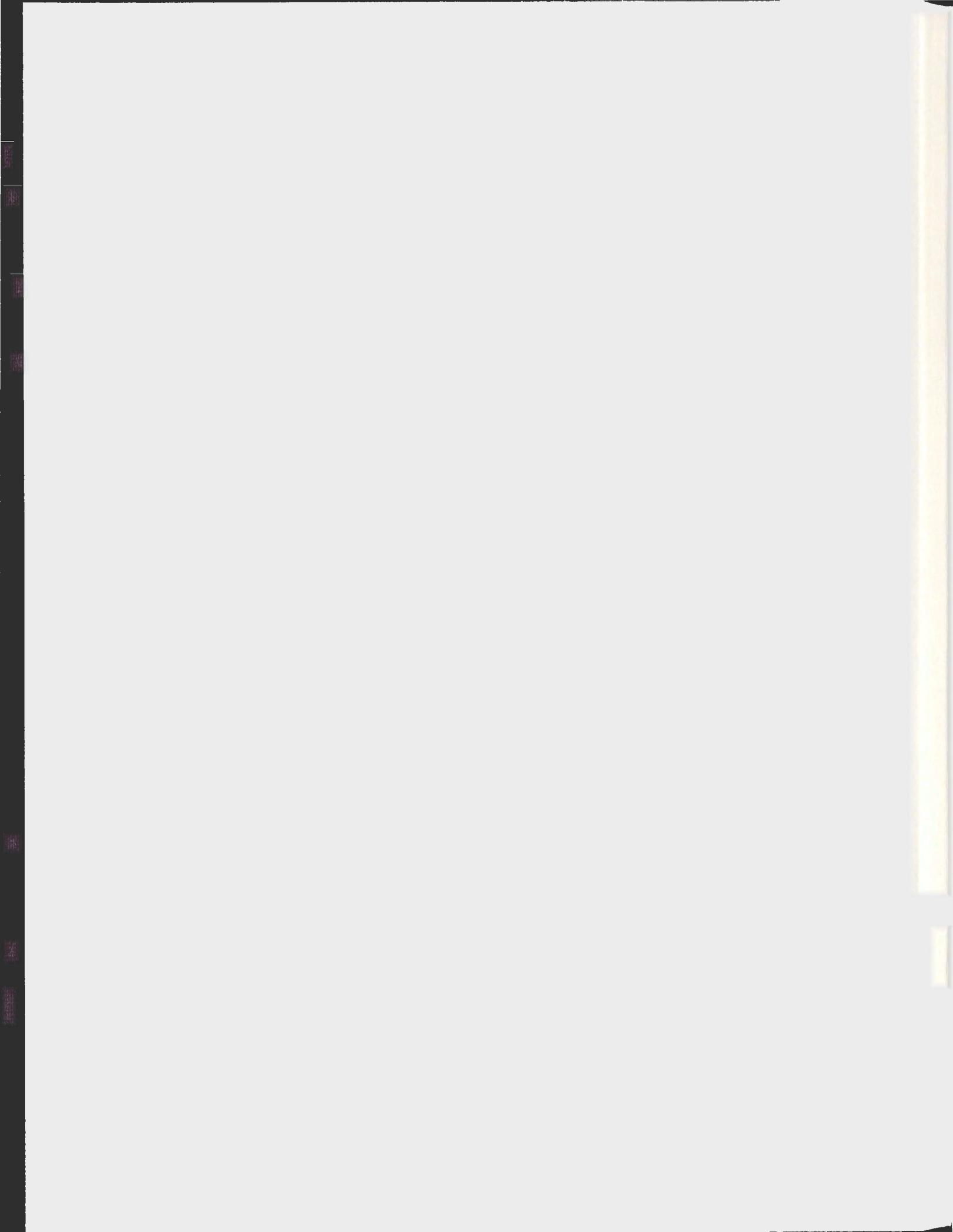


DISPERSAL AND HOME RANGE OF AGE 1  
GREENLAND COD (GADUS OGAC) IN  
NEWMAN SOUND, NEWFOUNDLAND

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**DISPERSAL AND HOME RANGE OF AGE 1 GREENLAND COD (*Gadus ogac*) IN  
NEWMAN SOUND, NEWFOUNDLAND**

**by**

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## Abstract

The stability of a population is largely dependent on the dispersal dynamics of the juvenile cohort. In the marine environment, dispersal range, mortality during dispersal, and site fidelity of juveniles contribute to the resilience and connectivity among populations. However, juvenile dispersal parameters are rarely investigated and quantified, even among species or populations of concern. I determined dispersal distances, site fidelity, and home range areas of 1 year old Greenland cod (*Gadus ogac*) in Newman Sound, a coastal fjord of Newfoundland, through the use of passive acoustic telemetry. A network of 26-32 fixed hydrophone listening stations monitored movements of 82 out of 84 juveniles surgically implemented with coded acoustic transmitters. Single and reciprocal transplant experiments between two coves approximately 3.5 km apart were carried out during October 2010 and November 2011, respectively. A behavioural dichotomy between “resident” and “disperser” fish was seen during both experiments. Individual dispersers moved on the km scale, associated with the timing of the onset and disappearance of the seasonal thermocline, and in the month of July during both years. Similar proportions of control and transplant fish visited opposite source coves, suggesting low site fidelity and/or low homing initiative in both sample populations. ANOVA analyses of the tagging periods identified season as the only significant predictor of home range size, with a general increase in home range from pre-winter to post-winter seasons, and no effect of fish capture or release location. Mean seasonal home range areas during both tagging periods exceed those documented for age 2-3 Atlantic cod in other studies, suggesting a less established residency in age 1 Greenland cod. High individuality in movement patterns and area usage indicate that factors

affecting dispersal, such as temperature, predation, and age, likely differ in importance across individuals in the age class.

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## **Table of Contents**

|                                 |      |
|---------------------------------|------|
| <b>Abstract</b> .....           | i    |
| <b>Acknowledgments</b> .....    | ii   |
| <b>Table of Contents</b> .....  | iv   |
| <b>List of Tables</b> .....     | vii  |
| <b>List of Figures</b> .....    | viii |
| <b>List of Appendices</b> ..... | x    |

### **Chapter 1: Introduction and Overview**

|   |    |
|---|----|
| 1.1 Life history of Greenland cod ( <i>Gadus ogac</i> ) .....                               | 1  |
| 1.2 Distribution, movements, and habitat associations<br>of Greenland and Atlantic cod..... | 4  |
| 1.3 Acoustic telemetry introduction, history, and applications .....                        | 7  |
| 1.4 Acoustic telemetry advantages and disadvantages .....                                   | 10 |
| 1.5 Chapter structure and hypotheses .....  | 12 |
| 1.6 References .....  | 14 |

|                                      |    |
|--------------------------------------|----|
| <b>Co-authorship Statement</b> ..... | 20 |
|--------------------------------------|----|

### **Chapter 2: Home range of juvenile age 1 Greenland cod (*Gadus ogac*) in a Newfoundland fjord**

|                                    |    |
|------------------------------------|----|
| 2.1 Abstract .....                 | 21 |
| 2.2 Introduction .....             | 22 |
| 2.3 Methods .....                  | 24 |
| 2.3.1 Study site .....             | 24 |
| 2.3.2 Hydrophone positioning ..... | 25 |
| 2.3.3 Tagging .....                | 25 |
| 2.3.4 Home range analyses .....    | 27 |

|                                      |    |
|--------------------------------------|----|
| 2.3.5 Standard length analyses ..... | 27 |
| 2.4 Results .....                    | 28 |
| 2.4.1 Acoustic tracking .....        | 28 |
| 2.4.2 Home range analyses .....      | 29 |
| 2.4.3 Standard length analyses ..... | 30 |
| 2.5 Discussion .....                 | 31 |
| 2.6 Acknowledgements .....           | 39 |
| 2.7 References .....                 | 40 |

**Chapter 3: Site fidelity of transplanted age 1 Greenland cod in Newman Sound, Newfoundland**

|  |    |
|--|----|
| 3.1 Abstract .....                                 | 57 |
| 3.2 Introduction .....                             | 58 |
| 3.3 Methods .....                                  | 61 |
| 3.3.1 Hydrophone positioning .....                 | 61 |
| 3.3.2 Experimental design .....                    | 62 |
| 3.3.3 Least cost path analyses .....               | 62 |
| 3.3.4 Standard length and residency analyses ..... | 63 |
| 3.4 Results .....                                  | 64 |
| 3.4.1 Acoustic tracking and residency .....        | 64 |
| 3.4.2 Movement patterns .....                      | 64 |
| 3.4.3 Large movements: timing and patterns .....   | 66 |
| 3.5 Discussion .....                               | 66 |
| 3.6 Acknowledgements .....                         | 73 |
| 3.7 References .....                               | 74 |

**Chapter 4: Summary**

4.1 Home range and dispersal potential of age 1 Greenland cod .....92  
4.2 Implications and future study .....94  
4.3 References .....98

**Appendix 1: Data processing and home range calculation for a passive acoustic telemetry network in Newman Sound, Newfoundland**

A1.1 Introduction .....100  
A1.2 Methods .....102  
A1.2.1 Data processing .....102  
A1.2.2 Generating position estimates .....102  
A1.2.3 Least cost path analyses .....103  
A1.2.4 Distance and rate of movement analyses .....104  
A1.2.5 Home range analyses .....105  
A1.3 Conclusion .....109  
A1.4 References .....111

**Appendix 2: Individual detection plots for fish tagged in the 2010-2011, and 2011-2012 experiments .....116**

**List of Tables**

Table 2.1 Summary of detection data for the 2010-2011 and  
2011-2012 tagging experiments .....53

## List of Figures

|  |    |
|--|----|
| Figure 2.1 Map of Newman Sound, Newfoundland, indicating the positions of Heffern's Cove and Buckley's Cove .....  | 45 |
| Figure 2.2 Positions and 500 m detection radii of the VR2/VR2W hydrophones deployed in Newman Sound, Newfoundland by November 2011 .....   | 46 |
| Figure 2.3. Cumulative density of the tracking periods of individual Greenland cod detected during the 2010-2011 (Year 1) and 2011-2012 (Year 2) tagging seasons .....                       | 47 |
| Figure 2.4. Proportional frequency distributions of seasonal home ranges.....  | 48 |
| Figure 2.5. Seasonal mean home ranges for the a) 2010-2011 and b) 2011-2012 tagging periods .....  | 49 |
| Figure 2.6. Home range areas of fish with sufficient numbers of positions for all three season calculations during the a) 2010-2011 and b) 2011-2012 tagging season .....                    | 50 |
| Figure 2.7 Boxplots of home range areas calculated solely for the month of May during both experiment years .....  | 51 |
| Figure 2.8 Scatterplot of initial standard length (cm) and tracking period of transplanted fish from Buckley's Cove for the 2011-2012 season .....   | 52 |
| Figure 3.1 Positions and 500 m detection radii of the VR2/VR2W hydrophones deployed in Newman Sound, Newfoundland by November 2011 .....   | 79 |
| Figure 3.2 Experimental designs for the a) 2010-2011 tagging experiment and b) 2011-2012 tagging experiment .....  | 80 |
| Figure 3.3 Detection plots of the a) 2010-2011 and b) 2011-2012 tagging experiments .....  | 81 |
| Figure 3.4. Frequency of tagged age 1 Greenland cod detected by varying numbers of receivers during the 2010-2011 and 2011-2012 experiments .....  | 83 |
| Figure 3.5. Movement patterns exhibited by individuals tagged in year 1 (2010-2011) and year 2 (2011-2012), defined as proportions of each experiment type excluding early mortalities ..... | 84 |

|  |     |
|--|-----|
| Figure 3.6. Detection plots of control fish 29916 and transplant fish 29950 exhibiting movement to opposite release cove during the 2010-2011 tagging season .....   | 85  |
| Figure 3.7. Detection plots of Buckley’s Cove transplant fish 4947 and Heffern’s Cove transplant fish 4952 exhibiting movement to their cove of origin during the 2011-2012 tagging season .....   | 86  |
| Figure 3.8. Example of control fish 29921, that visited the opposite source cove and then returned to its release site, and transplant fish 29937 that visited the opposite source cove and then continued dispersing elsewhere in the 2010-2011 experiment .....                    | 87  |
| Figure 3.9. Example Buckley’s Cove transplant fish 3964 and Buckley’s Cove control fish 4942 that travelled to and were last detected in the opposite source cove in the 2011-2012 experiment .....  | 88  |
| Figure 3.10. Example of Heffern’s Cove transplant fish 4957 that visited the opposite source cove but then continued elsewhere, and Buckley’s Cove control fish 4934 that visited the opposite source cove, but then returned to its release site, in the 2011-2012 experiment ..... | 89  |
| Figure 3.11. Detection plot of Buckley’s Cove transplant fish 4937, that visited the opposite source cove, then returned to its release site, and then returned to the opposite cove again in the 2011-2012 experiment .....   | 90  |
| Figure 3.12. Number of fish exhibiting movements >800 m for the a) 2010-2011 and b) 2011-2012 tagging experiments .....  | 91  |
| Figure A1 ModelBuilder tool for extracting areas of 95% kernel utilization distributions that were solely in the water .....   | 115 |

**List of Appendices**

Appendix 1: Data processing and home range calculation for a passive acoustic telemetry network in Newman Sound, Newfoundland .....100

Appendix 2: Individual detection plots for fish tagged in the 2010-2011, and 2011-2012 experiments .....116

## **Chapter 1: Introduction and Overview**

### **1.1 Life history of Greenland cod (*Gadus ogac*)**

Greenland cod, sometimes referred to as rock cod in Newfoundland, is a demersal marine fish that spans Arctic and subarctic waters from Greenland south to Newfoundland and New England, and west to Alaska (Scott and Scott 1988, Rose 2007). In Canada, it extends south to Nova Scotia, north to Baffin Island, and west to the Beaufort Sea and Hudson and James Bays (Mikhail and Welch 1989). The species associates mainly with coastal regions, perhaps in response to food availability (Mikhail and Welch 1989, Morin et al. 1991). Greenland cod can be characterised as a “cold water” species. Seasonal distributions are defined by temperature, as shown for individuals in James Bay that avoid waters  $>10^{\circ}\text{C}$  (Morin et al. 1991). High levels of glycoprotein antifreeze in the blood of Atlantic and Greenland cod serve as an adaptation for colder waters (Van Voorhies 1978, Goddard et al. 1992). The James Bay study attributed higher species activity at night than during day to avoidance of warmer water temperatures and visual predators (Morin et al. 1991), though their study did not examine age-class specific dynamics. Morin et al. (1991) suggested that “avoidance of high temperatures, coupled with the search for food, could account for Greenland cod distribution on the daily and seasonal time scales”.

Contrastingly, in Newman Sound, Newfoundland, age 0+ juveniles occupy shallow waters (Laurel et al. 2003, 2004; Sheppard 2005), where water temperatures can reach  $17^{\circ}\text{C}$  (Cote et al. 2002), though they may move to deeper waters as they age, similar to Atlantic cod (Gregory and Anderson 1997). Furthermore, age 0 Pacific cod, *Gadus macrocephalus*, (of which Greenland cod is actually a subspecies; Coulson et al.

2006) occurred in greater abundances in areas with relatively warmer water temperatures (Hurst et al. 2012). At the local scale, selection may favour warmer temperatures for growth (Hurst et al. 2010). Shallow waters in Newman Sound offer increased protection for vulnerable juveniles as well, especially in eelgrass, *Zostera marina* (Gotceitas et al. 1997, Linehan et al. 2001, Thistle et al. 2010, Warren et al. 2010). Shallow, warmer waters may offer the most ideal combination of protection from predators and sufficient feeding and growth opportunities for young juveniles (Thistle et al. 2010).

Studies from Hudson Bay and Western Greenland document consistent, opportunistic feeding on a variety of benthic organisms (Mikhail and Welch 1989, Nielsen and Andersen 2001). Large individuals prefer fish, particularly capelin when abundant, followed by crustaceans and polychaetes (Nielsen and Andersen 2001). Feeding also occurs under ice, and in winter, populations in James Bay favour small fish, polychaetes, and mysids (Morin et al. 1991). The species has been described as a “carnivorous dead-end” in Arctic food webs, because they are unimportant as prey for marine mammals and birds in the Hudson Bay region (Mikhail and Welch 1989). However, in other areas, natural mortality occurs from predation by invertebrates, fish, birds, and mammals (Scott and Scott 1988), especially on juveniles. For instance, tethering experiments in Newfoundland indicate predominant predators of juvenile cod include sculpins (*Myoxocephalus* spp.), white hake (*Urophycis tenuis*), Atlantic cod (*G. morhua*), and larger Greenland cod (Linehan et al. 2001, Laurel et al. 2003). Other potential predators include river otters (*Lontra canadensis*) (Cote et al. 2009), cormorants (*Phalacrocorax carbo*), (Ottera et al. 1999), and osprey (*Pandion haliaetus*) (Linehan et al. 2001).

Published information regarding life history characteristics of Greenland cod remains scant; however, reported life spans range from 12 years (Mikhail and Welch 1989) to 21 years (Morin and Dodson 1986). Overall reported maximum size ranges from 1.2 kg (Mikhail and Welch 1989) to 10 kg (Rose 2007). Individuals in Hudson Bay and James Bay populations reach maturity and spawn at ~3 years (Mikhail and Welch 1989, Morin et al. 1991). Greenland cod spawn demersal eggs (Scott and Scott 1988) any time from February to June depending on latitude. After a short pelagic period of a month or so, juveniles settle to the seabed in the nearshore (Scott and Scott 1988, Mikhail and Welch 1989, Morin et al. 1991) in a single recruitment pulse often associated with a coastal downwelling event (Ings et al. 2008). In contrast, their better studied congener, Atlantic cod, spawns pelagically later in the spring, between March and June, often at depths of 100s of meters (Scott and Scott 1988). Atlantic cod individuals often exhibit a reproductive "bet-hedging strategy". Unlike Greenland cod, there are multiple recruitment pulses several weeks apart where unsynchronized reproductive efforts are merged and driven by onshore/offshore winds to settle into nearshore habitats (Methven and Bajdik 1994, Grant & Brown 1998, Ings et al. 2008), where they co-occur with Greenland cod of similar size. Pelagic larvae and pelagic juveniles 25-50 mm long are transported by currents (Pepin and Helbig 1997) and onshore winds (Ings et al. 2008) into the nearshore where they settle to the seabed and adopt a demersal lifestyle thereafter (Methven and Bajdik 1994).

Demersal eggs may be an adaptation in response to high larval and juvenile mortality in surface Arctic waters at the northern extent of Greenland cod's range (Morin et al. 1991). Demersal larvae are generally larger and more developed than pelagic larvae

(Snelgrove et al. 2008), so Greenland cod larvae may maintain coastal associations more effectively than Atlantic cod. Conversely, greater passive transport by advection of the pelagic larvae of Atlantic cod may increase inter-annual recruitment variability (Bradbury et al. 2003). Although egg and larval dispersal potential both differ between the two species, they co-occur as demersal juveniles in Newfoundland coastal waters, where both prefer similar complex habitat, particularly eelgrass, as a refuge from predation (Linehan et al. 2001, Laurel et al 2003). In Newman Sound in Oct-Nov, age 1 *G. ogac* had a mean length 17.2 +/- 0.8 cm SL compared to a mean length of 16.7 +/- 1.2 cm SL for age 1 *G. morhua*.

## **1.2. Distribution, movements, and habitat associations of Greenland and Atlantic cod**

The dispersal and movement patterns of Atlantic cod have been studied much more intensely than those of Greenland cod. Initial tagging studies of Atlantic cod by Templeman (1979) suggested discrete populations of early life stages likely influenced by specific hydrographic forces and feeding conditions. He reported three distinct adult Atlantic cod populations in Newfoundland including Labrador, northeastern Newfoundland, and eastern Newfoundland populations. However, Atlantic cod on the Northeast Newfoundland Shelf have become concentrated in the southern part of the range since 1989, and mature fish have been nearly absent from the Labrador population since 1990 (deYoung and Rose 1993). Additionally, large spawning aggregations can arise in different areas through immigration and dispersal, as was observed in 1995 in Smith Sound Newfoundland (Rose et al. 2011).

Atlantic cod in Newfoundland exhibit diel and seasonal activity patterns, with more wide-ranging movements between deep, cold resting sites and warm, shallow feeding areas during summer (Clark and Green 1990). Previous telemetry studies document shallow water home ranges for age 2-3 Atlantic cod (Clark and Green 1990, Cote et al. 2004). Large-scale trawl sampling suggests segregated size distributions in various areas around Newfoundland with age 0s restricted to the inshore (<55 km from the coast), age 1+ found more in inshore than offshore, and age 2-3 becoming more widespread along and across the shelf (Dalley and Anderson 1997). Overlapping distributions of Greenland cod and Atlantic cod in Greenland within the 0-200 m depth range suggest that interspecific competition may be possible (Nielsen and Andersen 2001).

The rate and extent of movement by gadids varies with life-stage and size, as well as season and geographic location. Previous studies indicate that the majority of age 0 and age 1 Atlantic cod occur in nearshore environments (Dalley and Anderson 1997, Anderson and Gregory 2000), highlighting its importance as a nursery habitat. Greenland cod have been described as relatively sedentary, not moving “more than a few kilometres, remaining in their home inlet for life” (Mikhail and Welch 1989). Early studies on Atlantic cod juveniles suggest that juveniles 2 years and younger do not migrate seasonally to offshore waters (Anderson and Gregory 1997). Tupper and Boutilier (1995) found that juvenile age 0 Atlantic cod in Nova Scotia exhibited extreme site fidelity and territoriality, with home ranges  $\sim 100 \text{ m}^2$ , although home range area increased with size. In contrast, mark-recapture studies in Newman Sound by Laurel et al. (2004) indicated greater spatial and temporal movements among both Greenland and Atlantic age 0 cod,

which they attributed to habitat complexity or adaptive characteristics (Laurel et al. 2004). Age 1 Atlantic cod in Newfoundland occur in deeper waters than age 0s during the day, but then move shoreward at night where they actively forage for prey and locate conspecifics (Grant and Brown 1998). Age 2-3 individuals move to deeper waters in late November in Newfoundland (Cote et al. 2004), having occupied shallower seabeds (10-30 m) in the summer months. Activity of age 2-3 Atlantic cod sometimes correlates with substrate but not with temperature (Cote et al. 2002, 2003).

Observations from submersibles in Placentia Bay, Newfoundland showed that bottom substrate, water depth, and bathymetric relief all determine juvenile cod (< 4 years) distributions (Gregory and Anderson 1997). Previous work suggests limited movement by young juvenile Greenland cod (age 0-1), which venture less than a few hundred metres during spring and autumn (Sheppard, 2005). High predation risk in the area may limit these movements. Age 0 Atlantic and Greenland cod individuals in Newfoundland closely associate with eelgrass habitats (Gotceitas et al. 1997, Laurel et al. 2003), increasing in abundance proportionally with eelgrass percent cover (Laurel et al. 2003, Warren et al. 2010). Intermediately-complex eelgrass sites support the highest density of age 0 Atlantic and Greenland cod, perhaps by providing sufficient refuge from predation while simultaneously providing good feeding opportunities (Thistle et al. 2010). However, this response is density-dependent, because when high-quality patches are saturated with individuals, aggregations increase over lower quality patches, such as sand and gravel (Laurel et al. 2004). The ability of age 1 Atlantic cod individuals to perceive habitat over larger distances likely explains increased patchiness of age 1 juveniles relative to age 0 individuals (Methven et al. 2003). Indeed, increased shoaling

behaviour may explain the decoupling of age 1 Atlantic cod individuals from eelgrass habitat compared to younger juveniles (Methven et al. 2003). Substrates such as pebble-gravel provide cover for age 1 (Newfoundland - Gregory and Anderson 1997) and large age 0 Atlantic cod (George's Bank - Lough et al. 1989); their mottled colouring may provide protection from predation through crypsis (Gregory and Anderson 1997).

Acoustic telemetry offers an opportunity to observe individual juvenile cod movements to investigate where, when, and how far they actually move, which can provide insight into fitness consequences (or lack thereof) to movement, as well as site fidelity and overall contribution of the life stage to dispersal.

### **1.3 Acoustic telemetry introduction, history, and applications**

Relative to their terrestrial counterparts, aquatic and marine ecosystems impose additional logistical difficulty for ecologists interested in studying *in situ* behaviours and processes. Generally, terrestrial organisms can be observed more easily in their natural habitat, and our own terrestrial-based existence probably facilitates a more intuitive understanding. Nonetheless, cryptic or wide-ranging terrestrial organisms present similar scientific issues as marine or aquatic species. Furthermore, direct observation of any organism, in any environment, introduces varying degrees of observer bias on the behaviour of focal animals. Acoustic telemetry technology presents an opportunity to examine individual-based movements of fish in order to answer a wide range of behavioural questions with minimal bias over a period of weeks, months or even years. Biotelemetry allows scientists to observe animal ecology from a distance, effectively removing most bias and enabling detailed data collection, even on more elusive species.

The earliest form of telemetry started in the 1960s utilizing very-high frequency (VHF) radio-collars to study grizzly bears and elk in Yellowstone National Park (Craighead 1982, Craighead et al. 1995). Although revolutionary, early VHF technology required scientists to track collared individuals in the field with a directional receiver and antenna. VHF has since evolved to triangulate the position of any incoming detections from a transmitter in the area (i.e., a collared animal) using stations placed in the field. But the ability for remote measurement of movements of wide-ranging organisms soon appealed to terrestrial and marine researchers alike. In 1978, the French Space Agency (CNES), the National Aeronautics and Space Administration (NASA), and the National Oceanic and Atmospheric Administration (NOAA) created the Argos system to track movements using satellites combined with worldwide mobile and fixed receiving stations. The system remains in use today. Argos began satellite tracking of transmitters placed in terrestrial animals, or marine animals that surfaced periodically (e.g., marine mammals). When the animal surfaces one or more satellites relays a signal of its position to a receiving station on Earth. Satellite technology provided a means to track wide-ranging fishes (Block et al. 2011), birds (e.g., migrating whooper swans *Cygnus cygnus*, Pennycuick et al. 1996), marine mammals (e.g., blue whales *Balaenoptera musculus*, Mate et al. 1999) and other marine animals (e.g., green turtles *Chelonia mydas*, Godley et al. 2003) that would have otherwise been impossible to observe *in situ*.

Despite the appeal of satellite tag technology, high costs prohibit its use for small- to medium-scale studies, or for less mobile organisms, or for the majority of marine animals that never surface, such as most fish species. Water quickly absorbs radio waves used in VHF technology, limiting their utility to a narrow range. Radio wave

absorption in high conductivity waters (e.g., brackish estuaries and ocean water, plus saline lakes) renders such technology virtually useless. Ultrasonic acoustic transmitters and receiver technology offer a workable solution. Ultrasonic transmitters emit a sound, such as a sequence of pings, that travels as a sound wave through the water until detected by an acoustic receiver (i.e., hydrophone). Passive acoustic monitoring and tracking in marine environments was developed based on these principles.

Initial passive acoustic monitoring designs included a small number of submerged, omnidirectional, multi-channel, independent receivers (Voegeli et al. 2001) deployed within a study area to detect the presence or absence of individuals "tagged" with an acoustic transmitter. This design has since developed such that smaller, single-channel, independent receivers can detect transmitter tags with unique acoustic signal codes that allow individual-based movement analyses (Voegeli et al 1998, Lacroix and Voegeli 2000). Passive monitoring offers a cost-effective method that allows both long-term monitoring and/or monitoring of many individuals in a specific study area. Other developments in acoustic telemetry include cable and radio-linked systems, in which single acoustic signals are detected at multiple receivers simultaneously, facilitating detection of fine-scale movements by hyperbolic positioning or triangulation (Cote et al. 1998, 2003). However, the expense and logistics of deploying multiple receivers and interconnected cables generally limits these systems to coverage of small areas (e.g. 0.05 km<sup>2</sup>, Cote et al. 2003).

Passive acoustic telemetry arrays have generally been deployed in one of two patterns. "Gates" or "curtains" of receivers can examine movement along a migration route (Finstad et al. 2005), in narrow geographic "bottlenecks" that create a directed path

(Walsh et al. 2012), or across bays and inlets to detect specific movements (Stark et al. 2005). Recent developments in acoustic technology have also led to deployments of receivers in arrays or grids to look at movement in a specific study region (e.g. Heupel et al. 2004; Abecassis et al. 2008, 2009; March et al. 2010, Alós et al. 2011, 2012; Marshall et al. 2011), such as a marine protected area (MPA, e.g. Egli and Babcock 2004). Importantly, passive acoustic systems do not provide fine-scale position estimates, but instead indicate whether a fish is within the tested detection range of the receiver (e.g. < 500 m). Positioning receivers in such a way that detection ranges overlap can provide more detail in long-term movement patterns (Heupel et al. 2006). However, precision can often be limited.

Passive acoustic telemetry enables a wide variety of behavioural and process-based studies, including residency (e.g. March et al. 2011), home range (e.g. Heupel et al. 2004), repeated movements (e.g. Marshel et al. 2011), habitat use (e.g. Espinoza et al. 2011), mortality estimates (e.g. Welch et al. 2004), emigration or dispersal rates (e.g. Finstad et al. 2005), or MPA effectiveness (e.g. Green and Starr et al. 2011). Evolving technology allows application of passive acoustic monitoring not only to a variety of fish and elasmobranchs, but also to different life stages within a species. For example, recent development of increasingly smaller tags - such as the Vemco™ V7 acoustic tags I used - allow tracking of fish as small as 15 cm SL (Standard Length). Examining movement patterns of different age classes can elucidate ontogenetic shifts in behavior that are often required to develop effective management and conservation policy in fisheries.

#### **1.4 Acoustic telemetry advantages and disadvantages**

Cost represents the most common disadvantage to using any current form of biotelemetry. Indeed, GPS collars cost between \$2000 - \$8000 each (Hebblewhite and Haydon 2010). Passive acoustic telemetry is comparatively more affordable - for example, Vemco V7 transmitter tags cost ~\$400 each. However, acoustic receivers cost between \$1500 each, which can limit the spatial extent and actual coverage in a study. Receivers are also labour-intensive to deploy and retrieve. Another disadvantage linked to higher cost is smaller sample sizes. Typically, reliable statistical inference for simple questions (i.e. 2 outcomes) requires tagging >20 individuals; smaller sample populations associated with biotelemetry work, particularly involving more complicated questions, can lead to poor population-level inference (Lindberg and Walker 2007). Specific disadvantages or limitations of passive acoustic telemetry include the initial labour investment in setting up the acoustic array, the need for individuals to remain within the executed hydrophone array in order for any data to accrue, and the inability to achieve metre level resolution without opting for more expensive radio-linked systems (Heupel et al. 2006). Large datasets resulting from fine-scale data collection can also create data management issues, such as preserving data integrity and consistency, avoidance of data redundancy, and data quality filtering and storage (Cagnacci et al. 2010). Relating fine-scale movements to coarser-scale assessments of resource availability and behaviour represents the most challenging limitation to biotelemetry (Hebblewhite and Haydon 2010). The difficulty in identifying patterns corresponding to specific behaviours is further compounded by scale-dependent differences in movements (Hebblewhite and Haydon 2010). The broad applicability and usage of passive acoustic telemetry constrain development of any standard analyses (Heupel et al. 2006).

Ecology is fundamentally spatial, and “movement is the glue that ties ecological processes together” (Cagnacci et al. 2010). Therefore, despite the limitations of passive acoustic telemetry, many studies embrace its advantages. Telemetry allows researchers to gather data on even very cryptic species and in areas unsafe for researchers (Heupel et al. 2006). It eliminates observer bias and allows simultaneous observations of multiple individuals for long periods of time. Passive acoustic telemetry also has the distinct advantage of data acquisition not requiring recapture of tagged individuals (Heupel et al. 2006). Biotelemetry has improved habitat modelling and conservation, increased understanding in the mechanisms of migration, and contributed to ecology knowledge (Hebblewhite and Haydon 2010), especially of vital ecological rates. These discoveries have helped conservation and management, and in some cases helped in assessing direct conservation impacts (Hebblewhite and Haydon 2010). Furthermore, biotelemetry aids in projecting the impacts of climate change on study organisms, an application that will prove increasingly necessary in the future (Hebblewhite and Haydon 2010). Ultimately, increasing our understanding of how and why animals move will provide insights into fitness consequences of movement or lack thereof. In short, biotelemetry represents the most viable current option for observing *in situ* movements of individuals.

### **1.5 Chapter Structure and Hypotheses**

In this thesis, I incorporate passive acoustic telemetry technology to document the dispersal and residency of age 1 Greenland cod in Newman Sound, Newfoundland. In Chapter 2, I investigate whether home range size differs among seasons, among transplanted and control (non-transplanted) fish, and among fish from two different source locations. In Chapter 3, I explore the dispersal of individuals in a single (2010-11)

and reciprocal (2011-12) transplant experimental design. Specifically, I test whether transplanted fish undertake larger movements than resident individuals, and whether these movements are consistent with a tendency towards homing ability. I conclude with Chapter 4, where I consider the implications of my results for both Greenland cod ecology and also for that of Atlantic cod of similar size. Juvenile Greenland cod are a proxy for juvenile Atlantic cod in that they exhibit very similar behaviours (e.g. Laurel et al. 2003), and are also subspecies of Pacific cod. Therefore, home range, site fidelity, and dispersal distance estimates of juvenile Greenland cod from my study will prove valuable for management and conservation beyond the area of my study in two separate oceans, and for two separate commercially exploited species.

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## **Co-authorship Statement**

### **Chapter 2: Home range of juvenile age 1 Greenland cod (*Gadus ogac*) in a Newfoundland fjord**

M. Shapiera designed the 2011-2012 reciprocal transplant experiment, collected data, performed the data analyses, and prepared the manuscript. R.S. Gregory designed the 2010-2011 single transplant experiment, contributed ideas, advised on data processing and analyses, and assisted with data collection. P.V.R. Snelgrove contributed ideas, and advised on data processing and analyses. All co-authors contributed to the editing of the manuscript.

### **Chapter 3: Site fidelity of transplanted age 1 Greenland cod in Newman Sound, Newfoundland**

M. Shapiera designed the 2011-2012 reciprocal transplant experiment, collected data, performed the data analyses, and prepared the manuscript. R.S. Gregory designed the 2010-2011 single transplant experiment, contributed ideas, advised on data processing and analyses, and assisted with data collection. P.V.R. Snelgrove contributed ideas, and advised on data processing and analyses. All co-authors contributed to the editing of the manuscript.

## **Chapter 2: Home range of juvenile age 1 Greenland cod (*Gadus ogac*) in a Newfoundland fjord**

### **2.1 Abstract**

I used recent improvements in acoustic transmitter technology to advance the limited knowledge on the home range extent of juvenile Greenland cod, *Gadus ogac*. Specifically, I tagged 84 individual age 1 Greenland cod in Newman Sound, Newfoundland over two years. I captured individuals from two different coves and released them in a single transplant design in October 2010 and a reciprocal transplant design in November 2011. I tracked individuals with a network of 26-32 hydrophones, and converted detection data to position estimates for calculation of seasonal home range areas. Mean seasonal home range areas during both tagging periods exceed those documented for age 2 Atlantic cod in other studies, suggesting a less established residency in age 1 of this congener species. Individual home range area varied considerably across individuals and over time in both study years. However, ANOVA analyses of the tagging periods identified season as the only significant predictor of home range size, with a general increase in home range from pre-winter to post-winter seasons, and no effect of fish capture or release location. Temperature and fish age/size both may have influenced increase in home range size over both study years. Knowledge of the home range size of age 1 cod is critical for understanding recruitment as well as for effective management and conservation efforts.

## 2.2 Introduction

Understanding the spatial and temporal ecology of wild populations is crucial for effective management and conservation efforts. In particular, individual home range size can inform reserve design or reveal potential anthropogenic effects in a geographic region. Home range size can be related to substrate use (Cote et al. 2003, 2004, Alós et al. 2011), habitat shape and boundaries (Topping et al. 2005), predation (Heupel et al. 2004), as well as behaviour and efficiency of movement (Cote et al. 2002). For marine fish in particular, home range area can give insight to population dispersal (Bradbury et al. 2008) or connectivity between nursery and adult habitats (Abecasis et al. 2009), and can help target areas most important to include in marine protected areas (Marshall et al. 2011). Knowledge of home range can be critical for designing effective monitoring programs for commercially or recreationally harvested species (Cote et al. 2003, Alós et al. 2011).

Home range area and movement patterns likely change with age, necessitating long-term or stage-specific studies in order to fully understand a population's dispersal dynamics. However, for some species such as Greenland cod, *Gadus ogac*, little research currently is published on individual movement at any life stage or spatial scale. Fortunately, extensive accounts have been published of its congener, Atlantic cod (*Gadus morhua*), which document the movements of that species over both space and time through mark-recapture methods (Laurel et al. 2003, 2004, Robichaud and Rose 2004) and acoustic telemetry (Cote et al. 2002, 2003, 2004, Lindholm et al. 2007). Results indicate no relationship between activity of age 2-3 Atlantic cod and temperature, but do link activity to substrate in some instances (Cote et al. 2002, 2003). Age 2-3 individuals move to deep water in late November in the area of Newman Sound, Newfoundland

(Cote et al. 2004). Acoustic telemetry methods showed that age 2-3 Atlantic cod home ranges span 6.0 ha on average (2.1 ha median) in late autumn and early winter (Cote et al. 2004). At age 0, both cod species prefer complex habitats such as eelgrass, *Zostera marina*, likely as a refuge from predation (Laurel et al. 2003), but this response is density-dependent (Laurel et al. 2004). Consequently, age 0-1 *Gadus* spp. are thought to have smaller distributions, with movements on the order of hundreds of metres (Sheppard 2005), and reported home range areas ranging from ~100 to thousands of m<sup>2</sup> (Tupper and Boutilier 1995, Laurel et al. 2004). No previously published studies have examined movement for age 1+ individuals of either species, largely due to logistical constraints and technological limitations. However, recent advances in acoustic telemetry technology have facilitated the opportunity to conduct individual-based age 1 movement studies.

Passive acoustic telemetry was developed to gather data for marine and aquatic species for long periods of time, without introducing direct observer bias. Usage distributions in a study area can be inferred by combining acoustic telemetry data with geographic information and statistical analyses. My goal was to estimate positions of tagged age 1 Greenland cod released in a single transplant (October 2010) and a reciprocal transplant design (November 2011), both of which included control, non-transplanted groups. I then generated home range estimates during pre-winter, winter, and post-winter seasons. Specifically, I set out to test three null hypotheses:

1. Seasonal home range sizes are similar in transplanted and non-transplanted fish.
2. Seasonal home range sizes are similar in fish collected from two different coves.
3. Home range sizes are similar across seasons.

Greenland cod has recently been identified as a subspecies of the commercially exploited Pacific cod, *Gadus macrocephalus* (Coulson et al. 2006). In addition, juvenile Greenland cod are a proxy for juvenile Atlantic cod in that they exhibit very similar behaviours (e.g. Laurel et al. 2003). Therefore, home range estimates of juvenile Greenland cod will prove valuable for management and conservation beyond the area of my study in two separate oceans and for two separate commercial fisheries.

## **2.3 Methods**

### **2.3.1 Study Site**

Newman Sound is a 41 km long by 1.5-3 km wide fjord of Bonavista Bay, Newfoundland, adjacent to Terra Nova National Park. A sill, which rises to a depth of 18 m, divides the sound into an inner and outer basin, with maximum depths of 55 m and >300 m, respectively. Eelgrass dominates the shallow subtidal vegetation, particularly on southern shores such as in Heffern's Cove (HC, Figure 2.1), a small (100-600 m wide by ~500 m long) cove in the outer sound. Mud and kelp (*Agarum cribrosum*) occur in the deepest areas of the cove and eelgrass dominates shallower (< 5 m) areas (Robert Gregory, unpublished data). Kelp and eelgrass also similarly dominate Buckley's Cove (BC, Figure 2.1), a ~300-600 m wide by 500m long, 20-m deep site located in the inner sound (Cote et al. 2002). Temperature loggers placed in HC and BC indicate mean daily water temperatures ranged from ~-0.3°C in mid-February 2011 to ~13.7°C in early August 2011, and -1.4°C in mid-February 2012 to 14.4°C in mid-August 2012. All tagged fishes for the single displacement and reciprocal transplant experiments were captured from HC and BC.

### **2.3.2 Hydrophone positioning**

In 2010, Fisheries and Oceans Canada deployed a network of Vemco™ hydrophones in Newman Sound, including 12 fixed-station VR2W hydrophones within Heffern's Cove and an additional 14 fixed-station far-field VR2 hydrophones throughout the sound for use in this study. Hydrophones are underwater receivers that detect a series of acoustic pings emitted from a transmitter within their range, decode the signal to indicate a unique ID code, and store the date, time and tag ID. All hydrophones have a tested detection radius of ca. 500 m, which may vary with environmental conditions, (Figure 2.2), and were positioned 1 m off the seafloor to optimize detection of cod. The VR2W near-field receivers include Bluetooth® wireless technology, with a 16MB memory, and were also used for a separate Vemco Positioning System, whereas the far-field VR2 receivers, with a 2MB memory, were positioned to capture larger-scale movements. On November 8-10, 2011, I deployed six additional VR2W receivers within Buckley's Cove to achieve higher resolution during the second year of this study. Data retrieval occurred on five occasions (December 2010, May 2011, November 2011, June 2012 and November 2012) when I recovered hydrophones and transferred data to a laptop computer for further analysis. Once data were downloaded, I then redeployed hydrophones at their original positions for further logging of tagged age 1 Greenland cod positions.

### **2.3.3 Tagging**

I captured 42 age 1 year old Greenland cod by beach seine in each of two years (October 2010 and November 2011) from Buckley's and Heffern's Coves. Individuals

were held in buckets of saltwater before Vemco Ltd™ V7 acoustic tags were surgically implanted in their body cavities. After I measured each fish, a transmitter was inserted into the body cavity through a small (~2 cm) incision off centre of the midline of the belly, halfway between the pelvic girdle and the anus; and then stitched closed with two sutures. Fresh seawater was circulated over the gills throughout the procedure, and only sterilized materials were used during surgery. The entire surgical procedure for each fish was conducted within 30 seconds. No anaesthetic was used during the procedure due to cod's high sensitivity in the field to common anaesthetics such as clove oil. Protocol for surgeries was approved through DFO (NAFC-2010-03). Fish were held for 24 hours before release in order to ensure tagged individuals were not showing ill effects from the tags or the tagging procedure.

Tags were held near a VR100 acoustic receiver prior to implantation. The VR100 generated an output audible to the human ear, verifying that individual tags were "active". V7 transmitters were 7 mm diameter, 18 mm long, and weighed 0.7 g in water and operate at a frequency of 69 kHz. Transmitters were factory coded to emit a sequence, consisting of six pings, , with an average  $240 \pm 70$  second delay between sequences. I randomized delay time to decrease the probability of a "collision" – i.e., overlap of sequence transmission among two or more tags – and to increase battery life and sample size. The sequence contained a unique identification number which was decoded and stored by each hydrophone which detected the transmission.

The study encompassed two separate experiments: a single displacement to HC on 8 October 2010, and a reciprocal transplant between the two coves on 9 and 23 November 2011. In 2010, we captured 21 fish from both HC and BC, and released all 42

tagged fish in HC. These fish were tracked until 9 November 2011. In 2011, on November 9 and 23, we captured 28 fish from BC and 14 from HC, releasing half of the fish in their cove of origin, and half in the other cove. These fish were tracked until 14 November 2012.

#### **2.3.4 Home range analyses**

I calculated position estimates over hourly time intervals (see Simpfendorfer et al. 2002) from receiver files, after eliminating spurious, single detections over the span of 24 hours for each fish with a single detection filter. I then used position estimates to calculate 95% kernel utilization distribution (KUD) areas, standardized by a Monte Carlo approach (Farrugia et al. 2011), across pre-winter, winter, and post-winter seasons for each year (see Appendix 1 for complete information on data processing and analyses). I considered position estimates up until one year after the tag activation date in the home range analyses. I modelled the seasonal home ranges for each year separately using GLM models in R software (R 2.14.1 software, R Development Core Team 2010). I examined transplant status (transplant vs. control) and season effects in the 2010 dataset. In the 2011 dataset, I examined cove of origin, transplant status and season effects. For each analysis of variance (ANOVA) performed on the models, the unbalanced design required type II SS analysis (see Appendix 1). I considered but subsequently rejected the use of non-parametric tests. Although data were not normally distributed, and did not meet ANOVA assumptions, I validated my ANOVA results using a randomization test for each year (1000 iterations of the ANOVA F statistics,  $\alpha < 0.05$ ).

#### **2.3.5 Standard length analyses**

To determine if initial standard length (SL) affected the number of days a fish was detected by receivers or the calculated seasonal home ranges, I calculated a series of linear regressions. Using SL as the independent variable, I calculated regressions predicting the tracking period, and pre-winter, winter, and post-winter home ranges using the *stats* package in R ( R 2.14.1 software, R Development Core Team 2010) for the 2010 and 2011 tagging periods.

## **2.4 Results**

### **2.4.1 Acoustic tracking**

Between 8 October 2010 and 9 November 2011, the remote receiver array detected 41 of the 42 tagged individuals (Table 2.1a) for periods ranging from 25 to 399 days. The majority were detected for <125 days (Figure 2.3). Clustering of position estimates for six cod within a 2500-5000 m<sup>2</sup> area suggests mortality of these particular individuals or tag loss during the first month at large during the 2010 experiment. Continued detection of these transmitters (29913, 29914, 29919, 29920, 29928 and 29947) strongly suggests that the transmitter sank to the bottom and continued to emit a signal following mortality or tag expulsion. Accordingly, the acoustic tracking summary and the home range analyses use only the first month of position estimates for these individuals.

Between 9 November 2011 and 14 November 2012, the receiver array detected 41 of 42 tagged individuals (Table 2.1b) for periods spanning 4 to 369 days. The majority were detected for <150 days (Figure 2.3). Clustering of position estimates for one cod (4951) within a 400m<sup>2</sup> area suggests mortality of this particular individual or tag loss

during the first month at large during the 2011 experiment. Continued signal emission strongly suggests the transmitter sank to the bottom and continued to emit a signal following mortality or tag expulsion. Consequently, the acoustic tracking summary and home range analyses use only the first month of position estimates for this individual.

#### **2.4.2 Home range analyses**

Where sufficient positions ( $N \geq 100$ ) were obtained, I estimated average home range size for each individual across seasons using a Monte Carlo standardized 95% KUD (Figure 2.4). For the 2010-2011 tagging period, pre-winter individual home range areas ranged from  $0.010 \pm 0.002 \text{ km}^2$  to  $3.705 \pm 1.395 \text{ km}^2$ , with a mean value of  $0.295 \text{ km}^2$ . Winter home range area spanned from  $0.017 \pm 0.006 \text{ km}^2$  to  $14.619 \pm 0.392 \text{ km}^2$ , with a mean value of  $1.455 \text{ km}^2$ . Post-winter home range area ranged from  $0.036 \pm 0.007 \text{ km}^2$  to  $8.425 \pm 1.502 \text{ km}^2$ , with a mean value of  $3.392 \text{ km}^2$ . Of the 41 fish detected, only pre-winter home range calculations were possible for 19 fish, and post-winter home range calculations were only possible for 7 fish. Initial ANOVA results suggested no significant effect of transplant status ( $F_{1,57}=0.165$ ,  $p=0.687$ ), or cove-by-season interaction ( $F_{2,56}=0.552$ ,  $p=0.579$ ), but a significant season effect on home range area ( $F_{2,56}=5.793$ ,  $p=0.005$ ). Randomization tests (1000 iterations) confirmed the significant season effect ( $p=0.015$ ). Visualization of the seasonal mean home ranges shows a general positive trend in home range size over time (Figure 2.5a); however, home ranges in 6 fish with sufficient position data for all 3 seasons showed substantial individual variation in this trend (Figure 2.6a).

In the 2011-2012 tagging period, pre-winter home ranges ranged from  $0.005 \pm 0.002 \text{ km}^2$  to  $6.303 \pm 0.336 \text{ km}^2$ , with a mean value of  $0.420 \text{ km}^2$ . Winter home ranges ranged from  $0.013 \pm 0.002 \text{ km}^2$  to  $6.610 \pm 0.285 \text{ km}^2$ , with a mean value of  $1.161 \text{ km}^2$ . Post-winter home ranges ranged from  $0.012 \pm 0.001 \text{ km}^2$  to  $5.283 \pm 0.374 \text{ km}^2$ , with a mean value of  $1.759 \text{ km}^2$ . Of the 41 fish detected, only pre-winter home range calculations were possible for 15 fish. Though 14 fish were detected into the post-winter season, 7 fish were only detected within the month of May. These fish were excluded from the post-winter seasonal home range group in the ANOVA analyses. However, comparisons of calculated May home range areas between the two years (N=5 for 2010 and N=7 for 2011) revealed similar mean monthly home range size, and large variability (Figure 2.7). Initial ANOVA results suggested a significant season effect on home range size ( $F_{2,65}=3.211$ ,  $p=0.048$ ), but no significant effects of cove of origin ( $F_{1,66}=0.048$ ,  $p=0.827$ ), transplant status ( $F_{1,66}=0.418$ ,  $p=0.521$ ), cove-by-transplant status interaction ( $F_{1,66}=0.639$ ,  $p=0.427$ ), cove-by-season interaction ( $F_{2,65}=1.268$ ,  $p=0.289$ ), transplant status-by-season interaction ( $F_{2,65}=0.216$ ,  $p=0.806$ ), and cove-by-transplant status-by-season interaction ( $F_{1,66}=0.014$ ,  $p=0.907$ ). Randomization tests (1000 iterations) confirmed the significant season effect ( $p=0.045$ ). Visualization of the seasonal mean home ranges suggested a general positive trend in home range size over time (Figure 2.5b), but as in the 2010 tagging experiment, individual fish with home range estimates for all 3 seasons (N=4) varied from this trend (Figure 2.6b).

#### **2.4.3 Standard length analyses**

During the 2010 tagging period, I observed no significant correlation between initial standard length and the tracking period ( $R^2=0.006$ ,  $t_{39}=0.470$ ,  $p=0.641$ ), pre-winter

95% KUD area ( $R^2=0.025$ ,  $t_{34}=-0.932$ ,  $p=0.358$ ), winter 95% KUD area ( $R^2=0.046$ ,  $t_{14}=-0.825$ ,  $p=0.423$ ) or post-winter 95% KUD area ( $R^2=0.036$ ,  $t_5=0.434$ ,  $p=0.682$ ). All fish were grouped together for home range regressions because no transplant status effect was found in the ANOVA analysis. Separate regressions for transplant and control fish with tracking period revealed no significant relationships.

During the 2011 tagging period, I observed no significant relationship between the initial standard length and either pre-winter 95% KUD area ( $R^2=0.009$ ,  $t_{35}=0.577$ ,  $p=0.568$ ), winter 95% KUD area ( $R^2=0.004$ ,  $t_{22}=0.299$ ,  $p=0.768$ ), or post-winter 95% KUD area ( $R^2=0.082$ ,  $t_5=0.287$ ,  $p=0.789$ ). However, linear regression indicated a significant positive relationship between initial standard length and tracking period ( $R^2=0.1808$ ,  $t_{39}=2.896$ ,  $p=0.0062$ ; Figure 2.8). Separate regressions for transplant status and cove of origin groups with tracking period revealed a significant relationship only for BC transplants ( $R^2=0.383$ ,  $t_{12}=2.735$ ,  $p=0.018$ , Figure 2.8).

## **2.5 Discussion**

This study is the first to quantify seasonal home range areas of individual age 1 cod. Results challenge previous assumptions of the relatively limited movement of this age class and species of cod. Passive acoustic tracking proved successful for this age class, with detections for 82 of 84 tagged individuals at some point in the hydrophone array over two experiment years. Previous studies documented home ranges (particularly 95% KUDs) for a variety of marine species (see Kramer and Chapman 1999 for review), including coral reef fish (Marshall et al. 2011, Topping and Szedlmayer 2011), fish associated with seagrasses (March et al. 2010, Alós et al. 2011), elasmobranchs (Espinoza et al. 2011, Farrugia et al. 2011), commercially fished species (Cote et al.

2003, 2004, Parsons et al. 2003, Topping et al. 2005, Bradbury et al. 2008, Alós et al. 2012), endangered species (Simpfendorfer et al. 2010), and juvenile sharks in nursery habitats (Rechisky and Wetherbee 2003, Heupel et al. 2004, Yesier et al. 2008). Typically, home range analysis focuses on species or life stages that show residency within a specific area, or species with relatively small home ranges. A partial review suggested that fish may limit their activity to a home range for increased efficiency in resource use, particularly feeding and refuge site use (Kramer and Chapman 1999). Some adult Atlantic cod populations are known to be relatively sedentary residents of coastal areas (Robichaud and Rose 2004, Neat et al. 2006), and Atlantic juvenile cod generally occur in the nearshore environment (Dalley and Anderson 1997, Anderson and Gregory 2000). In my study, home range areas ranged from 1000s m<sup>2</sup> to km<sup>2</sup>, indicating a dichotomy between fish that stayed resident, and fish that dispersed from release sites, though this dichotomy was not related to transplant status or cove of origin. For instance, some control and transplant fish dispersed in both years. In fact, home ranges surpassing 1 km<sup>2</sup> were equally evident in control and transplant fishes in the 2010 experiment (N=10), and near equally in the 2011 experiment (N=9). Home range and dispersal behaviour are likely linked, but there is a bias in data collection. Fish moving outside of the near-field arrays are less likely to be detected due to lower saturation of far-field hydrophones, and so there is a lower probability of acquiring sufficient positions for seasonal home range estimates. Thus there may be a bias towards home range estimates for residents, and dispersing fish that spend some time in both the near- and far-field arrays (which would increase position estimates for the individual). The dichotomy between residents and dispersers is somewhat seen in the home range frequency

distributions, but the larger home ranges may be underrepresented. However, the home ranges of dispersing individuals suggested larger movements and deviations from more sheltered, protected areas. Indeed, mean seasonal home range areas during both tagging periods exceed those documented for age 2 Atlantic cod (Cote et al. 2004, Bradbury et al. 2008). It is possible that age 1 cod represent a transition point where individuals become less strictly associated with complex habitat than age 0+ cod, but retain a less defined home range than the larger age 2-3 cod. Of the three initial hypotheses, namely that cod home range does not change with cove of origin, transplant status and season, I can reject only the last one. The area of the home ranges differed significantly over time, but not among fish from different coves, or among transplant and control fish.

Age 0 cod select shallow coastal waters to reduce predation risk, including cannibalism by conspecifics (Bogstad et al. 1994), by limiting encounter rates (Gotceitas et al. 1997, Grant and Brown 1998b, Linehan et al. 2001) and confining their movements to a few hundred to a few thousand metres (Grant and Brown 1998b, Laurel et al. 2004). However, as fish grow, predation risk usually declines (Miller et al. 1988, Paradis et al. 1996) and metabolic costs of remaining vigilant may be lowered (Lima and Dill 1990), making fish more willing to leave coastal nurseries to forage or explore open, previously more dangerous areas (Cote et al. 2003, 2004). Indeed, age 1+ Atlantic cod juveniles occur further from shore during the day, moving shoreward at night to feed on prey and younger conspecifics (Clark and Green 1990, Grant and Brown 1998ab). Age 1 Greenland cod likely follow a similar strategy as they grow larger. Although the significant season (time) effect on home range area in this study was consistent with such a hypothesis, I could not test it because individuals were never recaptured and re-

measured. However, initial standard length did not correlate significantly with seasonal home range sizes in either tagging period, suggesting that body size is not the only potential factor affecting home range size.

Age 1 Greenland cod in general used a relatively smaller area during the pre-winter season than in winter and post-winter seasons. However, there was large variation in the average area being used by the individuals from both coves within and across seasons. Certainly, the fish that had home range estimates for each season show several different trends in area used over time. Larger mean home range size observed for winter seasons in comparison to pre-winter reflects fish generally expanding their home range, perhaps moving into deeper and ice-free waters. The disappearance of the thermocline in the winter season could result in movements to deeper waters, as seen in age 2-3 Atlantic cod in mid-November (Cote et al. 2004). Likewise, when younger and smaller Atlantic cod in Norway were fitted with acoustic tags, they showed a preference for deeper waters in the winter season than in warmer spring and summer periods (Espeland et al. 2010). Juvenile Atlantic cod age 1-4 years in the southern Gulf of St. Lawrence moved to deeper waters >100m in winter as well (Hanson 1996). Conversely, Clark and Green (1991) found that age 3 cod from Conception Bay, Newfoundland, exhibited seasonal temperature preferences that were not explicitly linked to ambient temperature, but perhaps to an internal cycle. Growth and metabolism of Atlantic cod have been shown to fluctuate seasonally; for instance, in lower water temperatures, cod exhibit lower appetite (Levesque et al 2005), lower amino acid incorporation (Foster et al 1992), and increased use and subsequent decreases in liver lipid stores (Black and Lowe 1986, Lambert and Dutil 1997). In addition to temperature, decreases in the photoperiod during the winter

season are also linked with changes in internal hormone and metabolite concentration (Levesque et al 2005). Movement to deeper water in winter may hold physiological and/or energetic efficiency benefits similar to those seen in diel vertical migrations (Clark and Green 1991). It may also be a strategy to lower basal metabolic rates during a period of lower food conversion efficiency (Levesque et al. 2005) and prey availability, particularly if swim speeds remain the same from fall to winter (Cote et al. 2002). Adult Atlantic cod in the Gulf of St. Lawrence migrated in correlation to photoperiod changes, but time of migration was influenced by cooling bottom temperatures (Comeau et al. 2002). The influences of lower temperature and photoperiod on internal metabolism, and the resultant stasis in growth, could allow age 1 individuals to divert more energy towards exploratory movements during the winter season. In addition, a decrease in photoperiod could potentially limit visual predation on the still vulnerable age 1 class, allowing them to move further away from more sheltered habitats, such as eelgrass, which younger age classes actively choose for protection (Gotceitas et al. 1997, Renkawitz et al 2011).

During the post-winter season, individuals will have likely grown larger than at release, and therefore, may be less inhibited by predators. As well, as water temperatures rise and metabolism starts to increase after the winter period, individuals may be forced to search a wider area to acquire enough food to support a higher metabolic rate (Levesque et al. 2005). Furthermore, diel migration as a means of following prey and regulating metabolism (Lough et al. 1989, Clark and Green 1991, Espeland et al. 2010) may be influencing larger movements that result in larger home range size. For instance, occupying deeper, cooler, and thus metabolically less demanding water would decrease

the cost of digestion (Soofiani and Hawkins 1982), allowing for more resource allocation towards movement (Brown et al. 1989). Prey selection may also change during this time, in tandem with changing temperatures, photoperiod, and prey distributions. For instance, a shift to feeding on more mobile, larger prey may be occurring, in contrast to the higher proportion of small fish, mysids, and polychaetes eaten during colder periods (Morin et al. 1991). Feeding on larger prey may necessitate a higher degree of movement and area use by the growing cod juveniles in the post-winter period. Conversely, some individuals did not show an increase in home range area during the post-winter season. It is possible that these individuals occupied small areas that saw a large increase in productivity associated with the spring season; hence it would be more beneficial to stay and maximize growth benefits. Another possibility is that these individuals were in too poor condition to make larger movements; Comeau et al. (2002) and Cote et al. (2004) respectively suggested a link between an adult and juvenile Atlantic cod's condition and propensity to migrate.

A crude estimate of natural mortality can be inferred from cumulative distributions of individual tracking periods in both experiments. In general, 50% of the fish had tracking periods greater than 4-5 months, but by 6-7 months only 25-35% of fish were still being detected. This decline in detections is consistent with the natural mortality of age 1 Greenland cod in the wild (up to 1% daily; Sheppard 2005). It is possible that tagging surgeries may have resulted in early mortalities, but care was taken to select only fish which had attained sufficient size to ensure tags were <2% of total body weight. It is also possible that some tags could have been expelled, and disappeared from the array. Mortality estimates from this study are crude at best because the study

area was not entirely enclosed by the receiver network. Therefore, fish that stop being detected could have emigrated from the area. However, an examination of the last detections of all fish (see Appendix 2) indicated that only 1 fish during the first year (29944) and 3 fish during the second year (3974, 4936, and 4957) were last detected on the most eastern placed hydrophones on either the north or south shores. Of these fish, one from the year 2 study (3974) was detected on a hydrophone located ~15 km from the array (John Bratley, personal communication) on October 14, 2012, 5 months after it was last detected in the Newman Sound array. Thus, there is evidence that individuals are capable of emigrating out of the area, but that only a maximum of ~5% of the tagged fish did so. A significant relationship between initial standard length and tracking period was found only in the 2011 study. Separate linear regressions for each experimental group revealed that only BC transplants (N=14) exhibited a significant positive relationship. This relationship was largely driven by smaller (15.5-16.5cm) BC fish transplanted to HC had short tracking periods ( $\leq 70$  days), exhibiting early mortality, tag expulsion, or movement to an area with no acoustic coverage. In general, low variation in body size at tagging could explain the lack of effect of body size on home range area and/or tracking period.

Age 1 Greenland cod showed variability in home range size through both years of my study. Movements of this age class appear to be largely contained within the sound, but these movements increase as fish age and grow larger. Newman Sound is adjacent to Terra Nova National Park, which aside from a recreational fishing period offers protection for cod species living in the area. It is likely that a high proportion of the regular movements of this age class are contained within an area near the park that offers

protection. The stability of populations relies on the dispersal dynamics of the juvenile stage, and I have demonstrated that the dispersal range of age 1 Greenland cod is far greater than expected given the more limited home ranges of younger and older conspecifics. Home range area estimates from my study would serve as valuable biological parameters for management and/or conservation efforts (e.g. in designating an effectively-sized or structure marine protected area) for either Pacific or Atlantic cod. Specifically, given that juveniles of the congener Atlantic cod are found in the same area in Newfoundland, it would be beneficial to establish explicit protection for coastal marine environments such as Newman Sound. Further study on habitat associations is needed to most effectively provide protection for cod species and allow for maximum recruitment.

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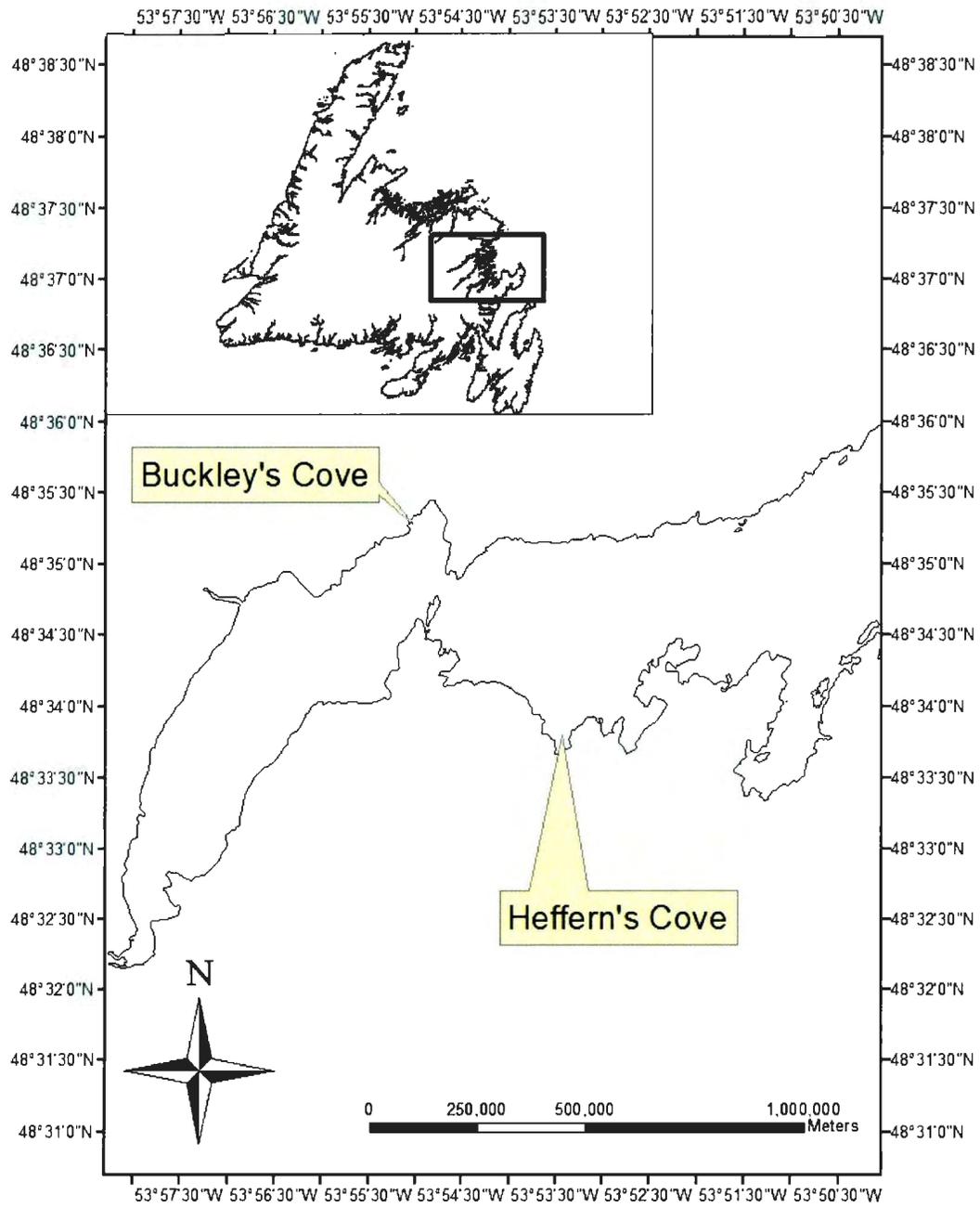


Figure 2.1. Map of Newman Sound, Newfoundland, indicating the positions of Heffern's Cove and Buckley's Cove. NAD 1983 UTM Zone 21 projection.

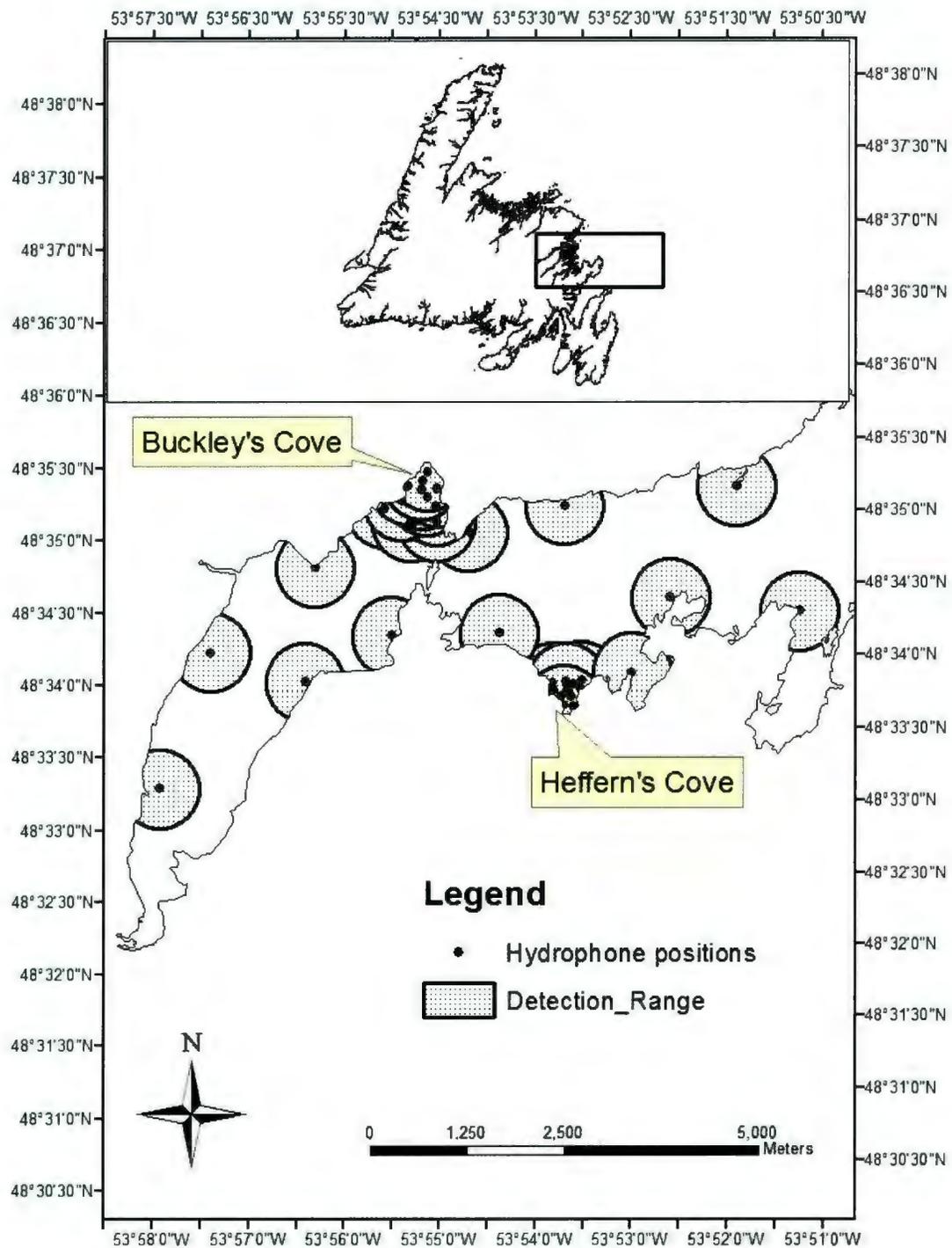


Figure 2.2. Positions and 500 m detection radii of the VR2/VR2W hydrophones deployed in Newman Sound, Newfoundland by November 2011. NAD 1983 UTM Zone 21 projection.

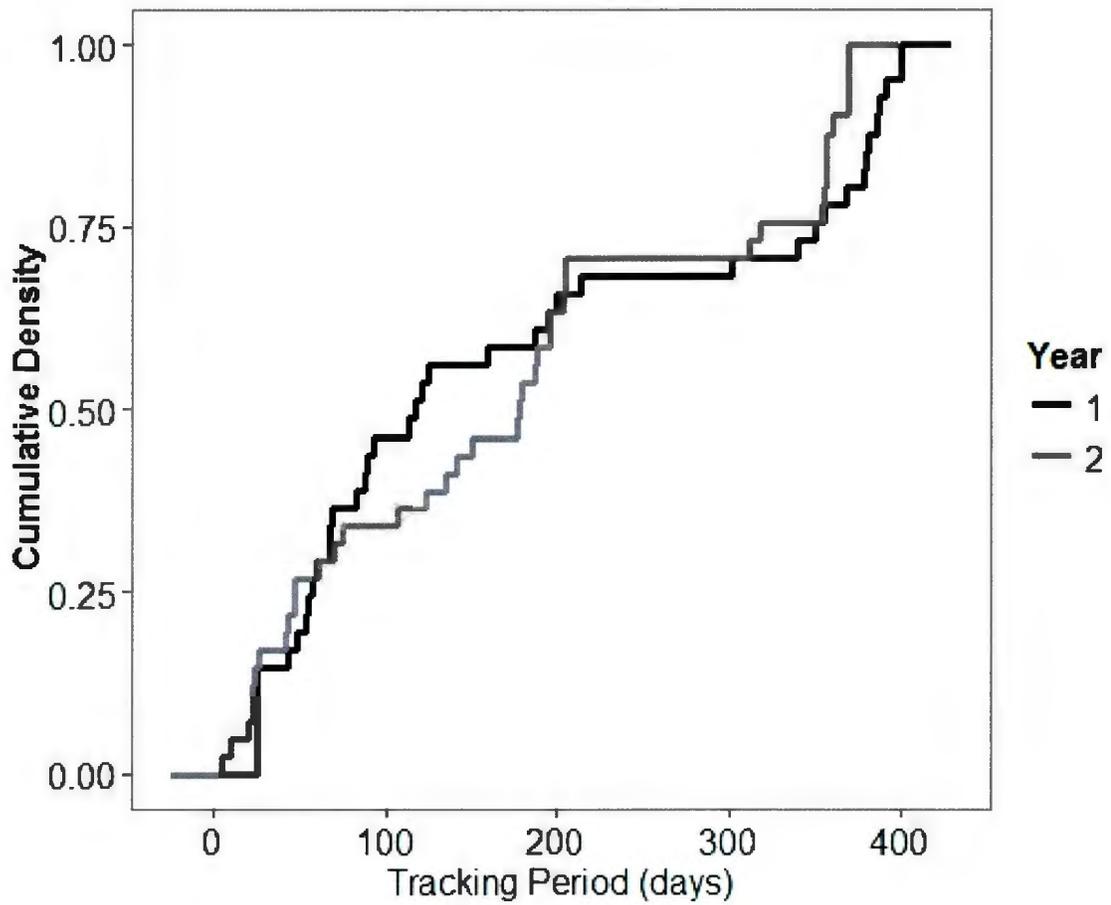


Figure 2.3. Cumulative density of the tracking periods of individual Greenland cod detected during the 2010-2011 (Year 1) and 2011-2012 (Year 2) tagging seasons.

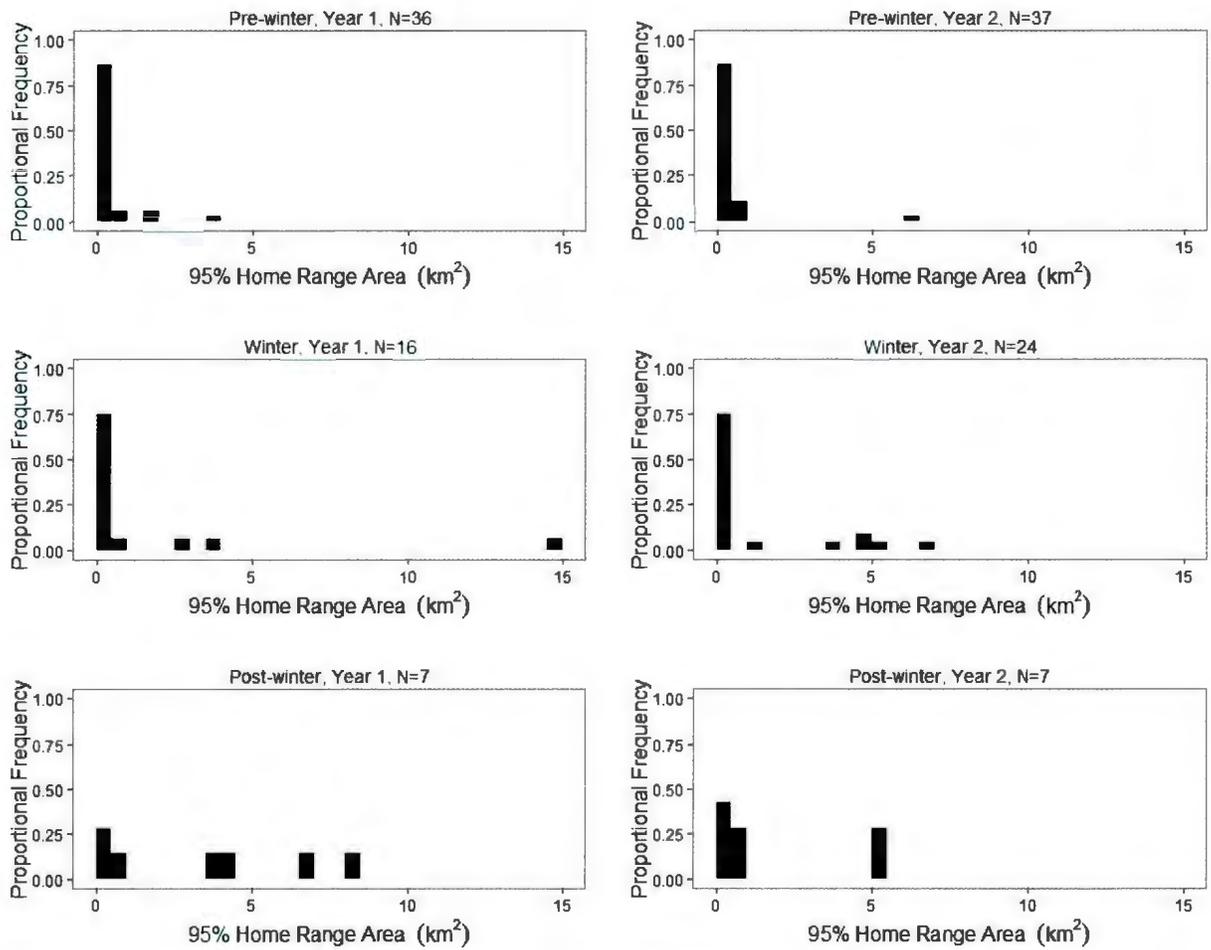


Figure 2.4. Proportional frequency distributions of seasonal home ranges. Panels on the left and right showcase home ranges from the 2010-2011, and 2011-2012 tagging seasons, respectively. Seasons and sample sizes are indicated above each panel.

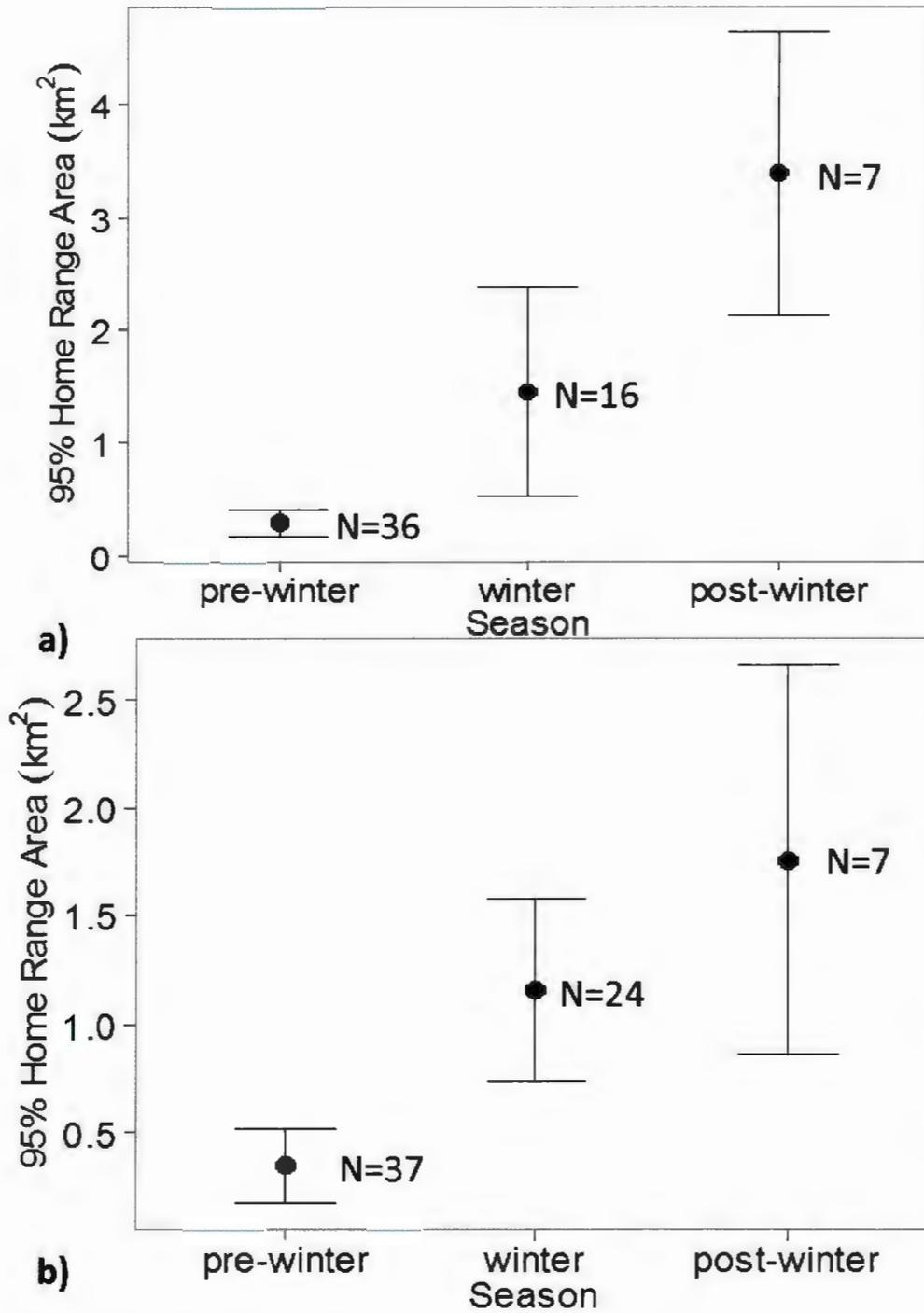


Figure 2.5. Seasonal mean home ranges for the a) 2010-2011 and b) 2011-2012 tagging periods. Error bars indicate one standard error.

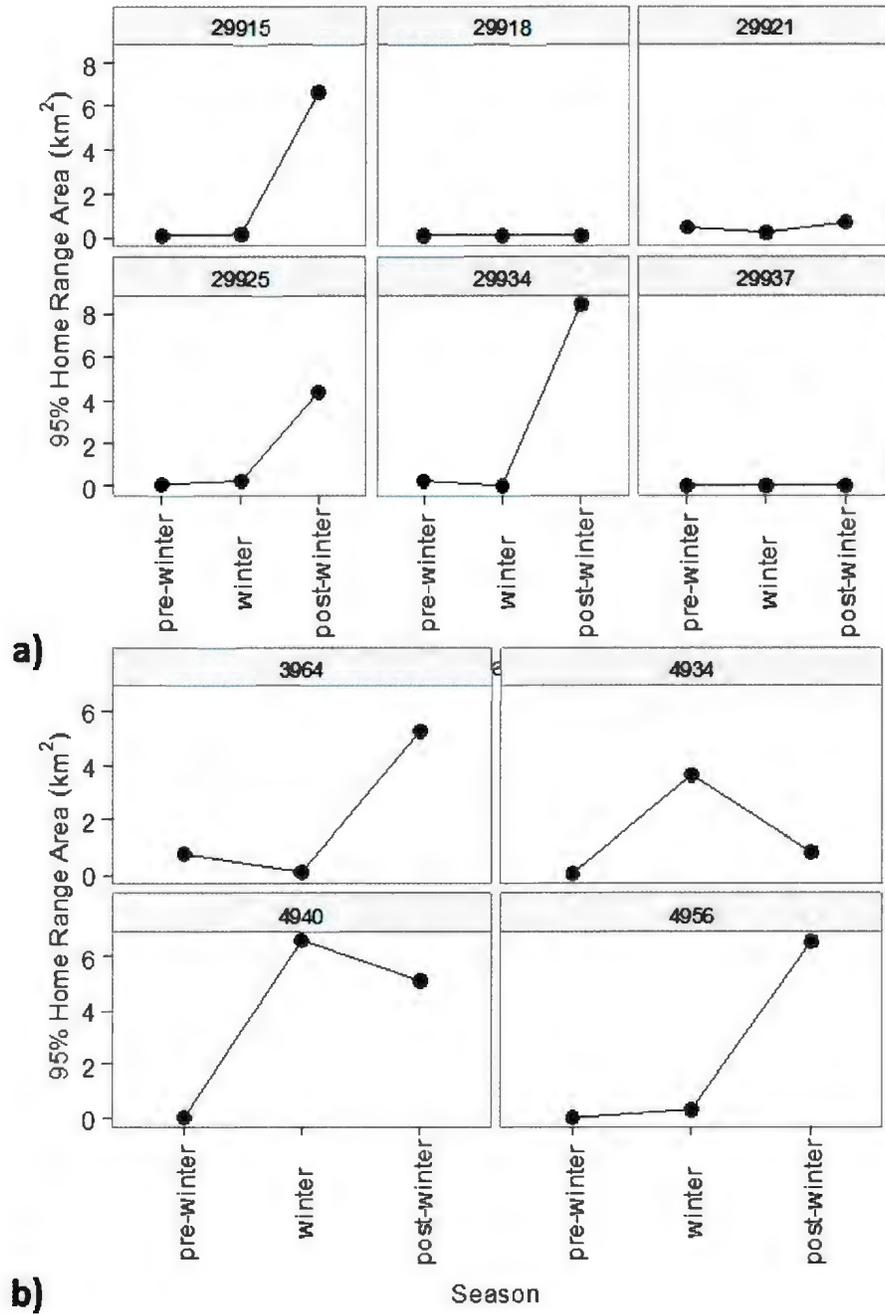


Figure 2.6. Home range areas of individual fish with sufficient numbers of positions for all three season calculations during the a) 2010-2011 and b) 2011-2012 tagging season. Tag IDs are indicated on top of each facet plot.

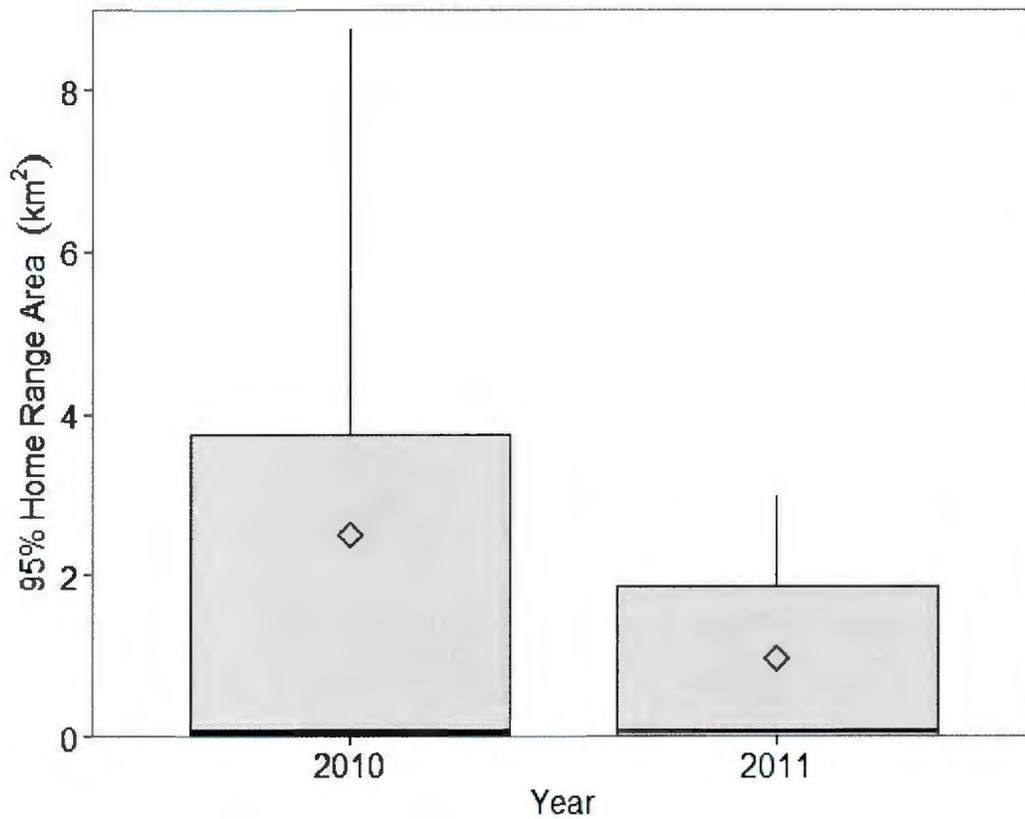


Figure 2.7. Boxplots of home range areas calculated solely for the month of May during both experiment years. Diamonds indicate group means. Solid black lines indicate median home range area values. Inter-quartile ranges are represented as the vertical length of each box. Solid lines extend to the maximum values.

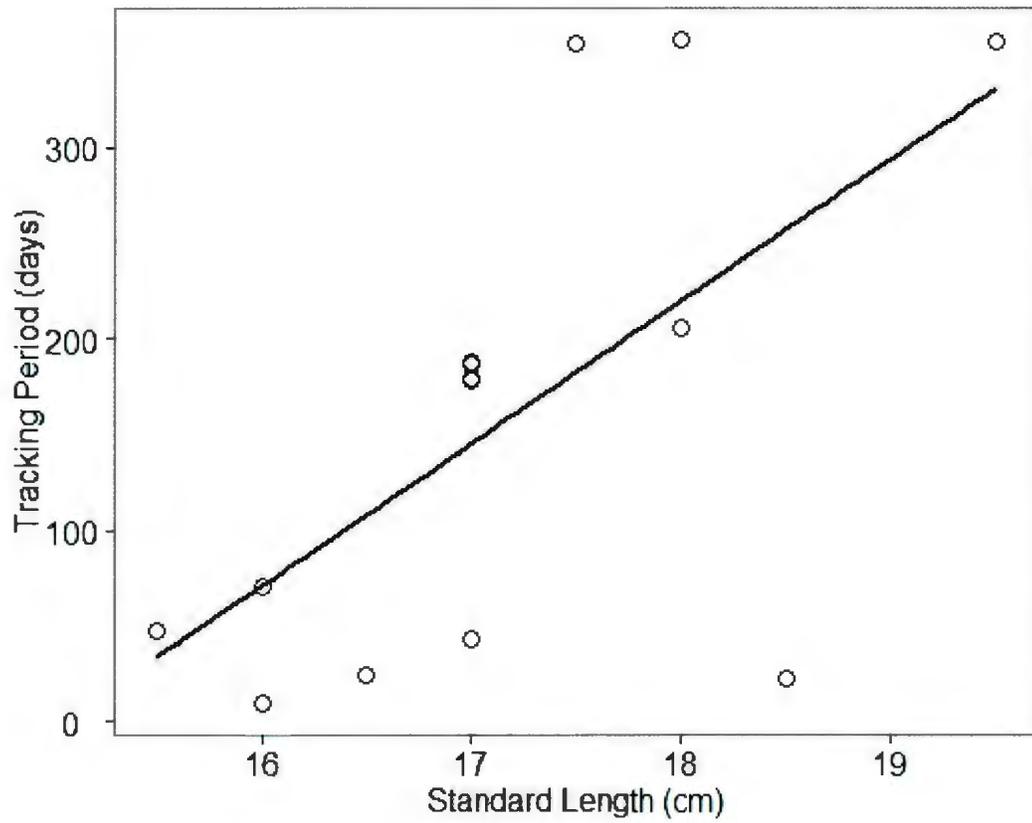


Figure 2.8. Scatterplot of initial standard length (cm) and tracking period (days) for the transplanted fish from Buckley's Cove in the 2011-2012 season. The black line represents the fitted linear model: Tracking period = -1118 + 74.3\*Standard length.

Table 2.1a. Summary of detection data for the 2010-2011 tagging season. HC= Heffern's Cove, BC= Buckley's Cove. Fish that likely exhibited early mortality denoted by EM.

| Tag ID | SL (cm) | Cove of Origin | Tracking Period | Days Detected | Last day detected |
|--------|---------|----------------|-----------------|---------------|-------------------|
| 29912  | 14      | HC             | 117             | 19            | 31/01/2011        |
| 29913  | 16      | HC             | EM              | EM            | 08/11/2011        |
| 29914  | 15      | HC             | EM              | EM            | 09/11/2011        |
| 29915  | 16      | HC             | 340             | 154           | 11/09/2011        |
| 29916  | 16      | HC             | 67              | 43            | 12/12/2010        |
| 29917  | 15.5    | HC             | 355             | 24            | 26/09/2011        |
| 29918  | 16.5    | HC             | 399             | 399           | 09/11/2011        |
| 29919  | 15.5    | HC             | EM              | EM            | 08/11/2011        |
| 29920  | 15      | HC             | EM              | EM            | 08/11/2011        |
| 29921  | 16.5    | HC             | 379             | 302           | 20/10/2011        |
| 29922  | 17      | HC             | 187             | 25            | 11/04/2011        |
| 29923  | 17      | HC             | 67              | 66            | 12/12/2010        |
| 29924  | 16      | HC             | 301             | 122           | 03/08/2011        |
| 29925  | 15      | HC             | 378             | 199           | 19/10/2011        |
| 29926  | 16.5    | HC             | 124             | 110           | 07/02/2011        |
| 29927  | 15.5    | HC             | 159             | 70            | 14/03/2011        |
| 29928  | 16      | HC             | EM              | EM            | 09/11/2011        |
| 29929  | 16.5    | HC             | 380             | 65            | 21/10/2011        |
| 29930  | 15.5    | HC             | 113             | 11            | 27/01/2011        |
| 29931  | 16.5    | HC             | 194             | 194           | 18/04/2011        |
| 29932  | 16      | HC             | 399             | 397           | 09/11/2011        |

Table 2.1a continued. Summary of detection data for the 2010-2011 tagging season. HC= Heffern's Cove, BC= Buckley's Cove.

| Tag ID | SL (cm) | Cove of Origin | Tracking Period | Days Detected | Last day detected |
|--------|---------|----------------|-----------------|---------------|-------------------|
| 29933  | 18      | BC             | 387             | 50            | 28/10/2011        |
| 29934  | 17      | BC             | 391             | 280           | 01/11/2011        |
| 29935  | 17      | BC             | 59              | 22            | 04/12/2010        |
| 29936  | 17.5    | BC             | 43              | 43            | 18/11/2010        |
| 29937  | 16      | BC             | 350             | 321           | 21/09/2011        |
| 29938  | 17      | BC             | 57              | 9             | 02/12/2010        |
| 29939  | 17      | BC             | 121             | 121           | 04/02/2011        |
| 29940  | 17.5    | BC             | 68              | 68            | 13/12/2010        |
| 29941  | 16      | BC             | 88              | 58            | 02/01/2011        |
| 29942  | 16      | BC             | 214             | 11            | 08/05/2011        |
| 29943  | 16.5    | BC             | 386             | 331           | 27/10/2011        |
| 29944  | 16.5    | BC             | 82              | 50            | 27/12/2010        |
| 29945  | 16      | BC             | 54              | 30            | 29/11/2010        |
| 29946  | 17      | BC             | 368             | 171           | 09/10/2011        |
| 29947  | 17.5    | BC             | EM              | EM            | 09/11/2011        |
| 29948  | 19      | BC             | 92              | 89            | 06/01/2011        |
| 29949  | 17      | BC             | 199             | 14            | 23/04/2011        |
| 29950  | 16      | BC             | 89              | 86            | 03/01/2011        |
| 29951  | 15      | BC             | 48              | 15            | 23/11/2010        |
| 29952  | 15.5    | BC             | 0               | 0             | NA                |
| 29953  | 18.5    | BC             | 53              | 22            | 28/11/2010        |

Table 2.1b. Summary of detection data for the 2011-2012 tagging season. HC= Heffern's Cove, BC= Buckley's Cove.

| Tag ID | Release Date | SL (cm) | Cove of Origin | Transplant or Control | Tracking Period | Days Detected | Last day detected |
|--------|--------------|---------|----------------|-----------------------|-----------------|---------------|-------------------|
| 3962   | 23/11/2011   | 15.5    | BC             | Transplant            | 47              | 47            | 08/01/2012        |
| 3963   | 23/11/2011   | 17      | BC             | Control               | 356             | 184           | 14/11/2012        |
| 3964   | 23/11/2011   | 18      | BC             | Transplant            | 356             | 356           | 14/11/2012        |
| 3965   | 23/11/2011   | 17      | BC             | Transplant            | 43              | 7             | 04/01/2012        |
| 3966   | 23/11/2011   | 19.5    | BC             | Transplant            | 355             | 352           | 13/11/2012        |
| 3967   | 23/11/2011   |         | BC             | Control               | 312             | 93            | 01/10/2012        |
| 3968   | 23/11/2011   | 16      | BC             | Transplant            | 70              | 16            | 31/01/2012        |
| 3969   | 23/11/2011   | 18      | BC             | Transplant            | 205             | 186           | 14/06/2012        |
| 3970   | 23/11/2011   | 16      | BC             | Control               | 26              | 25            | 18/12/2011        |
| 3971   | 23/11/2011   | 18      | BC             | Control               | 356             | 71            | 14/11/2012        |
| 3972   | 23/11/2011   | 16.5    | BC             | Control               | 41              | 41            | 02/01/2012        |
| 3973   | 23/11/2011   | 18      | BC             | Control               | 75              | 70            | 05/02/2012        |
| 3974   | 23/11/2011   | 17      | BC             | Transplant            | 178             | 154           | 18/05/2012        |
| 3975   | 23/11/2011   | 17      | BC             | Control               | 61              | 61            | 22/01/2012        |
| 4934   | 09/11/2011   | 15      | BC             | Control               | 369             | 318           | 14/11/2012        |
| 4935   | 09/11/2011   | 16      | BC             | Transplant            | 10              | 9             | 18/11/2011        |
| 4936   | 09/11/2011   | 15.5    | BC             | Control               | 176             | 171           | 02/05/2012        |
| 4937   | 09/11/2011   | 17      | BC             | Transplant            | 179             | 163           | 05/05/2012        |
| 4938   | 09/11/2011   | 17.5    | BC             | Control               | 205             | 184           | 31/05/2012        |
| 4939   | 09/11/2011   | 18.5    | BC             | Transplant            | 22              | 22            | 30/11/2011        |
| 4940   | 09/11/2011   | 20      | BC             | Control               | 369             | 312           | 13/11/2012        |

Table 2.1b continued. Summary of detection data for the 2011-2012 tagging season. HC= Heffern's Cove, BC= Buckley's Cove. Fish that likely exhibited early mortality denoted by EM.

| Tag ID | Release Date | SL (cm) | Cove of Origin | Transplant or Control | Tracking Period | Days Detected | Last day detected |
|--------|--------------|---------|----------------|-----------------------|-----------------|---------------|-------------------|
| 4942   | 09/11/2011   | 16      | BC             | Control               | 135             | 41            | 22/03/2012        |
| 4943   | 09/11/2011   | 17.5    | BC             | Transplant            | 354             | 134           | 29/10/2012        |
| 4944   | 09/11/2011   | 17      | BC             | Control               | 107             | 92            | 23/02/2012        |
| 4945   | 09/11/2011   | 16.5    | BC             | Transplant            | 24              | 7             | 02/12/2011        |
| 4946   | 09/11/2011   | 16.5    | BC             | Control               | 20              | 20            | 28/11/2011        |
| 4947   | 09/11/2011   | 17      | BC             | Transplant            | 187             | 95            | 13/05/2012        |
| 4948   | 09/11/2011   | 17      | HC             | Transplant            | 203             | 48            | 29/05/2012        |
| 4949   | 09/11/2011   | 15      | HC             | Transplant            | 123             | 7             | 10/03/2012        |
| 4950   | 09/11/2011   | 17.5    | HC             | Control               | 360             | 93            | 04/11/2012        |
| 4951   | 09/11/2011   | 17      | HC             | Control               | EM              | EM            | 18/06/2012        |
| 4952   | 09/11/2011   | 15      | HC             | Transplant            | 150             | 39            | 06/04/2012        |
| 4953   | 09/11/2011   | 19.5    | HC             | Control               | 141             | 7             | 28/03/2012        |
| 4954   | 09/11/2011   | 19      | HC             | Transplant            | 195             | 18            | 21/05/2012        |
| 4955   | 09/11/2011   | 18      | HC             | Control               | 369             | 82            | 14/11/2012        |
| 4956   | 09/11/2011   | 20      | HC             | Control               | 369             | 334           | 13/11/2012        |
| 4957   | 09/11/2011   | 18      | HC             | Transplant            | 195             | 121           | 21/05/2012        |
| 4958   | 09/11/2011   | 16.5    | HC             | Transplant            | 0               | 0             | NA                |
| 4959   | 09/11/2011   | 18      | HC             | Control               | 318             | 271           | 22/09/2012        |
| 4960   | 09/11/2011   | 17.5    | HC             | Transplant            | 47              | 42            | 25/12/2011        |
| 4961   | 09/11/2011   | 17      | HC             | Control               | 4               | 4             | 12/11/2011        |

## **Chapter 3: Site fidelity of transplanted age 1 Greenland cod in Newman Sound, Newfoundland**

### **3.1 Abstract**

My study documented movement of 84 tagged age 1 Greenland cod (*Gadus ogac*) in Newman Sound, Newfoundland, from October 2010 to November 2012. Individuals were captured from two coves and released in a single (N=42, 2010) and in a reciprocal (N=42, 2011) transplant design. A network of 26-32 hydrophones tracked the movement of fish at the release sites and throughout the Sound. Many fish, particularly transplants, moved on a km scale, representing far greater distances than previously presumed, particularly during late fall, early spring, and July of both experiment years. I observed a behavioural dichotomy in both years, with some fish (40% in 2010-11 and 28% in 2011-12) remaining in their cove of release for the entire tagging period (“residents”), and the other individuals moving away to other areas (“dispersers”). Greater proportions of control fish (individuals tagged and released at their capture location) remained resident compared to transplant fish in both experiments. However, not all transplanted dispersers travelled back to their source cove. Indeed, similar proportions of control and transplant fish visited opposite source coves, suggesting low site fidelity and/or low homing initiative in the sample population. Factors affecting dispersal tendency such as spatial cognition, predation, and temperature likely differ in importance across individuals given the large variability in movement. The perpetuity of a population depends on the dispersal dynamics of the juvenile cohort, and my study indicates the dispersal range of age 1 Greenland cod is far larger and varied than previously assumed.

### 3.2 Introduction

The distribution and movement of organisms and populations resides at the core of ecology. Spatial ecology - the understanding of the spatial structure of populations - rivals population demographics and metapopulation dynamics in importance (Hanski 1998). In ecosystems, the landscape interacts with the biology of organisms to influence how they disperse within it, a process referred to as functional connectivity (Crooks and Sanjayan 2006). Dispersal, the process by which living organisms expand the space where they live, not only determines the range of a species or population, but also affects its capacity to respond to changing environmental conditions (Cote et al. 2010). Movement of individuals can affect gene flow (Bohonak 1999), metapopulation dynamics (Hanski 1998), as well as management applications such as functioning of marine protected areas (Grüss et al. 2011). However, the decision to disperse from a currently occupied area includes energetic and risk costs to individuals that vary across space and time (Bowler and Benton 2005).

Metapopulation theory links dispersal with landscapes, under the premise that migration connects a network of habitat patches in which a species occurs in local populations (Hanski 1998). Initially, this theory revolved around the idea of idealized habitat patches. However, researchers now recognize sometimes weak matches between environment and species' distribution, and looser links than previously assumed. Therefore, ideas of functional connectivity are more complex than initially envisaged. In particular, Pulliam's (1988) idea of "source" populations (those with high reproductive output, productivity and habitat quality) and "sink" populations (those with low reproductive output, productivity and poor habitat quality) initially became prevalent.

But Kristan's (2003) idea of ecological traps, or poor-quality habitats that attract individuals, indicates that source-sink dynamics and habitat quality links are not always straightforward. There is a potential dichotomy within a metapopulation of individuals that choose to disperse versus those that choose to stay in their natal patch. Simple metapopulation models of the development of evolutionarily stable dispersal behaviour often operate on the assumption that the product of the probability of an individual surviving a time interval, and the fitness of an individual given survival, must be equal between dispersers and residents (Hamilton and May 1977, Ronce et al. 2000).

Seemingly, mortality risks associated with dispersal balance the benefits of dispersing to a nearby population. However, current condition may affect an individual's decision to disperse, resulting in changing resident/disperser dynamics. In addition to directed movements in the form of emigration and immigration, individuals can also become lost (vagrants) from their natal areas – i.e. the “member-vagrant” hypothesis of Sinclair and Iles (1989). In addition, individuals in specific age classes may experience natal homing (e.g. Dittman and Quinn 1996, Neat et al. 2006), affecting demographic membership in a population.

Spatial learning in fish is thought to be controlled by the telencephalon in teleost fishes (Broglia et al. 2003). The costs of learning for a fish include making mistakes, the energetic costs of processing the information, and, perhaps most importantly with regards to this study, increased juvenile vulnerability (Johnston 1982). However, the benefits of keeping track of location and orientating, other than for homing purposes, are numerous. For instance, food availability changes over space and time, and if those changes are predictable, foraging efficiency will increase if fish have learned the spatial locations of

the best prey patches (Hughes and Blight 2000). Furthermore, memory and learning may allow vulnerable juveniles to avoid high predator density habitats (Brown et al 2003), and to know the locations of shelters for future use, thus actually decreasing vulnerability. The energetic and fitness costs to learning likely mean that ecological demand structures the type of learning involved (Odling-Smee and Braithwaite 2008). Spatial learning is likely more important in populations or individuals that remain within a familiar area all their lives (Dodson 1988) or live in stable habitats (Odling-Smee and Braithwaite 2003a). Whether or not the mechanism behind spatial learning is the use of critical distance (Bovet 1987), landmarks, compass orientation, inertial guidance, and/or social cues likely varies with specific environmental factors and ecology of the species (Odling-Smee and Braithwaite 2003ab, 2008). Transplant studies provide an opportunity to examine whether individuals navigate back to a source location, implying some form of spatial learning and/or homing ability and initiative.

Ontogenetic changes in dispersal behaviour are likely the norm, not the exception. Knowledge of juvenile dispersal, though inherently lacking in most species, is necessary to effectively manage and conserve species and populations. For example, among marine fish, post-larval individuals' realized dispersal will be determined by mortality during dispersal, potential range of dispersal, and site fidelity (often linked to risk of predation or patch value). All contribute to the resilience and stability of a given population. Estimating dispersal distances of early life stages is particularly difficult in marine ecology (Halpern and Warner 2003).

Recent advances in acoustic telemetry allowed me to tag Greenland cod (*Gadus ogac*) individuals as young as 1 year old. My study aimed to quantify individual dispersal

distances of juvenile Greenland cod and examine site fidelity using passive acoustic telemetry. Individual age 1 cod were captured and released in the same location, or alternatively were captured then released in a location approximately 3.5 km away. High site fidelity was defined as an individual remaining in the cove of release for the duration of the tagging experiment. My initial null hypotheses were:

1. Individuals exhibit very short distance movements, on the order of a few 100 m, similar to age 0+ *Gadus* spp. (e.g., Sheppard 2005).
2. Transplanted and control fish will exhibit similar dispersal distances and patterns.

### **3.3 Methods**

#### **3.3.1 Hydrophone positioning**

I deployed an acoustic hydrophone network to capture the fine (~5 m) and course scale (~0.5-1.0 km) coastal movements of individual age 1 cod. A “near-field” array of 12 fixed-station VR2W (Vemco Ltd™) hydrophones was deployed in Heffern’s Cove in 2010, along with a “far-field” array of 14 fixed-station VR2 (Vemco Ltd™) hydrophones throughout Newman Sound (Figure 3.1, see Appendix 1 for details). All hydrophones have a tested detection radius of ca. 500 m (Figure 3.1). On 8-10 November, 2011, I deployed six additional VR2W receivers within Buckley’s Cove to achieve higher resolution at this release site during 2011-12. Hydrophones in far-field array were positioned to maximize coverage throughout the sound by placing them ~1 km from each other, targeting coastal areas that were the assumed preference of the individuals (e.g. Sheppard 2005). These coastal areas were targeted further with the near-field array arrangement.

### **3.3.2 Experimental Design**

To investigate dispersal and residency in age 1 Greenland cod, I carried out two tagging experiments in Newman Sound, one from 8 October 2010 to 8 November 2011 and the other from 9 November 2011 to 14 November 2012. In October 2010, I collaborated with other scientists from Fisheries and Oceans Canada to capture 42 age 1 individuals, 21 from Buckley's Cove (BC) and 21 from Heffern's Cove (HC), and released them in HC (Figure 3.2a, see Chapter 3 for details of the tagging procedure). On 9 November 2011, I captured 28 additional fish, again half from each of the two study coves. However, in this experiment, I followed a reciprocal transplant design after performing tagging surgeries, releasing half of the HC fish into BC, and half of the BC fish into HC. The remaining ("control") individuals were released close to their capture location (Figure 3.2b). I supplemented this experiment with 14 more individuals, captured on 23 November 2011 in BC, and released half in both coves. These designs allowed me to examine potential homing behaviour, differences in dispersal between two areas, and overall dispersal of the tagged individuals.

### **3.3.3 Least Cost Path Analysis**

I initially processed the hydrophone data (see Appendix 1) to obtain position estimates for each individual. The minimum resolution of hydrophone positions in the far-field array used in this study was 500 m. Estimating positions using a weighted mean approach over a certain time interval results in a location estimate rather than simply a presence within a receiver's range. To link these positions temporally, I carried out "least cost path" analyses for individual fish using ArcGIS and R software (see Appendix 1).

Least cost paths allowed characterization of basic movement so fish could be grouped as either "resident" in cove of release, "visitors" to the opposite cove, or "dispersing" to completely new areas. I also determined how many stations (defined as the far-field array stations plus one station each for the near-field arrays) each fish visited. Using ArcGIS, I determined the distance of each step length of the least cost paths, which allowed differentiation between larger and smaller movements. "Large" movements were defined as any movement >800 m, which was approximately the shortest distance between any two far-field hydrophones. I filtered out small movements from the dataset using R software to examine these large movements more closely. The number of fish associated with large movements was plotted against a monthly time line to indicate potential times of the year where dispersal was highest, and whether there were differences between transplant and control individuals, or among fish from the two source coves.

### **3.3.4 Standard Length and Behaviour Analyses**

I investigated potential differences in initial standard length between resident and dispersing fish using a two-sample t test for each experiment year separately. To investigate potential differences in behaviours among experimental groups, I used a Pearson's chi-squared test for each experiment separately. In the year 1 single transplant experiment, I evaluated the response variable behaviour (resident, visited opposite cove, dispersed elsewhere) across two treatment groups (control and transplant). In the year 2 reciprocal transplant, the same three behaviour variables were compared among four treatment groups (BC control, BC transplant, HC control, and HC transplant). The null hypothesis for each test was equal proportions of behaviours across all treatment groups, i.e. that behaviour is independent of treatment group. As a result of low sample size,

some treatment groups included <5 fish, and results were therefore evaluated further using a randomization test for each year (1000 iterations of the chi-squared test following randomization,  $\alpha < 0.05$ ). A separate chi-squared analysis for year 2 pooled the fish into only transplant and control groups.

### **3.4 Results**

#### **3.4.1 Acoustic Tracking and Residency**

A total of 82 individuals of the 84 tagged fish were detected at some point in the hydrophone array (Figure 3.3, see Table 2.1ab) during the two-year study. Six fish in experiment 1 (29913, 29914, 29919, 29920, 29928 and 29947), and one fish in experiment 2 (4951) exhibited signs of early mortality or tag loss, within the first month, as evidenced by the extreme clustering of tag positions. These fish were not included in movement analyses. Individuals were detected by between 1-12 far-field stations (Figure 3.4.)

#### **3.4.2 Movement patterns and behaviour analyses**

Movement patterns by individual fish were variable (see Appendix 2). Excluding early mortalities, 40% of fish in year 1 and 28% in year 2 remained resident (Figure 3.5). We found no significant differences in initial standard length between resident and dispersing fish in year 1 ( $t=0.529$ ,  $df=39$ ,  $p=0.60$ ) or in year 2 ( $t=1.10$ ,  $df=38$ ,  $p=0.23$ ). Chi-squared analyses indicated that proportions of fish exhibiting the specific movement behaviours (residency, visiting the opposite cove, or dispersing elsewhere) were independent of treatment groups in both year 1 ( $X^2=1.444$ ,  $df=2$ ,  $p=0.486$ ) and year 2 ( $X^2=7.090$ ,  $df=6$ ,  $p=0.313$ ). Randomization tests confirmed these results (1000 iterations

each,  $p_{\text{year1}}=0.428$ ,  $p_{\text{year2}}=0.320$ ). No significant differences in behaviour proportions between treatment groups were found when fish in year 2 were pooled into transplant status (i.e. transplanted vs. control) groups ( $X^2=1.210$ ,  $df=2$ ,  $p=0.546$ ), again confirmed by randomizations ( $p=0.600$ ). Therefore, similar proportions of control and transplant fish remained resident in both years. All control residents in year 1 were originally from HC (N=7), whereas in year 2, more control residents were from BC (N=6) compared to HC (N=1). Similar proportions of control individuals (38%, N=6) and transplant (26%, N=5) visited the opposite source location (BC) in year 1 (Figure 3.6). Similar proportions of control individuals (25%, N=5), and transplant individuals (35%, N=7) visited the opposite source location from their release in year 2 as well. Additionally in year 2, 67% of fish visiting the opposite cove were originally from BC (N=8), while 33% were originally from HC (N=4; Figure 3.7). Other individuals left their cove of release, but travelled to areas other than the opposite cove (Figure 3.5). Of these dispersing individuals, 70% (N=7) in year 1, and 53% (N=9) in year 2 were transplants. Though some control and transplant individuals visited the opposite source cove (Figure 3.5), only a portion remained once reaching that site. In fact, no individuals from year 1 remained in the opposite source cove once they reached it, rather, they continued dispersing elsewhere (N=8) or returned to their initial cove of release (N=3; Figure 3.8). Both control (N=6) and transplant fish (N=5) continued dispersing after reaching the opposite release cove. In year 2, five fish (2 BC transplants, 1 BC control, 1 HC transplant, 1 HC control) were last detected at the opposite source cove (Figure 3.9), though 3 disappeared from the array for long periods of time. But other fish continued dispersing elsewhere (N=3; 1 HC transplant, 1 BC transplant, 1 BC control), or returned

to their release site (N=3; 1 BC transplant, 1 BC control, 1 HC control; Figure 3.10). One fish (BC transplant; Figure 3.11) visited the opposite cove, returned to its release site, then returned again to the opposite cove.

### **3.4.3 Large movements: timing and patterns**

Large movements (>800 m) were documented in every month of the year 1 and year 2 experiments (Figure 3.12). More large movements occurred in late fall and early spring during both years. Transplanted individuals were responsible for 52% of large movements in year 1, compared to 43% in year 2. Furthermore, in year 2, 29% of large movements were by fish originally from HC, and 71% were by fish originally from BC. In year 1, large movements (irrespective of the number of fish making those movements) were more frequent in July 2011 than in other months (Figure 3.12). In year 2, the greatest numbers of large movements were also in July 2012 (Figure 3.12).

## **3.5 Discussion**

Many individual age 1 Greenland cod dispersed on a kilometre scale, particularly during late fall/early winter, and early spring. This level of movement was unexpected, and indicates larger dispersal and movement patterns among age 1 individuals than previous mark-recapture studies in Newman Sound had suggested (Laurel et al. 2004, Sheppard 2005). A behavioural dichotomy was evident in both years, with some fish remaining in their cove of release for the entire tagging period (“residents”), and the others moving to other areas (“dispersers”). Resident and disperser strategies have been documented in organisms spanning voles (Myers and Krebs 1971), mole rats (O’Riain et al. 1996), brook charr (Grant and Noakes 1987), Trinidad killfish (Fraser et al. 2001),

common lizards (Cote and Clobert 2007) to humans (Jokela et al. 2008). My study adds to this knowledge by showing that juvenile Greenland cod exhibit divergent residency and dispersive characteristics which are widely variable among individuals.

On a population level, adult Atlantic cod can exhibit different movement patterns, including sedentary and dispersive behaviours (Robichaud and Rose 2004). On an individual level, acoustically tagged cod in Norway exhibited high between-individual variability in activity (swimming speeds; Fernö et al. 2011). Furthermore, age 2-3 juveniles in Newman Sound displayed variation in site-fidelity to autumnal home ranges with the onset of winter (Cote et al. 2004). Juvenile stages of Mediterranean coastal fish exhibited variable dispersal, which was attributed to density effects and personality traits such as boldness (Di Franco et al. 2012). Previous work documented variation in dispersal habits in marsh harriers (*Circus aeruginosus*), and suggested that short-term variation in environmental conditions might promote route flexibility (Vardanis et al. 2011). Intrinsic differences between individuals, such as sex, body size, and condition may also account for some variation in dispersal patterns (Bowler and Benton 2005), though were not accounted for in the current study. The decision to disperse or not likely results from myriad parameters that include spatial cognition, homing tendency, predation risk, density, habitat characteristics and abiotic factors (e.g., temperature, oxygen). Variability in movements seen in this study suggests that these parameters may affect individuals differently.

Intrinsic homing ability or site fidelity may contribute to an individual's decision to remain in a patch or disperse, particularly in a transplant experiment. On the one hand, natal site fidelity can lead to locally distinct populations that can affect specific life

history adaptations, reproductive success, and overall population structure (Cury 1994, Dittman and Quinn 1996). On the other hand, dispersing to colonize new areas may create genetic mixing opportunities (Cury 1994) as well as exposure to new habitats. Salmonids in particular exhibit strong homing behaviours, where even juveniles can use olfactory cues to effectively waypoint their home stream (Dittman and Quinn 1996). Radiated shanny in Newfoundland that used very small areas ( $<3 \text{ m}^2$ ), are able to home using olfactory cues (Goff and Green 1978). Even spawning coastal Atlantic cod in the North Sea largely originate from nearby nurseries (Neat et al. 2006), suggesting homing to natal grounds, and adult Newfoundland cod stocks may follow established migratory routes (Templeman 1974, Rose 1993). Unfortunately, juvenile fish are particularly difficult to link to homing behaviour as a result of high mortality (Thorrold et al. 2001), but the high numbers of tagged fish in this study made it possible to address the possibility of homing in age 1 Greenland cod.

My results suggest no prevalent intrinsic homing initiative in the age 1 class that drives individuals to return to areas they formerly occupied. Similar proportions of transplanted and control individuals left their release site during both tagging studies, however, not all dispersers travelled to the opposite source cove. Adult Atlantic cod exhibited a negative non-linear relationship between return success and transplant distance, suggesting an important omnidirectional “attractor” necessary to realize direction (Robichaud and Rose 2002). At the scale of my transplant experiments ( $\sim 3.5 \text{ km}$ ), individuals may have been unable to perceive attractors such as habitat or abiotic cues, to orient themselves towards their capture site. Because transplanted individual cod may rely on familiar landmarks to navigate (e.g., Windle and Rose 2005)

and likely had no previous experience with the transplant sites, they may have been unable to position themselves relative to their capture sites. Correspondingly, the control fish that stayed resident may have recognized landmarks upon their release, and remained in that environment. Conversely, the age 1 cohort may simply not be attached to a capture site at all, and may simply choose to expand their range and learn new spatial information to make informed decisions about foraging, predator avoidance, etc. before committing to a more defined home range. Indeed, more transplanted fish visited their cove of origin but then continued dispersing, and similar proportions of control and transplant fish dispersed to opposite coves, suggesting no strong fidelity to capture and/or release sites.

Predation can be a major structuring force in marine communities, particularly for juvenile fish (Lima and Dill 1990, Gregory and Anderson 2000). In particular, predation impacts individual decisions on when and where to feed, and what to eat (Lima and Dill 1990). For instance, because *Gadus* spp. are prey for visual predators (Linehan et al. 2001), individuals may make decisions on when to feed based on light levels and predator activity. Indeed, diel vertical migration (Clark and Green 1991), and diel foraging and activity patterns (Grant and Brown 1998) have been documented as anti-predator behaviours in Atlantic cod and other species (e.g., salmon juveniles - Clark and Levy 1988). Coinciding with these behaviours are decisions such as depth selection or feeding location. Age 0 cod are more likely to inhabit shallow areas with decreased predation (Linehan et al. 2001), but the larger age 1 class may be able to exploit deeper waters (Clark and Green 1991), particularly as predation risk tends to decrease with increasing size (Miller et al. 1988, Paradis et al. 1996). Certainly, the large movements displayed in

this study indicate that age 1 Greenland cod are able to occupy deeper water for at least some period of time.

During my study, tagged individuals remained "at large" for periods up to one year. Therefore, individuals likely encountered a wide range of temperature conditions, which could have affected behaviour and movement. Certainly, increased temperatures have been linked to increased food intake and growth rate (Brown et al. 1989), as well as determining the primary growth seasons (Levesque et al. 2005) for juvenile Atlantic cod. Previous work documented winter movements to deeper waters in mid-November in age 2-3 Atlantic cod (Cote et al. 2004), so it is possible that the age 1 Greenland cod exhibited similar movements. Indeed, during both my tagging experiments, many large movements occurred in November, which could indicate individuals chose to leave their shallow locations to reside in cooler, less metabolically costly deeper waters (Soofiani and Hawking 1982). Likewise, a substantive increase in large movements during the March-May period in both experiments coincided with a rise in water temperature above 4 °C in the Sound. Movements from deep to shallow waters at this time would likely offer prey-rich waters in the warmer shallows (Clark and Green 1990), particularly as individual metabolisms begin to increase with temperature and the high growth rate season begins (Levesque et al. 2005).

Density within populations of a species has the potential to affect dispersal rates and patterns. For example, increased emigration was documented in the common lizard when population density increased and exploitative and interference competition were high for all individuals, irrespective of kinship (Léna et al. 1998). Density has also been shown to affect habitat selection on local and regional scales in a variety of juvenile cod

species (Laurel et al. 2004, Hurst et al. 2012), where distributions are expanded, perhaps into lower-quality habitats, when local population density is high. High release density and increased competition may explain more large movements (>800 m) in the first weeks of the studies, but not for the remaining months where large movements occurred.

Habitat type and variability may affect rates of dispersal. For instance, nearly all snapper associated with rocky reef habitats in New Zealand were resident, whereas individuals found over habitats that included soft sediments were far more mobile (Parsons et al. 2011). Furthermore, the spatial configuration of habitat patches (structural connectivity, Crooks and Sanjayan 2006) can interact with how landscape (functional connectivity) affects the behaviour of organisms. Post-settlement age 0 Atlantic cod have been shown to select complex habitats, particularly eelgrass (Gotceitas et al. 1995, 1997), with the highest density levels associated with habitat patches of intermediate complexity (Thistle et al. 2010). Fish in a habitat with abundant food and shelter are more likely to have a smaller home range, and thus limited dispersal (Tupper and Boutilier 1995, Kramer and Chapman 1999). Immigration to a new patch is likely affected by the size of the new patch (i.e., a larger patch is more likely to be discovered), its isolation (Hanski et al. 1998), and other habitat cues such as presence of conspecifics (Turchin 1987). Individual foraging tactics and diet variability may also influence the kind of habitat sought by a juvenile individual, as was seen in a young-of-year brook charr (Grant and Noakes 1987). Large dispersal movements exhibited by age 1 Greenland cod in my study suggest less coupling to shallow eelgrass habitat than age 0s, perhaps because they are larger and faster, and therefore incur less predation risk.

Age 1 Greenland cod tagged in my two experiments showed extreme variability in movement and dispersal. Transplanted fish did not travel back to their source site significantly more than control fish overall, and many that did return did not stay, suggesting lower site fidelity in the age 1 class in comparison to age 2-3 cod. A large subset of fish from each tagging study moved far greater distances than initially expected, indicating a much greater contribution to connectivity than previously thought. Large movements occurred during times of substantial change in water temperature. Further integration of behavioural studies like mine with physiological studies could provide insight to the proximate determinants of dispersal in a study population. The stability of a population relies on the dispersal dynamics of the juvenile cohort, including mortality, range, and site fidelity. Clearly, the dispersal range of age 1 Greenland cod is far greater than supposed. It is imperative that this age group, so often neglected in past ecological studies, be further studied in a time when environments and population dynamics are changing more than ever before.

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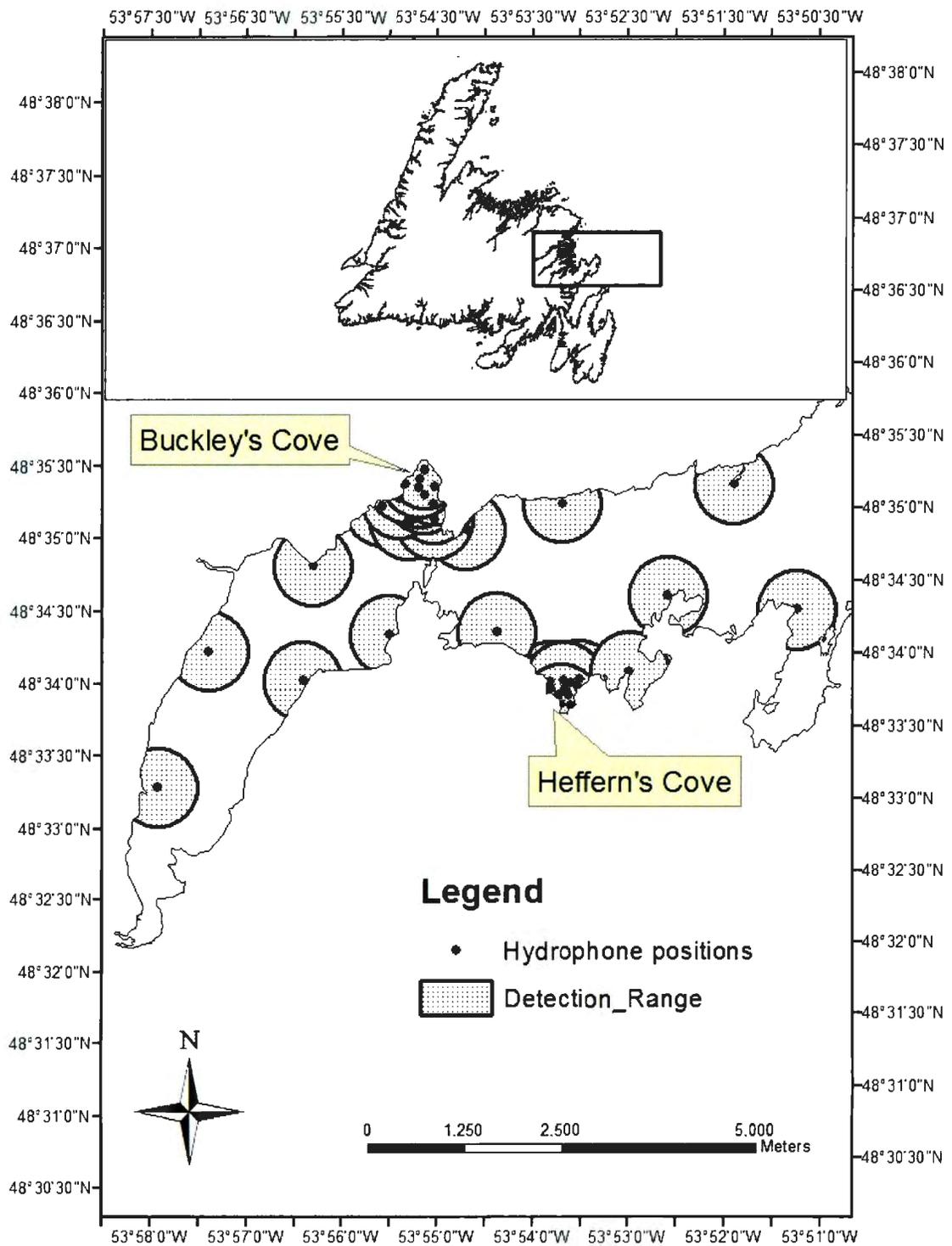


Figure 3.1. Positions and 500 m detection radii of the VR2/VR2W hydrophones deployed in Newman Sound, Newfoundland by November 2011. Coves of release (Buckley's Cove, Heffern's Cove) are indicated. NAD 1983 UTM Zone 21 projection.

October 7-8 2010

November 9 and 23, 2011

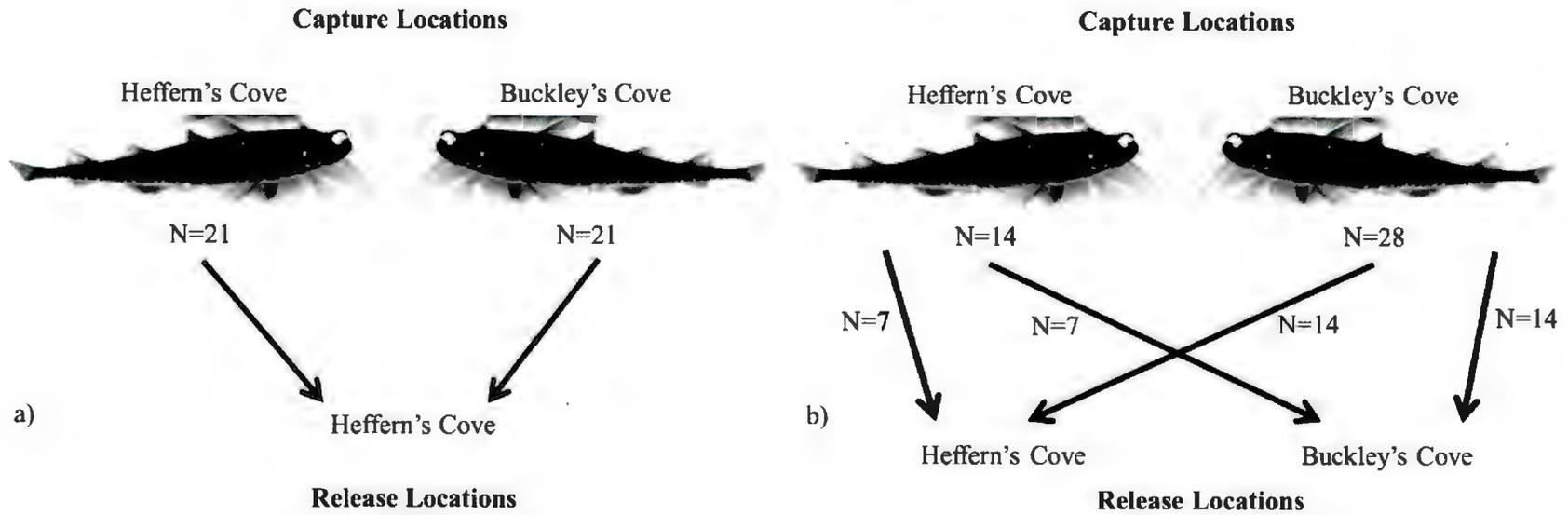


Figure 3.2. Experimental designs for a) the 2010-2011 tagging experiment and b) 2011-2012 tagging experiment. Arrows represent release after tagging surgery. Tagging dates are indicated in the upper left of each design panel.

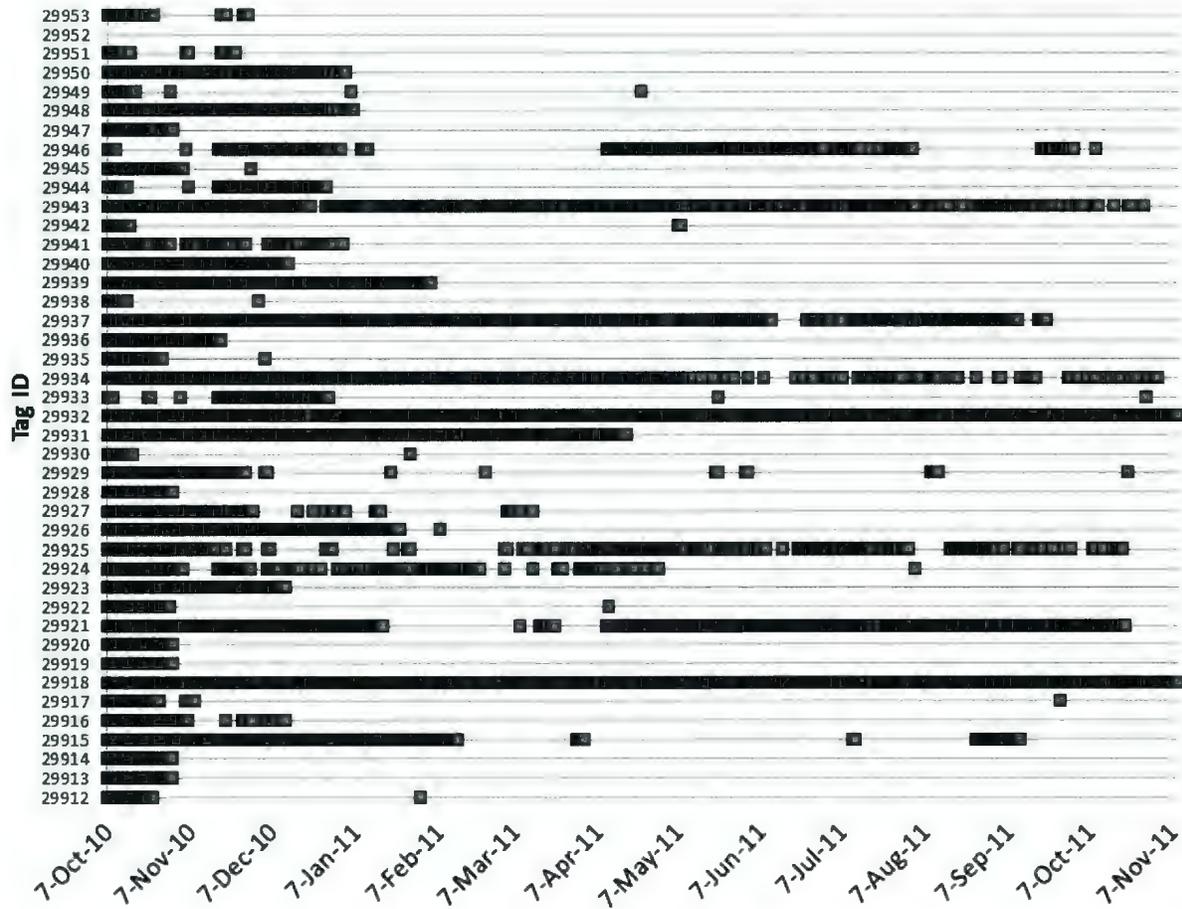


Figure 3.3a. Detection plot of the 2010-2011 tagging experiment (N=42) showing times at which individuals were detected over the 13 month period.



Figure 3.3b. Detection plot of the 2011-2012 tagging experiment (N=42) showing times at which individuals were detected over the 13 month period. Tag IDs beginning with 49 were released 9 November 2011, whereas tag IDs beginning with 39 were released 23 November 2011.

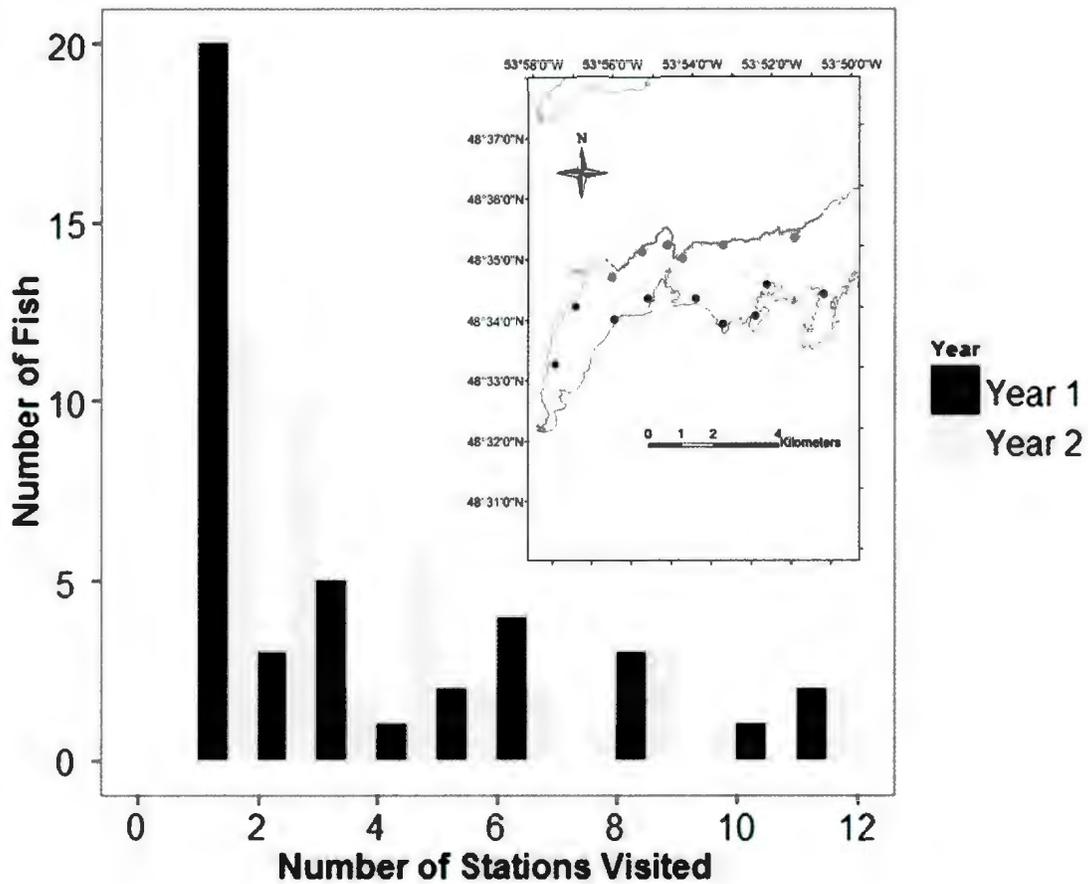


Figure 3.4. Frequency of tagged age 1 Greenland cod detected by varying numbers of receivers during the 2010-2011 experiment (Year 1, black bars) and the 2011-2012 experiment (Year 2, grey bars). Hydrophone receiver stations are indicated in the inset map

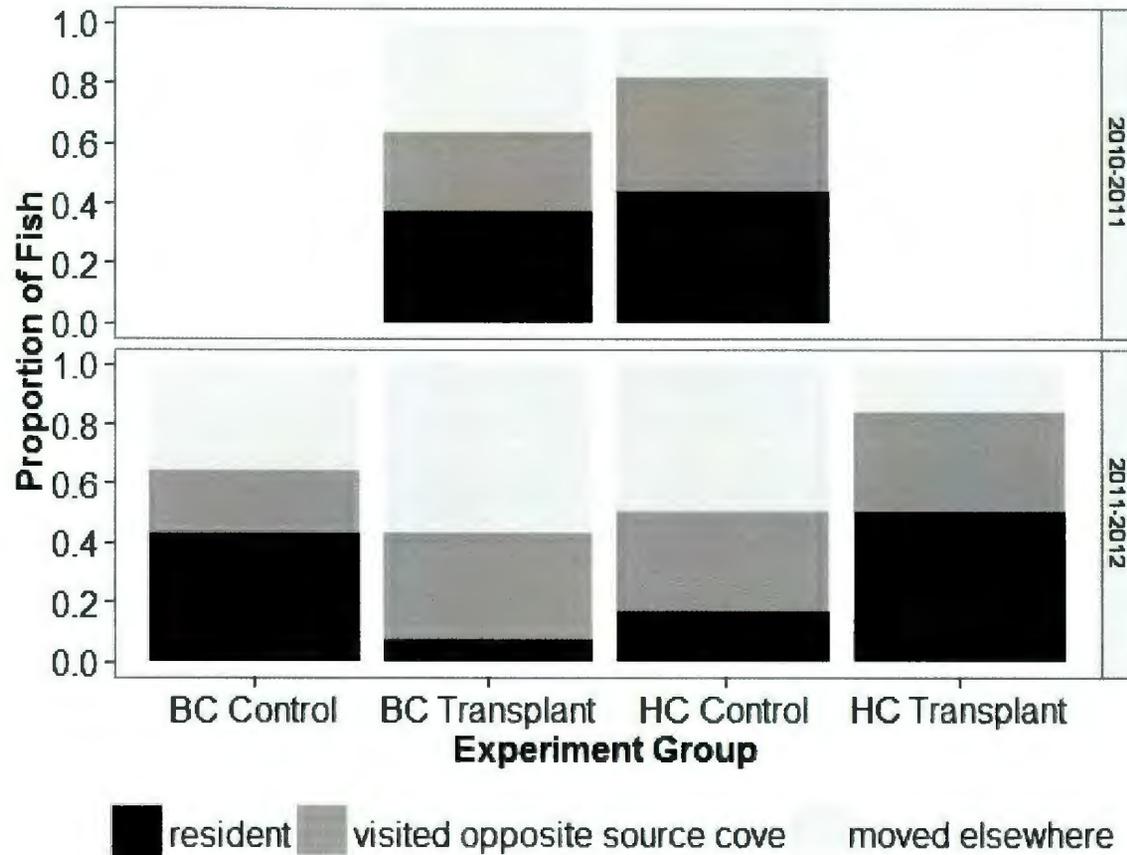


Figure 3.5. Movement patterns exhibited by individuals tagged in year 1 (2010-2011, top facet) and year 2 (2011-2012, bottom facet), defined as proportions of each experiment type excluding early mortalities. Experiment groups indicate firstly the cove of origin (BC=Buckley's Cove, HC=Heffern's Cove) and transplant status (transplant vs. control) of the fish.

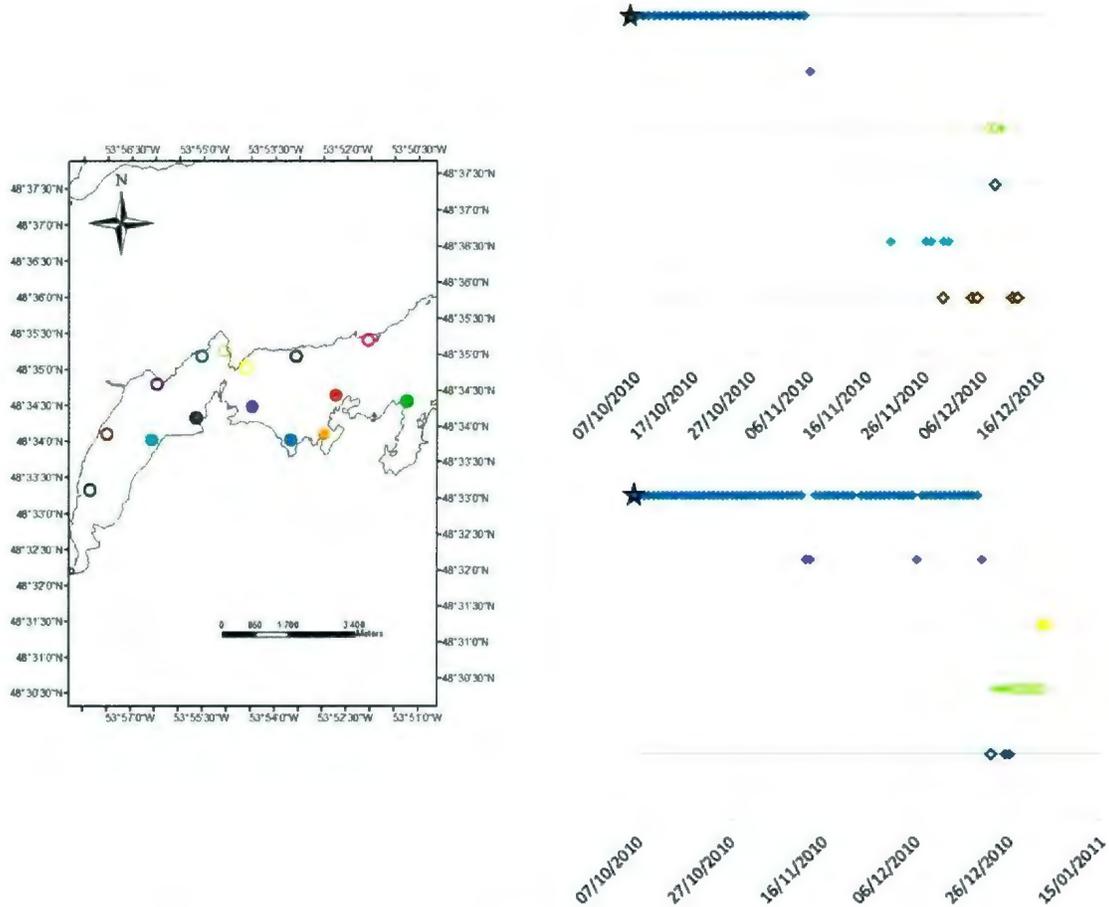


Figure 3.6. Detection plots of control fish 29916 (top) and transplant fish 29950 (bottom) released in Heffern's Cove that exhibited movement to opposite release cove during the 2010-2011 tagging season. Stars indicate release date. Stations in detection plots are shown progressing west to east as you move upwards. Open detection markers indicate stations on the north-northwestern shore, while closed markers indicate stations on the south-southwestern shore. Heffern's Cove is denoted by the solid blue markers, whereas Buckley's Cove is denoted by the open olive green markers.

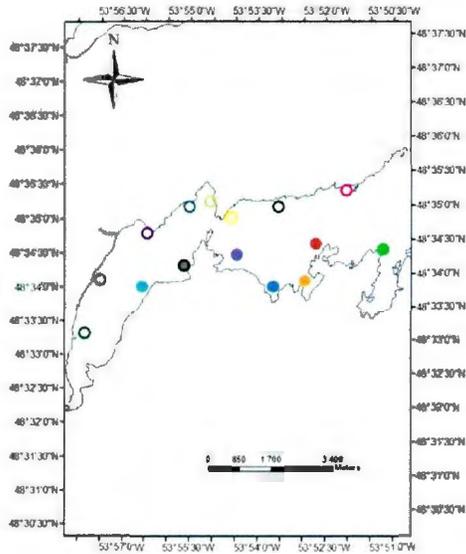


Figure 3.7. Detection plots of Buckley's Cove transplant fish 4947 (top) and Heffer's Cove transplant fish 4952 (bottom) exhibiting movement to their cove of origin. Stars indicate release date. Stations in detection plots are shown progressing from west to east as you move upwards. Open detection markers indicate stations on the north-northwestern shore, while closed markers indicate stations on the south-southwestern shore. Heffer's Cove is denoted by the solid blue markers, while Buckley's Cove is denoted by the open olive green markers.

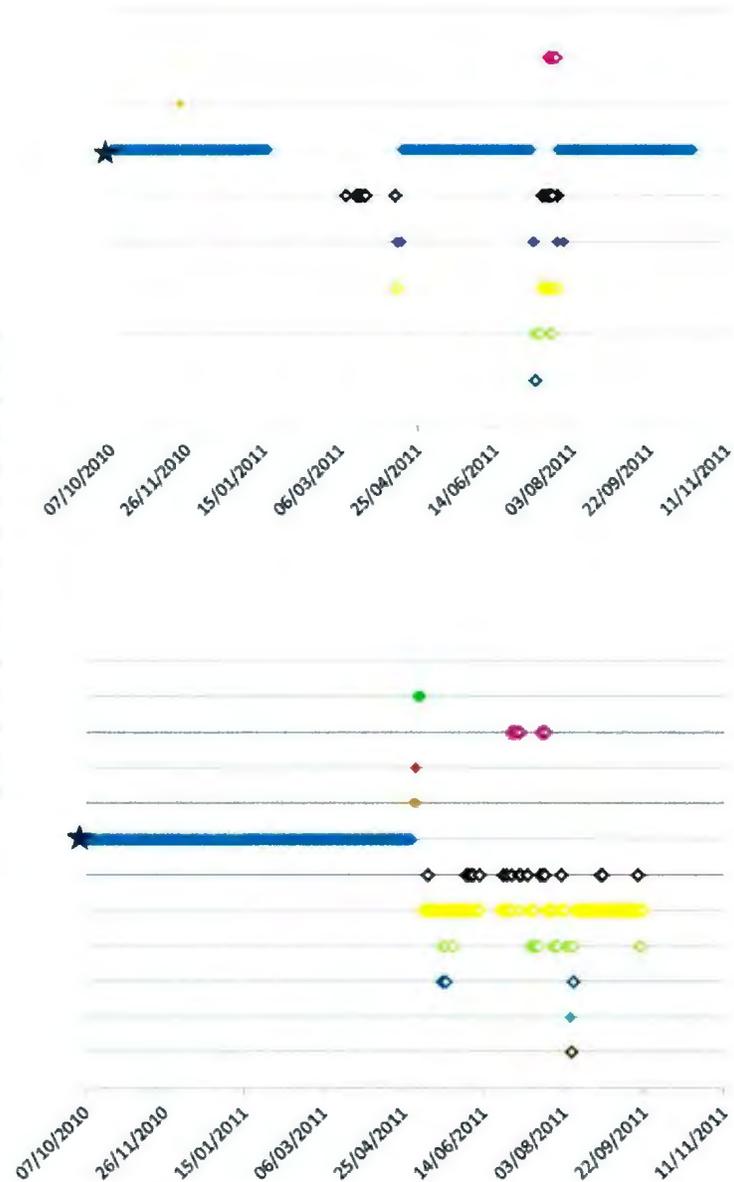
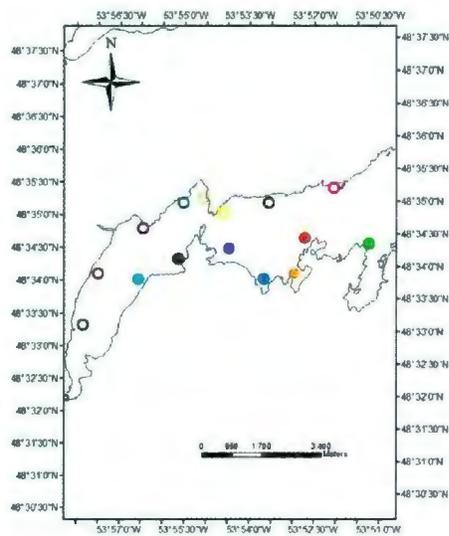


Figure 3.8. Example of control fish 29921 (top) that visited the opposite source cove (Buckley’s Cove, olive green open marker) and then returned to its release site in Heffern’s Cove, and transplant fish 29937 (bottom) that visited the opposite source cove and then continued dispersing elsewhere in the 2010-2011 experiment. Stars indicate release date. Stations in detection plots are shown progressing from west to east as you move upwards. Open detection markers indicate stations on the north-northwestern shore, while closed markers indicate stations on the south-southeastern shore.

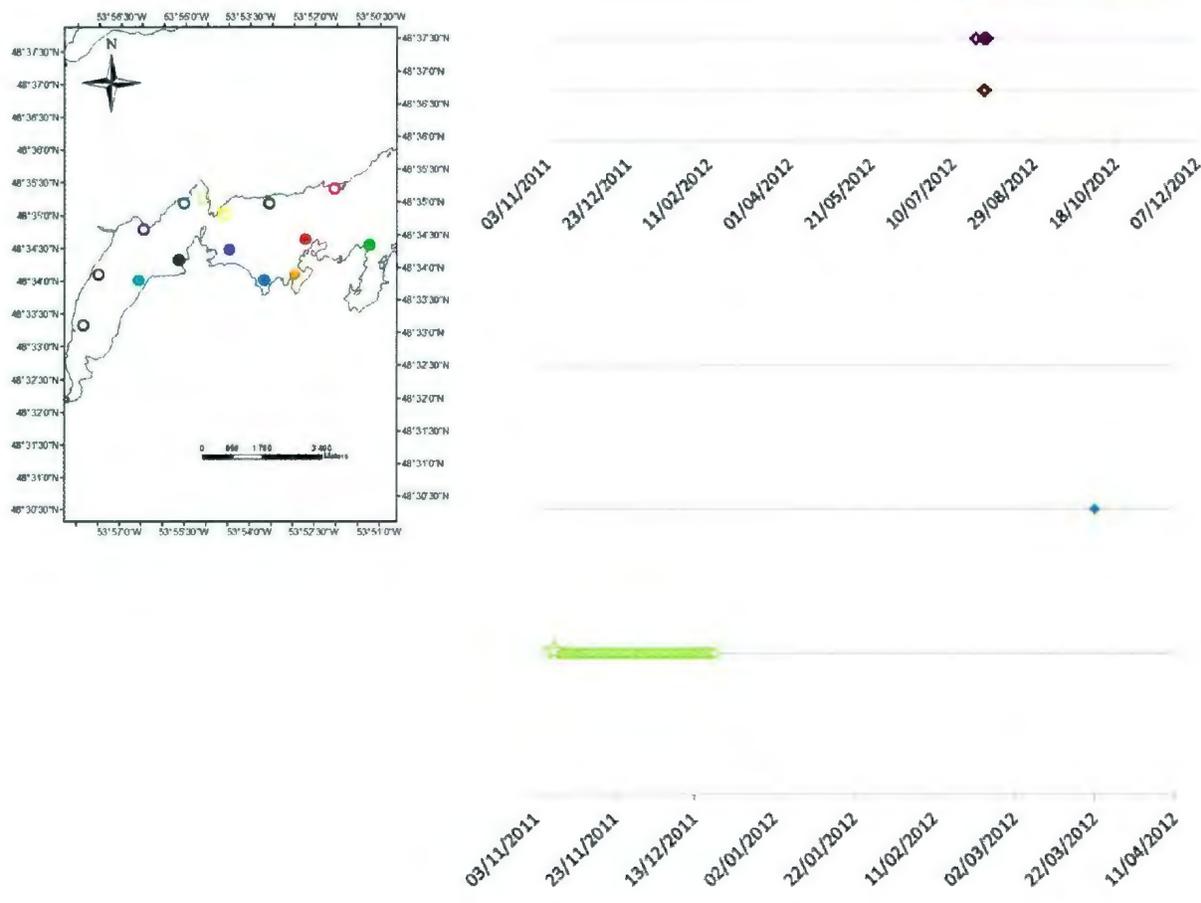


Figure 3.9. Example of Buckley’s Cove transplant fish 3964 (top) and control fish 4942 (bottom) that travelled to and were last detected in the opposite source cove (green olive and blue solid markers respectively) in the 2011-2012 experiment. Stars indicate release date. Stations in detection plots are shown progressing from west to east as you move upwards. Open detection markers indicate stations on the north-northwestern shore, while closed markers indicate stations on the south-southeastern shore.

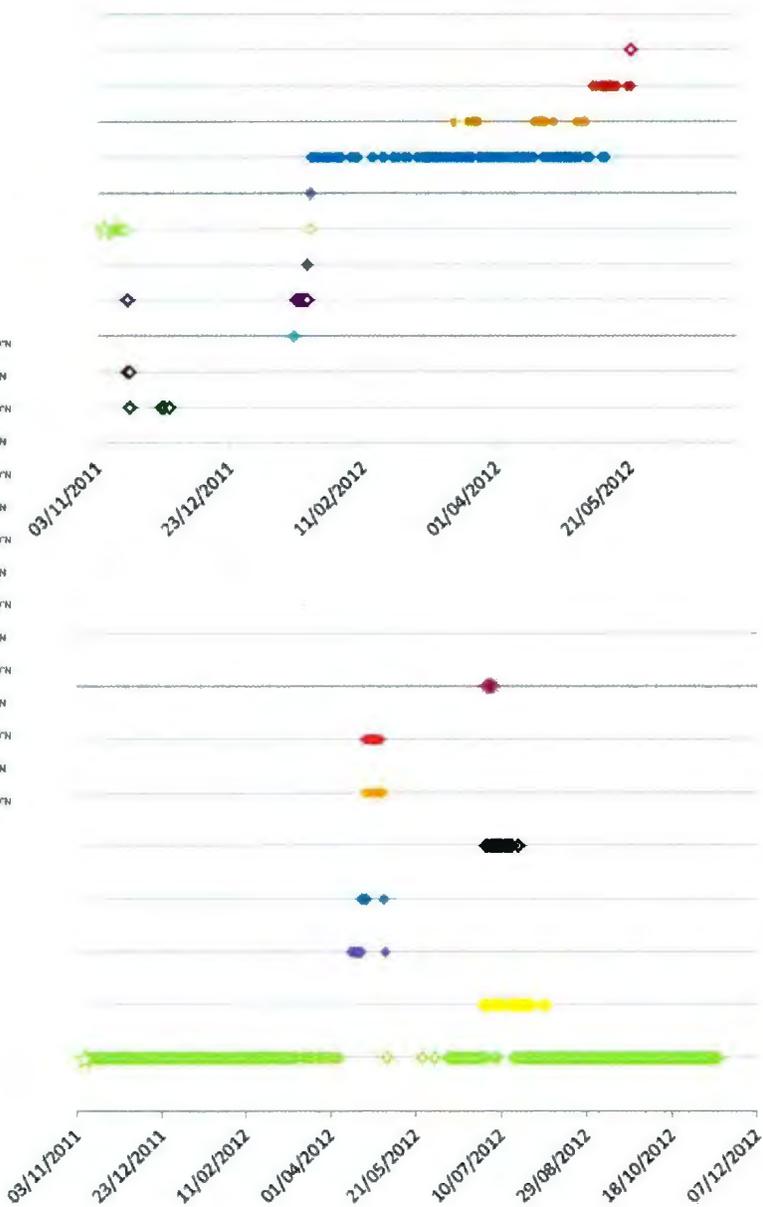
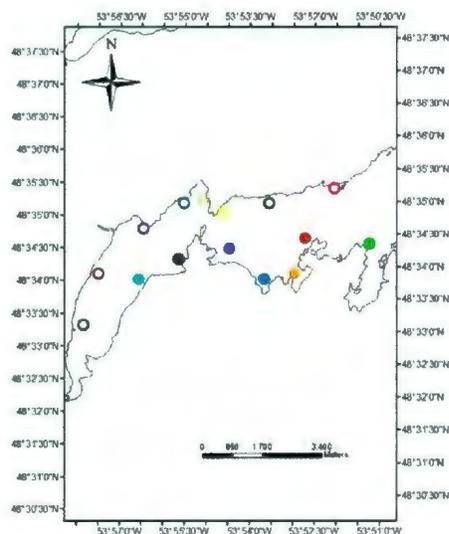


Figure 3.10. Example of Heffern's Cove transplant fish 4957 (top) that visited the opposite source cove (Heffern's Cove , blue solid marker), but then continued elsewhere, and Buckley's Cove control fish 4934 (bottom) that visited the opposite source cove (Heffern's Cove, blue solid marker), but then returned to its release site (Buckley's Cove, green open marker) in the 2011-2012 experiment. Stars indicate release date. Stations in detection plots are oriented more easterly at the top. Open detection markers indicate stations on the north-northwestern shore, while closed markers indicate stations on the south-southeastern shore.

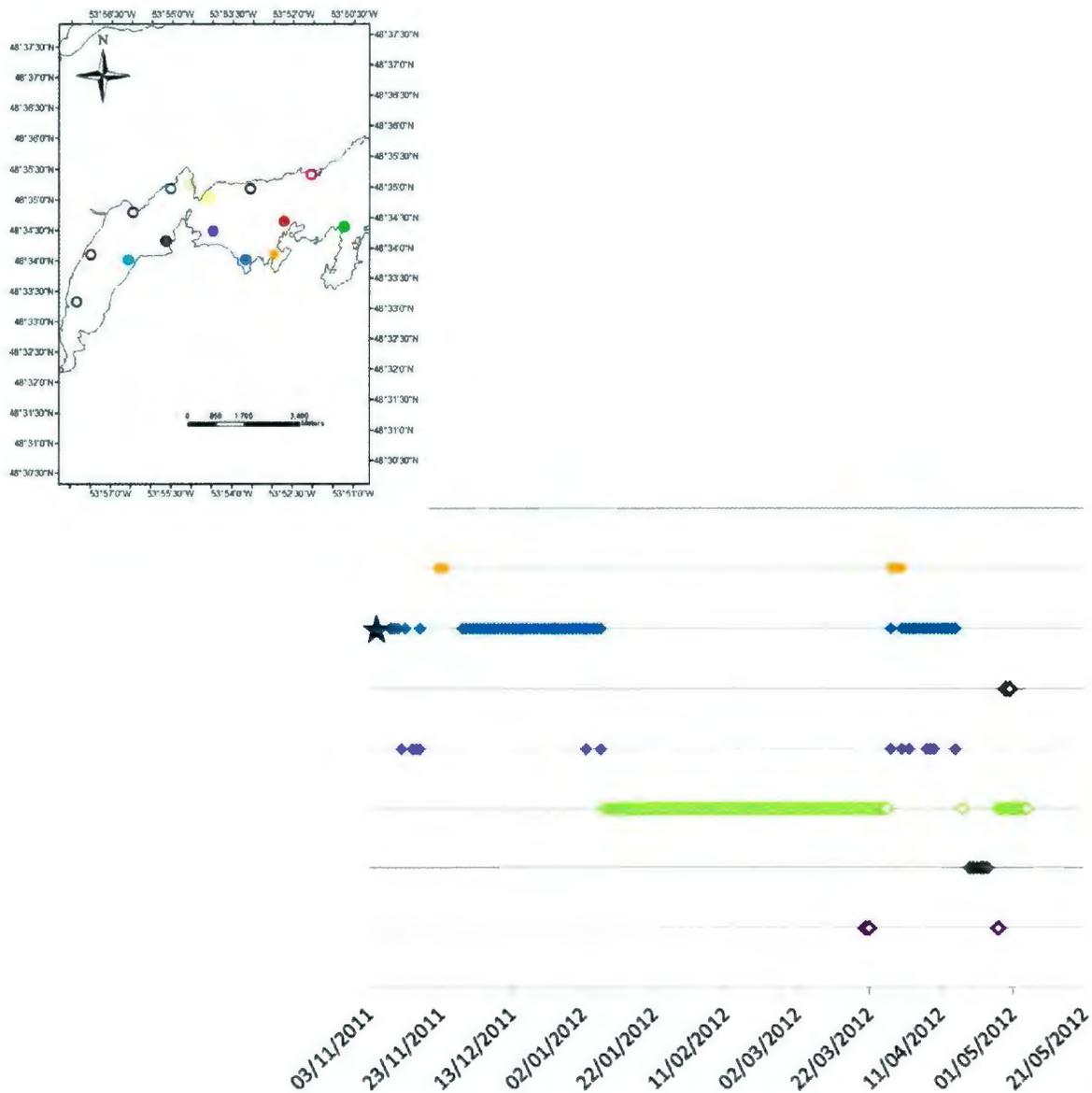


Figure 3.11. Detection plot of Buckley's Cove transplant fish 4937, that visited its source cove (Buckley's Cove, green open marker), then returned to its release site (Heffern's Cove, blue solid marker), and then returned to the opposite cove again in the 2011-2012 experiment. Stars indicate release date. Stations in detection plots move from west to east as you move upwards. Open detection markers indicate stations on the north-northwestern shore, while closed markers indicate stations on the south-southeastern shore

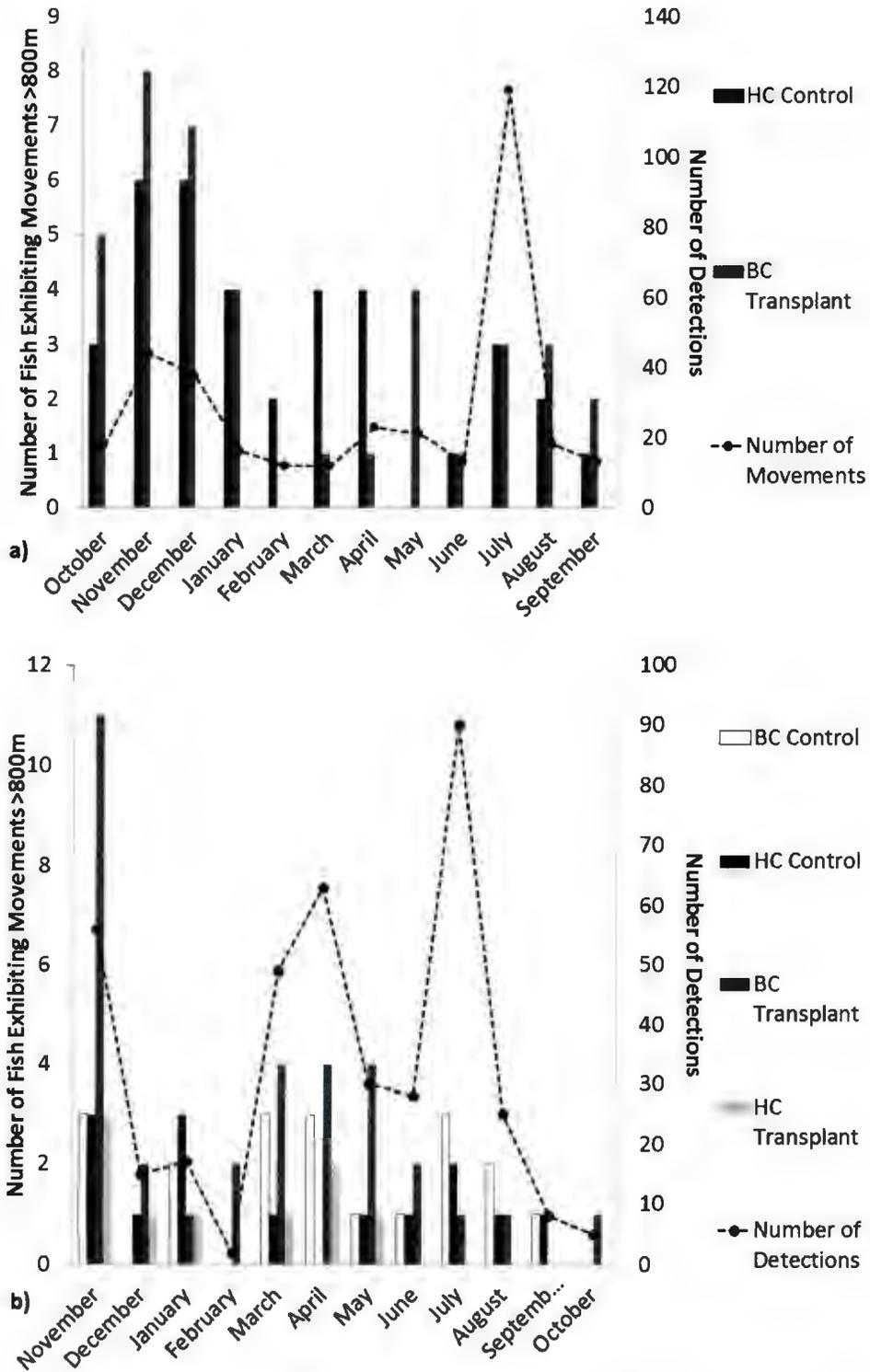


Figure 3.12. Number of fish exhibiting movements >800 m for the a) 2010-2011 and b) 2011-2012 tagging experiments. Tagged cod are categorized by their cove of capture (BC=Buckley's Cove, HC= Heffern's Cove), and their experiment type (control or transplant). The number of detections indicates the number of movements >800 m made during each month

## Chapter 4: Summary

### 4.1 Home range and dispersal potential of age 1 Greenland cod

Surprisingly, age 1 Greenland cod tagged in my study travelled distances and inhabited seasonal home range areas on kilometre scales. Recognition of higher dispersal capability in the age 1 class is critical for understanding coastal cod population dynamics, and for effective population management. Seasonal home range size generally increased with age during both years of tagging experiments. However, home range size ranged greatly among individuals. Specifically, some fish in both the 2010 and 2011 experiments inhabited roughly the same area across all seasons, in contrast to the general increase in mean home range area across seasons. No significant differences in seasonal home range size were found between control and transplant fish, or between fish from the two different capture coves, in either year. Effective management initiatives and practices should therefore acknowledge intrinsic individuality in juvenile cod movement. For example, my study suggests that if implementing a marine protected area or monitoring program for juvenile cod, the behaviour dichotomy between residents and dispersers needs to be addressed in the design. Areas monitored or managed need to be large enough to capture both these behaviour groups.

Individuals in my study occupied larger seasonal home ranges than those previously documented for younger and older gadid juveniles. Age 0 Atlantic and Greenland cod occupy more compact areas in coastal Nova Scotia (100s of  $m^2$ ; Tupper and Boutilier 1995) and Newfoundland (1000s of  $m^2$ ; Laurel et al. 2004, Sheppard 2005). Age 2-3 Atlantic cod in Newman Sound occupied a median of 2.1 ha during late autumn and early winter (Cote et al. 2004). It is possible that varying methods used for home range calculation (SCUBA, mark-

recapture, manual tracking, passive acoustic telemetry) could contribute to differences among locations and age classes. However, acoustic telemetry delineates home range more accurately than mark-recapture methods, which are limited to a straight-line distance from the point of capture and point of recapture (Zeller 1999), and also provide more comprehensive and long-term coverage than manual tracking methods. Home ranges were maintained into the winter season by 30% of the sample populations in the Cote et al. (2004) study; remaining individuals migrated to deeper waters in winter. Similarly, I observed a behavioural dichotomy between “residents” and “dispersers” in my age 1 sample populations, with more of the latter in both years. More dispersing individuals likely resulted in higher overall average home ranges across all seasons (minimum 0.420 km<sup>2</sup>, maximum 3.392 km<sup>2</sup>).

Large movements (~km scale) were documented in every month of the tagging experiments, but especially in the late fall, early spring, and July of both years. These large movements couple well with observed increases in average seasonal home range across pre-winter to post-winter seasons. Age 2-3 Atlantic cod move to deeper water as the summer thermocline disappears (Cote et al. 2004), as do age 1-4 cod in the Gulf of St. Lawrence (Hanson 1996), and smaller cod in Norway (Espeland et al. 2010). Many age 1 Greenland cod in my study exhibited similar behaviour, suggesting that deep waters benefit juvenile gadids during the colder winter season. Movement to deeper water may offer physiological benefits during times of decreased appetite and metabolism (linked to decreasing temperatures), and changing internal metabolites (linked to changes in photoperiod). However, the tendency for some tagged individuals to remain at the release sites, occupying similar, smaller home range areas than dispersing individuals throughout a given year, suggests additional winter strategies other than movement to deep water. These age 1s could be exhibiting small-scale habitat selection,

choosing to remain in highly productive shallower areas to maximize growth benefits.

Conversely, poorer condition may drive an individual's decision to remain in shallow areas that provide greater protection from predation.

In both years, similar proportions of control fish remained resident compared to transplant fish. Many fish, particularly transplants, dispersed from the release sites, but did not travel to the opposite source site. In fact, similar numbers of control and transplant fish travelled to opposite source sites. My results suggest no prevalent intrinsic homing ability exists in age 1 cod, though individuals at this age could learn and sense surroundings at smaller scales than the transplant design of this study. Adult Atlantic cod exhibit negative non-linear relationships between return success and transplant distance (Robichaud and Rose 2002), and likely rely on habitat or abiotic cues to navigate (Windle and Rose 2005); younger congeners may well exhibit similar behaviour. However, age 1 individuals more likely exhibit weaker site fidelity than older juveniles and adults, as suggested by transplanted fish that returned to their source site but then dispersed to other areas, and control fish that left their release site. Larger movements in the study may be more exploratory in nature. Gathering information (learning) about habitat, foraging success, predator presence, etc. in the area would allow individuals to make a more informed decision on where to commit to a smaller home range, as seen in age 2-3 juveniles. Likewise, in my study I gathered information about the dispersal potential of the age 1 individuals, which can be implemented in marine spatial planning or ecosystem-based management for more informed regulations, monitoring protocols, and population management decisions.

#### **4.2 Implications and future study**

Effective marine reserve planning requires consideration of dispersal distances of target species. However, these distances are challenging to estimate (Halpern and Warner 2003). Connectivity of populations underpins ecosystem-based marine spatial planning (Foley et al. 2010), in part because it is important for maintaining the structure and function of ecosystems (Mumby and Hastings 2008). Additionally, connectivity ensures population replenishment, population persistence or recovery during times of disturbance or environmental change, and maintenance of genetic diversity (Foley et al. 2010). My study focuses on active movement of age 1 juvenile Greenland cod and reveals kilometre+ scale movements, indicating a higher contribution to connectivity than previously supposed. The more commercially significant congener species, Atlantic cod, coexists with Greenland cod in coastal Newfoundland as juveniles, so inferences on dispersal potential can be made between the two species. Greenland cod are often described as more sedentary and coastal-associated than Atlantic cod, but my results indicate that juveniles travel larger distances than expected. Therefore, juvenile Atlantic cod in the area could move equal, if not larger distances. Larger dispersal distances and weak site fidelity imply highly connected metapopulations in Newman Sound. Correspondingly, reserves to protect nursery areas for economically and culturally significant Atlantic cod in Newfoundland will likely have to be larger than previously assumed in order to ensure appropriate protection for vulnerable juvenile stages.

Multiple sustainability goals for conservationists and other stakeholders (e.g., harvesters) add challenge to designing effective marine protected areas (MPAs) and reserves (Halpern and Warner 2003). Use of spatial information such as dispersal distance is critical to the success of both parties. Modelling efforts indicate that increased spatial information on larval dispersal can be used to increase fishery values significantly, largely through better targeted areas for fishery

closures and for harvesting (Costello et al. 2010). Better dispersal information and modelling can also advise the design of larger marine reserve networks (Costello et al. 2010), which likely would support higher diversity, density, and biomass (MacArthur and Wilson 1967, Halpern 2003). My study contributes such dispersal information.

Dispersal information is required at all stages of ontogeny because marine species often change habitat and move at different scales as they develop. Furthermore, some life stages may be more vulnerable than others, and should receive higher degrees of protection. For instance, closing key nursery areas to fishing would likely help preserve future populations (Grüss et al. 2011). For effective management, protection of sufficient areas requires knowledge of the limit of immature individual dispersal. Likewise, behaviour polymorphisms, such as the “dispersers” and “residents” seen in this study, must be considered in placement and establishment of marine protected areas because some individuals may have better survival than others in the reserve. Over time, this behavioural dichotomy could affect the diversity of the proposed protected population (Grüss et al. 2011). Fisheries managers should consider movements associated with changing temperature regimes, such as the movements to deeper waters at the end of fall made by certain individuals in my tagged populations. On a related note, climate change may influence both seawater temperatures and current movements which could, in turn, affect where and when juvenile gadids disperse.

Other aspects of juvenile dispersal, including habitat selection and temperature and/or depth preferences require further study. Passive acoustic telemetry networks proved highly successful in providing a comprehensive database of juvenile cod movements, and therefore offer a valuable tool for these future investigations. Juvenile cod dispersal may vary with location depending on environmental conditions, so translating my observations to larger-scale

processes requires investigations on other local populations, and eventually studies at regional scales. Further understanding and certainty regarding age 1 Atlantic cod dispersal potential will arise from direct comparisons between age 1 Greenland and Atlantic cod dispersal potential through additional acoustic studies. My work provides estimates of age 1 juvenile cod dispersal distance and site fidelity for research scientists and fisheries managers. Incorporation of these estimates into movement models or marine spatial planning will result in more informed management of gadid species in Newfoundland. Juveniles moving on scales of kilometres, as exhibited by my study, may be effectively protected or managed with the use of relatively modest-sized but strategically placed MPAs. My study does not address whether the disperser/resident dynamic is genetically linked, a learned behaviour, or a mixture of both. If the disperser/resident dynamic is genetically linked, a larger MPA would be necessary to assure no exclusion of a certain phenotype (dispersers). If the dynamic is entirely behavioural, smaller MPAs placed in core areas used by each of the groups would likely be effective.

### 4.3 References

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## **Appendix 1: Data processing and home range calculation for a passive acoustic telemetry network in Newman Sound, Newfoundland**

### **A1.1 Introduction**

Biotelemetry has allowed scientists to follow the detailed movements of a variety of terrestrial and aquatic species, and accumulate massive quantities of data. Telemetry data have the potential to answer many questions at the forefront of spatial ecology if the design and execution of the study matches the type and scale of questions being asked. Knowledge of positions over time can allow scientists to infer the sample population's behaviour, dispersal, and interactions with the environment. However, there are inherent challenges, both technical and analytical, in working with large datasets. Technical issues include preserving data integrity and consistency, avoidance of data redundancy, filtering and storage, and management of different data types (Cagnacci et al. 2010). Analytical issues include dealing with mismatched scales between tracked movements and the related environment (Turchin 1998, Hebblewhite and Haydon 2010), and matching the correct temporal scale to observed behaviours to ensure analysis of biologically relevant movement behaviours (Turchin 1998).

The analytical issues with telemetry data must be addressed even before a study is carried out to ensure valid and biologically relevant results. For passive acoustic telemetry, questions such as “what is the study objective?” and “what are the suggested temporal and spatial scales in the study?” need to be considered in order to answer more technical questions such as “how many receivers should be deployed?”, “where should they be deployed?”, and, “how long should data be collected?” (Heupel et al. 2006). Hypotheses concerning movement behaviours need to be made prior to data collection and analyses to ensure receiver networks will address the right

questions. Presently, the study objectives in passive acoustic telemetry studies involve a dichotomy where researchers try to determine if the sample population exhibits residency, and/or whether larger movements, such as dispersal and/or emigration movements, occur. Only after these two initial questions are answered can more detailed hypotheses on home range size, relationship between movement and environmental factors, and timing of dispersal be addressed.

Analysis of telemetry data requires a spatial database. Information in the database can come from hydrophone receivers, direct observations, environmental sensors, and maps, among other sources (Urbano et al. 2010). Once data are compiled into a database, statistics software and geographic information systems (GIS) are needed to process and filter the data, and then carry out the analyses. Herein lays a major issue with acoustic telemetry technology. The broad applicability of the technology results in numerous studies of different scale and design, all requiring slightly different processing and analysis techniques. Consequently, no standard analyses for the technology have been developed (Heupel et al. 2006); likewise, no standard software is used. For example, an investigating survey of software tools for calculating home range yields a surprising selection (e.g. Animal Movement Extension for ESRI ArcView: Hooge and Eichenlaub 2000; Hawth's Tools Extension for ESRI ArcGIS: Beyer 2004; HRT extension for ESRI ArcGIS: Rodgers et al. 2005; *adehabitat*: Analysis of habitat selection by animals for R software: Calenge 2009; *adehabitatHR*: Home range estimation for R software: Calenge 2011; Geospatial Modelling Environment: Beyer 2012). Perhaps the most powerful current toolset in processing and analysing acoustic telemetry data is the pairing of the open-source, globally used R software (R Development Core Team 2010), with a GIS such as ArcGIS (ESRI). In this chapter, I outline and explain the methodology and analyses I used to extract information from the initial receiver files. Specifically, I develop a new data analysis approach, adapting and

incorporating existing methods to address questions concerning residency and dispersal of age 1 Greenland cod.

## **A1.2 Methods**

### **A1.2.1 Data processing**

I retrieved date and time of detection, a unique tag identification (ID), and receiver ID from hydrophones and uploaded the data to a Vemco User Environment (VUE) database. Files for each fish were then exported from VUE for data processing using R software. The date and time field was converted to a POSIXct class for further manipulations in R. For each fish, I then calculated the time difference in seconds between successive detections. Single detections, defined as a lone detection over 24 hours for an individual fish, were interpreted as spurious and thus filtered out of the data, consistent with common practice (March et al. 2010, Alós et al. 2011).

### **A1.2.2 Generating Position Estimates**

Previous researchers used average positions occupied over defined time intervals, or centres of activity (COA Simpfendorfer et al. 2002), successfully in acoustic telemetry studies in the marine environment (Heupel et al. 2004, March et al. 2010, Alós et al. 2011). Passive acoustic telemetry networks, though less labour-intensive than active tracking, can only provide positions of individual transmitters within the omnidirectional range of detection of the hydrophones in the network (500 m in this case). COAs are weighted position estimates of individual transmitters based on known hydrophone positions in an array design, that increase precision from a presence/absence dataset to a position-based dataset. COA calculation requires selection of a time interval appropriate to the duration and spatial extent of the study. Previous

use of hourly time bins (Simpfendorfer et al. 2002, March et al. 2010, Alós et al. 2011) has proven effective in capturing the subtleties of diel movements as well as more general long-term movement patterns. Using the *plyr* package (Wickham 2012) in R, I generated COAs for each individual over hourly time intervals using arithmetic means of longitude and latitude weighted by the number of detections per receiver defined as:

$$\bar{X}_{\Delta t} = \frac{\sum_{i=1}^n R_i X_i}{\sum_{i=1}^n R_i} \quad \text{and} \quad \bar{Y}_{\Delta t} = \frac{\sum_{i=1}^n R_i Y_i}{\sum_{i=1}^n R_i} \quad (\text{from Simpfendorfer et al. 2002})$$

where  $n$  = the number of receivers in the array,  $R_i$  = the number of receptions at the  $i$ th receiver during  $\Delta t$ ,  $X_i$  = the X coordinate of the  $i$ th receiver, and  $Y_i$  = the Y coordinate of the  $i$ th receiver. The COA approach assumes all receivers have equal detection ranges and probability of detection of any given transmitter.

### **A1.2.3 Least cost path analysis**

To better visualize the movements of individual fish over time, I connected point locations of individuals to produce least cost paths. A least cost path is the most efficient track between two points based on an underlying cost surface that highlights the probability and/or risk (“cost”) of moving within the study area. Least cost paths are superior to paths using Euclidean distance in small scale, coastal areas because they ensure inferred tracks only pass through water. Using ArcGIS, I created a cost raster surface, downloading CanVec vector data from Geogratis (NTS sheet 2C12). I then converted the water shapefiles to raster format using the “Feature to Raster” tool, choosing the smallest cell size possible to maximize resolution. From there, I used the “Reclassify” tool to allocate a value of 1 to all cells containing water, and a value of 999 to all cells containing land, effectively creating a cost surface. The cost raster was then converted

using the “Raster to ASCII” tool for input into R software. I then converted the file back to raster format using the R *raster* package (Hijmans and van Etten, 2012), and aggregated the raster by a factor of 10, to facilitate efficient computation in R. Using the package *gdistance* (van Etten 2011), the inverse of the cost raster was then converted to a transition object. Transition objects represent a conductance surface (paths are more likely to travel through cells with values closer to 1 than to zero) used in the command "shortestPath()", which mimics the least cost path tool in ArcGIS. Least cost paths were then calculated between each successive point, for each individual fish, and written to shapefiles using the package *maptools* (Lewin-Koh and Bivand 2012). Using the least cost paths, I categorized movements for comparisons based on experimental design.

#### **A1.2.4 Distance and rate of movement analyses**

I determined distances between position estimates for each fish by calculating the length of each step of the least cost paths in ArcGIS. Rate of movement was determined by dividing this distance by the time interval between each successive pair of points. I then applied a conservative speed filter to the position estimates for each fish, eliminating any detections resulting from a rate of movement faster than two body lengths per second. I chose this threshold as a conservative method of eliminating detections that might represent a transmitter ingested by a predator. Cod can move up to 10 body lengths per second over short distances (Gregory and Anderson 1997), but probably cannot sustain this speed over the hour time intervals of the position estimates. Overall, this filter eliminated 0.4% of detections in 2010, and 0.03% in 2011.

Throughout the course of the study, many path steps for the fish indicated detection by only one receiver, effectively generating a path step of length 0. To investigate the timing of movements to different receivers, I placed a distance filter on the datasets. Using R, I isolated

detections associated with movements of >800 m, which approximated the shortest distance between receivers outside of the two capture and release sites in my experiments. The resulting dataset thus included only larger movements among far-field stations, and was used to compare amounts and timing of movements between control and transplant fish, and fish from different coves.

### **A1.2.5 Home range analyses**

To calculate the extent of individual home ranges, I used kernel utilization distributions (KUDs) to provide the probability density of an individual's location in a plane (Worton 1989), using 95% KUDs to delineate the home range. Kernel methods are not dependent on parametric assumptions, and are used for both univariate and multivariate probability density estimation (Worton 1989). Using a bivariate normal density kernel, the kernel density estimator for  $n$  observations at a point  $(x,y)$  on a plane is defined as:

$$\frac{1}{2\pi nh^2} \sum_{i=1}^n \exp\left(-\frac{d_i^2}{2h^2}\right),$$

(from Worton 1995)

where  $h$  is the smoothing parameter, and  $d$  is the distance of the  $i$ th observation from the point (Worton 1995). This equation represents a probability density function (the kernel) applied to each known position, constructing the estimate for the  $n$  components of the point (Worton 1989). The smoothing parameter determines the amount of variation in the  $n$  components of the estimate (Worton 1989); the smaller the  $h$ , the more detail present in the utilization distribution. Kernels are referred to as “fixed” or “adaptive”, depending on whether or not the smoothing parameter is fixed over the plane (Worton 1989). In the R package *adehabitatHR* (Calenge 2011), the

function “kernelUD” uses the *ad hoc* method by default on the given data to estimate the smoothing parameter. For a fixed bivariate normal kernel, the method is defined as:

$$h = \sigma n^{-1/6}$$

where  $\sigma$  represents the estimate of variance for the (x,y) location, or:

$$\sigma = 0.5(\sigma(x) + \sigma(y)) \text{ (from Worton 1995)}$$

Once the KUD is calculated, a contour can be generated for 95% probability to represent home range area. To produce a contour, the study site is divided into a high resolution grid, and the probability associated with each cell of the grid is calculated using the volume of the cell (Worton 1995). In the R package *adehabitatHR*, the grid is user-specified, which allows various scales of locational data. Area within the 95% contour is calculated by selecting the smallest number of cells whose probability is 95% (Worton 1995).

Because KUDs depend on sample size, and the number of detections varied for each individual and for each time period examined, I used a Monte Carlo simulation approach (Farrugia et al 2011). For each fish, and for each time period, 100 positions were randomly chosen 100 times. I then calculated KUDs for each of the 100 replicates, extracted the vertices of the 95% area contours using the *adehabitatHR* package, and wrote each collection of 95% polygons to a shapefile for viewing in ArcGIS. Using ModelBuilder, I used the Erase and Calculate Areas tools to extract only the water area of each 95% KUD replicate, for each season and fish (Figure A1). Once the land area was excluded, I calculated the average area and standard deviation for the 100 replicates representing one fish. This procedure produced an average home range area for each individual, for each of three time periods it was detected in, for

the 2010-2011 and 2011-2012 datasets, chosen to reflect ambient water temperatures in Newman Sound. The winter season was defined by average water temperature  $\leq 4$  °C (~December-April). I defined periods on either side of the winter season as “pre-winter” (October-November 2010, November 2011) and “post-winter” (~May-October 2011, ~May-October 2012), respectively. Average daily water temperature data were obtained from four thermographs moored at a depth of 3m in Newman Sound throughout the duration of my study year by Fisheries and Oceans Canada.

I separated the two experimental years (October 2010 to October 2011 and November 2011 to October 2012) for statistical analyses because they differed in design and used two different batches of acoustically tagged individuals. However, I modelled the seasonal home ranges for both experiments using GLM models in R software, examining different effects based on initial design. For each analysis of variance (ANOVA) performed on the models, the unbalanced design required the more powerful type II SS analysis. These tests allowed me to test the effects of transplant status (“transplant” and “control” [i.e. “replanted”]) and season for the 2010-2011 experiment, and cove of origin, season, and transplant status for the 2011-2012 experiment.

Because R uses a type I SS by default, and adds each effect sequentially to the model, results depend on model term order (Langsrund 2003). Furthermore, with unbalanced data, sample size influences results. Many other statistical software packages use type III SS analysis, adjusting each effect for all other model terms. Parameters in this type of analysis must be constrained, usually where the sum of parameters is equal to zero for any subscript considered, in order to produce unique estimates (Langsrund 2003). The major criticism of type III tests, however, is that they test main effects in the presence of interactions, requiring unsatisfactory

hypotheses that often lack inferential interest (Nelder and Lane 1995) and thus produce unsatisfactory results. For example, a type III SS analysis could produce a significant interaction effect (AB) but an insignificant main effect (A). That result suggests an unrelated effect of A on each level of B but null average effects, which makes no inferential sense (Nelder and Lane 1995). Another major criticism is that unnecessarily constraining the parameters can lead to confusing results. Nelder (1994) argues that when considering a model that includes interactions between effects, that interaction doesn't tell us *how* the main effects interact. Constraining parameters is not part of the intrinsic model, so why should it be safe to assume the effects of A summed over the levels of B equal zero? The decision to set constraints on the parameters is arbitrary at best, and highly inaccurate at worst.

In type II SS analyses, each effect is adjusted for all other interaction terms that do not contain that effect (Langsrund 2003), effectively assuming non-significant interactions. No constraints are placed on the parameters. In actuality, a type II analysis for a two-way ANOVA design (as seen in the 2010-2011 tagging experiment) involves two Type I analyses, using the order A-B-AB, and B-A-AB (Langsrund 2003). For an ANOVA with three effects (as seen in the 2011-2012 tagging experiment), for example, there is no adjustment in the main effect A for the interaction AB, AC, or ABC in a type II SS analysis (Langsrund 2003). Non-adjustment makes intuitive sense; for example, testing for the effect of AB while acknowledging the presence of ABC lacks inferential meaning. Type II SS analysis is actually more powerful in examining interactions. For example, a significant ABC interaction in a three-way design would suggest an AB interaction, but one can test this inference with two independent tests (AB and ABC), given the non-adjustment (Langsrund 2003).

I considered but rejected the use of non-parametric tests. Although the data were not normally distributed, and thus did not meet ANOVA assumptions, I used a randomization test approach to validate my ANOVA results. Randomization tests are more powerful than non-parametric tests because actual numeric values drive sampling distribution of a statistic based on repeated random computations of the statistic (Edgington 1964). The proportion of the statistics in the sampling distribution that exceed the actual statistic then determine significance (Edgington 1964). Thus, decisions on whether to accept or reject the null hypothesis follow examination of numerous permutations from random sampling (Fisher 1971). If the statistics found in the sampling distribution are <5% likely to be equal to or larger than the actual statistic, then the result is considered significant.

For each experiment, I obtained F statistics for each effect in the ANOVA based on a Gaussian distribution, then randomized home range areas for each separate experiment. I then recomputed the ANOVA test for the randomized data and the F statistics for each effect were obtained, repeating the procedure 1000 times to produce frequency distributions representing each effect's F statistics in an experiment. Finally, I compared the initial observed outcome (F statistic) for each effect to the distribution of outcomes for that effect, to calculate a probability level. If this probability level was <5%, the test statistic was deemed significant. The randomization test approach was directed towards effects that appeared significant after the initial ANOVA type II SS analysis, but I also checked for the effects that did not appear significant.

### **A1.3 Conclusion**

Acoustic telemetry experiments allowed me to observe and calculate individual age 1 Greenland cod movements and home range areas. Incorporation of R software and ArcGIS for the processing of data obtained from transmitters and hydrophones deployed in the field provided an integrated methodology that produced both descriptive and hypothesis-driven results. In summary, I took the following approach in data processing:

1. Single detections were filtered out of original hydrophone files using R.
2. Position estimates based on the known locations of the hydrophones were calculated using a weighted mean over hour time bins, with number of detections per receiver as the weighting factor, using R.
3. Position estimates were connected to represent movement tracks using a least cost path approach, integrating R and ArcGIS.
4. Distances between points were calculated from the least cost paths using ArcGIS, rate of movement was calculated, and a speed filter and distance filter implemented using R.
5. A Monte Carlo approach in R standardized the number of positions used to calculate the home range of each fish, for each season. 95% KUD areas were calculated for each Monte Carlo permutation, and averaged for each fish, for each season.
6. An ArcGIS model tool was used to extract solely the water areas for each calculated average home range area.
7. A GLM and ANOVA approach in R examined different experimental design effects on the calculated seasonal home range areas. Results were confirmed with randomization tests.

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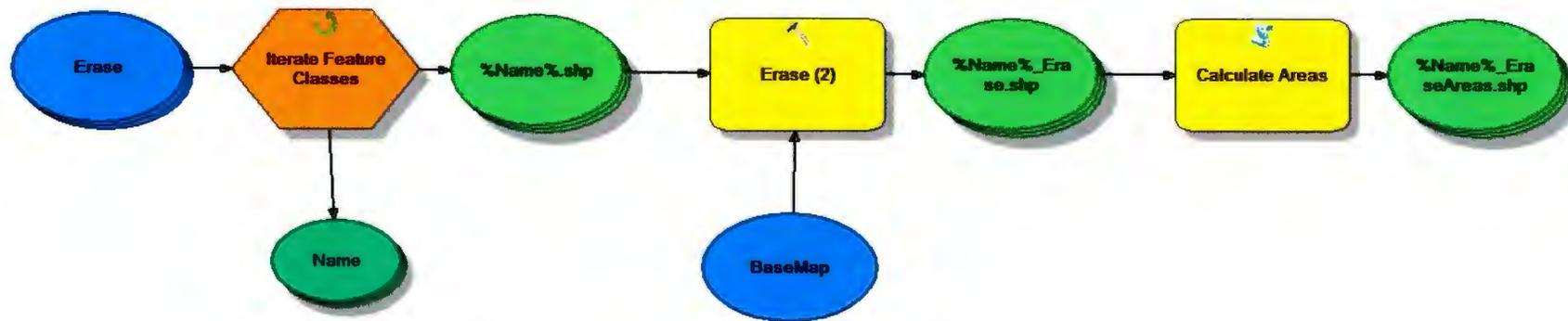


Figure A1 ArcGIS ModelBuilder tool for extracting areas of 95% kernel utilization distributions that were solely in the water. In line substitution (i.e. %Name%) was used to iterate the process for all files. Blue ovals indicate data folders of feature classes (“Erase” = folder of home range polygons, “BaseMap”=map of Newfoundland). The orange hexagon denotes an iteration tool used to loop through all feature classes in the Erase folder for incorporation into the model. Yellow squares indicate ArcGIS tools used to extract and calculate water areas in  $m^2$ . Green circles indicate outputs of the iteration and tools are indicated by the green circles.

**Appendix 2: Individual detection plots for fish tagged in the 2010-2011, and 2011-2012 experiments.**

Figure A2a. Detection plots of transplant fish tagged during the 2010-2011 experiment that left Heffern's Cove. Stars indicate release date. Stations in detection plots are shown progressing from west to east as you move upwards. Open detection markers indicate stations on the north-northwestern shore, while closed markers indicate stations on the south-southeastern shore. Tag IDs are indicated on the y axes.

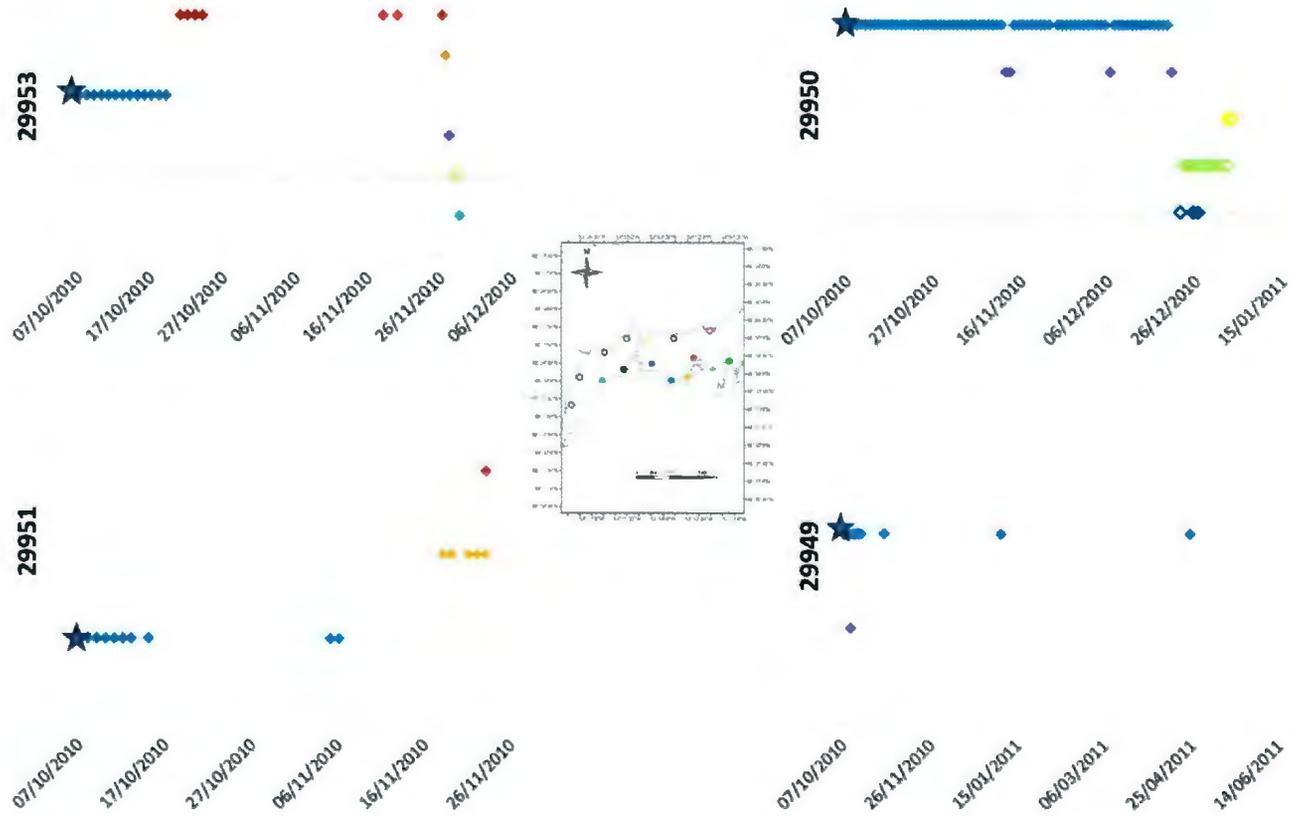


Figure A2a continued. Detection plots of transplant fish tagged during the 2010-2011 experiment that left Heffern's Cove. Stars indicate release date. Stations in detection plots are shown progressing from west to east as you move upwards. Open detection markers indicate stations on the north-northwestern shore, while closed markers indicate stations on the south-southeastern shore. Tag IDs are indicated on the y axes.

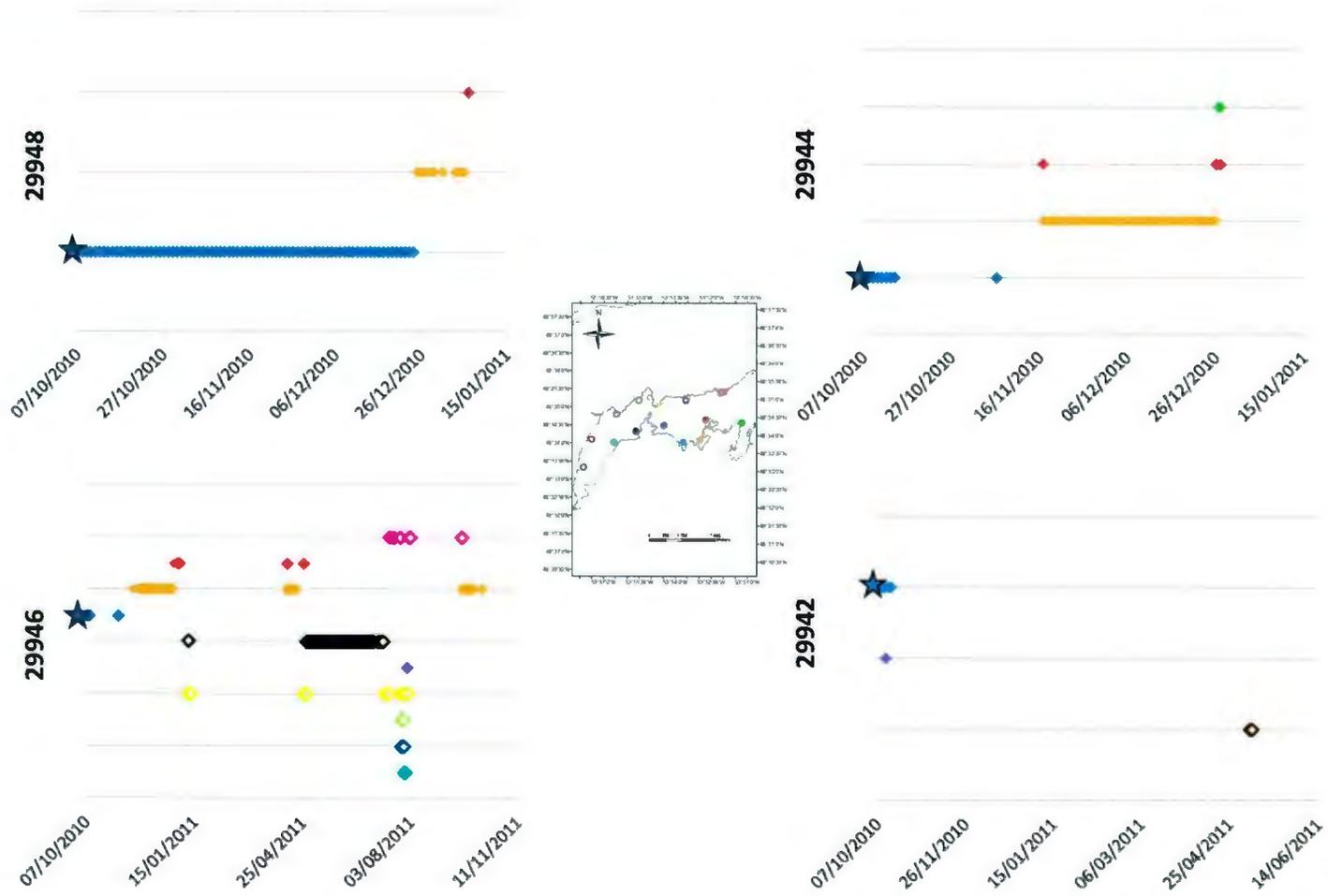


Figure A2a continued. Detection plots of transplant fish tagged during the 2010-2011 experiment that left Heffern's Cove. Stars indicate release date. Stations in detection plots are shown progressing from west to east as you move upwards. Open detection markers indicate stations on the north-northwestern shore, while closed markers indicate stations on the south-southeastern shore. Tag IDs are indicated on the y axes.

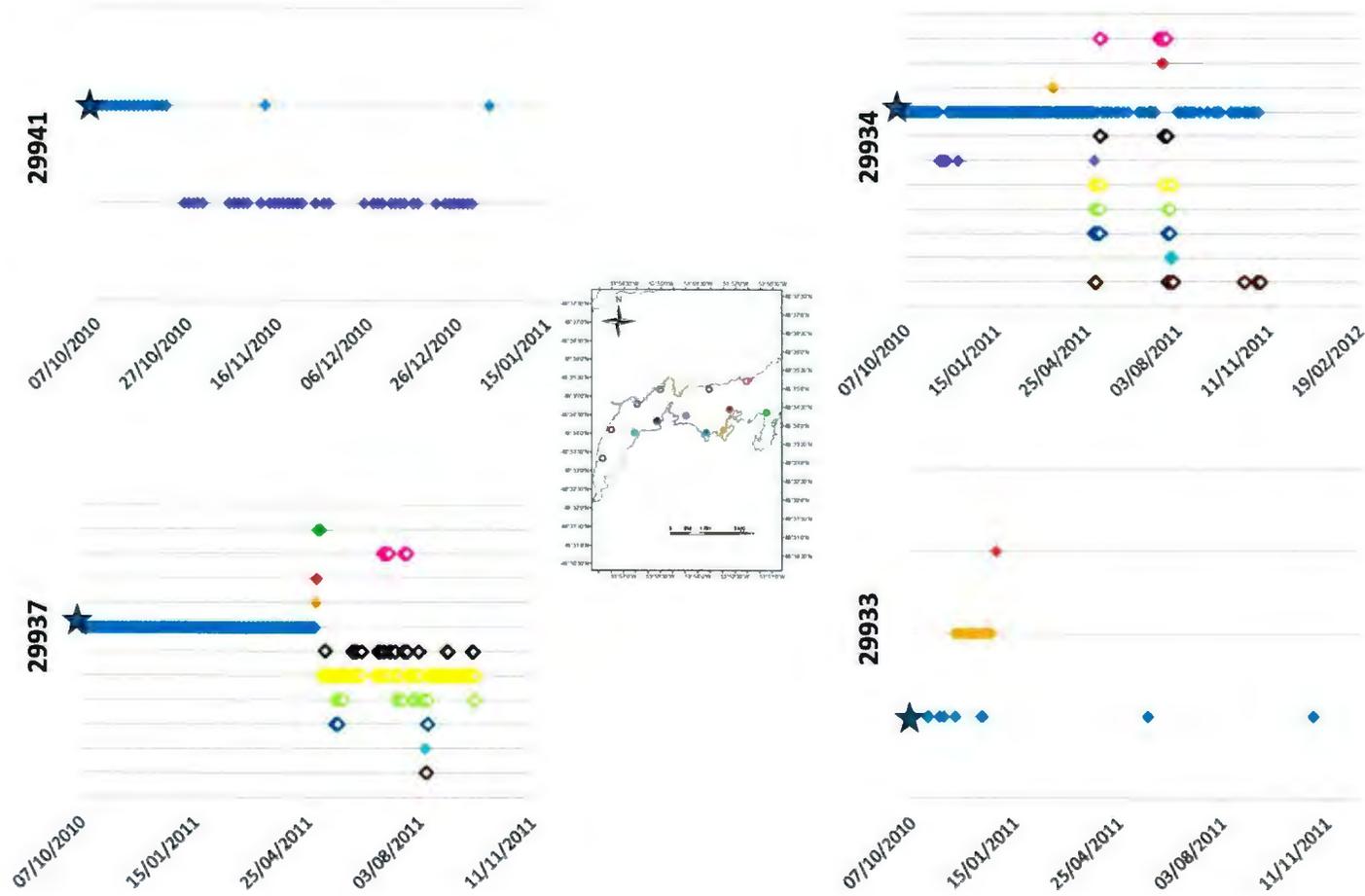


Figure A2b. Detection plots of control fish tagged during the 2010-2011 experiment that left Heffern's Cove. Stars indicate release date. Stations in detection plots are shown progressing from west to east as you move upwards. Open detection markers indicate stations on the north-northwestern shore, while closed markers indicate stations on the south-southeastern shore. Tag IDs are indicated on the y axes.

119

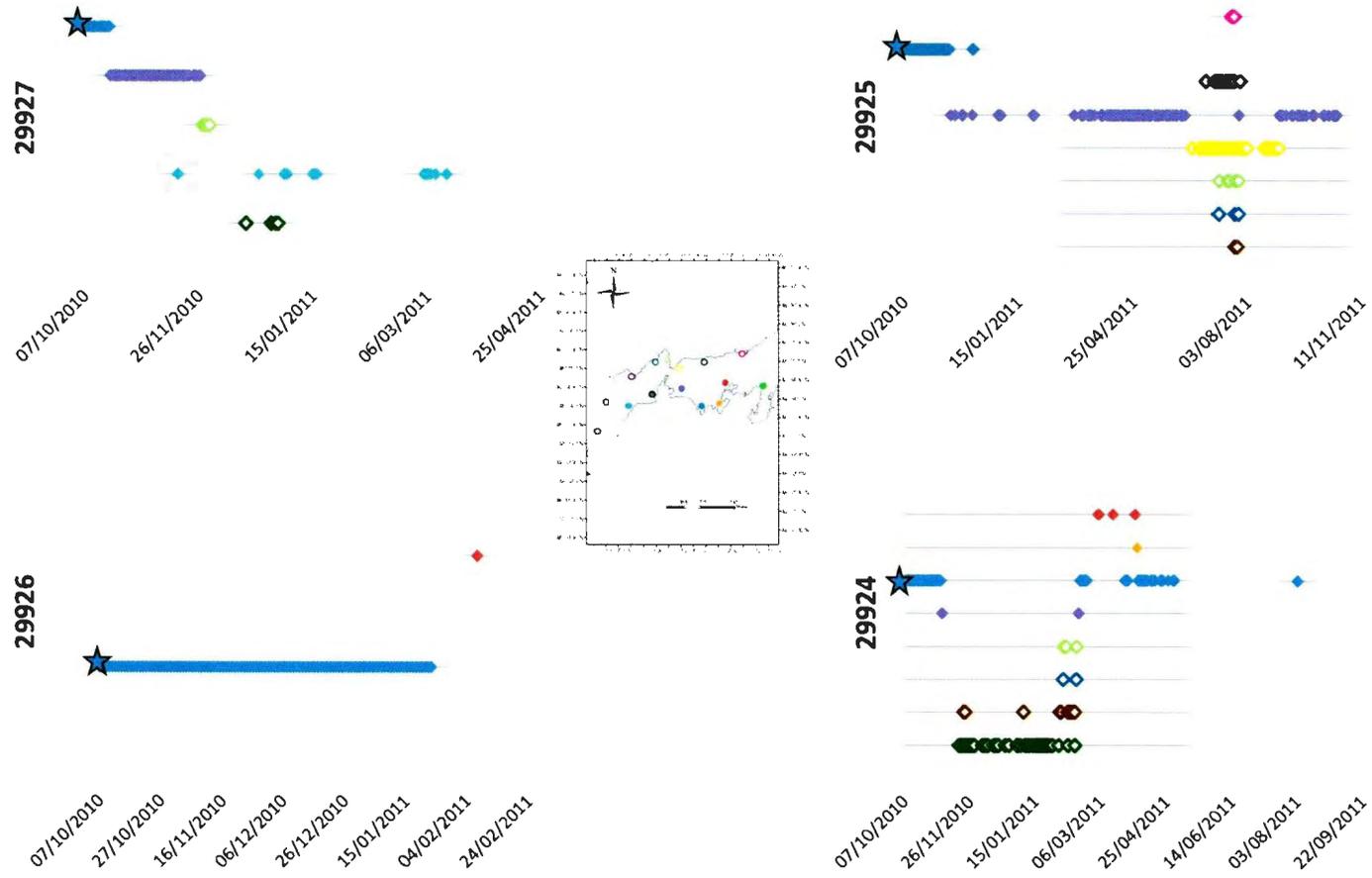


Figure A2b continued. Detection plots of control fish tagged during the 2010-2011 experiment that left Heffern's Cove. Stars indicate release date. Stations in detection plots are shown progressing from west to east as you move upwards. Open detection markers indicate stations on the north-northwestern shore, while closed markers indicate stations on the south-southeastern shore. Tag IDs are indicated on the y axes.

120

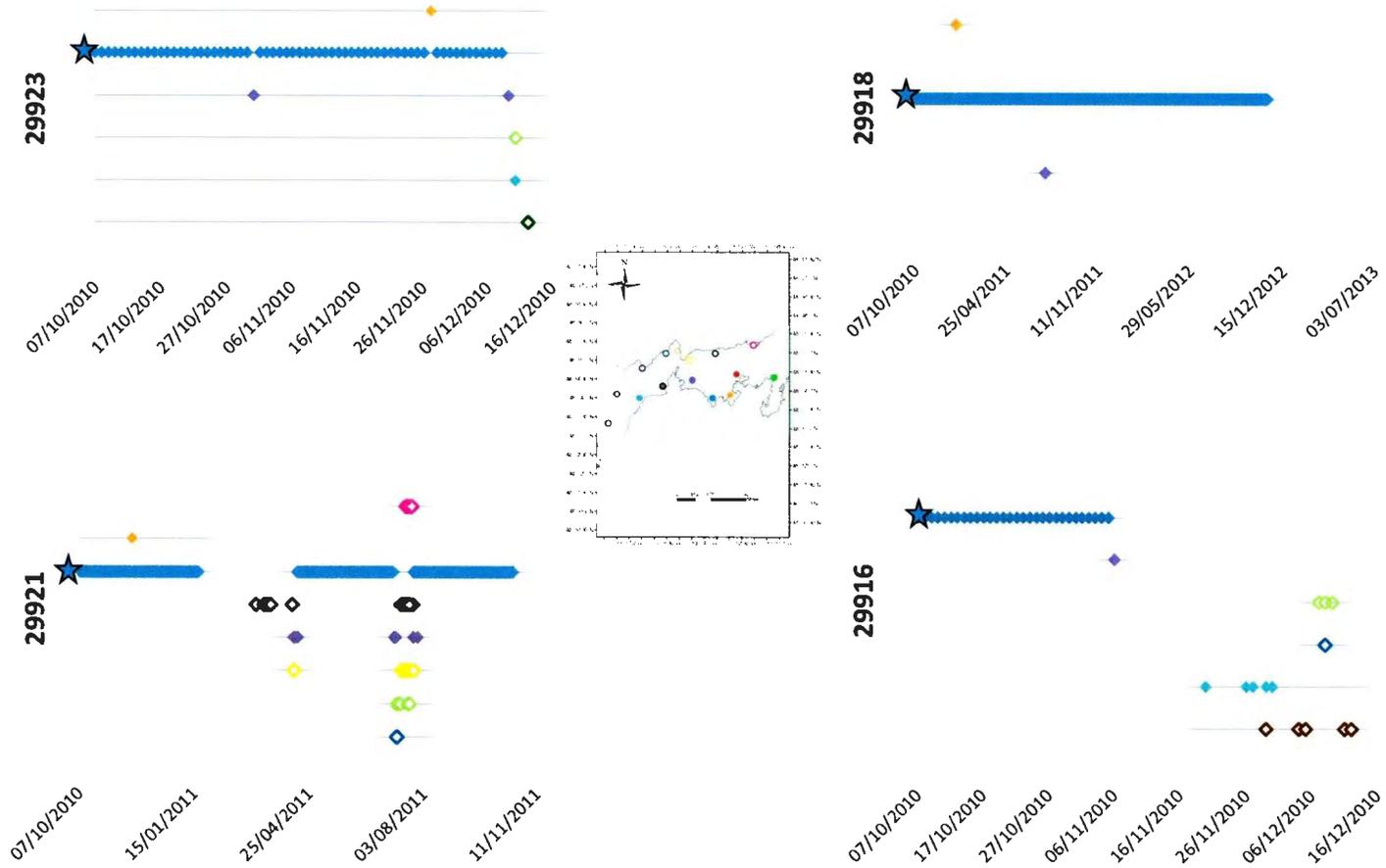


Figure A2b continued. Detection plots of control fish tagged during the 2010-2011 experiment that left Heffern's Cove. Stars indicate release date. Stations in detection plots are shown progressing from west to east as you move upwards. Open detection markers indicate stations on the north-northwestern shore, while closed markers indicate stations on the south-southeastern shore. Tag IDs are indicated on the y axes.

121

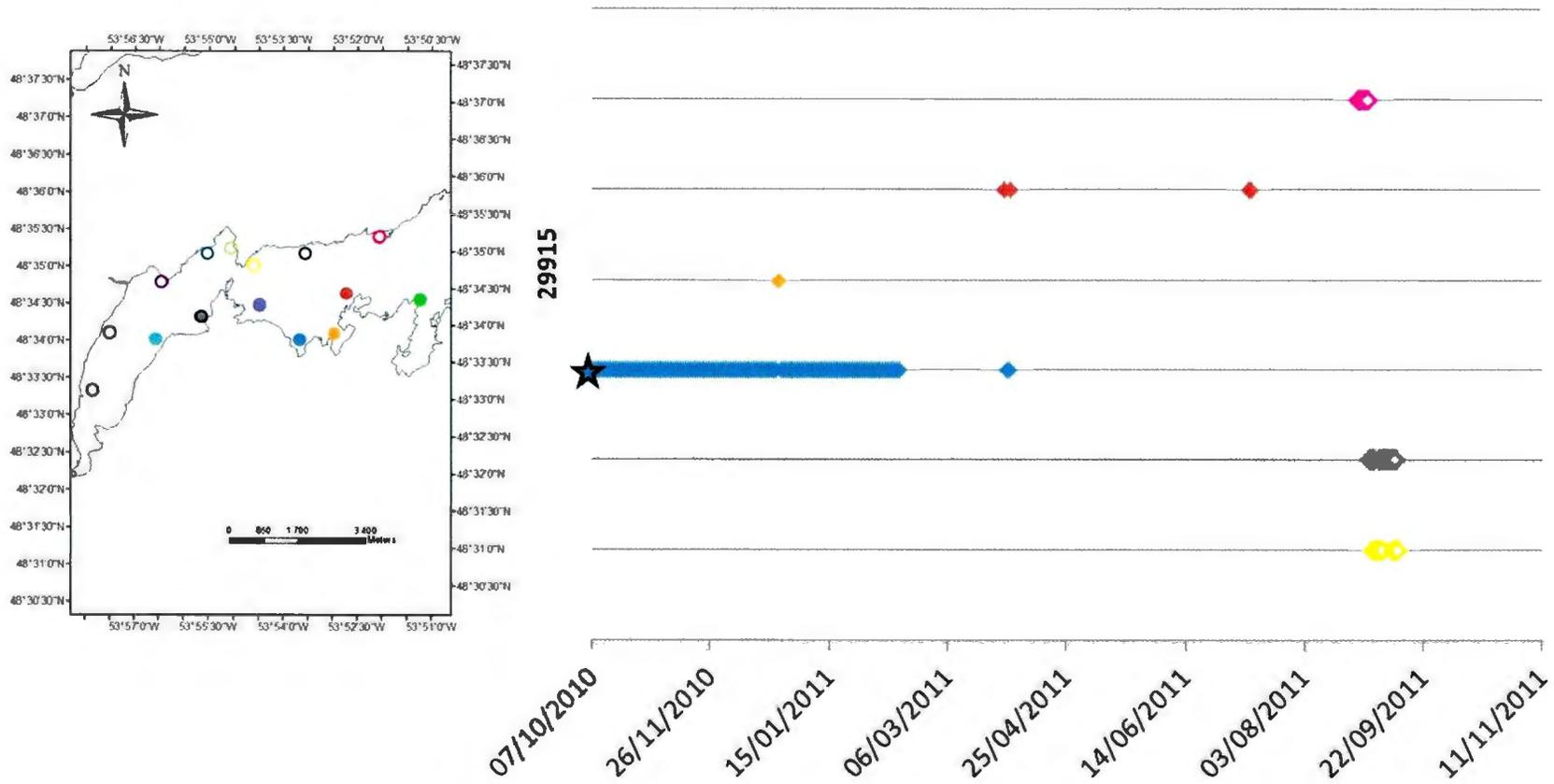


Figure A2c. Detection plots of transplant fish tagged during the 2010-2011 experiment that remained resident. Stars indicate release date. Stations in detection plots are shown progressing from west to east as you move upwards. Tag IDs are indicated on the y axes.

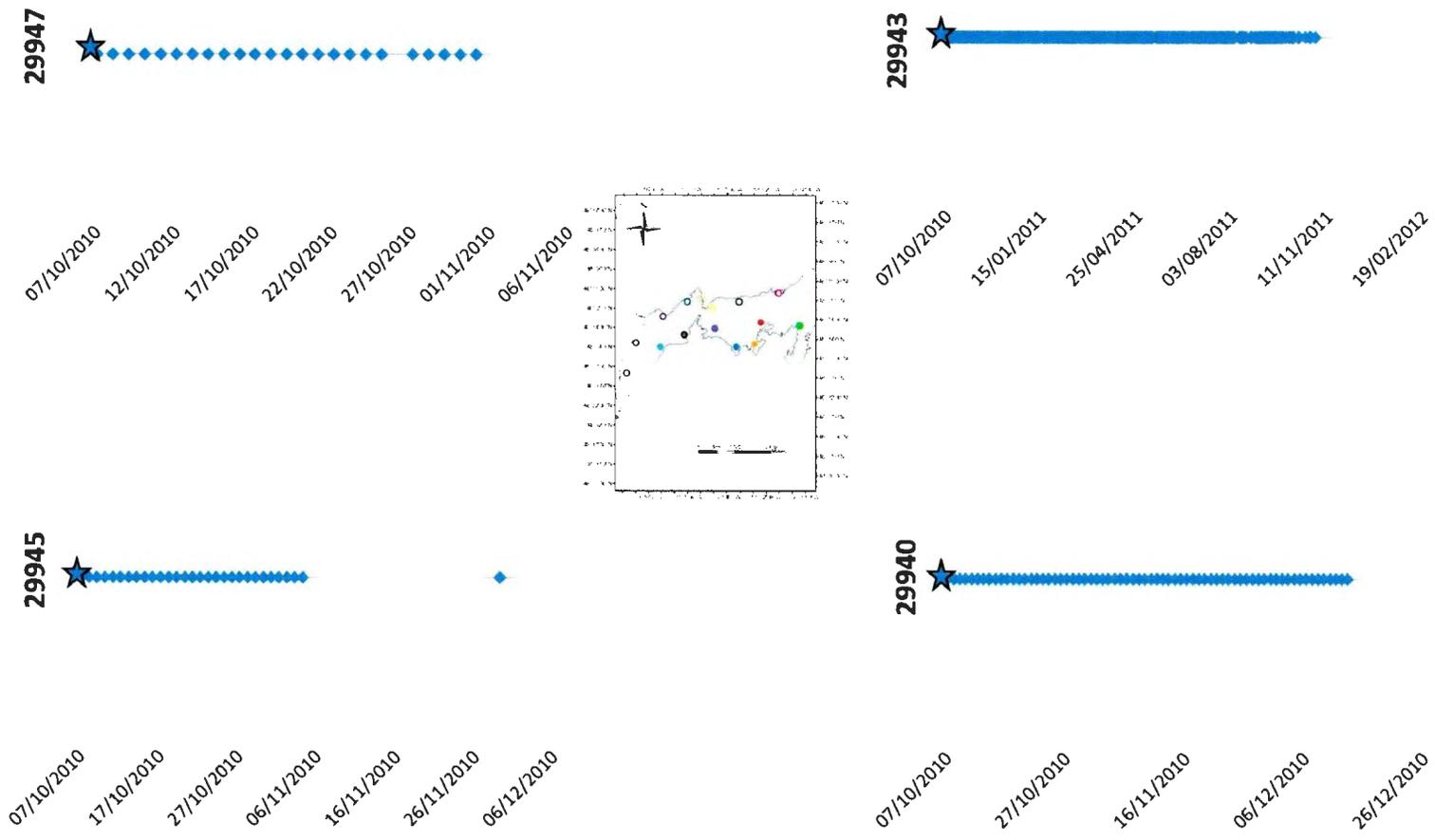


Figure A2c continued. Detection plots of transplant fish tagged during the 2010-2011 experiment that remained resident. Stars indicate release date. Stations in detection plots are shown progressing from west to east as you move upwards. Tag IDs are indicated on the y axes.

123

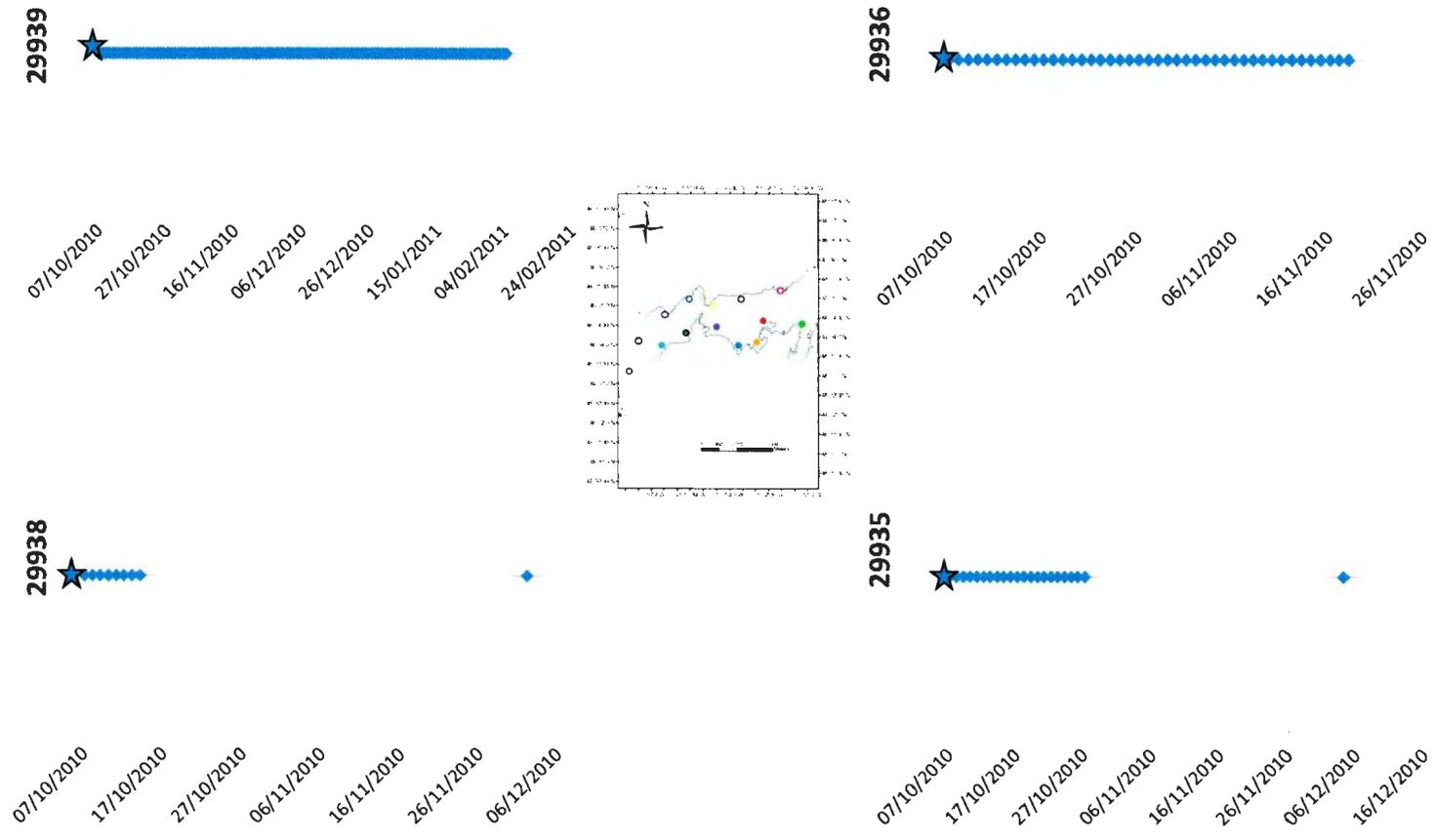


Figure A2d. Detection plots of control fish tagged during the 2010-2011 experiment that remained resident. Stars indicate release date. Stations in detection plots are shown progressing from west to east as you move upwards. Tag IDs are indicated on the y axes.

124

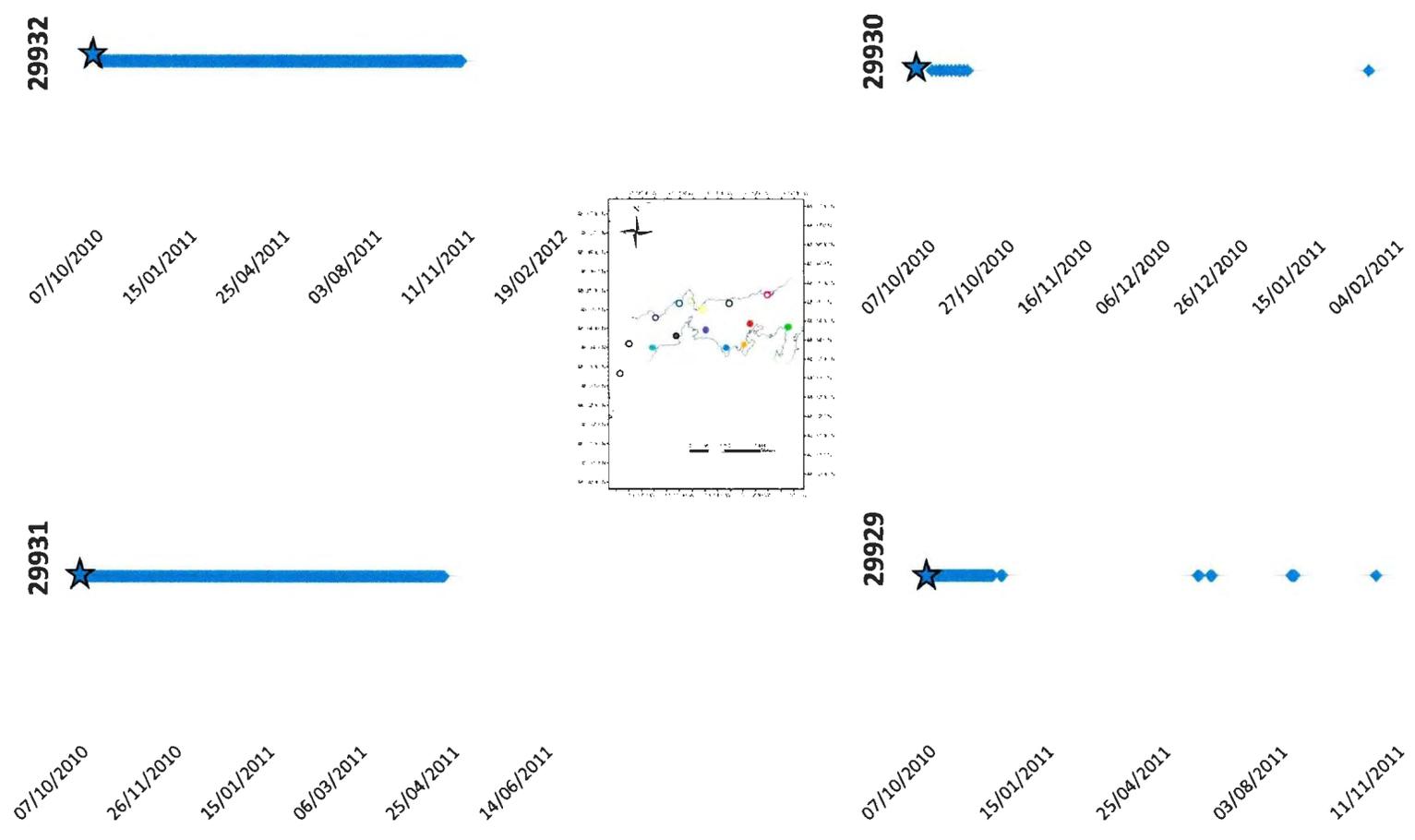


Figure A2d continued. Detection plots of control fish tagged during the 2010-2011 experiment that remained resident. Stars indicate release date. Stations in detection plots are shown progressing from west to east as you move upwards. Tag IDs are indicated on the y axes.

125

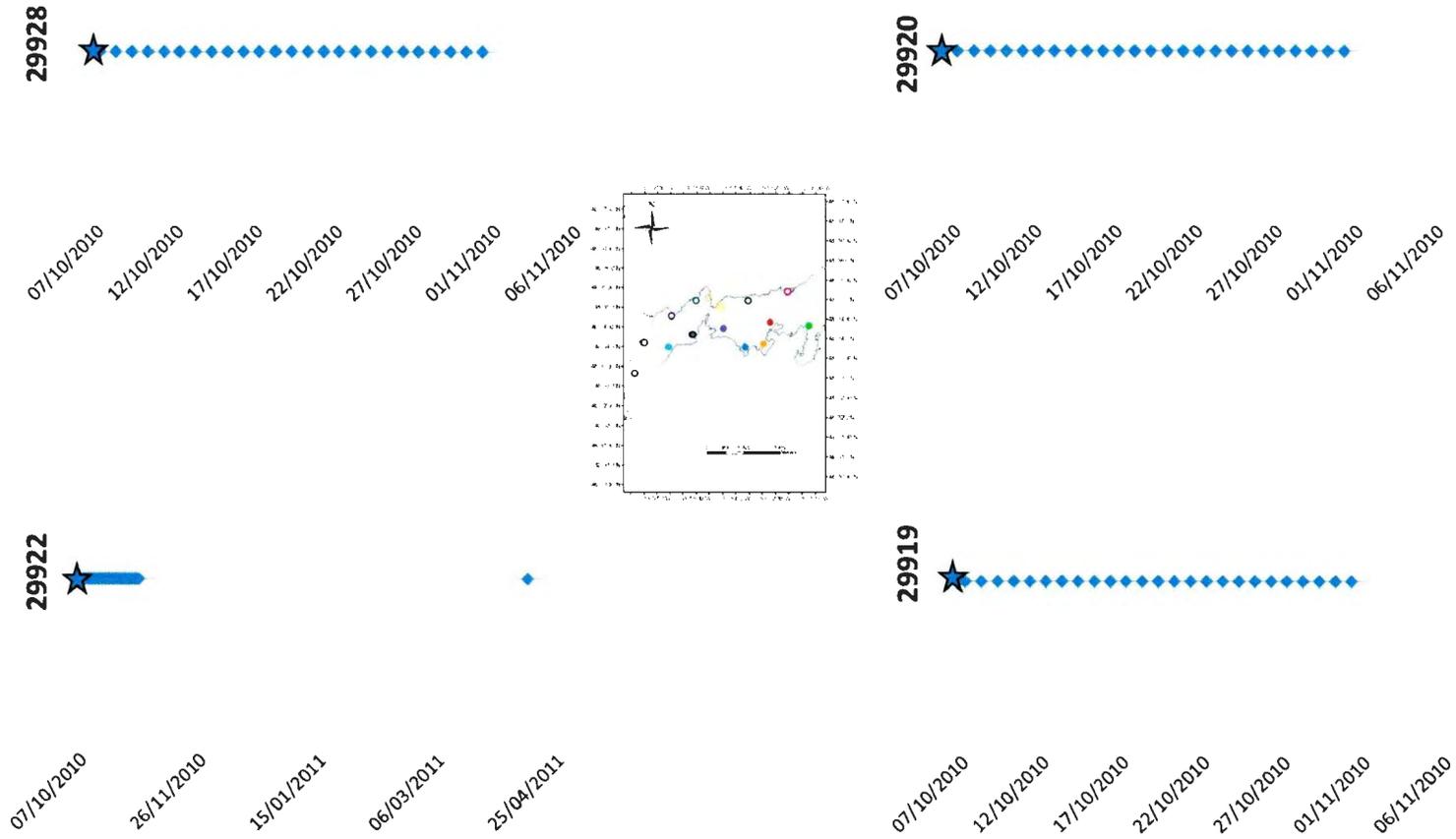


Figure A2d continued. Detection plots of control fish tagged during the 2010-2011 experiment that remained resident. Stars indicate release date. Stations in detection plots are shown progressing from west to east as you move upwards. Tag IDs are indicated on the y axes.

126

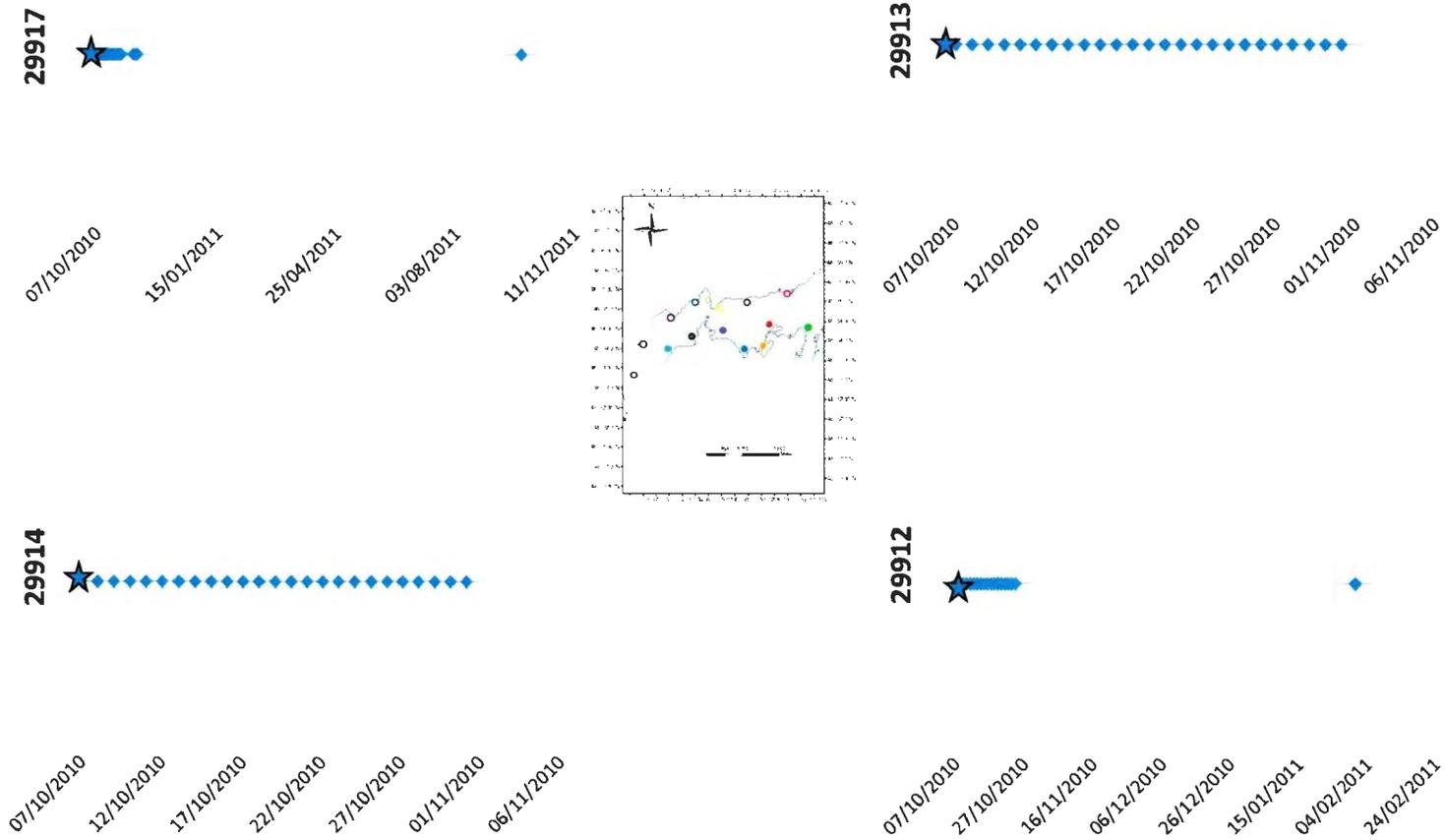


Figure A2e. Detection plots of Buckley's Cove transplant fish tagged during the 2011-2012 experiment that left Heffern's Cove. Stars indicate release date. Stations in detection plots are shown progressing from west to east as you move upwards. Open detection markers indicate stations on the north-northwestern shore, while closed markers indicate stations on the south-southeastern shore. Tag IDs are indicated on the y axes.

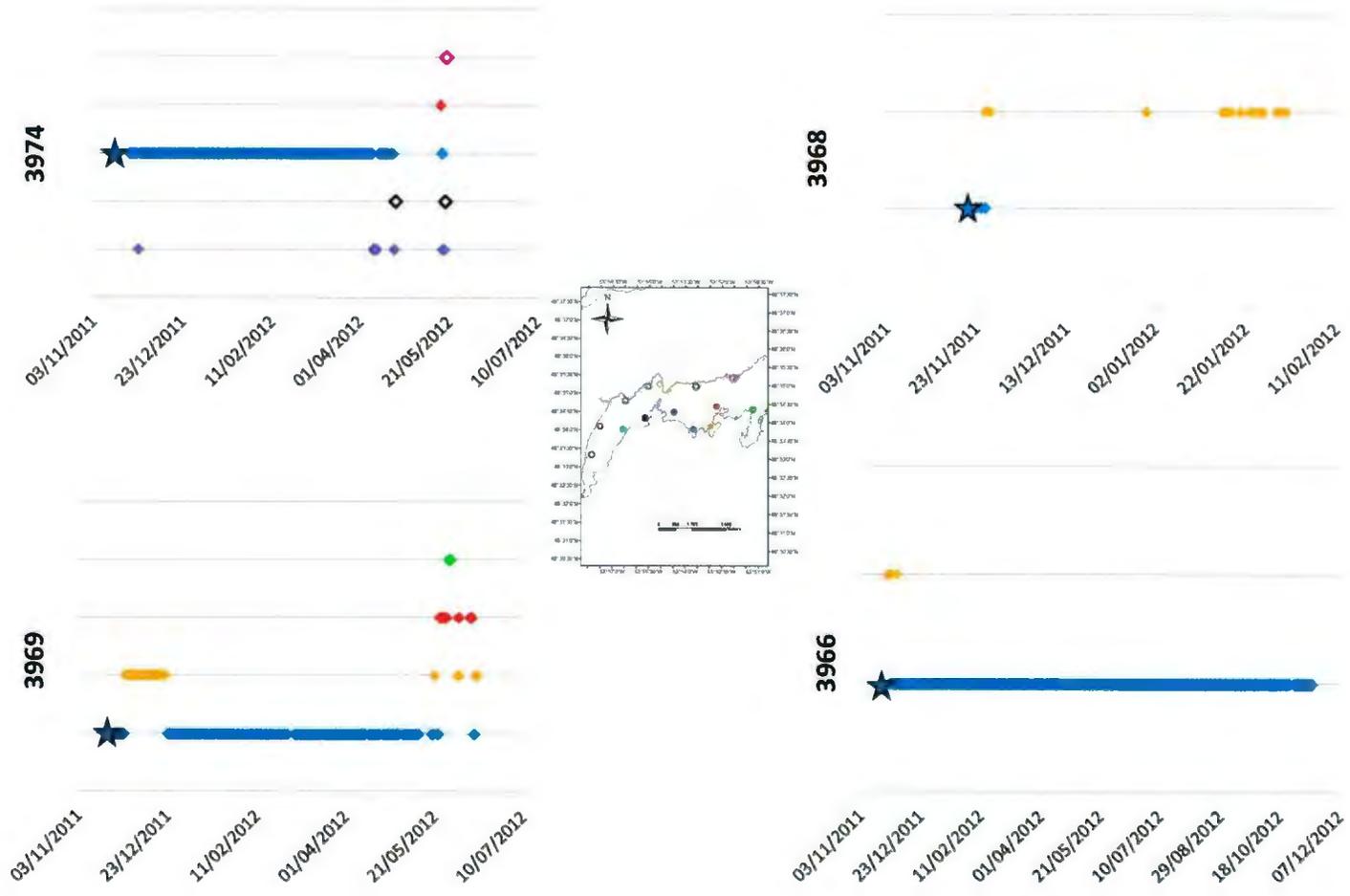


Figure A2e continued. Detection plots of Buckley's Cove transplant fish tagged during the 2011-2012 experiment that left Heffern's Cove. Stars indicate release date. Stations in detection plots are shown progressing from west to east as you move upwards. Open detection markers indicate stations on the north-northwestern shore, while closed markers indicate stations on the south-southeastern shore. Tag IDs are indicated on the y axes.

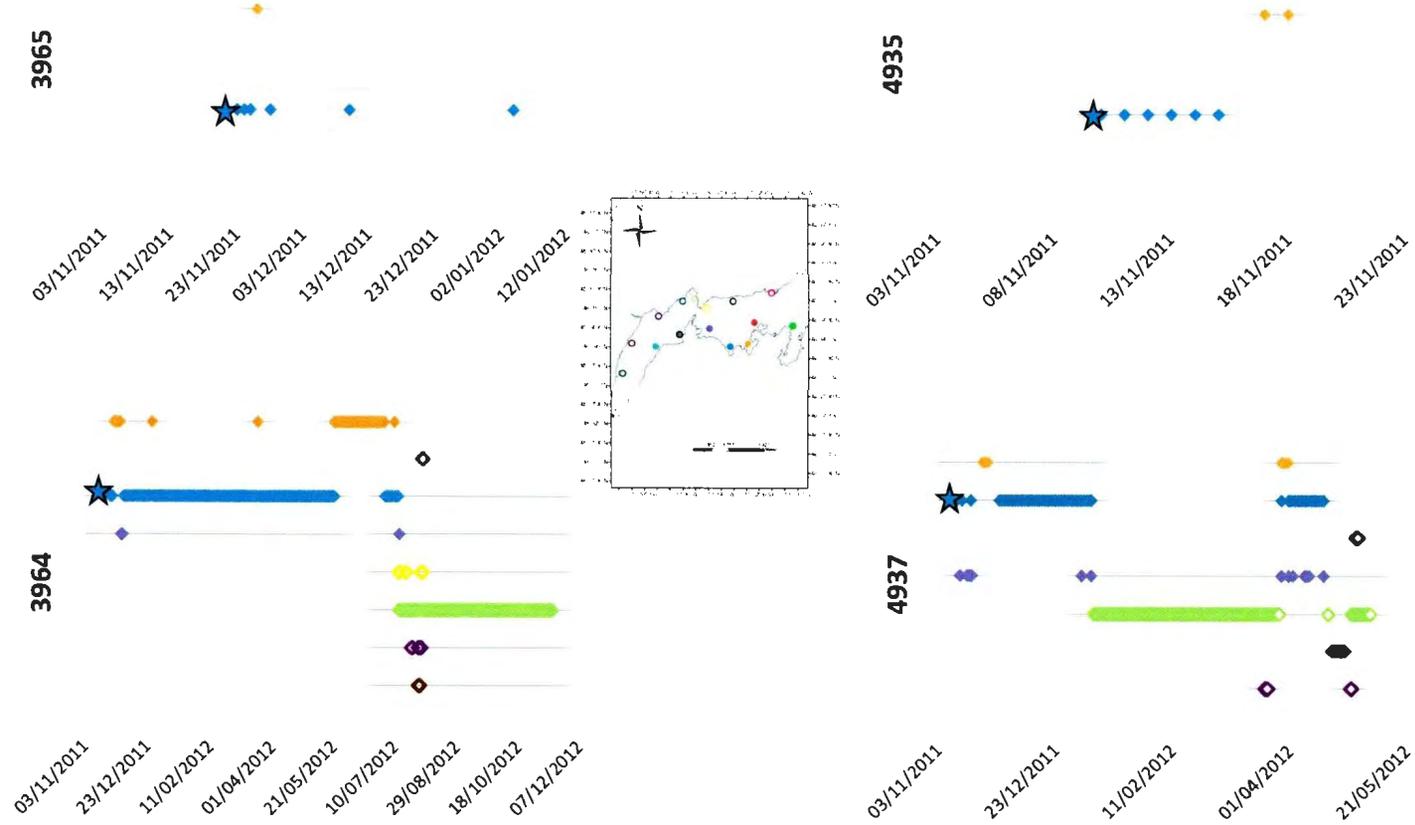


Figure A2e continued. Detection plots of Buckley's Cove transplant fish tagged during the 2011-2012 experiment that left Heffern's Cove. Stars indicate release date. Stations in detection plots are shown progressing from west to east as you move upwards. Open detection markers indicate stations on the north-northwestern shore, while closed markers indicate stations on the south-southeastern shore. Tag IDs are indicated on the y axes.

129

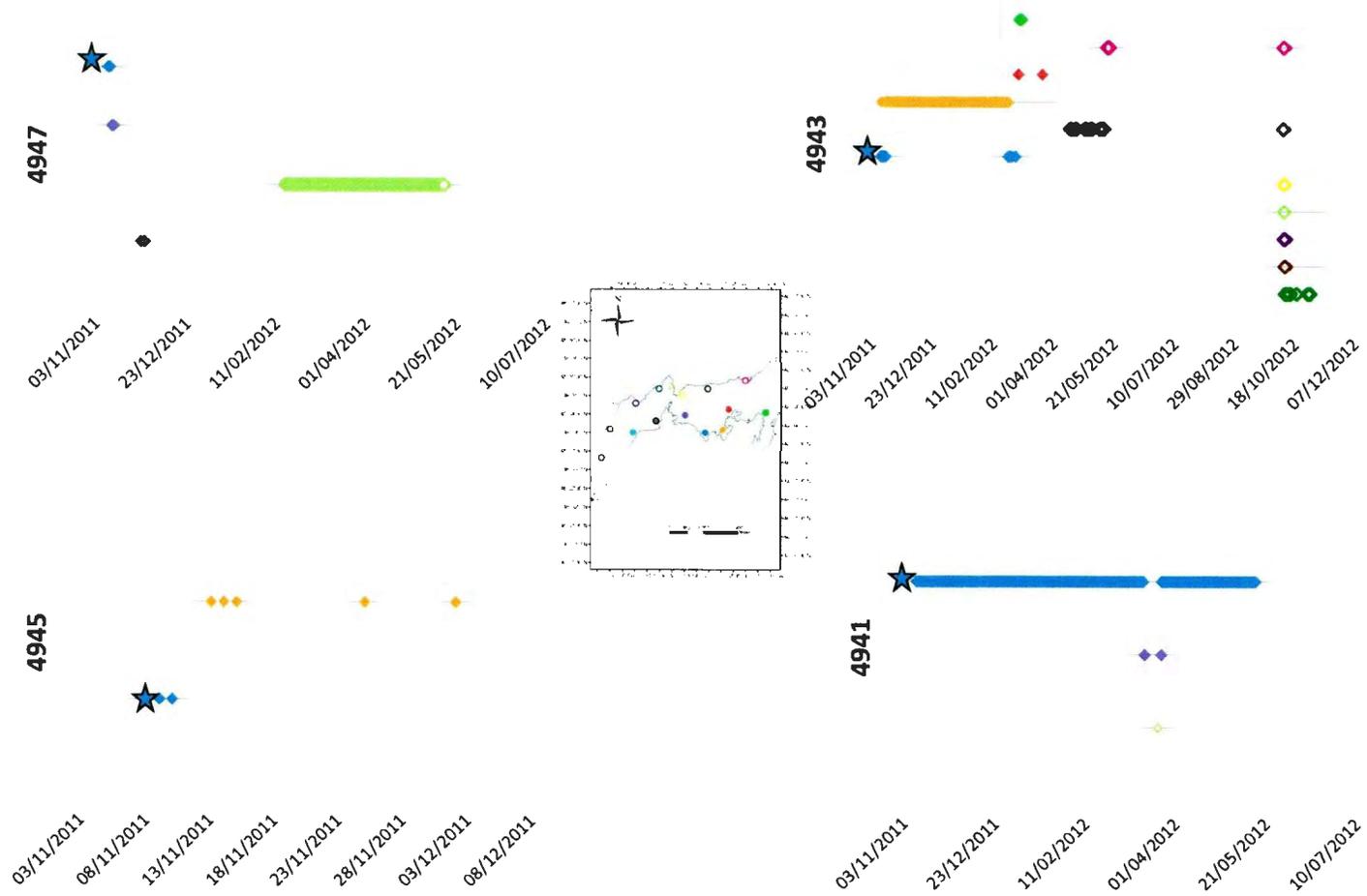


Figure A2e continued. Detection plots of Buckley's Cove transplant fish tagged during the 2011-2012 experiment that left Hefferm's Cove. Stars indicate release date. Stations in detection plots are shown progressing from west to east as you move upwards. Open detection markers indicate stations on the north-northwestern shore, while closed markers indicate stations on the south-southeastern shore. Tag IDs are indicated on the y axes.

130

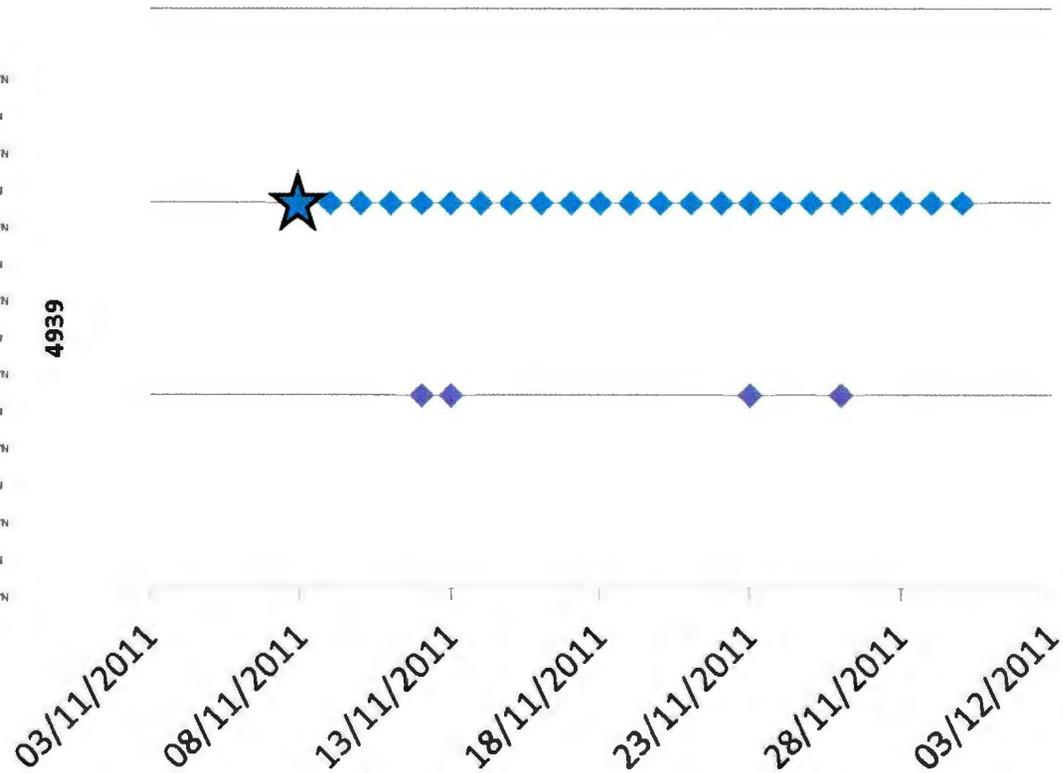
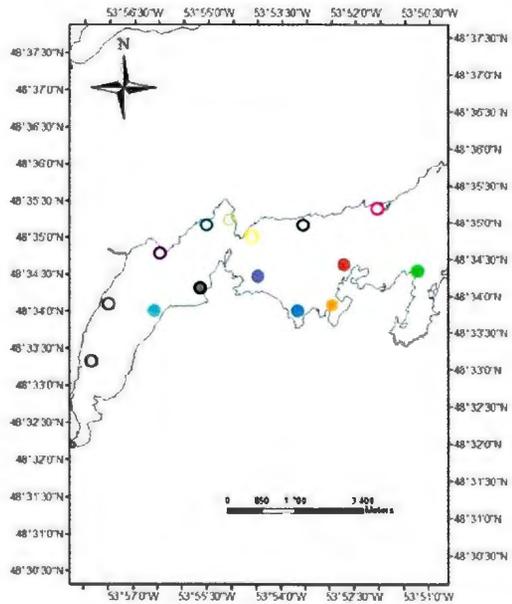


Figure A2f. Detection plots of Heffern's Cove transplant fish tagged during the 2011-2012 experiment that left Buckley's Cove. Stars indicate release date. Stations in detection plots are shown progressing from west to east as you move upwards. Open detection markers indicate stations on the north-northwestern shore, while closed markers indicate stations on the south-southeastern shore. Tag IDs are indicated on the y axes.

131

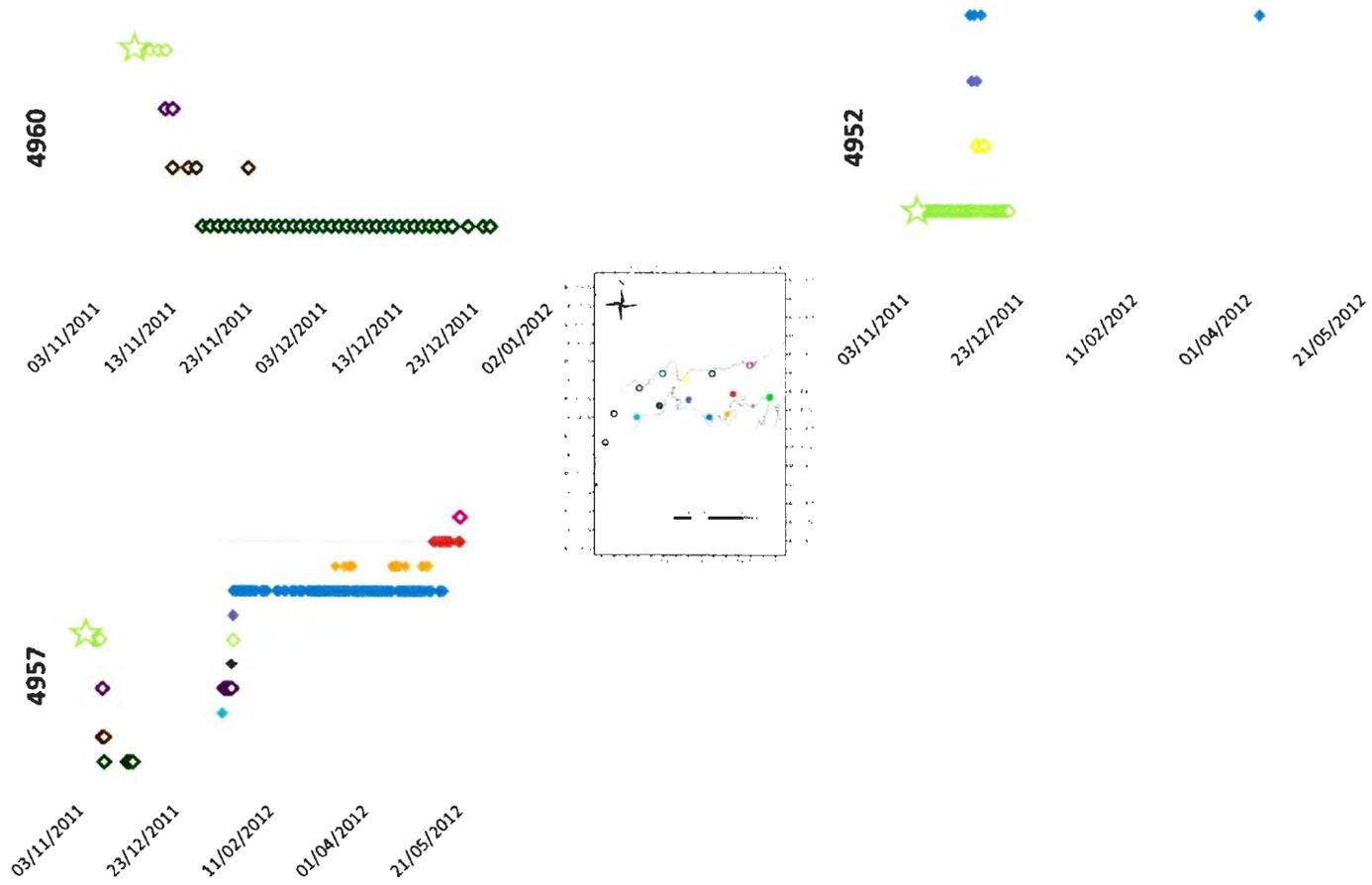


Figure A2g. Detection plots of Buckley's Cove control fish tagged during the 2011-2012 experiment that left Buckley's Cove. Stars indicate release date. Stations in detection plots are shown progressing from west to east as you move upwards. Open detection markers indicate stations on the north-northwestern shore, while closed markers indicate stations on the south-southeastern shore. Tag IDs are indicated on the y axes.

132

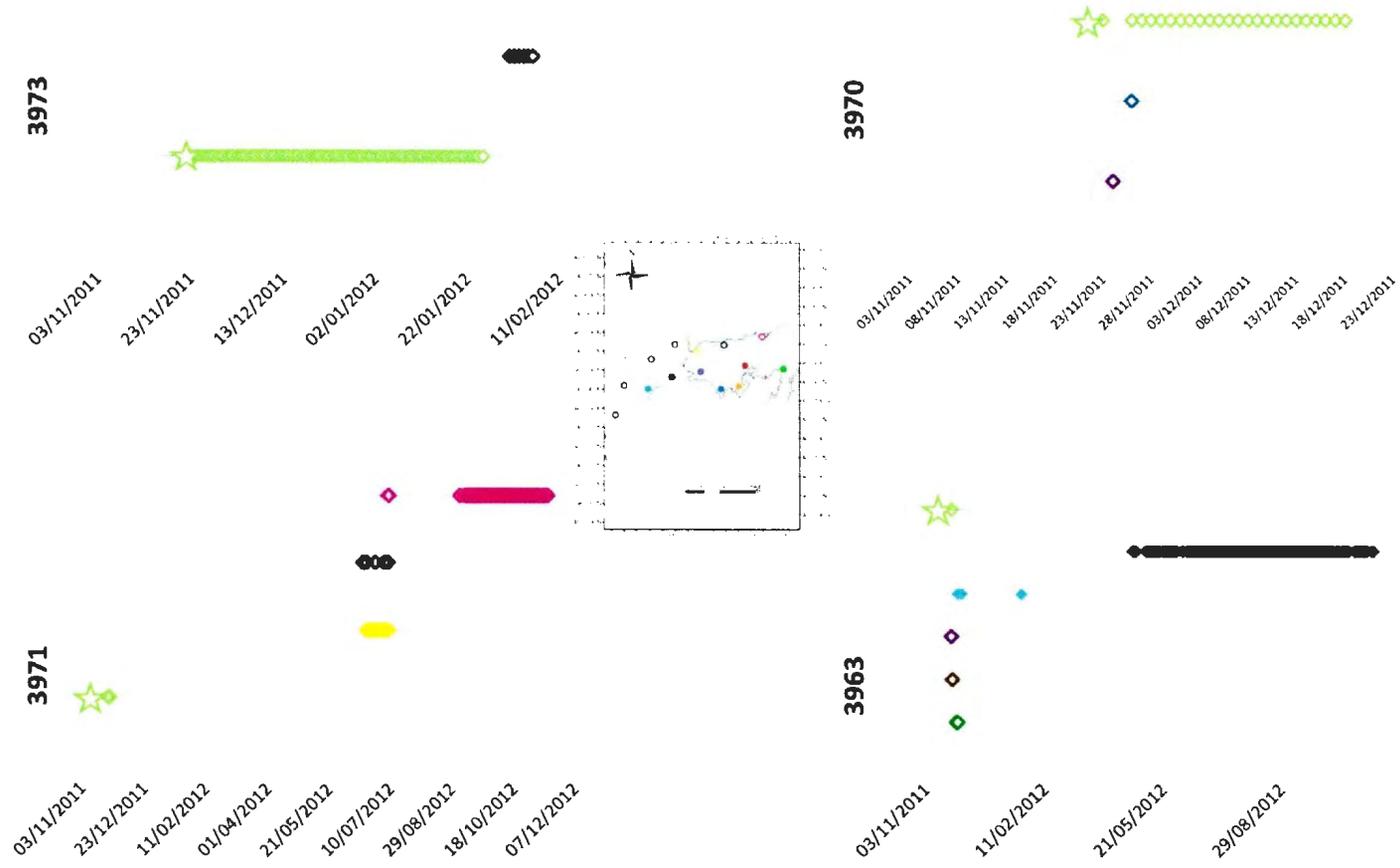


Figure A2g. Detection plots of Buckley's Cove control fish tagged during the 2011-2012 experiment that left Buckley's Cove. Stars indicate release date. Stations in detection plots are shown progressing from west to east as you move upwards. Open detection markers indicate stations on the north-northwestern shore, while closed markers indicate stations on the south-southeastern shore. Tag IDs are indicated on the y axes.

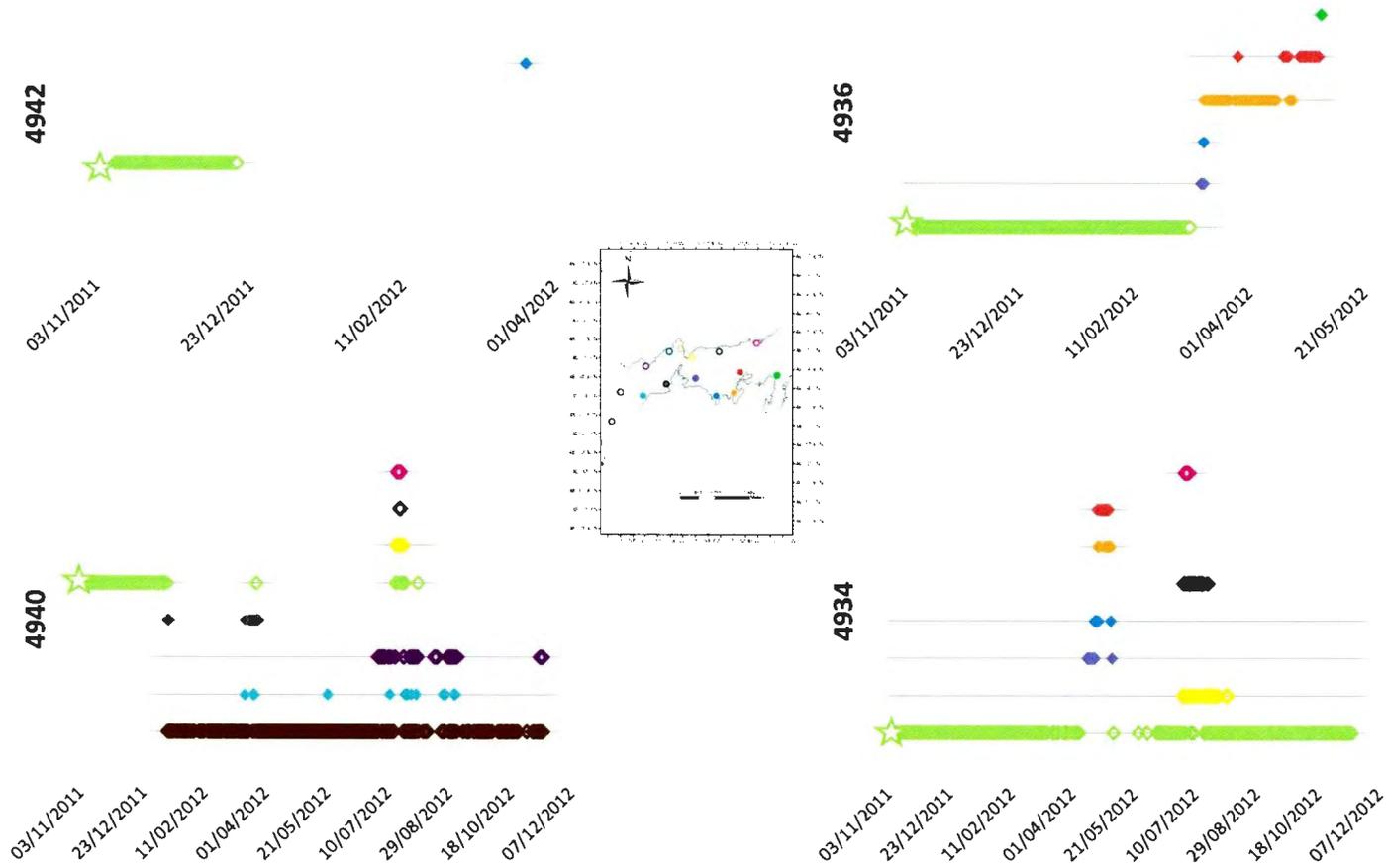


Figure A2h. Detection plots of Heffern's Cove control fish tagged during the 2011-2012 experiment that left Heffern's Cove. Stars indicate release date. Stations in detection plots are shown progressing from west to east as you move upwards. Open detection markers indicate stations on the north-northwestern shore, while closed markers indicate stations on the south-southeastern shore. Tag IDs are indicated on the y axes.

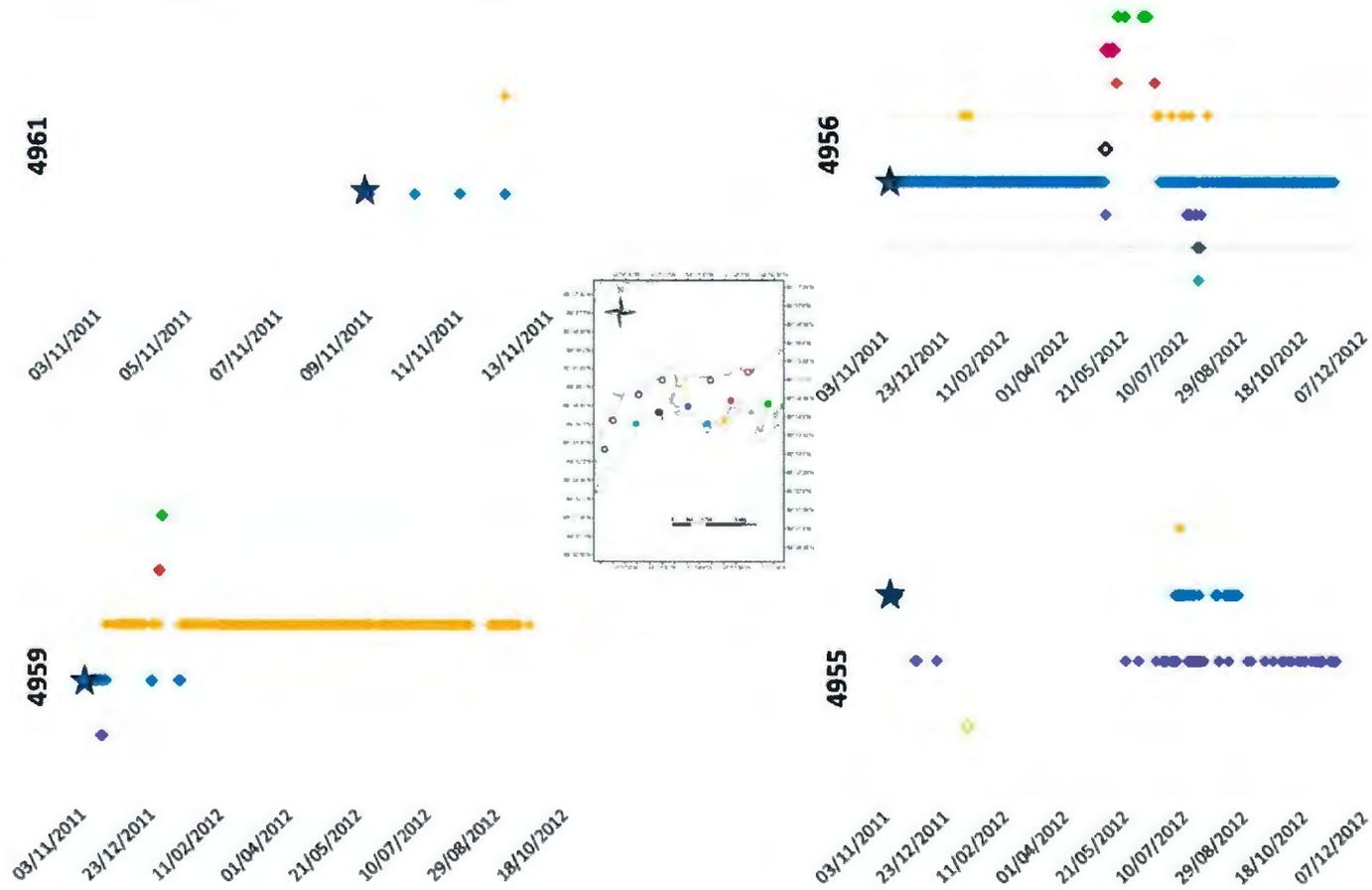


Figure A2h continued. Detection plots of Heffern's Cove control fish tagged during the 2011-2012 experiment that left Heffern's Cove. Stars indicate release date. Stations in detection plots are shown progressing from west to east as you move upwards. Open detection markers indicate stations on the north-northwestern shore, while closed markers indicate stations on the south-southeastern shore. Tag IDs are indicated on the y axes.

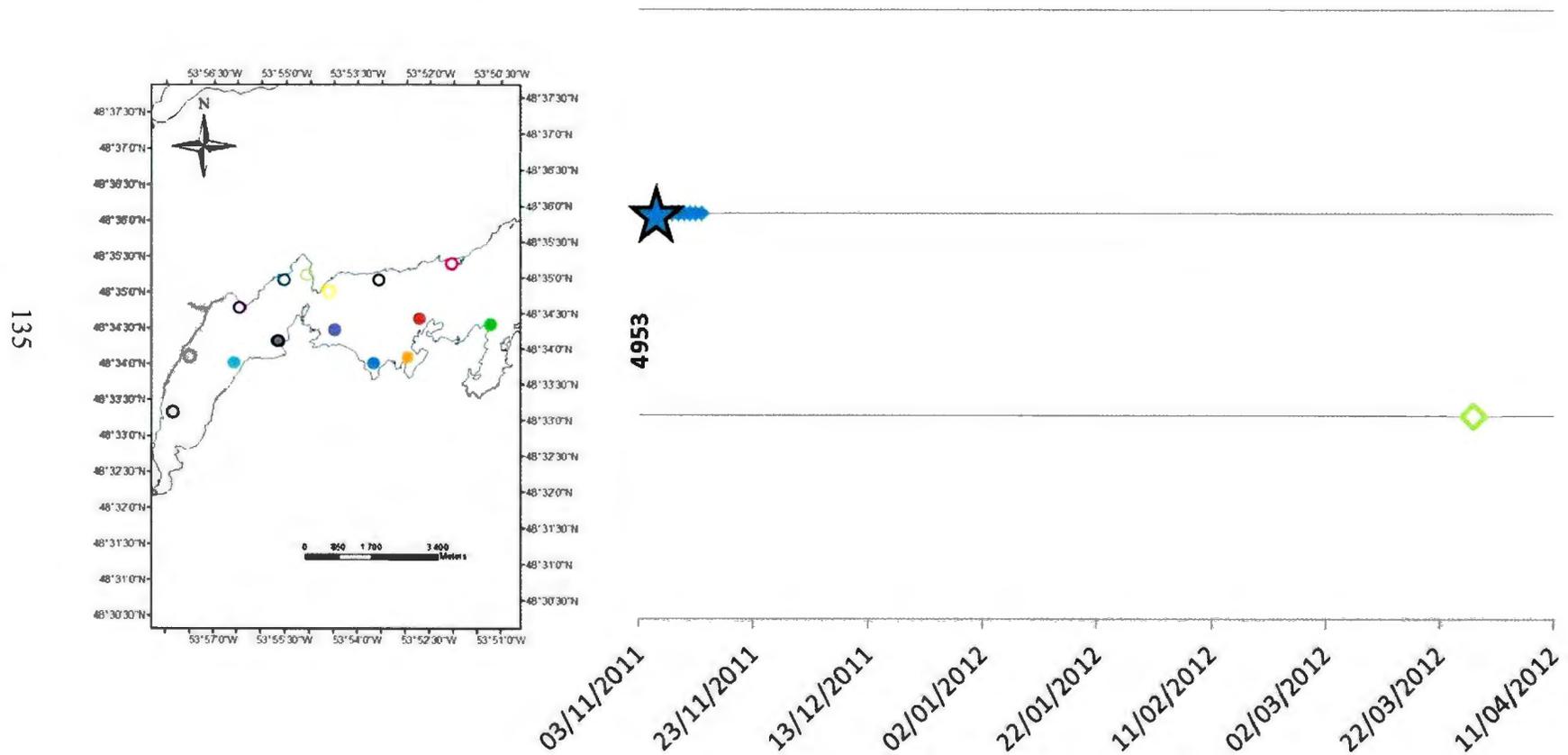


Figure A2i. Detection plots of transplant fish tagged during the 2011-2012 experiment that remained resident. Stars indicate release date. Stations in detection plots are shown progressing from west to east as you move upwards. Tag IDs are indicated on the y axes.

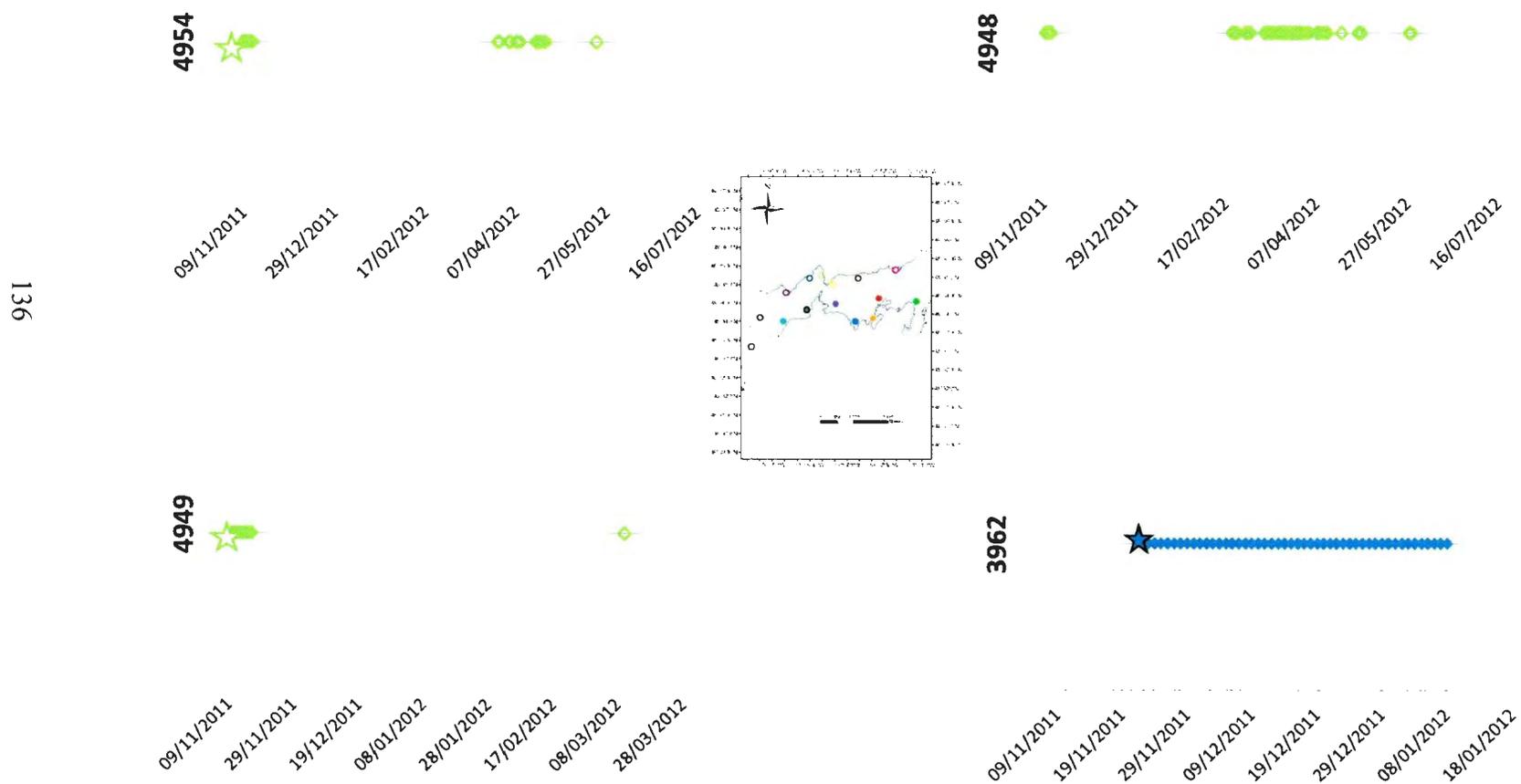


Figure A2i. Detection plots of control fish tagged during the 2011-2012 experiment that remained resident. Stars indicate release date. Stations in detection plots are shown progressing from west to east as you move upwards. Tag IDs are indicated on the y axes.

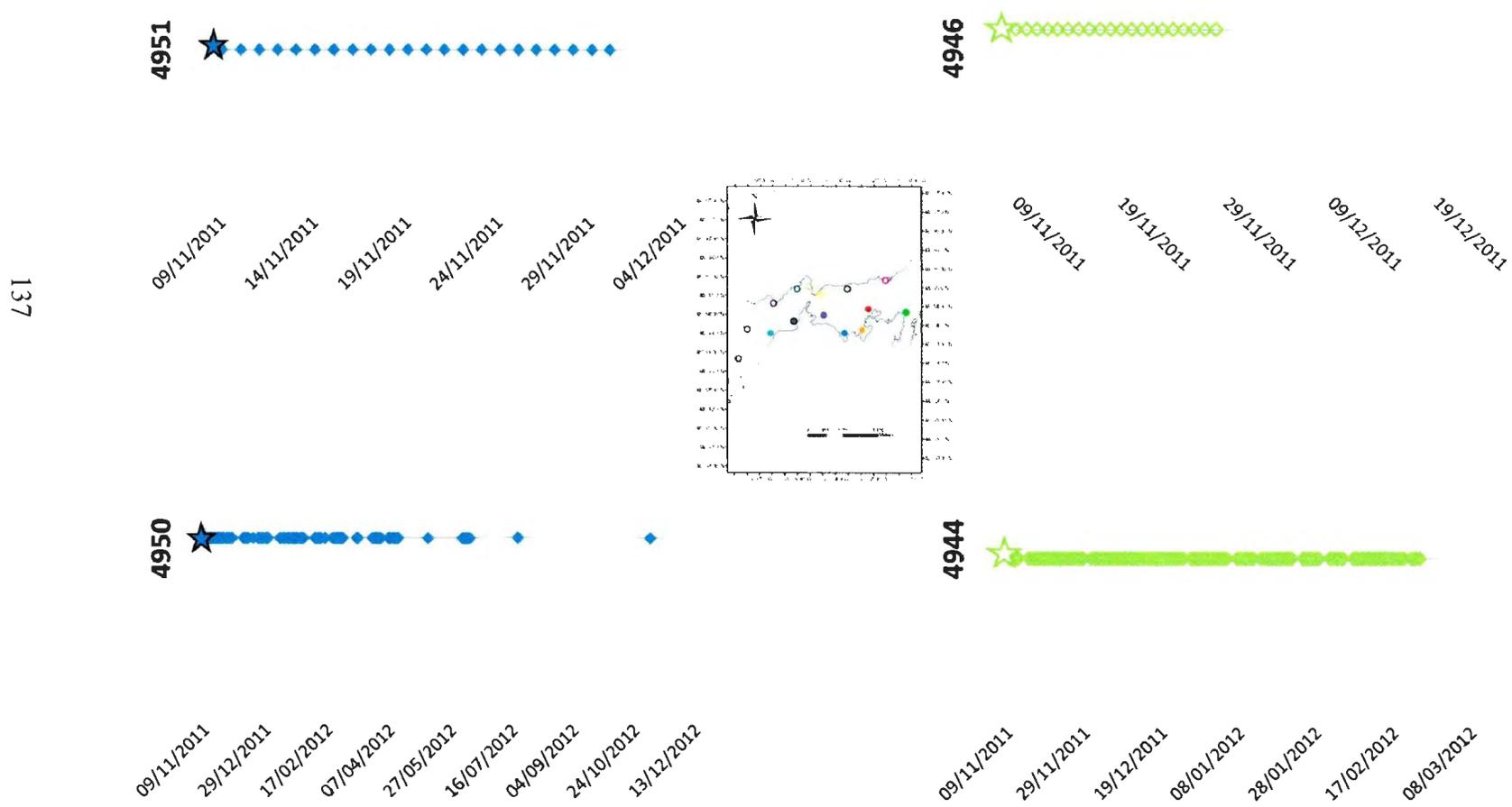


Figure A2i. Detection plots of control fish tagged during the 2011-2012 experiment that remained resident. Stars indicate release date. Stations in detection plots are shown progressing from west to east as you move upwards. Tag IDs are indicated on the y axes.

