in such situations single or quasi-replicated surveys should be regarded as minimal estimates of the numbers of fish using the grounds over a spawning season. I believe that the use of complementary telemetric and acoustic surveys, as demonstrated here for Atlantic cod, may have use in many survey situations.

8.6 Acknowledgements

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Table 8-1: Total length of the 27 female and 21 male cod tagged at Bar Haven, April 1998.

Fish	TL (cm)
31f	83
32f	76
33f	75
34f	77
35f	74
37f	69
38f	78
42f	77
46f	78
47f	75
48f	76
49f	86
50f	75
54f	76
57f	65
66f	64
68f	66
78f	65
90f	72
96f	72
102f	78
107f	87
114f	76
118f	82
126f	83
160f	72
170f	70

Fish	TL (cm)
31m	73
32m	69
35m	81
36m	72
37m	77
38m	76
42m	78
47m	67
49m	74
50m	84
54m	82
57m	81
66m	76
68m	88
78m	75
90m	83
102m	76
107m	74
114m	81
126m	76
160m	79

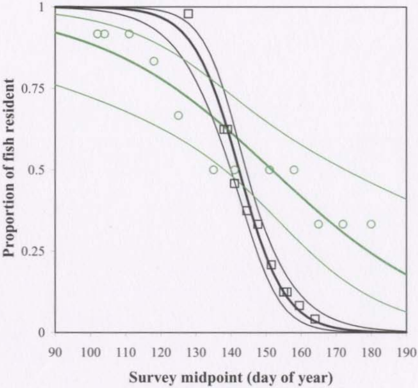
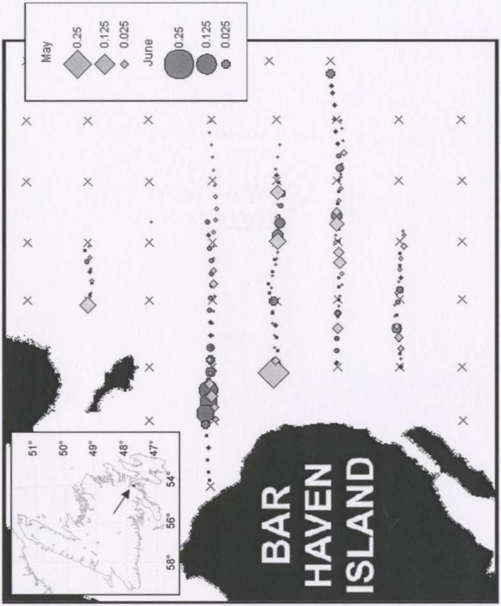


Figure 8-1: The decline in number of Bar Haven residents over time in 1998 (squares, black lines) and 2000 (circles, green lines). For comparison between years, the number of residents is shown as a proportion of the maximum number of residents for that survey year. Fitted curves and 95% confidence bounds are shown as bold and light lines, respectively.

Figure 8-2: The distribution of cod densities (in fish per square metre) on the part of the Bar Haven spawning ground covered during both acoustic surveys (9 May and 7 June 1998). Inset: The island of Newfoundland, with box showing location of the Bar Haven study area.


May
0.25
0.125
0.025
June
0.25
0.125
0.025
BAR
HAVEN
ISLAND
51°
50°
49°
48°
47°
58°
56°
54°

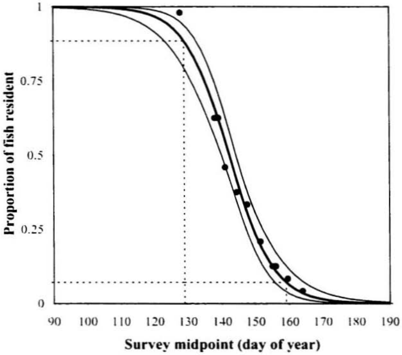


Figure 8-3: The evacuation model for the 1998 telemetric survey on the Bar Haven spawning ground. The vertical axis is the proportion of tagged fish that are resident during each survey. The horizontal axis is the mid-date of each survey. Each point represents one survey of the ground. The bold and thin solid lines are the regression and 95% confidence limits, respectively. The dotted lines show the proportion of tagged fish predicted to be resident during the acoustic surveys of 9 May (day 129) and 7 June (day 159).

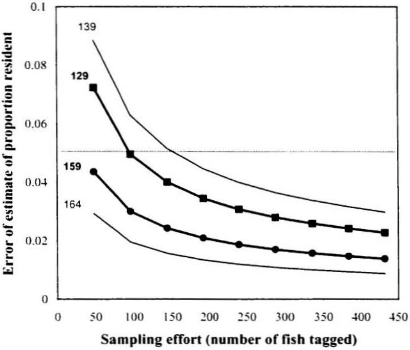


Figure 8-4: The reduction of error with sampling effort for the 1998 Bar Haven evacuation model. Each line shows the model's error behaviour for a given day. Lines in bold (days 129 and 159) correspond to the acoustic survey days. Light lines are examples of other days during the spawning season. Error is calculated as half the difference between the upper and lower confidence limits around model predictions. The horizontal axis shows sampling effort (as the number of fish tagged). The dotted line shows the precision of ± 0.05.

9 The annual distribution and relative abundance of demersal juveniles in a large coastal Atlantic cod fishery in Newfoundland.

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9.1 Abstract

Although knowledge of demersal juvenile cod abundance is likely to be more useful for prediction of year-class strength than that of any previous life-stage, there has been no previous attempt to quantify, or even to describe the distribution or abundance of demersal juvenile cod (*Gadus morhua*) in Placentia Bay, Newfoundland (currently the site of the most active coastal cod fishery in the Northwest Atlantic), part of the most commercially fished cod stock in Newfoundland. In this study, age 0 cod catch was monitored in conjunction with 29 explanatory variables from September to December, 1997-1999 at sites located throughout the bay. Catch was modelled using principal components regression with an error structure following the negative binomial distribution. Although age 0 cod catch was consistently higher at a number of sites in the northern part of the bay, it varied among years and months. Increases in overall catch for any given period were accompanied by an increase in the number of occupied sites. Catch models and presence-absence models that excluded terms for temperature, salinity, and depth had significantly lower maximum likelihood values than models including them. However, eelgrass (*Zostera marina*) cover was not important. Many species loaded heavily on the principal components that were important to catch (and presence-absence) of age 0 cod. Those that loaded positively include rock gunnel (*Pholis gunnellus*), rock crab (*Cancer irroratus*), Atlantic snailfish (*Liparis atlanticus*), thorny skate (*Raja*

radiata), sculpins (*Myoxocephalus octodecemspinosus*, *M. scorpius*, and *M. aenaeus*), age 1 *G. morhua* and smelt (*Osmerus mordax*). Those that loaded negatively were larval capelin (*Mallotus villosus*), hake (*Urophycis tenuis*), cunner (*Tautogolabrus adspersus*), Atlantic salmon (*Salmo salar*), lumpfish (*Cyclopterus lumpus*) and winter flounder (*Pseudopleuronectes americanus*). *Gadus ogac*, age 2+ *G. morhua*, and brook trout (*Salvelinus fontinalis*) showed no heavy loading on any principal component that was important to age 0 cod catch. When only hauls containing cod were examined, no factors explained catch rates. This study demonstrates that age 0 cod surveys, such as those conducted in Europe, can generate ranked year-class predictions, but that more quantitative predictions are complicated by density-dependent site-use. Consistency among sites of ranked catch from year-to-year allows identification of important, temporally stable nursery grounds within the bay. Perhaps the most surprising result of this study is that 29 feasible explanatory variables failed to provide reasonable predictions of catch rates.

9.2 Introduction

For almost a century fishery managers have tried to find relationships between spawner biomass and year-class strength (Ricker, 1954; Beverton and Holt, 1957; Deriso, 1980; Cushing, 1995). However, few attempts have been successful (Cushing, 1995; Myers et al., 1996) due in part to the tremendous variance in recruitment that is observed for most stocks. Many authors believe that recruitment variance is driven largely by the year-to-year variation in pre-recruit mortality rate (e.g., Hjort, 1914; Lasker, 1975; Cushing, 1995), and much effort in the last 100 years has been directed at understanding and predicting this rate.

The focus of many pre-recruit mortality studies has been starvation of exogenously feeding larvae, including classic papers describing the "critical period" (Hjort, 1914), "match-mismatch" (Cushing, 1972) and "stable ocean" (Lasker, 1975) hypotheses. However, evidence for a relationship between prey availability and recruitment has been elusive (May, 1974; Dahlberg, 1979; Leggett and DeBlois, 1994). Many studies have shown that marine fish larvae are infrequently food limited (Cushing, 1983; Sissenwine, 1984; but see Kiørboe et al., 1988; those cited in Bailey and Houde, 1989; Sinclair, 1989), and that prey concentrations at sea are sufficiently high (to allow efficient feeding) as a result of small-scale turbulence (Mackenzie and Leggett, 1991). Other major themes of research are Sinclair's (1989) member-vagrant hypothesis (varying hydrographic conditions could affect the number of individuals that are retained in areas favourable for survival) and the effects of predation on variability in early life history survival (Bailey and Houde, 1989).

One of the reasons a great deal of research has focused on larval mortality rate is that very small year-to-year fluctuations can result in large variations in larval abundance, because initial cohort numbers are so large (Ware, 1975; Houde, 1987). In years of high survival through the larval stage, the density of post-metamorphose individuals could swamp their predators, causing reduced rates of juvenile mortality. Thus, strong recruitment could be directly attributable to survival through the larval stage (Smith, 1985). However, density dependent mortality during the post-metamorphose stage can dampen variations resulting from such larval processes (Bailey and Houde, 1989; Tyler et al., 1997), which can explain why larval abundance tends not to be a good predictor of recruitment (Peterman et al., 1988; Bradford and Cabana, 1997).

Although instantaneous mortality rates are higher in the late-larval than the juvenile stage (Ware, 1975), the duration of the latter stage is often longer (Sissenwine, 1984; Smith, 1985; Bradford and Cabana, 1997). Sissenwine (1984) compared absolute mortality (i.e., rate times duration) for several George's Bank fish stocks and found it to be greater for juvenile than for larval stage fish. Bradford and Cabana (1997) reasoned that the larger the proportion of mortality that has occurred up to a life stage in question, the better that stage will predict recruitment. Bradford (1992) found correlations between recruitment and abundance of earlier life stages (egg or early larvae) were weaker than those for later stages (metamorphosing and later-stage larvae). Knowledge of demersal juvenile abundance is therefore likely to be more useful for prediction of year-class strength of adults than that of any earlier life-stages.

The study of recruitment variability is as alive today as it was 100 years ago. After the closure of the Atlantic cod (*Gadus morhua*) fisheries throughout the Northwest Atlantic in the early 1990's, few stocks have shown signs of biomass increase (Anderson and Rose, 2001), most have not recovered, and many continued to decline during nearly a decade of drastically reduced fishing pressure (Hutchings, 2000). The failure of many stocks to recover has been attributed to poor recruitment (e.g., Lilly et al., 1999; but see Castonguay, 2000; Hunt and Hatt, 2000; Swain and Chouinard, 2000). Furthermore, it has been proposed that recovery of the overfished stocks cannot occur until abiotic and biotic environmental conditions required for successful growth and recruitment have prevailed for several generations (Rose et al., 2000a). However, knowledge of which environmental factors are requirements for successful recruitment is poor, despite many years of study (e.g., Koslow et al., 1987; Cohen et al., 1991; Myers et al., 1993a; Hansen et al., 1994).

The collapse and lack of recovery of offshore cod stocks has resulted in an increase in the relative economic importance of coastal stocks. This has been accompanied by an increase in interest and study of coastal cod (e.g., Smedbol and Wroblewski, 1997; Brattey, 2000; Green and Wroblewski, 2000; Lawson and Rose, 2000a). Although the Department of Fisheries and Oceans in recent years extended their traditional annual research surveys into nearshore areas for the first time, fishers have argued that their coverage is inadequate (Davis et al., 1994). Recruitment estimates from these cruises were likely flawed since the large ocean-going vessels typically must avoid the shoal areas where young cod are likely to be found (Davis et al., 1994; Dalley and Anderson, 1997). For Placentia Bay cod, part of the only actively fished cod stock in Newfoundland, there has never been any attempt to quantify, or even to describe the distribution or abundance of demersal juveniles.

In most parts of the Northwest Atlantic, any monitoring of juvenile cod has been sporadic at best. In one recent attempt, Ings et al. (1997) were marginally successful in predicting year-class strength from Northeast coast demersal juvenile cod catches. These authors showed that recruitment could be more readily predicted using a few consistently positioned monitoring locations rather than with a larger number of hauls that varied in position.

The purpose of the present study was to acquire initial baseline information about juvenile cod distribution and ecology, including the identification of potential nursery sites in the bay. Age 0 cod were sampled at sites throughout Placentia Bay for three consecutive years. The distribution of cod was described for the three years of study, and the relative abundance compared among years and sites. Another objective was to identify physical and biotic factors that may influence the distribution and abundance of cod in the bay, and thus be associated with strong year classes.

9.3 Materials and Methods

9.3.1 The Survey Sites

Several criteria had to be met for a site to be considered part of the survey. Initially, only sites with eelgrass (*Zostera marina*) were considered, given the well published affinity of juvenile cod for that habitat (e.g., Gotceitas et al., 1997). Eelgrass sites throughout the bay were identified through conversation with local people, and by mapping the nearshore bottom from a small craft using a mask and snorkel. Sites had to be free of obstructions so a bottom seine could pass easily over the habitat with the lead-line remaining on the bottom, and without being snagged on rocks. Since bottom topography affects the catchability of the seine, I chose only flat bottomed sites to allow comparison of catch among sites. Sites also had to be distributed throughout the bay, and be accessible by small craft through to the end of December.

In 1997, 18 permanent sites were selected, and in 1998, five more sites (Fig. 9–1, Appendix B–1) were added to the survey. Three of these sites were chosen in a manner similar to that described above, and increased coverage of the bay into the Eastern and Central Channels (areas previously inaccessible because a slower boat was used in 1997). The two other new sites had no eelgrass growing nearshore, and were chosen for comparison to the eelgrass sites. In October 1998 a 24th site was added. All sites were marked with flagging tape to ensure the same swath was sampled on every visit. Detailed notes describing each site were taken in case the flagging tape vanished between sampling periods, and a handheld GPS was used to identify latitude and longitude.

9.3.2 Sampling Protocol

The gear used for the survey was a 25 m bottom seine hauled by two people toward the shore after being deployed from a small boat. The seine is described in detail in Lear et al. (1980), and deployment of the seine is described in Schneider et al. (1997). A standardised area of 880 m^2 was sampled on each haul of the seine (16 m along shore x 55 m offshore) and the net extended up to 2 m off the bottom.

Once a month, a complete survey of all sites was conducted from September to December, 1997-1999 (a total of 12 surveys). To make each survey as synoptic as possible, all sites were sampled in as short a period as possible at the start of every month, in an order that was largely determined by weather. Sampling at any site was not confined to a particular tide level or time of day, although all sampling was done during daylight hours.

At each site, two beach seine hauls were done in immediate succession. The two seine-haul locations were fixed at each site, and approximately 30-100 meters apart. The locations were far enough apart to be treated as independent, but close enough to be similar in depth, eelgrass cover, salinity, and exposure. The occurrence of any snags during all hauls was recorded. The time, depth (except in 1997), temperature, and salinity were also recorded for each haul of the seine, approximately 55 m offshore. Temperature and salinity were measured with a probe at the surface and at approximately 1.5 m depth. Depth in 1998 and 1999 was determined using a weighted line marked at 1 m intervals. Using tide tables (Anonymous, 1996, 1997, 1998), the measured depths were partitioned into a "depth at zero tide" (which was constant for each haul location) and a "tidal height". Tide tables were again used to back-calculate the 'observed' water depth for each set in 1997 using the depth at zero tide for every location.

The standard length and taxon of every fish caught in each set was recorded, and whenever possible, fish were returned alive to the sea. In a number of seine hauls, sticklebacks (*Gasterosteus aculeatus*, *G. wheatlandi*, and *Pungitus pungitus*) and smelt (*Osmerus mordax*) were caught in great numbers, thus sub-sampling was required to ensure maximal survival, and to get home before dark. Sub-sampling was achieved by evenly splitting the catch until about 100 individuals remained. Counts were scaled back up by 2^s, where **s** is the number of splits. Taxa of which less than 5 individuals were caught over the course of the study (including 4-beard rockling, *Enchelyopus cimbrius*, Banded gunnel, *Pholis fasciata*, pollack, *Pollachius virens*, and eelpout, Zoarcidae) were not included in these analyses.

Polymodality in length distributions for each of the 12 bay-wide surveys was used to divide the catch of cod into length classes that corresponded to age groups: age 0 cod were less than 120 mm, with the majority less than 95 mm; age 1 cod were generally between 101 and 215 mm. Cod treated as age 2+ ranged from 199 mm to 480 mm. The Placentia Bay cod caught in the present study were somewhat larger at age than the northeast Newfoundland coast cod studied by Methven and Schneider (1998).

9.3.3 Other Parameters Measured

Three measures of eelgrass cover were recorded for both seining-locations at all 23 sites. Data were collected by filming the substrate along a strip transect which extended perpendicular to shore from the "mid tide mark" out to 55 m (approx. the distance off shore fished by the seine) using a hand-held video camera. The transect consisted of a pair of white ropes, held parallel and 3 ft (0.91 m) apart by metal rods attached every 5 m along the length. The rope was marked every meter with flagging tape, thus the substrate could be divided into 55 bins of 1m by 0.91 m. When viewing the videotape, it was possible to visually estimate the percent of substrate covered by eelgrass within each bin. The three measures of eelgrass cover derived from the videotapes were number of bins containing eelgrass, the mean percent cover (averaged over all bins), and the mean percent cover in non-zero bins.

9.3.4 Statistical Analyses

The counts of age 0 cod used as the dependent variable throughout most of the analyses were not normally distributed (Shapiro Wilk $W = 0.17$; $p < 0.0001$). They followed more closely the negative binomial distribution (Anscombe, 1950) typical of seine data. The distribution was strongly skewed with a modal count of zero, and a few rare large values. Since standard transformation techniques (Sokal and Rohlf, 1995) were not able to normalise the distribution, a method described in Power and Moser (1999), which followed McCullagh and Nelder (1989), was used to model the relations between the number of age 0 cod caught and the explanatory variables of interest. The predicted catch for haul **i** (μ_i), modelled with **p** explanatory variables (including the intercept), was

$$\mu_i = \exp(\eta_i) = \exp\left(\sum_{j=1}^{p} \beta_j X_{ij}\right). \qquad \text{(eq. 9-1)}$$

The negative binomial parameter, **k**, was also allowed to be a function of the explanatory variables as

$$k_i = \sum_{j=1}^{p} \kappa_j X_{ij}\,. \qquad \text{(eq. 9-2)}$$

Using the logarithmic link function, the parameterisation of the negative binomial distribution was:

$$\ell = \sum_{i=1}^{n} \left[\ln\left(\frac{\Gamma(Y_i + k_i)}{\Gamma(k_i)\Gamma(Y_i + 1)} \right) + Y_i \left(\eta_i + \ln\left(\frac{1}{k_i + \exp(\eta_i)} \right) \right) + k_i \ln\left(\frac{k_i}{k_i + \exp(\eta_i)} \right) \right]$$

(eq. 9-3)

(where $\Gamma(\cdot)$ is the gamma function). Through iteration, 2**p** parameters (κ_j, β_j) were estimated to maximise this likelihood. The significance of variables was determined by comparing the likelihood estimate of a model including the variable of interest with that of a reduced model. Since I could find no published formula for the standard error of parameters estimated under a negative binomial error structure (McCullagh and Nelder, 1989; Crawley, 1993; Power and Moser, 1999), standard deviations were determined by bootstrapping.

Ideally, a fully factorial 3-way ANOVA would test for the effects of site, month and year on age 0 catch rate. However, since only two hauls were made at each combination of site-month-year, and the negative binomial linear model estimates two parameters per cell, the model exhausts all degrees of freedom. Since no data was collected in 1997 at the five sites that were added in the second year, four separate ANOVAs were carried out. The effect of SITE was examined for the 18 sites sampled in 1997 in the first ANOVA, and then for the 23 sites sampled in 1998-1999 in the second ANOVA. In the third ANOVA, the effects of YEAR and MONTH were examined for the three years in which 18 sites were sampled. In the fourth ANOVA, these temporal effects were examined for two years in which the remaining five sites were sampled. When YEAR*MONTH interactions were significant, nested effects were examined. Since four tests were performed instead of one, the alpha was adjusted to account for the inflated probability of type I error. Effects were considered significant at $\alpha' = 0.0125$ (i.e., $\alpha' = \alpha/4$). The negative binomial linear model was adapted for categorical variables using indicator variables (Neter et al., 1996) whereby dummy variables were coded 1, except for the first which was coded 0 across all other dummy variables for that effect. Data for the 24th site was not included because it was only sampled in just over half the months of the study.

In order to assess the relative importance of several possible mechanisms influencing catch rates, nine physical variables (day of year, time of day, depth, tidal height, and both temperature and salinity at and 1.5m below the surface) were measured in association with each of 490 beach seine hauls throughout Placentia Bay (no physical data were collected in September 1997). Also, catch rates of 19 other fish taxa and of crabs were recorded (Table 9–1). To use the raw data as predictors would have caused problems because of the high degree of colinearity among the 29 variables (see Tabachnick and Fidell, 2001). Thus, 29 new orthogonal variables (called PC1 through PC29) were created with the scores from a Principal Components Analysis. These principal component scores were used as the predictor variables in models of age 0 cod catch presented below. Because of instrument failure, sudden changes in weather, and sampling errors, data for all 29 variables could not be gathered for every haul. As a result, only 470 of the 526 seine hauls could be included in the PCA.

An "abundance model" was generated using the negative binomial method with the 29 PCs as predictor variables and the number of age 0 cod caught as the response. A "presence model" was generated using a logistic regression

$$p(\mathit{presence}) = 1 - \frac{1}{1 + \exp(\beta_0 - (\sum_{j=1}^{p} \beta_j X_{ij}))} . \qquad \text{(eq. 9-4)}$$

(where β_0 is the intercept) with the 29 PCs as predictor variables and the presence or absence of age 0 cod in a given haul (coded as 1's and 0's) as the ordinal response. A "non-zero model" was generated to determine the factors that affect the quantity of cod caught, when present. The non-zero model included only the 178 seine hauls that contained age 0 cod, and used the 29 PCs as predictor variables, and number of cod as the response. In all cases, variables were removed from the model in increasing order of effect size, until further removal resulted in a model with significantly worse fit (based on the deviation criterion, see Neter et al., 1996).

In addition to the 29 variables measured for each haul, there were three measures of eelgrass cover recorded. These could not be included in the above models because they would artificially deflate the variance since the same number would appear for all the hauls at a given location. As such, the effect of three measures of eelgrass cover on age 0 cod catch were analysed separately using the negative binomial model.

9.4 Results

9.4.1 Age 0 Cod Catch Rates

In 1997, a total of 117 age 0 cod were caught in 144 beach seine hauls at 18 sites. In each of 1998 and 1999, 184 beach seine hauls were made at 23 sites. In total, 1266 and 208 age 0 cod were caught in 1998 and 1999, respectively. The average catch rate of age 0 cod was 0.81, 6.88 and 1.13 fish haul^{-1} in 1997-1999, respectively. Figures 9–2 through 9–4 show the number of age 0 cod caught at each site during the four monthly surveys of the three study years.

Spatial trends in catch of age 0 cod during the first year, and during the last two years were examined with two separate ANOVAs (Tables 9–2a,b). In both tests, the saturated model was rejected in favour of the null model in which the negative binomial parameter was not a function of SITE (1997: Dev = 5.484; df = 17; p = 0.966. 1998-1999: Dev = 21.504; df = 22; p = 0.490). However, there were highly significant differences in catch among sites observed in 1997 (among the 18 sites, Dev = 46.428; df = 17; p < 0.001), as well as in the last two years of the study (among all 23 sites, Dev = 130.964; df = 22; p < 0.001). Mean catches at Bar Haven North were significantly higher than all other sites in 1997, and were second only to Great Brule in 1998-1999 (Table 9-2), a site not sampled in the first year. The sampling sites at King's Island and Ship Harbour were also consistently better for age 0 cod than others examined. Also, catches of age 0 cod were consistently poor at several locations including the sampling sites at Fair Haven, Swift Current and Boat Harbour. There are clear differences among sites that are somewhat consistent among years (Figs. 9-2 to 9-4; Table 9-2).

Temporal trends in catch of age 0 cod were examined separately for the 18 original sites and for those added in the second year (Tables 9–3 and 9–4). In both tests, the saturated model was rejected in favour of the null model in which the negative binomial parameter was not a function of MONTH and YEAR (18 sites: Dev = 9.408; df = 11; p = 0.584, 5 sites: Dev = 8.970; df = 7; p = 0.255). However, in both tests, there was a significant interaction between MONTH and YEAR (18 sites: Dev = 17.818; df = 6; p = 0.007, 5 sites: Dev =15.856; df = 3; p = 0.001), indicating that the pattern of catch among months in one year did not necessarily correspond to that in other years (see Figs. 9–2 through 9–4, Tables 9–3 and 9–4). For the 18 original sites, the effect of MONTH was significant within all years (Table 9-3a). November 1998 was the month with the greatest catch, followed by October, then December. In 1997 and 1999, however, the catches increased continuously from September to December (Table 9–3b). Similarly, the analysis of the five newer sites also showed a strong effect of MONTH within all years (Table 9–4a). At these five newer sites catch rates peaked in November in both 1998 and 1999, but in the former year, October and December catches were substantial, while October catches in the latter year were poor (Table 9–4b).

The mean length of age 0 cod caught in Placentia Bay varied over time within each year (Fig. 9–5). During the early parts of each survey year, average lengths increased with time. However, nearing the end of each year, the larger cod were not caught, and catches became dominated by small (< 45 mm) cod.

The age 0 cod in Placentia Bay appeared to show density-dependent habitat use. As the number of cod caught in a given month increased, so did the number of sites at which cod were present (Fig. 9-6; proportion of sites with cod = -0.031 + 0.13 • ln (abundance); r^2 = 0.95; the intercept was not significantly different from zero (t = -0.77), but the slope was (t = 13.38; $p < 0.0001$)). The asymptotic relationship was linearized by $\log_e$ transforming abundances. The response variable was presented as proportions of the total number of sites examined to account for the increase in number of study sites in 1998.

9.4.2 Potential Correlates of Age 0 Cod Catch

The matrix of partial correlations among the 20 taxa that were caught in association with age 0 cod is shown in Table 9–5. There were complex interconnections between rock gunnel, radiated shanny, cunner, hake, sticklebacks, rock crab, sculpins and winter flounder. There were also less complex correlations of rock gunnel with lumpfish; sticklebacks with skate; age 2 cod with brook trout; winter flounder and rock crab with sand lance; and sculpins with Atlantic snailfish, brook trout and Atlantic salmon. There were no significant associations among capelin, age 1 cod, herrings, *Gadus ogac* or smelt and any other taxa measured. In all, 21 of 190 pairwise comparisons showed significant correlation, only 9.5 of which could be expected by chance at α=0.05.

The matrix of partial correlations among the 9 physical variables is shown in Table 9–6. There were many significant interconnections among the variables. As would be expected, there were significant correlations between the two measures of temperature, between the two measures of salinity, and between depth and tidal height. Also, both measures of temperature were negatively related to Julian day. Salinity at depth was significantly correlated with tidal height, both measures of temperature, and the number of times the net became snagged during a haul. Also, surface salinity was related to tidal height. Only time of day was significantly correlated with no other physical variable measured. In all, 11 of 45 pairwise comparisons showed significant correlation, only 2.25 of which could be expected by chance at α=0.05.

A high degree of colinearity was observed among the 20 biological and 9 physical variables measured, both in the raw data (Table 9–7), and among the principal components scores (not shown). All 29 variables were used in a principal components analysis to generate 29 new variables ("principal components", or "PCs") that were orthogonal, thus not colinear. The strongest-loading variables are shown for each of the 29 PCs in Table 9–8. The 29 PCs were subsequently used as the predictor variables in models of age 0 cod catch presented below.

9.4.3 Modelling Age 0 Cod Catch

For the saturated model 60 parameters were estimated, including a β and κ for each of the 29 variables and an intercept. The negative binomial parameters, κ_j, could not be removed from the model without significantly reducing the fit (Dev = 79.766; df = 29; p < 0.001), indicating that the negative binomial parameter was a function of the explanatory variables. The model was reduced stepwise until further removal of variables resulted in a less parsimonious fit. The final (reduced) model included only 7 of the original 29 variables, and didn't differ significantly from the saturated model (Dev = 14.468, df = 44; p = 1). The variables that remained were PC1, PC3, PC5, PC11, PC14, PC19, and PC27. Any further removal of variables resulted in significant changes in the model's maximum likelihood (Dev = 7.834, df = 2; p = 0.020). The overall fit of the reduced model is poor ($r^2 < 1\%$), however, it does provide information on the relative importance of the physical and biological factors to age 0 cod catch rates. The biological and physical variables that influenced the catch of age 0 cod were determined from the loadings on the PCs that were retained in the reduced model. Coefficients of the reduced model (Table 9–9) and sign of the loadings (Table 9–8) determined the direction of each effect.

Age 0 cod catches were higher in hauls of higher salinity (PC3), lower temperature (or later in the year, PC1) and in deeper water (PC5). In this study, 99.5% of salinities were between 17.07 and 34.62 ppt at depth, and between 0.37 and 33.63 ppt at the surface. For temperatures, 99.5% of observations were between 2.5 and 18.31 °C at depth, and between 0.6 and 19 °C at the surface. In 1998 and 1999, 99.5% of depths were between 0.65 and 12.75 m. Also important to the model was the principal component related to the way salinities differed between the surface versus depth (PC27). There were conflicting results regarding the influence of time of day (PC3, PC5). And there was no effect of snags or tidal height on catch rates.

Many species loaded heavily on the principal components that were important to catch of age 0 cod. Loadings that were consistently positive include rock gunnel (PC3, PC5, PC27), rock crab (PC3, PC11), Atlantic snailfish (PC11, PC14), and skate (PC5, PC11). Other positive associations included sand lance (PC11), sculpins (PC27), age 1 cod (PC5) and smelt (PC5). Loadings that were consistently negative include capelin (PC 11, PC14), hake (PC1, PC11) and cunner (PC1, PC5). Other negative associations included Atlantic salmon (PC3), lumpfish (PC14) and winter flounder (PC27). There were conflicting results regarding the influence of radiated shanny (PC3, PC5, PC27), and herrings (PC

11, PC14) on catch rates. There was no apparent association of age 0 cod with *Gadus ogac*, 2+ cod, or brook trout.

Given the negative binomial abundance model's lack of ability to predict abundance of age 0 cod in a seine haul, the probability of catching cod in a given haul (i.e., the "presence/absence of cod") was subsequently modelled as a function the 29 variables. The saturated model, for which 30 parameters (one per explanatory variable, plus an intercept) were estimated, explained almost 20% of the variance in the presence/absence of age 0 cod. The model was reduced stepwise until further removals resulted in significantly different likelihood estimates. The final (reduced) model included only 9 of the original 29 variables, and didn't differ significantly from the saturated model (Dev = 19.541; df = 20; $p \approx 0.5$). The variables that remained were PC1, PC2, PC3, PC5, PC8, PC23, PC24, PC28, and PC29. Any further removal of variables resulted in significant changes in the model's maximum likelihood (Dev = 4.040, df = 1; $p < 0.05$). Although the fit of the reduced presence-model was low ($r^2 = 16.3\%$), it was a considerable improvement over the abundance-model described above. Despite the poor fit, the model can nonetheless assess the relative importance of the various physical and biological factors to the presence or absence of cod. Again, the variables that influenced the model were determined from the loadings (Table 9–8) on the PCs that were retained in the reduced model. Coefficients of the reduced model (Table 9–10) and sign of the loadings determined the direction of each effect.

Cod were more likely to be present in hauls of lower temperature (or later in the year, PC1), higher salinity (PC2, PC3, PC8, PC24), and in deeper water (PC2, PC5). There was also an influence of PCs related to how the temperature differed between the surface versus depth (PC29), how temperatures differed from the negative relationship with date

(PC28), and how depth deviated from its relation with tidal height (PC23). There was a small negative association with tidal height as well. There were conflicting results regarding the influence of time of day (PC3, PC5, PC8, PC23), snags (PC8, PC23).

Many species loaded heavily on the principal components that were important to catch of age 0 cod. Loadings that were consistently negative include Atlantic salmon (PC2, PC3, PC24) and hake (PC1, PC24). Other negative associations included sand lance (PC8) lumpfish (PC8) and winter flounder (PC2). There were conflicting results regarding the influence of most other taxa caught. There was no apparent association of age 0 cod with *Gadus ogac*, 2+ cod, brook trout, capelin, herrings or Atlantic snailfish.

The distribution of age 0 cod catch, when present (i.e., only the seine hauls in which cod catch was non-zero) was also highly skewed. The distribution was non-normal (Shapiro Wilk $W = 0.28$; $p < 0.0001$), had a mode of 1, and could not be normalised with any standard transformations. The negative binomial linear model could not be fitted for the non-zero model, since only 178 seine hauls included age 0 cod, and there would only be about three observations per parameter to be estimated. However, a standard linear regression model yielded no significant coefficients ($r^2 = 0.052$, Adjusted $r^2 < 0$).

There was no detectable effect of eelgrass cover on catch of age 0 cod. To avoid problems associated with colinearity among the three variables, the scores of three principal components were used as explanatory variables in the negative binomial model. The negative binomial parameter was not a function of the eelgrass cover (Dev = 5.234; df = 3; $p = 0.156$), and none of the three PCs explained a significant amount of variance in the mean catch of age 0 cod (Dev = 6.228; df = 3; $p = 0.101$).

9.5 Discussion:

9.5.1 Temporal and Spatial Distribution of Catches

The catch rates of age 0 cod were poor in 1997 and 1999 (0.81 and 1.13 fish per haul). Only in 1998, when the overall catch was five times greater than in either other year, did catch rates (6.88 fish per haul) resemble those reported from other Newfoundland bays. Average late September to late October catch rates for Northeast Newfoundland bays during recent years (1992-1995) ranged from 1.8 fish per haul in St. Mary's Bay to 45 fish per seine in Bonavista Bay (Smedbol et al., 1998). Concurrent to this study (1997), a survey of Northeast Newfoundland Bays showed mean catch rates ranging from 1.7 fish per haul in Conception Bay to 75.5 fish per haul in Trinity Bay, and in St. Mary's Bay, the only other South Coast bay surveyed, catch rates were 4.4 cod per seine (Methven et al., 1998). For fair comparison between this and the surveys of the other Newfoundland bays, one might consider only the September and October catches, however, this would result in even lower catch rates for Placentia Bay, since September was poor relative to other months, and November was consistently the peak month for age 0 cod catches. Methven and Bajdik (1994) found the peak period of juvenile cod in Trinity bay to be somewhat earlier than that for Placentia Bay (August-November).

The strong interaction between month and year indicated that the pattern of catch among months in one year did not necessarily correspond to that in other years (see Figs 9–2 to 9–4). In all years, November was the month of greatest catch rates. However, depending on the year, October or December was second best. In all years, September catch rates were lowest. The catch during a given month varied among years for September and October due to considerably higher catches in 1998 relative to 1997. However, December catch rates were similar among all years, and those for November were different at the 18 original sites but not significantly different at the $\alpha'=0.0125$ level at the five newly added sites.

The mean length of age 0 cod caught in Placentia Bay varied over time within each year (Fig. 9–5). Earlier in the season average lengths were approximately 36 mm - 85 mm. By November, larger fish (66 mm – 95 mm) were caught, possibly representing growth of the cohort that was present in prior months. Nearing the end of each year, the larger cod disappeared, and catches became dominated by small (< 45 mm) cod, which certainly were the result of later spawning events, and were possibly not fully settled at the time of capture. The fate of the disappearing larger fish is not known. It is possible that they moved into deeper water as surface temperatures declined later in the year. There is evidence that smaller cod, which produce antifreeze glycoproteins, are more likely to move into colder areas (Goddard et al., 1997).

The spatial and temporal trends in the catch of age 0 cod could not be examined using a fully-factorial three-way ANOVA on SITE, MONTH and YEAR because only two hauls were done at each combination of these. Under a standard linear model, two observations per cell would be enough, however, since the negative binomial model estimates twice as many parameters as the standard linear model, the degrees of freedom become exhausted at less than three observations per cell. The analysis was further complicated by the addition of five sites in the second year of the study, creating a large number of empty cells in 1997. However, it is interesting to note that a standard (i.e., normal error distribution) 3-way ANOVA on the data from the latter two years in which all sites were sampled (2 years * 4 months * 23 sites) showed no significant second order interaction ($F_{66,184} = 0.71$; $p= 0.95$). The problem of empty cells was avoided by evaluating the effect of site with two separate ANOVAs (one with a single year of data at 18 sites, and another with two years of data at 23 sites) and the effect of YEAR and MONTH with another pair of ANOVAs (one with three years of data at 18 sites, and another with two years of data at five sites). Since this technique inflated the probability of type I error, the alpha was adjusted to account for the number of tests performed ($\alpha' = \alpha/4 = 0.0125$). An advantage of this technique is that the data was split into different sections, thus the model made with one section of the data could be tested against those in the other section. For example, the mean predicted catch for the 18 sites during 1997 was significantly correlated with that at the same sites during 1998-1999 ($r_s = 0.53$; $p < 0.05$), and 10 out of 18 sites were within two ranks of the predicted value. This confirms that sites were of consistent quality, and relative catch rates could be forecasted from these models.

The sites in the northern part of the bay generally yielded larger catches of age 0 cod than those in other parts of the bay. This could be the result of local spawning in the northern part of the bay (which was observed in every year considered here, L. Mello and G. Rose, unpublished data, Lawson and Rose, 2000b) if it is assumed that there is a mechanism for the retention of eggs and larvae in the spawning vicinity. Local retention is likely in the Bar Haven area. Drifters released at Bar Haven during the 1997 spawning season were most often recovered among the islands in the northern part of the bay, and along the west coast of Merasheen Island (Bradbury et al., 2000), matching the distribution of age 0 juveniles described in this study. Retention of eggs and larvae in the northern part of the bay is consistent with the variable and relatively weak currents (Schillinger et al., 2000), complex bottom topography (as per Mullineaux and Mills, 1997), and presence of many small islands, particularly on the western side of the bay.

The two sites with gravel substrate were not among the lowest in terms of age 0 catch rates. In fact, catch rates were significantly higher at these two sites than at 13 of the 21 eelgrass sites. However, catches at these two sites were restricted to November and December, when small, possibly pelagic cod were caught at large number of sites around the bay. The cod caught at these sites were not necessarily associated with the substrate. In fact, when the seine was pulled, they could have been passing through the area, looking for substrate appropriate for settlement. However, it should be noted that there are clearly factors other than eelgrass that influence the distribution of age 0 cod, and many of the sites with the densest eelgrass cover yielded near zero catch rates.

The age 0 cod in Placentia Bay appeared to show density-dependent habitat use. As the number of cod caught in a given month increased, so did the number of sites at which cod were present (Fig. 9–6). The asymptotic relationship indicated that the proportion of sites used by cod increased much less rapidly than abundance, and that some sites would only be used at extremely high abundances. Since there is autocorrelation in the relationship (presence of cod, Y, is a function of the number of cod, X), the exact p values of this relationship should be interpreted with caution. However, it is clear that the autocorrelation would be zero under the scenario of increasing abundance without an increase in number of occupied sites (all additional cod go to sites already occupied). Thus, with increasing degrees of density-dependent range fluctuation, there must be increasing autocorrelation. As such, the degree of autocorrelation is the test of interest, not an artefact of it. For Placentia Bay cod, the relationship was very strong, showing clear density dependent habitat use. At low numbers, only a few sites were occupied, but as the number of individuals increased, there was spillover into other sites. Schneider et al. (1997) did not find evidence for density-dependent range fluctuation for age 0 cod along the Northeast coast of Newfoundland. However, the geographic scale of the study was large relative to this one. There could have been supply differences among different parts of the northeast coast that could have clouded the results. Although the same possibility is true for Placentia Bay, it is less likely. Presumably, the sites occupied under low abundances are of superior quality, and that the spillover at larger numbers is into suboptimal habitats (MacCall, 1990). If this were the case, then sites at which cod were present when abundances were low could be identified as prime candidates for protective measures, especially during periods when recruitment is likely to be poor. However, given density dependent spillover, protection of those habitats will be less effective at larger abundances, and protection of additional sites may be desirable. It should be noted that the patterns observed here are not necessarily the result of redistribution of individuals. The same pattern could result from differential settlement and predation processes among sites. When predation is high, for example, cod could be eradicated from lower quality sites. Whereas, when predation is low, a greater abundance of cod may survive, even at poorer quality sites. Geographic contraction means that sampling a single site cannot provide complete information about the relative abundance for comparison among years. For example, many sites showed an increase in catch rate in 1998, however they did not show the five-fold increase that was characteristic of the overall catch rate for that year. Given that sites of highest catch rates were consistent among years, it appears that range contracted consistently towards the same sites in both 1997 and 1999. One of the goals of this study was to test whether the level of quality that appears to be associated with these "preferred" sites is a function of the suite of physical and biological variables discussed below.

9.5.2 Correlates of Catch Rates

The principal components on which temperature, salinity and depth loaded heavily could not be removed from the abundance-model or presence-model without significant change in the likelihood estimates. Physiological temperature and salinity tolerances likely limit the distribution or abundance of most species. Upper and lower temperature boundaries for survival, and dome-shaped survivorship and growth curves have been shown for many fish species (Fry, 1971; Brett, 1979), thus it is reasonable to assume that catch would not be a linear function of these variables. Typically, if a response is assumed to be a quadratic function of a certain variable, the model should include both the variable and its square. However, inclusion of squared terms in the principal components regression would make the output even more difficult to interpret than usual. And given that the actual explanatory power of the model is so slight (and would likely not be greatly improved by adding squared terms), conclusions are limited to a statement about the relative importance of temperature and salinity to age 0 cod; I draw no conclusions about the form of the relationships.

The range of temperatures and salinities observed in Placentia Bay between 1997-1999 were similar to those observed in Trinity Bay between 1982 and 1990 (Methven and Bajdik, 1994). Methven and Bajdik observed no relationship between temperature on catch of age 0 cod over the range –1 °C to 17 °C. In this study, temperatures below the surface ranged from 2 °C to 18.5 °C. Rose and Leggett (1988) did not observe adult cod outside of the range –0.5 °C to 8 °C, and other authors found the range to be even smaller (e.g., Jean, 1964; Scott, 1982). In this study no age 0 cod were caught in waters greater than 15.5 °C, and no large catches were made beyond 10 °C. The salinities over which Methven and Bajdik (1994) found no relationship with age 0 cod catch was 22 ppt – 32 ppt. In this study, cod were caught throughout the range of observed salinities (16 ppt - 36 ppt), but no large catches were made at salinities below 23 ppt. This and the study of Methven and Bajdik (1994) conflict with respect to the importance of temperature and salinity to age 0 cod catch. This difference could be the result of testing a great number of variables simultaneously (this study) versus testing the effects of each variable in separate tests as the lone predictor (Methven and Bajdik, 1994). For example, if temperature is driven by another, external variable, and that variable does not influence cod catches, then in a single-variable test, temperature will appear unimportant. However, if within each level of the external variable, temperature plays a significant role, then both variables would be needed in the model simultaneously to observe the effect of temperature. If the graphical method used by Methven and Bajdik (1994) had been applied to the present data, a conclusion similar to theirs would have been drawn. However, both salinity and temperature were important to the fit of the multiple regression model used here.

In this study, age 0 cod catch was found to be greater at deeper sites, when all else was equal. Again, this is in conflict with previous reports. Linehan et al. (2001) tethered age 0 *Gadus* sp. in Bonavista Bay, and found a significant positive relationship between predation rate and depth. Thus, within a substrate type (regardless of which one) cod were found to have higher survivorship at shallower locations. While fish in deeper areas may be subject to greater risk of predation by aquatic predators, individuals in shallower regions can be more susceptible to avian predation (Dickman, 1995). The relative rates of avian and fish predation in Placentia and Bonavista Bays are not known, but could explain some of the differences observed between this and the study of Linehan et al. (2001).

In the literature, there is conflicting evidence about several aspects of juvenile cod ecology. For example, in Nova Scotia (Tupper and Boutilier, 1995), age 0 cod were reported to be highly territorial, yet marking studies in Bonavista Bay (Hancock, 2000) and in Trinity Bay (Grant and Brown, pers. comm.; Robichaud and Rose, unpublished data) showed that few cod could be recaptured in the same place over time. In addition, age 0 cod were preferentially found in cobble habitat in shallow and deep waters of Nova

Scotia (Lough et al., 1989; Tupper and Boutilier, 1995) and in Newfoundland lab studies (Gotceitas and Brown, 1993; Gotceitas et al., 1995). However, a seining and diving study in Bonavista Bay (Gotceitas et al., 1997) showed that few *in situ* age 0 cod could be found away from eelgrass habitats. Furthermore, juvenile cod were found to spend nights near the bottom in both Placentia (Lawson and Rose, 1999) and in Trinity Bays (Grant and Brown, 1999), but were found to spend nights in the water column in Bonavista Bay (Laurel and Gregory, unpublished data). Thus it is feasible that preferences for salinity, temperature or depth vary among sampling locations, and may be a function of the predator field, food availability, and/or water conditions in the areas of study.

Eelgrass cover was not an important predictor of cod catch rates in this study. There were a large number of cod caught at the two non-gravel sites. Sites of greatest eelgrass density were among the best for cod (Bar Haven north) and among the worst (Swift Current). Gorman (2002) found that intermediate-sized eelgrass patches were best for age 0 *Gadus* sp., since they afforded more protection than smaller patches, but contained fewer predators than large patches. Furthermore, Gotceitas et al. (1997) found that cod in Bonavista Bay were distributed almost entirely in eelgrass habitats, yet cod collected from these same locations showed significant preference for cobble over eelgrass habitats in the lab. Only under the threat of predation and only at certain eelgrass densities could cod in the lab be coaxed into eelgrass habitats (Gotceitas et al., 1995). In Nova Scotian waters, age 0 cod preferred cobble more than other substrates in both shallow-water (Tupper and Boutilier, 1995) and in offshore-bank environments (Lough et al., 1989). It is possible that differences in predation risk, in conjunction with (or perhaps resulting from) differing age 0 densities among the regions, generated the differences in eelgrass preference observed among these various studies.

The results of the abundance model and presence model were quite similar. Given that catches were overwhelmingly zero, and that larger values were increasingly rare, 77% of the catch data were either zeros or ones. This means that the two models could vary by a maximum of 23%. In addition, the abundance model did not fit the data very closely, largely because it failed to predict the magnitude of the very large catches. Thus, the abundance model resembles the presence-absence model even more closely than 77%. Given that the non-zero model showed no important effects, it can be concluded that factors which were significant in the abundance model were important mostly as a result of their influence on the presence or absence of cod.

An interesting result is the positive association of age 0 cod with the predatory sculpins and age 1 cod. The result suggests that predation pressure from these groups is not very strong. However, older *Gadus* sp. (*G. ogac* and *G. morhua*) were the most frequent predator of tethered age 0 in Bonavista Bay (R. Gregory, pers. comm.). Furthermore, cannibalism of age 0 by older cod has been reported in holding tanks (Otteraa and Lie, 1990) and in the wild by (Bjoernstad et al., 1999; Grant and Brown, 1999). Other biotic associations include a consistent negative association with cunner, which Linehan et al. (2001) found to be minor predators of tethered cod.

The negative association with capelin is of interest. It should be noted that the capelin caught in this study were small, almost entirely 40-50 mm in length. They were not the sort of capelin traditionally associated with cod-diets. Furthermore, it should be noted that age 0 cod feed mostly on copepods and a few benthic items, and do not switch to fish until they have reached a larger size (Grant and Brown, 1999).

Gadus ogac, which are widely distributed in the eelgrass habitat of age 0 cod, are commonly mistaken for *G. morhua* at small sizes. As they are congeners, they have been pooled in several studies (e.g., Linehan et al., 2001), since they are assumed to share diet, predators, habitat and behaviours with *G. morhua*. The lack of association between *G. ogac* and *G. morhua* observed in this study may reveal differences in the ecology and distribution of these species. Here, *G. ogac* tended to be more widely distributed, in greater numbers, and of greater size than *G. morhua*.

A key result of this study is that none of the factors studied provided any power to predict catch rates and juvenile cod densities. Yet it is likely that something determines density, because in the three years studied, distributions were not random, but systematic with respect to various sites. One possible factor that was not measured was distance downstream of a spawning ground. Differences in supply could be an overriding factor determining the distribution of these fish. However, this assumes that larval and post-metamorphose-pre-settlement cod cannot greatly influence their distribution, which may not be true (Campana et al., 1989). Another possible factor is food supply. However, marine fish larvae are infrequently food limited (Cushing, 1983; Sissenwine, 1984; those cited in Bailey and Houde, 1989; Sinclair, 1989) and Grant and Brown (1999) found that demersal juvenile cod feed on similar items. Still other factors include site-exposure (or frequency of storms), abundance of avian predators, eelgrass patchiness (Gorman, 2002) or fractal dimension of eelgrass beds (Wells, 2002).

9.5.3 Statistical Models

Catch data is most likely to be distributed as a negative binomial. Zero catches are most common, the frequency of larger values decreases monotonically, and only integer observations are possible. Transformations can reduce the length of the tail of the distribution, but they cannot normalise this type of data because there will always be a large frequency of one single value, and a monotonic decrease in frequency in only one direction. Assuming a normally distributed error structure when modelling catch data can thus lead to problems interpreting coefficients and probability values. As an alternative, catch data is frequently modelled as a Poisson distribution (because it is included in several statistic packages). Although Poisson is a special case of the negative binomial distribution (when k approaches infinity) real data rarely follow Poisson exactly. An advantage of the negative binomial model is that k is an estimated parameter. Assuming k is infinity (without testing it) is analogous to assuming a normal distribution of error without confirmation.

A disadvantage of the negative binomial model is that a large number of parameters must be estimated to fit the data. As a result, degrees of freedom are lost from the error term, reducing the power of the test. Further, a larger minimum number of observations are required per cell, which can be problematic for complex, multi-factorial analyses of variance. The iterative approach to parameter estimation can be sensitive to initial values and may converge on a local maximum likelihood, rather than the global maximum.

Using principal component regression effectively removed the colinearity among the 29 variables of interest. However, it made interpretation of the model results more difficult. For example, the suite of PCs that remained in the reduced model were both negatively and positively associated with a number of the original 29 variables. Another disadvantage of the principal components regression is that all 29 variables will be required to calculate the scores of the 29 PCs in order to use of the model to forecast catch. Moreover, the model will suffer from the error associated with the measurement of each of the 29 original variables. Thus parsimony is not really the goal of model reduction in the case of the principal components regression. Rather, the model is reduced to a subset of the original set of PCs in order to identify the relative importance of the original explanatory variables, for example, as a starting point for future study.

9.5.4 Age 0 Cod as Management Tool

The rank of the sites from greatest to lowest age 0 catch rate remained fairly consistent among years. For example, catches at Great Brule and Bar Haven North were consistently greater than any others in the bay. This inter-year consistency of ranked catches (and possibly of quality) among sites allows identification of important, temporally stable nursery grounds within the bay. Decisions about nursery ground protection could therefore be made without much study beyond that reported here. However, if abundance of demersal juveniles increases, there will be a concomitant decline in the relative importance of these sites. Cod will expand their distribution into a greater number of sites, each of which increases in relative importance. If a management goal were to ensure a constant proportion of fish being protected, a greater number of sites would need to be protected at higher abundances.

The tight relationship between abundance and the proportion of sites occupied by cod throughout the bay has interesting implications for management. On one hand, it implies that managers might simply measure the presence or absence of cod at a series of sites, rather than spending time counting fish. On the other hand, the expansion of distribution with increased abundance will make it difficult to make year-class predictions beyond the assessment of rank. From this study, it is possible to make the prediction that the year class strengths will be 1997 < 1999 << 1998. The 1999 year class will be marginally stronger than that in 1997, and both will be a great deal weaker than that of 1998. It is not possible to confidently predict that the 1998 year class will be five times stronger than those of 1997 and 1999, because one does not have absolute knowledge of every site in the bay. It is not possible to assess the rate at which the sites studied here increase in catch with increased abundance over the whole bay (i.e., everywhere, including unsampled locations).

Perhaps the most surprising result of this study is that predictive power for catch rates was so low. That the catch rate, ranked among sites, was consistent among years, indicated that something influences distribution. However, no factor studied here was capable of forecasting catch with any precision. All factors examined had potential influence, and despite some proving to be important, none had predictive power. It is apparent that no simple surrogate for age 0 cod can be used by fishery managers to forecast year-class strength.

9.6 Acknowledgements

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Table 9-1: Method of measurement for each parameter included in the age 0 cod catch models. Cod, *Gadus morhua* , were divided into length classes that corresponded to size differences. Age 0 cod ranged between 15 and 122 mm.

parameter name	measurement
Atlantic snailfish	count of *Liparis atlanticus*
Capelin	count of *Mallotus villosus* (majority were juvenile, approx 45 mm)
Cod age 1	count of *Gadus morhua* , between 101 and 215 mm
Cod age 2+	count of *Gadus morhua* , between 199 and 480 mm
Rock crab	count of *Cancer irroratus*
Cunner	count of *Tautogolabrus adspersus*
Rock gunnel	count of *Pholis gunnellus*
Hake	count of *Urophycis tenuis*
Herrings	count of *Clupea harengus* , includes some *Alosa sapidissima*
Lumpfish	count of *Cyclopterus lumpus*
Gadus ogac	count of *Gadus ogac* (majority were < 110 mm)
Radiated shanny	count of *Ulvaria subbifurcata*
Atlantic salmon	count of *Salmo salar* (majority had parr marks)
Brook trout	count of *Salvenilus fontinalis* (all had parr marks)
Sand lance	count of *Ammodytes americanus*
Sculpins	count of *Myoxocephalus octodecemspinosus* , *M. Scorpius* , *M. aenaeus*
Skate	count of *Raja radiata*
Smelt	count of *Osmerus mordax*
Sticklebacks	count of *Gasterosteus aculeatus* , *G. wheatlandi* , *Pungitus pungitus*
Winter flounder	count of *Pseudopleuronectes americanus*
julien day	days from Jan 1
time of day	minutes from midnight
depth (m)	distance of bottom (m) from surface at 55 m from shore
tidal height (m)	observed depth minus the depth-at-no-tide for site
T surf (°C)	°C within 10 cm of surface
S surface (ppt)	ppt within 10 cm of surface
T depth (°C)	°C at about 1.5 m from surface
S depth (ppt)	ppt at about 1.5 m from surface
number of snags	small snags remedied by jiggling the net =1 larger snags that required removing the lead-line from the bottom =2

Table 9-2a: Parameter Estimates for effect of SITE on age 0 cod catch in 144 beach seine hauls at 18 locations in 1997. Means and standard deviations are from 550 bootstraps of the reduced model.

Parameter	Parameter mean	Parameter Std Dev	catch mean	catch Lower CL	catch Upper CL
k	0.4374	0.1403			
intercept (Baine Hr.)	-24.6390	2.2785	0.0	0.0	0.0
Bar Haven North	26.1643	2.6137	4.6	2.1	10.2
Bar Haven South	24.1507	3.8953	0.6	0.2	1.7
Boat Hr.	-18.6920	0.0000	0.0	0.0	0.0
Clattice Hr.	15.9047	9.0714	0.0	0.0	0.0
Fair Haven	-18.6920	0.0000	0.0	0.0	0.0
Fox Hr.	16.8195	9.3200	0.0	0.0	0.0
King's Is.	24.8964	3.7516	1.3	0.5	3.5
Little Bay	15.8077	9.0660	0.0	0.0	0.0
North Hr.	15.9314	3.6700	0.0	0.0	0.0
North-East Arm	23.2513	9.3161	0.2	0.0	1.7
Sandy Hr.	21.6165	6.5212	0.0	0.0	0.2
Ship Hr.	24.9704	8.7548	1.4	0.2	8.4
South-East Arm	16.4791	3.7150	0.0	0.0	0.0
Southern Hr.	-18.6920	0.0000	0.0	0.0	0.0
Spanish Room	16.7661	8.7825	0.0	0.0	0.0
Swift Current	-18.6920	0.0000	0.0	0.0	0.0
Woody Is.	23.7755	2.9424	0.4	0.2	1.0

Table 9-2b: Parameter Estimates for effect of SITE on age 0 cod catch in 368 beach seine hauls at 23 locations between 1998-1999. Means and standard deviations are from 500 bootstraps of the reduced model.

Parameter	Parameter mean	Parameter Std Dev	catch mean	catch Lower CL	catch Upper CL
k	0.3033	0.0344			
intercept (Baine Hr.)	-0.8100	1.3255	0.4	0.4	0.5
Bar Haven gravel site	2.2344	1.4596	4.2	3.1	5.5
Bar Haven North	3.1465	1.3908	10.3	7.8	13.7
Bar Haven South	1.5684	1.4729	2.1	1.6	2.8
Boat Hr.	-0.6920	3.9020	0.2	0.1	0.4
Clattice Hr.	2.2085	1.6176	4.0	3.0	5.5
Fair Haven	-21.8200	1.3681	0.0	0.0	0.0
Fox Hr.	-3.5657	1.5459	0.0	0.0	0.0
Great Brule	4.0448	1.7703	25.4	18.5	34.9
Hr. Buffett	1.8879	5.9494	2.9	1.4	6.2
King's Is.	2.3745	1.4508	4.8	3.6	6.3
Kingwell	2.1764	1.3436	3.9	3.0	5.2
Little Bay	-0.3926	2.5085	0.3	0.2	0.4
North Hr.	-0.3255	2.2513	0.3	0.2	0.5
North-East Arm	-0.2596	3.5489	0.3	0.2	0.6
Sandy Hr.	0.9599	1.7960	1.2	0.8	1.6
Ship Hr.	0.8938	1.3650	1.1	0.8	1.4
Ship Is. gravel site	2.1018	1.4244	3.6	2.7	4.8
South-East Arm	0.1503	1.4107	0.5	0.4	0.7
Southern Hr.	2.1810	1.3783	3.9	3.0	5.2
Spanish Room	2.0528	1.3953	3.5	2.6	4.6
Swift Current	-6.8952	8.4284	0.0	0.0	0.0
Woody Is.	-0.1645	3.0445	0.4	0.2	0.6

Table 9-3a: The effect of MONTH nested within YEAR on catch of age 0 cod catch in 144 beach seine hauls per year at 18 locations, 1997-1999. The "Saturated model" includes 4 κ and 4 β parameters (1 intercept and 3 month parameters). The "Unique k" model tests whether the negative binomial parameter is a function of MONTH. The effect of MONTH is tested by comparing model including terms versus a more reduced model.

Effect tests	Model	Likelihood	Compare	Deviance	df	chi sq P
1997						
Saturated Model	κ_j, β_m	-120.836				
Unique k	k, β_m	-121.979	κ_j, β_m	2.286	3	0.512
MONTH in 1997	k, β	-132.923	k, β_m	21.888	3	0.000
1998						
Saturated Model	κ_j, β_m	-270.487				
Unique k	k, β_m	-271.586	κ_j, β_m	2.198	3	0.532
MONTH in 1998	k, β	-283.002	k, β_m	22.832	3	0.000
1999						
Saturated Model	κ_j, β_m	-129.870				
Unique k	k, β_m	-130.667	κ_j, β_m	1.594	3	0.661
MONTH in 1999	k, β	-146.247	k, β_m	31.160	3	0.000

Table 9-3b: Parameter estimates for the effect of MONTH nested within YEAR on catch of age 0 cod catch in 144 beach seine hauls at 18 locations, 1997-1999. Means and standard deviations are from 1000 bootstraps of the reduced model.

Parameter	Parameter mean	Parameter Std Dev	catch mean
1997			
k	0.1726	0.0485	
β dec (int)	0.5185	0.3577	1.7
β nov	-0.6564	0.7105	0.9
β oct	-1.3990	0.6495	0.4
β sep	-23.5964	0.0937	0.0
1998			
k	0.3038	0.0697	
β dec (int)	1.1442	0.2877	3.1
β nov	0.5363	0.4560	5.4
β oct	0.1889	0.8180	3.8
β sep	-2.2335	0.5360	0.3
1999			
k	0.2643	0.0643	
β dec (int)	0.6446	0.3152	1.9
β nov	-0.4530	0.5387	1.2
β oct	-3.5534	3.9073	0.1
β sep	-10.4172	9.2971	0.0

Table 9-4a: The effect of MONTH nested within YEAR on catch of age 0 cod catch in 40 beach seine hauls per year at 5 locations, 1998-1999. The "Saturated model" includes 4 κ and 4 β parameters (1 intercept and 3 month parameters). The "Unique k" model tests whether the negative binomial parameter is a function of MONTH. The effect of MONTH is tested by comparing model including terms versus a more

Effect tests	Model	Likelihood	Compare	Deviance	df	chi sq P
1998						
Saturated Model	κ_j, β_m	-121.878				
Unique k	k, β_m	-125.792	κ_j, β_m	7.828	3	0.050
MONTH in 1998	k, β	-135.042	κ_j, β_m	26.328	6	<0.001
1999						
Saturated Model	κ_j, β_m	-47.272				
Unique k	k, β_m	-47.557	κ_j, β_m	0.569	3	0.904
MONTH in 1999	k, β	-56.662	k, β_m	18.210	3	0.000

Table 9-4b: Parameter estimates for the effect of MONTH nested within YEAR on catch of age 0 cod catch in 40 beach seine hauls at 5 locations, 1998-1999. Means and standard deviations are from 1000 bootstraps of the reduced model.

Parameter	Parameter mean	Parameter Std Dev	catch mean
1998			
κ dec (int)	4.834773	66.1992	
κ nov	8.509657	215.3352	
κ oct	20.10582	201.4532	
κ sep	133.4612	393.9908	
β dec (int)	1.684958	0.3983	5.4
β nov	1.716509	0.7297	30.0
β oct	1.10544	1.4395	16.3
β sep	-1.589196	0.5885	1.1
1999			
κ	26.21144	162.0509	
β dec (int)	0.7869441	1.0240	2.2
β nov	0.6151535	1.3266	4.1
β oct	-9.13481	9.3323	0.0
β sep	-26.9081	0.0081	0.0

Table 9-5: Partial correlations among the 20 taxa caught along with age 0 cod in 490 beach seine hauls between 1997-1999. Values below the diagonal are correlation coefficients partialed with respect to all other variables. Values above the diagonal are probabilities for the corresponding correlations.

Variable	Atlantic snailfish	capelin	cod age 1	cod age 2+	rock crab	cunner	rock gunnel	hake
Atlantic snailfish	•	ns	ns	ns	ns	ns	ns	ns
capelin	-0.01	•	ns	ns	ns	ns	ns	ns
cod age 1	-0.01	-0.01	•	ns	ns	ns	ns	ns
cod age 2+	-0.01	-0.02	0.05	•	ns	ns	ns	ns
rock crab	-0.02	-0.03	-0.01	0.02	•	< 0.001	< 0.001	ns
cunner	-0.01	-0.02	-0.04	-0.02	0.33	•	ns	< 0.001
rock gunnel	0.00	0.03	0.05	-0.05	0.26	0.01	•	ns
hake	0.00	-0.02	-0.02	-0.01	-0.09	0.21	0.03	•
herrings	0.00	-0.01	-0.01	-0.01	-0.01	0.01	-0.01	0.00
lumpfish	-0.02	-0.02	-0.04	0.01	-0.03	-0.05	0.15	-0.05
Gadus ogac	-0.01	-0.02	0.03	0.04	-0.02	-0.01	0.01	0.02
radiated shanny	-0.07	-0.01	-0.03	0.01	0.01	-0.05	0.34	0.20
Atlantic salmon	-0.05	-0.01	-0.02	-0.03	-0.02	-0.02	-0.05	-0.07
brook trout	-0.05	-0.01	-0.01	0.14	0.06	-0.04	-0.05	-0.02
sand lance	0.01	-0.01	-0.01	-0.01	0.19	-0.08	-0.08	-0.03
sculpins	0.20	-0.02	0.02	-0.03	0.06	-0.01	-0.05	-0.05
skate	-0.01	-0.01	0.09	-0.03	-0.03	0.04	-0.05	-0.04
smelt	-0.01	-0.03	0.03	-0.03	-0.04	-0.04	0.06	0.04
sticklebacks	-0.01	-0.04	-0.03	0.03	0.00	-0.02	0.16	0.11
winter flounder	-0.06	-0.01	0.05	0.02	0.16	-0.03	0.04	0.38

con't...

Table 9-5 con't.

Variable	herrings	lumpfish	*Gadus ogac*	radiated shanny	Atlantic salmon	brook trout	sand lance	sculpins
Atlantic snailfish	ns	ns	ns	ns	ns	ns	ns	< 0.001
capelin	ns	ns	ns	ns	ns	ns	ns	ns
cod age 1	ns	ns	ns	ns	ns	ns	ns	ns
cod age 2+	ns	ns	ns	ns	ns	< 0.01	ns	ns
rock crab	ns	ns	ns	ns	ns	ns	< 0.001	ns
cunner	ns	ns	ns	ns	ns	ns	ns	ns
rock gunnel	ns	< 0.01	ns	< 0.001	ns	ns	ns	ns
hake	ns	ns	ns	< 0.001	ns	ns	ns	ns
herrings	•	ns	ns	ns	ns	ns	ns	ns
lumpfish	-0.01	•	ns	ns	ns	ns	ns	ns
Gadus ogac	0.01	-0.03	•	ns	ns	ns	ns	ns
radiated shanny	0.01	-0.05	-0.01	•	ns	ns	ns	< 0.001
Atlantic salmon	0.00	-0.02	-0.01	-0.06	•	ns	ns	< 0.001
brook trout	0.00	-0.02	-0.01	-0.03	-0.02	•	ns	< 0.001
sand lance	0.00	0.01	0.00	0.01	-0.01	-0.02	•	ns
sculpins	-0.01	-0.03	-0.02	0.35	0.22	0.20	-0.06	•
skate	-0.01	0.01	0.02	0.02	-0.04	-0.01	0.00	0.00
smelt	-0.01	0.08	0.05	-0.03	0.00	0.00	-0.01	-0.03
sticklebacks	0.00	-0.04	-0.02	-0.07	0.21	0.01	0.00	-0.03
winter flounder	-0.01	0.03	-0.01	-0.09	0.07	-0.05	0.09	0.28

con't...

Table 9-5 con't.

Variable	skate	smelt	stickle-backs	winter flounder
Atlantic snailfish	ns	ns	ns	ns
capelin	ns	ns	ns	ns
cod age 1	ns	ns	ns	ns
cod age 2+	ns	ns	ns	ns
rock crab	ns	ns	ns	< 0.001
cunner	ns	ns	ns	ns
rock gunnel	ns	ns	< 0.001	ns
hake	ns	ns	< 0.02	< 0.001
herrings	ns	ns	ns	ns
lumpfish	ns	ns	ns	ns
Gadus ogac	ns	ns	ns	ns
radiated shanny	ns	ns	ns	ns
Atlantic salmon	ns	ns	< 0.001	ns
brook trout	ns	ns	ns	ns
sand lance	ns	ns	ns	< 0.05
sculpins	ns	ns	ns	< 0.001
skate	•	ns	< 0.01	ns
smelt	0.04	•	ns	ns
sticklebacks	0.12	-0.03	•	< 0.05
winter flounder	0.02	-0.01	-0.10	•

Table 9-6: Partial correlations among the 9 physical variables measured for 490 beach seine hauls between 1997-1999. Values below the diagonal are correlation coefficients partialed with respect to all other variables. Values above the diagonal are probabilities for the corresponding correlations.

Variable	julien day	time of day	depth (m)	tidal height (m)	Temperature surface (ºC)	Salinity surface (ppt)	Temperature depth (ºC)	Salinity depth (ppt)	number of snags
julien day	•	ns	ns	ns	< 0.001	ns	< 0.05	ns	ns
time of day	-0.05	•	ns	ns	ns	ns	ns	ns	ns
depth (m)	0.03	-0.02	•	< 0.001	ns	ns	ns	ns	ns
tidal height (m)	-0.06	0.01	0.40	•	< 0.05	< 0.001	ns	< 0.001	ns
T surf (ºC)	-0.34	0.03	0.06	-0.09	•	ns	< 0.001	< 0.01	ns
S surface (ppt)	0.02	-0.02	0.07	-0.18	0.09	•	ns	< 0.001	ns
T depth (ºC)	-0.10	-0.03	-0.04	0.06	0.89	-0.06	•	< 0.01	ns
S depth (ppt)	-0.05	0.01	-0.03	0.15	-0.13	0.54	0.12	•	< 0.001
number of snags	0.00	-0.02	0.06	-0.04	-0.01	0.08	0.00	-0.21	•

Table 9-7: Pairwise correlations among physical and biological variables that are significant beyond the Bonferroni adjustment for 29 variables and 406 possible pairwise comparisons.

Variable	by Variable	Correlation	Signif Prob
depth (m)	rock crab	-0.173	0.00012070
depth (m)	sculpins	-0.2362	0.00000010
julien day	cunner	-0.3757	0.00000000
julien day	hake	-0.2911	0.00000000
julien day	rock gunnel	-0.1899	0.00002320
S depth (ppt)	sculpins	-0.2623	0.00000001
S surface (ppt)	sculpins	-0.2238	0.00000090
T depth (°C)	rock crab	0.1929	0.00002220
T depth (°C)	cunner	0.3757	0.00000000
T depth (°C)	hake	0.3214	0.00000000
T depth (°C)	rock gunnel	0.2219	0.00000100
T surface (°C)	rock crab	0.1895	0.00002990
T surface (°C)	cunner	0.3748	0.00000000
T surface (°C)	hake	0.3219	0.00000000
T surface (°C)	rock gunnel	0.2135	0.00000240
time of day	sticklebacks	0.1932	0.00001660

Table 9-8: The strongest-loading variables on each of 29 principal components (PCs) from the biological and physical variables measured in association with 470 beach seine hauls between 1997-1999. Only loadings greater than or equal to 0.20 are shown.

Component name:	PC1	PC2	PC3	PC4
% of total variance:	13.0%	8.0%	5.6%	4.9%
	0.48 - T depth	0.49 - sculpins	0.41 - S surface	0.53 - tidal ht.
	0.48 - T surface	-0.34 - S depth	0.41 - S depth	0.49 - depth
	-0.47 - julian day	0.32 - w. flounder	0.31 - shanny	-0.42 - sticklebacks
	0.26 - cunner	-0.31 - S surface	0.29 - gunnel	-0.26 - time of day
	0.25 - hake	0.27 - shanny	-0.25 - Atl. salmon	-0.21 - Atl. salmon
		-0.26 - depth	-0.23 - time of day	0.19 - shanny
		0.23 - rock crab	0.23 - rock crab	
		0.2 - hake	-0.2 - sticklebacks	
		0.2 - Atl. salmon		

PC5	PC6	PC7	PC8	PC9
4.6%	4.4%	4.2%	4.0%	3.9%
0.37 - skate	-0.39 - lumpfish	0.38 - sand lance	-0.55 - # of snags	0.51 - brook trout
0.35 - cod age 1	0.34 - S depth	0.35 - cod age 1	0.36 - sand lance	0.45 - cod age 2+
0.32 - smelt	-0.33 - smelt	0.33 - cod age 2+	-0.33 - cod age 1	-0.37 - w. flounder
0.3 - time of day	0.32 - brook trout	0.33 - # of snags	0.31 - lumpfish	0.27 - gunnel
0.26 - gunnel	0.31 - cod age 2+	0.33 - rock crab	0.23 - tidal ht.	-0.27 - hake
0.26 - depth	-0.28 - gunnel	-0.24 - shanny	0.22 - time of day	-0.21 - sand lance
0.26 - sticklebacks	0.27 - tidal ht.	0.24 - cunner	-0.22 - S surface	
-0.22 - cunner	0.23 - sculpins	-0.22 - snailfish	0.22 - smelt	
0.21 - shanny	-0.22 - # of snags	-0.22 - Atl. salmon		

Table 9-8 con't.

PC10	PC11	PC12	PC13	PC14
3.8%	3.6%	3.6%	3.4%	3.3%
-0.37 - smelt	0.46 - snailfish	0.5 - *G. ogac*	0.56 - capelin	0.76 - herrings
-0.36 - *G. ogac*	0.42 - skate	-0.37 - snailfish	0.53 - *G. ogac*	0.33 - capelin
0.36 - Atl. salmon	-0.38 - capelin	0.36 - Atl. salmon	-0.28 - lumpfish	0.3 - lumpfish
-0.28 - hake	-0.28 - hake	-0.31 - capelin	0.27 - cunner	-0.24 - snailfish
0.28 - sticklebacks	0.27 - sand lance	0.3 - herrings		
-0.27 - snailfish	0.24 - rock crab	-0.25 - skate		
0.24 - rock crab	0.22 - herrings	-0.24 - cod age 1		
0.23 - gunnel		-0.23 - time of day		
0.22 - sand lance				
0.21 - tidal ht.				

PC15	PC16	PC17	PC18	PC19
3.2%	3.1%	3.0%	2.9%	2.8%
-0.37 - brook trout	0.39 - Atl. salmon	0.55 - smelt	-0.44 - skate	-0.46 - time of day
0.37 - snailfish	0.39 - lumpfish	-0.34 - lumpfish	0.43 - cod age 1	0.36 - sand lance
0.35 - cod age 2+	0.33 - cod age 1	-0.33 - *G. ogac*	0.33 - smelt	0.33 - capelin
-0.34 - skate	-0.33 - shanny	0.27 - cunner	0.31 - sand lance	0.31 - skate
0.26 - sand lance	-0.3 - sand lance	0.24 - cod age 2+	-0.29 - cod age 2+	0.27 - brook trout
0.25 - sticklebacks	0.25 - snailfish	0.24 - snailfish	-0.23 - cunner	-0.24 - rock crab
-0.25 - smelt	0.21 - *G. ogac*	0.21 - depth	0.2 - capelin	0.21 - # of snags
0.24 - time of day		0.2 - Atl. salmon	0.2 - brook trout	-0.2 - cunner
0.22 - herrings				0.2 - snailfish

Table 9-8 con't.

PC20	PC21	PC22	PC23	PC24
2.7%	2.4%	2.1%	2.0%	1.7%
-0.43 - sticklebacks	0.45 - # of snags	0.43 - cunner	0.49 - depth	0.5 - sculpins
-0.39 - hake	0.43 - brook trout	-0.39 - w. flounder	-0.48 - tidal ht.	-0.4 - Atl. salmon
-0.31 - cod age 1	-0.39 - cod age 2+	-0.36 - gunnel	0.34 - cunner	0.35 - sticklebacks
0.3 - time of day	0.26 - time of day	0.33 - shanny	-0.26 - rock crab	0.32 - S surface
0.29 - sculpins	0.24 - snailfish	0.27 - hake	0.25 - time of day	-0.3 - hake
0.26 - # of snags	0.22 - S surface	0.27 - lumpfish	-0.21 - smelt	0.22 - cunner
0.24 - shanny	0.22 - S depth	0.22 - S depth	-0.2 - # of snags	-0.2 - gunnel
-0.22 - brook trout				
0.21 - Atl. salmon				

PC25	PC26	PC27	PC28	PC29
1.4%	1.3%	1.2%	0.2%	0.04%
0.51 - rock crab	0.43 - S surface	0.51 - S depth	0.81 - julien day	0.73 - T surface
-0.36 - gunnel	0.35 - gunnel	0.48 - sculpins	0.46 - T depth	-0.68 - T depth
-0.35 - w. flounder	-0.35 - shanny	-0.38 - shanny	0.35 - T surface	
0.34 - hake	0.31 - tidal ht.	-0.36 - S surface		
-0.33 - cunner	-0.3 - w. flounder	-0.21 - w. flounder		
0.29 - depth	-0.28 - S depth	0.21 - gunnel		
-0.23 - S depth	0.27 - hake			
0.21 - S surface	-0.26 - depth			
0.2 - sculpins				

Table 9-9: Parameter estimates for the reduced negative binomial model of the effect of PCs on the catch of age 0 cod in 470 beach seine hauls at 24 locations between1997-1999. Means and standard deviations are from 1646 bootstraps of the reduced model.

Parameter	Parameter mean	Parameter Std Dev
κ int	0.1782	0.0325
κ PC1	-0.0243	0.0086
κ PC3	0.0016	0.0104
κ PC5	0.0198	0.0170
κ PC11	-0.0041	0.0131
κ PC14	0.0307	0.0239
κ PC19	-0.0209	0.0156
κ PC27	-0.0287	0.0284
β int	0.8130	0.2710
β PC1	-0.2842	0.1439
β PC3	0.6892	0.1353
β PC5	0.1291	0.2218
β PC11	0.2660	0.3160
β PC14	-0.4498	0.3202
β PC19	0.2647	0.3060
β PC27	0.0411	0.3952

Table 9-10: Parameter estimates for the reduced logistic regression model of the effect of PCs on the presence or absence of agr 0 cod in the catch of 470 beach seine hauls at 24 locations between 1997-1999.

Parameter	Parameter mean	Parameter Std Error	ChiSquare	Prob > ChiSq	Parameter Upper CL	Parameter Lower CL
Intercept	0.7427	0.1165	40.6200	<.0001	•	•
β PC1	0.4028	0.0666	36.6200	<.0001	0.5382	0.2765
β PC2	0.1529	0.0778	3.8600	0.0495	0.3108	0.0037
β PC3	-0.3660	0.0969	14.2600	0.0002	-0.1790	-0.5606
β PC5	-0.2919	0.1009	8.3600	0.0038	-0.0993	-0.4967
β PC8	0.2255	0.1067	4.4700	0.0345	0.4427	0.0221
β PC23	-0.4374	0.1522	8.2600	0.0041	-0.1408	-0.7393
β PC24	-0.5800	0.1833	10.0100	0.0016	-0.2293	-0.9499
β PC28	1.4309	0.4510	10.0700	0.0015	2.3266	0.5547
β PC29	-3.4836	1.0931	10.1600	0.0014	-1.3805	-5.7032

Note that in the logistic model, lower coeffcients result in a greater probability of presence.

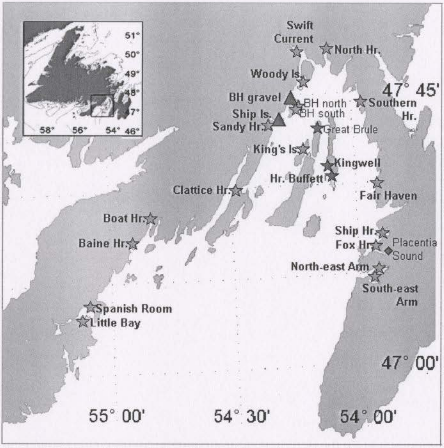


Figure 9–1: Map of Placentia Bay, showing the location of the 18 sites sampled in all 3 years (lightly shaded stars), the 3 eelgrass sites added in 1998 (dark shaded stars), the 2 sites with gravel substrate (triangles), and the site (Placentia Sound) used only in some of the analyses (Diamond). Note that the position of Bar Haven north has been displaced to the north-east for presentation purposes, so it could be distinguished on the map from Bar Haven south. Bar Haven is abbreviated to BH. Inset: The island of Newfoundland, with box showing location of the Placentia Bay study area.

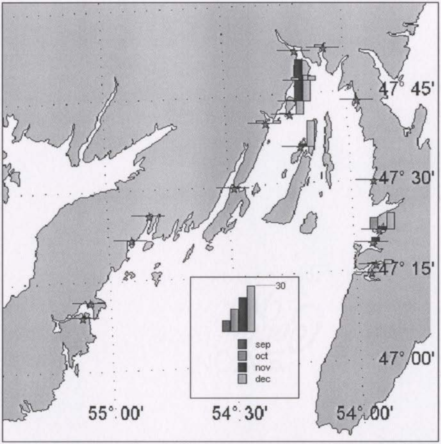


Figure 9–2: Location and catch of 0-group cod at each of the 18 sites in 1997. The bars represent catch (in number of fish) for September (leftmost bar), October (second bar), November (third bar) and December (rightmost bar). Catch in September was 0 at all sites. Note that scale of bars are different from Figures 3 and 4. Note that the position of Bar Haven north has been displaced to the north-east for presentation purposes.

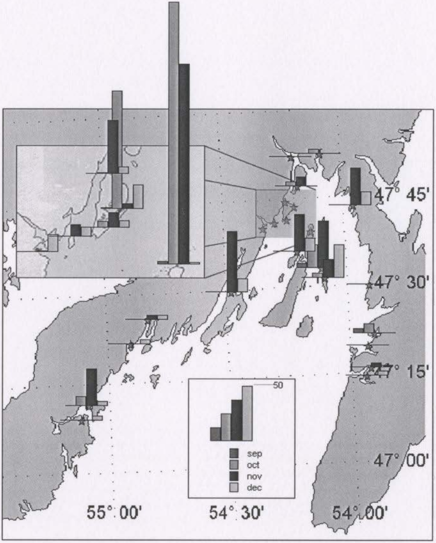


Figure 9–3: Location and catch of 0-group cod at each of the 23 sites sampled throughout 1998. The bars represent catch (in number of fish) for September (leftmost bar), October (second bar), November (third bar) and December (rightmost bar). Inset: a magnification of the Bar Haven area. Scales are identical for main map and for inset. Note that scale of bars are different from Figures 2 and 4. Note that the position of Bar Haven north has been displaced to the north-east for presentation purposes.

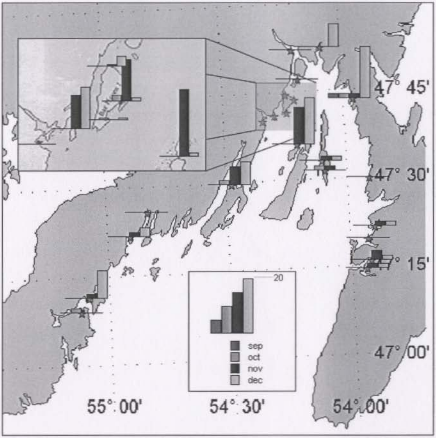
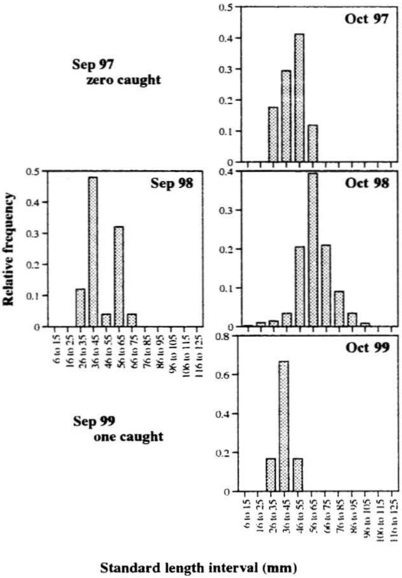
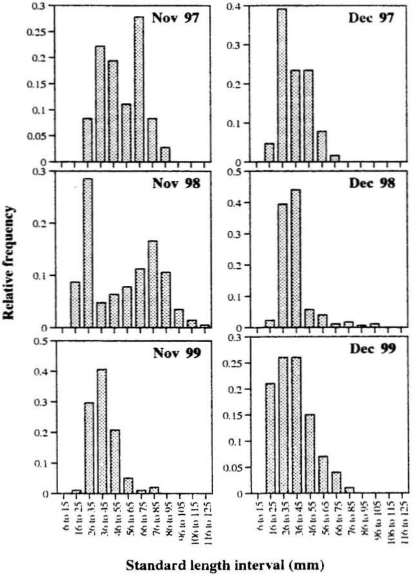


Figure 9–4: Location and catch of 0-group cod at 23 sites sampled in 1999. The bars represent catch (in number of fish) for September (leftmost bar), October (second bar), November (third bar) and December (rightmost bar). Inset: a magnification of the Bar Haven area. Scales are identical for main map and for inset. Note that scale of bars are different from Figures 3 and 4. Note that the position of Bar Haven north has been displaced to the north-east for presentation purposes.

Figure 9–5: Relative frequency of standard lengths of age 0 cod (binned by 10 mm intervals) for each of the four months surveys in 1997 through 1999. Length distributions for September are in the leftmost column. Those for October, November and December are in the second, third and last columns, respectively. Length distributions for 1997 are in the topmost row. Those for 1998 and 1999 are in the middle and bottom rows, respectively. Note no age 0 were caught in September 1997, and only 1 in September 1999. Note that the scale of the bars is different in every panel


Sep 97
zero caught
Oct 97
Sep 98
Oct 98
Sep 99
one caught
Oct 99
Relative frequency
0
0.1
0.2
0.3
0.4
0.5
0.6
0.8
6 to 15
16 to 25
26 to 35
36 to 45
46 to 55
56 to 65
66 to 75
76 to 85
86 to 95
96 to 105
106 to 115
116 to 125
Standard length interval (mm)


Nov 97
Dec 97
Nov 98
Dec 98
Nov 99
Dec 99
Relative frequency
Standard length interval (mm)
0
0.05
0.1
0.15
0.2
0.25
0.3
0.4
0.5
6 to 15
16 to 25
26 to 35
36 to 45
46 to 55
56 to 65
66 to 75
76 to 85
86 to 95
96 to 105
106 to 115
116 to 125

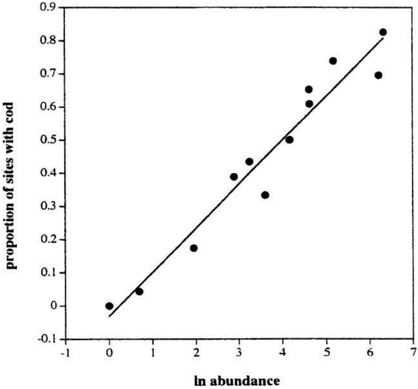


Figure 9–6: Distribution expansion with abundance. Proportion of total number of sites surveyed that had age 0 cod in the catch, versus the natural logarithm of the overall abundance (number of age 0 cod caught) in the bay. Each point represents one survey month. The line is a standard least squares regression $Y = -0.031 - 0.13X$ ($r^2 = 0.95$; the intercept is not significantly different from zero).

10 Summary

Stock structure forms the spatial and biological basis for assessment and management of commercial fisheries. The development and maintenance of structure depends on the segregation of spawning groups during reproduction (Templeman, 1979). Furthermore, eggs and larvae produced must be distributed in such a way that allows maturing individuals to eventually join their parent population. For small-scale population structure to exist in Atlantic cod, a broadcast spawner, two biological processes must be limited: 1) dispersal of eggs and larvae; and 2) straying of adults among spawning grounds.

The extent of local retention of spawning products at the Bar Haven spawning ground in Placentia Bay was explored by examining the timing, magnitude and distribution of the various life-stages (from spawning through to juvenile recruitment) for three consecutive years. In 1997, spawning rate declined after that observed in April in 0 °C waters, and early stage eggs were plentiful, but late stage eggs and larvae were few. Poor recruitment of demersal juveniles followed. In comparison, peak spawning in 1998 was at least one month later, and occurred in 11 °C water. Although fewer early stage eggs were produced in 1998, larger numbers of late stage eggs and larvae were observed within the bay, and stronger local recruitment of demersal juveniles resulted. Transport of eggs and larvae into the bay was not observed, suggesting that recently settled juveniles within the bay were of local origin. In all years, demersal juveniles were distributed in the head of the bay and on the western side (downcurrent from Bar Haven), suggesting retention of Bar Haven spawning products within the bay. The similarity in distribution of early and late stage eggs within a given year was further evidence of local retention. Thus the extent of local retention was related to the timing (or temperature) of spawning, whereby later spawning in warmer water led to faster egg development and larval growth, and enhanced local retention.

Straying of adults among spawning grounds may be limited if individuals repeatedly and precisely return to the same location each time they spawn (homing) or if the home range of individuals is small relative to the distance among spawning grounds (site fidelity). The pervasiveness of site fidelity, homing and resultant population structure was reviewed for all major stocks of Atlantic cod in the North Atlantic. Cod populations can be classified into four categories based on their migratory behaviour: First, populations that perform long-distance migrations and accurately home to spawning grounds; Second those that home less accurately; Third, those that exhibit strong site fidelity, and can be found year-round within a relatively small geographic range; Fourth, populations that disperse or tend to move within large geographic areas. Although the relative proportion of these behavioural categories across the range of the species could not be accurately determined (because of the limitations of conventional tagging studies under review, and the subjectivity with which behaviours are assigned to a category), cod migratory behaviour was highly variable throughout all parts of its range, and no category was limited to inshore or offshore environments, or to any part of the North Atlantic range.

The degree of cod homing has traditionally been assessed by tagging individuals and recording the date and location of release, and of subsequent recapture in the fishery. Since individuals cannot be tracked over extended periods of time, the rates of homing and straying are difficult to assess using this method. For example, it can never be known if an individual was caught in its preferred location, or whether it was en route (see Tåning, 1940). However, advancements in underwater telemetric techniques now allow many observations of tagged individuals to be made over several years. Thus, residency times at spawning grounds can be now assessed as well as the extent of multi-year homing.

The extent of homing to the Bar Haven ground was explored using underwater acoustic telemetry. For three consecutive spawning seasons, adult cod tagged at the Bar Haven spawning ground in Placentia Bay, Newfoundland were monitored. Two-thirds of the tagged fish were relocated during the study, all within ten km of the tagging site, the majority within a few 100 meters. No tagged fish were relocated at other known spawning grounds or elsewhere in the bay. Homing rates to Bar Haven in the two years after release were 39% and 53% returning after adjustments for the number of tags captured in the fishery. Multi-year homing was observed in 26% of cod tagged. This study provides the first direct evidence that long-distance migrant cod may exhibit fidelity to a specific spawning ground over multiple years.

Factors affecting Bar Haven cod's ability to home were explored by tagging and displacing 23 large spawners in small groups up to 35 km from Bar Haven. Overall, approximately 60% of the fish homed to the grounds. Homing success was negatively related to distance of the release sites from the spawning ground, irrespective of current directions or known spawning routes. Transplanted groups did not stay together. Females and males homed at approximately equal rates, although more females homed successfully from distant sites. Underwater landmarks and celestial clues were unlikely to be important homing mechanisms in Placentia Bay. Of any navigatory mechanism explored, the data are most consistent with the orientation towards an omnidirectional "attractor" at the spawning ground that dissipates with distance, such as a characteristic sound or geophysical signature. Individual variability in ability to navigate (or tendency to home) was evident.

Individual differences were further explored using acoustic telemetry to monitor the movements of 48 spawning cod (21 male, 27 female) tagged and released on the Bar Haven spawning ground. Over three consecutive spawning seasons the distribution of individuals was monitored over a grid of listening stations on the spawning ground. Thirty tagged cod were relocated acoustically and fifteen caught in the fishery (including seven of the former) during this study. Only eight were never observed. On average, males stayed on the spawning ground at least 9.5 days, and females 18.6 days. The rate of departure from the spawning grounds varied among years. There was no effect of body length on the timing of departure from the spawning ground, for either males or females. Males departed from the grounds earlier than females. The relocation rates for males were greater than for females in all years, suggesting that females move in and out of male-dominated spawning aggregations.

In this thesis I also developed a telemetric management tool to assess of the independence of a set of abundance estimates from serial surveys. Assessing the spawning abundance of marine fishes is difficult if spawning periods exceed the residency of individual fish on the spawning grounds. For Atlantic cod, which has a protracted spawning period, biotelemetric surveys were used to estimate the rate at which individual fish vacate the spawning ground and develop a method to adjust multiple acoustic survey results to account for spawner turnover. Two acoustic surveys conducted one month apart (May and June 1998) on the Bar Haven spawning ground yielded abundance estimates of 220 000 and 210 000 fish of mean length 63 cm. Rates of evacuation from the spawning ground, observed over two separate spawning seasons, were modelled as logistic decay functions with good fit. My method estimated that only 8.8% of the fish counted during the second survey were present during the first, and that between 400 976 and 420 842 fish were actually present within the survey zone over the full spawning season.

I also explored another potential management tool in this thesis, namely the use of proxy variables to forecast recruitment to the Bar Haven spawning group. Proxy variables are indices that can reliably predict the value of a variable of interest. Since demersal juvenile abundance is likely to be a better predictor of year-class strength than that of any previous life-stage (Bradford, 1992), age 0 cod catch was sued as a measure of recruitment. Age 0 cod were collected from 24 sites throughout Placentia Bay from September to December of 1997 through 1999. Age 0 catch was modelled using principal components regression with an error structure following the negative binomial distribution. Although age 0 cod catch was consistently higher at a number of sites in the head of the bay, it varied among years and months, and increases in overall catch for any given period was accompanied by an increase in the number of sites occupied by cod. Catch rate and presence/absence models which included temperature, salinity, and depth were significantly different than more reduced models, but eelgrass cover could be removed from a model without significantly affecting its maximum likelihood estimate. Age 0 cod showed positive associations with several inshore species including rock gunnel, rock crab, Atlantic snailfish, thorny skate, smelt and age 1 cod. Catch of age 0 cod also showed negative associations with larval capelin, hake, cunner, Atlantic salmon, lumpfish and winter flounder. There were no detectable associations with *Gadus ogac*, cod aged two or older, or brook trout. When only hauls containing cod were examined, no factors explained catch rates. This study demonstrates that simple age 0 cod surveys can generate ranked year-class predictions, but that more quantitative predictions are complicated by density-dependent site-use. Consistency among sites of ranked catch from year-to-year allows identification of important, temporally stable nursery grounds within the bay. Perhaps the most surprising result of this study is that 29 feasible explanatory variables failed to provide reasonable predictions of catch rates.

Overall, the thesis illustrates the diverse patterns of migration and distribution of cod throughout its range, from sedentary to highly migratory, a feature that may explain the success of this species in the North Atlantic. That the Bar Haven cod show both the required features of fine scale population structure, homing and retention, may provide the answer to the question of why this spawning area, of the known grounds in Placentia Bay, has been the most consistently occupied since observations began in 1996 (G. A. Rose, personal communication, Lawson and Rose, 2000a). Together with genetic evidence (Ruzzante et al., 1998) this thesis demonstrates strong potential for population structure at scales much smaller than those of current fisheries management, important results given that management over inappropriate scales can result in local depletions and overall reductions in productivity (Hilborn and Walters, 1992; Frank and Brickman, 2000). The future of cod in Placentia Bay will likely depend on the resolution of population structure and on management at appropriate geographic scales. Recently, partly as a result of this work, the Fisheries Resource Conservation Council recommended that the fishery for cod in the head of Placentia Bay be open only to fishers in the local area (i.e., closed to those in other parts of 3Ps, see FRCC, 2001), a first step toward smaller-scale management.

The same issues that are important to consider for Placentia Bay cod management could also apply to other groups of cod, especially those in coastal regions of the North Atlantic. Whether or not similar arguments could also apply to other broadcast spawning species with wide-spread distribution and localised spawning grounds, I leave open to further research.

11 Literature cited

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Appendix A – Fish tagging procedures

A total of 71 cod, including 39 females (lengths 64 to 98 cm) and 32 males (lengths 67 to 98 cm) were tagged and released. In 1998, 48 cod, including 27 females (lengths 64 to 87 cm) and 21 males (lengths 67 to 88 cm) were tagged and released (Appendix Table A1). In 2000, 23 cod, including 12 females (lengths 70 to 98 cm) and 11 males (lengths 75 to 95 cm) were tagged and released (Appendix Table A2). All procedures were approved by the Memorial University animal research committee.

Fish collection

On 19 April 1998, 84 cod (total lengths: 34 to 102 cm; mean: 59.5 cm) were removed from a spawning aggregation, located acoustically at 47° 44.57' N 54° 12.75' W (within the Bar Haven spawning area). On 20 April, another 133 cod (total lengths: 37 to 92 cm; mean: 68.1 cm) were caught under similar conditions between 47° 44.13' N 54° 11.31' W and 47° 44.38' N 54° 11.24' W. A total of 217 cod (total lengths: 34 to 102 cm; mean: 64.8 cm) were taken from aggregations using feathered hooks. The fish were in water near 0 °C, at depths between 30 and 50 m.

Between 3–4 April 2000, approximately 85 cod (total lengths: 45 to 89 cm; mean 65.7 cm) were removed from a spawning aggregation, located acoustically at 47° 45.25' N 54° 13.20' W (within the Bar Haven spawning area). Fish were caught using feathered hooks. The fish were in water near 0 °C, at depths between 30 and 50 m.

Fish that were large (and therefore possibly in spawning condition) were transferred to holding tanks. Smaller fish were measured and returned alive to the sea.

Fish holding

The fish were held in two holding tanks, each measuring approximately 1.3 m x 1.3 m with a depth of about 1.3 m. One of the tanks was made of hard plastic, and the other was a collapsible tank. The tanks held approximately 2200 L when full. Onboard pumps supplied a continuous flow of seawater into the tanks. Water overflowed over the tops, which were covered except while fish were being added or removed from the tanks.

Prior to tagging, fish with difficulty righting themselves, and those with bloated peritoneal cavities were returned alive to the ocean. Cod that appeared to be in good condition, and were oriented toward the bottom of the tanks were selected preferentially for tagging.

Fish surgery

Candidates for tagging were removed from the holding tanks, placed on wooden measuring board, and wrapped in wet sponges, making sure that the head was covered. Fish were kept still by holding down the head and caudal peduncle, although few fish attempted to move beyond the initial escape response. Fish were measured to the nearest centimetre, were turned ventral side-up, and were sexed by inserting a small piece of tubing (a "cannula") into the cloaca. The cannula, after being pushed up about 7 centimetres (depending on fish size) and retracted, contained either milt or eggs. For all females, the proportion of eggs that were hydrated in each cannula was recorded.

For each fish, an individually-coded ultrasonic transmitter (Lotek Model CAFT16-2; size: 82 mm long, 16 mm diameter; weight: 35.9 g in air, 18.1 g in water; 66 and 76 kHz for males and females, respectively) was surgically implanted into the peritoneal cavity. To implant the transmitter in the fish, a 1 cm incision was made 3 mm away from and parallel to the mid-ventral line starting about 3 mm anterior to the pelvic girdle. The incision was only deep enough to penetrate the peritoneum (e.g., Adams et al., 1998). The transmitter was implanted through the incision and gently pushed posteriorly into the body cavity. For fish that bled, an intraperitoneal antibiotic was pipetted into the incision to prevent infection. The incision was closed with three uninterrupted, non-absorbable sutures, evenly spaced across the incision. The surgical implantation procedures took approximately 2 minutes. New scalpels and sutures were used for each individual tagged.

The surgical implantation procedures used were based on the methods outlined in (Murphy and Willis, 1996), except that anesthetic was not applied. Other researchers in the area (pers. comm., J. Wroblewski, Memorial University of Newfoundland) found that cod treated with anesthetic commonly died, possibly as a result of reduced levels of metabolic activity associated cold water. In this study, the water was near 0 °C, and the fish were found to be sufficiently sedate.

Post-tagging procedures

Immediately after surgery, an external spaghetti tag was anchored on the left side adjacent to the first dorsal fin, and the tagged fish were returned to the holding tanks.

In 1998, the tagged fish were held for up to ten hours, and those that appeared to be robust and in excellent condition were released at the location where they were caught.

In 2000, the tagged fish were observed fro between 2 and 30 hours, and those that appeared to be robust and in excellent condition were released in small groups (3-4 fish) at various locations throughout Placentia Bay.

Appendix Table A1: Length, sex and maturity state of Atlantic cod caught and released on April 19-20 1998 at Bar Haven, Placentia Bay. Also shown: the specifications of the Lotek acoustic tags that were surgically implanted into each fish.

					Tag Information			
Fish No.	Sex	Maturity State	Total Length (cm)	Catch and Release Date	Tag Code	Tag Freq. (kHz)	Echo Value	Serial Number
beacon				4/18/98	129	65.5	219	9804057
f31	f	matc	83	4/20/98	31	65.5	194	9804056
f32	f	mata	76	4/20/98	32	65.5	194	9804055
f33	f	mata	75	4/20/98	33	65.5	194	9804054
f34	f	matc	77	4/20/98	34	65.5	194	9804053
f35	f	matb	74	4/20/98	35	65.5	194	9804052
f37	f	mata	69	4/20/98	37	65.5	194	9804050
f38	f	mata	78	4/20/98	38	65.5	194	9804049
f42	f	mata	77	4/20/98	42	65.5	219	9804048
f46	f	mata	78	4/20/98	46	65.5	219	9804047
f47	f	matc	75	4/20/98	47	65.5	244	9804046
f48	f	mata	76	4/20/98	48	65.5	244	9804045
f49	f	mata	86	4/20/98	49	65.5	244	9804044
f50	f	matc	75	4/19/98	50	65.5	244	9804043
f54	f	matc	76	4/19/98	54	65.5	219	9804042
f57	f	mata	65	4/19/98	57	65.5	219	9804041
f66	f	mata	64	4/19/98	66	65.5	219	9804040
f68	f	mata	66	4/19/98	68	65.5	219	9804039
f78	f	matc	65	4/19/98	78	65.5	219	9804038
f90	f	mata	72	4/19/98	90	65.5	219	9804037
f96	f	mata	72	4/19/98	96	65.5	219	9804036
f102	f	matc	78	4/19/98	102	65.5	219	9804035
f107	f	mata	87	4/19/98	107	65.5	219	9804034
f114	f	mata	76	4/19/98	114	65.5	219	9804033
f118	f	mata	82	4/20/98	118	65.5	219	9804032
f126	f	mata	83	4/20/98	126	65.5	219	9804031
f160	f	matb	72	4/20/98	160	65.5	219	9804030
f170	f	matc	70	4/20/98	170	65.5	219	9804029

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Appendix Table A1: con't

					Tag Information			
Fish No.	Sex	Maturity State	Total Length (cm)	Catch and Release Date	Tag Code	Tag Freq. (kHz)	Echo Value	Serial Number
m31	m	ripe	73	4/20/98	31	76.8	194	9804028
m32	m	ripe	69	4/20/98	32	76.8	194	9804027
m35	m	ripe	81	4/20/98	35	76.8	194	9804024
m36	m	ripe	72	4/20/98	36	76.8	194	9804023
m37	m	ripe	77	4/20/98	37	76.8	194	9804022
m38	m	ripe	76	4/20/98	38	76.8	194	9804021
m42	m	ripe	78	4/20/98	42	76.8	219	9804020
m47	m	ripe	67	4/20/98	47	76.8	244	9804018
m49	m	ripe	74	4/20/98	49	76.8	244	9804016
m50	m	ripe	84	4/20/98	50	76.8	244	9804015
m54	m	ripe	82	4/19/98	54	76.8	219	9804014
m57	m	ripe	81	4/20/98	57	76.8	219	9804013
m66	m	ripe	76	4/20/98	66	76.8	219	9804012
m68	m	ripe	88	4/20/98	68	76.8	219	9804011
m78	m	ripe	75	4/20/98	78	76.8	219	9804010
m90	m	ripe	83	4/20/98	90	76.8	219	9804009
m102	m	ripe	76	4/20/98	102	76.8	219	9804007
m107	m	ripe	74	4/20/98	107	76.8	219	9804006
m114	m	ripe	81	4/20/98	114	76.8	219	9804005
m126	m	ripe	76	4/20/98	126	76.8	219	9804003
m160	m	ripe	79	4/20/98	160	76.8	219	9804002

Appendix Table A2: Length, sex and maturity state of Atlantic cod caught on April 3-4 2000 at Bar Haven, and released at various locations and times throughout Placentia Bay. Also shown: the specifications of the Lotek acoustic tags that were surgically implanted into each fish.

					Holding			Tag Information			
Fish No.	Release site	Sex	Maturity State	Total Length (cm)	Catch Time	Release Time	Time in Hold (h)	Tag Code	Tag Freq. (kHz)	Echo Value	Serial Number
f137	Bar Haven	f	matb	74	4/3/00 13:00	4/3/00 15:00	2.0	137	65.5	269	279
f161	Bar Haven	f	mata	87	4/3/00 13:00	4/3/00 15:00	2.0	161	65.5	269	271
m104	Bar Haven	m	ripe	84	4/3/00 13:00	4/3/00 15:00	2.0	104	76.8	319	236
m109	Bar Haven	m	ripe	95	4/3/00 13:00	4/3/00 15:00	2.0	109	76.8	319	235
f150	E.Cheese Island	f	matb	98	4/3/00 13:00	4/3/00 16:40	3.7	150	65.5	319	274
f162	E.Cheese Island	f	matc	70	4/3/00 13:00	4/3/00 16:40	3.7	162	65.5	319	270
m62	E.Cheese Island	m	ripe	78	4/3/00 13:00	4/3/00 16:40	3.7	62	76.8	294	263
m91	E.Cheese Island	m	ripe	84	4/3/00 13:00	4/3/00 16:40	3.7	91	76.8	269	262
f149	Haystack Bank	f	matb	85	4/3/00 13:00	4/4/00 16:35	27.6	149	65.5	269	275
f154	Haystack Bank	f	mata	83	4/4/00 13:00	4/4/00 16:35	3.6	154	65.5	269	272
m59	Haystack Bank	m	matp	75	4/3/00 13:00	4/4/00 16:35	27.6	59	76.8	294	266
m60	Haystack Bank	m	matp	80	4/4/00 13:00	4/4/00 16:35	3.6	60	76.8	294	265
f142	Clattice Harbour	f	mata	80	4/4/00 13:00	4/5/00 12:00	23.0	142	65.5	319	276
f168	Clattice Harbour	f	mata	79	4/4/00 13:00	4/5/00 12:00	23.0	168	65.5	319	269
m92	Clattice Harbour	m	ripe	82	4/4/00 13:00	4/5/00 12:00	23.0	92	76.8	319	261
m97	Clattice Harbour	m	ripe	80	4/4/00 13:00	4/5/00 12:00	23.0	97	76.8	269	239
f138	Isle Valen	f	mata	95	4/4/00 13:00	4/5/00 13:20	24.3	138	65.5	319	278
f153	Isle Valen	f	mata	95	4/4/00 13:00	4/5/00 13:20	24.3	153	65.5	*	273
m98	Isle Valen	m	ripe	80	4/4/00 13:00	4/5/00 13:20	24.3	98	76.8	319	238
m110	Isle Valen	m	ripe	80	4/4/00 13:00	4/5/00 13:20	24.3	110	76.8	269	234
f79	Southern Head	f	mata	79	4/4/00 13:00	4/5/00 18:15	29.3	79	65.5	219	267
f167	Southern Head	f	mata	74	4/4/00 13:00	4/5/00 18:15	29.3	167	65.5	269	268
m61	Southern Head	m	ripe	82	4/4/00 13:00	4/5/00 18:15	29.3	61	76.8	294	264

* not known

Appendix Table B1: Global position (in decimal degrees) of the 24 sites surveyed for 0-group cod in Placentia Bay, 1997-1999.

SITE	N	W
Original 18 sites		
Baine Harbour	47.364	54.894
Bar Haven north	47.710	54.214
Bar Haven South	47.709	54.215
Boat Harbour	47.431	54.818
Clattice Harbour	47.496	54.473
Fair Haven	47.496	53.913
Fox Harbour	47.324	53.930
King's Island	47.600	54.197
Little Bay	47.157	55.107
North Harbour	47.872	54.082
North-east Arm	47.261	53.921
Sandy Harbour	47.671	54.330
Ship Harbour	47.357	53.900
South-east Arm	47.240	53.941
Southern Harbour	47.722	53.958
Spanish Room	47.195	55.075
Swift Current	47.868	54.198
Woody Island	47.784	54.180
Sites added Sept 1998		
Bar Haven gravel site	47.743	54.234
Great Brule	47.656	54.135
Harbour Buffett	47.522	54.089
Kingwell	47.551	54.102
Ship Island gravel site	47.685	54.283
Site added Oct 1998		
Placentia Sound	47.307	53.880

Appendix Table C1: Table of tag relocations

fish *	date	LAT	LONG
54f	May 5 98	Between Little Woody I. and Shag Rk.	
66f	May 5 98	Between Little Woody I. and Shag Rk.	
38m	May 5 98	Release location	
114m	May 7 98	N 47 ° 43.85'	W 54 ° 10.00'
126m	May 7 98	N 47 ° 43.85'	W 54 ° 11.54'
160m	May 7 98	N 47 ° 44.38'	W 54 ° 11.54'
32m	May 7 98	N 47 ° 44.38'	W 54 ° 10.71'
37f	May 7 98	N 47 ° 43.85'	W 54 ° 11.54'
42m	May 7 98	N 47 ° 44.38'	W 54 ° 11.54'
114m	May 8 98	N 47 ° 43.85'	W 54 ° 10.00'
31f	May 8 98	N 47 ° 42.33'	W 54 ° 9.25'
32m	May 8 98	N 47 ° 44.38'	W 54 ° 10.71'
36m	May 8 98	N 47 ° 42.06'	W 54 ° 10.00'
37f	May 8 98	N 47 ° 43.85'	W 54 ° 11.54'
47m	May 8 98	N 47 ° 43.85'	W 54 ° 9.63'
54m	May 8 98	N 47 ° 43.85'	W 54 ° 10.72'
78m	May 8 98	N 47 ° 44.90'	W 54 ° 12.20'
114f	May 10 98	N 47 ° 43.99'	W 54 ° 12.04'
37f	May 10 98	N 47 ° 43.82'	W 54 ° 11.67'
37m	May 10 98	N 47 ° 44.61'	W 54 ° 11.75'
38f	May 10 98	N 47 ° 43.88'	W 54 ° 11.94'
47f	May 10 98	N 47 ° 43.71'	W 54 ° 11.82'
48f	May 10 98	N 47 ° 44.96'	W 54 ° 10.88'
54f	May 10 98	N 47 ° 43.71'	W 54 ° 11.82'
54m	May 10 98	N 47 ° 45.12'	W 54 ° 10.69'
126m	May 18 98	N 47 ° 44.38'	W 54 ° 10.00'
38f	May 18 98	N 47 ° 43.87'	W 54 ° 12.10'
126m	May 19 98	N 47 ° 44.38'	W 54 ° 10.00'
31m	May 19 98	N 47 ° 43.35'	W 54 ° 10.71'
36m	May 19 98	N 47 ° 43.35'	W 54 ° 8.50'
37f	May 19 98	N 47 ° 44.38'	W 54 ° 12.20'
38f	May 19 98	N 47 ° 43.91'	W 54 ° 12.18'
47m	May 19 98	N 47 ° 43.85'	W 54 ° 9.25'

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Appendix Table C1 con't

fish *	date	LAT			LONG		
48f	May 19 98	N	47 °	43.84'	W	54 °	9.61'
54m	May 19 98	N	47 °	44.90'	W	54 °	9.25'
126m	May 20 98	N	47 °	43.84'	W	54 °	9.70'
31m	May 20 98	N	47 °	43.44'	W	54 °	10.85'
47m	May 20 98	N	47 °	44.02'	W	54 °	9.06'
78m	May 20 98	N	47 °	44.77'	W	54 °	12.13'
126m	May 21 98	N	47 °	47.33'	W	54 °	9.55'
31m	May 21 98	N	47 °	43.27'	W	54 °	11.08'
47m	May 21 98	N	47 °	43.86'	W	54 °	9.59'
78m	May 21 98	N	47 °	44.84'	W	54 °	13.11'
57f	May 22 98	N	47 °	46.44'	W	54 °	9.03'
66f	May 22 98	N	47 °	45.74'	W	54 °	8.3'
68f	May 22 98	N	47 °	45.96'	W	54 °	8.06'
126f	May 24 98	N	47 °	44.65'	W	54 °	11.71'
126m	May 24 98	N	47 °	44.17'	W	54 °	9.80'
48f	May 24 98	N	47 °	44.56'	W	54 °	11.08'
54f	May 24 98	N	47 °	44.70'	W	54 °	11.34'
78m	May 24 98	N	47 °	44.56'	W	54 °	11.11'
126m	May 25 98	N	47 °	44.05'	W	54 °	9.91'
48f	May 25 98	N	47 °	44.43'	W	54 °	10.70'
78m	May 25 98	N	47 °	44.31'	W	54 °	11.33'
126m	May 26 98	N	47 °	44.36'	W	54 °	10.00'
31m	May 26 98	N	47 °	43.43'	W	54 °	8.69'
48f	May 26 98	N	47 °	44.36'	W	54 °	10.94'
57f	May 26 98	N	47 °	46.85'	W	54 °	8.49'
66f	May 26 98	N	47 °	45.50'	W	54 °	9.26'
78m	May 26 98	N	47 °	44.38'	W	54 °	11.24'
57f	May 28 98	N	47 °	46.90'	W	54 °	8.50'
31m	May 31 98	N	47 °	43.50'	W	54 °	8.51'
48f	May 31 98	N	47 °	44.42'	W	54 °	11.45'
31m	Jun 1 98	N	47 °	43.67'	W	54 °	8.19'
48f	Jun 1 98	N	47 °	44.42'	W	54 °	11.46'
66f	Jun 1 98	N	47 °	45.63'	W	54 °	9.33'

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Appendix Table C1 con't

fish *	date	LAT			LONG		
126f	Jun 5 98	N	47 °	46.86'	W	54 °	8.25'
66f	Jun 5 98	N	47 °	46.01'	W	54 °	9.82'
66f	Jun 8 98	N	47 °	44.40'	W	54 °	11.39'
57m	Jun 9 98	N	47 °	41.74'	W	54 °	10.23'
57m	Jun 12 98	N	47 °	41.12'	W	54 °	11.05'
57m	Jun 14 98	N	47 °	41.13'	W	54 °	10.80'
31m	Apr 8 99	N	47 °	45.75'	W	54 °	12.84'
50m	Apr 8 99	N	47 °	45.75'	W	54 °	12.84'
160m	Apr 8 99	N	47 °	45.75'	W	54 °	12.84'
31m	Apr 9 99	N	47 °	45.72'	W	54 °	12.93'
68m	Apr 9 99	N	47 °	45.72'	W	54 °	12.93'
31m	Apr 9 99	N	47 °	45.75'	W	54 °	12.87'
48f	Apr 9 99	N	47 °	45.75'	W	54 °	12.87'
68m	Apr 9 99	N	47 °	45.75'	W	54 °	12.87'
160m	Apr 9 99	N	47 °	45.75'	W	54 °	12.87'
48f	Apr 13 99	N	47 °	45.75'	W	54 °	12.88'
50f	Apr 13 99	N	47 °	45.75'	W	54 °	12.88'
160m	Apr 13 99	N	47 °	45.75'	W	54 °	12.88'
50f	Apr 13 99	N	47 °	45.77'	W	54 °	12.68'
160m	Apr 13 99	N	47 °	45.77'	W	54 °	12.68'
90m	May 4 99	N	47 °	44.73'	W	54 °	12.85'
90m	May 4 99	N	47 °	45.15'	W	54 °	13.17'
31m	May 4 99	N	47 °	44.11'	W	54 °	11.40'
31m	May 13 99	N	47 °	44.79'	W	54 °	8.50'
48f	May 13 99	N	47 °	43.86'	W	54 °	9.39'
114m	May 14 99	N	47 °	45.02'	W	54 °	4.20'
114m	Dec 3 99	N	47 °	44.71'	W	54 °	11.75'
49m	Dec 3 99	N	47 °	44.71'	W	54 °	11.75'
114m	Dec 3 99	N	47 °	44.58'	W	54 °	11.56'
42f	Dec 3 99	N	47 °	44.58'	W	54 °	11.56'
49m	Dec 3 99	N	47 °	44.58'	W	54 °	11.56'
114m	Dec 3 99	N	47 °	44.53'	W	54 °	11.77'
107f	Dec 4 99	N	47 °	23.79'	W	54 °	0.66'

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Appendix Table C1 con't

fish *	date	LAT			LONG		
f142 CL	Apr 8 00	N	47°	30.31'	W	54°	25.71'
f154 HB	Apr 8 00	N	47°	42.49'	W	54°	5.84'
f162 CH	Apr 8 00	N	47°	42.49'	W	54°	5.84'
f168 CL	Apr 8 00	N	47°	29.76'	W	54°	26.96'
m92 CL	Apr 8 00	N	47°	29.79'	W	54°	26.6'
m97 CL	Apr 8 00	N	47°	29.59'	W	54°	27.54'
f154 HB	Apr 9 00	N	47°	47.26'	W	54°	9.59'
f162 CH	Apr 9 00	N	47°	42.62'	W	54°	5.83'
f167 SH	Apr 9 00	N	47°	47.36'	W	54°	11.11'
f79 SH	Apr 9 00	N	47°	46.88'	W	54°	9.46'
m104 BH	Apr 9 00	N	47°	45.91'	W	54°	12.71'
m109 BH	Apr 9 00	N	47°	43.79'	W	54°	11.57'
m61 SH	Apr 9 00	N	47°	48.29'	W	54°	8.35'
m62 CH	Apr 9 00	N	47°	50.26'	W	54°	8.59'
m91 CH	Apr 9 00	N	47°	45.35'	W	54°	12.59'
f137 BH	Apr 10 00	N	47°	45.82'	W	54°	12.88'
f154 HB	Apr 10 00	N	47°	47.12'	W	54°	10.36'
f154 HB	Apr 10 00	N	47°	47.57'	W	54°	10.82'
f167 SH	Apr 10 00	N	47°	47.17'	W	54°	10.18'
f167 SH	Apr 10 00	N	47°	47.49'	W	54°	10.87'
f79 SH	Apr 10 00	N	47°	45.42'	W	54°	11.51'
m104 BH	Apr 10 00	N	47°	45.86'	W	54°	12.97'
m109 BH	Apr 10 00	N	47°	44.08'	W	54°	11.33'
m61 SH	Apr 10 00	N	47°	49.48'	W	54°	8.20'
m62 CH	Apr 10 00	N	47°	48.93'	W	54°	7.95'
m91 CH	Apr 10 00	N	47°	45.34'	W	54°	12.58'
f137 BH	Apr 11 00	N	47°	45.93'	W	54°	12.66'
f162 CH	Apr 11 00	N	47°	42.58'	W	54°	6.17'
f167 SH	Apr 11 00	N	47°	47.49'	W	54°	11.62'
f79 SH	Apr 11 00	N	47°	45.13'	W	54°	11.28'
m104 BH	Apr 11 00	N	47°	45.90'	W	54°	12.84'
m109 BH	Apr 11 00	N	47°	44.05'	W	54°	11.71'
m61 SH	Apr 11 00	N	47°	50.41'	W	54°	9.53'

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Appendix Table C1 con't

fish *	date	LAT			LONG		
m62 CH	Apr 11 00	N	47 °	49.63'	W	54 °	7.79'
m91 CH	Apr 11 00	N	47 °	45.19'	W	54 °	12.75'
f138 IV	Apr 12 00	N	47 °	29.98'	W	54 °	24.04'
f142 CL	Apr 12 00	N	47 °	30.08'	W	54 °	26.14'
f168 CL	Apr 12 00	N	47 °	30.12'	W	54 °	26.03'
m92 CL	Apr 12 00	N	47 °	30.10'	W	54 °	26.07'
m92 CL	Apr 12 00	N	47 °	30.32'	W	54 °	25.83'
f137 BH	Apr 13 00	N	47 °	45.86'	W	54 °	13.01'
f154 HB	Apr 13 00	N	47 °	45.70'	W	54 °	13.21'
f162 CH	Apr 13 00	N	47 °	42.66'	W	54 °	6.15'
f167 SH	Apr 13 00	N	47 °	46.93'	W	54 °	9.69'
f79 SH	Apr 13 00	N	47 °	45.82'	W	54 °	12.96'
m104 BH	Apr 13 00	N	47 °	45.67'	W	54 °	12.97'
m109 BH	Apr 13 00	N	47 °	43.88'	W	54 °	11.88'
m61 SH	Apr 13 00	N	47 °	51.09'	W	54 °	10.22'
m91 CH	Apr 13 00	N	47 °	45.49'	W	54 °	12.90'
f154 HB	Apr 20 00	N	47 °	46.01'	W	54 °	12.58'
f167 SH	Apr 20 00	N	47 °	44.85'	W	54 °	11.79'
f79 SH	Apr 20 00	N	47 °	45.76'	W	54 °	12.63'
m104 BH	Apr 20 00	N	47 °	45.32'	W	54 °	12.58'
m109 BH	Apr 20 00	N	47 °	43.96'	W	54 °	11.04'
m60 HB	Apr 20 00	N	47 °	43.03'	W	54 °	11.60'
m61 SH	Apr 20 00	N	47 °	45.45'	W	54 °	12.65'
m91 CH	Apr 20 00	N	47 °	45.02'	W	54 °	13.29'
f154 HB	Apr 27 00	N	47 °	45.99'	W	54 °	12.64'
f167 SH	Apr 27 00	N	47 °	44.44'	W	54 °	11.86'
f79 SH	Apr 27 00	N	47 °	44.35'	W	54 °	11.53'
m104 BH	Apr 27 00	N	47 °	44.53'	W	54 °	11.83'
m61 SH	Apr 27 00	N	47 °	44.66'	W	54 °	12.43'
m61 SH	Apr 27 00	N	47 °	44.47'	W	54 °	11.28'
m91 CH	Apr 27 00	N	47 °	44.46'	W	54 °	11.00'
f154 HB	May 3 00	N	47 °	42.85'	W	54 °	11.92'
f167 SH	May 3 00	N	47 °	44.82'	W	54 °	11.66'

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Appendix Table C1 con't

fish *	date	LAT			LONG		
m104 BH	May 3 00	N	47 °	45.00'	W	54 °	13.22'
m61 SH	May 3 00	N	47 °	44.48'	W	54 °	10.85'
m91 CH	May 3 00	N	47 °	44.64'	W	54 °	10.94'
m104 BH	May 14 00	N	47 °	44.42'	W	54 °	11.01'
m109 BH	May 14 00	N	47 °	42.84'	W	54 °	11.93'
m91 CH	May 14 00	N	47 °	44.43'	W	54 °	10.86'
f168 HB	May 20 00	N	47 °	47.44'	W	54 °	11.81'
f168 HB	May 20 00	N	47 °	46.78'	W	54 °	12.64'
m109 BH	May 20 00	N	47 °	44.41'	W	54 °	11.69'
f142 CL	May 30 00	N	47 °	43.67'	W	54 °	11.65'
m109 BH	May 30 00	N	47 °	44.08'	W	54 °	11.42'

* Release locations are noted for fish tagged in 2000. Abbreviations are as in Table 6-2.