

Turnover time and annual migration of *Clupea harengus* Atlantic herring
on the German Bank and Scot's Bay spawning grounds:
a mark and recapture study

by

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ABSTRACT

This study examined eleven years of mark and recapture data to quantify turnover time, defined as the time required for individuals to aggregate, spawn and exit the spawning area, of *Clupea harengus* Atlantic herring on the German Bank and Scot's Bay spawning grounds off eastern Canada. Herring migrating from the Scot's Bay spawning ground have a shorter mean turnover time and faster dispersal rate than German Bank herring. Most post-spawned Scot's Bay herring migrated to the approaches of the Bay of Fundy where they mixed with German Bank herring. German Bank herring were more broadly distributed, occurring near the approaches of the Bay of Fundy, throughout the Gulf of Maine, and on Scotian Shelf. No mixing of the two populations occurred during spawning indicating self-sustaining reproductively isolated populations. The two populations only mixed during feeding and overwintering. Population specific turnover times calculated in this study improve current methods of estimating spawning stock biomass, thereby reducing the risk of overexploiting the resource.

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LIST OF SYMBOLS AND ABBREVIATIONS

~	Approximately
°	Degrees
>	Greater Than
<	Less Than
#	Number
%	Percent
α	Alpha
$\bar{\alpha}$	Mean Angle
ACON	A Contouring Application
ANOVA	Analysis of Variance
cm	Centimeter
df	Degrees of Freedom
E	East
F	Analysis of Variance Test Statistic
HDPS	Hydroacoustic Data Processing Software
k	Instantaneous Rate of Change
km	Kilometer
km ²	Square Kilometer
m	Meter
mm	Millimeter
n	Number
N	North

p	p Value
P_t	Mean Cumulative Proportion
r^2	Regression
S	South
SE	Standard Error
SSB	Spawning Stock Biomass
t	Days at Large
t	Two-Tailed t-statistic
TAC	Total Allowable Catch
TL	Total Length
W	West
$\bar{x}$	Mean
z	Rayleigh's Critical Value

CHAPTER 1: GENERAL INTRODUCTION

1.1 Herring biology and migration

In the western Atlantic, *Clupea harengus* herring is a highly abundant and broadly distributed fish species ranging from northern Labrador (60°N) to Cape Hatteras, North Carolina (35°N) (Scott and Scott, 1988; Collette and Klein-MacPhee, 2002; Melvin et al., 2009). Herring exist as many discrete spawning populations that mix with other populations of herring when overwintering and during summer when intensively feeding (Blaxter and Hunter, 1982; Stephenson *et al.*, 2009). Herring first mature and spawn at three or four years of age (23 to 28 cm Total Length [TL]) with a median size at maturity of approximately 25 cm TL in the western Atlantic (Collette and Klein-MacPhee, 2002; Power *et al.*, 2009). A maximum age of 18 years (39 cm TL) was recorded in the Gulf of Maine, although some studies report herring >20 years (Collette and Klein-MacPhee, 2002). Herring spawn 1-1.4 mm diameter demersal eggs that are non-buoyant, adhesive and adhere to the substrate, algae or each other. Spawning occurs in shallow water during spring and deeper water in autumn (Haegele and Schweigert, 1985; Able and Fahay, 2010). Time of spawning in the western Atlantic Ocean is population dependent (Lambert, 1987; Lambert and Messieh, 1989; Melvin *et al.*, 2009). Spring spawners, defined as spawning before July 1 (Melvin *et al.*, 2009) dominate the northern portion of the range. Autumn spawners, those spawning from July 1 onwards, dominate in the south (Melvin *et al.*, 2009). Both spawning types occur in the central portion of the range (Lambert, 1987; Lambert and Messieh, 1989; Melvin *et al.*, 2009).

Adult herring undertake a generally predictable migration each year for the purposes of spawning, overwintering and feeding (Harden Jones, 1968; McKeown,

1984; Nottestad *et al.*, 1999; Stephenson *et al.*, 2009). Herring spawn once per year (Blaxter and Hunter, 1982) in discrete locations to which they are presumed to return (Cushing, 1967; Wheeler and Winters, 1984; Stephenson *et al.*, 2009). Their high abundance, schooling habit, conventional migration patterns and repeated use of defined spawning grounds have made herring a lucrative species for commercial fisheries in the eastern and western Atlantic (Blaxter and Hunter, 1982).

1.2 Herring fishery – eastern Canada

Herring support one of the largest commercial fisheries in Atlantic Canada. Landings from all stocks exceed 113,000 metric tonnes per year and have an expected value in excess of \$44 million (DFO, 2012). Herring are also a key prey species for fish, marine mammals and sea birds (Read and Brownstein, 2003; Overholtz and Link, 2007). Due to their commercial significance and ecological importance Atlantic herring are one of the most intensively studied species in the world (Blaxter and Hunter, 1982; Skaret *et al.*, 2003; Kanwit and Libby, 2009).

In the Scotia-Fundy region of Atlantic Canada, the fishery primarily targets dense summer feeding, overwintering, or spawning aggregations and has been dominated by purse seine, weir and gillnet gear types (Power *et al.*, 2010). The largest single fishery in the Scotia-Fundy region is the summer purse seine fishery which occurs from May to October in the Bay of Fundy and off southwest Nova Scotia. The fishery is primarily directed towards pre-spawning, feeding aggregations during May and June and dense spawning aggregations on the spawning grounds (German Bank and Scot's Bay) from July to October (Melvin and Power, 1999; Power *et al.*, 2010).

Atlantic herring populations in the Scotia-Fundy region are managed under a global “total allowable catch” (TAC) (Melvin *et al.*, 2002). Prior to 1995, these populations were assessed as a single stock complex, however, concentrated fishing effort on individual spawning components within the region led to significant declines in abundance and the collapse of major spawning populations throughout the 1980s and 1990s (Melvin *et al.*, 2002; Stephenson *et al.*, 2009). High fishing pressure due to the introduction of highly mobile purse seining fleets in the 1970s, which currently account for more than 80% of total annual landings in the Gulf of Maine and Bay of Fundy (Power *et al.*, 2009), has had deleterious impacts on local populations (Kanwit and Libby, 2009; Stephenson *et al.*, 2009). In 1980 the Seal Island population off southwest Nova Scotia, as well as the Trinity Ledge population in 1991, collapsed due to high fishing pressure and have shown minimal signs of improvement (Smedbol and Stephenson, 2001; Melvin *et al.*, 2002; Stephenson *et al.*, 2009). Stock assessments in 1995 recognized these concerns and the quota was reduced from 151,500 tonnes in 1994 to 80,000 tonnes in 1995 (Melvin *et al.*, 2002) and is currently fixed at 50,000 tonnes (Power *et al.*, 2010).

An additional management strategy implemented in the Maritimes region of Atlantic Canada follows a “survey, assess, and then (if warranted) fish” approach for herring on key spawning grounds (Melvin *et al.*, 2002; Power *et al.*, 2009). Department of Fisheries and Oceans Canada (DFO) research scientists have been estimating and monitoring the abundance of spawning herring using hydro-acoustic surveys since 1997 (Melvin *et al.*, 2002, 2004). Industry led acoustic surveys are conducted by commercial fishing vessels using Hydroacoustic Data Processing Software (HDPS) 9320 automated logging systems that are designed for quantitative fish biomass estimates (Melvin *et al.*,

2002). Currently, there are 14 systems deployed on commercial purse seine vessels in the region, which typically conduct 5-6 surveys per year on a given spawning ground. Surveys begin once spawning fish arrive on the spawning ground and continue until herring are gone (Power *et al.*, 2010). Acoustic surveys are separated by intervals of approximately 10 to 14 days to allow for herring turnover (Power *et al.*, 2010). Turnover is defined as the length of time required for herring to aggregate, spawn and exit the spawning area (Melvin *et al.*, 2004). It is assumed that spawning herring in the Bay of Fundy and off southwest Nova Scotia move onto the spawning grounds in runs or waves with a complete turnover every 10 to 14 days (Power *et al.*, 2002; Maxner *et al.*, 2010).

Acoustic surveys on the spawning grounds are considered to provide a reliable estimate of biomass at the time of surveying; however, a summation of multiple surveys over the spawning season is required to estimate total spawning biomass and may be biased by introducing uncertainties in the overall approach (Power *et al.*, 2009). The current acoustic survey method is dependent on the elapsed turnover time of spawning fish on the spawning ground to avoid double counting of fish during repeated surveys (Stephenson *et al.*, 1999; McPherson *et al.*, 2003). If herring do not move completely off the spawning ground or if the assumed turnover time is incorrect, spawning stock biomass estimates will be biased with possible deleterious impacts to the population and the fishery.

A number of tagging studies have been conducted by Fisheries and Oceans Canada in the Bay of Fundy, off southwest Nova Scotia and on the Scotian Shelf to address the assumption of turnover time on the spawning ground and to better understand current seasonal movements of these exploited populations. Tagging studies have provided fundamental information with important management implications,

however, despite intensive research and an extensive literature on the biology of Atlantic herring, there remains a number of uncertainties associated with spawning ground turnover times of Atlantic herring and current seasonal movements (Kanwit and Libby, 2009; Stephenson *et al.*, 2009).

1.3 Objectives

The overall objective of my thesis is to utilize Fisheries and Oceans Canada mark and recapture tagging data to investigate important sources of uncertainty associated with determining spawning stock biomass for two important spawning populations of herring off southwest Nova Scotia and in the Bay of Fundy: German Bank and Scot's Bay. Chapter II addresses the first objective, determining turnover time of herring that are aggregated on these two spawning grounds. Multiple years of mark and recapture tagging data from German Bank (6 years) and Scot's Bay (3 years) were used to determine the time required for tagged fish to vacate the spawning grounds. Chapter III addresses the second objective, describing seasonal movements of adult herring away from the German Bank and Scot's Bay spawning grounds. Distances traveled and times at large of tagged fish from 11 years of tagging data were used to illustrate the migratory patterns of these herring populations to determine dispersal rates from the spawning grounds, the locations of important feeding grounds and the time spent by individuals on them, and to provide information on population integrity and connectivity. The new mark and recapture data examined in Chapter III are summarized using a novel approach that plots distance (km) against time (days) as done for herring (Kanwit and Libby, 2009) and cod (*Gadus morhua*) (Howell *et al.*, 2008) in the Gulf of Maine.

Chapters II and III are presented in article format for publication and will be submitted to a peer reviewed journal after discussion with the co-authors Martin, J.R., Methven, D. A., Melvin, G.D. and MacDonald, B.A.

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CHAPTER 2: ESTIMATING TURNOVER TIME OF *CLUPEA HARENGUS* ATLANTIC HERRING ON GERMAN BANK AND SCOT'S BAY SPAWNING GROUNDS USING MARK AND RECAPTURE DATA

2.1 Abstract

A tagging study was conducted to investigate turnover time of *Clupea harengus* Atlantic herring on the German Bank and Scot's Bay spawning grounds during the spawning season. Recapture data from herring caught on the spawning ground within the same spawning season have been examined to quantify the time required for tagged herring to vacate the spawning grounds and to determine if this varies annually and between spawning populations. Mean turnover time for Atlantic herring in Scot's Bay is slightly quicker (14.54 days for 90% of the population) compared to German Bank (16.09 days for 90% of the population). However, when individual years are considered separately (German Bank: 6 years; Scot's Bay: 3 years) there is considerable variability among years within a population in the time required to reach 90% turnover (6 to 20 days on German Bank; 7 to 17 days in Scot's Bay). Turnover times calculated in this study have important management implications, and provided information necessary to accurately estimate spawning stock biomass with acoustic surveys.

2.2 Introduction

Migrations of animals inhabiting terrestrial and aquatic environments are typically associated with the use of resources that cannot be met by a single habitat (Dingle and Drake, 2007). Fish in northern temperate habitats typically undertake three main types of migrations each year: spawning, feeding and overwintering (Harden Jones, 1968; McKeown, 1984; Lucas and Baras, 2001; Secor, 2002). Migrations have evolved in response to predictable oceanic features such as areas of high productivity where food is expected to be abundant and feeding optimal, overwintering areas where conditions are favorable for saving energy, and spawning areas where conditions are most beneficial for finding mates, spawning and survival of eggs and larvae (Harden Jones, 1968; Sinclair and Iles, 1985; Nottestad *et al.*, 1999; Dingle and Drake, 2007). The time spent at these locations depends on numerous factors including food availability (Hay, 1985; Sinclair and Iles, 1985; Corten, 2000; Corten, 2001), temperature (Hay, 1985; Ware and Tanasichuk, 1989; Corten, 2001), and size of the site (Sinclair and Iles, 1985), amongst others.

One method of examining migration is by mark and recapture (Harden Jones, 1968; Blaxter and Hunter, 1982; Schwarz *et al.*, 1993). Tagging individuals with external tags followed by their subsequent recapture provides information on patterns of migration, and rates of movement (McKeown, 1984). Mark and recapture information can also be used to estimate population size, identify sites of ecological and conservation importance, and to quantify turnover times (Kaiser, 1995; Lehnert and Kremenetz, 2005; Maxner *et al.*, 2010). Turnover time is variously defined, but for herring it is the time required for individuals to aggregate, spawn and exit the spawning area (Melvin *et al.*, 2004).

Since 1997 the calculation of spawning stock biomass (SSB) for herring in the Bay of Fundy and off southwest Nova Scotia has been based on hydro acoustic surveys conducted on the spawning grounds when herring are highly aggregated (Melvin et al., 2002). The frequency that surveys are conducted should be similar to the turnover time that herring remain on the spawning ground. Acoustic surveys are currently conducted at an assumed herring turnover time of 10 to 14 days to estimate the total SSB for a specific ground (Power et al., 2002; Clark, 2006; Maxner et al., 2010). Accurate estimates of turnover time are important for determining SSB and recommending catch levels (Stephenson et al., 1999). Surveys that are conducted too frequently risk double counting fish and overestimating SSB. Surveys that are conducted at intervals greater than the turnover time risk underestimating SSB diminishing potential socioeconomic benefits from fisheries. This can also affect the scientific advice given to management and the exploitation rates of the populations (Melvin and Power, 1999; Stephenson et al., 1999; McPherson et al., 2003; Power et al., 2009).

The objective of this study was to determine turnover times of herring on two well established and important herring spawning grounds off eastern Canada: German Bank off southwest Nova Scotia and Scot's Bay in the inner Bay of Fundy. Estimates of turnover times based upon mark and recapture data have seldom been reported for fish other than herring. In this study we modified the turnover time calculation methods of Clark (2006) and Maxner *et al.* (2010) to estimate the time herring remain on the spawning grounds and to determine if this varied annually within and between these spawning populations. Turnover times were then used to quantify the proportion of herring that remained on the spawning grounds at the time of repeated surveys during the spawning season.

2.3 Materials and methods

2.3.1 Description of study sites

This study examined herring collected and tagged on German Bank and Scot's Bay spawning grounds (Figure 2.1). The German Bank spawning ground spans approximately 646 km² with depths ranging from 50 to 80 m (Melvin and Power, 1999). Spawning occurs from mid-August to mid-October (Power *et al.*, 2010). During the non-spawning season, German Bank is an important feeding area for juvenile and adult herring and supports an active fishery during pre-spawning from April to mid-August (Power *et al.*, 2009). The Scot's Bay spawning ground covers approximately 636 km² with spawning occurring at depths of 46 to 60 m from early-July to early September (Melvin and Power, 1999; Power *et al.* 2010). The Scot's Bay population migrates to feeding and overwintering areas throughout the Bay of Fundy and off Nova Scotia when spawning is finished in September (Clark, 2006). Both spawning grounds are located in tidally energetic areas characterized by vertically well-mixed water and a bottom consisting of gravel substrate that is free from silting (Sinclair and Tremblay, 1984; Sinclair and Iles, 1985; Haegele and Schweigert, 1985; Hay *et al.*, 2001a; Colette and Klein-MacPhee, 2002).

2.3.2 Tagging

Data for this study came from herring tagged on German Bank (51,432 tagged) and Scot's Bay (14,046 tagged) spawning grounds by Fisheries and Oceans Canada personnel during the spawning period (Table 2.1). Tagging continued throughout the spawning season, but varied annually due to weather and availability of personnel (Table 2.1). Herring were caught in purse seine nets used by the commercial fishery. For a

description of this fishery and the purse seines used to capture herring, refer to Power *et al.* (2010) and Hart and Reynolds (2002). Live herring were transferred from the purse seine by dip net to a holding tank (~ 218 litres) on deck of the fishing vessel prior to being tagged. The holding tank contained ambient running seawater pumped from the sea surface and typically held approximately 150 herring at a time. Only adult fish (>23 cm; Power *et al.*, 2009) in spawning condition and no indication of injury were tagged.

A Floy tagging gun (Floy Tag and Mfg., Inc.) was used to insert a tag between the pterygiophores supporting the finrays of the dorsal fin. The FD-94 Anchor tags are 6 cm long, brightly coloured with an individual identification number and return address:

DFO/SABS NB E5B 2L9;

where: ##### represents a number unique to each tagged herring.

Herring that were caught each year in the commercial fishery were transported to fish processing plants where fish with tags were identified and matched to the fishing vessel that landed that catch. The date and location where the tagged fish were caught was then determined from the official log books kept by each vessel. From this information it is possible to determine the number of days each fish was at large and to ensure that only tags recaptured on the same spawning ground during the same spawning season were considered in the calculations of turnover time described below. A lottery was held each December as an incentive for fish processing plant employees to report recaptured fish. Individuals who returned tags with information on recapture date and location to the Fisheries and Oceans Canada St. Andrews Biological Station, St.

Andrews, New Brunswick were entered in the lottery to win one of three cash prizes (\$1000, \$500 and \$250).

2.3.3 Data analyses

A common method of analyzing mark and recapture data from commercial fisheries is to adjust the number of recaptured fish by the total weight of all fish caught (Wheeler and Winters, 1984a, b; Flostrand *et al.*, 2009; Maxner *et al.*, 2010). Adjusting recapture data by catches is important since the number of recaptured fish is dependent on the catch of the commercial fishery (Wheeler and Winters, 1984a, b; Stobo and Fowler, 2009). As such, both non-catch adjusted and catch adjusted methods were used to quantify turnover times of herring on German Bank and Scot's Bay spawning grounds. These methods are described below.

For the non-catch adjusted method, a two dimensional matrix consisting of days at large (columns) and tagging date (rows) was constructed showing the number of recaptured fish. Recaptured fish were summed for each day at large and a percentage was calculated for each day at large based on the total number of fish recaptured on the spawning ground in that year. The cumulative proportion was then calculated for each year that tagging data was available for German Bank (1998, 2001, 2005, 2009, 2010, 2011) and Scot's Bay (1998, 2005, 2006) (Table 2.1). A mean cumulative proportion of recaptured fish was then calculated across all years for each spawning ground leading to plots of mean cumulative proportions of recaptured fish against days at large (Figures 2.2 and 2.3). For the catch-adjusted method of calculating turnover time, the number of recaptured fish was divided by the total weight of all fish caught on the same day and

expressed as the number of recaptured fish per 1000 tonnes of herring for each day at large.

To determine the proportion of herring remaining on the spawning ground at any one time (i.e. turnover time) I calculated k , the instantaneous rate of change using Equation 1.

Equation 1:
$$P_t = 1 - e^{(-kt)}$$

k is equal to the slope of $\ln(1 - P_t)$ plotted against days at large (t) with the y intercept set to zero (Figure 2.4). The instantaneous rate of change of recaptured fish can then be multiplied by the days at large following Equation 1 to determine the mean cumulative proportion of fish that have left the spawning ground (P_t) if tagged fish are assumed to behave no differently than non-tagged fish.

2.4 Results

2.4.1 Recapture rates

Recapture rates of tagged herring on the spawning ground varied annually from 0.1 (1999) to 0.9% (2009) on German Bank and from 0.0 (1999) to 3.0% (2005) in Scot's Bay (Table 2.1). In 1999, only one herring out of 821 tagged was recaptured on German Bank, while none of the 2832 tagged herring were recaptured in Scot's Bay. Consequently, turnover times could not be estimated for either population in 1999. When these data were removed, recapture rates ranged from 0.3 (1998) to 0.9% (2009) on German Bank and from 0.9 (1998) to 3.0% (2005) in Scot's Bay (Table 2.1).

2.4.2 Turnover time variability

Most variability in the proportion of recaptured herring, when calculated at a daily resolution, occurred within the first several days after tagging. After 5 days at large, the cumulative proportion of (non-catch adjusted) recaptured herring ranged from 19 - 98% for German Bank (Figure 2.2) and 57 - 84% for Scot's Bay (Figure 2.3). Results were similar when recapture rates were adjusted by daily catches (German Bank: 7 - 92%; Scot's Bay: 58 - 86%) (Figures 2.2 and 2.3). Hence, there was considerable variability in the proportion of recaptured fish amongst years regardless of method (Figures 2.2 and 2.3). Variability in the proportion of recaptured fish was greater for German Bank (6 years of tagging) compared to Scot's Bay (3 years) (Table 2.1; Figures 2.2 and 2.3). Much of the variability for German Bank was influenced by two years (2001, 2005) during which there was less than six days of tagging each year (Table 2.1). Both methods (non-catch adjusted and catch adjusted) showed very similar patterns of cumulative recaptures with overlapping standard errors despite the considerable variability observed among years during the first several days at large (Figures 2.2 and 2.3). Regressions for the instantaneous rate of change (k) of recaptured fish fit the data well as indicated by high r -squared values for both German Bank ($r^2=0.973$) and Scot's Bay ($r^2=0.854$) (Figure 2.4).

2.4.3 Turnover times

Averaged turnover times for 50, 90 and 99% of recaptured herring from German Bank were 5.32, 17.66 and 35.32 days, respectively for the non-catch adjusted method and 4.84, 16.09 and 32.18 days, respectively for the catch adjusted method (Figure 2.5). Averaged turnover times were similar for Scot's Bay but slightly quicker at 4.03, 13.37

and 26.74 days for 50, 90 and 99% of recaptured herring, respectively for the non-catch adjusted method and 4.38, 14.54 and 29.07 days, respectively for the catch adjusted method (Figure 2.6). Two tagged fish caught on German Bank (October 12, 2005 and September 16, 2010) were recaptured on days with very low catches in the commercial fishery (2 and 11 tonnes), resulting in an over representation of the proportion of recaptured herring when adjusted by daily catches. If these two recaptures are considered to be outliers and excluded from the daily catch adjustment method, average turnover times increased from 4.84 to 5.23 days, from 16.09 to 17.38 days, and from 32.18 to 34.76 days for 50, 90 and 99% of recaptured herring, respectively (Figure 2.5). These two outliers represent just 0.73% (2 of 273, Table 2.1) of the recaptured herring from German Bank.

2.5 Discussion

2.5.1 Turnover times

Precise calculation of herring turnover times are necessary to determine the proportion of herring that remain on the spawning grounds at the time of repeated acoustic surveys to adjust for double counting of fish in order to calculate accurate estimates of spawning stock biomass (SSB) (Stephenson *et al.*, 2009). Surveys that are conducted too frequently risk double counting those herring that have not yet left the spawning ground since the previous survey. Double counting results in an overestimate of the SSB and could lead to changes in management such as increasing fishing quotas, which can be detrimental if population size was smaller than calculated (Stephenson *et al.*, 1999; McPherson *et al.*, 2003). Since 1997, acoustic surveys on the spawning

grounds have been conducted according to an assumed herring turnover time of 10 to 14 days to calculate SSB (Melvin *et al.*, 2002).

Reports of turnover times from herring on the spawning ground are limited (McPherson *et al.*, 2003) despite their importance for management purposes (Stephenson *et al.*, 1999; McPherson *et al.*, 2003; Power *et al.*, 2009). Previous studies on herring in Atlantic Canada have reported spawning ground turnover times of <6 days at Devastation Shoal (McPherson *et al.*, 2003), 10 days in Scot's Bay (Paul, 1999), 10 days for 75% of the population to turnover on German Bank (Paul, 1999), 14 days for 80% of the population to turnover in Scot's Bay (Clark, 2006), and 21 days for 93% of the population to turnover on German Bank (Maxner *et al.*, 2010). With the exception of McPherson *et al.* (2003), which was not a mark and recapture study, all of the above data used to estimate turnover times have been re-examined in the current study, with the addition of two previously unexamined years of mark recapture data (German Bank: 2010, 2011). Turnover times in this study were 87% (German Bank) and 89% (Scot's Bay) after 14 days using the daily catch adjusted method. This indicates that on average approximately 13 and 11% of the German Bank and Scot's Bay population, respectively, are being double counted when acoustic surveys are conducted at 14 day intervals. The proportion of double counted herring increases to 24 and 21% if surveys are conducted every 10 days.

The Scot's Bay population turns over more frequently than the German Bank population. This was evident for both the non-catch adjusted (German Bank: 18 days, Scot's Bay: 13 days, for 90% turnover) and catch adjusted (German Bank: 16 days, Scot's Bay: 15 days, for 90% turnover) methods of estimating turnover time. The catch adjusted method of turnover time calculation is considered more appropriate given that

the number of recaptured fish is dependent on (weighted by) the catch of the commercial fishery (Wheeler and Winters, 1984a, b; Flostrand *et al.*, 2009). It is also important to note that estimates of turnover time based on mark and recapture data are generally underestimates of the actual values given that individual fish may arrive on the spawning ground before they are first captured and may have remained for sometime after the date they were recaptured as noted by Kaiser (1995) for migratory birds. Hence, this suggests a more cautious approach when calculating turnover times using mark and recapture methods. Regardless of the method, estimation of turnover time can be influenced by a wide range of factors, both methodological and biological.

2.5.2 Methodological limitations to estimating turnover times

In terms of methodology, this study is heavily dependent on recapture rates of tagged herring. Low recapture rates on the German Bank and Scot's Bay spawning grounds (German Bank: $\bar{x} = 0.5\%$; Scot's Bay: $\bar{x} = 1.3\%$) are attributed to the confined temporal and spatial scales of the study. Only fish recaptured on the spawning ground during the same spawning season (~2.5 months) were considered in the analyses, i.e., the recapture rates reported here are typically for only a 75 day period when fishing occurred on the spawning ground. Additional fish were recaptured elsewhere months and years later, but are not included in the analyses because these were not relevant to the calculation of turnover time on the spawning ground. Consequently, it is not surprising that recapture rates for this study were typically less than 1%. Recapture rates for other species are often calculated for other purposes, and hence are higher given that rates are usually calculated over several years and are not restricted to fish recaptured in a small area, such as a spawning ground. Tagging studies in the northwest Atlantic

reported recapture rates of 30% (Templeman, 1974) and 20% (Fowler and Stobo, 1999) for *Gadus morhua* Atlantic cod, 15% for *Hippoglossoides platessoides* American plaice, 10% for *Pollachius virens* pollock and 5% for *Melanogrammus aeglefinus* haddock (Fowler and Stobo, 1999). Recapture rates as high as 2.6% have been reported for Atlantic herring off Maine and New Hampshire (Kanwit and Libby, 2009), 3.8% off eastern Newfoundland (Wheeler and Winters, 1984b) and 4.8% in the Gulf of St. Lawrence (Stobo and Fowler, 2009). Detection rates in processing plants are also important and have been reported to be as low as 33% (Kanwit and Libby, 2009).

Factors that reduce fishing effort also affect the number of tagged herring that are recaptured (Wheeler and Winters, 1984a; Beentjes and Francis, 1999; Kanwit and Libby, 2009). If fishing effort is reduced due to weather conditions, quota restrictions or to the availability of fish, the number of recaptured fish will also be reduced, hence the importance of using catch-adjusted data to mitigate this limitation. In addition, fishing is typically only conducted in specific areas and the lack of fishing in a particular area clearly does not preclude herring from being there (Power *et al.*, 2010).

2.5.3 Biological limitations to calculating turnover times

Additional uncertainties to calculating turnover times may also arise from biological factors including the assumptions that German Bank and Scot's Bay spawning populations are closed populations at the time of spawning and that spawning herring actually turnover (i.e. depart after spawning). This assumption is important because intermixing of individuals from different populations during spawning may interfere with population specific turnover times. Alternatively, tagging studies provide strong evidence that herring of different populations do not intermix during spawning (Wheeler

and Winters, 1984b; Sinclair and Iles, 1985; Stephenson *et al.*, 2009), rather, they exhibit a high degree of spawning ground fidelity, spawning with the same population on the same spawning ground each year (Cushing, 1967; Hourston, 1982; Wheeler and Winters, 1984a; Hay *et al.*, 2001b; Flostrand *et al.*, 2009). For this reason, German Bank and Scot's Bay are assumed to be closed populations. This assumption is investigated further in Chapter III for the German Bank and Scot's Bay populations. Furthermore, it has been suggested that in contrast to spring spawners, fall spawning herring (which includes both German Bank and Scot's Bay populations) leave the spawning ground and move to deeper water as soon as they have spawned (Jean, 1956; Lambert, 1984). Additionally, the near absence of spent fish in commercial catches during fall spawning support a rapid departure from the spawning ground (Jean, 1956; Lambert, 1984; Stephenson *et al.*, 2009).

Turnover times may also be influenced by partial migrations away from the spawning grounds. Partial migration describes the situation where migratory and resident (non-migratory) individuals spawn with the same population (Jonsson and Jonsson, 1993; Pulido, 2011; Chapman *et al.*, 2012). If German Bank or Scot's Bay herring exhibit a degree of partial migration, some tagged fish may immediately move off the spawning ground (migratory) while others may reside there, or nearby, longer after spawning (resident) which would increase the variability in turnover time calculations and consequently affect accurate SSB estimates.

Factors that influence the timing of spawning may also affect turnover time. If environmental conditions are poor during the spawning season, spawning may be delayed. Herring may then reside on the spawning grounds longer increasing the turnover time. In contrast, if conditions are suitable for spawning, turnover time may be

expected to be shorter. Temperature has been reported to influence the timing of spawning in marine fish (Hutchings and Myers, 1994; Carscadden *et al.*, 1997; Wieland *et al.*, 2000), including herring (Sinclair and Tremblay, 1984; Hay, 1985; Lambert, 1987; Lambert and Messieh, 1989; Ware and Tanasichuk, 1989; Winters and Wheeler, 1996). Hence, varying temperatures within and between spawning seasons may result in turnover time variation.

Numerous factors not yet known may affect the turnover time of Atlantic herring on the spawning ground that in this study was slightly shorter for Scot's Bay (14.54 days for 90% of the population) compared to German Bank (16.09 days for 90% of the population), however, when individual years are considered separately (German Bank: 6 years; Scot's Bay: 3 years) there is considerable variability among years within a population ranging annually from 6 to 20 days on German Bank and from 7 to 17 days in Scot's Bay for 90% turnover.

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Table 2.1: Summary of tagging on German Bank and at Scot's Bay used to determine turnover times of adult herring on their spawning grounds. To quantify turnover times, only fish that were tagged and recaptured on the same spawning ground during spawning season are considered in the evaluation.

Spawning ground tagging location	Year	Tagging dates	Number of tagging days	Number of fish tagged on spawning ground	Number of tags returned from spawning ground	Percent recaptured on spawning ground
German Bank	1998	Aug. 20 - Sep. 22	14	9730	30	0.3
	1999	Sep. 21 - Sep. 22	2	821	1	0.1
	2001	Sep. 17 - Sep. 19	3	9402	47	0.5
	2005	Aug. 30 - Oct. 05	5	8487	43	0.5
	2009	Aug. 19 - Sep. 30	15	10333	94	0.9
	2010	Aug. 19 - Oct. 12	10	6036	22	0.4
	2011	Aug. 24 - Sep. 29	12	6623	36	0.5
Scot's Bay	1998	Aug. 23 - Aug. 25	2	2367	21	0.9
	1999	Aug. 11 - Aug. 21	2	2832	0	0.0
	2005	Jul. 28 - Aug. 24	4	5047	150	3.0
	2006	Jul. 28 - Aug. 20	3	3800	45	1.2

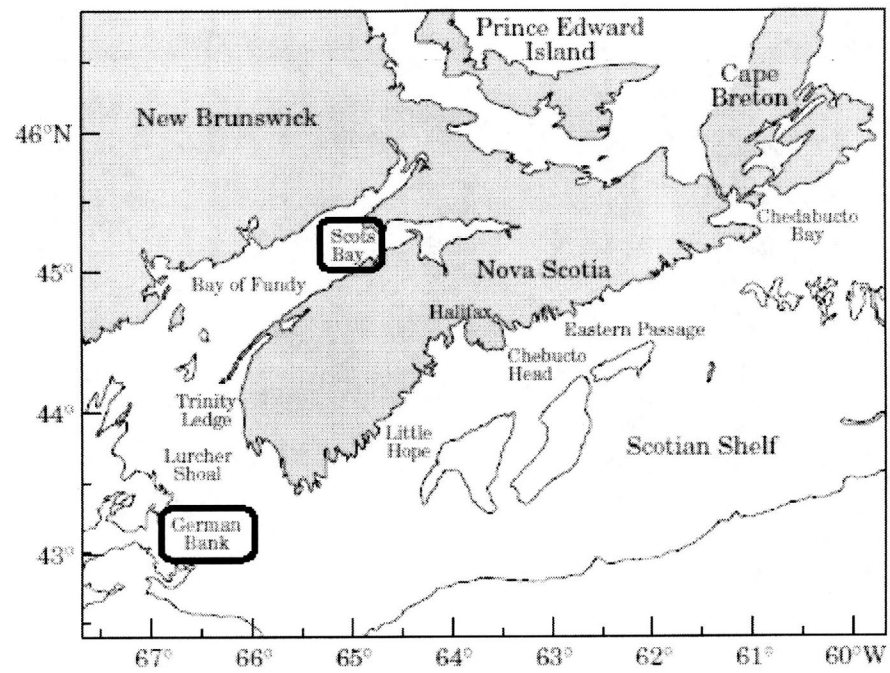


Figure 2.1: Locations of German Bank and Scot's Bay spawning grounds off eastern Canada (Melvin *et al.*, 2002).

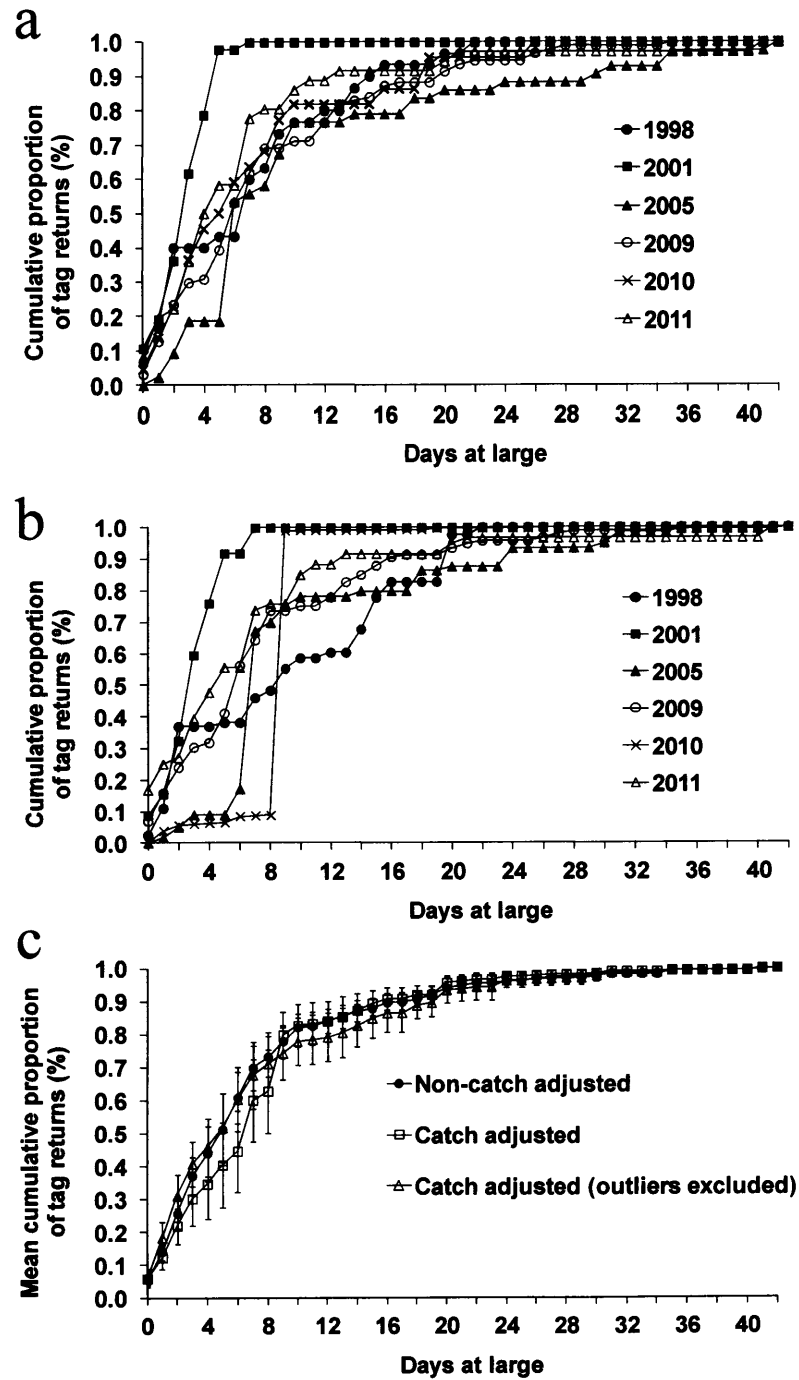


Figure 2.2: Cumulative proportions of (a) non-catch adjusted and (b) catch adjusted recaptured Atlantic herring on the German Bank spawning ground and (c) non-catch adjusted and catch adjusted mean cumulative proportions with all years combined at a daily resolution. Error bars are one standard error above and below the mean.

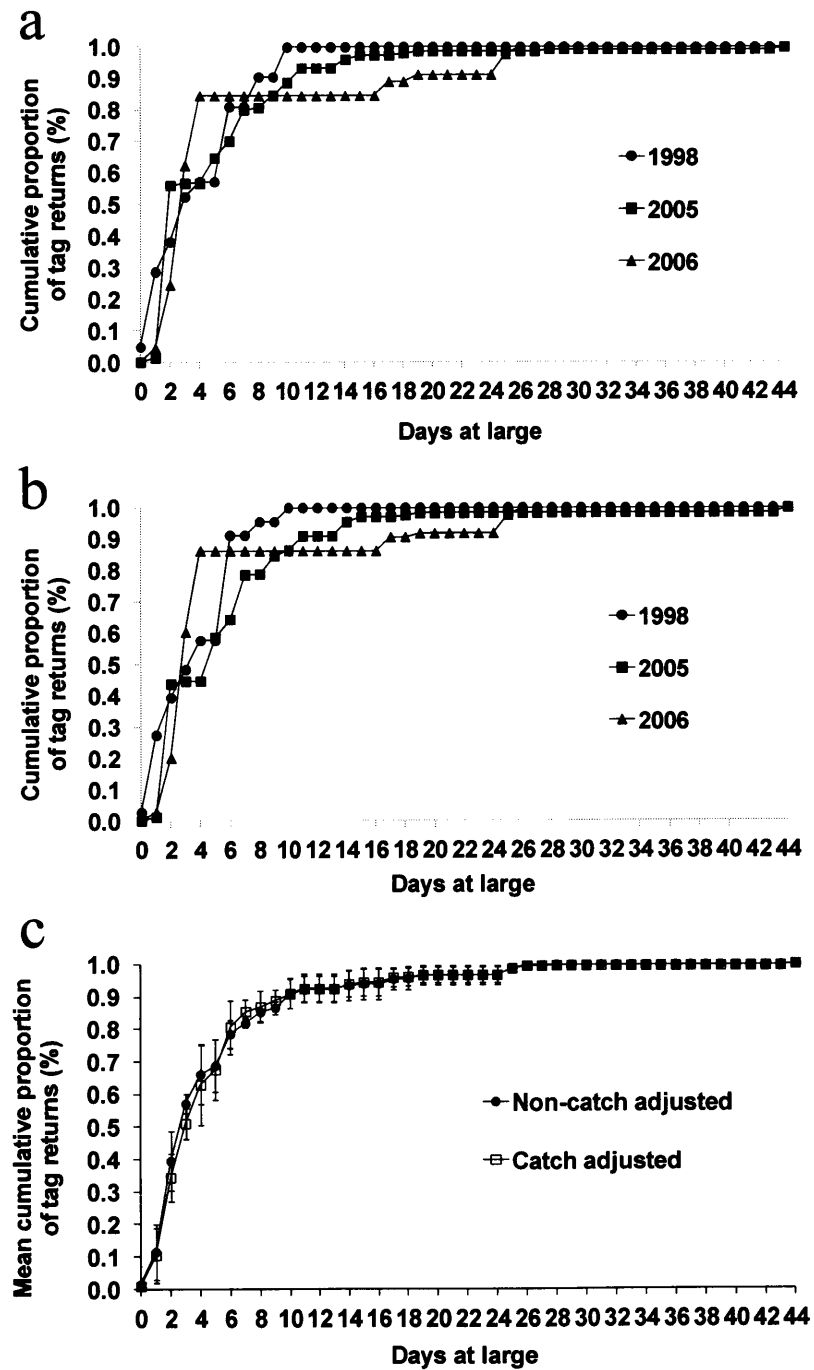


Figure 2.3: Cumulative proportions of (a) non-catch adjusted and (b) catch adjusted recaptured Atlantic herring on the Scot's Bay spawning ground and (c) non-catch adjusted and catch adjusted mean cumulative proportions with all years combined at a daily resolution. Error bars are one standard error above and below the mean.

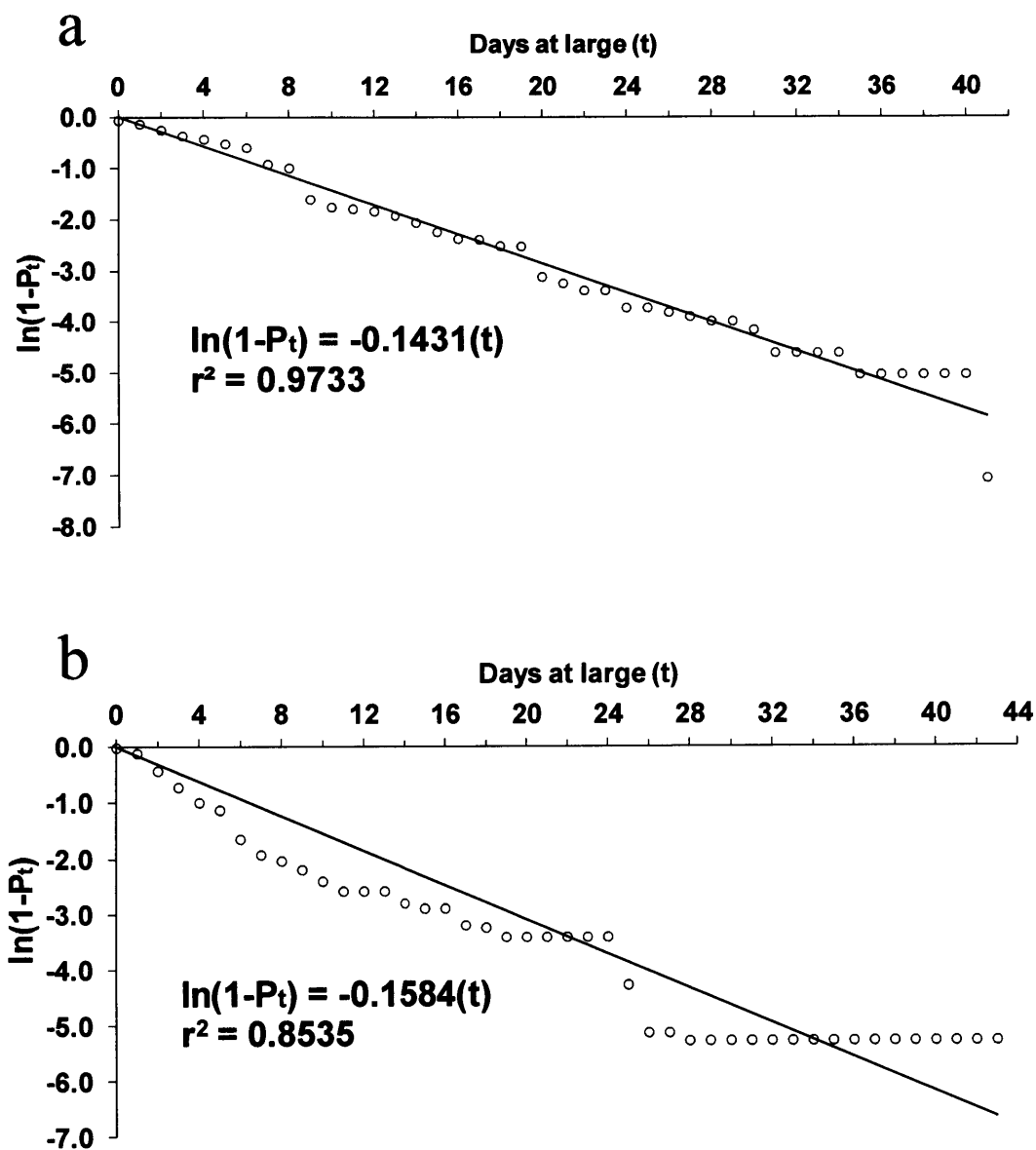


Figure 2.4: Example of regression analysis of the mean cumulative proportion of recaptured herring ($\ln(1-P_t)$) on (a) German Bank and at (b) Scot's Bay for the catch adjusted method where the slope is equal to the instantaneous rate of change (k) of recaptures during the spawning season.

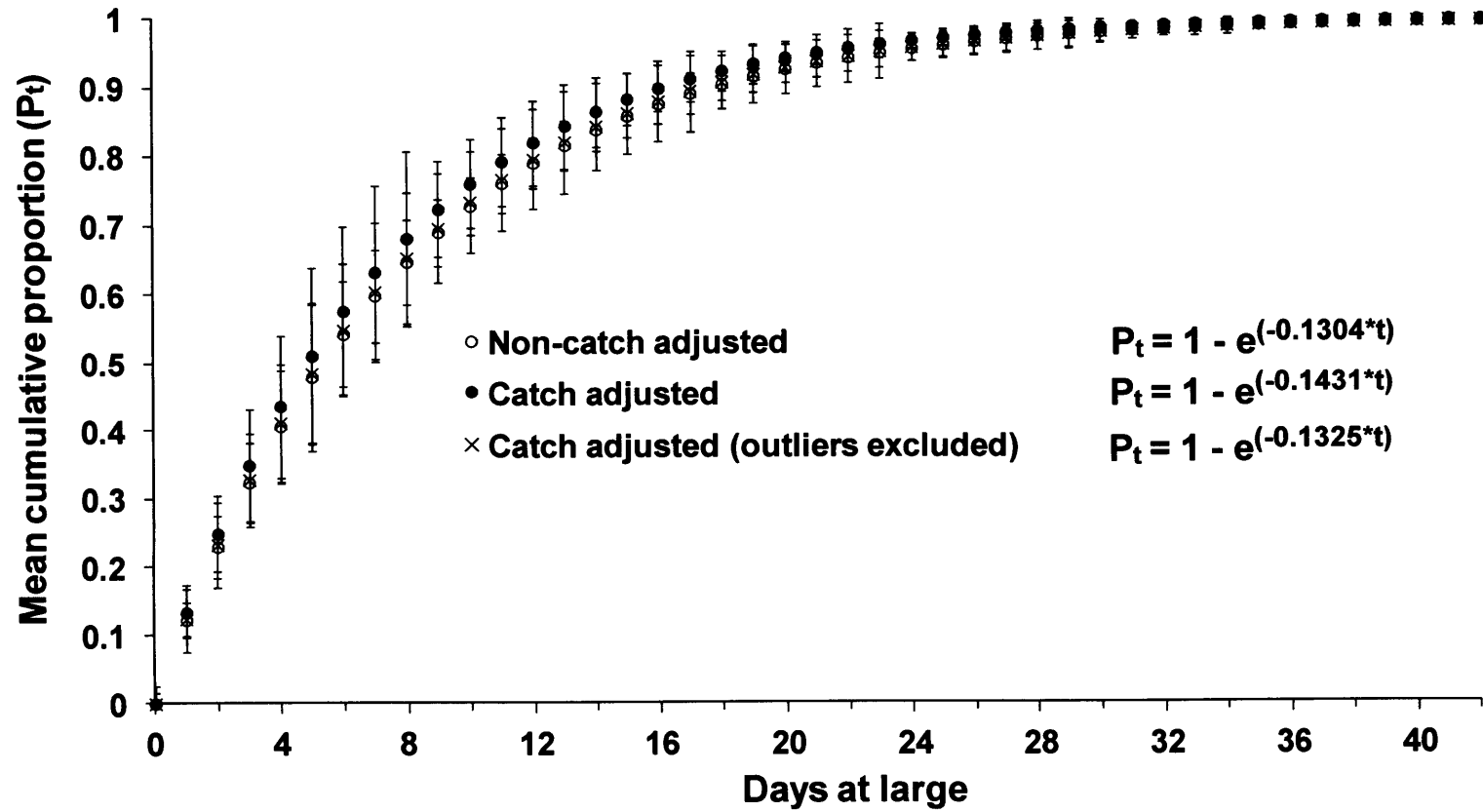


Figure 2.5: Non-catch adjusted and catch adjusted mean turnover times for Atlantic herring on the German Bank spawning ground. Error bars are one standard error above and below the mean.

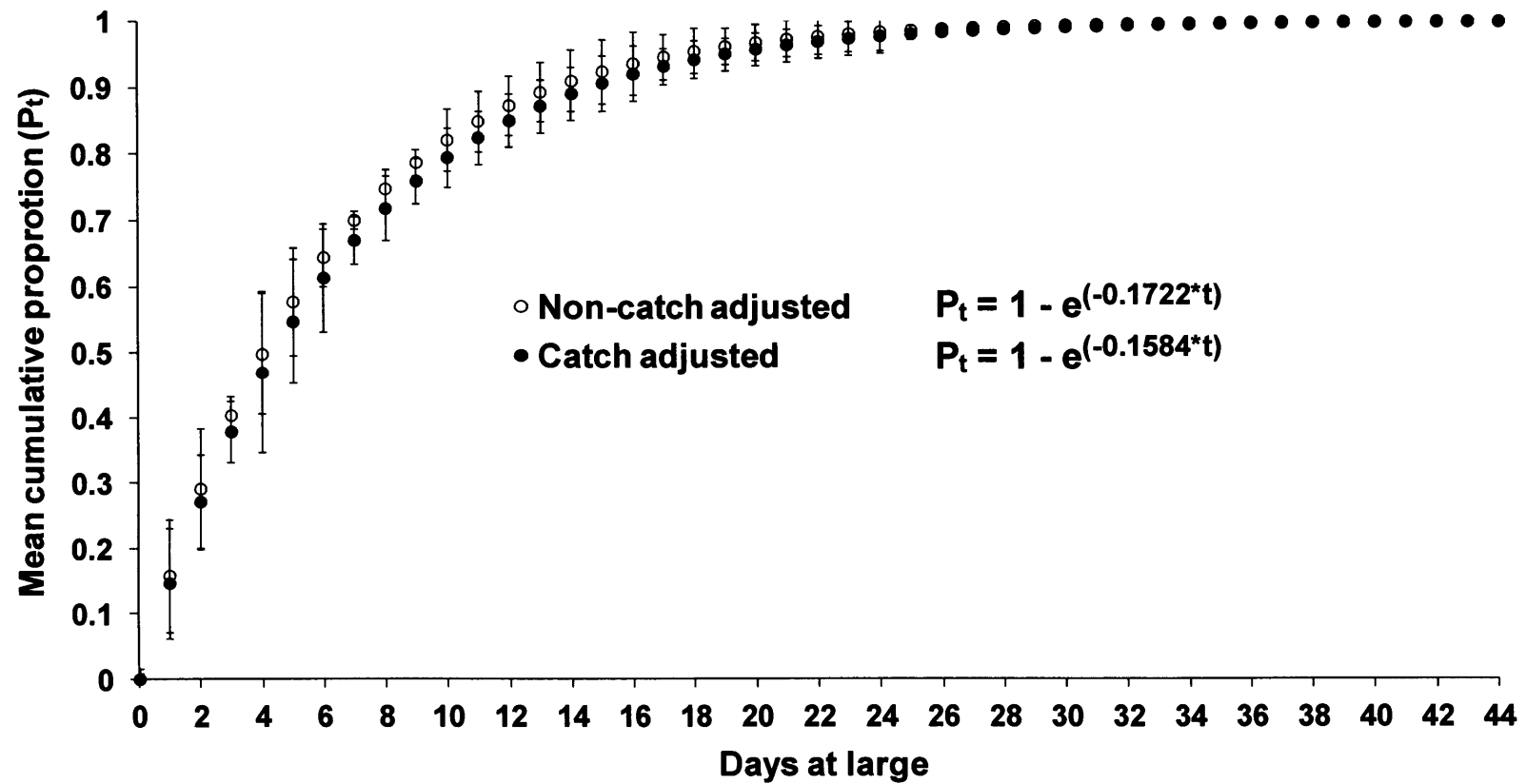


Figure 2.6: Non-catch adjusted and catch adjusted mean turnover times for Atlantic herring on the Scot's Bay spawning ground. Error bars are one standard error above and below the mean.

CHAPTER 3: MIGRATION BETWEEN SPAWNING AND FEEDING GROUNDS OF *CLUPEA HARENGUS* ATLANTIC HERRING IN THE BAY OF FUNDY AND OFF SOUTHWEST NOVA SCOTIA USING MARK AND RECAPTURE DATA

3.1 Abstract

Eleven years of mark and recapture data were examined to determine the seasonal movements of two populations of *Clupea harengus* Atlantic herring off eastern Canada: German Bank and Scot's Bay. Distance traveled was plotted against time at large to compare the migratory patterns of these populations and to determine locations and times spent at feeding grounds, dispersal rates from the spawning grounds, and to provide information on population integrity and connectivity. German Bank herring were more broadly distributed when feeding and were recaptured near the approaches of the Bay of Fundy, throughout the Gulf of Maine and on the offshore banks of the Scotian Shelf. More than 99% of herring tagged on the Scot's Bay spawning ground were recaptured within the Bay of Fundy. During feeding, these herring were distributed primarily off southwest New Brunswick, Grand Manan Island and Long Island shore, Nova Scotia. There was no significant difference in the distances moved between German Bank and Scot's Bay herring. Dispersal from the spawning ground was significantly greater for herring spawning in Scot's Bay after 3-4 ($p=0.002$), 5-8 ($p<0.0001$), 9-16 ($p<0.0001$) and >16 ($p=0.031$) days at large. Outside of the spawning season, both populations tended to occur in the approaches of the Bay of Fundy where they mixed during feeding. There was no mixing of the two populations during the spawning season supporting the assumption that herring spawn as a closed population.

3.2 Introduction

Adult fish typically undertake annual migrations for the purposes of spawning and feeding (Harden Jones, 1968; McKeown, 1984; Dingle and Drake, 2007). Migratory routes between spawning and feeding habitats are related to water currents which provide directional cues and can increase travel speed and decrease energy requirements of the migrant (Harden Jones, 1968; Smith, 1985; Binder *et al.*, 2011). Migrations from spawning to feeding areas are said to be denatant (in the direction of the current), while return spawning migrations are contranatant (against the current) and are energy demanding (Harden Jones, 1968; Nottestad *et al.*, 1999; Slotte and Fiksen, 2000). Despite the energetic costs, migrations are thought to be an adaption towards improved fitness and subsequently increased population size (Nikolskii, 1963; Roff, 1988) where factors such as environmental conditions, availability of food and favourable reproductive conditions are considered to be important (McKeown, 1984; Nottestad *et al.*, 1999; Dingle and Drake, 2007).

In the northwest Atlantic, *Clupea harengus* herring is a highly migratory schooling pelagic fish species ranging from northern Labrador (60°N) to Cape Hatteras, North Carolina (35°N) (Scott and Scott, 1988; Collette and Klein-MacPhee, 2002; Melvin *et al.*, 2009). Tagging studies have been conducted in the northwest Atlantic since the 1950s to examine herring migration patterns and population structure (McKenzie and Skud, 1958; Stobo and Fowler, 2009). In the Maritimes region of eastern Canada, the last large scale tagging program was conducted 30-40 years ago (Stobo and Fowler, 2009), around the same time as the introduction of the highly mobile and efficient purse seine fishing gear. Since this time, there have been major changes in herring distribution and the relative abundance of major spawning components (Paul,

1999; Melvin *et al.*, 2002; Power *et al.*, 2010), including the loss of several spawning populations due to fishing pressure and poor recruitment (Smedbol and Stephenson, 2001; Stephenson *et al.*, 2009). Continuous examination of the movements of these migratory fish and their population dynamics is an essential step for management of commercial fisheries.

Northwest Atlantic herring first mature and spawn at three or four years of age (23 to 28 cm Total Length [TL]) (Collette and Klein-MacPhee, 2002; Power *et al.*, 2010) and then begin a predictable annual migration between spawning and feeding grounds, which often involves traveling considerable distances in short periods (Creaser *et al.*, 1984; Lambert, 1987; Stephenson *et al.*, 2009). There is an extensive literature indicating herring exhibit a high degree of fidelity towards population specific spawning grounds (Blaxter and Holliday, 1963; Hay, 1985; Slotte, 2001; Stephenson *et al.*, 2009), while the locations of overwintering and summer feeding grounds can vary and include herring from more than one population (Sinclair and Iles, 1985; Scott and Scott, 1988; Stephenson *et al.*, 2009; Stobo and Fowler, 2009). Although migration routes are relatively stable (Harden Jones, 1968; Corten, 2002), changes in migration routes between spawning and feeding grounds can occur when populations become unstable due to stock collapse (Dragesund *et al.*, 1997; Huse, 2002), strong recruitment (Dragesund *et al.*, 1997; Huse, 2002), high exploitation (Dragesund *et al.*, 1997; Melvin *et al.*, 2009) or changes in environmental factors (Corten, 2001; Huse, 2002; Melvin *et al.*, 2009).

The objective of this study is to examine 11 years of mark and recapture data for two commercially important herring populations (German Bank and Scot's Bay) off eastern Canada. Distances traveled and times at large were plotted to document the

migratory patterns of these populations at lower population sizes and determine i. locations and times spent at feeding grounds, ii. dispersal rates from the spawning grounds, and to iii. provide information on population integrity and connectivity.

3.3 Materials and methods

3.3.1 Tagging and recapture of herring

All herring examined in this study were adults greater than 23 cm in TL (Power *et al.*, 2009) in spawning condition that were tagged on German Bank (1998, 1999, 2001, 2005, 2009, 2010, 2011) and Scot's Bay (1998, 1999, 2005, 2006) spawning grounds by Fisheries and Oceans Canada personnel during the spawning period (Table 3.1; Figure 2.1). Herring were caught in purse seine nets used by the commercial fishery. For a description of this fishery and the purse seines used to capture herring, refer to Power *et al.* (2010) and Hart and Reynolds (2002). Tagging procedures and a more detailed description of the study sites are provided in Chapter II (Section 2.3).

Herring that are caught each year in the commercial fishery were transported to fish processing plants where fish with tags are identified and matched to the fishing vessel that landed that catch. The date and location where the tagged fish were caught was then determined from the official log books kept by each vessel. It is then possible to determine the number of days each fish was at large and the distances traveled between where it was tagged and subsequently recaptured. Because the actual distance traveled by each recaptured fish is not known, minimum straight line distances between the tag application site and recapture location are used in this study and in most other tagging studies on herring (Hay and McKinnell, 2002; Kanwit and Libby, 2009) and other species (*Solea solea*: Koutsikopoulos *et al.*, 1995; *Polyprion oxygeneios*: Beentjes

and Francis, 1999; *Gadus morhua*: Howell *et al.*, 2008). An annual lottery of three cash rewards (\$1000, \$500 and \$250) was held each December as an incentive for fish processing plant employees to submit recaptured tags and recapture information to the Fisheries and Oceans Canada Biological Station in St. Andrews, New Brunswick.

3.3.2 Data analyses

The distance traveled by each recaptured fish was plotted against the number of days at large for all years combined for each spawning population (German Bank and Scot's Bay) to develop time and distance plots as done previously for *Gadus morhua* cod (Howell *et al.*, 2008) and herring (Kanwit and Libby, 2009) in the Gulf of Maine. A straight trajectory distance between the release location and recapture location was calculated using A Contouring Application (ACON) (Black, 1991). In cases where a straight trajectory created a path through land, a non-linear distance was calculated by measuring the most direct route around the land mass.

Recaptured herring from all years were arbitrarily grouped by the number of days at large (0-1, 2, 3-4, 5-8, 9-16 and >16 days at large) separately for German Bank and Scot's Bay to compare distances (km) moved by tagged fish. A two-way analysis of variance (ANOVA) was conducted to examine the effect of population and days at large on distances moved; however, the data did not meet the assumption of homogeneity of variances when untransformed (Levene's test: $F_{13, 599} = 37.27$, $p < 0.0001$) or transformed (square root: $F_{13, 599} = 25.29$, $p < 0.0001$; $\log_{10}(x+1)$: $F_{13, 599} = 8.15$, $p < 0.0001$). The two-way ANOVA was decomposed and a one-way ANOVA was used to compare distances moved between populations. t-tests were then conducted to compare distances moved

between populations at the following temporal scales (0-1, 2, 3-4, 5-8, 9-16 and >16 days at large). Statistical tests were performed using IBM SPSS Version 20 at $\alpha = 0.05$.

The direction (degrees from true north: N=0°, E=90°, S=180°, W=270°) traveled by each recaptured fish was calculated using ACON software and plotted against distance traveled for that same fish. Rayleigh's test was conducted following procedures described by Zar (1999) to determine whether herring recaptured on and off the spawning grounds had a preferred direction traveled after tagging by calculating the mean angle of dispersion. Separate analyses were done for herring recaptured on and off the spawning grounds so that the preferred direction traveled by fish that moved off the spawning ground was not influenced by those that remained on the spawning ground. Mean angles of dispersion were also calculated for each temporal bin (0-1, 2, 3-4, 5-8, 9-16 and >16 days at large) for herring recaptured off the spawning ground to temporally investigate post-spawning movements of tagged herring.

3.4 Results

3.4.1 Recapture summary and locations

A total of 65,478 herring were tagged on German Bank (n=51,432) and Scot's Bay (n=14,046) spawning grounds (Table 3.1, Figure 3.1). Overall recapture rates of tagged herring were 0.81% for German Bank and 2.90% for Scot's Bay. Recaptured fish were removed from the analyses if time of recapture or recapture location was not provided. Removal of these data reduced recapture rates to 0.68% for German Bank (n=349) and 1.88% for Scot's Bay (n=264) (Table 3.1).

Most herring tagged on German Bank were recaptured there either during the same spawning season (0 – 42 days at large: n=273, 78.22%), the following spawning

season (338 – 400 days at large: $n=22$, 6.30%), or two spawning seasons after being tagged (714 – 768 days at large: $n=5$, 1.43%) (Figures 3.2 and 3.3). In addition, three (0.86%) fish were recaptured on German Bank prior to the beginning of the spawning season (July 31, 2008; July 8, 2011; July 29, 2012) after 298, 306 and 1059 days at large, respectively (Figure 3.3). A similar pattern was observed for Scot's Bay recaptures with 73.11% ($n=193$) being recaptured on the spawning ground during the same spawning season (0 – 44 days at large) and 0.38% ($n=1$) recaptured during the following spawning season after 348 days at large (Figures 3.2 and 3.3).

Tagged herring were commonly recaptured in the Bay of Fundy during the non-spawning season (Figure 3.2) by the commercial purse seiner fleet and by stationary fishing weirs. Intermixing of these populations occurred in late fall and in summer at three areas near the entrance of the Bay of Fundy: Fundy Isles off southwest New Brunswick (German Bank: 6.52%, Scot's Bay: 55.07%), off Long Island shore, Nova Scotia (German Bank: 8.70%, Scot's Bay: 26.09%) and off Grand Manan Island, N.B. (German Bank: 26.09%, Scot's Bay: 13.04%) (Figure 3.2). Fish recaptured at the entrance of the Bay of Fundy accounted for 41.31% of the recaptured herring that vacated German Bank and 97.10% that vacated Scot's Bay. Other German Bank recaptures were taken on Trinity Ledge/Lurcher off Yarmouth, N.S. ($n=4$; 8.70%; a distance of 48.14 – 68.27 km) during the summer and fall purse seine fishery (Power *et al.*, 2010), in the Gulf of Maine ($n=7$; 15.22%; 142.82 – 524.10 km) during the American fall and winter purse seine and trawl fishery (Collette and Klein-MacPhee, 2002; Kanwit and Libby, 2009) and from the offshore banks of the Scotian Shelf ($n=12$; 28.26%; 326.62 – 370.61 km) during the early summer purse seine fishery (Table 3.2, Figure 3.2) (Power *et al.*, 2010).

Herring that were tagged together in some instances were subsequently recaptured together in the same catch suggesting that fish remain together for an extended period of time. A total of 83 (24.64%) herring that were tagged on German Bank were recaptured with at least one other herring that was tagged at the same time and location. The number of fish recaptured together ranged from two to 12 and this occurred on 31 different occasions. A much larger proportion ($n=176$, 66.67%) of recaptured fish tagged in Scot's Bay were recaptured with at least one other fish at the same time and location with numbers ranging from two to 49 fish recaptured together at one time on 36 occasions. Most multiple fish that were recaptured together were taken on their respective spawning grounds during the same spawning season that they were tagged (German Bank: 90.36%, Scot's Bay: 86.36%). Others were recaptured together over considerable periods and distances including two tagged herring recaptured together 253 days later on the offshore banks of the Scotian Shelf 344.43 km away from German Bank.

3.4.2 Dispersal rates

In general, with increasing time after tagging, dispersal (km traveled) from the spawning ground increased for both German Bank and Scot's Bay herring (Table 3.2). Distance traveled was generally greater for German Bank herring (Table 3.2) given that most fish tagged in Scot's Bay remained within the Bay of Fundy (Figure 3.2).

A two-way analysis of variance (ANOVA) was conducted to examine the effects of population and days at large on the distance traveled by tagged herring; however, the data did not meet the assumptions of homogeneity of variances when untransformed (Levene's test: $F_{13, 599} = 37.27$, $p < 0.0001$) or transformed (square root transformed: $F_{13,$

$_{599} = 25.29, p < 0.0001$; $\log_{10}(x+1)$ transformed: $F_{13, 599} = 8.15, p < 0.0001$). A one-way ANOVA using untransformed data with variances being homogeneous (Levene's test: $F_{1, 611} = 2.17, p = 0.141$) was used to compare distances moved by tagged fish between populations. There was no significant difference in the distances moved between populations ($F_{1, 611} = 2.949, p = 0.086$). Separate t-tests were then conducted to investigate differences in distances moved between populations for each of the six temporal bins representing days at large (i.e. 0-1, 2, 3-4, 5-8, 9-16, >16) (Table 3.2). The untransformed data violated the assumption of homogeneity of variance for all temporal bins except 0-1; consequently the data were $\log_{10}(x+1)$ transformed. This resulted in only two bins violating the assumption of homogeneity (3-4: $p < 0.0001$, >16: $p < 0.0001$). t-tests, like ANOVA, are robust to violation of the assumptions (Zar, 1999) and results are reported for the t-tests on all temporal bins (Table 3.2) in conjunction with non-parametric Kruskal Wallis tests which provided the same findings as the t-tests for all temporal bins except >16 days at large where the t-test indicated a significant difference between the two populations in distance moved (Table 3.2) compared to the Kruskal Wallis test (0-1 days: $p = 0.111$; 2 days: $p = 0.294$; 3-4 days: $p = 0.030$; 5-8 days: $p < 0.0001$; 9-16 days: $p < 0.0001$; >16: $p = 0.070$). A significant difference in the distances moved by tagged fish first occurs at 3-4 days at large ($p = 0.002$), becoming highly significant at 5-8 ($p < 0.0001$) and 9-16 ($p < 0.0001$) days at large (Table 3.2) and remains significant for >16 days at large ($p = 0.031$).

Significant differences between distances moved by German Bank and Scot's Bay herring is related to faster dispersal rates and hence shorter residency times for herring spawning in Scot's Bay (Table 3.2). Considerable movement away from Scot's Bay occurred as early as two days after tagging with six fish recaptured at distances

greater than 140 km (146.2 – 201.6 km) (Table 3.2). Of the 69 fish recaptured outside Scot's Bay, 45 (65.22%) were recaptured within 16 days at distances ranging from 68.3 – 268.8 km (average 152.7 km, generally within the Bay of Fundy). In contrast, only 9 (19.57%) of the 46 fish recaptured away from German Bank were recaptured within 16 days at distances ranging 48.1 – 181.3 km (average 130.7 km).

3.4.3 Movement of herring on and off the spawning grounds

There was no significant trend in mean direction traveled by fish recaptured on the German Bank spawning ground; however, there was a tendency to move southeast on the spawning ground, a mean distance of 7.0 km ($\alpha = 88^\circ$; $z = 1.26$; $p > 0.20$). Overall, there was a significant trend to move north into the Bay of Fundy (41.31%) for herring that left German Bank ($\alpha = 1^\circ$; $z = 8.83$; $p < 0.001$); however, this result masks the fact that smaller, but noteworthy, proportions were recaptured in the Gulf of Maine (15.22%) and on the offshore banks of the Scotian Shelf (28.26%) (Figure 3.2). The number of tagged herring recaptured off German Bank within 16 days was minimal ($n=9$, Table 3.3); therefore, mean angles of dispersion were not calculated for this small number of herring.

In contrast, herring recaptured on the Scot's Bay spawning ground ranged from 0 to 34.9 km and were primarily recaptured inshore of where they were tagged, usually near the coast of Nova Scotia (Figure 3.2) indicated by a significant mean direction traveled ($\alpha = 143^\circ$; $z = 33.05$; $p < 0.001$). Movement away from Scot's Bay was exclusively southwest towards the entrance of the Bay of Fundy ($\alpha = 253^\circ$; $z = 65.25$; $p < 0.001$) with significant mean angles of dispersion for all days at large temporal bins (Table 3.3). As time after tagging increased (i.e., 0-1, 2, 3-4, 5-8, 9-16, > 16 days at

large), the mean direction traveled shifted (Table 3.3) indicating the initial movements after spawning were generally towards the New Brunswick side of the Bay of Fundy to the Fundy Isles off southwest New Brunswick, followed by movements to the south off Grand Manan Island and continuing off Long Island shore on the Nova Scotia side of the Bay of Fundy.

3.5 Discussion

This study explored eleven years of mark and recapture data from herring tagged on the German Bank and Scot's Bay spawning grounds during the spawning season to understand movements and distributions of these two commercially important populations. Given the importance of the commercial fishery in this mark and recapture study, I first discuss how the fishery influences my interpretation of herring movement and distribution.

3.5.1 Interpreting seasonal movements in relation to the fishery

The most significant limitation to studying seasonal movements of herring in this mark and recapture study is that it relies entirely on the time and location of the commercial fishery, i.e. herring are recaptured and reported only for times and locations where a commercial fishery (usually herring) occurs.

Many factors can influence when and where the commercial fishery takes place including management regulations (e.g., quota restrictions), market conditions, the availability of fish (abundance), accessibility to fishing grounds and fuel costs (Power *et al.*, 2010). In the Scotia-Fundy region, a substantial reduction of the total allowable catch (TAC) due to decreasing herring abundance in 1995 effectively reduced fishing

efforts on many traditional fishing grounds (Melvin *et al.*, 2002). Consequently, fishing has been concentrated in fewer areas that are more accessible and closer to market, thereby reducing the distance traveled and fuel costs (Power *et al.*, 2010). Restricted coverage of the commercial fishery in this region consequently affects how seasonal movements are interpreted relative to historical reports when the herring fishery was much more broadly distributed. Hence, the lack of fishing in a particular area clearly does not preclude herring from being there (Power *et al.*, 2010).

Given the restricted coverage of the commercial fishery in the Scotia-Fundy region it is not surprising that most recaptured herring in this study came from relatively few fishing grounds. The largest proportions of annual catches from the Scotia-Fundy region are typically taken off Grand Manan Island during summer feeding and on German Bank during fall spawning, with smaller proportions taken in Scot's Bay, Long Island shore, and off southwest Nova Scotia (Gannet/Dry Ledge) (Power *et al.*, 2010). Smaller fisheries also exist in this region that are managed outside of the TAC including a weir/shutoff fishery off southwest New Brunswick that primarily relies on aggregations of juvenile herring believed to originate from coastal Maine during summer and fall, a roe gillnet fishery along the eastern coast of Nova Scotia during fall spawning, and a purse seine fishery on the offshore banks of the Scotian Shelf during May and June (Power *et al.*, 2010). With the exception of recaptures taken in the Gulf of Maine during the American winter purse seine and trawl fishery, virtually all herring recaptures were from the fishing grounds described above.

One way of mitigating this limitation is to conduct acoustic surveys in areas that no longer have active fisheries or have not traditionally been fished. Industry led acoustic surveys have been conducted on the Trinity Ledge spawning ground off

southwest Nova Scotia since 1999 to document the amount of spawning fish (Melvin *et al.*, 2002); however, since the fishery collapsed in 1991, virtually no spawning has occurred (DFO, 2013). Conducting acoustic surveys during the overwintering period would be most beneficial given the absence of fisheries during this time and hence lack information on overwintering migrations.

Interpreting seasonal movements of a highly migratory, pelagic fish species like herring based on mark and recapture data collected by the commercial fishery typically does not provide a complete representation of their movements and distribution, i.e. the lack of fishing in a particular area clearly does not preclude herring from being there (Power *et al.*, 2010). The proposed migration patterns formulated below are based on the timing and location of recaptured herring, dispersal rates from the spawning grounds, mean angles of dispersion, historical reports of herring distribution and general fish migration theory.

3.5.2 Migration between spawning and feeding grounds

Post-spawning movements of German Bank and Scot's Bay herring differed in where tagged fish went after spawning, and the rates that they left the spawning grounds. German Bank herring were broadly distributed, occurring near the approaches of the Bay of Fundy, throughout the coastal Gulf of Maine as far south as Rhode Island, and on the offshore banks of the Scotian Shelf. This contrasts with Scot's Bay herring that, with the exception of two fish, did not leave the Bay of Fundy. Both populations were present in the approaches of the Bay of Fundy, specifically off Grand Manan Island, off Long Island shore, and in the Fundy Iles area off southwest New Brunswick where they mixed presumably for the purpose of feeding during fall and summer, an observation supported

by Stobo and Fowler (2009) for herring mark and recapture data from 1973-1983.

Feeding grounds at the entrance of the Bay of Fundy are approximately 89.5 – 181.3 km from the German Bank spawning ground and approximately 104.2 – 211.2 km from the Scot's Bay spawning ground.

Dispersal from the spawning ground was greatest for German Bank herring with one recapture taken over 520 km from the tagging site, but was significantly faster for herring from Scot's Bay. Several fish tagged in Scot's Bay were first recaptured just two days later near the entrance of the Bay of Fundy having traveled up to 201 km.

Comparable rates for German Bank herring were not observed until >16 days at large. Similar rates of dispersal have been reported for herring tagged in the Gulf of Maine and off southern New England with recaptures taken more than 200 km away from the tagging site within the first two days (Kanwit and Libby, 2009).

The extensive post-spawning migrations and hence wide distribution of German Bank herring is likely influenced by the counter clockwise currents of the Gulf of Maine that flow north from southern Nova Scotia (near German Bank) towards the Bay of Fundy before extending south along coastal Maine and New Hampshire to Cape Cod, Massachusetts (Townsend *et al.*, 2001; Pettigrew *et al.*, 2005). During spawning, German Bank herring generally reside on the spawning ground for two to three weeks, with some remaining there up to six weeks. There was no significant movement on the spawning ground; however German Bank herring tend to move southeast on the bank after tagging before departing the spawning ground. A lack of fisheries south of German Bank precludes information on whether herring continue to move off the bank in this direction when spawning is finished. Based on the calculated mean angle of dispersion (Table 3.3), most herring depart German Bank and migrate north with the residual flow

(Pettigrew *et al.*, 2005) to feeding grounds at the entrance of the Bay of Fundy some 90 to 180 kilometers away off Grand Manan Island, Long Island shore and off southwest New Brunswick. German Bank herring remain at the feeding grounds for up to two months where they mix with Scot's Bay herring, an observation also reported by Stobo and Fowler (2009). A small proportion of German Bank herring remain at the entrance of the Bay of Fundy throughout the overwintering and summer feeding periods while a large proportion migrate southwest to the Gulf of Maine with the residual current (Pettigrew *et al.*, 2005) to traditionally reported overwintering areas along coastal Maine and New Hampshire as far south as Rhode Island (Kanwit and Libby, 2009; Stobo and Fowler, 2009). German Bank herring remain in the Gulf of Maine during winter forming part of the mixed populations taken in the American fall and winter purse seine and trawl fishery (Collette and Klein-MacPhee, 2002; Kanwit and Libby, 2009) and then migrate back to the Bay of Fundy to feed in the spring and summer (Stobo and Fowler, 2009). For some German Bank herring, the return migration against the current to the German Bank spawning ground from summer feeding grounds in the Bay of Fundy occurs more than a month before the spawning season begins in mid-August, an expected finding given that German Bank is reported to be an important feeding ground for juvenile and adult herring that supports an active fishery during pre-spawning from April to mid-August (Power *et al.*, 2009).

An unknown proportion of the German Bank population leaves the spawning ground and moves eastward to overwinter along coastal Nova Scotia as reported previously for this population (Waters *et al.*, 2000; Mouland *et al.*, 2003; Waters and Clark, 2004). Due to the absence of a winter fishery along the coast of Nova Scotia since 2002 (Power *et al.*, 2010), recapture information for this traditionally reported

overwintering location is limited (Waters *et al.*, 2000; Mouland *et al.*, 2003; Waters and Clark, 2004; Stobo and Fowler, 2009). Given historical reports of herring distribution, in addition to a single tagged herring recapture off Chebucto Head, Nova Scotia in January, 2000 in this study and the presence of German Bank herring east of Nova Scotia on the offshore banks of the Scotian Shelf during May and June (Figure 3.2), it is likely that German Bank herring continue to move east after spawning. These herring overwinter along the coast before moving offshore to feed during spring and early summer. The return migration to the German Bank spawning ground from the offshore banks of the Scotian Shelf begins as early as May where herring likely feed close to or on the spawning ground prior to spawning (Power *et al.*, 2009).

The high rate of dispersal away from Scot's Bay may not be unusual given the strong tidal currents in the Bay of Fundy (Desplanque and Mossman, 2004; Lacroix and Knox, 2005). Bay of Fundy currents have a counter clockwise residual flow (Watson, 1936; Dadswell *et al.*, 1983) that can provide a directional cue for post-spawning herring migrating from spawning to feeding grounds (Smith, 1985). Feeding grounds at the entrance of the Bay of Fundy are highly productive (Sinclair and Iles, 1985) and are some 105 to 210 kilometers from the Scot's Bay spawning ground. The well-mixed, nutrient rich waters of the Bay of Fundy promote excellent feeding grounds for what is believed to be a diverse mixture of resident and migrant herring populations that cohabit the bay during feeding with many other marine fish, birds and mammals (Scott and Scott, 1988; Diamond and Devlin, 2003; Baumgartner and Mate, 2005; Stobo and Fowler, 2009). Indeed, herring are a key component of the marine food web and are fed upon by many species of fish (Overholtz, 2006), sea birds (Huettmann *et al.*, 2005) and marine mammals (Overholtz and Link, 2007). After residing on the Scot's Bay

spawning ground for approximately two weeks, the residual currents carry post-spawning (spent, energy depleted) herring along the New Brunswick coastline (direction of the current) to the Fundy Iles off southwest New Brunswick in as little as two days and judging from the calculated mean angles of dispersion (Table 3.3), Scot's Bay herring move across the entrance of the Bay of Fundy to feed off Grand Manan Island and off Long Island shore, Nova Scotia. An unknown proportion of Scot's Bay herring apparently remain near the approaches of the Bay of Fundy throughout the year supporting previous reports that this population largely resides in the Bay of Fundy (Stobo and Fowler, 2009). Caution regarding this observation is required given that the herring fishery in the Scotia-Fundy region typically ends in November (i.e. recapture data is typically not available in this region from December to April) (Power *et al.*, 2010). Furthermore, based on previous tagging studies on overwintering herring off eastern Nova Scotia (Mouland *et al.*, 2003) and the recapture of two herring off southwest Nova Scotia (i.e. outside of the Bay of Fundy) in this study, it is likely some as of yet unknown proportion of Scot's Bay herring leave the Bay of Fundy to join other populations of herring (e.g. German Bank) in their overwintering migration toward the Gulf of Maine or east of Nova Scotia. Given that relatively few herring were tagged in Scot's Bay (n=14,046) compared to German Bank (n=51,432) and the absence of a winter fishery in the coastal Nova Scotia region, it is not surprising that there is an absence of Scot's Bay recaptures from these overwintering areas. Feeding continues at the entrance of the Bay of Fundy in spring where energy reserves are replenished and used for the return migration back to Scot's Bay spawning ground in June and July (Harden Jones, 1968; Nottestad *et al.*, 1999; Slotte and Fiksen, 2000).

The return migration route from the entrance of the Bay of Fundy to the Scot's Bay spawning ground is unclear. A return spawning migration against the current, as predicted by theory (Harden Jones, 1968; McKeown, 1984), is unnecessary given the counter clockwise circulation of the Bay of Fundy (Watson, 1936; Dadswell *et al.*, 1983). Hence, herring can return to Scot's Bay by simply following the residual current from Long Island shore to Scot's Bay in the inner Bay of Fundy (Figure 2.1). In contrast, Scot's Bay herring may move against the residual current, but take advantage of selective tidal stream transport by hugging the bottom where current flow is reduced during the ebb as reported for *Pleuronectes platessa* (plaice) in the North Sea (Metcalf *et al.*, 1990) and *Oncorhynchus nerka* (sockeye salmon) in the Fraser River Estuary, British Columbia (Levy and Cadenhead, 1995).

3.5.3 Population integrity and connectivity

This study supports the assumption that herring spawn as a closed population given that no intermixing was evident from recaptures of tagged fish during the spawning season. German Bank and Scot's Bay herring exhibited a high degree of integrity by spawning exclusively with the same population on the same spawning ground annually, an observation supported by studies of other herring populations from the Atlantic and Pacific Oceans (Cushing, 1967; Hourston, 1982; Wheeler and Winters, 1984a, b; Hay, *et al.*, 2001; Secor *et al.*, 2009; Jech and Stroman, 2012).

Outside of the spawning season, fish from both populations routinely mix in common feeding areas near the entrance of the Bay of Fundy indicating connectivity between populations at that time and location. Intermixing of different populations is common for herring during overwintering and feeding (Wheeler and Winters, 1984b;

Sinclair and Iles, 1985; Scott and Scott, 1988; Secor *et al.*, 2009). It has also been reported for Atlantic cod (*Gadus morhua*) (Templeman, 1974), Atlantic salmon (*Salmo salar*) (Saunders, 1981), American shad (*Alosa sapidissima*) (Dadswell *et al.*, 1983), mackerel (*Scomber scombrus*) (Sinclair and Iles, 1985), and Chinook salmon (*Oncorhynchus tshawytscha*) (Bugaeu and Myers, 2009).

Although herring from different spawning populations mix outside of the spawning season, schooling aggregations from each population tend to remain together maintaining population integrity. There are several instances where multiple fish that were tagged together were subsequently recaptured together after traveling great distances or after being at liberty for considerable periods. Two fish tagged together on German Bank (September 7, 2010) traveled a minimum of 344 km before being recaptured together 253 days later offshore of eastern Nova Scotia. Similar observations are reported for *Clupea pallasii* Pacific herring that remain together within aggregations for periods of 6 months to several years while moving over considerable distances (Hay and McKinnell, 2002). Although mixing allows for population connectivity, schooling of individuals of the same population maintains population integrity (Stephenson *et al.*, 2009).

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Table 3.1: Summary of mark and recapture data for German Bank and Scot's Bay used in this study.

Spawning ground tagging location	Year	Tagging dates	Number of tagging days	Number of fish tagged on spawning ground	Number of recaptured fish	Percent recaptured
German Bank	1998	Aug. 20 - Sep. 22	14	9730	34	0.3
	1999	Sep. 21 - Sep. 22	2	821	2	0.2
	2001	Sep. 17 - Sep. 19	3	9402	56	0.6
	2005	Aug. 30 - Oct. 05	5	8487	58	0.7
	2009	Aug. 19 - Sep. 30	15	10333	104	1.0
	2010	Aug. 19 - Oct. 12	10	6036	41	0.7
	2011	Aug. 24 - Sep. 29	12	6623	54	0.8
	Totals		61	51432	349	
Scot's Bay	1998	Aug. 23 - Aug. 25	2	2367	24	1.0
	1999	Aug. 11 - Aug. 21	2	2832	6	0.2
	2005	Jul. 28 - Aug. 24	4	5047	204	4.0
	2006	Jul. 28 - Aug. 20	3	3800	30	0.8
	Totals		11	14046	264	

Table 3.2: Summary of days at large and mean distances traveled (km) by herring tagged on German Bank and at Scot's Bay during the spawning season. n = number of recaptured herring. Statistics refer to t-tests between distances traveled by recaptured German Bank and Scot's Bay herring. * = significant.

Days at large	Population								<i>t</i>	<i>df</i>	<i>p</i>
	German Bank				Scot's Bay						
	n	mean	S.E.	range	n	mean	S.E.	range			
0 to 1	35	6.56	1.22	0 - 21	8	9.28	1.58	3 - 12	1.76	41	0.086
2	36	8.28	1.52	0 - 48	82	16.79	4.85	0 - 202	0.30	116	0.767
3 to 4	46	7.20	0.87	0 - 21	47	49.19	9.99	2 - 211	3.23	91	0.002 *
5 to 8	90	13.27	3.65	0 - 161	54	41.45	7.82	1 - 176	7.16	142	<0.001 *
9 to 16	46	12.92	4.78	0 - 181	40	58.47	11.19	2 - 269	5.64	84	<0.001 *
>16	75	108.44	16.43	0 - 524	32	99.40	9.86	1 - 155	2.18	105	0.031 *
>365	21	54.85	20.32	0 - 346	1	297.85					

Table 3.3: Summary of days at large, mean distances traveled (km) and mean direction traveled (a degrees) by herring recaptured off the German Bank and Scot's Bay spawning grounds. a = mean direction (degree), z = Rayleigh's test critical value, p = Rayleigh's p value, and * = significant.

Days at large	Population														
	German Bank								Scot's Bay						
	n	mean	S.E.	range	a	z	p	n	mean	S.E.	range	a	z	p	
0 to 1	0							0							
	2	1	48.14		338			7	154.14	16.14	69 - 202	268	6.02	<0.001	*
3 to 4	0							14	150.34	7.83	68 - 211	261	13.68	<0.001	*
5 to 8	6	135.19	17.97	49 - 161	349	2.67	>0.05	11	152.87	4.54	126 - 176	254	10.72	<0.001	*
9 to 16	2	158.47	22.79	136 - 181	340			13	154.44	10.36	112 - 269	254	12.34	<0.001	*
>16	33	235.34	22.78	50 - 524	1	3.60	<0.05 *	23	132.79	2.96	104 - 155	249	21.84	<0.001	*
>365	4	221.34	54.36	100 - 346	36			1	297.85			208			

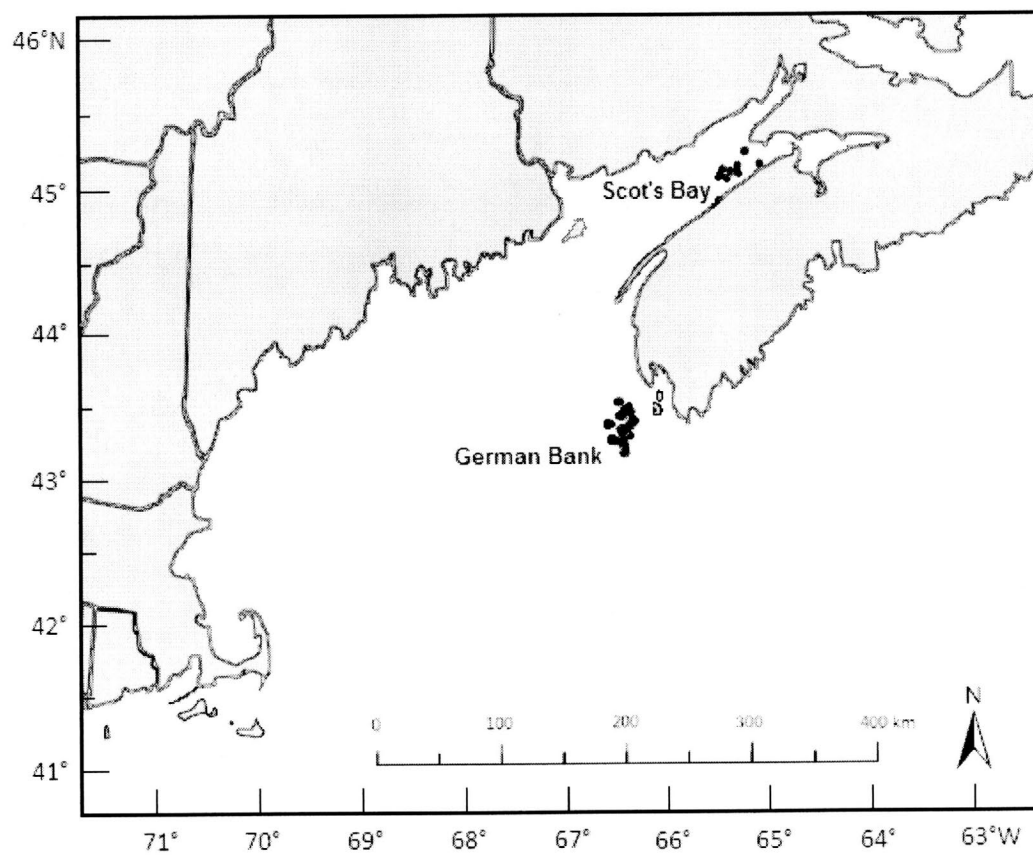


Figure 3.1: Locations where Atlantic herring were tagged on German Bank (1998, 1999, 2001, 2005, 2009, 2010, 2011) and at Scot's Bay (1998, 1999, 2005, 2006) during the fall spawning seasons. Some points represent multiple fish released at the same location.

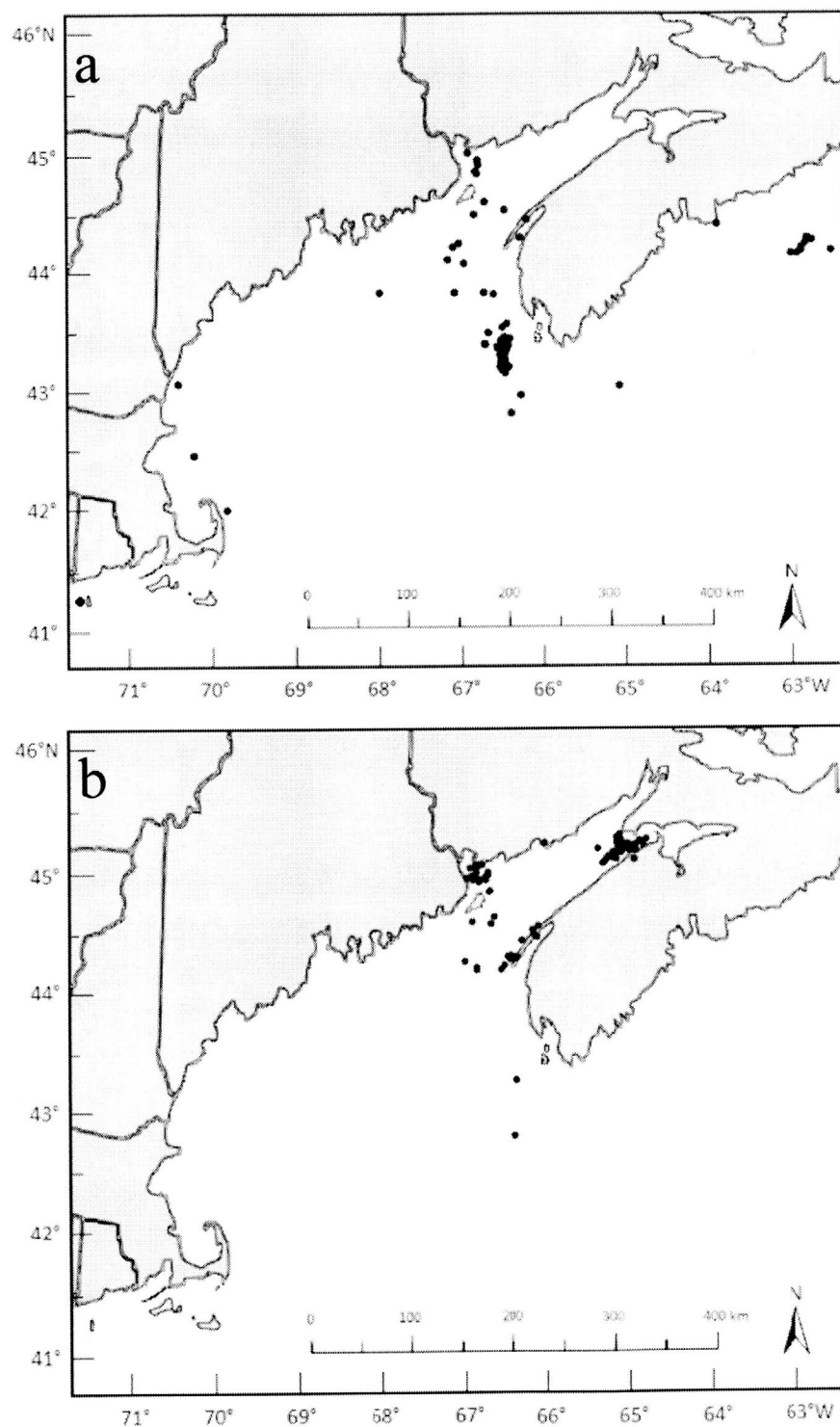


Figure 3.2: Recapture locations for Atlantic herring tagged on (a) German Bank and at (b) Scot's Bay. Some points represent multiple recaptures at the same location.

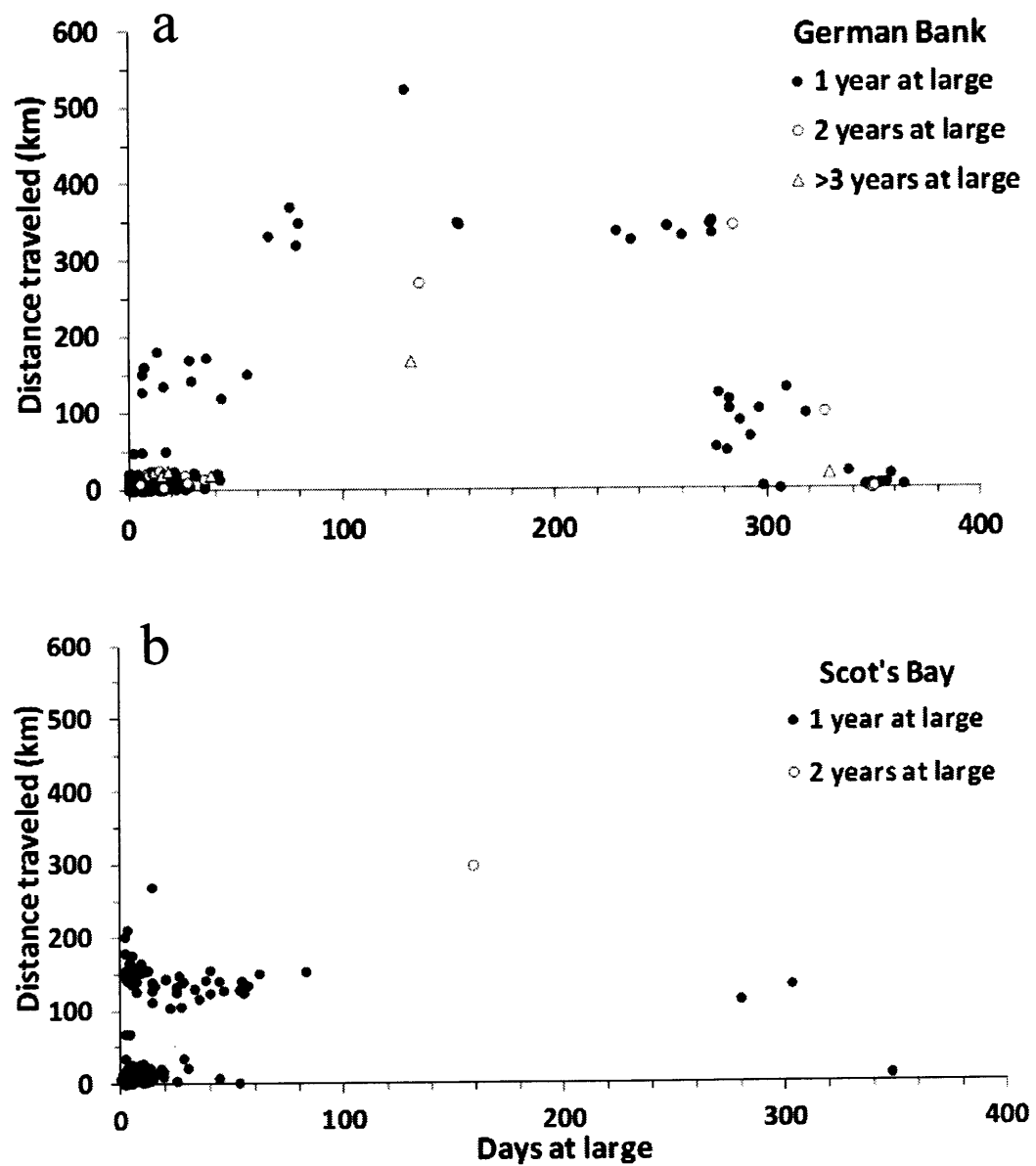


Figure 3.3: Time at large and distance traveled for herring tagged on (a) German Bank and at (b) Scot's Bay during the spawning season.

CHAPTER 4: GENERAL SUMMARY AND CONCLUSIONS

4.1 Summary and conclusions

Mark and recapture data collected over nine spawning seasons were used to calculate turnover times of spawning Atlantic herring (*Clupea harengus*) on two commercially important and well established spawning grounds off eastern Canada: German Bank off southwest Nova Scotia and Scot's Bay in the inner Bay of Fundy. Quantifying turnover time is important for determining spawning stock biomass and recommending catch levels (Stephenson *et al.*, 1999). Mean turnover time for Atlantic herring on Scot's Bay is slightly shorter (14.54 days for 90% of the population) compared to German Bank (16.09 days for 90% of the population), however, when individual years are considered separately (German Bank: 6 years; Scot's Bay: 3 years) there is considerable variability among years within a population ranging annually from 6 to 20 days on German Bank and from 7 to 17 days in Scot's Bay for 90% turnover. Variability in population specific turnover times can be influenced by a variety of factors including the effects of variable environmental factors (e.g., temperature) on time of spawning (Wright and Trippel, 2009), but also our low recapture rates of approximately 1%.

The results presented in Chapter II have several important implications that directly apply to the management of the Atlantic herring fishery in eastern Canada. Accurate estimates of herring spawning stock biomass (SSB) rely on the summation of multiple acoustic surveys conducted on the spawning ground during the spawning season. The calculation of herring turnover times, defined as the time required for individuals to aggregate, spawn and exit the spawning area, are necessary to determine

the proportion of herring that remain on the spawning ground at the time of repeated surveys to avoid double counting of fish (Stephenson *et al.*, 2009). Surveys that are conducted too frequently risk double counting those herring that have not yet left the spawning ground since the previous survey. Double counting results in an overestimate of the SSB and could affect the scientific advice given to management (Stephenson *et al.*, 1999; McPherson *et al.*, 2003). By calculating turnover times and thus the proportion of herring that are double counted during repeated surveys, SSB estimates can be adjusted accordingly. Currently, surveys are conducted according to an assumed herring turnover time of 10 to 14 days to calculate SSB (Melvin *et al.*, 2002). Turnover times calculated in this study suggest that surveys can be conducted at 14 day intervals, however, only 87 and 89% of the German Bank and Scot's Bay population will have turned over by this time, respectively. This means that if a second survey is conducted 14 days later, 13 (German Bank) and 11% (Scot's Bay) of the estimated SSB from the previous survey will be double counted. Hence, to determine a more accurate estimate of SSB, 13 and 11% must be deducted from survey #2 and those following. The interval between surveys can vary during the spawning season when weather conditions prevent the deployment of expensive hydro acoustic equipment on these offshore spawning grounds. The proportion of double counted herring can then be calculated by using turnover time equations developed for each population where the number of days between surveys is multiplied by the instantaneous rate of change of recaptured fish.

These results also indicate that turnover times differ between populations and that SSB estimates should be calculated accordingly based on turnover time equations developed for each population. Furthermore, both non-catch adjusted and catch adjusted turnover times were very similar with overlapping standard errors, however, given that

adjusting recaptures takes into account variable catches, it is recommended that turnover times be based on catch adjusted data.

The major limitation to calculating accurate estimates of turnover times in this study was low recapture rates of tagged herring from the commercial fishery. To improve turnover time estimates, future studies should consider that recapture rates of approximately 1% result in considerable variability among years and populations. To achieve a greater recapture rate and thus improve turnover time estimates within the confined temporal and spatial scales, a greater number of herring must be tagged and efforts should be made to tag and to fish daily. This is difficult and costly when the spawning grounds are located in deep water at considerable distances offshore. Detection rates in processing plants are also important and have been reported to be as low as 33% (Kanwit and Libby, 2009); hence the significance of a lottery as an incentive for fish processing plant employees to return recaptured tags. Tagging herring using small acoustic transmitters would provide another method of determining how quickly marked herring disperse from the spawning grounds (Smith *et al.*, 2009). Herring are rather delicate fish and lose their scales easily when handled (Stobo *et al.*, 1992); hence great care would have to be used when implanting transmitters.

Turnover time estimates can also be improved by investigating factors that affect timing of spawning within and among spawning seasons. For example, colder temperatures may delay spawning (Hay, 1985; Ware and Tanasichuk, 1989), thus increasing turnover time on the spawning ground. Finally, one important uncertainty associated with the calculation of turnover times on the spawning ground is whether herring spawn as a closed population, i.e. there being no intermixing of populations during the spawning season.

Post-spawned German Bank herring were in general more broadly distributed than Scot's Bay herring, occurring near the approaches of the Bay of Fundy, throughout the Gulf of Maine as far south as Rhode Island, and on the offshore banks of the Scotian Shelf. In contrast, most Scot's Bay tagged herring were returned from within the Bay of Fundy. Both populations tended to occur in the approaches of the Bay of Fundy, specifically off Grand Manan Island, off Long Island shore, and in the Fundy Isles area off southwest New Brunswick where they mixed for the purposes of feeding (Stobo and Fowler, 2009). Herring spawning in Scot's Bay had significantly higher rates of dispersal and a shorter residency time on the spawning ground compared to German Bank herring validating conclusions made in Chapter II. The high rates of dispersal are not uncommon (Kanwit and Libby, 2009) and are likely related to the relatively strong residual current of the Bay of Fundy (Dadswell *et al.*, 1983).

Migrations by adult herring tagged on German Bank consist of two apparent post-spawning movements: a westward and eastward migration. The westward migration begins with a northward movement with the residual current (Pettigrew *et al.*, 2005) to feeding grounds at the entrance of the Bay of Fundy where they remain for up to two months mixing with Scot's Bay herring (Stobo and Fowler, 2009). Some German Bank herring remain at the approaches of the Bay of Fundy for the overwintering period, while a larger proportion of the population begin a southwestward migration with the residual current (Pettigrew *et al.*, 2005) to overwintering grounds in the Gulf of Maine, specifically along coastal Maine, New Hampshire and as far south as Rhode Island. They remain in the Gulf of Maine for the winter and then move northeast back to the approaches of the Bay of Fundy to feed during spring and summer. In late summer or early fall, pre-spawning German Bank herring begin migrating south against the current

to the German Bank spawning ground to spawn between mid-August and mid-October (Power *et al.*, 2009).

Some German Bank herring leave the spawning ground and move eastward to overwinter along coastal Nova Scotia as reported previously for this population (Waters *et al.*, 2000; Moulund *et al.*, 2003; Waters and Clark, 2004). Gaps exist in the data due to the absence of a winter fishery off eastern Nova Scotia since 2002 (Power *et al.*, 2010); however, one German Bank herring was recaptured during the overwintering period off Chebucto Head, Nova Scotia prior to the end of that fishery. Strong evidence of an eastward migration is based on the presence of German Bank herring on the offshore banks of the Scotian Shelf during May and June. Although information during the overwintering period is negligible, it is likely German Bank herring continue to overwinter along coastal Nova Scotia and then move offshore to feed during spring and early summer. Interestingly, the majority of recaptures east of German Bank were taken in the later years of the study (2011 and 2012) suggesting an important proportion of German Bank herring migrate eastward after spawning. The return migration to the German Bank spawning ground from the offshore banks of the Scotian Shelf begins as early as May where they likely feed close to or on the spawning ground prior to the spawning season (Power *et al.*, 2009).

For herring spawning in Scot's Bay, post-spawning migrations to feeding grounds at the entrance of the Bay of Fundy are undoubtedly influenced by the counter clockwise current (Watson, 1936; Dadswell *et al.*, 1983). After residing on the Scot's Bay spawning ground for approximately two weeks, the residual currents carry post-spawning herring along the New Brunswick coastline (direction of the residual flow) to feeding grounds near the Fundy Isles off southwest New Brunswick, off Grand Manan

Island, N.B. and Long Island shore, Nova Scotia. Most Scot's Bay herring were recaptured at the approaches of the Bay of Fundy during fall and spring suggesting the population may largely reside in the Bay; however, mark and recapture information during the overwintering period is lacking. Previous tagging studies reported movements from overwintering locations in the Gulf of Maine (Kanwit and Libby, 2009) and off eastern Nova Scotia (Mouland *et al.*, 2003) to the Scot's Bay spawning ground; however, this study provides no support for these observations. In contrast, tagging studies conducted on the Scot's Bay spawning ground in the early 1980s reported recaptures in the Gulf of Maine and off Cape Breton Island, Nova Scotia during overwintering (Stobo and Fowler, 2009). Reduced fishing effort on overwintering herring in the Scotia-Fundy region during the time of this study ultimately limits the information available for these traditionally reported overwintering areas (Mouland *et al.*, 2003; Stobo and Fowler, 2009). Furthermore, relatively few herring were tagged in Scot's Bay (n=14,046) compared to German Bank (n=51,432), so it is not surprising that there were no Scot's Bay herring recaptured in the Gulf of Maine or off eastern Nova Scotia considering only 2.0 and 0.3% of all German Bank recaptures came from these overwintering locations, respectively. Two Scot's Bay herring were recaptured off southwest Nova Scotia near German Bank providing some evidence of migrations outside of the Bay of Fundy. For these reasons, it is believed that some Scot's Bay herring leave the Bay of Fundy to join larger populations (e.g. German Bank) and begin their migration to common overwintering grounds in the Gulf of Maine and off eastern Nova Scotia, while an unknown proportion of the population remains at the approaches of the Bay of Fundy. Feeding continues at the entrance of the Bay of Fundy in spring when energy reserves are replenished (Harden Jones, 1968; Nottestad *et al.*, 1999; Slotte

and Fiksen, 2000) and used for the return migration back to Scot's Bay spawning ground in June and July.

A major limitation to this study is related to the restricted coverage of the commercial fishery that in turn limits the information on herring distribution based on mark and recapture. For example, there is very limited information for overwintering herring in the Scotia/Fundy region because fishing is primarily directed against summer feeding and fall spawning aggregations in the Bay of Fundy and on the major spawning grounds (German Bank and Scot's Bay) (Power *et al.*, 2010). One way of mitigating this limitation is by conducting acoustic surveys in areas that no longer have active fisheries. This would be most beneficial during the overwintering period given the lack of fisheries and hence information on overwintering migrations of German Bank and Scot's Bay herring. Tagging herring with small acoustic transmitters could also effectively track the movements of herring without the obligation of the commercial fishery (Smith *et al.*, 2009).

The absence of intermixing during the spawning season confirm that herring spawn as a closed population, filling the last knowledge gap associated with calculating turnover times. Outside of the spawning season, fish from both populations routinely mix in common feeding areas near the entrance of the Bay of Fundy suggesting connectivity between populations (Stephenson *et al.*, 2009). The nutrient rich waters of the Bay of Fundy support a diverse mixture of juvenile and adult herring from several populations as well as many other marine fish, birds and mammals (Scott and Scott, 1988; Diamond and Devlin, 2003; Baumgartner and Mate, 2005; Stobo and Fowler, 2009). Although mixing of different populations occurs during feeding and

overwintering, herring from the same population tend to remain together for extended periods maintaining population integrity (Stephenson *et al.*, 2009).

Due to their commercial significance and importance in the marine ecosystem Atlantic herring are one of the most intensively studied marine fish species in the world (Blaxter and Hunter, 1982; Kanwit and Libby, 2009). Despite an extensive literature on the biology of herring, information on current seasonal movements and population dynamics has been lacking. However, examination of several years of mark and recapture data has provided fundamental information relevant to the migratory movements, population structure and spawning biology of two populations of Atlantic herring in the northwest Atlantic that can in turn be implemented for future management of the resource. Further research is recommended to improve variable turnover time estimates and to better understand changing herring distribution as an expanding fishery exploits an already vulnerable species.

4.2 Literature cited

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