THE INFLUENCE OF SPATIAL AND TEMPORAL SCALE IN DETECTING OFFSHORE RECRUITMENT SIGNALS OF ATLANTIC COD (*GADUS MORHUA*) BASED ON COASTAL JUVENILE SURVEYS

by

© Emma L.L. Cooke

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Abstract

The moratorium on the Newfoundland Atlantic cod (*Gadus morhua*) fishery in 1992 motivated studies on the factors influencing population stability and tools to forecast future cod abundance. Unfortunately, short-duration time series compromised most efforts to link life stages. I used coastal seine surveys of juveniles (age-0 and -1) to predict offshore pre-adult (age-3) cod abundance at multiple spatial scales (individual bays to offshore regions), temporal scales (short and long-term time series from 7 to 18 years in length) and environmental and biological factors influencing recruitment signal strength. These analyses detected strong recruitment signals among all early age classes from the Newman Sound Survey (1995 – 2013) and demonstrated interactions between juvenile abundance and environmental variables. In contrast, a strong recruitment signal was only detectable from a single bay using the shorter Fleming Survey (1992 – 1997, 2001). For both surveys, recruitment signal strength varied with distance from the index sites, among management zones, and between areas of known ecological and biological significance. Studies evaluating year-class strength often overlook the value of coastal juvenile surveys. These results demonstrate the utility of using information from long-duration coastal seine surveys when forecasting adult population strength. The implications of my results could help stakeholders prepare for socio-economic implications of poor recruitment years, and can be used in management decision-making.

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List of Abbreviations and Symbols

COSEWIC	Committee on the Status of Endangered Wildlife in Canada
D^2	Explained deviance
DFO	Fisheries and Oceans Canada
EBSA	Ecologically and Biologically Significant Area
FAO	Food and Agriculture Organization
GLM	Generalized Linear Model
ICES	International Council for the Exploration of the Sea
LM	General Linear Model
MPA	Marine Protected Area
NAFO	Northwest Atlantic Fisheries Organization
R^2	Coefficient of determination
SD	Standard Deviation
SE	Standard Error
SSB	Spawning Stock Biomass

Co-authorship Statement

The research described in this thesis was designed and conceptualized by E.L.L. Cooke, with assistance from committee members R.S. Gregory and P.V.R. Snelgrove. R.S. Gregory, P.V.R. Snelgrove, and D. Cote assisted with thesis preparation, writing, and presentation of data. All data analyses were conducted by E.L.L. Cooke, with assistance from D. Cote. Authorship of Chapters 2 and 3 will evolve as the manuscripts mature; however, E.L.L. Cooke will be lead author and those who made significant contributions to manuscript development will be included.

Chapter 1: General Introduction

Fisheries provide vital food, income, and livelihood for millions of people worldwide. Anticipated growth in world population by >50% by 2050 will require a significant increase in fisheries and aquaculture production (FAO 2016). However, the productivity of many commercial marine fisheries is highly sensitive to anthropogenic and environmental stressors (e.g., fishing pressure and climate change), and can be exacerbated by phenomena such as fishery-induced evolution (Caddy and Agnew 2004, Olsen et al. 2004, Brander 2007). These pressures, along with changing habitat and food availability, can lead to shifts in age structure, distribution, and variability in recruitment success and natural mortality in wild fish populations (Sætre et al. 2002, Perry et al. 2005, Olsen et al. 2011, Ottersen et al. 2013). The combination of these factors can compromise the sustainability of a fishery or hinder the recovery of overexploited populations.

In order to reduce population decline of fishery species with high recreational or commercial value, scientists and managers have developed strategies and tools to facilitate population growth and sustain ecosystem function. The most common of these strategies include designing and enacting marine protected areas (MPAs), fishing gear restrictions, and implementing fishing quotas or closures (Sissenwine 1984, Berkeley 2004, Hilborn et al. 2004, Worm et al. 2009). In order to measure the impacts on fish populations and set appropriate limits and quotas on harvest levels, management routinely conducts assessments on important fish stocks. Classic fishery assessment models use biological and catch data and estimates of mortality to assess current and future stock abundance and growth (Megrey and Wespestad

1988). This task becomes particularly challenging when exploited fish population decline to the point of collapse but remain both ecologically and socioeconomically valuable.

Fisheries managers have sought better prediction capacity of future stock strength for over a century (Hjort 1914). The possibility of forecasting adult offshore recruitment from early age classes (i.e., eggs, larvae, juveniles) could improve harvest strategies and help to plan for socio-economic cost of low recruitment years, but only recently has access to extensive long-term datasets increased the feasibility of this type of approach. However, predicting future stock status has proven difficult because of high spatiotemporal variability in survival and recruitment of early age classes for marine fishes. Nonetheless, many population assessments include abundance indices of early age classes for year-class strength (Dorn et al. 2017, ICES 2018).

Atlantic cod (*Gadus morhua*) offers an ideal model species for studies of recruitment dynamics (Ings et al. 1997, Kristiansen et al. 2011). Historically, Atlantic cod was widely distributed geographically, and one of the most abundant populations occurred off the northeastern coast of Newfoundland and Labrador (Fahay et al. 1999). Unfortunately, overexploitation and environmental stressors led to the subsequent fishery closure for Atlantic cod in this region, also known as NAFO (Northwest Atlantic Fisheries Organization) divisions 2J3KL – i.e., “northern cod” – in 1992 (Taggart et al. 1994, Halliday and Pinhorn 2009). Since the 1992 moratorium, the northern cod stock has shown only minimal signs of recovery, and was even listed as endangered by COSEWIC (2010) (DFO 2018). Despite modest increases in the past decade, its Spawning Stock Biomass (SSB) remains below the conservation limit reference point (DFO 2018). The historical economic and ecological importance of Atlantic cod has motivated increasing efforts to detect a recruitment signal and forecast adult abundance using estimates of juvenile year-class strength (Ings et al. 1997, Laurel et al. 2017). Although intuitively obvious, the proportional relationship between abundance of adults and juveniles in many fish populations has proven challenging to test empirically. The high mortality rates during early age classes attributed to predation and low body condition complicate efforts to link juvenile and adult abundance (Copeman et al. 2008, Houde 2008, Kristiansen et al. 2011). Moreover, the geographic separation between juvenile and adult cod populations requires distinctly different sampling methods to avoid bias and underrepresentation of age classes (Dalley and Anderson 1997, Williams et al. 2011). Despite these complications, some studies have successfully detected a recruitment signal among early age classes (e.g., Ings et al. 1997, Laurel et al. 2017); however, no study has attempted to link these recruitment signals to the offshore cod stock. As a result, current stock assessments do not consider year-class strength derived empirically from juvenile cod surveys (Cadigan 2016, DFO 2018).

I address the suitability of using coastal seine surveys of juveniles (age-0 and age-1) to predict offshore pre-adult (age-3) Atlantic cod abundance in Newfoundland at varying spatial and temporal scales. Researchers consider the abundance of age-3 cod as "recruitment" into the Newfoundland fishery assessment because this is the earliest age at which a trawl survey effectively samples cod (DFO 2016). In addition, I consider several environmental factors to assess their influence on predictive relationships. My thesis is organized into two separate data chapters (Chapters 2 and 3). The time series used in each chapter differs in spatial and temporal scale and resolution, allowing a unique opportunity to compare recruitment signal strength in different contexts, in the same geographic region. In Chapter 2 I investigate the use of the Newman Sound Juvenile Survey, collected bi-weekly in Bonavista Bay, Newfoundland over almost two decades, in forecasting offshore Atlantic cod recruitment. I determine the predictive relationship between annual estimates of juvenile cod (age-0 and -1) and offshore abundance indices of pre-adult cod (age-3) over an 18-year period (1996 – 2013). In Chapter 3, I investigate the use of the Fleming Survey in forecasting offshore Atlantic cod recruitment using annual sampling from four bays over a 7-year period (1992 – 1997, 2001). In Chapter 4, I discuss the overall implications of my results, considering the differences in recruitment signals based on the different spatial and temporal scales examined, and comparing the strengths and limitations of both approaches.

Chapter 2: Spatial, temporal, and environmental influences on Atlantic cod (*Gadus morhua*) recruitment signals in Newman Sound, Newfoundland

Abstract

Information from coastal seine surveys is useful for monitoring juveniles of Atlantic cod (*Gadus morhua*), and forecasting future population strength at older age classes. I analyzed juvenile (age-0 and -1) cod population components in Newman Sound, Newfoundland, to predict offshore pre-adult (age-3) cod recruitment at multiple spatial and temporal scales, and the factors influencing recruitment signal strength. Generalized linear models revealed significant relationships between juvenile (age-0 and -1) and pre-adult (age-3) abundance. The strength of these relationships varied with distance from nursery habitats and among fisheries management zones. Additionally, water temperature, predator abundance, and chlorophyll-a level during early life stages appeared to influence the strength of the relationships between juvenile and adult abundance. However, the strength of recruitment signal influence by both biological and environmental factors varied over time, highlighting the value of long duration time series. The potential to forecast pre-adult abundance from juveniles could aid in planning for low recruitment years, and improve inferences on the response of cod population abundance to future environmental changes.

Introduction

Many of the world’s most valuable marine fish stocks (e.g., Atlantic cod, *Gadus morhua*; Baltic Sea sprat *Sprattus sprattus*; herring *Clupea harengus* L.) exhibit strong recruitment variability, driven by a mixture of environmental and anthropogenic drivers that often lead to depleted fish populations (e.g., Sætre et al. 2002, Baumann et al. 2006, Stige et al. 2013, Rose and Rowe 2015). Along with the goal of an ecologically sustainable fishery, managers are often pressured to make decisions based on the socio-economic impacts of sudden cuts to fishing quotas (Copes 1996, National Research Council 1998). Surveys of early life stages that improve understanding of recruitment variability could potentially contribute to adult stock assessments of many commercially valuable marine fishes by improving predictions of future stock strength (Sissenwine 1984, Houde 1987, 2008). Fisheries managers have pursued better prediction of future recruitment for over a century (Hjort 1914) because improved prediction would provide time for fishery managers, industry, and subsistence fishermen to prepare for the socio-economic and ecological effects of fluctuating fish stocks (Gulland 1989).

Estimates of cohort strength in marine fishes often use adult abundance (e.g., Spawning Stock Biomass, SSB) (Stige et al. 2013) because many confounding factors (e.g., predation, advection, temperature) limit the utility of early life stages (e.g., eggs and larvae) for such estimates. Several studies have attempted to link the abundance of early life stages and adult fish in order to forecast adult population abundance, or detect a ‘recruitment signal’ (Hjort 1914, Sissenwine 1984, Ings et al. 1997, Laurel et al. 2016). However, successful application of juvenile data to forecast adult abundance remains challenging, largely constrained by poor understanding of factors influencing juvenile survival and dispersal, and lack of long-term data series (e.g., Bradford 1992). One exception is in Norway, where long-duration juvenile fish surveys have been conducted for almost a century for integration into stock assessments - i.e., the Flødevigen surveys (Tveite 1971, Rogers et al. 2010). Nonetheless, linking pre-recruit and adult life stages remains a critical challenge in fisheries management (Sissenwine 1984), and a knowledge gap in understanding population connectivity still exists for many species.

As expected, many studies report better predictions of year-class strength from recruitment for life stages sampled closer to the age-at-recruitment (Stige et al. 2013, Laurel et al. 2017). Most researchers consider juvenile fish surveys better predictors of future adult offshore recruitment than egg and larvae surveys because juveniles are less vulnerable to predation and starvation, and easier to track (Stige et al. 2013). Further, sampling difficulties (e.g., larval behaviour, advection) and unsuitable spatial coverage limit accuracy of larval abundance and mortality estimates (Taggart and Leggett 1987). Nevertheless, even beyond the larval stages, demersal juveniles of many commercial fish species remain at substantial risk to high natural mortality, particularly in the absence of suitable nursery habitat (e.g., haddock, Atlantic cod, and walleye pollock, Nassau grouper – *Epinephelus striatus* - Sissenwine 1984, Sogard and Olla 1993, Jackson et al. 2001, Gillanders et al. 2003, Lilley and Unsworth 2014). Although older age classes (i.e., age-at-recruitment) allow better predictions of future population estimates as a result of decreased vulnerability and sampling complications, forecasting population abundance further in advance using pre-recruit data would add a considerable advantage for management given the ecological and socio-economic consequences of unexpected stock collapses.

The economic and ecological importance of Atlantic cod (hereafter cod) has provided impetus for numerous studies on factors that influence juvenile cod mortality and recruitment variability (e.g., Daewel et al. 2015, Horne et al. 2016, Laurel et al. 2017). Prior to the northern cod fishery collapse and subsequent moratorium in 1992 (Taggart et al. 1994), juvenile cod yielded a weak but detectable recruitment signal on a rank-scale using data from a survey covering most of northeast coastal Newfoundland (Ings et al. 1997). Combining data from the pre-collapse period with data immediately post-collapse also produced a detectable recruitment signal on a ratio-scale from one year to the next (Ings et al. 1997). Further, recent analysis of a short-term inshore survey, conducted in a similar northeast region of Newfoundland, identified a weak recruitment signal using age-0 abundance and a strong recruitment signal using age-1 abundance on a ratio scale (Laurel et al. 2017). Strong recruitment signals were similarly detected using age-1 indices of *G. morhua* and *G. macrocephalus,* in Norway and Alaska (Laurel et al. 2017). However, lack of long-duration time series, encompassing multiple generations, for many juvenile cod has generally compromised efforts to link early life stages of cod to recruitment variability at longer temporal scales after the collapse.

Juvenile cod are characterized by extreme vulnerability throughout the first few years of life. Different environmental and spatio-temporal factors may confound patterns and strength of observed predictive relationships of recruitment. Factors that contribute to variable survival and predictive ability include nursery habitat availability (Tupper and Boutilier 1995a, Warren et al. 2010), water temperature (Copeman et al. 2008), growth and body size (Tupper and Boutilier 1995b, Drinkwater 2005), productivity levels (e.g., phytoplankton blooms, (Kristiansen et al. 2011), and the presence of other fishes that may act as competitors, predators, or prey (Linehan et al. 2001, Laurel et al. 2003a). Interactions between environmental and biological factors using time-series data with high inter-annual variation in juvenile abundance may prove useful in forecasting year-class strength in cod.

Since its collapse in the early 1990s, the Northern cod stock has been slowly rebuilding, coinciding with spatial redistributions in the offshore (DeYoung and Rose 1993, DFO 2016, Rose and Rowe 2018). However, variation in predictive strength with spatial scale and delineating the spatial extent of recruitment signals from a juvenile index site remain poorly understood empirically for the Northern cod stock. Predictive potential within areas of possible ecological and biological significance characterized by high abundance also remains open to investigation. Spatial considerations may be important for improving predictions of stock strength given the substantial distributional shifts caused by movement from juvenile to adult habitats. Further, considering the dynamic nature of recruitment, assessing the temporal stability of recruitment signals may provide insight into the influence of environmental factors in predictive models over time. Spatio-temporal variability and stability in recruitment has been explored in marine fish populations (e.g., Sale et al. 1984, Stige et al. 2013), and determining how recruitment signals reflect this variability will enhance predictive utility.

In this study, I investigated the potential for nearshore seine surveys to detect recruitment signals in pre-adult abundance in coastal Newfoundland at multiple spatial scales. Using an extensive time-series dataset, I tested the hypothesis that recruitment signal varied at different spatial and temporal scales. Specifically, I examined the stability of prediction over time, and strength of recruitment signals with distance from the index site. Further, I hypothesized that consideration of environmental and biological factors in tandem with juvenile abundance would increase recruitment predictive capacity.

Methods

Juvenile sampling

Juvenile cod in Newman Sound, located in Bonavista Bay off the northeast coast of Newfoundland, have been monitored extensively over a 22-year period (1995 – 2017) (Fig. 2.1, Gregory et al. 2016). The area includes 12 nearshore sites, chosen based on presence of juvenile cod nursery habitat (e.g., eelgrass) (Gregory et al. 2016). Each site was sampled bi-weekly from

May to November, the period when juveniles appear, via seine hauls to determine abundances of fish species inhabiting these nearshore habitats. I analyzed data from a total of 2405 seine hauls in this study (1996, 1998 – 2015). Temporal gaps in the survey in 1995 and 1997 meant no data for those years.

Fish were sampled using a Danish bag seine net (25 m x 2 m; 9 mm mesh) deployed using a small motorized boat. At each site, the net was deployed by one person holding one warp of the net on shore, while two others backed the boat perpendicular to shore to a distance of 55 m. Once the net was fed into the water parallel to shore, the boat then returned to shore where a second person was placed on shore with the other warp. After the net sank to the bottom, both warps were then pulled in at an equal rate with both ends separated by 16 m in order to maintain a standardized seine area. Once the net approached shore, the two warps were pulled closer together to avoid fish escapement. A third person retrieved the cod end of the net once it reached shore. Any fish captured in the seine net were then transferred to a container with clean seawater. The total area sampled was 880 m^2 with the net sampling the lowermost 2 m of the water column. One seine haul was performed at each site ±2 hours from low tide, during daylight hours, during the periods of peak neap and spring tides (i.e., biweekly). All fish species caught in the seine net were identified, measured (mmSL, mm Standard Length), then released. We assigned tentative ages to all juvenile cod using pre-established length-age classes from the northeast Newfoundland coast (Dalley and Anderson 1997). These ages were subsequently modified where necessary by examining length frequencies of each year-class and, in some years, using otolith microstructure validation.. Moreover, biweekly sampling meant that we could follow a cohort through time, reducing the need for age validation.

All sites contained a mixture of bottom habitat including macrophytes – eelgrass (*Zostera marina*), kelp, and rockweed – overlaying mineral based substrates such as cobble, sand, and mud. Proportions of each habitat type varied among sites and years. Eelgrass coverage was estimated for each site annually using visual site inspections, aerial photos, or scuba transects (1996 – 2015).

Water temperature was measured using Vemco Mini-T (or T-II) thermographs set to record every 1 (2002 – 2016) to 4 hours (1998 – 2001) at four standardized locations in Newman Sound; thermographs were suspended 50 cm above the bottom at a depth of approximately 3 m. I express these records as mean daily mean temperatures (± 0.1ºC) hereafter. Daily water temperature readings across locations indicated minimal variation among locations.

Adult sampling

The northern cod stock encompasses the area off the northeast coast of Newfoundland and Labrador in NAFO zones 2J3KL (Fig 2.1). The northern cod stock assessment defines "recruitment" as the abundance of age-3 cod in the survey area – the age at which a trawl survey effectively samples cod (DFO 2016). Based on 7150 trawls available for data analysis (1998 – 2016), I derived an abundance index of age-3 cod from the Fisheries and Oceans (DFO) Fall Research Vessel (RV) survey, conducted annually from October to January.

Fisheries and Oceans Canada (DFO) began using a Campelen 1800 shrimp trawl in the Newfoundland region in 1995 to complete all bottom trawl surveys. This bottom trawl has three 40 m bridles with 4.3 m^2 polyvalent trawl doors weighing 1400 kg each. A rockhopper footrope (35.6 m) with rubber disks 356 mm in diameter form the bottom of the trawl. Mesh size is 80 mm in the wings, 60 mm in the square and first bellies, and 40 mm in the other bellies, extension, and codend. The codend also has a 7 m nylon liner with 12.5 mm mesh size. Trawls are deployed and towed at a speed of 3.0 knots for 15 minutes after the trawl contacts the sea floor. Trawls are conducted within "strata" in a stratified random survey within depth-stratified areas. The strata are areas defined to allocate sampling intensity and reduce sampling variability (Fig. 2.1). Each trawl is towed to maintain contact with the seabed within stratum boundaries and towed in the general direction of the next station or along the isobath (Walsh et al. 2009). After completion of each tow, the trawl is retrieved and fishes measured and recorded. Catch measurements include: fish species identification, count, length (cm, standard length), weight (kg), bottom temperature, depth, start and end latitude, and longitude. Rigid standardization of bottom trawl survey and fishing protocols was implemented to ensure consistent trawl performance (see Walsh and McCallum 1997 and Walsh et al. 2009 for full information on the specification and protocols).

For my analysis I used catch numbers provided by DFO, that were standardized to a mean catch over a trawl distance of 0.8 km (0.8 km / trawl path km) x catch/trawl. Trawls occurred in areas ranging from 57 – 499 m in depth among the 57-74 index strata (< 500 m depth) sampled each year. Each strata was sampled at least 2 times, with total annual trawl numbers across strata varying from 274 – 329.

Chlorophyll-a concentration

I assessed the role of primary production on recruitment by using peak phytoplankton biomass data (using chlorophyll-a concentration as a surrogate) provided by César Fuentes-Yaco, Bedford Institute of Oceanography, Fisheries and Oceans Canada. These data were based on satellite imagery (GLOBCOLOUR, GlobColour 2007), which were prepared using a semianalytical bio-optical model, the Garver, Siegel, and Maritorena (GSM) model (Maritorena and Siegel 2005, Maritorena et al. 2010). Analysis of phytoplankton blooms and development of biological points of interest followed methods from Fuentes-Yaco et al. (2016). A function was fit to the satellite-derived points using a five-parameter logistic equation (Fuentes-Yaco et al. 2013), modified following Ricketts and Head (1999). Spring and fall peak chlorophyll-a concentrations ($Log_{10}(mg \cdot m^{-3})$/day) were estimated for Bonavista Bay at a spatial resolution of 4 km (2003 – 2014)

Data Analyses

Recruitment signals

I assessed the suitability of using juvenile abundance (age-0 and -1) data to predict recruitment of age-3 abundance to the offshore fishery in northeastern Newfoundland. For models with age-3 as a response variable ($n_{Age\text{-}0} = 17$, $n_{Age\text{-}1} = 18$), I used a negative binomial Generalized Linear Model (GLM) with a log link to assess the relationship between age-0 and -1 cod and age-3 cod. After examining the residuals, I deemed a GLM unacceptable to assess the relationship between age-0 and age-1 cod. Therefore, for models predicting age-1 abundance from age 0 abundance ($n_{Age\text{-}0} = 18$), I used a General Linear Model (LM) with a normal error structure, log transforming the abundance of age-0 and age-1. A constant of 1 was added to juvenile abundance indices when necessary to account for the presence of zeros, and I set statistical significance at alpha = 0.05. I assessed recruitment signal strength using the coefficient of determination (R^2) of the model for LMs, and used explained deviance (D^2) for the GLMs, calculated as:

$$\mathrm{D}^2 = \frac{(null\ deviance - residual\ deviance)}{null\ deviance}$$

Explained deviance, the amount of deviance accounted for in a GLM, provides a measure of goodness of fit. Explained deviance is calculated using the null deviance and residual deviance. Null deviance describes how well the model predicts the response variable including only the intercept, whereas the residual deviance describes the unexplained deviance in the model that includes the independent variables (Guisan and Zimmermann 2000). I ran each model using juvenile data from the entire sampling period (July – November) and each month separately in order to determine the sampling period with the highest predictive power.

Spatial scale analysis

In order to extrapolate recruitment signal strength spatially from the juvenile survey, I ran each model using age-3 abundance in buffers increasing by 50 km, centred on Newman Sound, until I covered the entire 2J3KL area (i.e., buffers = 100 km, 150 km …850 km, Fig. 2.2). Buffers were cumulative rather than separate bands. I also examined recruitment signal strength among NAFO management areas by separating age-3 abundance within 2J, 3K, and 3L.

I considered recruitment signals within two groups of areas identified as potential Ecologically and Biologically Significant Areas (EBSAs) for cod as described herein, by DFO (Nadine Wells, Ecological Sciences Section St. John's, NL). To identify potential EBSAs, total cod biomass in each trawl set since 1996 was interpolated across the survey area (i.e., 2J3KL) by creating a raster file using kernel density and 400 km^2 cells. The raster file was then classified into 10 quantiles with zero biomass excluded. The cells containing the top 10th quantile of biomass were identified as potential EBSAs. I selected several areas and combined them into two groups, EBSA 1 and EBSA 2 based on the large separation in their geographical location (Fig. 2.3). I then ran each recruitment model using age-3 abundance within EBSA 1 and EBSA 2 separately.

Environmental and biological factors

I examined the potential influence of other environmental and biological factors on the relationships between abundance of early life stages and age 3 recruits by including the mean values of multiple environmental and biological factors as interaction terms with juvenile abundance in each of my models. These additional environmental and biological factors included: seasonal water temperature anomalies, winter duration, percent eelgrass cover, peak fall and spring chlorophyll-a concentration, mean October age-0 predator abundance, mean October age-1 prey abundance, mean October age-1 competitor abundance, and mean October body length (mmSL). Age-1 predator abundance was not analysed because our seine nets rarely catch predators of this size in the depths we sampled. I calculated winter duration as days when the water temperature was consistently below 1°C. I defined predator abundance as the mean abundance of piscivorous fish at least double the minimum length of age-0 cod in each month for each year. Competitor abundance was calculated as the mean abundance of piscivorous fish larger than the minimum length of age-1 cod in each month for each year. I calculated prey abundance as the mean abundance of juvenile gadids (i.e. *G. morhua* and *G. ogac*) at least half the minimum length of age-1 cod in each month for every year. Juvenile gadids are known prey for older conspecifics in Newfoundland (e.g., Gotceitas et al. 1997, Linehan et al. 2001). Depending on data availability, the residual degrees of freedom varied among the models containing environmental factors.

Temporal analysis

In order to examine environmental influence on the number of recruits at different temporal scales, I split the time series into seven-year sliding windows (i.e., 1998 – 2004, 1999 – 2005, etc.). I chose a seven-year sliding window to allow comparisons among studies using time series of similar length (e.g., Ings et al. 1997, Laurel et al. 2017). I assessed the relationship between each environmental factor, and juvenile abundance, with age-3 abundance in each seven-year period. This analysis assisted in evaluating variation in recruitment signal and the influence of environmental variables over time.

Results

Recruitment signals

Juvenile surveys later in the fall yielded stronger recruitment signals than earlier periods. For all models, pre-recruit abundance in October yielded the strongest recruitment signal across the entire stock area (Fig. 2.4). For the age-0 to -3 model, November suggested a potentially stronger signal; however, the model did not converge. I therefore used October data for all abundance values for the remainder of the analyses. The model comparing age-0 to -1 abundances produced the strongest recruitment signal ($R^2 = 0.56$; Fig 2.5a). The model comparing age-1 and age-3 abundance produced a slightly stronger recruitment signal ($D^2 = 0.32$; (Fig 2.5c) than the age-0 to -3 model ($D^2 = 0.29$; Fig 2.5b). All models were statistically significant ($p < 0.05$).

Spatial scale analysis

For all models, recruitment signals generally strengthened with increasing distance from the juvenile area (Table 2.1). The largest buffer (850 km), encompassing the entire NAFO

2J3KL survey area, yielded the strongest, and statistical significant recruitment signal for age-0 (Fig 2.6a). Similarly, the 750 km buffer yielded the strongest statistically significant recruitment signal for age-1, although the recruitment signals were almost identical from 600 – 850 km (Fig 2.6a). For the age-0 to -3 model, the recruitment signal was strongest in NAFO divisions 2J and 3K ($D^2 = 0.40$ and $D^2 = 0.36$, respectively, $p < 0.01$), in contrast to the virtually non-existent recruitment signal in 3L ($D^2 = 0.00060$, $p = 0.921$) (Fig 2.6b). Likewise, for the age-1 to -3 model, NAFO divisions 2J and 3K also yielded the strongest recruitment signal ($D^2 = 0.45$ and 0.35, respectively; $p < 0.01$) and I observed a very low, non-significant recruitment signal in 3L ($D^2 = 0.0062$, $p > 0.05$) (Fig 2.6a). When predicting the abundance of age-3 cod, both age-0 and age-1 abundance yielded a significant recruitment signal within EBSA 2 ($D^2 = 0.314$, $p = 0.006$; $D^2 = 0.336$, $p =0.002$; for age-0 and age-1, respectively). EBSA 1 did not yield a recruitment signal with either age-0 or age-1 abundance ($D^2 = 0.127$, $p > 0.05$; $D^2 = 0.142$, $p > 0.05$; for age-0 and age-1, respectively).

Environmental and biological factors

Of the main effects tested, percent eelgrass cover strongly predicted age-3 abundance for both age-0 and -1 models ($p < 0.01$, Table 2.2), but had no effect in predicting age-1 abundance from age 0s ($p > 0.05$, Table 2.3). Winter temperature, winter duration, and prey of age-1 cod, had no influence on the any predictive relationships ($p > 0.05$, Table 2.2 and 2.3). Summer and fall temperature interacted positively (and significantly) with age-1 abundance in predicting recruits ($D^2_{model} = 0.45$, $p < 0.05$). Both fall ($D^2_{model} = 0.77$, $p < 0.01$) and spring ($D^2_{model} = 0.67$, $p < 0.05$) chlorophyll-a level interacted positively with age-0 abundance in predicting age-3 abundance (Table 2.2). However, only fall chlorophyll-a level interacted with the age-1 indices ($D^2_{model} = 0.46$, $p < 0.05$, Table 2.2). The number of predators positively interacted in the age-0 to -3 model ($D^2_{model} = 0.35$, $p < 0.01$, Table 2.2), whereas the number of competitors for age-1 cod alone positively predicted age-3 abundance ($D^2_{model} = 0.45$, $p < 0.05$, Table 2.2). Standard length of age-1 cod weakly predicted age-3 abundance ($D^2_{model} = 0.32$, $p < 0.05$, Table 2.2). There were no strong ecological or statistical correlations among environmental variables.

Temporal analysis

In all models, the recruitment signals associated with environmental variables (irrespective of juvenile age class) and age-3 abundance varied over time. I detected significant recruitment signals using age-0 and age-1 abundance towards the end of the time series (cohorts 2004 and 2005 onwards, for age-1 and age-0, respectively; $D^2 = 0.56 – 0.74$, $p < 0.001$, Fig. 2.7a). Winter water temperature anomalies in Newman Sound were not significant contributors to the model throughout the time series ($p > 0.05$); however, settlement water temperature anomalies (summer/fall) in Newman Sound were significant towards the end of the time series (2005 onwards), $D^2 = 0.42 – 0.50$, $p < 0.05$, Fig. 2.7b). Winter duration in Newman Sound was significant from 1999 – 2005, and 2006 onwards ($D^2 = 0.35 – 0.62$, $p < 0.05$, Fig. 2.7b). Recruitment strength and statistical significance using predator and prey abundance, and chlorophyll-a concentration in Newman Sound as predictors varied greatly over time ($D^2 = 0.0044 – 0.83$, $p = 0.00 – 0.87$); yet signal strength was generally strong towards the end of the time series (2005 onwards), consistent with other density-independent indices (Fig 2.7c, d). However, the direction of the relationship often reversed through the time series. For example, the recruitment signal was strong using indices of peak chlorophyll-a concentration (2005 and 2006 onwards for spring and fall indices, respectively; $D^2 = 0.42 – 0.82$, $p < 0.05$); however, the relationship with recruits was negative for the last three 7-year periods (Table 2.4). I analyzed eelgrass cover as a predictor variable; however, the statistical model did not converge, likely because of insufficient annual variation in the source data.

Discussion

I identified recruitment signals between all early age classes and the offshore population components of cod in my analyses. As predicted, I detected a recruitment signal between early age classes (age-0 and age-1) in Newman Sound, and offshore recruits (age-3) in Newfoundland’s NAFO divisions 2J3KL. The strongest recruitment signal was between age-0 and age-1 abundance, whereas the weakest recruitment signal was between age-0 and age-3 abundance, as expected. All recruitment signals were strongest during October, when abundances and length distributions of early age classes were often greatest. High abundances likely result from multiple age-0 settlement pulses. Furthermore both age-0 and -1 abundances were high because winter migrations to deeper, warmer water may not occur until November (Cote et al. 2001, 2004).

I predicted a weak recruitment signal between age-0 and age-3 abundance because of the spatial and temporal lags between age classes. Age-0 cod occur most commonly in shallow nearshore areas containing nursery habitat such as eelgrass (Gotceitas et al. 1997, Laurel et al. 2003b). Cod often remain in a given habitat type, exploring a small home range with high site fidelity at this age (Pihl and Ulmestrand 1993, Cote et al. 2004). High site fidelity of juveniles and repeated sampling in the same location likely contribute to a stronger recruitment signal between age-0 and age-1 cod by minimizing spatial variation in abundance. In contrast, the temporal (2+ years) and spatial separation between juveniles and adult cod complicate the detection of recruitment signals based on indices from early life stages. Juvenile cod often remain close to coastal settlement habitats for 2-3 years, eventually migrating into deeper water

(Templeman 1974, Gregory and Anderson 1997, Cote et al. 2004). High variability in juvenile mortality throughout the first year may influence the weaker recruitment signal using age-0 abundance. Further, although juvenile cod occur in offshore bottom trawl surveys, they primarily occupy nearshore habitats and are more accurately sampled by nearshore seine surveys than by offshore surveys (Gotceitas et al. 1997, Tulk et al. 2017). Therefore, differences in sampling location and survey gear may contribute to the unexplained variance. As expected, recruitment signal strength increased when using age classes closer to recruitment (i.e., age-1). However, poorly sampled age-1 abundance, leading to underrepresentation of the age class in Newman Sound, may have weakened the recruitment signals of both the age-0 to age-1 and age-1 to age-3 models. Although seine surveys represented age-1 cod better than offshore surveys, past studies show that although age-1 cod may continue to use eelgrass habitat, they often select for less vegetated and deeper habitats (Bradbury et al. 2008; Cote et al. 2013). Age-1 cod may occur outside of the seine haul area in deeper habitats for reasons such as avoidance of unfavourable water temperature, population density, and diel migrations (Methven and Bajdik 1994, Robichaud and Rose 2006, Espeland et al. 2010). This movement may have caused underrepresentation in abundance of the age class in my study, reducing predictive potential.

Spatial scale

Identifying the origin of recruits in inshore and offshore regions remains a challenge (André et al. 2016). In the mid-1990s, offshore populations of cod had declined measurably and smaller aggregations were located inshore (DFO 2010). But in recent years, cod have distributed widely across the Newfoundland shelf, and fisheries managers continue to calculate a single annual abundance index for the entire 2J3KL region (DFO 2016). For all models, recruitment signals were strongest within the largest buffers (i.e., the majority of the 2J3KL region; 750 and

850 km buffer size for age-0 and -1, respectively). With limited tagging and genetic data, the dispersal, migrations, and location of recruits in the offshore remain largely unknown. However, a recent genetic study revealed a sibling relationship and broad relatedness between cod spanning management zones along the Newfoundland coast (Horne et al. 2016). Also, cod in both the inshore and offshore regions of Newfoundland demonstrate different migratory behaviours within and among regions (e.g., sedentary vs. dispersive, resident vs. migratory), seasonal intermingling and genetic distinction (Ruzzante et al. 1996, Brattey 1999, Robichaud and Rose 2004, Brattey et al. 2008). These studies may explain why I detected that a broad survey area showed the strongest recruitment signal because it better represented the many different aggregations and sub-populations of Atlantic cod within 2J3KL. The buffers I used were cumulative. Although analyzing recruitment signals within non-cumulative buffers (e.g., the abundance between 650-700 km and 700-750 km etc.) may provide further insight on spatial patterns, there was no reason to have expected this outcome to be the case a priori. Therefore, I did not conduct such an analysis. It is noteworthy that, given evidence of strong recruitment signals based on inshore abundance (Laurel et al. 2017), data from inshore strata might well strengthen the recruitment signal. Unfortunately, no abundance data were available in the inshore region (i.e., the first 50 km) at a comparable time scale with which I could explore these ideas further. Based on analysis of available data, estimates of future recruitment using Newman Sound juvenile abundance should consider an abundance index for the entire offshore. Newman Sound juvenile abundances appear to be useful for predicting abundance of recruits across a broad area. However, predictions from a single location should exercise caution given the limited spatial scale of juvenile sampling. Addition of more index sites could yield more robust results.

Using age-3 abundance as the response variable from 2J and 3K improved the recruitment signal for all models compared to that of the entire 2J3KL region. Despite moderately high correlations in abundances between 2J3KL zones (Tulk et al. 2017), the recruitment signal for 3L was nearly non-existent. Ever since the cod collapse in the late 1980s and early 1990s, 3L has yielded the lowest abundance of cod relative to 2J and 3K, and the slowest recovery (DFO 2016), limiting detection of any recruitment signal. Elevated abundance in 2J and 3K relative to 3L may result from capelin movement into these zones during the fall and winter months (DFO 2015). Capelin, a small forage fish, have historically been a primary food source for cod in Newfoundland (Templeman 1966). Recent studies suggest that the recovery of cod stocks strongly depends on the recovery of capelin stocks (Buren et al. 2014, DFO 2018). Thus, future work might consider whether the overlap of capelin presence with the timing of the fall RV survey, when cod feed in the area, could provide a more accurate cod abundance index for recruits. It is also highly possible that juveniles in Newman Sound do not provide a source for adult cod populations in 3L.

Environmental Factors

Investigations of interacting and additive effects of environmental variables on fish populations has become increasingly common in response to changing climate and slow recovery of commercial stocks (e.g., Britten et al. 2016, Zhang et al. 2016). Indeed, environmental variables can explain substantial variability in recruitment models (e.g., Zabel et al. 2011). I found high variation in the magnitude and direction of interactions between abundance and environmental variables on juvenile cod abundance. In my study, peak concentration of chlorophyll-a (both fall and spring) interacted positively and significantly with age-0 abundance. Similarly, peak concentration of chlorophyll-a in the fall interacted positively and significantly with age-1 abundance. These results indicate that in years with high peak chlorophyll-a concentration, the linear relationship between juveniles and recruits is stronger. Such an observation was not unexpected. High concentrations of chlorophyll-a (phytoplankton) enhance zooplankton production, both acting as a food source for early life stages of cod (Beaugrand et al. 2003, Bradbury et al. 2008, Kristiansen et al. 2011) and likely driving the strong relationship between juveniles and recruits. In the spring, greater food availability benefits larval cod growth as they drift in ocean currents and ultimately settle in nearshore habitats. In the fall, greater plankton production relative to summer periods likely promotes high growth, reducing the time newly settled juveniles are vulnerable to predators and starvation (Lomond et al. 1998, Beaugrand et al. 2003). When juvenile cod densities are low, the magnitude of the phytoplankton bloom may not act as the primary influence on juvenile growth and survival; however, when their densities are high, the amount of food likely becomes increasingly important in reducing competition for resources. Synchronous spawning and settlement events with the phytoplankton bloom may also influence the recruitment relationships (Hjort 1914, Sissenwine 1984, Cushing 1990, Platt et al. 2003).

Water temperature also greatly affects juvenile fish survival and recruitment (e.g., flounder, *Paralichthys dentatus*; Baltic Sea sprat, *Sprattus sprattus*; coral reef fishes) (e.g., Malloy and Targett 1991, Baumann et al. 2006, Figueira and Booth 2010). The effect of water temperature is location-dependent, and in Newfoundland water temperature correlates positively with body condition; favourable growth conditions support faster individual growth and greater accumulation of lipid stores (Otterlei et al. 1999, Planque and Fredou 1999, Copeman et al. 2008, Laurel et al. 2017). Faster growth likely reduces predation risk by increasing body size and predator avoidance ability. It also reduces chances of starvation during periods of low productivity and food availability such as the overwinter period (Copeman et al. 2008, Houde 2008). Although the potential response of cod to future climate change remains largely unknown, a recent study by Laurel et al. (2017) demonstrated the importance of temperature-dependent growth potential in estimating recruitment signals in three locations with known cod populations: Newfoundland, Alaska, and Norway. Their study found improved recruitment signals during favourable growth conditions in the settlement period before the first winter, when juveniles are highly vulnerable. However, water temperature anomalies from July to November positively influenced recruitment signals between age-1 and age-3 cod. Age-1 cod likely benefit from faster growth and increased chances of survival before they begin to migrate into deeper water.

Predator abundance interacted positively with recruitment; high predator abundance coincided with a positive relationship between age-0 cod and recruits. Although unexpected, this interaction may result from high correlation with age-0 abundance, and may simply reflect periods of high productivity. Alternatively, predators may positively influence recruitment by mediating cod abundance over winter, thus reducing density-dependent effects, such as competition and cannibalism.

Surprisingly, I observed no significant interaction between juvenile abundance and eelgrass through the entire time series. Eelgrass, considered ecologically significant species, are common along the coast of Newfoundland, but are vulnerable to anthropogenic and environmental stressors such as fishing activity and ice scour (DFO 2009, Warren et al. 2010). Although juvenile cod live within many structured habitats (e.g., cobble, rocky reefs, kelp etc.), they benefit from eelgrass beds through increased refuge (Gotceitas et al. 1997, Laurel et al. 2003a) and greater prey abundance (Renkawitz et al. 2011), ultimately leading to higher juvenile (age-0) density in eelgrass beds compared to unvegetated areas (Cote et al. 2013). Although several studies show positive effects of eelgrass on juvenile cod survival, it is possible that variables related to eelgrass other than total percent cover may influence juvenile abundance and could reveal stronger recruitment signals in my study area (e.g., patch size, number of patches, shoot density, Thistle et al. 2010). As a result of high, expanding eelgrass cover in Newman Sound coupled with low year-to-year variability, my analyses did not identify eelgrass statistically as a primary influence on recruitment signals in this system. Eelgrass remains a vital factor for juvenile cod survival, and analysis of eelgrass at different spatial scales may explain additional variation in recruitment (e.g., Thistle et al. 2010).

Consideration of environmental variables remains an important part of interpreting year-class strength in juvenile cod and forecasting adult abundance. However, my results are consistent with past studies in that the magnitude of environmental effects may interact with and depend on population density (Zabel et al. 2011, Ottersen et al. 2013).

Temporal Analysis

Although extended time series likely illustrate large-scale climate effects more strongly (e.g., the North Atlantic Oscillation), small-scale environmental factors likely influence fish abundance differently over short temporal scales of several years (e.g., Stige et al. 2006, Brunel and Boucher 2007, Nye et al. 2009, Zabel et al. 2011). Previous studies identified non-stationarity of recruitment-environment relationships as the necessary standard for interpreting most ecological time series (Stige et al. 2013, Feiner et al. 2015). I found environmental factors influenced recruitment at different times, often reversing trends, which may reduce their utility for forecasting recruitment (Britten et al. 2016). Nonetheless, my results show that environmental factors can enhance predictive strength, and studies should include environmental factors when interpreting stock-recruitment dynamics and forecasting population size of cod.

Conclusions

My study provides the first empirical evidence that information from nearshore seine surveys can be considered when forecasting adult population strength. As predicted, I detected a recruitment signal between Newman Sound coastal nursery habitats and the pre-adult northern cod population offshore. Recruitment signal strength varied among fisheries management zones and distance from juvenile cod nursery habitats. I also identified additional biotic and abiotic factors that appear to play a role in recruitment to the fishery: peak concentration of chlorophyll-a, water temperature, and predator abundance. Environmental variables should be considered when attempting to maximize predictive ability among fish populations. I also showed the relative influence of environmental and biological factors on recruitment signal strength shifted over time, highlighting the importance of ecological time series in fish recruitment studies.

Figures

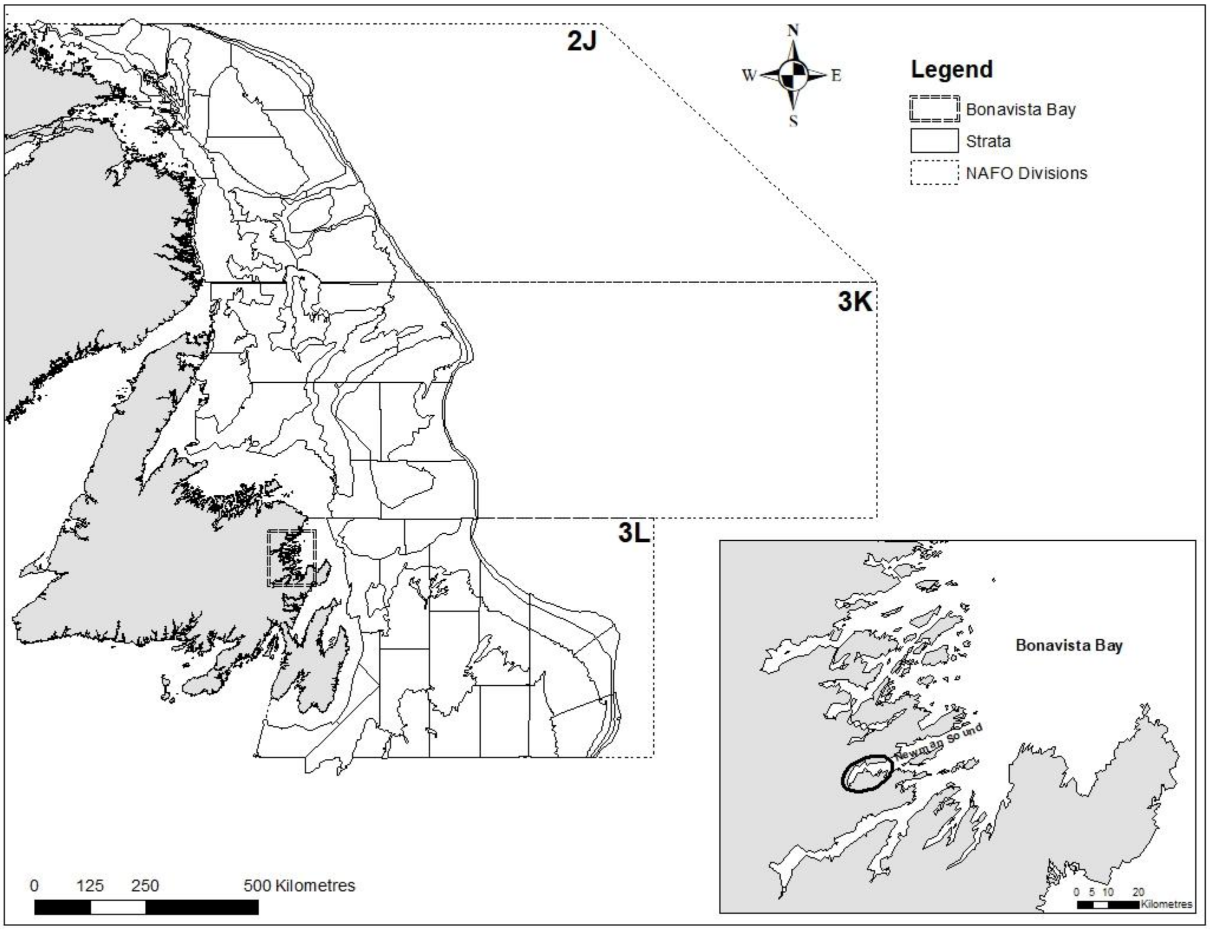


Figure 2.1. Newman Sound (oval in inset figure) with respect to NAFO fisheries management divisions 2J3KL and strata, off the northeast coast of Newfoundland.

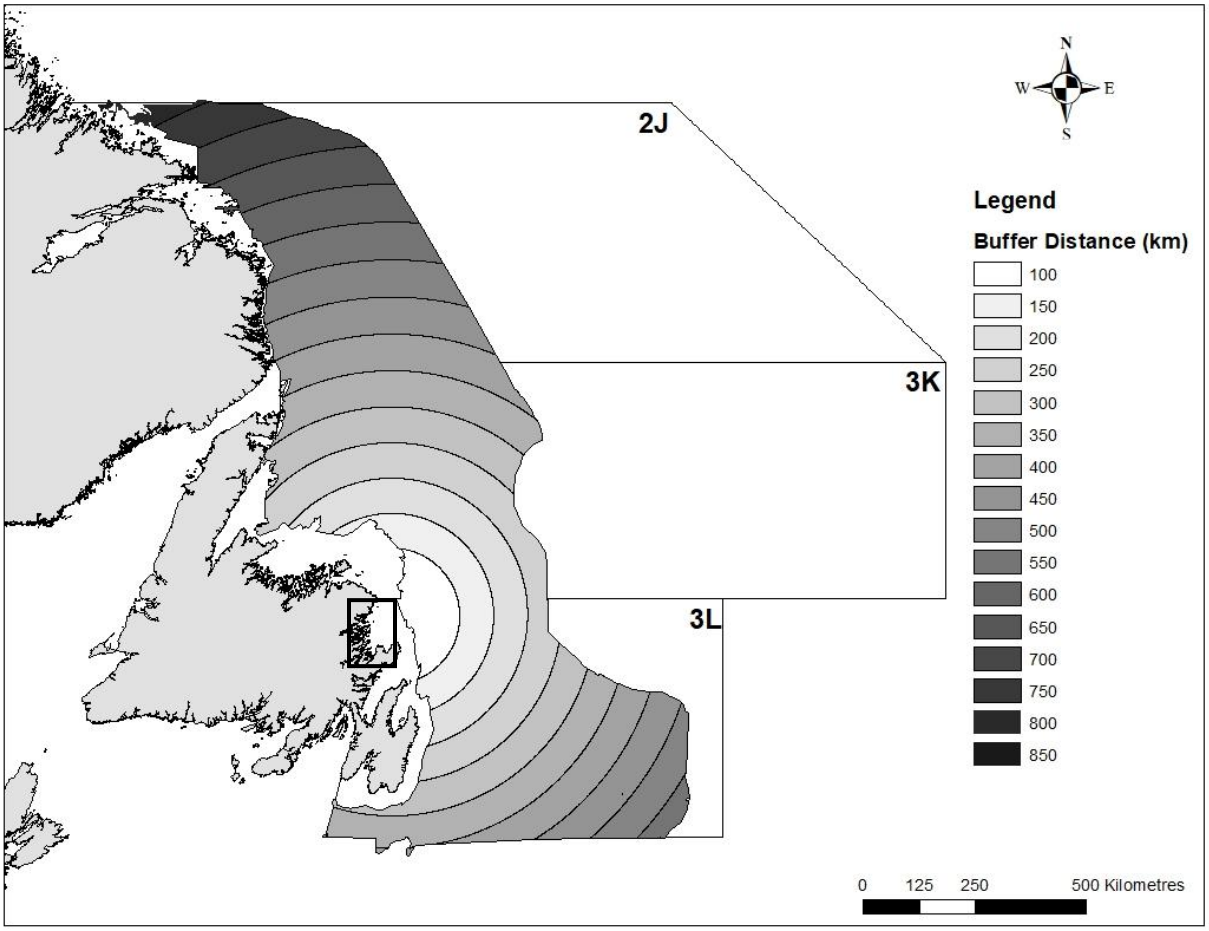


Figure 2.2. Buffers within NAFO divisions 2J3KL (100 – 850 km) from Newman Sound, Bonavista Bay (rectangle) used for spatial analysis of recruitment models.

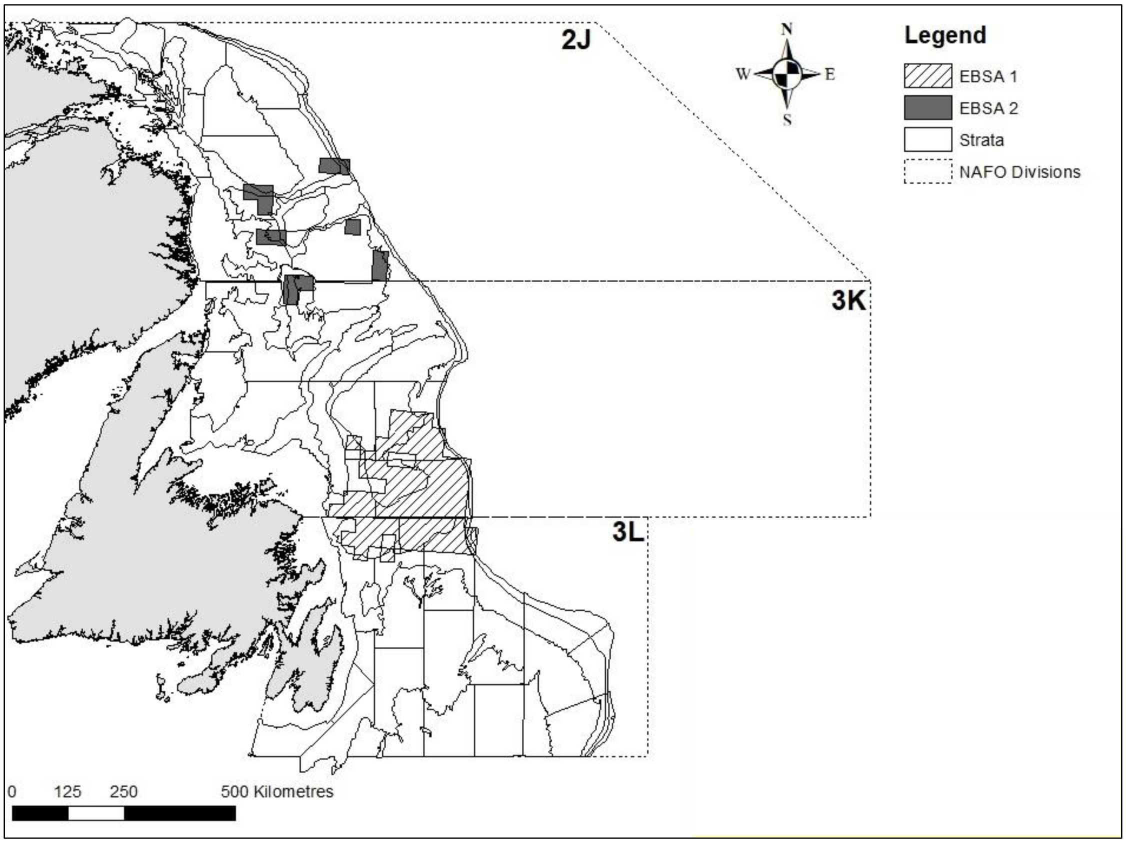


Figure 2.3. Potential Atlantic cod Ecologically and Biologically Significant Areas placement within NAFO divisions 2J3KL as of 2017.

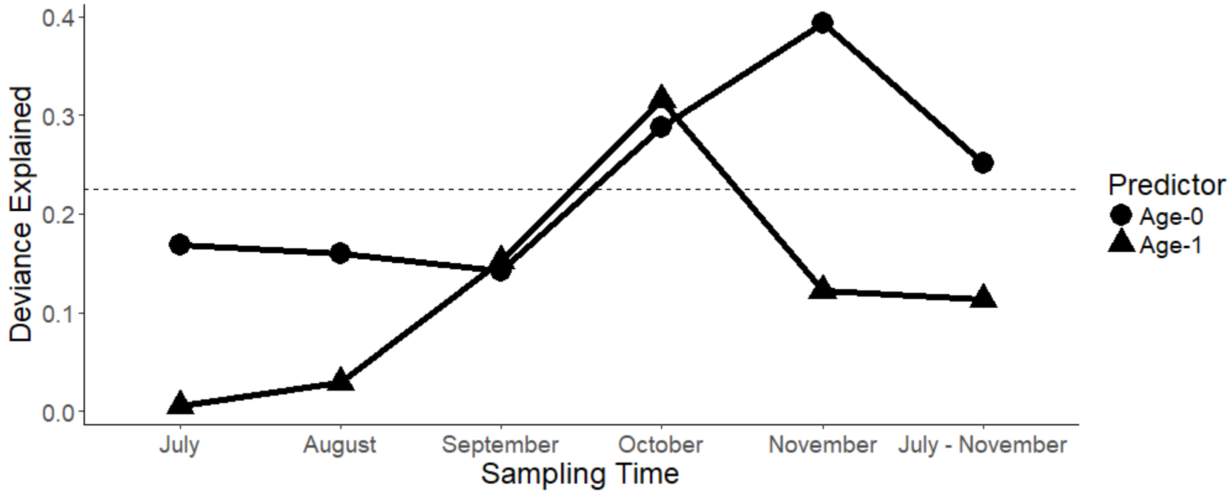


Figure 2.4. Age-3 recruitment signal strength between monthly juvenile abundance (mean catch·haul^{-1}) and the entire season (i.e., July – November) for predictor age classes (Age-0 and Age-1). Points above dashed line indicate statistically significant periods ($p < 0.05$).

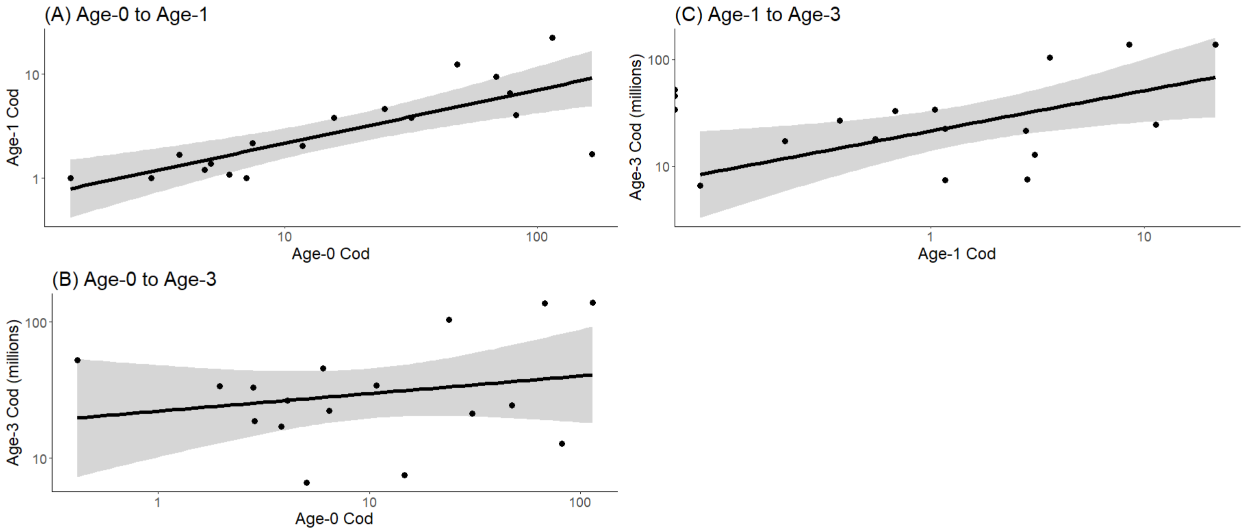


Figure 2.5. Recruitment signals between mean juvenile October (age-0 and -1) abundance in Newman Sound, Bonavista Bay and pre-adult (age-3) cod abundance in NAFO divisions 2J3KL (± SE). (A) Age-0 and -1; (B) Age-0 and -3; (C) Age-1 and -3.

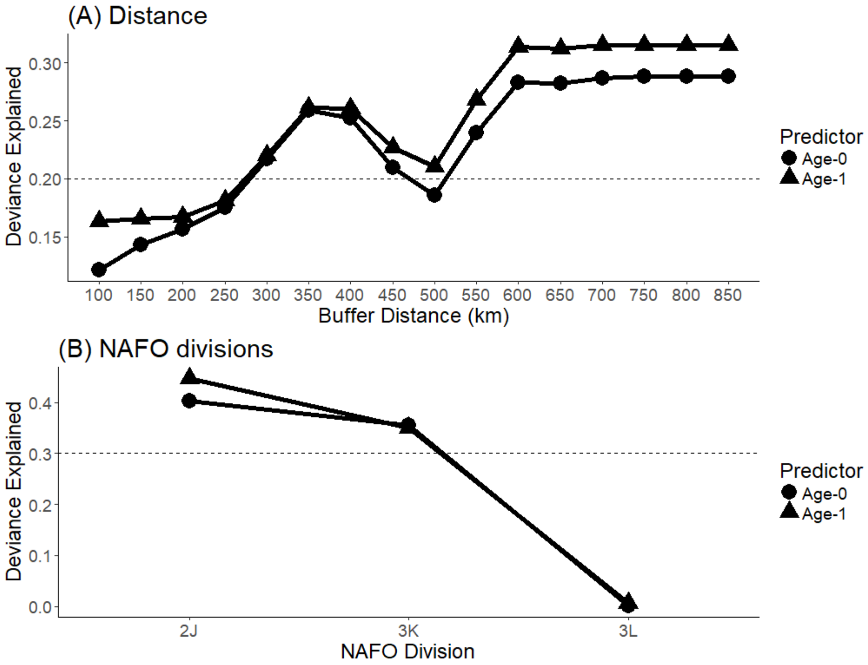
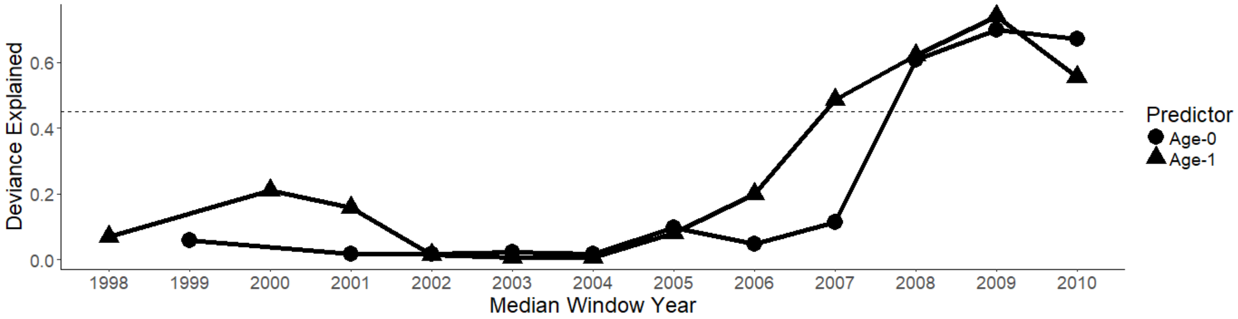
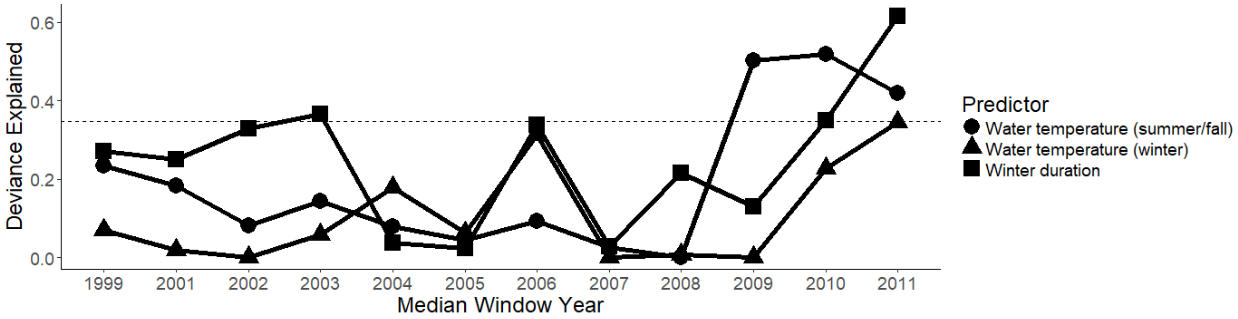


Figure 2.6. Age-3 recruitment signal strength from juvenile abundance (mean catch·haul^{-1}) between (A) increasing distance from nursery habitat and (B) NAFO divisions. Relationships represented by points above the dashed line are statistically significant ($p < 0.05$).

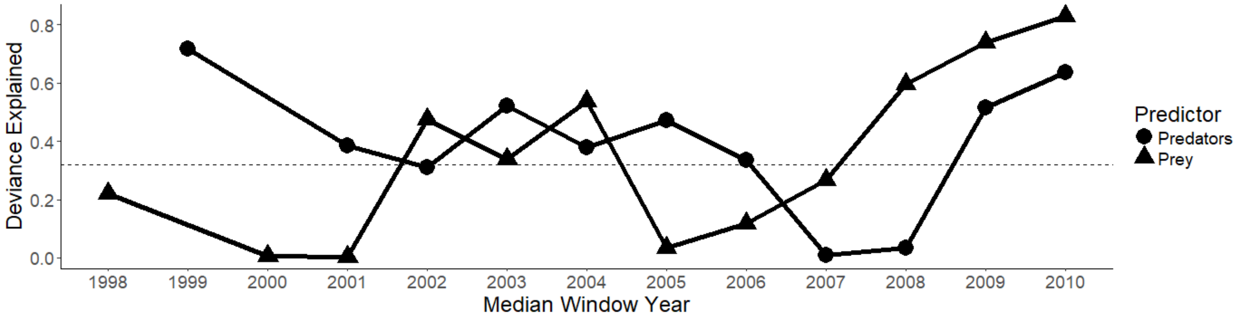
(A) Juvenile abundance



(B) Temperature



(C) Predator and prey abundance



(D) Chlorophyll-a concentration

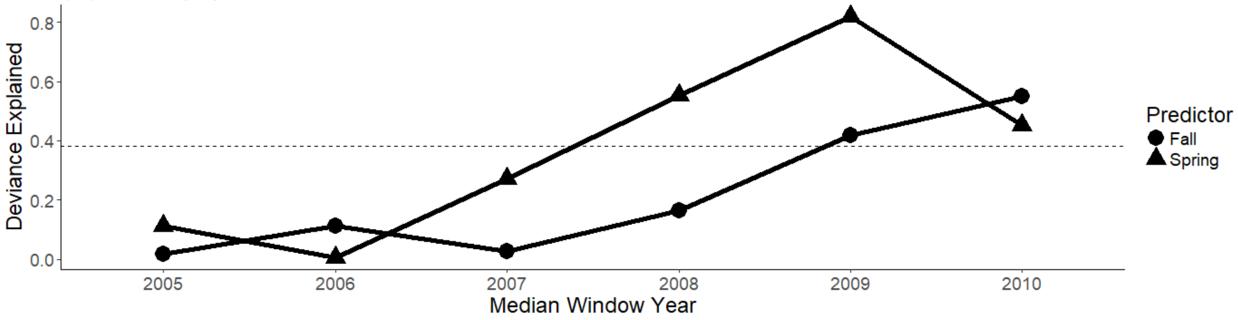


Figure 2.7. Age-3 recruitment signal strength in seven-year sliding windows using (A) age-0 and -1 abundance (mean catch·haul^{-1}), (B) age-0 predator and age-1 prey abundance (mean

catch·haul^{-1}), (C) water temperature anomalies and winter duration, and (D) peak spring and fall chlorophyll-a concentration. Relationships represented by points above the dashed line are statistically significant ($p < 0.05$)

Tables

Table 2.1. Generalized linear model results for recruitment signals of age-3 cod using age-0 and age-1 abundance at varying spatial scales (increasing distance from the juvenile survey area). Bold font signifies statistical significance ($p < 0.05$).

Age-0							
Buffer size (km)	Slope	DF	Deviance	Residual DF	Residual Deviance	*p* value	D^2
100	0.00741	1	20.6	15	18.2	0.124	0.121
150	0.00876	1	21.4	15	18.3	0.091	0.143
200	0.00893	1	21.7	15	18.3	0.080	0.156
250	0.00889	1	22	15	18.2	0.067	0.175
300	**0.0101**	**1**	**23.2**	**15**	**18.1**	**0.035**	**0.217**
350	**0.0114**	**1**	**24.5**	**15**	**18.1**	**0.017**	**0.259**
400	**0.0118**	**1**	**24.4**	**15**	**18.2**	**0.018**	**0.252**
450	**0.011**	**1**	**23.2**	**15**	**18.3**	**0.035**	**0.210**
500	0.0102	1	22.6	15	18.4	0.053	0.185
550	**0.0117**	**1**	**24.2**	**15**	**18.4**	**0.027**	**0.240**
600	**0.0128**	**1**	**25.6**	**15**	**18.4**	**0.016**	**0.283**
650	**0.0128**	**1**	**25.6**	**15**	**18.4**	**0.015**	**0.283**
700	**0.013**	**1**	**25.8**	**15**	**18.4**	**0.014**	**0.287**
750	**0.013**	**1**	**25.8**	**15**	**18.4**	**0.013**	**0.288**
800	**0.013**	**1**	**25.8**	**15**	**18.4**	**0.014**	**0.288**
850	**0.013**	**1**	**25.8**	**15**	**18.4**	**0.014**	**0.288**

Table 2.1. (continued)

Age 1							
Buffer size (km)	Slope	DF	Deviance	Residual DF	Residual Deviance	*p* value	D^2
100	0.052	1	23	16	19.2	0.065	0.163
150	0.058	1	23.3	16	19.4	0.058	0.165
200	0.058	1	23.4	16	19.4	0.060	0.167
250	0.057	1	23.6	16	19.3	0.055	0.181
300	**0.065**	**1**	**24.8**	**16**	**19.3**	**0.026**	**0.220**
350	**0.073**	**1**	**26.1**	**16**	**19.3**	**0.013**	**0.261**
400	**0.076**	**1**	**26.2**	**16**	**19.4**	**0.012**	**0.261**
450	**0.073**	**1**	**25.2**	**16**	**19.5**	**0.021**	**0.227**
500	**0.070**	**1**	**24.7**	**16**	**19.5**	**0.030**	**0.210**
550	**0.079**	**1**	**26.7**	**16**	**19.5**	**0.014**	**0.268**
600	**0.085**	**1**	**28.4**	**16**	**19.5**	**0.008**	**0.314**
650	**0.085**	**1**	**28.4**	**16**	**19.5**	**0.007**	**0.312**
700	**0.086**	**1**	**28.5**	**16**	**19.5**	**0.007**	**0.315**
750	**0.086**	**1**	**28.5**	**16**	**19.5**	**0.007**	**0.316**
800	**0.086**	**1**	**28.5**	**16**	**19.5**	**0.007**	**0.315**
850	**0.086**	**1**	**28.5**	**16**	**19.5**	**0.007**	**0.315**

Table 2.2. Generalized linear model results for recruitment signals of age-3 cod using age-0 and age-1 abundance with environmental interactions. Bold font signifies statistical significance (p < 0.05)

Age-0								
Response	Predictor	Slope	DF	Deviance	Residual DF	Residual Deviance	*p* value	Adjusted D^2
Age 3	Age-0	0.00217	1	27.6	13	18.3	0.804	0.183
	Settlement temperature	-0.762	1				0.412	
	Age-0 * Settlement temperature	0.0404	1				0.206	
Age 3	Age-0	0.00858	1	26.9	13	18.3	0.233	0.163
	Winter temperature	-0.588	1				0.438	
	Age-0 * Winter temperature	-0.00638	1				0.728	
Age 3	Age-0	0.031	1	29.2	13	18.2	0.532	0.231
	Winter duration	-0.0122	1				0.217	
	Age-0 * Winter duration	-0.000136	1				0.757	
Age 3	Age-0	0.00674	1	108	13	17.3	0.613	0.803
	Percent eelgrass	**0.0446**	**1**				**<0.001**	
	Age-0 * Percent eelgrass	0.0000689	1				0.670	
Age 3	Age-0	0.142	1	29.7	13	18.2	0.118	0.246
	Length	0.0109	1				0.624	
	Age-0 * Length	-0.002	1				0.157	
Age 3	**Age-0**	**0.00765**	**1**	**70.7**	**7**	**11.1**	**0.033**	**0.775**
	Fall chlorophyll-a	-0.173	1				0.586	
	Age-0 * Fall chlorophyll-a	**0.109**	**1**				**0.001**	

Table 2.2. (continued)

Response	Predictor	Slope	DF	Deviance	Residual DF	Residual Deviance	*p* value	Adjusted D^2
Age 3	Age-0	-0.0315	1	48.5	7	11.2	0.178	0.670
	Spring chlorophyll-a	1.78	1				0.457	
	Age-0 * Spring chlorophyll-a	**0.207**	**1**				**0.031**	
Age 3	Age-0	-0.0208	1	34	13	18	0.076	0.346
	Predators	-0.044	1				0.083	
	Age-0 * Predators	**0.00126**	**1**				**0.003**	
Age 1								
Response	Predictor	Slope	DF	Deviance	Residual DF	Residual Deviance	p-value	Adjusted D^2
Age 3	**Age-1**	**0.0601**	**1**	**42**	**14**	**19**	**0.024**	**0.450**
	Settlement temperature	-0.148	1				0.803	
	Age-1 * Settlement temperature	**0.365**	**1**				**0.013**	
Age 3	Age-1	-0.0394	1	38.6	14	19.1	0.521	0.399
	Winter temperature	-1	1				0.131	
	Age-1 * Winter temperature	-0.212	1				0.136	
Age 3	Age-1	-0.343	1	31.6	14	19.4	0.188	0.256
	Winter duration	-0.00666	1				0.476	
	Age-1 * Winter duration	0.00387	1				0.103	
Age 3	Age-1	0.168	1	92.4	13	17.4	0.183	0.768
	Percent eelgrass	**0.0501**	**1**				**<0.001**	
	Age-1 * Percent eelgrass	-0.00109	1				0.454	
Age 3	Age-1	-0.422	1	39.1	11	15.9	0.241	0.482
	Length	**0.0385**	**1**				**0.050**	
	Age-1 * Length	0.00438	1				0.096	

Table 2.2. (continued)

Response	Predictor	Slope	DF	Deviance	Residual DF	Residual Deviance	*p* value	Adjusted D^2
Age 3	**Age-1**	**0.126**	**1**	**31.4**	**8**	**12.4**	**<0.001**	**0.458**
	Fall chlorophyll-a	0.283	1				0.516	
	Age-1 * Fall chlorophyll-a	**0.908**	**1**				**0.024**	
Age 3	Age-1	0.057	1	24.5	8	12.5	0.794	0.300
	Spring chlorophyll-a	-4.14	1				0.293	
	Age-1 * Spring chlorophyll-a	0.000978	1				0.999	
Age 3	Age-1	-0.222	1	34.6	14	19.2	0.171	0.324
	Competitors	**0.176**	**1**				**0.031**	
	Age-1 * Competitors	0.0041	1				0.401	
Age 3	Age-1	-0.0266	1	38.6	14	19.1	0.661	0.399
	Prey	0.00703	1				0.102	
	Age-1 * Prey	0.000423	1				0.369	

Table 2.3. General linear model results for recruitment signals of age-1 cod using age-0 abundance (both log-transformed + 1) with and without environmental interactions. Bold font signifies statistical significance ($p < 0.05$)

Response	Predictor	DF	Slope	Residual DF	F Statistic	*p* value	Adjusted R^2
Age-1	**Age-0**	**1**	**0.513**	**16**	**4.798**	**<0.001**	**0.564**
Age-1	**Age-0**	**1**	**0.516**	**16**	**4.263**	**0.001**	**0.504**
	Settlement temperature	1	0.197		0.158	0.877	
	Age-0 * Settlement temperature	1	-0.025		-0.063	0.951	
Age-1	**Age-0**	**1**	**0.585**	**14**	**5.665**	**0.001**	**0.646**
	Winter temperature	1	-0.796		-0.583	0.569	
	Age-0 * Winter temperature	1	0.524		1.342	0.201	
Age-1	Age-0	1	0.768	14	1.322	0.207	0.550
	Winter duration	1	0.000		-0.019	0.985	
	Age-0 * Winter duration	1	-0.002		-0.429	0.675	
Age-1	Age-0	1	0.740	14	0.902	0.382	0.507
	Percent eelgrass	1	0.007		0.202	0.843	
	Age-0 * Percent eelgrass	1	-0.003		-0.282	0.782	
Age-1	Age-0	1	-0.604	14	-0.396	0.698	0.536
	Length	1	-0.053		-0.931	0.368	
	Age-0 * Length	1	0.018		0.731	0.477	
Age-1	**Age-0**	**1**	**0.430**	**9**	**3.072**	**0.013**	**0.532**
	Fall chlorophyll-a	1	-1.701		-1.109	0.296	
	Age-0 * Fall chlorophyll-a	1	1.009		1.290	0.229	
Age-1	**Age-0**	**1**	**1.386**	**9**	**2.364**	**0.042**	**0.729**
	Spring chlorophyll-a	1	3.165		0.519	0.616	
	Age-0 * Spring chlorophyll-a	1	-3.379		-1.791	0.107	

Table 2.3. (continued)

Response	Predictor	DF	Slope	Residual DF	F Statistic	*p* value	Adjusted R^2
Age-1	**Age-0**	**1**	**0.637**	**14**	**2.834**	**0.013**	**0.524**
	Predators	1	0.003		0.073	0.943	
	Age-0 * Predators	1	-0.004		-0.375	0.713	

Table 2.4. Generalized linear model results for recruitment signals using environmental and biological factors in 7-year sliding windows. Bold font signifies statistical significance (p < 0.05)

Time Window (Cohort year)	DF	Slope	Residual DF	*p* value	D^2
Mean Age-0					
1996 – 2002	1	0.00472	5	0.490	0.060
1998 – 2004	1	0.00241	6	0.709	0.016
1999 – 2005	1	-0.00273	6	0.701	0.019
2000 - 2006	1	-0.006	6	0.704	0.023
2001 – 2007	1	-0.00476	6	0.724	0.018
2002 – 2008	1	-0.00691	6	0.383	0.096
2003 – 2009	1	-0.0232	6	0.578	0.049
2004 – 2010	1	-0.0268	6	0.368	0.113
2005 – 2011	**1**	**0.0404**	**6**	**0.004**	**0.607**
2006 – 2012	**1**	**0.0211**	**6**	**<0.001**	**0.698**
2007 - 2013	**1**	**0.0142**	**6**	**<0.001**	**0.669**

Table 2.4. (continued)

Time Window (Cohort year)	DF	Slope	Residual DF	*p* value	D^2
Mean Age-1					
1995 – 2001	1	0.104	5	0.488	0.070
1997 – 2003	1	0.0528	6	0.196	0.21
1998 – 2004	1	0.0493	6	0.269	0.159
1999 – 2005	1	0.0158	6	0.768	0.014
2000 - 2006	1	-0.0144	6	0.820	0.008
2001 – 2007	1	-0.013	6	0.809	0.008
2002 – 2008	1	-0.0256	6	0.422	0.081
2003 – 2009	1	-0.336	6	0.191	0.199
2004 – 2010	**1**	**-0.4**	**6**	**0.010**	**0.485**
2005 – 2011	**1**	**0.254**	**6**	**0.003**	**0.621**
2006 – 2012	**1**	**0.166**	**6**	**<0.001**	**0.740**
2007 - 2013	**1**	**0.0715**	**6**	**0.002**	**0.555**
Winter Temperature					
1995 – 2001	1	-0.57	5	0.428	0.069
1997 – 2003	1	-0.425	6	0.662	0.019
1998 – 2004	1	0.0706	6	0.943	<0.001
1999 – 2005	1	-0.766	6	0.464	0.057
2000 - 2006	1	-1.78	6	0.190	0.178
2001 – 2007	1	-0.784	6	0.488	0.063
2002 – 2008	1	-1.09	6	0.067	0.312
2003 – 2009	1	-0.0187	6	0.972	<0.001
2004 – 2010	1	-0.0829	6	0.835	0.007
2005 – 2011	1	-0.0194	6	0.978	<0.001
2006 – 2012	1	-0.936	6	0.164	0.226
2007 - 2013	1	-1.2	6	0.056	0.344

Table 2.4. (continued)

Time Window (Cohort year)	DF	Slope	Residual DF	*p* value	D^2
Settlement Temperature					
1995 – 2001	1	-0.588	5	0.146	0.234
1997 – 2003	1	-0.56	6	0.148	0.184
1998 – 2004	1	-0.446	6	0.350	0.081
1999 – 2005	1	-0.723	6	0.174	0.143
2000 - 2006	1	-0.883	6	0.377	0.079
2001 – 2007	1	-0.592	6	0.495	0.045
2002 – 2008	1	0.536	6	0.404	0.094
2003 – 2009	1	-0.278	6	0.689	0.026
2004 – 2010	1	0.00901	6	0.986	<0.001
2005 – 2011	**1**	**1.18**	**6**	**0.016**	**0.503**
2006 – 2012	**1**	**1.59**	**6**	**0.008**	**0.518**
2007 - 2013	**1**	**1.79**	**6**	**0.019**	**0.418**
Winter Duration					
1995 – 2001	1	-0.0146	5	0.130	0.270
1997 – 2003	1	-0.0144	6	0.123	0.251
1998 – 2004	1	-0.0162	6	0.064	0.328
1999 – 2005	**1**	-0.0203	**6**	0.037	0.367
2000 - 2006	1	0.00644	6	0.639	0.037
2001 – 2007	1	0.00465	6	0.690	0.024
2002 – 2008	1	0.0102	6	0.073	0.338
2003 – 2009	1	0.00251	6	0.687	0.027
2004 – 2010	1	0.0057	6	0.211	0.215
2005 – 2011	1	0.00847	6	0.293	0.13
2006 – 2012	**1**	**0.0164**	**6**	**0.043**	**0.349**
2007 - 2013	**1**	**0.0264**	**6**	**0.001**	**0.615**

Table 2.4. (continued)

Time Window (Cohort year)	DF	Slope	Residual DF	*p* value	D^2
Age-1 Prey					
1995 – 2001	1	0.00488	5	0.241	0.221
1997 – 2003	1	0.000798	6	0.859	0.006
1998 – 2004	1	0.000796	6	0.872	0.004
1999 – 2005	**1**	**-0.0235**	**6**	**0.009**	**0.475**
2000 - 2006	**1**	**-0.0336**	**6**	**0.022**	**0.338**
2001 – 2007	**1**	**-0.035**	**6**	**<0.001**	**0.538**
2002 – 2008	1	-0.00428	6	0.607	0.035
2003 – 2009	1	-0.00804	6	0.325	0.118
2004 – 2010	1	-0.00912	6	0.099	0.267
2005 – 2011	**1**	**0.00717**	**6**	**0.005**	**0.595**
2006 – 2012	**1**	**0.00861**	**6**	**<0.001**	**0.738**
2007 - 2013	**1**	**0.00927**	**6**	**<0.001**	**0.829**
Age-0 Predators					
1996 – 2002	**1**	**-0.0668**	**5**	**<0.001**	**0.716**
1998 – 2004	**1**	**-0.0379**	**6**	**0.039**	**0.386**
1999 – 2005	1	-0.0421	6	0.066	0.31
2000 - 2006	**1**	**-0.0581**	**6**	**0.005**	**0.521**
2001 – 2007	**1**	**-0.0477**	**6**	**0.036**	**0.379**
2002 – 2008	**1**	**-0.0355**	**6**	**0.009**	**0.471**
2003 – 2009	**1**	**-0.0331**	**6**	**0.041**	**0.335**
2004 – 2010	1	-0.00601	6	0.813	0.009
2005 – 2011	1	0.0218	6	0.596	0.035
2006 – 2012	**1**	**0.0366**	**6**	**0.012**	**0.514**
2007 - 2013	**1**	**0.0396**	**6**	**<0.001**	**0.636**

Table 2.4. (continued)

Time Window (Cohort year)	DF	Slope	Residual DF	*p* value	D^2
Peak Spring Chlorophyll-a Concentration					
2002 – 2008	1	2.31	6	0.298	0.112
2003 – 2009	1	0.604	6	0.833	0.005
2004 – 2010	1	-4.04	6	0.095	0.271
2005 – 2011	**1**	**-7.62**	**6**	**0.005**	**0.552**
2006 – 2012	**1**	**-8.71**	**6**	**<0.001**	**0.818**
2007 - 2013	**1**	**-7.93**	**6**	**0.011**	**0.452**
Peak Fall Chlorophyll-a Concentration					
2002 – 2008	1	0.179	6	0.702	0.016
2003 – 2009	1	0.329	6	0.336	0.112
2004 – 2010	1	0.128	6	0.657	0.028
2005 – 2011	1	-0.528	6	0.248	0.163
2006 – 2012	**1**	**-1.07**	**6**	**0.030**	**0.419**
2007 - 2013	**1**	**-1.26**	**6**	**0.004**	**0.549**

Chapter 3: The effects of spatial and temporal scale on post-collapse recruitment signals of Atlantic cod (*Gadus morhua*) across the northeast coast of Newfoundland

Abstract

The coast-wide Fleming Survey conducted in four bays along the northeast coast of Newfoundland from 1992-1997 and in 2001 – provided an opportunity to evaluate the potential to use juvenile Atlantic cod (*Gadus morhua*) populations to predict future year-class strength of offshore recruits and a unique opportunity to examine recruitment signals at spatial scales from (within and across major bays) to offshore region. Generalized linear models reveal a significant relationship between juvenile (age-0) and pre-adult (age-3) abundance in the Northern cod stock. However, this relationship was only present in Trinity Bay, which contained a large and consistent spawning aggregation during a period of otherwise low productivity in coastal and offshore waters of northeast Newfoundland. Recruitment signal strength also varied with distance from the index sites and among management zones. Juvenile abundance should be used when forecasting future populations, but spatial and temporal scale and resolution adds an important consideration when interpreting recruitment signal strength.

Introduction

Shifts in environmental and anthropogenic stressors can lead to high spatiotemporal fluctuations in recruitment for marine fish populations (e.g., Atlantic cod, *Gadus morhua*; Atlantic mackerel *Scomber scombrus*; sardine *Sardina pilchardus* e.g., Santos et al. 2001, Robert et al. 2007, Stige et al. 2013, Laurel et al. 2016). These fluctuations can alter the ecological dynamics of exploited fish stocks and render a fishery unsustainable (Fréon et al. 2005, Hsieh et al. 2006). Obtaining accurate predictions of future stock strength, or detecting a “recruitment signal", benefits management, industry, and fishing communities by providing time to address the ecological and socio-economic consequences of poor productivity years (Gulland 1989). Classic fishery assessment models use biological and catch data, and estimates of mortality to assess current and future stock strength (Megrey and Wespestad 1988). Indeed, several studies have successfully demonstrated the predictive potential of using larval and juvenile estimates to forecast abundances of older age classes (e.g., Sissenwine 1984, Tveite 1992, MacKenzie et al. 2008, Stige et al. 2013). In general, predictions using life stages closer to the age-at-recruitment (e.g., juveniles) produce more accurate forecasts because individuals are easier to sample and less vulnerable to abrupt and unexpected changes in abundance caused by predation and starvation than earlier stages (Stige et al. 2013, Laurel et al. 2017). However, monitoring year-class strength of early life stages can allow a longer time period to adjust management decisions and socioeconomic expectations associated with low fishery productivity.

Understanding spatial patterns of fish population recruitment is critical to developing effective fisheries management and conservation policies. For example, the development of fisheries management zones and the placement of marine protected areas (MPAs) require knowledge on spatial ecology and population connectivity (Fogarty and Botsford 2007, Morris et al. 2014). Important spatial components of marine fish populations to consider include distribution, dispersal and migrations of fish through different life stages (Cowen et al. 2000, Palumbi 2004), and population structure (e.g., genetic similarity, Berkeley 2004, Reiss et al. 2009). Quantifying dispersal and movement patterns of individuals in a marine environment in order to detect a recruitment signal can be difficult (e.g., Cowen and Sponaugle 2009), particularly when tracking organisms across different life stages.

Many marine organisms disperse over large spatial scales during their pelagic larval phase, controlled in part by oceanographic processes, such as ocean currents and wind. High mortality during early life stages contributes to spatial differences in survival, year-class strength, and settlement success (Sale et al. 1984, McGurk 1986, Pepin and Helbig 1997). Numerous studies have demonstrated the value of nursery habitats as a source for adult populations of many marine species (Gillanders et al. 2003) and consequently, the relative output of recruits likely varies in time and space in association with the distribution of these habitats. Further, the distribution of adult fish may subsequently shift from juvenile distributions depending on changes in climate, food availability, and fishing pressure (Perry et al. 2005). Therefore, recruitment signals based on early life stages are likely to vary among regions and populations (e.g., Laurel et al. 2017) but identifying the appropriate spatial scales in management remains a crucial challenge for managing many marine fisheries (Sissenwine 1984).

Many studies have focused on Atlantic cod (hereafter cod) as a model species to study spatiotemporal variability in recruitment and population connectivity. After drifting into coastal habitats as larvae and pelagic juveniles, cod settle to the seabed. Post-settled juveniles remain highly vulnerable to predator mortality during the first few years of life (Anderson and Gregory 2000). Juvenile cod use nursery habitats (e.g., eelgrass *Zostera marina*) that provide refuge, food, and thermal conditions that promote high growth and survival (Laurel et al. 2003a, Bradbury et al. 2008, Copeman et al. 2008). Although extensive time series exist for juvenile cod - e.g., the Fleming Survey (Schneider et al. 1997), the Flødevigen surveys (Rogers et al. 2010), and the Newman Sound Juvenile Program (Gregory et al. 2016) - the spatial variation in recruitment signals from these juvenile index sites remains largely unknown. For example, differences in recruitment signals among embayments that may reveal recruitment patterns at the bay-scale have yet to be examined through to adults. Following the cod stock collapse in Newfoundland and Labrador, populations redistributed spatially in both inshore and offshore regions coinciding with the partial rebuilding of the Northern cod stock (DeYoung and Rose 1993, DFO 2016, Rose and Rowe 2018). Although past studies link juvenile cod genetically over broad spatial scales (> 500 km) in Newfoundland (Horne et al. 2016), whether recruitment signals respond at similar scales remains unclear.

A coast-wide survey conducted in Newfoundland – the “Fleming Survey” (Lear et al. 1980) – was completed annually pre- (1959 – 1964) and post-collapse (1992 – 1997, 2001) of the cod fishery and subsequent moratorium in 1992. The original objectives of the Fleming Survey were to monitor post-settlement juvenile cod populations (ages 0 – 2) and determine whether an index of year-class strength could be derived that predicted recruitment to the commercial fishery. Additional objectives for this survey included comparing fish lengths and abundance among years (Ings et al. 1997), evaluating the influence of abiotic factors on cod abundance, and evaluating the importance of large spawning events (Schneider et al. 1997). This annual seine survey targeted shallow coastal sites (< 10 m depth) that contain high densities of juvenile cod (< age-3) relative to deeper areas offshore (Dalley and Anderson 1997). The Fleming Survey was unique in allowing comparisons of abundance and recruitment signals before and after the cod fishery decline; it also used consistent sampling methodologies across five prominent bays along the northeast coast of Newfoundland. This dataset yielded weak recruitment signals between juvenile age classes (Ings et al. 1997) and a recruitment signal to the offshore 2J3KL stock pre-collapse (1959 – 1964, Ings et al. 1997). However, no study has attempted post-collapse extrapolation of inshore juvenile abundance to the offshore. Given the substantial spatial movements that cod undergo throughout early life stages to age-at-recruitment, spatial scale may prove important for revealing predictive relationships.

In this study, I investigated the potential for nearshore seine surveys to detect recruitment signals in pre-adult cod abundance in coastal Newfoundland following the cod fishery collapse. I tested the hypothesis that recruitment signals vary across spatial scales. Specifically, I examined whether recruitment signals differ among juvenile cod populations in four different bays on the northeast coast of Newfoundland. Further, I examined whether signals attenuate with distance from the juvenile sampling sites, between management zones, and within areas of ecological and biological importance for cod. Lastly, I hypothesized that biotic factors (i.e., juvenile body length and habitat type) related positively with pre-adult cod abundance offshore. Ultimately my goal was to evaluate the predictive potential of the Fleming Survey to forecast future recruit abundance in the Newfoundland and Labrador offshore.

Methods

Juvenile sampling

Sampling of juvenile cod populations in Trinity, Notre Dame, Bonavista, and Conception bays was conducted as part of the Fleming Survey. Between 24 and 33 sites were sampled annually from late September to late October (Fig 3.1). Each site was sampled using a beach seine to determine the abundance of fish species inhabiting nearshore habitats. My study analyzed data from 206 standardized seine hauls (1992 – 1997, 2001).

Three hauls were conducted using a Danish bag seine net (25 m x 2 m; 9 mm mesh) at each site. Following two consecutive hauls at the same location, a third haul was completed in an area immediately adjacent (see Chapter 2 for seine haul details). All fish caught were measured (mm SL), assigned a tentative age class based on length groups, and released. The length groups were: LG0 (< 97 mm), LG1 (97 – 192 mm), and LG2 (> 193 mm) (Schneider et al. 1997). I only used data from the first seine haul in my analyses in order to compare results directly with those reported in Chapter 2. Visual estimates of eelgrass coverage were taken at each site during the 1995, 1996 and 2001 surveys, and presence/absence values were derived for analysis.

Adult sampling

The northern cod stock encompasses the area off the northeast coast of Newfoundland and Labrador in NAFO divisions 2J3KL (Fig 3.1). The Newfoundland fishery assessment defines “recruitment” as the abundance of age-3 cod in the survey area – the age at which a trawl survey effectively samples cod (DFO 2016). Based on data from 1995 – 2004 available for my analysis, I derived an abundance index of age-3 cod from the Fisheries and Oceans (DFO) Fall Research Vessel (RV) survey, conducted annually from October to January using a Campelen 1800 shrimp trawl (see Chapter 2 for details of the trawl and the survey). Pre-1995 was not used for comparison due to a change in gear used in the RV survey in 1995.

For my analysis I used standardized catch numbers provided by DFO. Catch values were standardized to a mean catch over a trawl distance of 0.8 km (0.8 km / trawl path km) x catch/trawl. Trawls sampled areas ranging from 57 – 499 m in depth among the 57-74 index strata (< 500 m depth) sampled each year. Each stratum was sampled at least two times annually, with total trawl frequency across all strata varying from 274 – 329.

Recruitment signals

I assessed the suitability of using juvenile abundance (age-0 and -1) data to predict recruitment of age-3 abundance to the offshore fishery in northeastern Newfoundland. For models with age-3 as a response variable ($n_{\text{Age-0}} = 7$, $n_{\text{Age-1}} = 6$), I used a negative binomial Generalized Linear Model (GLM) with a log link to assess the relationship between age-0 and age-1, and age-3 cod. For models predicting age-1 abundance from age 0 abundance ($n_{\text{Age-0}} = 5$), I used a General Linear Model (LM) with a normal error structure to account for non-integer catch numbers. A GLM with an alternative error distribution was deemed unacceptable after examination of residuals. Age-0 and age-1 abundance were log transformed and a constant of 1 was added when necessary to juvenile abundance values pre-transformation to account for the presence of zeros. I set the statistical significance at alpha = 0.05. I assessed recruitment signal strength using the coefficient of determination (R^2) of the model for LMs, and used explained deviance (D^2) for the GLMs (see Chapter 2 for calculation details).

Spatial scale analysis

In order to evaluate spatial extrapolation of recruitment signal strength from the juvenile survey areas, I ran each model using age-3 abundance in buffers increasing by 50 km distances, centred on the mouth of each bay, until the buffer covered the entire 2J3KL area (i.e., buffers = 100 km, 150 km, 200 km…, Fig. 3.2a-d). I also examined recruitment signal strength among NAFO management areas by separating age-3 abundance within 2J, 3K, and 3L (Fig. 3.1) to further understand the spatial differences in signal strength.

I considered recruitment signals produced from potential Ecologically and Biologically Significant Areas (EBSAs) for cod identified by DFO (Nadine Wells, Ecological Sciences Section St. John’s, NL). Specifically, I selected several such areas and separated them into two groups, EBSA 1 and EBSA 2, based on geographical location (Fig. 3.3). EBSA 1 and EBSA 2 were located near Hawke Channel and the Bonavista Corridor, respectively. I selected these

EBSAs to determine if historically abundant areas reflected the recruitment signals of the entire stock. Each recruitment model was run using age-3 abundance within EBSA 1 and EBSA 2 separately (see Chapter 2 for details on EBSA calculations).

Environmental and biological factors

I tested for potential relationships between age-3 recruits and other environmental and biological factors by using juvenile body length and eelgrass habitat cover as predictor variables in the linear models. I calculated juvenile body length for both age-0 and -1 cod as the mean length (mmSL) of each age class in each year of the time series, for each bay. I calculated eelgrass cover as the proportion of sites that had eelgrass in each bay annually when data were available (1995, 1996 and 2001). A site was characterized as having eelgrass habitat if eelgrass covered over 10 percent of the survey area.

Results

Recruitment signals

The recruitment signals based on age 0 juveniles in Notre Dame ($D^2 = 0.258$, $p = 0.132$; Table 3.1; Fig. 3.4), Bonavista ($D^2 = 0.214$, $p = 0.174$; Table 3.2; Fig. 3.4), and Conception Bay were not significant ($D^2 = 0.013$, $p = 0.749$; Table 3.3; Fig. 3.4) over the entire 2J3KL region. Trinity Bay was the only bay that yielded a strong and significant positive recruitment signal when predicting age-3 from age-0 abundance in the entire 2J3KL region ($D^2 = 0.770$, $p < 0.001$; Table 3.4; Fig. 3.4). When using age-1 abundance, I found Bonavista Bay yielded the strongest recruitment signal ($D^2 = 0.301$, $p = 0.066$; Table 3.2; Fig. 3.4), however, it was not statistically significant. Recruitment signals for Trinity, Notre Dame, and Conception bays were weak ($D^2 < 0.02$, $p > 0.50$; Table 3.1, 3.3. & 3.4; Fig. 3.4). Capacity to predict age-1 abundance using age-0 abundance in any of the bays was poor at the scale of the entire 2J3KL region ($R^2_{NB} = 0.224$, p = 0.421; $R^2_{BB} = 0.204$, p = 0.446; $R^2_{TB} = 0.026$, p = 0.796; $R^2_{CB} = 0.373$, p = 0.274) (Table 3.5; Fig. 3.5).

Spatial scale analysis

Combining all four bays together to detect a coast-wide recruitment signal did not improve the recruitment signal strength, which was statistically non-significant for all models ($D^2_{age-0-3} = 0.006$, p = 0.823; $D^2_{age-1-3} = 0.014$, p = 0.772; $R^2_{age-0-1} = 0.003$, p = 0.812; Table 3.7; Fig 3.5-3.7).

Age 0-3

In Notre Dame Bay, the strongest recruitment signal ($D^2 = 0.615$, $p < 0.001$) coincided with the 250 km buffer, and buffers were statistically significant out to 400 km (Table 3.1; Fig. 3.4). All significant relationships were negative (i.e., high abundance of juveniles is associated with low numbers of recruits). The recruitment signal did not improve when using either EBSA grouping ($D^2_{EBSA1} = 0.441$, p = 0.015; $D^2_{EBSA2} = 0.208$, p = 0.210; Table 3.10); and EBSA 1 showed a statistically significant negative relationship with the Fleming data. Similarly, a significant negative signal for NAFO Division 3K also did not improve in strength from the 250 km buffer ($D^2_{3K} = 0.505$, p = 0.007; Table 3.9).

In Bonavista Bay, the strongest recruitment signal occurred with the 200 km buffer ($D^2 = 0.404$, p = 0.018), and buffers were statistically significant out to the 350 km buffer (Table 3.2; Fig. 3.4). All significant relationships were negative. The recruitment signal improved only for EBSA 1 ($D^2_{EBSA1} = 0.475$, p = 0.009; $D^2_{EBSA2} = 0.233$, p = 0.168; Table 3.10). The recruitment signal also improved at the scale of NAFO divisions 2J ($D^2_{2J} = 0.560$, p = 0.003) and 3K (D^2_{3K}

=0.431, p = 0.019, Table 3.9). However, only Division 2J exhibited a positive relationship between age-0 and age-3 abundance (Table 3.9).

In Trinity Bay, the strongest recruitment signal occurred with the 900 km buffer (i.e., the entire offshore region) ($D^2 = 0.770$, $p < 0.001$; Table 3.4; Fig.3.4); all significant relationships were positive. Relationships based on EBSAs were statistically significant and positive, but with a decreased recruitment signal for both areas compared to the entire offshore region ($D^2_{EBSA1} = 0.525$, $p = 0.014$; $D^2_{EBSA2} = 0.563$, $p = 0.003$; Table 3.10). Positive recruitment signals in NAFO divisions 3K ($D^2_{3K} = 0.742$, $p < 0.001$) and 3L ($D^2_{3L} = 0.552$, $p = 0.008$) were significant (Table 3.9) but weaker than the signal associated with the 900 km buffer.

In Conception Bay, the strongest recruitment signal coincided with the 100 km buffer ($D^2 = 0.530$, $p = 0.010$; Fig. 3.4), the only buffer with a positive relationship (Table 3.3). The recruitment signal weakened and was not statistically significant for either EBSA ($D^2_{EBSA1} = 0.080$, $p = 0.396$; $D^2_{EBSA2} = 0.044$, $p = 0.570$; Table 3.10) or for any NAFO division ($D^2_{2J} = 0.245$, $p = 0.134$; $D^2_{3K} = 0.001$, $p = 0.920$; $D^2_{3L} = 0.149$, $p = 0.207$; Table 3.9).

Age 1-3

In Notre Dame Bay, the strongest recruitment signal coincided with the 100 km buffer, but the relationship was not statistically significant ($D^2 = 0.026$, $p = 0.626$; Table 3.1; Fig. 3.4). The recruitment signal remained weak and statistically non-significant for both EBSAs ($D^2_{EBSA1} = 0.045$, $p = 0.543$; $D^2_{EBSA2} < 0.001$, $p = 0.960$; Table 3.10) and for the NAFO divisions ($D^2_{2J} = 0.020$, $p = 0.743$; $D^2_{3K} = 0.009$, $p = 0.797$; $D^2_{3L} = 0.142$, $p = 0.228$; Table 3.9).

In Bonavista Bay, the strongest positive recruitment signal occurred with the 850 km buffer (i.e., the entire offshore), but was not statistically significant ($D^2 = 0.301$, $p = 0.087$, Table 3.2; Fig. 3.4). The recruitment signal weakened and remained statistically non-significant for both EBSAs ($D^2_{EBSA1} = 0.130$, $p = 0.300$; $D^2_{EBSA2} = 0.237$, $p = 0.138$; Table 3.10) and for the NAFO divisions, with the exception of 3K ($D^2_{2J} = 0.048$, $p = 0.586$; $D^2_{3K} = 0.373$, $p = 0.0506$; $D^2_{3L} = 0.133$, $p = 0.247$; Table 3.9). All relationships were positive, but non-significant.

In Trinity Bay, the strongest recruitment signal coincided with the 100 km buffer, but was non-significant ($D^2 = 0.070$, $p = 0.526$; Table 3.4; Fig. 3.4). EBSA scale buffers did not meaningfully strengthen the recruitment signal ($D^2_{EBSA1} = 0.079$, $p = 0.462$; $D^2_{EBSA2} = 0.026$, $p = 0.687$; Table 3.10). Stronger recruitment signals for NAFO divisions 2J and 3L were, nonetheless, not statistically significant ($D^2_{2J} = 0.171$, $p = 0.274$; $D^2_{3K} = 0.001$, $p = 0.936$; $D^2_{3L} = 0.160$, $p = 0.249$; Table 3.9).

In Conception Bay, the strongest and only statistically significant recruitment signal occurred with the 100 km buffer ($D^2 = 0.662$, $p = 0.002$; Table 3.3; Fig. 3.4). The recruitment signals for each EBSA ($D^2_{EBSA1} = 0.066$, $p = 0.499$; $D^2_{EBSA2} = 0.067$, $p = 0.520$; Table 3.10) and NAFO division ($D^2_{2J} = 0.071$, $p = 0.520$; $D^2_{3K} < 0.001$, $p = 0.961$; $D^2_{3L} = 0.181$, $p = 0.221$; Table 3.9) were weak and non-significant.

Environmental and Biological Factors

A significant negative relationship between age-0 body length and age-3 coast-wide abundance emerged for Bonavista ($D^2 = 0.411$, $p = 0.0352$), Trinity ($D^2 = 0.636$, $p < 0.001$), and Conception Bays ($D^2 = 0.478$, $p = 0.0184$; Table 3.6), in contrast to no significant relationships between age-1 body length and age-3 abundance in any bay ($p > 0.05$; Table 3.6). The absence of any significant relationship between age-0 body length and age-1 abundance in any bays (Table 3.5) did not improve when combining all bays and considering body length and any early age classes (Table 3.7). The proportion of sites containing eelgrass habitat and the abundance of either age-0 or age-3 cod over the three years where eelgrass cover was quantified were not significantly related (Table 3.8).

Discussion

Recruitment Signals

Juvenile cod did not produce any consistent recruitment signals in the offshore (NAFO 2J3KL) across the northeast coast of Newfoundland. The abundance of age-0 and age-1 cod was unrelated within any bay. Similarly, age-1 abundance generally yielded weak recruitment signals in age-3 abundance for all bays. Of all populations, only age-0 cod from Trinity Bay predicted recruits in the offshore. This strong recruitment signal likely resulted from a large spawning aggregation in Smith Sound (Trinity Bay). Cod were observed spawning in Trinity Bay beginning in 1991 (Smedbol and Wroblewski 1997), and the Smith Sound spawning aggregation reported from 1995 to 2006 was considered the largest northern cod spawning group during this time (e.g., Rose 2003). Consistent spawning in inshore Trinity Bay likely sources strong juvenile abundance for Trinity Bay coastal sites, and may explain the detectable recruitment signal in my study. Egg densities in and adjacent to Smith Sound were significantly higher in 1995 compared to previous years (Smedbol et al. 1998). Nonetheless, at the coast-wide scale or within individual bays (Trinity and Conception bays) average catch of age-0 cod in 1995 did not increase detectably compared to the two previous years (Smedbol et al. 1998). However, the Smith Sound spawning aggregation persisted in subsequent years, with generally higher mean catch of age-0 cod in Trinity Bay than the other three bays after 1995. Therefore, a greater density of eggs and a broad range of juvenile abundances in Trinity Bay during the Fleming Survey likely contributed to the strong recruitment signal.

Combining all bays and increasing the spatial coverage did not improve recruitment signals. I predicted that aggregating cod abundance from multiple bays could account for spatial and temporal variability in juvenile abundance. Previous studies report a correlation scale for recruitment signals and genetic linkage of up to 500 km for cod in Newfoundland (Myers et al. 1995, 1997, Horne et al. 2016), which encompasses all bays analysed in my study. Moreover, a study in the 1990s reported no significant genetic differentiation among inshore cod sampled from Notre Dame, Trinity, Bonavista, and Conception Bays (Beacham et al. 2002). The weakened coast-wide recruitment signal indicates a persistent effect of individual bays, and weak correlations in recruitment dynamics at the time of the Fleming Survey.

Unlike Trinity Bay, the three other bays in my study may not have received a strong supply of eggs and larvae in the early 1990s. The proportion of eggs and larvae that reach nursery habitats depends largely on variations in location of spawning aggregations and ocean currents (Templeman 1981). The Labrador Current drives a strong larval drift north-to-south over the continental shelf, transporting larvae towards the northeast coast of Newfoundland (Pepin and Helbig 1997). Therefore, high production and recruitment of the northern cod stock depends on spawning in northern areas (Templeman 1966, DeYoung and Rose 1993, Pepin and Helbig 1997, Bradbury et al. 2008) and not necessarily from spawning in southern areas. Despite high concentrations of eggs in Smith Sound, models indicate limited dispersal of eggs and larvae outside Smith Sound, and limited connectivity from Trinity Bay to other coastal areas at this life-stage (Stanley et al. 2013). Spawning cod following the collapse were smaller and younger than historical norms, likely representing first-time spawners. Such spawners can have smaller eggs, lower hatching rates, and lower survival rates than older age classes (Trippel 1998). Ultimately spawning mass declined during the moratorium, with a subsequent decline in the distribution and abundance of pelagic juveniles (Anderson and Rose 2001). The timing of offshore migrations of cod overwinter and water temperature can influence variation in spawning time, and subsequent abundance of progeny (Smedbol and Wroblewski 1997). Furthermore, cod in Newfoundland are protracted spawners (Hutchings and Myers 1993, Stanley et al. 2013); because the Fleming Survey only samples each site once annually, the abundance of juveniles at a given sampling period is unlikely to represent the entire cohort, depending on spawning and settlement times, coupled with onshore wind events and coastal upwelling (Ings et al. 2008).

Spatial Scale Analysis

In general, recruitment signals from each bay (i.e. Conception, Bonavista, Trinity, and Notre Dame) to the entire offshore region (NAFO divisions 2J3KL) were weak. However, recruitment signals generally improved in buffers closer to the coast using age-0 cod (< 250 km for Notre Dame, Bonavista, and Conception bays). In the pre-collapse period, cod were distributed broadly across the Newfoundland shelf and occupied areas from northern Labrador to the southern Grand Banks (Rose 1992), with large aggregations and high concentrations historically located in areas such as the Bonavista Corridor (on the 3KL boundary) and Hawke Channel (2J) (Rose 1993). As the cod population collapsed, offshore cod declined sharply (Lilly et al. 1998). Cod distribution contracted dramatically, disappearing from areas they occupied historically. Cod did not increase appreciably in previously occupied areas until 2007, with distribution and abundance increases only recently observed in offshore regions (e.g., Bonavista Corridor, Hawke Channel, Belle Isle, Hamilton Banks; Mello and Rose 2008, Rose and Rowe

2015, DFO 2016). Tagging and genetic evidence of cod in the inshore region of Newfoundland, demonstrate both resident and migrant populations during the 1990s (Ruzzante et al. 1996, Brattey 1999). During the 1990s, hydroacoustic surveys also detected shifts in distribution of cod away from areas of historical distribution; the largest aggregations occurred primarily inshore in the 1990s and early 2000s (Bradbury et al. 2008). The stronger recruitment signal inshore may reflect the movement of cod inshore coinciding with population decline, but more likely reflects a persistent inshore population during this time. Dispersal was often local and restricted within embayments, despite high dispersal potential (Bradbury et al. 2008). In my study, the significant relationships between age-0 and age-3 cod in proximity to the coast were often negative. The temporal limitations of the Fleming Survey make it difficult to assess whether these negative relationships are biologically meaningful. Despite the absence of abundance data for the inshore region (i.e., the first 50 km) at a comparable time scale, recent studies detected strong recruitment signals in the inshore strata of 2J3KL using juvenile data from coastal seining in Newman Sound (Laurel et al. 2017). Further, analysis of separate NAFO divisions generally did not yield any improvements in signals than using the abundance for the entire 2J3KL region. This result suggests that abundances remained low, and any clear detection of population change through recruitment signals would require a further increase in abundances. Indeed recruitment correlations between NAFO divisions 2J, 3K, and 3L vary, especially when using short time series (Myers et al. 1993, Tulk et al. 2017). The inconsistent recruitment signals likely reflect shifts in distribution and movement behaviours of cod during this time (Anderson and Gregory 2000, Anderson and Rose 2001).

Environmental and Biological Factors

Abundances of age-3 cod were significantly related to body length of age-0 cod for all bays except Notre Dame. Higher growth rate, often promoted by high food availability and optimal thermal conditions, helps in predator avoidance (Houde 2008, Laurel et al. 2017). A large body length also suggests high lipid stores that promote survival overwinter and predator avoidance (Copeman et al. 2008). The relationships, however, were consistently negative (i.e., smaller mean body length correlated with greater age-3 abundance). Potentially, a “good year” may coincide with smaller mean body length because of a stronger pulse structure. A strong cohort could result from strong pulses or multiple age-0 settlement events, or “pulses”, arriving throughout the summer and fall as a result of wind and upwelling events (Ings et al. 2008, Gregory et al. 2016); thus, arrival of a new pulse just prior to the survey could result in small mean body length. Multiple settlement pulses help to reduce intra-specific competition by staggering sizes of new recruits, and reduces the risk of mortality to an entire year class from predation, environmental stressors, or mismatch with prey (Kristiansen et al. 2011). Unfortunately, I could not evaluate inter-annual variation in pulse structure with these data because each site was sampled only once during the annual survey. Indeed, many other factors not considered in this analysis may influence juvenile cod survival and predictive potential (e.g., phytoplankton abundance, seasonal water temperature, predator abundance (Anderson and Gregory 2000, Beaugrand et al. 2003, Houde 2008; Chapter 2)).

Conclusions

My study provides evidence that forecasts of adult population strength should consider information from nearshore seine surveys, but its utility may be context-dependent. Recruitment signals for the northern cod population varied among juvenile populations in different bays. Specifically, age-0 abundance in Trinity Bay provided the only strong recruitment signal to the entire offshore fish stock, likely reflecting the large spawning aggregation present in this area. Recruitment signal strength also varied among NAFO divisions, EBSAs, and distance from juvenile cod nursery habitats. In general, recruitment signals strengthened closer to juvenile inshore sites, reflecting changes in cod behaviour and distribution during the population's post-collapse period.

I have highlighted the importance of considering spatial scale when examining cod recruitment in Newfoundland. However, the short temporal coverage of the Fleming Survey dataset likely limits its utility in modeling and predicting current cod recruitment, and may have reduced the power of my statistical tests to detect significance. Because this survey was conducted before any recovery was evident in the stock post-collapse, the results may not reflect current spatial patterns or predictive potential along the northeast coast of Newfoundland. Understanding the value of dispersal patterns and population connectivity remains a critical challenge when developing effective spatial management tools and forecasting future fish populations.

Figures

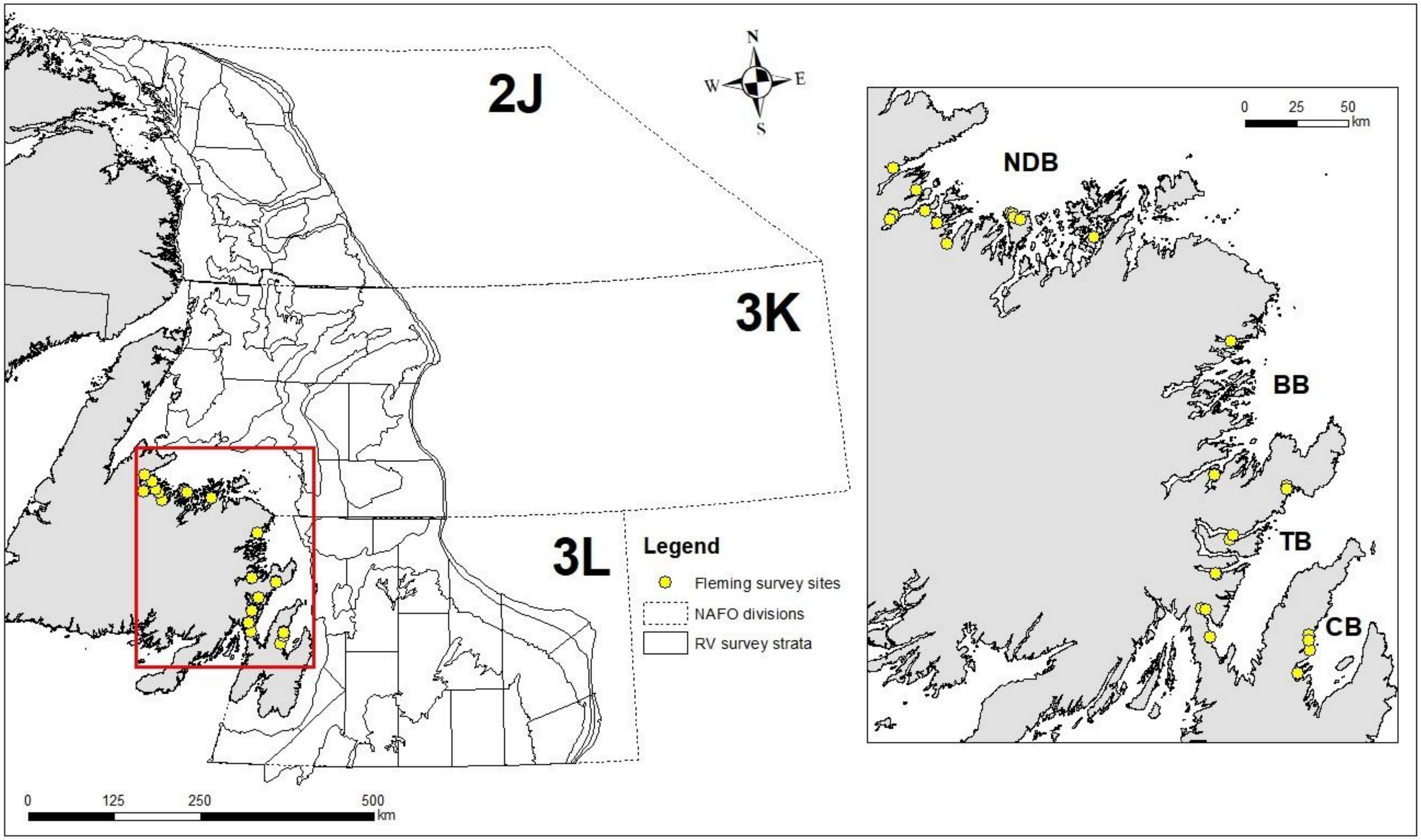
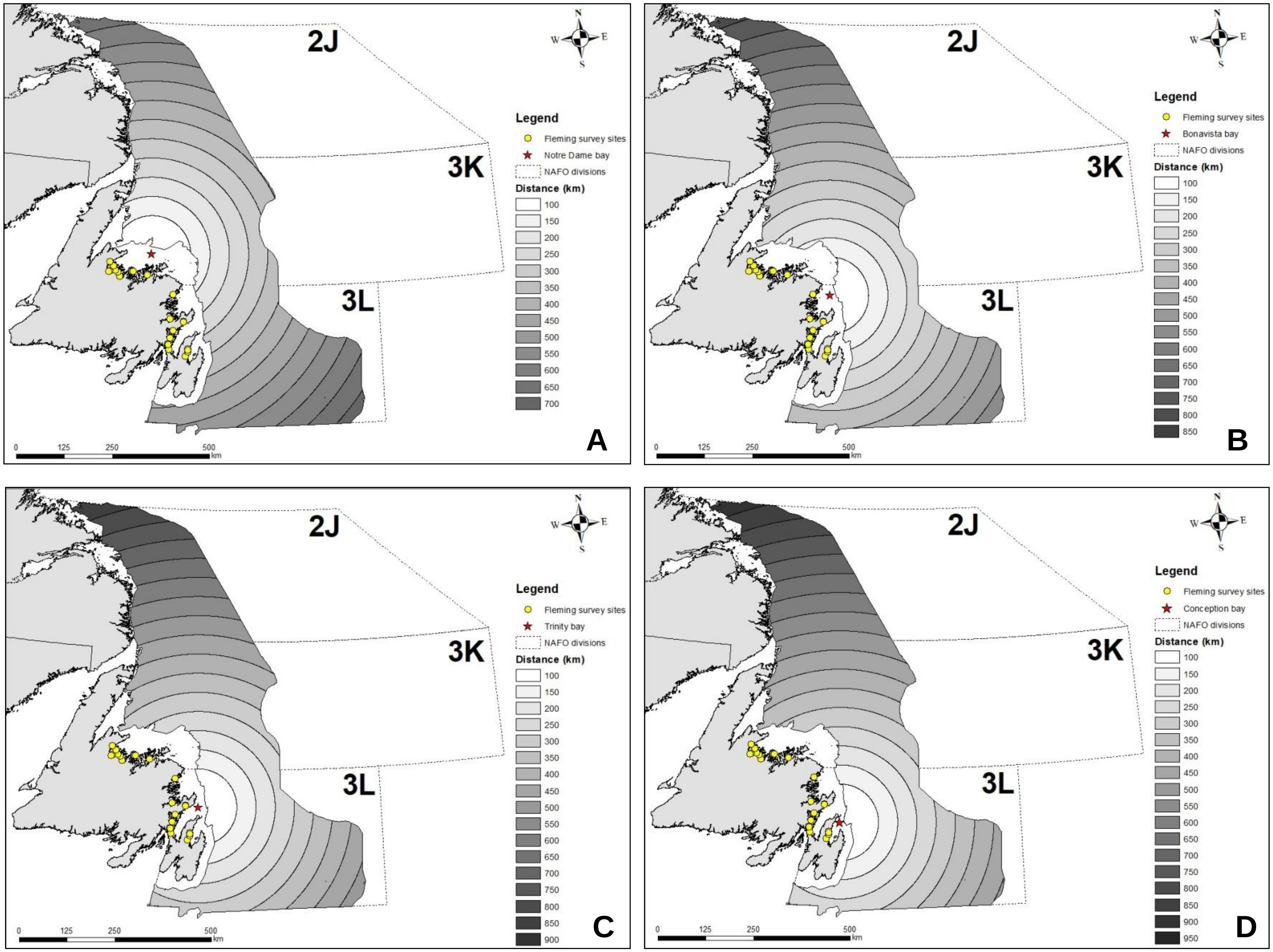

2J
3K
3L
N
W
E
S
Legend
Fleming survey sites
NAFO divisions
RV survey strata
0
125
250
500
km
NDB
BB
TB
CB
0
25
50
km

Figure 3.1. Fleming Survey (1992 – 1997, 2001) sampling sites with respect to NAFO fisheries management divisions 2J3KL and strata, off the northeast coast of Newfoundland in Notre Dame (NBD), Bonavista (BB), Trinity (TB), and Conception (CB) bays (inset).


2J
3K
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N
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Legend
Fleming survey sites
Notre Dame bay
NAFO divisions
Distance (km)
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400
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550
600
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700
0
125
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km
A
Legend
Fleming survey sites
Bonavista bay
NAFO divisions
Distance (km)
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Legend
Fleming survey sites
Trinity bay
NAFO divisions
Distance (km)
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700
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Legend
Fleming survey sites
Conception bay
NAFO divisions
Distance (km)
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750
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850
900
950
D

Figure 3.2. Buffers from (A) Notre Dame (100 – 700 km), (B) Bonavista (100 – 850 km), (C) Trinity (100 – 900 km), and (D) Conception (100 – 950 km) bays used for spatial analysis of recruitment models.

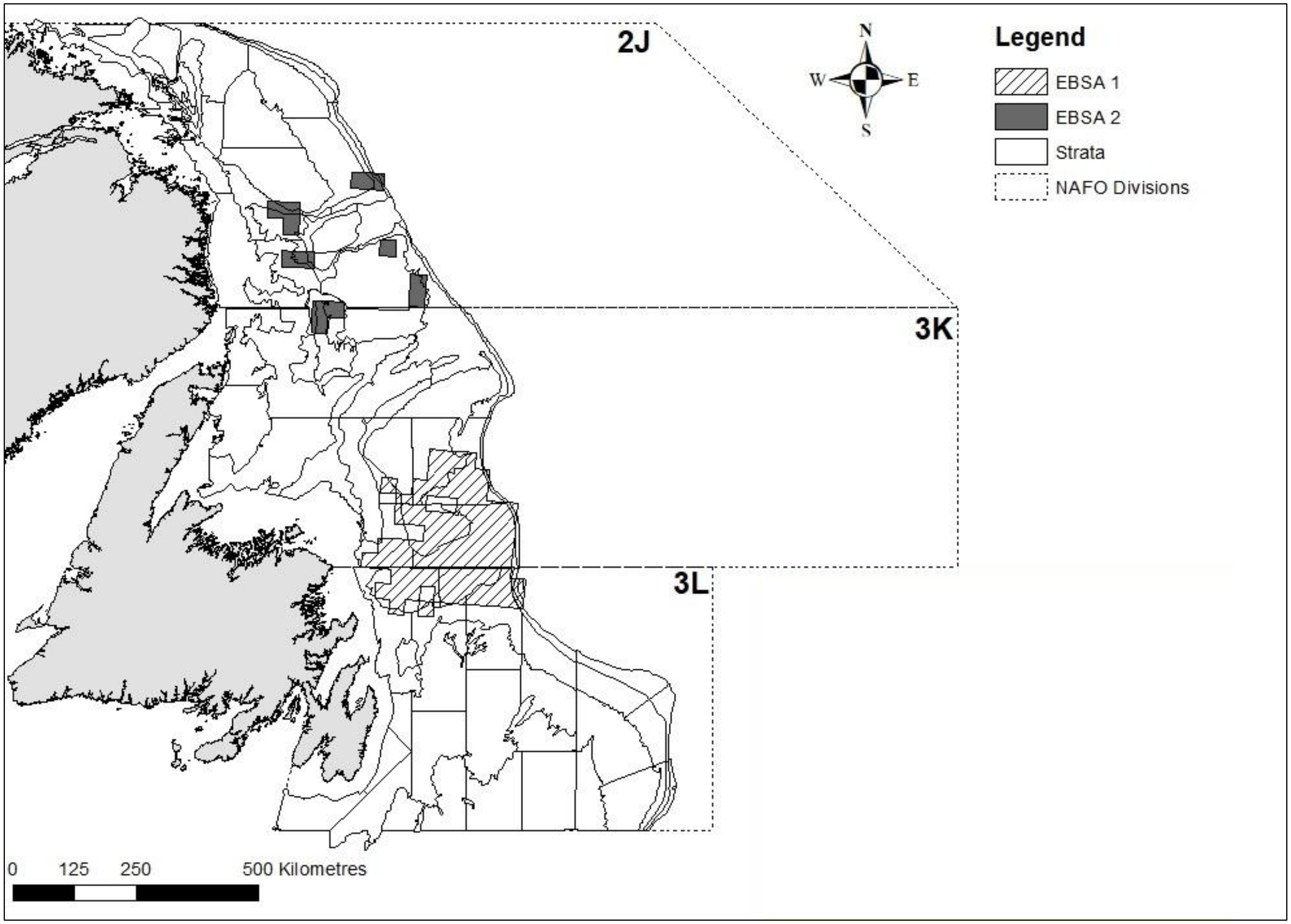
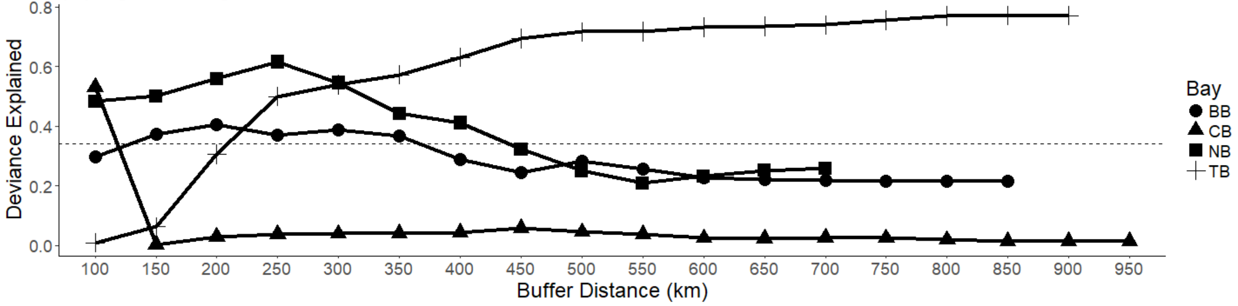


Figure 3.3. Potential Atlantic cod Ecologically and Biologically Significant Area (EBSA) placement within NAFO divisions 2J3KL described by DFO (Nadine Wells, Ecological Sciences Section St. John’s, NL).

(A) Age-0 to Age-3



(B) Age-1 to Age-3

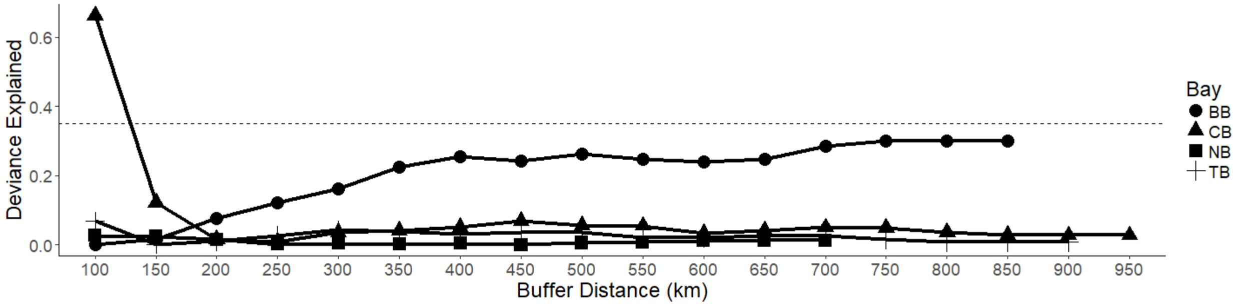


Figure 3.4. Age-3 recruitment signal strength from (A) age-0 abundance and (B) age-1 abundance (mean catch·haul^{-1}) with increasing distance from nursery habitat in Bonavista (BB), Conception (CB), Notre Dame (NB) and Trinity (TB) bays (1992 – 1997, 2001). Points above the dashed line are statistically significant ($p < 0.05$).

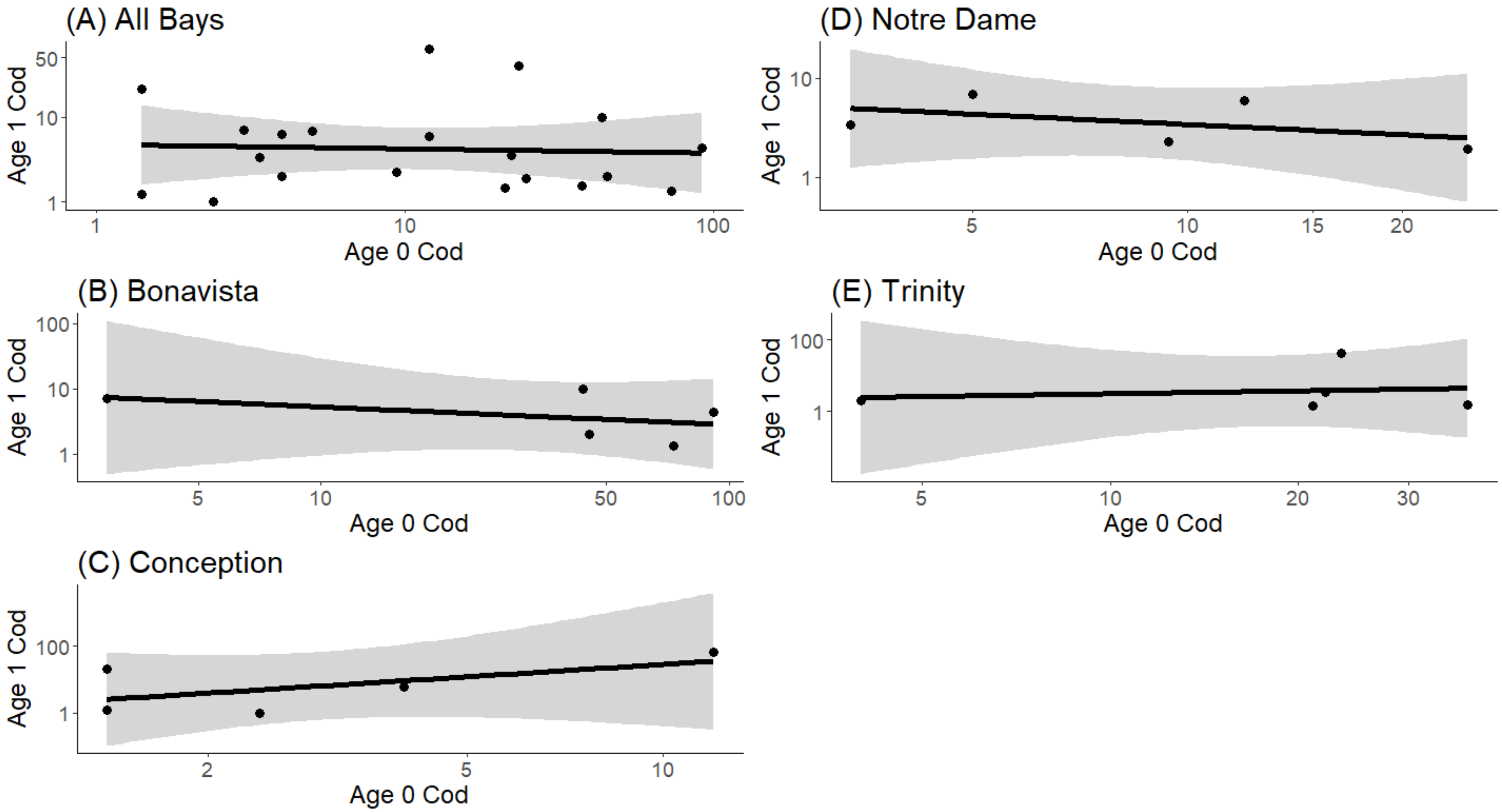


Figure 3.5. Recruitment signals between annual mean age-0 and age-1 cod abundance per seine haul (± SE) (1992 – 1997, 2001). (A) All bays combined (at each site); (B) Bonavista Bay; (C) Conception Bay; (D) Notre Dame Bay; and (E) Trinity Bay.

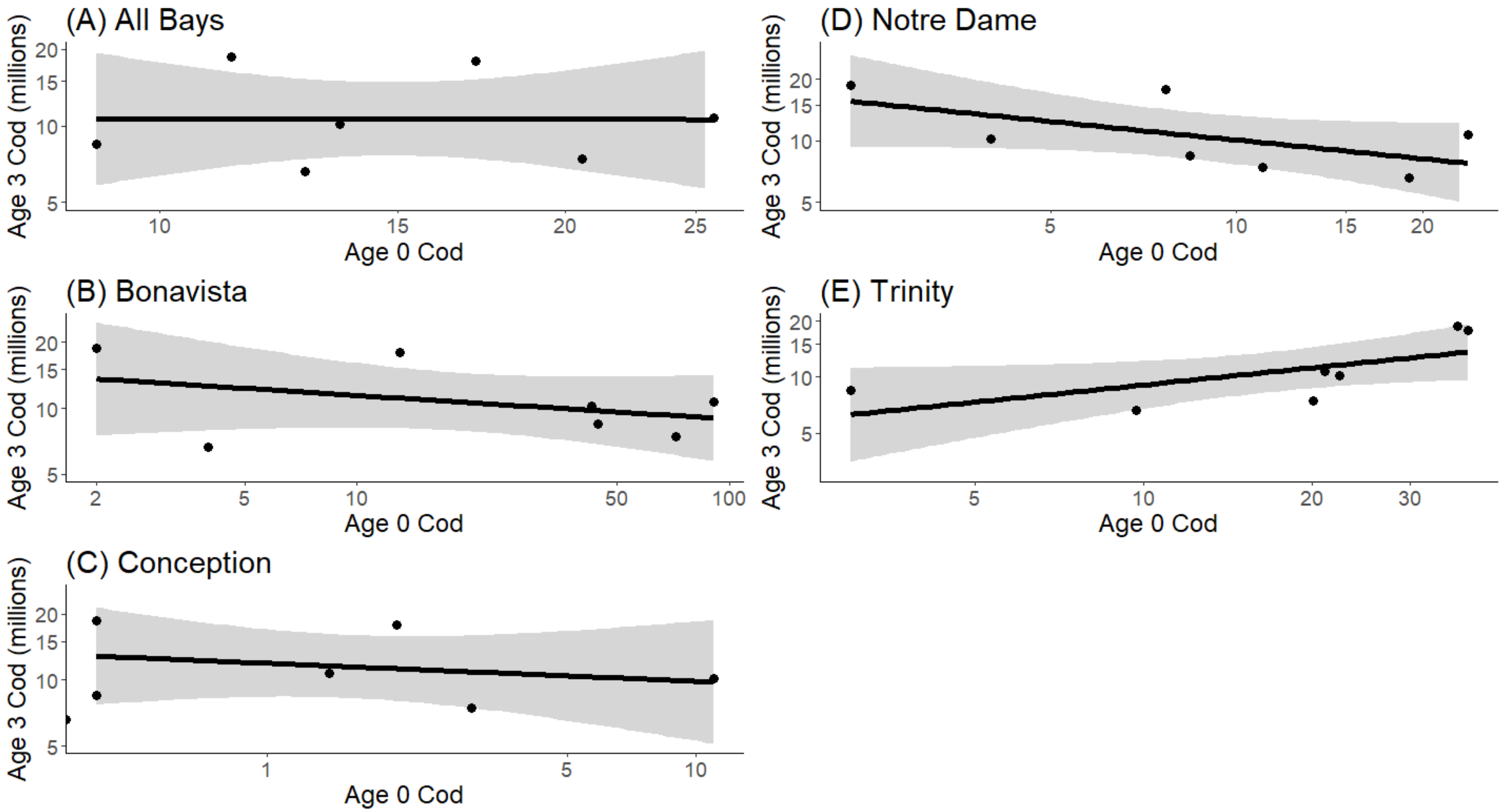


Figure 3.6. Recruitment signals between annual mean juvenile (age-0) abundance per seine haul and pre-adult (age-3) cod abundance in NAFO divisions 2J3KL (± SE) (1992 – 1997, 2001). (A) All bays combined; (B) Bonavista Bay; (C) Conception Bay; (D) Notre Dame Bay; and (E) Trinity Bay.

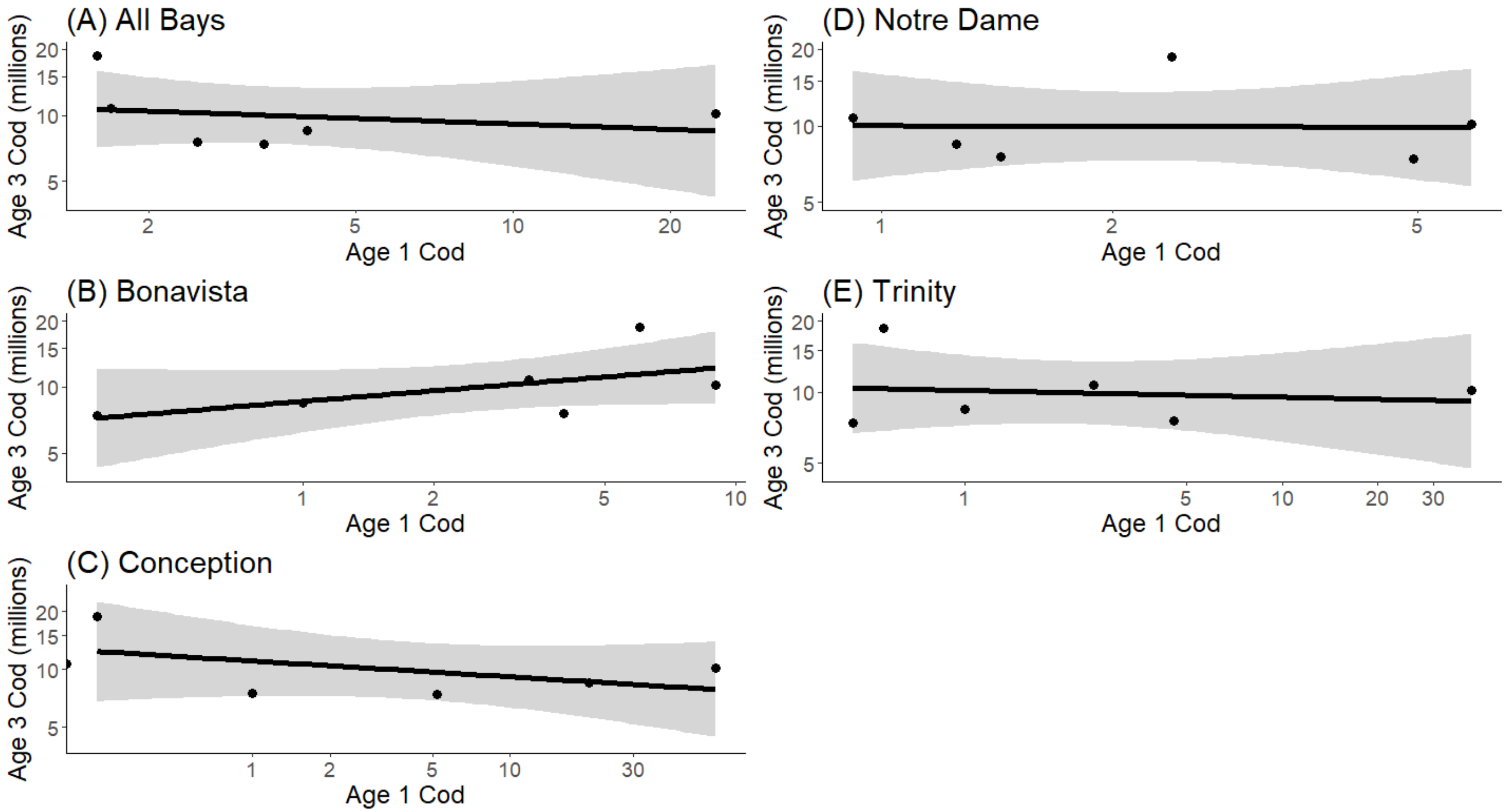


Figure 3.7. Recruitment signals between annual mean juvenile (age-1) abundance per seine haul and pre-adult (age-3) cod abundance in NAFO divisions 2J3KL (± SE) (1992 – 1997, 2001). (A) All bays combined; (B) Bonavista Bay; (C) Conception Bay; (D) Notre Dame Bay; (E) Trinity Bay.

Tables

Table 3.1. Generalized linear model results for recruitment signals of age-3 cod using age-0 and age-1 abundance at varying spatial scales (increasing distance from the juvenile survey area) from Notre Dame Bay (1992 – 1997, 2001). Bold font signifies statistical significance ($p < 0.05$).

Age-0								
Response	Buffer Size (km)	DF	Deviance	Residual DF	Residual Deviance	Slope	*p* value	D^2
Age-3	**100**	**1**	**13.8**	**5**	**7.13**	**-0.0458**	**0.009**	**0.483**
Age-3	**150**	**1**	**14.5**	**5**	**7.22**	**-0.0678**	**0.003**	**0.500**
Age-3	**200**	**1**	**16.1**	**5**	**7.12**	**-0.0543**	**0.001**	**0.558**
Age-3	**250**	**1**	**18.4**	**5**	**7.08**	**-0.0484**	**<0.001**	**0.615**
Age-3	**300**	**1**	**15.6**	**5**	**7.08**	**-0.0406**	**0.003**	**0.545**
Age-3	**350**	**1**	**12.7**	**5**	**7.08**	**-0.0327**	**0.017**	**0.442**
Age-3	**400**	**1**	**12**	**5**	**7.09**	**-0.0316**	**0.026**	**0.411**
Age-3	450	1	10.5	5	7.11	-0.0289	0.066	0.322
Age-3	500	1	9.48	5	7.11	-0.0248	0.127	0.249
Age-3	550	1	8.97	5	7.11	-0.0214	0.180	0.208
Age-3	600	1	9.27	5	7.12	-0.0234	0.158	0.232
Age-3	650	1	9.51	5	7.12	-0.0251	0.139	0.251
Age-3	700	1	9.6	5	7.13	-0.0259	0.132	0.258

Table 3.1. (continued)

Age-1								
Response	Buffer Size (km)	DF	Deviance	Residual DF	Residual Deviance	Slope	*p* value	D^2
Age-3	100	1	6.61	4	6.43	0.0689	0.626	0.027
Age-3	150	1	6.35	4	6.2	0.0404	0.673	0.024
Age-3	200	1	6.24	4	6.14	0.0261	0.747	0.015
Age-3	250	1	6.14	4	6.13	0.00838	0.913	0.002
Age-3	300	1	6.12	4	6.1	0.0107	0.873	0.004
Age-3	350	1	6.07	4	6.07	0.00466	0.932	0.001
Age-3	400	1	6.08	4	6.06	0.00798	0.874	0.004
Age-3	450	1	6.05	4	6.05	0.00165	0.972	<0.001
Age-3	500	1	6.08	4	6.04	-0.00853	0.850	0.006
Age-3	550	1	6.09	4	6.05	-0.0104	0.826	0.008
Age-3	600	1	6.15	4	6.08	-0.0166	0.787	0.011
Age-3	650	1	6.18	4	6.1	-0.0195	0.773	0.012
Age-3	700	1	6.19	4	6.11	-0.0206	0.768	0.013

Table 3.2. Generalized linear model results for recruitment signals of age-3 cod using age-0 and age-1 abundance at varying spatial scales (increasing distance from the juvenile survey area) from Bonavista Bay (1992 – 1997, 2001). Bold font signifies statistical significance ($p < 0.05$).

Age-0								
Response	Buffer Size (km)	DF	Deviance	Residual DF	Residual Deviance	Slope	*p* value	D^2
Age-3	**100**	**1**	**10.3**	**5**	**7.25**	**-0.0114**	**0.038**	**0.297**
Age-3	**150**	**1**	**11.5**	**5**	**7.2**	**-0.0113**	**0.021**	**0.373**
Age-3	**200**	**1**	**12.1**	**5**	**7.19**	**-0.0114**	**0.018**	**0.404**
Age-3	**250**	**1**	**11.4**	**5**	**7.21**	**-0.0108**	**0.032**	**0.369**
Age-3	**300**	**1**	**11.7**	**5**	**7.19**	**-0.0107**	**0.028**	**0.386**
Age-3	**350**	**1**	**11.3**	**5**	**7.16**	**-0.00913**	**0.038**	**0.367**
Age-3	400	1	10	5	7.14	-0.00713	0.089	0.288
Age-3	450	1	9.46	5	7.15	-0.0064	0.132	0.244
Age-3	500	1	9.95	5	7.16	-0.00724	0.010	0.281
Age-3	550	1	9.62	5	7.16	-0.00683	0.125	0.255
Age-3	600	1	9.25	5	7.16	-0.00627	0.158	0.226
Age-3	650	1	9.17	5	7.15	-0.00594	0.166	0.220
Age-3	700	1	9.11	5	7.14	-0.00559	0.171	0.217
Age-3	750	1	9.09	5	7.13	-0.00547	0.174	0.215
Age-3	800	1	9.08	5	7.13	-0.00546	0.175	0.214
Age-3	850	1	9.08	5	7.13	-0.00546	0.175	0.214

Table 3.2. (continued)

Age-1								
Response	Buffer Size (km)	DF	Deviance	Residual DF	Residual Deviance	Slope	*p* value	D^2
Age-3	100	1	6.31	4	6.31	-0.0029	0.970	<0.001
Age-3	150	1	6.31	4	6.22	0.0195	0.763	0.016
Age-3	200	1	6.67	4	6.16	0.0395	0.476	0.076
Age-3	250	1	6.96	4	6.12	0.0454	0.341	0.121
Age-3	300	1	7.27	4	6.1	0.05	0.262	0.160
Age-3	350	1	7.84	4	6.08	0.0532	0.169	0.225
Age-3	400	1	8.13	4	6.06	0.0522	0.135	0.254
Age-3	450	1	8.01	4	6.07	0.0536	0.145	0.242
Age-3	500	1	8.25	4	6.1	0.068	0.121	0.261
Age-3	550	1	8.11	4	6.1	0.0661	0.132	0.248
Age-3	600	1	8.01	4	6.09	0.0626	0.141	0.239
Age-3	650	1	8.09	4	6.09	0.062	0.133	0.247
Age-3	700	1	8.49	4	6.08	0.0643	0.100	0.284
Age-3	750	1	8.68	4	6.08	0.0654	0.088	0.300
Age-3	800	1	8.69	4	6.08	0.0655	0.087	0.301
Age-3	850	1	8.69	4	6.08	0.0655	0.087	0.301

Table 3.3. Generalized linear model results for recruitment signals of age-3 cod using age-0 and age-1 abundance at varying spatial scales (increasing distance from the juvenile survey area) from Conception Bay (1992 – 1997, 2001). Bold font signifies statistical significance ($p < 0.05$).

Age-0								
Response	Buffer Size (km)	DF	Deviance	Residual DF	Residual Deviance	Slope	*p* value	D^2
Age-3	**100**	**1**	**15**	**5**	**7.06**	**0.0619**	**0.010**	**0.530**
Age-3	150	1	7.16	5	7.14	-0.00524	0.888	0.003
Age-3	200	1	7.4	5	7.18	-0.0199	0.636	0.029
Age-3	250	1	7.59	5	7.32	-0.0312	0.574	0.036
Age-3	300	1	7.66	5	7.37	-0.0353	0.556	0.038
Age-3	350	1	7.65	5	7.35	-0.0346	0.555	0.039
Age-3	400	1	7.64	5	7.32	-0.0337	0.543	0.042
Age-3	450	1	7.77	5	7.32	-0.0393	0.481	0.058
Age-3	500	1	7.61	5	7.27	-0.0308	0.545	0.044
Age-3	550	1	7.53	5	7.24	-0.0268	0.580	0.038
Age-3	600	1	7.41	5	7.23	-0.0205	0.663	0.024
Age-3	650	1	7.39	5	7.21	-0.0196	0.667	0.024
Age-3	700	1	7.39	5	7.21	-0.0198	0.658	0.025
Age-3	750	1	7.37	5	7.19	-0.0189	0.662	0.024
Age-3	800	1	7.31	5	7.18	-0.0155	0.707	0.018
Age-3	850	1	7.27	5	7.17	-0.013	0.745	0.014
Age-3	900	1	7.26	5	7.17	-0.0128	0.749	0.013
Age-3	950	1	7.26	5	7.17	-0.0128	0.749	0.013

Table 3.3. (continued)

Age-1								
Response	Buffer Size (km)	DF	Deviance	Residual DF	Residual Deviance	Slope	*p* value	D^2
Age-3	**100**	**1**	**17.8**	**4**	**6.04**	**0.0113**	**0.002**	**0.662**
Age-3	150	1	6.95	4	6.11	0.0058	0.331	0.122
Age-3	200	1	6.2	4	6.1	0.0019	0.746	0.016
Age-3	250	1	6.18	4	6.13	-0.00157	0.808	0.009
Age-3	300	1	6.37	4	6.14	-0.00332	0.627	0.036
Age-3	350	1	6.41	4	6.14	-0.00357	0.602	0.042
Age-3	400	1	6.47	4	6.14	-0.00394	0.568	0.050
Age-3	450	1	6.67	4	6.21	-0.0056	0.502	0.068
Age-3	500	1	6.55	4	6.18	-0.0046	0.549	0.056
Age-3	550	1	6.51	4	6.16	-0.00421	0.556	0.055
Age-3	600	1	6.36	4	6.15	-0.00315	0.650	0.034
Age-3	650	1	6.39	4	6.13	-0.00329	0.616	0.041
Age-3	700	1	6.44	4	6.12	-0.0035	0.577	0.050
Age-3	750	1	6.43	4	6.11	-0.00338	0.581	0.049
Age-3	800	1	6.33	4	6.11	-0.00278	0.642	0.036
Age-3	850	1	6.28	4	6.11	-0.00241	0.683	0.028
Age-3	900	1	6.28	4	6.11	-0.00238	0.686	0.027
Age-3	950	1	6.28	4	6.11	-0.00238	0.687	0.027

Table 3.4. Generalized linear model results for recruitment signals of age-3 cod using age-0 and age-1 abundance at varying spatial scales (increasing distance from the juvenile survey area) from Trinity Bay (1992 – 1997, 2001). Bold font signifies statistical significance ($p < 0.05$).

Age-0								
Response	Buffer Size (km)	DF	Deviance	Residual DF	Residual Deviance	Slope	*p* value	D^2
Age-3	100	1	7.25	5	7.19	-0.00291	0.820	0.009
Age-3	150	1	7.67	5	7.19	0.00775	0.552	0.062
Age-3	200	1	10.3	5	7.18	0.0192	0.123	0.306
Age-3	**250**	**1**	**14.3**	**5**	**7.18**	**0.0296**	**0.020**	**0.499**
Age-3	**300**	**1**	**15.5**	**5**	**7.18**	**0.0316**	**0.012**	**0.538**
Age-3	**350**	**1**	**16.7**	**5**	**7.15**	**0.031**	**0.006**	**0.572**
Age-3	**400**	**1**	**19.2**	**5**	**7.11**	**0.0301**	**0.002**	**0.631**
Age-3	**450**	**1**	**23.1**	**5**	**7.09**	**0.0319**	**<0.001**	**0.693**
Age-3	**500**	**1**	**24.9**	**5**	**7.07**	**0.0314**	**<0.001**	**0.716**
Age-3	**550**	**1**	**25**	**5**	**7.07**	**0.0304**	**<0.001**	**0.717**
Age-3	**600**	**1**	**26.2**	**5**	**7.06**	**0.0298**	**<0.001**	**0.731**
Age-3	**650**	**1**	**26.6**	**5**	**7.06**	**0.0293**	**<0.001**	**0.734**
Age-3	**700**	**1**	**27.1**	**5**	**7.05**	**0.0288**	**<0.001**	**0.739**
Age-3	**750**	**1**	**28.7**	**5**	**7.05**	**0.0277**	**<0.001**	**0.755**
Age-3	**800**	**1**	**30.5**	**5**	**7.04**	**0.0272**	**<0.001**	**0.769**
Age-3	**850**	**1**	**30.6**	**5**	**7.04**	**0.0272**	**<0.001**	**0.770**
Age-3	**900**	**1**	**30.6**	**5**	**7.04**	**0.0272**	**<0.001**	**0.770**

Table 3.4. (continued)

Age-1								
Response	Buffer Size (km)	DF	Deviance	Residual DF	Residual Deviance	Slope	*p* value	D^2
Age-3	100	1	6.61	4	6.16	0.00747	0.526	0.068
Age-3	150	1	6.16	4	6.16	-0.00097	0.933	0.001
Age-3	200	1	6.19	4	6.13	-0.00249	0.812	0.009
Age-3	250	1	6.31	4	6.15	-0.00451	0.684	0.027
Age-3	300	1	6.4	4	6.13	-0.00542	0.602	0.042
Age-3	350	1	6.38	4	6.13	-0.00515	0.616	0.039
Age-3	400	1	6.31	4	6.12	-0.00436	0.667	0.030
Age-3	450	1	6.4	4	6.17	-0.00572	0.635	0.035
Age-3	500	1	6.39	4	6.16	-0.00553	0.634	0.036
Age-3	550	1	6.28	4	6.15	-0.00409	0.716	0.022
Age-3	600	1	6.27	4	6.13	-0.00386	0.717	0.021
Age-3	650	1	6.29	4	6.12	-0.00414	0.684	0.027
Age-3	700	1	6.28	4	6.12	-0.00398	0.688	0.026
Age-3	750	1	6.21	4	6.11	-0.00297	0.759	0.015
Age-3	800	1	6.16	4	6.11	-0.00209	0.826	0.008
Age-3	850	1	6.15	4	6.11	-0.00198	0.835	0.007
Age-3	900	1	6.15	4	6.11	-0.00197	0.835	0.007

Table 3.5. General linear model results for recruitment signals of age-1 cod using age-0 abundance and age-0 body length (mmSL) from each bay (1992 – 1997, 2001). Bold font signifies statistical significance ($p < 0.05$).

Notre Dame Bay							
Response	Predictor	DF	F Statistic	Residual DF	Slope	*p* value	R^2
Age-1	Age-0	1	0.866	3	-0.347	0.421	0.224
Age-1	Age-0 body length	1	0.456	3	-0.0241	0.548	0.132
Bonavista Bay							
Response	Predictor	DF	F Statistic	Residual DF	Slope	*p* value	R^2
Age-1	Age-0	1	0.767	3	-0.276	0.446	0.204
Age-1	Age-0 body length	1	1.48	3	-0.0397	0.310	0.331
Trinity Bay							
Response	Predictor	DF	F Statistic	Residual DF	Slope	*p* value	R^2
Age-1	Age-0	1	0.0796	3	0.261	0.796	0.026
Age-1	Age-0 body length	1	0.128	3	0.0245	0.744	0.041
Conception Bay							
Response	Predictor	DF	F Statistic	Residual DF	Slope	*p* value	R^2
Age-1	Age-0	1	1.78	3	1.22	0.274	0.373
Age-1	Age-0 body length	1	0.435	3	0.0754	0.557	0.127

Table 3.6. Generalized linear model results for recruitment signals of age-3 cod in 2J3KL using age-0 and age-1 body length (mmSL) from each bay (1992 – 1997, 2001). Bold font signifies statistical significance ($p < 0.05$).

Notre Dame Bay								
Response	Predictor	DF	Deviance	Residual DF	Residual Deviance	Slope	*p* value	D^2
Age-3	Age-0 body length	1	8.06	5	7.15	-0.0176	0.381	0.113
Age-3	Age-1 body length	1	6.11	4	6.11	-0.00122	0.948	<0.001
Bonavista Bay								
Response	Predictor	DF	Deviance	Residual DF	Residual Deviance	Slope	*p* value	D^2
Age-3	**Age-0 body length**	**1**	**12**	**5**	**7.1**	**-0.0247**	**0.035**	**0.411**
Age-3	Age-1 body length	1	8.84	4	6.07	0.0311	0.082	0.313
Trinity Bay								
Response	Predictor	DF	Deviance	Residual DF	Residual Deviance	Slope	*p* value	D^2
Age-3	**Age-0 body length**	**1**	**19.4**	**5**	**7.06**	**-0.0318**	**<0.001**	**0.636**
Age-3	Age-1 body length	1	7.41	4	6.09	0.0132	0.285	0.178
Conception Bay								
Response	Predictor	DF	Deviance	Residual DF	Residual Deviance	Slope	*p* value	D^2
Age-3	**Age-0 body length**	**1**	**11.6**	**4**	**6.07**	**-0.0215**	**0.018**	**0.478**
Age-3	Age-1 body length	1	5.65	3	5.08	0.0118	0.422	0.101

Table 3.7. Generalized linear model results for recruitment signals of age-3 cod in 2J3KL using juvenile (age-0 and age-1) cod abundance and body length (mmSL), and general linear model recruits for recruitment signals of age-1 cod using age-0 abundance and body length, from Bonavista, Notre Dame, Trinity, and Conception bays combined (1992 – 1997, 2001). Bold font signifies statistical significance ($p < 0.05$).

Age-0 to Age-3								
Response	Predictor	DF	Deviance	Residual DF	Residual Deviance	Slope	*p* value	D^2
Age-3	Age-0	1	7.21	5	7.17	-0.00593	0.823	0.006
Age-3	Body length	1	10.6	5	7.11	-0.0234	0.091	0.330
Age-1 to Age-3								
Response	Predictor	DF	Deviance	Residual DF	Residual Deviance	Slope	*p* value	D^2
Age-3	Age-1	1	6.19	4	6.11	-0.00472	0.772	0.014
Age-3	Body length	1	7.12	4	6.09	-0.123	0.288	0.144
Age-0 to Age-1								
Response	Predictor	DF	F Statistic	Residual DF		Slope	*p* value	R^2
Age-1	Age-0	1	0.0581	18		-0.0508	0.812	0.003
Age-1	Body length	1	0.0213	18		-0.0254	0.885	0.001

Table 3.8. General linear model results for relationships between the proportion of sites containing eelgrass along the northeast coast of Newfoundland (1995, 1996, 2001), and age-0 and age-3 cod abundance in 2J3KL (1992 – 1997, 2001). Bold font signifies statistical significance ($p < 0.05$).

Response	Predictor	DF	F Statistic	Residual DF	Slope	*p* value	R^2
Age-0	Eelgrass	1	0.1273	10	7.705	0.729	-0.086
Age-3	Eelgrass	1	0.0190	10	-826792	0.893	-0.098

Table 3.9. Generalized linear model results for recruitment signals of age-3 cod in each NAFO division (2J3KL) using age-0 and age-1 abundance from each bay (1992 – 1997, 2001). Bold font signifies statistical significance ($p < 0.05$).

Age-0									
Bay	Response	NAFO Division	DF	Deviance	Residual DF	Residual Deviance	Slope	*p* value	D^2
Notre Dame	Age-3	2J	1	9.21	5	7.09	0.0205	0.167	0.230
Notre Dame	**Age-3**	**3K**	**1**	**14.3**	**5**	**7.1**	**-0.0401**	**0.007**	**0.505**
Notre Dame	Age-3	3L	1	9.6	5	7.41	-0.0436	0.163	0.228
Bonavista	**Age-3**	**2J**	**1**	**16**	**5**	**7.05**	**0.00754**	**0.003**	**0.560**
Bonavista	**Age-3**	**3K**	**1**	**12.5**	**5**	**7.11**	**-0.00856**	**0.019**	**0.431**
Bonavista	Age-3	3L	1	10.1	5	7.39	-0.0108	0.122	0.265
Trinity	Age-3	2J	1	7.13	5	7.12	-0.00103	0.920	0.001
Trinity	**Age-3**	**3K**	**1**	**27.4**	**5**	**7.05**	**0.028**	**<0.001**	**0.742**
Trinity	**Age-3**	**3L**	**1**	**16.2**	**5**	**7.25**	**0.0388**	**0.009**	**0.552**
Conception	Age-3	2J	1	9.39	5	7.09	0.0445	0.134	0.245
Conception	Age-3	3K	1	7.2	5	7.19	-0.00433	0.920	0.001
Conception	Age-3	3L	1	8.76	5	7.45	-0.0838	0.207	0.149

Table 3.9. (continued)

Age-1									
Bay	Response	NAFO Division	DF	Deviance	Residual DF	Residual Deviance	Slope	*p* value	D^2
Notre Dame	Age-3	2J	1	6.23	4	6.11	0.0233	0.743	0.020
Notre Dame	Age-3	3K	1	6.18	4	6.12	0.019	0.797	0.010
Notre Dame	Age-3	3L	1	7.39	4	6.34	-0.151	0.228	0.142
Bonavista	Age-3	2J	1	6.41	4	6.11	0.0249	0.586	0.048
Bonavista	Age-3	3K	1	9.69	4	6.08	0.075	0.051	0.373
Bonavista	Age-3	3L	1	7.31	4	6.34	0.0947	0.247	0.133
Trinity	Age-3	2J	1	7.35	4	6.09	0.00973	0.274	0.171
Trinity	Age-3	3K	1	6.13	4	6.12	0.000812	0.936	0.001
Trinity	Age-3	3L	1	7.54	4	6.33	-0.0194	0.249	0.160
Conception	Age-3	2J	1	6.57	4	6.11	0.0038	0.520	0.071
Conception	Age-3	3K	1	6.12	4	6.12	-0.00031	0.961	<0.001
Conception	Age-3	3L	1	7.72	4	6.33	-0.0128	0.221	0.181

Table 3.10. Generalized linear model results for recruitment signals of age-3 cod in each Ecologically and Biologically Significant Area (EBSA) (1 and 2) using age-0 and age-1 abundance from each bay (1992 – 1997, 2001). Bold font signifies statistical significance ($p < 0.05$).

Age-0									
Bay	Response	EBSA	DF	Deviance	Residual DF	Residual Deviance	Slope	*p* value	D^2
Notre Dame	**Age-3**	**1**	**1**	**12.9**	**5**	**7.21**	**-0.0533**	**0.015**	**0.441**
Notre Dame	Age-3	2	1	9.04	5	7.16	-0.024	0.210	0.208
Bonavista	**Age-3**	**1**	**1**	**13.7**	**5**	**7.19**	**-0.0126**	**0.009**	**0.475**
Bonavista	Age-3	2	1	9.34	5	7.16	-0.006	0.168	0.233
Trinity	**Age-3**	**1**	**1**	**15.1**	**5**	**7.17**	**0.0305**	**0.014**	**0.525**
Trinity	**Age-3**	**2**	**1**	**16.2**	**5**	**7.09**	**0.0268**	**0.003**	**0.563**
Conception	Age-3	1	1	7.96	5	7.33	-0.048	0.396	0.080
Conception	Age-3	2	1	7.52	5	7.19	-0.0245	0.570	0.044
Age-1									
Bay	Response	EBSA	DF	Deviance	Residual DF	Residual Deviance	Slope	*p* value	D^2
Notre Dame	Age-3	1	1	6.5	4	6.21	-0.0597	0.543	0.045
Notre Dame	Age-3	2	1	6.23	4	6.23	0.005	0.960	<0.001
Bonavista	Age-3	1	1	7.12	4	6.19	0.0633	0.300	0.130
Bonavista	Age-3	2	1	8.09	4	6.18	0.087	0.138	0.237
Trinity	Age-3	1	1	6.73	4	6.2	-0.00963	0.462	0.079
Trinity	Age-3	2	1	6.39	4	6.23	-0.00556	0.687	0.026
Conception	Age-3	1	1	6.65	4	6.21	-0.00559	0.499	0.066
Conception	Age-3	2	1	6.66	4	6.22	-0.00545	0.520	0.067

Chapter 4: Conclusions

In this thesis, I demonstrated the utility of coastal juvenile cod seine surveys for predicting the abundance of recruits entering the Northern cod stock (2J3KL), using juvenile cod abundance data from two long-term coastal monitoring programs. Recruitment signals were detected from juvenile abundance to offshore regions using both time series analysed in Chapters 2 and 3 (the Newman Sound and Fleming Surveys, respectively); however, the strength of these recruitment signals varied with spatial and temporal scales likely reflecting the state of cod populations during the two surveys periods and the characteristics of both datasets. Following the Northern cod stock collapse, spawning biomass was substantially lower than historical levels, the distribution of the Northern cod stock contracted, and the distribution and abundance of juveniles consequently contracted and declined (Anderson and Rose 2001). Not until 2007 were aggregations observed in areas historically occupied in the offshore (Mello and Rose 2008). Here, I contrast the results in Chapters 2 and 3 and how they likely reflect differences in the time periods and durations of the time series in the context of the status of the fishery when their component data were collected.

The Newman Sound Survey (Chapter 2) gave the strongest recruitment signals from juveniles when considering the entire adult Northern cod stock, whereas the Fleming Survey (Chapter 3) showed inconsistent overall recruitment signals, but generally stronger inshore recruitment signals. These results are consistent with changes in cod behaviour that occurred in the first decade post collapse (1992 – 1997, 2001), when the shorter Fleming Survey was conducted. In the post-collapse years (after 1992), cod distribution contracted dramatically from the offshore and greater concentrations of cod occurred inshore, coinciding with a decline in abundance. Cod may have avoided risky migrations offshore in search of food and available habitat because coastal areas would have had sufficient food to support the stock at low abundance (Anderson 1964, Ribalet et al. 2010, Finstad and Hein 2012). However, when cod abundance began to increase in the mid-late 2000s, competition may have forced individuals to migrate further from the coast in search of food. This re-expansion of cod in the offshore is reflected in the strong recruitment signals over a broader area from the Newman Sound time series in Chapter 2. The Newman Sound Survey extended from low abundance years post-collapse further into the recovery period. In contrast, because the Fleming Survey occurred during the early years after the collapse, before any substantial stock re-growth, and the associated shift in distribution and behaviour may have eliminated recruitment signals.

Recruitment signals strength also differed between potential Ecologically and Biologically Significant Areas (EBSAs) and among NAFO divisions. Potential EBSAs, characterized by consistently high biomass, generally did not influence the recruitment signal strength from either the Fleming or Newman Sound Surveys. The EBSAs likely contain the highest biomass of cod within the time series because these habitats support the depth, habitat, and water temperatures preferred by sub-adult and adult cod (i.e. age 3+); however, they did not strengthen predictive relationships compared to those signals detected in the other spatial analysis. These EBSAs were chosen based on data that included age classes other than age-at-recruitment (age-3). However, areas of importance for age-3 cod may differ from those favoured by older adult age classes and focusing on such locations could reveal stronger predictive relationships in future analyses. Further, since these EBSAs consistently reflect the highest abundance of cod year-to-year in this region, they do not necessarily reflect fluctuations in juvenile abundance or adult abundances elsewhere in the offshore. Cod may be aggregating in these areas first and spilling out into less ideal habitat once the carrying capacity of the area has been reached (MacCall 1990), producing a consistently high catch rate. Therefore, these EBSAs may be inappropriate for detecting recruitment signals.

In Chapter 2, recruitment signals from Newman Sound were statistically strong in the entire offshore, but particularly in both NAFO divisions 2J and 3K, whereas 3L indicated virtually no recruitment signal. In contrast, Chapter 3 showed low and inconsistent recruitment signals in the whole offshore region, as well as when separating NAFO divisions. Inconsistent recruitment signals across management zones in Chapter 3 overall suggest that abundances were too low during that period to yield a broad-scale signal, at least for the number of years that were available for analysis in the Fleming Survey dataset. Forecasting of population change through recruitment signals will require a larger change in abundance (i.e. effect size) or a longer time series to increase the statistical power. The stock only began to rebuild within the past decade (post-Fleming Survey) (Mello and Rose 2008), and abundance in 2J and 3K rose faster than in 3L (DFO 2018), a change reflected in the recruitment signals from the longer Newman Sound time series. Indeed, limiting the Newman Sound Survey to the same time span as the Fleming Survey, yielded similar non-significant results, and no detectable recruitment signals prior to 2005 (see Chapter 2). Therefore, I attribute the inconsistent and unclear recruitment signals in the Fleming Survey described in Chapter 3 to the short time series during a period of low abundance.

In addition to the effect of spatial and temporal scale on recruitment signals, the resolution of sampling adds limitations to both surveys. The Newman Sound Survey, conducted in Bonavista Bay, is temporally extensive (1995 – present) with fine temporal resolution (bi-weekly) and captures a broad spectrum of abundances over an extended period of time. This survey provided understanding of variation within a single coastal area over time with greater statistical power than the Fleming Survey. Repeated sampling also reduces measurement error associated with spatial variation in the population, likely contributing to the strong recruitment signals year-to-year. However, because only one area was sampled, extrapolation of results to other locations requires caution. Unlike the Newman Sound Survey, the Fleming Survey sampled several bays along the northeast coast of Newfoundland, thus providing a broader spatial perspective on juvenile Atlantic cod. The Fleming Survey offers a unique opportunity that the Newman Sound Survey does not – the comparison of recruitment signals, and relative importance of juveniles in different bays immediately following the cod collapse. This information could benefit fisheries management in determining which nursery habitats contribute most to adult stocks. Areas with strong recruitment signals could indicate which nursery areas supply offshore recruits and provide insight on connectivity between coastal habitats and offshore regions. However, the Fleming Survey was temporally less extensive than the Newman Sound Survey, providing a single abundance estimate annually for each site during a historically low period of cod abundance. Despite the extensive spatial scale of the Fleming Survey, the coarse temporal resolution may have implications regarding recruitment signal strength because settlement pulses of juvenile cod occur multiple times through the summer and fall. Therefore, if the full pulse structure of a given cohort was not evident during the specific sampling window that year, the sample would under-represent the year-class and the recruitment signal would not accurately reflect year-class strength. Assessing the correlation of pulse strength among settlement pulses within years (using the Newman Sound Survey) may indicate whether a single abundance measurement is the most useful index for determining recruitment signals in the future.

Long-duration time series are also crucial for identifying patterns and effects of environmental variables on recruitment. My results for both Chapter 2 and 3 are generally consistent with previous studies that emphasize the non-stationarity of environmental variables in ecological time series (Stige et al. 2013, Feiner et al. 2015). In both Chapter 2 and 3, the influence of environmental factors on recruitment varied over time, even reversing in trend, thus reducing their utility in forecasting recruitment (Britten et al. 2016). A longer time series over multiple time frames would facilitate documentation of the effects of slowly changing environmental factors, identifying any nonlinear relationships, and revealing relationships with environmental variables. Long duration and high resolution time series can also strengthen statistical power to detect significant relationships. Although the Newman Sound and Fleming surveys have spatial and temporal limitations respectively, the results from both of these surveys identify broad spatial patterns in recruitment signals that are unlikely to arise from chance alone.

Both surveys have strengths and limitations with regard to spatial and temporal scale and resolution, but ultimately future surveys should continue as long-term monitoring programs to capture ecosystem shifts, variability in abundance, and relative importance of environmental variables over space and time. Continued monitoring of coastal nursery habitats will also aid in quickly identifying environmental and anthropogenic threats (e.g., coastal development, climate change, habitat degradation), and facilitating the protection and restoration of these areas accordingly (e.g., designation of MPAs and EBSAs). Seine surveys offer a cost-effective, relatively quick sampling method to provide accurate estimates of juvenile cod that offshore trawl surveys cannot (Dalley and Anderson 1997, Williams et al. 2011), allowing relatively rapid assessments of year-class strength and environmental degradation, potentially years before they might appear in the fishery. In addition to monitoring and analysing juvenile abundance, assessing larval supply offers one additional mechanism to evaluate the relative value of nursery habitats (Beck et al. 2001). Chapter 3 identified differences in recruitment signals among bays.

Trinity Bay was the only bay that provided a strong recruitment signal for the entire offshore. Noting the presence of a large spawning aggregation in Smith Sound, Trinity Bay during the Fleming Survey (Rose 2003), I suggest examining spawning location, aggregation size, and ocean circulation models in the future (e.g., Stanley et al. 2012, 2013), in addition to juvenile abundance to better understand the success of recruitment signals in all areas. This aspect may be particularly helpful when using short time series or during periods of low abundance.

Coastal seine surveys clearly contain important information for predicting offshore cod recruitment. Using early age classes to detect recruitment signals can assist managers in forecasting stock strength. The spatial and temporal scale and context of the fishery survey remain important for interpreting these recruitment signals however. My study of the link between juvenile and pre-adult Atlantic cod abundance along the northeast coast of Newfoundland provides insight into the importance of collecting early life history data and creating long duration ecological time series. Specifically, my findings highlight how knowledge of juvenile abundance in nursery habitats can be used for understanding and forecasting fluctuations in stock abundance, potentially supporting fisheries management decisions.

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