

Fleet Dynamics around a Seasonal Regulatory Closure on the Scotian Shelf.

by

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A Thesis submitted to the Faculty of Graduate Studies of
The University of Manitoba
in partial fulfilment of the requirements of the degree of

MASTER OF SCIENCE

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Abstract

I investigate aspects of fleet dynamics in a mobile gear, groundfish fishery, on the Scotian Shelf; an area subject to a seasonal area closure. Firstly, the direct impacts of the closure on the redistribution of fishing effort and the resultant catch rates of those “fishing the line” (FTL) were examined. Effort was found to concentrate within 30km of the closure boundary. Two areas of potential FTL strategy were identified, which produced variable catch rate trends. East of the closure, areas of highest catch rate corresponded to areas of greatest effort, while to the west, catch rate was often equalized throughout the region, analogous to the ideal free distribution (IFD). Secondly, two effort distributional models were compared: an IFD-based isodar model and a discrete choice model. The isodar was determined to be the preferred model because of both its consistently superior predictive performance and its greater simplicity.

Acknowledgements

Foremost I thank my advisor, Darren Gillis, for his support, guidance and wisdom, without which this thesis would not be possible. I feel fortunate to have had you as my supervisor. I also thank the rest of my committee, Jim Hare and Gary Crow, for your constructive comments and input throughout this process.

Many thanks, to those at Fisheries and Oceans Canada who supported this project, specifically, Peter Comeau, Jerry Black, and Peter Hurley. As well, I thank my lab-mate, Colin Charles, who allowed me to consistently bounce ideas off of him. Finally, I thank my parents for their unwavering support; without which, who knows where I'd be.

Funding was provided primarily through a Discovery Grant to Dr. D.M. Gillis from the Natural Sciences and Engineering Research Council (NSERC), Canada.

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Chapter 1

General Introduction

The focus of my MSc thesis is an examination of fleet dynamics within a mobile gear fishery in a region subject to a seasonal area closure on the Scotian Shelf. The analysis is divided into two major projects. The first project (Chapter 2) examines of the direct effects of the area closure on the redistribution of fishing effort within the fishery as well as a micro-distributional examination of fishing effort in areas directly adjacent to the closure and its resultant influence on catch rate. The second project (Chapter 3) is a comparative analysis of two effort distribution models within the fishery: an isodar model (Morris 1987) based on the ideal free distribution (IFD; Fretwell and Lucas 1970) and a multinomial logistic regression model (McFadden 1974) examining individual location choice among distinct fishing regions. Table 1.1 lists the abbreviations used throughout the thesis.

The fishery examined is the NAFO Division 4X groundfish otter trawl fishery. 'Otter trawl' refers to the method of fishing where a net is towed from the back (stern) of a vessel with the mouth of the net kept open with use of otter boards, rectangular boards mounted to the sides of the net, which use hydrodynamic forces to prevent the mouth from closing. The mouth is kept open vertically with use of floats at the top and weights at the bottom. The funnel-shaped net is towed at approximately 4 knots collecting fish in the 'cod end', the cone shaped trailing end of the net. In this fishery trawls last on average 3 to 4 hours or until the cod end is sufficiently full, which captains can monitor with use of catch sensors attached to the net. The vessels in this fleet target groundfish, which encompass larger demersal species such as gadiformes and flatfish. Catch levels are regulated using a species specific individual transferable quota (ITQ) system, primarily targeting haddock (*Melanogrammus aeglefinus*), redfish (*Sebastes* spp.), and pollock (*Pollachius virens*), with limited targeting of Atlantic cod (*Gadus morua*), winter flounder (*Pseudopleuronectes americanus*), and silver hake (*Merucius bilinearis*).

Fleet dynamics was first identified by Hilborn (1985) as an important component of fisheries science, also including: population dynamics, processing, and marketing. Hilborn further categorized fleet dynamics into four groups: 1) investment/disinvestment, 2) effort allocation, 3) harvest efficiencies, and 4) keeping/discarding of catch. He then highlighted that little research had been conducted in these areas despite their importance in understanding fisheries and making accurate abundance estimates. Species abundance is often estimated utilizing commercial catch rate (catch-per-unit-effort; CPUE) information, which can be misleading when elements of fleet dynamics are not considered. Hilborn and Walters (1992) described two patterns in which CPUE is not proportional to fish abundance; hyperstability and hyperdepletion. Hyperstability occurs when species abundances decreased faster than commercial CPUE; that is CPUE remains relatively stable even though abundances are declining. Hyperdepletion is the reverse, when decreases are found in CPUE while abundance levels remain unchanged or at least are much less decreased. Both of these situations can be catastrophic to a fishery if quota levels are set based on the resultantly misleading CPUE estimates. Hyperstability has been blamed on the collapse of northern cod in the early 1990s (Swain and Wade 1993; Rose and Kulka 1999). As cod abundance declined, rather than density decreasing, its distribution contracted, maintaining CPUE levels, and leaving fisheries managers unaware of the magnitude of the problem they were about to face. Additionally, hyperstability has been found in George's Bank haddock (Crecco and Overholts 1990) and in a meta-analysis of European gadiformes and flatfish fisheries (Harley et al. 2001). Hyperdepletion has been less commonly mentioned in the literature and most commonly occurs with cryptic species that can access an area of refuge within a fishery. Hilborn and Walters (1992) suggest hyperdepletion may have occurred in post World War II South Australia rock lobster (*Jasus novaehollandiae*). This was due to the fishers initially targeting small, high density aggregations of lobsters in the early phases of fishery, but

as the fishery developed effort shifted to larger aggregations which had a lower density leading to decreased CPUE without an associated decrease in abundance.

Another situation where CPUE may not be proportional to abundance results from the predictions of the IFD, when applied to a fisheries context. Developed by Fretwell and Lucas (1970), the IFD was initially applied to nest site choice in birds but has since been more widely applied to generally describe the spatial distribution of foraging animals. In this sense the IFD predicts that among a number of distinct foraging sites, foragers distribute themselves in a manner that equalizes the proportion of resource among them. The IFD has been applied in fisheries research to describe the behaviour of fish, their prey and their harvesters (Gillis 2003). There are a number of assumptions that must be met for the IFD to develop within a fishery: 1) there must be spatially distinct stock components utilized within the fishery; 2) the fishers must be free to move between the distinct stock components; 3) information about quality of fishing success must be exchanged within the fleet so that fishers have ideal knowledge of the environment; 4) vessels must be of equal competitive ability; and 5) competition between vessels must exist and be in the appropriate form (Gillis 2003). Competition can occur in two forms, exploitative and interference competition (Goss-Custard 1980).

Exploitative competition is the result of a decrease in the local abundance of target fish due to the presence of other fishing vessels in the area but this style of competition does not lead to the IFD (Gillis and Peterman 1998). For the classic IFD to be created the competition must be through interference. Two types of interference competition exist; direct and indirect (Goss-Custard 1980). Direct interference is when increased density of vessels on a fishing ground leads to decreased efficiency of the individual vessels; for example, in a mobile gear fishery when a vessel must divert from its desired path because another is in the way. Indirect

interference results from the effect of vessels on the behaviour of the prey, such as when fishing disturbs the prey and drives them into less accessible habitats. Using a mathematical model, Gillis and Peterman (1998) found that within a fishery where the IFD is possible, even low levels of interference can cause a breakdown in the correlation between CPUE and abundance. Historically it has been very difficult to experimentally test for the existence of interference competition, with few examples in the primary literature. Abrahams and Healey (1993) experimentally manipulated the density of three trawler vessels. Increased density led to a decrease in catch rate of the primary target species, chinook salmon (*Oncorhynchus tshawytscha*), likely due to interference; however, the catch rate of spiny dogfish (*Squalus acanthias*) increased with the same densities, demonstrating how density can have a significant yet variable effect on catch rate. Gillis (1999) examined the course trajectory of trawling vessels on the Scotian Shelf targeting silver hake and was able to infer interference due to deviations from a linear course. Finally, Rijnsdrop et al. (2000) made use of the convenient fact that a portion of the Dutch beam trawl fleet stays in port for one week during an Urk holiday. This resulted in a 10% increase in catch rate for the vessels that continued to fish relative to the prior week. In addition, the reference area did not experience any change in density or catch rate. This led the researchers to conclude that interference was present in the fishery. Though it is likely that in any natural system some of the assumptions of the IFD will be violated, the predictions of the IFD have been shown to be robust to these violations (Milinski and Parker 1991; Gillis et al. 1993; Vogues et al. 2005). This robust nature of the predictions of the IFD makes it a good first approximation of the effort distribution of vessels when multiple fishers are targeting a number of distinct fishing grounds.

This project will investigate aspects of fleet dynamics in the otter trawl groundfish fishery in NAFO Division 4X on the Scotian Shelf. This region is subject to a seasonal area closure,

the Brown's Bank spawning closure, from February 1st to June 15th annually. Seasonal area closures and permanent marine protected areas (MPAs) have become an increasingly used management strategy in recent years and as a result have received much research attention. The benefits of MPAs to fish species have been widely researched and consistently found to cause increases in density, biomass, diversity, and individual size (Gell and Roberts 2002; Halpern 2003). MPAs are also hypothesized to benefit adjacent fisheries through spillover from the reserve into the fished area. This benefit is often inferred from studies of commercial catch and effort statistics (Roberts et al. 2001; Murawski et al. 2005; Goni et al. 2006; 2010). However, some direct experimental evidence of the spillover effect has been found (Ashworth and Ormand 2005; Forcada et al. 2009). Often fishers will attempt to capitalize on spillover from the reserve by concentrating their effort at the boundary line of a MPA, which is termed 'fishing the line' (FTL; Gell and Roberts 2002). Less work has been conducted on the effects of seasonal closures but they too can have a substantial effect on effort distribution (Fogarty and Murawski 1998; Pastoors et al. 2000; Dinmore et al. 2003; Murawski et al. 2005; Poos and Rijnsdorp 2007).

The purpose of this thesis is to address the aspects of fleet dynamics that may be important to the relationship between catch rate (CPUE) and abundance. Specifically, I want to examine the patterns in displacement of effort around a regulatory closure and the performance of alternative behaviour models in representing these effort distributions. Chapter 2 will investigate the relationship between fishing effort and catch rate for those vessels employing FTL strategy. Three potential relationships are expected: 1) a correspondence between effort and abundance; 2) an equalization of catch rate in the FTL region, analogous to the predictions of the IFD; and 3) concentrated line fishing leading to a 'prey depression' at the boundary. An understanding of this relationship is important in the field of fisheries science because in the case of the latter two hypotheses the relationship between catch rate and abundance becomes

disassociated and therefore managers must consider the distribution of fishing effort as well as catch rate when estimating stock abundances from commercial log book data. Chapter 3 extends the analysis to examine how all effort is distributed throughout the fishery with a comparative analysis of two effort distribution models: IFD-based isodars; and a discrete choice random utility model. This again tests the applicability of the IFD to a fishery with the associated implications for the relationship of catch rate and abundance. Moreover, it is a comparison of a simple ecological model to a detailed econometric model which can provide insight for managers into the best perspective to take when using patterns of spatial effort to inform management decisions. Overall, this project improves the understanding of the relationship between abundance and commercial catch rate through the use of novel techniques that can be readily applied to additional fisheries.

References

- Abrahams, M.V., and Healey, M.C. 1993. Some consequences of variation in vessel density: a manipulative experiment. *Fish. Res.* **15**: 315-322.
- Ashworth, J.S., and Ormond, R.F.G. 2005. Effects of fishing pressure and trophic group on abundance and spillover across boundaries of a no-take zone. *Biol. Cons.* **121**: 333-344.
- Crecco, V., and Overholtz, W.J. 1990. Causes of density-dependent catchability for Georges Bank haddock *Melanogrammus aeglefinus*. *Can. J. Fish. Aquat. Sci.* **47**: 385-394.
- Dinmore, T.A., Duplisea, D.E., Rackham, B.D., Maxwell, D.L., and Jennings, S. 2003. Impact of a large-scale area closure on patterns of fishing disturbance and the consequences for benthic communities. *ICES J. Mar. Sci.* **60**: 371-380.

- Fretwell, S.D., and Lucas, H.L. 1970. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheor.* **19**: 16-36.
- Fogarty, M.J., and Murawski, S.A. 1998. Large-scale disturbance and the structure of marine systems: fishery impact on Georges Bank. *Ecol. Appl.* **8**: S6-S22.
- Forcada, A., Valle, C., Bonhomme, P., Criquet, G., Cadiou, G., Lenfant, P., and Sanchez-Lizaso, J.L. 2009. Effects of habitat on spillover from marine protected areas to artisanal fisheries. *Mar. Ecol. Prog. Ser.* **379**: 197-211.
- Gell, F. R., and Roberts, C. M. 2002. *The Fishery Effects of Marine Reserves and Fishery Closures.* WWF-US, 1250 24th Street, NW, Washington, DC 20037, USA.
- Gillis, D.M. 1999. Behavioral inferences from regulatory observer data: catch rate variation in the Scotian Shelf silver hake (*Merluccius bilinearis*) fishery. *Can. J. Fish. Aquat. Sci.* **56**: 288-296.
- Gillis, D.M. 2003. Ideal free distributions in fleet dynamics: a behavioural perspective on vessel movement in fisheries analysis. *Can. J. Fish. Aquat. Sci.* **81**: 177-187.
- Gillis, D.M., and Peterman, R.M. 1998. Implications of interference among fishing vessels and the ideal free distribution to the interpretation of CPUE. *Can. J. Fish. Aquat. Sci.* **55**: 37-46.
- Gillis, D.M., Peterman, R.M., and Tyler, A.V. 1993. Movement dynamics in a fishery: application of the ideal free distribution to spatial allocation of effort. *Can. J. Fish. Aquat. Sci.* **50**: 323-333.

- Goni, R., Hilborn, R., Diaz, D., Mallol, S., and Adlerstein, S. 2010. Net contribution of spillover from a marine reserve to fishery catches. *Mar. Ecol. Prog. Ser.* **400**: 233-243.
- Goni, R., Quetglas, A., and Renones, O. 2006. Spillover of spiny lobster *Palinurus elephas* from a marine reserve to an adjoining fishery. *Mar. Ecol. Prog. Ser.* **308**: 207-219.
- Goss-Custard, J.D. 1980. Competition for food and interference among waders. *Ardea* **68**: 31-52.
- Halpern, B.S. 2003. The impact of marine reserves: do reserves work and does reserve size matter? *Ecol. Appl.* **13**: S117-S137.
- Harley, S.J., Myers, R.A., and Dunn, A. 2001. Is catch-per-unit-effort proportional to abundance? *Can. J. Fish. Aquat. Sci.* **58**: 1760-1772.
- Hilborn, R., and Walters, C.J. 1992. Quantitative fisheries stock assessment: choice, dynamics, and uncertainty. Chapman and Hall, London.
- Hilborn, R. 1985. Fleet dynamics and individual variation: why some people catch more fish than others. *Can. J. Fish. Aquat. Sci.* **42**: 2-13.
- McFadden, D. 1974. Conditional logit analysis of qualitative choice behavior. *In* *Frontiers in Econometrics*. Edited by P. Zarembka. Academic Press, New York. pp. 105-142.
- Milinski, M., and Parker, G.A. 1991. Competition for resources. *In* *Behavioural ecology*. 3rd ed. Edited by J.R. Krebs and N.B. Davies. Blackwell Scientific Publications, Oxford. pp. 137-168.
- Morris, D.W. 1987. Spatial scale and the cost of density-dependent habitat selection. *Evol. Ecol.* **1**: 379-388.

- Murawski, S.A., Wigley, S.E., Fogarty, M.J., Rago, P.J., and Mountain, D.G. 2005. Effort Distribution and catch patterns adjacent to temperate MPAs. *ICES J. Mar. Sci.* **62**: 1150-1167.
- Rijnsdorp, A.D., Dol, W., Hoyer, M., and Pastoors, M.A. 2000. Effects of fishing power and competitive interactions on the effort allocation on the trip level of the Dutch beam trawl fleet. *ICES J. Mar. Sci.* **57**: 927-937.
- Roberts, C.M., Bohnsack, J.A., Gell, F., Hawkins, J.P., and Goodridge, R. 2001. Effects on marine reserves on adjacent fisheries. *Science* **294**: 1920-1923.
- Pastoors, M.A., Rijnsdorp, A.D., and Van Beek, F.A. 2000. Effects of a partially closed area in North Sea ("plaice box") on stock development of plaice. *ICES J. Mar. Sci.* **57**: 1014-1022.
- Poos, J.J., and Rijnsdorp, A.D. 2007. An "experiment" on effort allocation of fishing vessels: the role of interference competition and area specialization. *Can. J. Aquat. Sci.* **64**: 304-313.
- Rose, G.A., and Kulka, D.W. 1999. Hyperaggregation of fish and fisheries: how catch-per-unit-effort increased as the northern cod (*Gadus morhua*) declined. *Can. J. Fish. Aquat. Sci.* **56**: 118-127.
- Swain, D.P., and Wade, E.J. 1993. Density-dependent geographic distribution of Atlantic cod (*Gadus morua*) in the Southern Gulf of St. Lawrence. *Can. J. Fish. Aquat. Sci.* **50**: 725-733.
- Voges, E., Gordo, A., and Field, J.G. 2005. Dynamics of the Namibian hake fleet and management connotations: application of the ideal free distribution. *Sci. Mar.* **62**: 285-293.

Tables and Figures

Table 1.1. List of abbreviations uses throughout the thesis

Abbreviation	Meaning
AR	AutoRegressive
ARMA	AutoRegressive Moving Average
CPUE	Catch Per Unit Effort
DTL	Distant To the closure boundary Line
FTL	Fishing The Line
GAM	Generalized Additive Model
GEE	Generalized Estimation Equation
GLM	Generalized Linear Model
GNLS	Generalized Non-linear Least Squares
IBE	Effort inside the Brown's Bank area
IFD	Ideal Free Distribution
ITQ	Individual Transferable Quota
LOA	Length Over All (of a fishing vessel)
MA	Moving Average
MPA	Marine Protected Area
OBE	Effort outside the Brown's Bank area
RMSE	Root Mean Square Error
RUM	Random Utility Model
TAC	Total Allowable catch
VPA	Virtual Population Analysis
VPUE	Value Per Unit Effort

Chapter 2

Fishing the Line: Catch and effort distribution around the seasonal haddock (*Melanogrammus aeglefinus*) spawning closure on the Scotian Shelf.

Abstract

Area closures have become a common regulatory strategy in multispecies fisheries. As a result there has been a substantial amount of primary research investigating the effects of implementing permanent marine protected areas (MPAs). Far fewer studies, however, have examined the effect of seasonal or temporary closures. In this study, I examined the impact the Brown's Bank seasonal spawning closure had on the spatial distribution of fishing effort, as well as how the fleet utilized a 'fishing the line' (FTL) strategy. Vessel locations and catch information were available from log book data provided by Fisheries and Oceans Canada, for the years 2004 to 2008. Using a generalized estimation equation (GEE), no simple effect of the closure on the amount of effort on or around Brown's Bank was found. Instead, the effort that was displaced from the bank when the closure was in effect became concentrated within 30km from the boundary line. Within this distance from the line, two primary areas of effort concentration were identified during the closed period, one along each of the east and west boundary lines. Within these areas catch trends with distance from the line were analysed using generalized additive models (GAMs), which revealed differing results between regions and among years. In the east, the areas of highest catch rates were targeted most frequently, whether this was at or away from the line. While in the west region, vessels distributed themselves in a way that commonly saw catch rates equalized within the region, consistent with the IFD. Consistently among years, there was an attraction of vessels to areas near the closure boundary lines, suggestive of line fishing behaviour, though to somewhat varying degrees, depending on vessel spatial distribution and target species.

Introduction

The use of fishery closures and marine protected areas (MPA) has increased in popularity amongst regulatory agencies and become a common management strategy in multispecies fisheries. MPAs, also called marine reserves and no-take zones, are areas where fishing is prohibited, in an attempt to give an exploited stock an area of refuge within a fished region. This is expected to assist in stock recovery and maintenance of a species' spawning stock. Empirical evidence of the effectiveness of marine reserves is mounting with the finding that the establishment of marine reserves leads to increases in biomass, abundance, density, body size, and egg production in a time period as short as 2-5 years (Gell and Roberts 2003). From a review of 89 separate studies on marine reserves, Halpern (2003) reported that the benefits of marine reserves extended to all functional groups within the community (carnivorous fishes, herbivorous fishes, planktivorous fishes/invertebrate eaters, and invertebrates) and that effects were seen regardless of reserve size.

Reserves are expected to benefit adjacent fisheries through two mechanisms: 1) export of larvae from inside the reserve to areas outside, and, 2) spillover of adults into the fished area around the reserve. Using a theoretical model, Neubert (2003) determined that the optimal harvesting strategy for a fishery always included the incorporation of marine reserves, and evidence of this benefit to adjacent fisheries is prominent within the primary literature with examples representing a diverse array of species and varying climatic conditions, e.g. ground fish on the Scotian Shelf (Fisher and Frank 2002), game fish in Florida and reef fish in St Lucia (Roberts et al. 2001), and lobster species in New Zealand (Kelly et al. 2002) and the Mediterranean (Goni et al. 2006). The mechanism underlying the achievement of these benefits, however, is not always clear. Fishers attempt to capitalise on the spillover effect by changing their fishing patterns, increasing effort along the boundaries of the reserves, termed 'fishing the

line' (FTL; McClanahan and Mangi 2000; Murawski et al. 2005; Goni et al. 2006; Jaworski et al. 2006). Kellner et al. (2007) investigated trends in abundance and catch rate around a MPA for species of differing motilities that result from using different fishing strategies, a uniformly distributed fleet, a competitive fleet where each vessel is attempting to optimize its individual success, and a coordinated fleet where total catch of the fleet is optimized, using a theoretical model. With a uniform distribution of effort, catch rates and abundance were highest at the boundary and decreased with distance. In a competitive fishery, individual success was maximized when a portion of the fleet targeted the line, with remaining vessels targeting areas away from the line. This led to CPUE being equalized among harvesters and is analogous to the ideal free distribution (IFD; Fretwell and Lucas 1970; Gillis 2003). The coordinated fleet led to a more complex effort distribution, where a greater proportion of effort was directed at the line, so that almost all the fish spilling over from the reserve were captured. This resulted in a depression in both abundance and catch rate at the boundary but overall provided the greatest total catch for the fleet. In addition, for both a competitive and cooperative fleet, when targeting a species with increased mobility, Kellner et al. (2007) found a greater proportion of the fleet should target the line to achieve optimal catch rates.

The localized depression in catch rate, or 'prey depression' pattern, at the reserve boundary line Kellner et al. (2007) predicted in a coordinated fleet has been found in practice when intensive line fishing exists, though typically in more artisanal fisheries where the fleet was not necessarily cooperative (McClanahan and Mangi 2000; Willis et al. 2003; Abesamis and Russ 2005; Goni et al. 2006; Kellner et al. 2007). In a study of spillover of spiny lobster (*Palinurus elephas*) in the Columbretes Island marine reserve (CIMR) in the western Mediterranean, Goni et al. (2006) found that there was a localized depression of catch-per-unit-effort (CPUE) at the boundary of the reserve followed by a plateau that extended to 1500m away from the reserve.

This localized depression in CPUE was attributed to depleted lobster stock near the boundary due to intensive line fishing; 75% of all fishing sets were within 1km of the reserve boundary. Other studies provided less evidence of a concentrated FTL strategy but concluded it was likely the cause of the prey depression found (McClanahan and Mangi 2000; Willis et al. 2003; Kellner et al. 2007). An FTL strategy has the potential benefit to fishers that it may lower fishing cost associated with searching behaviour compared to fishing regions farther away from the reserve boundary. Instead fishers can assume that spillover from the reserve will provide a continuous supply of fish that is either equal to or greater than that of areas farther away with decreased searching costs. This leads to the potential of equal profitability for fishers near the boundary despite depressed catch rates.

This study focused on a seasonal spawning closure, rather than a permanent MPA, the Brown's Bank spawning closure. While it is unlikely seasonal spawning closures provide the same level of biological benefit to the protected species that permanent closures do, it has been demonstrated that they do lead to a redistribution of fishing effort spatially and temporally (Fogarty and Murawski 1998; Pastoors et al. 2000; Dinmore et al. 2003; Murawski et al. 2005; Poos and Rijnsdrop 2007). Dinmore et al. (2003) found that with the establishment of the 'plaice box', a seasonal closure in the North Sea, fishing effort became more homogeneously distributed throughout the year with the development of a strong FTL component at the boundary of the closure. Upon the reopening of a New England seasonal closure Murawski et al. (2005) observed a sharp increase in effort within the closed area even though the average CPUE remained the same or was lower. Little work has been conducted examining the specific line fishing practices of vessels near the boundaries of seasonal closures.

This study examined the distributional response of vessels to a regulatory closure and how FTL practices are utilized amongst the fleet. First, the amount of effort directed towards Brown's Bank was contrasted between the open and closed period. Second, it was determined whether the success of a particular trawl affected the distance a vessel moved, which provides insight into how vessel distributions correspond to underlying catch rates. Finally, in areas where effort was concentrated near the boundary line, catch rate trends with distance from the line were examined using generalized additive models (GAM; Hastie and Tibshirani 1990). Three potential catch rate trends with respect to distance were considered: 1) 'Simple tracking hypothesis', where the greatest amount of effort correspond to the areas with the greatest catch rates, regardless of location; 2) 'IFD hypothesis', where catch rates are equalized throughout the region; and 3) 'Prey depression hypothesis', where intensive line fishing leads to a depression of catch rates at the boundary of a closed area.

Methods

Study site

The Brown's Bank spawning closure is situated in NAFO Division 4X off the south coast of Nova Scotia (Figure 2.1). The closure was first instituted in 1970 by the International Commission for the Northwest Atlantic Fisheries (ICNAF) along with two other areas in Subarea 5 including the Canadian part of George's Bank. Concerned with the high catch rates of haddock (*Melanogrammus aeglefinus*) during pre-spawning and spawning aggregation, the closures were instituted in an effort to protect the spawning stock, reduce the total exploitation rate, and spread the catch more evenly throughout the year (Halladay 1988). As a result, the positions of the closures were based on spawning data and not commercial catch rates. Since its initial creation, the Brown's Bank closure has decreased slightly in size but the duration of the closure

has increased from two months to four and a half months. Currently the area is closed from February 1st to June 15th each year, with fishing occurring through the remainder of the year, subject to quota restrictions.

It is conceivable that given the complex nature of haddock courtship behaviour (Hawkins et al. 1967), the number of eggs fertilized per female could be reduced by disturbances from fishing; however, the closures were not instituted with the intent to have any effect on the spawning success of haddock (Halladay 1988). At the same time that the closures were created, total allowable catch (TAC) quotas were instituted in the haddock fishery and together these measures were projected to decrease landings by 20% (Halladay 1988).

The data set

Logbook data were obtained from the Department of Fisheries and Oceans Canada for the otter trawl groundfish fishery in NAFO Division 4X for the years 2005-2008. This data set contains information for each individual trawl in which a groundfish species was caught using mobile gear. Each record included the date, time and coordinates for the start of each trawl, the total catch, catch broken down by species, duration of the trawl, and vessel characteristics: length overall and gross tonnage. In addition, there was a unique identifier for each trawl, trip and vessel in the data set; however, to maintain privacy the vessel identifiers were assigned arbitrarily and were not consistent between years.

All trips with missing information on the start time or duration of a trawl were removed. Additionally, trips were removed when the start times were not unique between different trawls, when the position of the trawl was obviously incorrect (e.g. off the continental shelf), or if the distance traveled between trawls was unreasonable in the time reported (e.g. resulted in

an average speed of greater than $25\text{km}\cdot\text{h}^{-1}$). In total, 736 unique trips were removed from the data set representing 25% of the all trips available.

Catch value instead of raw catch data was used for analysis to account for the differential values of target species and the multispecies nature of the fishery. A monthly average price was calculated for the species caught in highest abundance (i.e. at least 100 tonnes total catch over the four years of the data set), from which a total catch value for each trawl was calculated and converted to value per unit effort (VPUE) and used in analysis. Price information was obtained from the PEI Department of Fisheries, Aquaculture and Rural Development (available online at <http://www.gov.pe.ca/>, last accessed May 2011), who have compiled weekly fish prices for Nova Scotia harbours from 2001 to the present.

Standardization

The analysis was restricted to vessels in tonnage classes 2 and 3 (25 - 150 tonnes). This represents on average 84% of the individual vessels that entered the fishery each year. All analyses were conducted in R 2.12.1 (R Development Core Team 2010). To allow catch rates of vessels of different sizes to be directly comparable they must be standardized to remove the effect of fishing power (Westrheim and Foucher 1985; Bishop et al. 2008) and varying fish abundance among years. Standardization utilized a linear model and was fitted to \log_{10} transformed VPUE with year, available vessel characteristics, length overall (LOA) and gross tonnage, and time of day, as predictors, expressed as:

$$(1) \quad \log_{10}(\text{VPUE}_i) = \beta_0 + \sum_{k=1} \beta_k X_i$$

where VPUE_i represents the expected catch rate ($\text{\$}\cdot\text{hour}^{-1}$) for trawl i , and β_k are the estimated coefficients from predictors X_i . Temporal periods within a year, such as month or week, as well

as spatial position of effort, were not considered for standardization as maintaining this variability was important in later analysis. The year effect represents variation in annual abundance and was forced in the model as the first predictor with additional predictors added based on an *a priori* improvement in R^2 of 0.5% when added to the model (Vignaux 1996; Maunder and Punt 2004; Bishop et al. 2008). Zero catches were few in number, 70 trawls, and deemed to not have much influence; thus zero trawls were excluded from the coefficient estimates.

VPUE for a standard vessel, s , was calculated from the above model, using the most common values of each variable to define the standard vessel. The fishing power, q , of each trawl was calculated as:

$$(2) \quad q = \text{VPUE}_i / \text{VPUE}_s$$

VPUE from each set was then divided by its respective fishing power to give VPUE standardized to the standard vessel size and year. Standardized VPUE will be referred to simply as VPUE.

Closure directed effort

To investigate how vessel effort distribution responds to the closure, the number of trawls per week directed towards Brown's Bank was summed and modeled in comparison to the amount of effort directed elsewhere. Effort directed towards Brown's Bank was defined as all trawls within a set distance from the closure boundary; this encompasses effort directly on the bank during the open months as well as the concentration of effort near the boundaries of the closure displaced from the bank itself during the closed months. The distance from the boundary chosen to define vessels directing effort towards Brown's Bank was 30km as this is the approximate distance from the boundary line to which the annual FTL concentration extended;

determined through visual assessment of trawl positions. The model was also run using 10km and 20km distances to assess the robustness of the results to the choice of distance. Weekly summed effort was used because the number of trawls was not uniform across week days, with typically less effort Friday through Sunday.

The full model was fit using weekly effort directed towards Brown's Bank (Inside Brown's Effort; IBE) as the response variable; weekly effort directed elsewhere (Outside Brown's Effort; OBE), a binomial closure variable, and week as a continuous variable from 1 to 52, were the predictors. All possible main effects and interactions were fitted in the full model.

$$(3) \quad \log(\mathbb{E}[IBE_i]) = \beta_0 + \beta_1(OBE_i) + \beta_2(Closure_i) + \beta_3(Week_i) + \beta_4(OBE_i \times Closure_i) + \beta_5(OBE_i \times Week_i) + \beta_6(Closure_i \times Week_i) + \beta_7(OBE_i \times Closure_i \times Week_i),$$

where $\text{Var}[IBE_i] \sim \phi \times \mu_i$

Interpretation of this model is simplified somewhat by the dichotomous nature of closure. The main effect of closure represents a fixed change in effort corresponding to the onset of regulation. Interactions with closure indicate relationships that are unique to the closure period, while main effects and simple interactions with week are common between the open and closed period. Thus, a change in the proportion of effort directed towards the closure during the regulatory period would be represented by a significant OBE×Closure interaction.

Initial model fitting was conducted with a generalized linear model (GLM; McCullagh and Nelder 1989), using a Poisson error distribution as the model was for count data, and its canonical link function, the log link. This model, however, was highly overdispersed, which can result in underestimated standard errors and inaccurate p-values. Moreover, there was strong residual temporal autocorrelation between observations, violating the independence assumption of a GLM, again leading to erroneous p-values (Zuur et al. 2009). To combat this, a

generalized estimation equation (GEE; Liang and Zeger 1986) was used. A GEE is similar to a GLM but allows for the use of alternative correlation matrix structures to account for autocorrelation. In addition, the GEE does not make distribution assumptions thus resolving the overdispersion issue (Zuur et al. 2009).

The full model was then fitted as a GEE for distances 30, 20 and 10km from the boundary line using the geepack library in R (Hojsgaard et al. 2005). An AR1 correlation structure was employed using years as blocks. This type of correlation structure is appropriate for data sampled on regular time intervals where the correlation between observations is expected to decrease with increased time between samples (Zuur et al. 2009). Model simplification was conducted using Wald tests to compare reduced models to the full model. Coefficients with non-significant results were removed from the model (Zuur et al. 2009).

Vessel movement

To determine how catch success influenced vessel movement binomial models were developed and fit as generalized additive models (GAM; Hastie and Tibshirani 1990). Initially the data were modeled with GLMs; however, this demonstrated a lack of fit when tested using a Hosmer-Lemeshow test, indicating that the predictions significantly differed from what was expected given the data set. Using GAMs allows the models to more accurately conform to the data, giving a more representative trend and reliable predictions. The models were fitted as a binomial regression using cubic regression splines as the smoothing term. The mgcv package was used for model creation (Wood 2006).

Vessel movement was defined by the distance traveled between the start of consecutive trawls. The end position of a trawl was not available. The threshold defining a move was set to the median distance between the start of consecutive trawls for the entire data set, which was

8.2km. The catch success of a particular trawl was defined as the difference between the VPUE and the fleet wide average over the previous seven days, to give Δ VPUE. If Δ VPUE was greater than 0, the current trawl was more successful than the fleet and if Δ VPUE was less than 0, the vessel was currently less successful than the fleet. I then expect a vessel with a positive Δ VPUE to have a greater probability of staying and a vessel with a negative Δ VPUE to be more likely to move. A 7-day period was chosen for analysis again for reasons described above. The choice of this period was examined through preliminary analysis using Δ VPUE calculated from 1 day and 3 days (the approximate mean length of a trip), which resulted in greater AIC values than the 7 day model (Δ AIC: 0.17, 29.28 respectively).

Three separate models were created. The first utilized the full data set and included only smoothed Δ VPUE as a predictor. This model demonstrated the general trend Δ VPUE has on movement and was used as a graphical representation. Following this, the data set was divided into the closed and open period with additional predictors entered into the model as unsmoothed, parametric parameters, to further identify factors influencing movements. Additional predictors tested included: distance to the closure boundary line (DTL; for the closed period), vessel length, trawl duration, and time of day. Akaike's information criterion (AIC; Akaike 1974) was utilized for model fitting.

Fishing the Line

To begin, effort concentrations along and near the boundary lines were identified and determined to be potential FTL concentrations. Two primary FTL concentrations were identified that appear consistently among the years examined; one along the east boundary and a second on the northern part of the west boundary, hereafter referred to as the east and west FTL regions (Figure 2.1).

The spatial distribution of catch rates was examined for each FTL region and year separately to investigate the prey depression hypothesis. VPUE of each region was modeled with a GAM against the smoothed distance from and along the boundary line (as transverse Mercator projections in km, adjusted to the FTL regions, easting and northing), using a gamma error distribution and a log link, so:

$$(4) \quad \log(\mathbb{E}[VPUE_i]) = f(\text{Easting}, \text{Northing}) \text{ where } VPUE_i \sim \text{Gamma}$$

where f is the smoothing function, in this case a thin plate spline which allows for the simultaneous smoothing of multiple isotropic predictors (Wood 2006). Again the mgcv R library was utilized for model fitting. Response values from these models were then graphically compared to the effort distribution within the FTL regions.

Results

Standardization

Year fished and LOA were the only variables found to increase the model R^2 more than the *a priori* threshold of 0.5%, and therefore were the only predictors included in the model (Table 2.1). Time and gross tonnage did not have sufficient effect on R^2 to be included in the final model, nor did the interaction of LOA with year. The interactions of gross tonnage with year and time with year were not considered after their main effects were found to not impact the predictive nature of the model. The final model including only year and LOA accounted for 8.4% of the catch rate variability. There was a significant positive relationship of VPUE with LOA and significant differences between years (Table 2.2). As a result VPUE was standardized to a vessel 44' in length (the most frequent boat length), fishing in 2005 (the year with the greatest VPUE).

Closure directed effort

The general reaction of the fleet to the closure coming into effect was examined by dividing the fished region into two areas: where effort was directed towards Brown's Bank (IBE), and away from Brown's Bank (OBE), with the threshold for the division set to 30, 20 and 10km from the closure boundary line. The total catch value and average catch rate during the open and closed periods for each area definition are summarized in Table 2.3. IBE during the closed period, which represents potential line fishing activity, produced greater average catch rates (VPUE) than OBE; however OBE represented a larger number of trawls resulting in greater total catch values. During the open period, IBE produced greater average VPUE (for all distances from the line) and total catch value (for 30 and 20km distances) than OBE.

Results of the generalized estimation equations (GEE) examining the relationship between IBE and OBE, week, and closure period are presented in Table 2.4. The results for 30 and 20km distances from the line were almost identical, with the same parameters being included in the final model, and very similar coefficient estimates of similar significance. These results differed from the 10km model, however, indicating potential differences in effort distributions with varying distances from the boundary line.

30 and 20km model

There was a strong positive relationship of IBE with OBE indicating proportionality between the amount of effort directed towards Brown's Bank and away from it. The significant negative interaction between OBE and week, however, suggests that the relationship between IBE and OBE was not constant, decreasing over the course of the year. There was no simple trend with closure present; thus, the implementation of the closure did not have an immediate effect on the number of trawls beginning within 20 or 30km of the boundary. Instead, the effort that was directly on Brown's Bank during the open period became concentrated within 20km

from the boundary line when the closure was in effect. There were, however, more complex relationships with closure, in the form of two-way and three-way interactions. The significant positive interaction between closure and week indicates an increasing number of trawls near Brown's Bank over the course of the closure; this followed a general trend of increasing effort in the fishery during the closure. This becomes evident with the significance of the negative three-way interaction between OBE, closure, and week, indicating a decrease in the proportion of effort directed towards Brown's Bank over the course of the closure, relative to effort elsewhere.

Figure 2.2a gives a graphical representation of how the proportion of IBE within 30km of the boundary changes over time. There is an apparent periodicity to the plot, where the proportion of effort was generally higher at the beginning of the closure period, declines throughout the closure and then increased to a second peak during the open period. This decline during the closure period is the realization of the negative three-way interaction between, OBE, week and closure period. The mean trend, characterized by the loess curve, varies around approximately 50%, and illustrates that fishers utilized Brown's Bank at similar proportions among and throughout different years.

10km model

There were a number of key differences between the 10km model and the others. Most notable was a significant negative relationship with closure, indicating a decrease in the number of trawls beginning within 10km of Brown's Bank when the closure came into effect (median IBE closed: 17, median IBE open: 25). There was also a positive interaction between OBE and closure indicating that when total effort was high, a greater amount was directed towards the IBE area when the closure was in effect. There was no longer an interaction between OBE and week

suggesting the relationship between IBE and OBE was more consistent throughout the open period than in the 20 and 30km models. All other parameters were the same as the previous models, differing only in magnitude.

The proportion of IBE within 10km of the boundary followed a similar trend to the 30km area (Figure 2.2b). There was an overall decrease in the average proportion, however, especially during the closure period, but this is not surprising as the area available for fishing was much smaller. In addition, the declines during the closure period appear to be greater and steeper, possibly representing the decline in total effort in this area during the closure period. Nonetheless, there were a number of weeks where a substantial portion, sometimes greater than 50%, of the total fleet effort was concentrated within this relatively small area, suggesting times when an FTL strategy was commonly employed within the fishery.

Movement

Results for the generalized additive logistic movement models are presented in Table 2.5. From the full data set a significant negative trend between vessels moving to new trawling location and $\Delta VPUE$ is evident (Figure 2.3). This follows the expected pattern with vessels more likely to stay in the same region when they achieved a positive $\Delta VPUE$ and were more likely to move when $\Delta VPUE$ was negative. The trend was highly significant, however, it only accounted for ~2% of the total deviance indicating that, not surprisingly, relative catch rate was not the only factor influencing vessel movements. By dividing the data set into the distinct time periods, of when the closure was and wasn't in effect, additional factors including distance from the closure boundary line (DTL) could be investigated.

During the closure, DTL did have a significant positive effect on movement. This indicates that vessels fishing closer to the boundary line are somewhat less inclined to move

greater distances, possibly due to increased clustering near the boundary, indicative of a FTL strategy. Vessel length, however, had a greater effect with larger vessels travelling further distances between sets than smaller ones. Finally, and somewhat surprisingly, trawl duration had a significant negative coefficient indicating vessels tend to travel less distance between trawls when fishing for longer time periods. During the open period only vessel length was a significant contributor to movement. With an additional parameter added to the closed and open period models still only 3.4% and 2.5% of the deviance was explained. Nevertheless, these factors remain significant contributors to the choice of whether to remain fishing in a particular region or move to a new area. Of the vessels that were more successful than the fleet average (n=5613), significantly more (60.2%) stayed in the same area, and of the vessels that were less successful than the fleet average (n=12273), significantly more (54.7%) moved to a new area following that set. This further supports a vessel's increased probability of moving from, or remaining in, an area depending on its current catch rate relative to the fleet.

Fishing the line

There were two primary concentrations of effort near the boundary of the Brown's Bank spawning closure (Figure 2.1), one along the east boundary (the east FTL region) and a second along the northern part of the west boundary (the west FTL region). A significant proportion of the fleet exploited the FTL regions while fishing. An average of 51% of vessels that fish in a given year utilized at least one of the two primary FTL regions during the closed period, but this varied among years, 56%, 66%, 53%, and 30% in 2005 to 2008 respectively. A third potential FTL area exists, along the southeast boundary; however, this area was not as consistently fished as the others among years. In addition, the vessel distribution was limited by the continental shelf. The average distance from the line was 3.3km and ranged from 0.6 to 8.7km. The resolution of the

log book data used was too coarse to discern trends with distance on this scale. As a result this third region is not considered in the analysis.

The two primary FTL regions (east and west) differed in many ways. First and foremost they differed in target species. Haddock made up 89% of the catch weight in the east FTL region and only 6% in the west region. In the west region redfish (*Sebastes* spp.) was the fish caught in highest abundance, making up 56% of the total catch weight, while pollock (*Pollachius virens*), accounted for 34%. In addition, there were disparities in VPUE (east: 330.1 $\$/\text{hour}^{-1}$, west: 463.6 $\$/\text{hour}^{-1}$), average trawl duration (east: 3.8 hours, west: 1.8 hours), median distance traveled between the start of consecutive trawls (east: 7.78km, west: 3.95km), and the average number of vessels fishing each day fishing that took place (east: 8.5, west: 4.4). Despite these differences, there was substantial overlap in the vessels that fished these regions. An average of approximately 46% of vessels that fished either of the FTL regions fished in both of them, suggesting vessels employed multiple strategies over the course of a year. Overall effort was fairly evenly distributed between the two regions with a total of 1415 trawls in the east and 1451 in the west, in the years examined; however, again this was quite variable between years. In the east most of this effort was in 2005 and 2006, 425 and 531 trawls respectively, with 246 and 214 trawls during 2007 and 2008. In the west the vast majority of the effort came from 2005 with 799 trawls, this sharply declined in 2006 with 145 sets, recovered somewhat in 2007 with 326 trawls, and again declined in 2008 to 181 trawls.

Trends with distance from and along the boundary lines were examined with GAMs of VPUE against trawl starting position, with each year and FTL region examined separately. Much like other characteristics, trends in VPUE with distance were quite variable between FTL regions as well as among years. At least some effort directly at the line was present in all years in both

the east and west region, but this was most evident in 2005 and 2007 as well as some in 2006 in the east FTL region (Figures 2.4 and 2.5). In the east region all years had a significant trend in VPUE with distance from and along the line but in the west the trend was only significant in 2005 and 2006 (Table 2.6). This indicates that VPUE did not vary significantly throughout the west region in 2007 and 2008 while in other years and in the east region there existed VPUE hotspots where catch rates were elevated relative to other positions in the region. In 2005 and 2006 in the east region, VPUE was decreased nearer to the boundary, increasing to its maximum 10 – 20km off the line before decreasing again (Figure 2.4a and b). This follows the pattern of a prey depression; however, when examining the effort distribution, it appears that more trawls began where catch rates were highest rather than concentrating near the boundary, corresponding more closely with the simple tracking hypothesis, that effort concentration will most closely correspond to areas of high catch rates, rather than illustrating a prey depression pattern. The trend in 2008 was similar but the total amount of effort within the region was much reduced as was the extent and significance of the distance to line trend. This trend was reversed in 2007, with VPUE and effort highest at the boundary and decreasing with distance. Although the total amount of effort in the region was reduced from the years previous, there was more targeted line fishing than in other years with greater than 60% of all trawls beginning within 5km of the closure boundary, representing to the greatest number of trawls and highest total catch this close to the boundary, in the east region.

In the west region, significant trends in VPUE with distance from and along the line existed in 2005 and 2006 (Table 2.6). In 2006 there was very little effort within the region and the significant pattern present was due primarily to five trawls with very high catch rates (>5000 $\$/\text{hour}^{-1}$, which was over 5 times the mean for this region in 2006 when excluded). When the extreme trawls were removed the model lost significance and the resultant plot (not shown)

appears much more like that of 2007. In contrast, in 2005 there was a considerable amount of effort within the region and a highly significant VPUE pattern. Effort appeared to be fairly well distributed throughout the region with concentrations near the boundary as well as away from the line. VPUE remained high at the boundary despite high effort, and then decreased before again increasing away from the line. A substantial amount of the effort was concentrated in the areas of high catch rates but there was also a considerable amount where the catch rate was reduced. There were a number of trawls beginning very close to the boundary in 2007, however, no distance to line trend is present. Nor was there a trend present in 2008, but again, effort was quite low as was catch rate variability. The patterns observed in 2007, 2008, and in 2006 when the trawls with unusually high catch rates were removed, are consistent with the predictions of the IFD, in that VPUE appeared similar throughout the region.

Discussion

The implementation of the Brown's Bank spawning closure each year caused the effort directed towards Brown's Bank during the open season, in the otter trawl groundfish fleet, to become concentrated within an area extending 30km from the closure boundary. The amount of effort directed towards Brown's Bank (Inside Brown's Effort; IBE) was proportional to the effort directed elsewhere in the fishery (Outside Brown's Effort; OBE). There was no simple effect of the closure period on IBE for the 20 or 30km models. This indicates that the effort directed towards Brown's Bank when the closure was open was displaced to the surrounding area within 30km from the boundary when it was closed. Within 10km from the boundary, however, there was a significant decrease in the amount of IBE during the closed period, which could be interpreted as a change in strategy between the open and closed period, with a decreased emphasis on targeting the Brown's Bank area during the closure. Although, as there was no change in the amount of effort within 20km from the boundary, it is more likely that the total

amount of area available to fish within 10km from the boundary was not enough to support all the effort that was directed upon Brown's Bank during the open period, for the entire duration of the closed period. This limits the physical amount of space available to begin a trawl, but moreover, what is important is the physical space available to move to once trawling. The median distance between trawls, 8.2 km, can give a rough estimate of the distance covered. This suggests that the boundary can limit the area a vessel has to manoeuvre and that it may be more beneficial to begin a trawl somewhat farther away from the boundary. Competition may also play a role in vessels distribution around the closure. In addition to preventing fishing in an area due to occupying physical space, the presence of other vessels affects potential profitability of an area as a result of exploitative and interference competition (Goss-Custard 1980; Rijnsdrop et al. 2000; Gillis 2003).

In addition, more complex effort trends existed when the closure was in effect. The interaction of closure and week was significant but this simply follows a general increase in the total amount of effort during that time period. Also the negative three-way interaction between OBE, closure and week was significant. This suggests a decrease in the proportion of effort directed towards Brown's Bank over the course of the closure and likely follows the underlying haddock distribution. Fishers initially target pre-spawning aggregations during the early months of the closure, though these aggregations then dissipate following spawning, which occurs in late April/early May on Brown's Bank, necessitating that those fishers targeting haddock move to new areas (Page and Frank 1989). This behaviour is consistent with historical catch patterns, prior to the closure being put in place (Halliday 1988). Overall, the effect of the closure was to displace effort directed towards Brown's Bank to the surrounding areas, concentrating effort near the boundaries of the closure.

Since the rationale behind my hypothesis was that fishing success drives effort distributions it was important to determine how catch rate influences location choice when fishing. The relative success of a trawl, calculated by subtracting the current VPUE from the fleet wide average from the previous 7 days, was modeled against movement using a generalized additive logistic regression model. The results were as expected with vessels that were experiencing greater success more likely to remain fishing in the same area while vessels doing worse than the fleet more likely to travel a distance greater than the movement threshold to begin their next trawl. Murawski et al. (2005) found similar results showing that the current catch rate of a fishing set was a significant predictor of vessel movement in a logistic model, as well as finding vessel size to have an influence. Contrary to our results, however, they found that proximity to an area closure was not a factor influencing movement decisions; though Murawski's investigation examined permanent year round closure rather than a seasonal closure like the one in this study. Surprisingly, in this study trawl duration had a negative impact on movement suggesting that less distance was travelled between the starting points of consecutive trawls as trawl length increased. This was unexpected because one would assume a greater distance would be travelled while fishing these longer trawls. Perhaps the negative coefficient was due to an increase in nonlinear trawls with increasing trawl length.

A number of studies have examined vessel movements on a coarser scale than this study, typically examining movements between statistical divisions or 30 X 30 nmi grid squares, with varying results (Eales and Wilen 1986; Vignaux 1996; Holland and Sutinen 1999; 2000; Hutton et al. 2004; Marchal et al. 2009). Vignaux (1996) and Hutton et al. (2004) determined that vessel movements were not influenced by the catch rates of other vessels; however, Holland and Sutinen (1999; 2000) found the success of other vessels did impact vessel movements. In addition, Holland and Sutinen (1999) found that implementing a seasonal closure

had no effect on the overall movement in or out of a statistical area and suggested that any effort displaced from the region due to the closure was offset by additional effort drawn in to target the boundary lines of the closure. This result is analogous to results of the GEE model in this study. Catch rates then, are expected to be the primary driving force behind vessel movement and positioning.

Two primary concentrations of effort near the boundary of the closure were observed, the east and west FTL regions. These were areas of increased fishing activity near the boundary of the reserve, which could be identified visually in spatial plots of trawl starting positions, and reoccurred annually during the closure period. This indicates an attraction to these areas to potentially capitalize on spillover from the closed area. In both regions, a significant amount of the effort was exerted in very close proximity to the boundary, consistent with FTL strategy. The spatial patterns in VPUE adjacent to closure boundaries were quite variable between regions and among years. Typically in the east FTL region, the areas of greatest effort concentration corresponded to the areas of highest VPUE, whether this was at the boundary line, such as in 2007, or away from it, as in 2006. Patterns in this region most closely corresponded to the simple tracking hypothesis; that effort concentrations would be found in areas of highest catch rate. In 2005, VPUE was reduced at the boundary line in a pattern that could be associated with a prey depression; however, the amount of effort in this area was not greatly increased, which is the expected driving force behind a prey depression (Goni et al. 2006). Even in 2007, in which greater than 60% of all effort in the east regions was located within 5km of the boundary line, catch rates remained higher at the boundary than elsewhere in the region. This could be representative of increased spillover from the closure, sustaining high catch rates despite increased effort concentration at the boundary, or alternatively may indicate a decreased likelihood of a prey depression occurring in this type of fishery. In previous studies where a prey

depression was noted, the fisheries were more artisanal in nature and the target species were typically less motile reef species (McClanahan and Mangi 2000; Willis et al. 2003; Abesamis and Russ 2005) or lobster (Goni et al. 2006). In addition, Kellner et al. (2007) predicted that any prey depression near a boundary line will be less for target species with increased motility. It is unlikely that the seasonal nature of the closure played a role, as Maury and Gascuel (2001) found using a theoretical model, that localized depression, which they termed 'local overfishing', can develop rapidly with intense localized fishing.

In the west FTL region, again there was a consistent FTL strategy employed within the region; however, the resultant catch trends differed greatly from the east region. VPUE was typically more even throughout the region, and did not differ significantly in 2007, 2008 and when 5 outlying points were removed in 2006. This is consistent with the predictions of the IFD and corresponds to the outcome expected in a competitive fishery from Kellner et al. (2007). In 2005, the VPUE trend with distance from the boundary line was significant, indicating differing catch rates within the region; however, areas of low catch rate have values that are not lower than in other years in this region. Instead VPUE was elevated at the boundary and again approximately 15 – 20km away from it. The IFD has been commonly applied in fisheries research when examining the relationship between vessel distributions and catch rates, and becomes important when making inferences about underlying resource distributions (Gillis 2003). This study provides a possible application of this on a micro-distributional scale where catch rates may not accurately represent underlying prey distributions until vessel concentration patterns are accounted for. The recognition of IFD patterns in fisheries is important because it can lead to a breakdown in the relationship between commercial catch rates and abundance. When fishers act like ideal, free predators the distribution of effort can give a better representation of underlying abundance than catch rate estimates (Swain and Wade 2003). Within the west FTL

region an examination of effort patterns would give a better understanding of the underlying prey distribution than VPUE, which shows little variability. In the east FTL region this is less of a concern as areas of high effort and VPUE correspond quite well; though even in this non-IFD scenario effort may still represent abundance quite well. It then becomes important for managers to consider effort distribution as well as catch rate when conducting stock assessments of exploited species. The application of the IFD on a macro-scale, throughout all fished areas within this fishery, will be further examined in a future study, where catch and effort distributions between multiple areas will be examined (Chapter 3).

Vessels concentrated their effort near the boundaries of the Brown's Bank spawning closure when the closure was in effect. There exist two primary areas where this concentration occurred though they differ in many aspects including target species and resultant average catch rate. Analysis of catch trends with distance from the boundary line revealed differing results between these regions and among years. In the east, the areas of highest catch rates were targeted most frequently, whether this was at or away from the line. While in the west region, vessels distributed themselves in a way that commonly saw catch rates equalized within the region, consistent with the IFD. Overall, the distribution of effort around the Brown's Bank spawning closure illustrates the diverse nature of 'line fishing' within a multispecies, mobile gear, commercial fleet. Effort generally responded to relative catch rates which varied with target species and even among years in response to fish availability. However, rather than dissipating evenly throughout the open fishing areas in response to the closure, effort consistently became concentrated in nearby adjacent regions due to displaced effort remaining near the closure and/or an attraction of additional vessel to line fishing areas for its assumed benefit.

References

- Abesamis, R.A., and Russ, G.R. 2005. Density-dependent spillover from a marine reserve: Long-term evidence. *Ecol. Appl.* **15**: 1798-1812.
- Akaike, H. 1974. A new look at statistical model identification. *IEEE Trans. Automat. Contr.* **AC-19**: 716-722.
- Bishop, J., Venables, W. N., Dichmont, C. M., and Sterling, D. J. 2008. Standardizing catch rates: is logbook information by itself enough? *ICES J. Mar. Sci.* **65**: 255-266.
- Dinmore, T.A., Duplisea, D.E., Rackham, B.D., Maxwell, D.L., and Jennings, S. 2003. Impact of a large-scale area closure on patterns of fishing disturbance and the consequences for benthic communities. *ICES J. Mar. Sci.* **60**: 371-380.
- Eales, J., and Wilen, J. E. 1986. An examination of fishing location choice in the pink shrimp fishery. *Mar. Resour. Econ.* **2**: 331-351.
- Fisher, A.D., and Frank, K.T. 2002. Changes in finfish community structure associated with an offshore fishery closed area on the Scotian Shelf. *Mar. Ecol. Prog. Ser.* **240**: 249-265.
- Fogarty, M.J., and Murawski, S.A. 1998. Large-scale disturbance and the structure of marine systems: fishery impact on Georges Bank. *Ecol. Appl.* **8**: S6-S22.
- Fretwell, S.D., and Lucas, H.L. 1970. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheor.* **19**: 16-36.
- Gell, F.R., and Roberts, C.M. 2003. Benefits beyond boundaries: the fishery effects of marine reserves. *Trends Ecol. Evol.* **18**: 448-455.

- Gillis, D.M. 2003. Ideal free distributions in fleet dynamics: a behavioural perspective on vessel movement in fisheries analysis. *Can. J. Fish. Aquat. Sci.* **81**: 177-187.
- Goni, R., Quetglas, A., and Renones, O. 2006. Spillover of spiny lobster *Palinurus elephas* from a marine reserve to an adjoining fishery. *Mar. Ecol. Prog. Ser.* **308**: 207-219.
- Goss-Custard, J.D. 1980. Competition for food and interference among waders. *Ardea* **68**: 31-52.
- Halliday, R.G. 1988. Use of seasonal spawning area closures in the management of haddock fisheries in the Northwest Atlantic. *NAFO Sci. Coun. Studies* **12**: 27-36.
- Halpern, B.S. 2003. The impact of marine reserves: Do reserves work and does reserve size matter? *Ecol. Appl.* **13**: S117-S137.
- Hastie, T.J., and Tibshirani, R.T. 1990. Generalized additive models. Chapman and Hall, London.
- Hawkins, A.D., Chapman, K.J., and Symond, D.J. 1967. Spawning of haddock in captivity. *Nature* **215**: 923-925.
- Hojsgaard, S., Halekoh, U., and Yan, J. 2005. The R Package geepack for generalized estimating equations. *J. Stat. Soft.* **15**: 1-11.
- Holland, D.S., and Sutinen, J.G. 1999. An empirical model of fleet dynamics in New England trawl fisheries. *Can. J. Fish. Aquat. Sci.* **56**: 253-264.
- Holland, D.S., and Sutinen, J.G. 2000. Location choice in New England fisheries: old habits die hard. *Land Econ.* **76**: 133-149.

- Hutton, T., Mardle, S., Pascoe, S., and Clark, R.A. 2004. Modelling fishing location choice within mixed fisheries: English North Sea beam trawlers in 2000 and 2001. *ICES J. Mar. Sci.* **61**: 1443-1452.
- Jaworski, A., Solmundsson, J., and Ragnarsson, S.R. 2006. The effects of area closures on the demersal fish community off the east coast of Iceland. *ICES J. of Mar. Sci.* **63**: 897-911.
- Kellner, J.B., Tetreault, I., Gaines, S.D., and Nisbet, R.M. 2007. Fishing the line near marine reserves in single and multispecies fisheries. *Ecol. Appl.* **17**: 1039-1054.
- Kelly, S. 2002. The value of a spillover fishery for spiny lobster around a marine reserve in northern New Zealand. *Coast. Manage.* **30**: 153-166.
- Liang, K.Y., and Zeger, S.L. 1986. Longitudinal data analysis using generalized linear models. *Biometrika* **73**: 13-22.
- Marchal, P., Lallemand, P., and Stokes, K. 2009. The relative weight of traditions, economics, and catch plans in New Zealand fleet dynamics. *Can. J. Fish. Aquat. Sci.* **66**: 291-311.
- Maunder, M.M., and Punt, A.E. 2004. Standardizing catch and effort data: a review of recent approaches. *Fish. Res.* **70**: 141-159.
- Maury, O. and Gascuel, D. 2001. 'Local overfishing' and fishing tactics: theoretical considerations and applied consequences in stock assessment studies with a numerical simulator of fisheries. *Aquat. Living Resour.* **14**: 203-210.
- McClanahan, T.R., and Mangi, S. 2000. Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. *Ecol. Appl.* **10**: 1792-1805.

- McCullagh, P., and Nelder, J.A. 1989. Generalized Linear Models. Chapman & Hall, London.
- Murawski, S.A., Wigley, S.E., Fogarty, M.J., Rago, P.J., and Mountain, D.G. 2005. Effort distribution and catch patterns adjacent to temperate MPAs. ICES J. Mar. Sci. **62**: 1150-1167.
- Neubert, M.G. 2003. Marine reserves and optimal harvesting. Ecol. Lett. **6**: 843-849.
- Page, F.H., and Frank, K.T. 1989. Spawning time and egg stage duration in northwest Atlantic haddock (*Melanogrammus aeglefinus*) stocks with emphasis on Georges and Browns Bank. Can. J. Fish. Aquat. Sci. **46**: 68-81.
- Pastors, M.A., Rijnsdrop, A.D., and Van Beek, F.A. 2000. Effects of a partially closed area in North Sea ("plaice box") on stock development of plaice. ICES J. Mar. Sci. **57**: 1014-1022.
- Poos, J.J., and Rijnsdorp, A.D. 2007. An "experiment" on effort allocation of fishing vessels: the role of interference competition and area specialization. Can. J. Aquat. Sci. **64**: 304-313.
- R Development Core Team. 2010. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0.
- Rijnsdorp, A.D., Dol, W., Hoyer, M., and Pastors, M.A. 2000. Effects of fishing power and competitive interactions on the effort allocation on the trip level of the Dutch beam trawl fleet. ICES J. Mar. Sci. **57**: 927-937.
- Roberts, C.M., Bohnsack, J.A., Gell, F., Hawkins, J.P., and Goodridge, R. 2001. Effects on marine reserves on adjacent fisheries. Science **294**: 1920-1923.

- Swain, D.P., and Wade, E.J. 2003. Spatial distribution of catch and effort in a fishery for snow crab (*Chionectes opilio*): test of predictions of the ideal free distribution. *Can. J. Fish. Aquat. Sci.* **60**: 897-909.
- Vignaux, M. 1996. Analysis of spatial structure in fish distribution using commercial catch and effort data from the New Zealand hoki fishery. *Can. J. Fish. Aquat. Sci.* **53**: 963-973.
- Westrheim, S.J., and Foucher, R.P. 1985. Relative fishing power for Canadian trawlers landing Pacific cod (*Gadus macrocephalus*) and important shelf cohabitants for major offshore areas of western Canada, 1966-81. *Can. J. Fish. Aquat. Sci.* **42**: 1614-1626.
- Willis, T.J., Millar, R.B., and Babcock, R.C. 2003. Protection of exploited fishes in temperate regions: high density and biomass of snapper *Pagrus auratus* (Sparidae) in northern New Zealand marine reserves. *J. Appl. Ecol.* **40**: 214:227.
- Wood, S.N. 2006. *Generalized Additive Models: An Introduction with R*. Chapman and Hall/CRC, Boca Raton.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., and Smith, G.M. 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York.

Tables and Figures

Table 2.1. Summary of R^2 values in the stepwise model fitting process for the vessel catch rate standardization model. Predictors were modeled against log-transformed catch rate value. Year and available vessel characteristics were considered in the model, as well as interactions with year but only after the main effects were modeled. Year was forced as the first predictor with others added iteratively in the order of greatest increase in model R^2 , as long as that increase was greater than 0.5%, following the method of Vignaux (1996).

Variables	1	2	3
Year	1.3	-	-
LOA	-	8.36	-
Time	-	1.37	8.38
Gross tonnage	-	5.18	8.36
Year:LOA	-	-	8.61

Table 2.2. The vessel catch rate standardization model controlling for influences of vessel length and year fished on catch rate (as value per hour fished; all species). LOA is length overall, in feet. Only vessels of tonnage class (TC) 2 and 3 were included in the model, range 25:150 tonnes.

Source	Df	Sum Sq	Mean Sq	F value	p value
Year	3	75.162	25.054	94.301	<0.0001
LOA	1	410.324	410.323	1544.423	<0.0001
Residuals	20023	5319.726	0.266	NA	NA

Parameter	Estimate	SE	t value	p value	Retransformed
Intercept	1.412	0.0261	54.086	<0.0001	25.801
Year 2005	0.000				
Year 2006	-0.139	0.010	-13.352	<0.0001	0.726
Year 2007	-0.078	0.010	-8.123	<0.0001	0.836
Year 2008	-0.022	0.011	-2.045	0.0409	0.951
LOA	0.018	0.000	39.299	<0.0001	1.042

Table 2.3. The total catch (in value) and catch rate (VPUE) data for effort directed toward Brown’s Bank (IBE) and away from it (OBE) during the closed and open periods.

Period	Area	Distance	Number of Sets	Total Catch Value (\$1000)	Average VPUE
Closed	IBE	30	4977	8585.66	371
		20	3976	6937.19	384
		10	2280	4149.22	390
	OBE	30	5832	8022.05	232
		20	6833	9670.52	245
		10	8529	12458.49	271
Open	IBE	30	5573	9353.07	276
		20	4859	8153.64	276
		10	4012	6787.60	278
	OBE	30	3716	5141.15	204
		20	4430	6340.57	216
		10	5277	7706.61	224

Table 2.4. Effort directed towards Brown’s Bank (IBE) modelled by effort directed away from it (OBE), a binomial closure effect (1: closed, 0: open), and continuous (1:52) week variable using a generalized estimation equation (GEE). IBE is defined as all effort within a set distance from the closure boundary, which was varied as 30, 20 or 10 km. The model was reduced through the use of Wald tests. Significant results are in boldface type.

Models	Parameters	Coefficients	SE	Wald	p-value
30 km	Intercept	3.521	0.046	5838.995	<0.0001
	OBE	0.012	0.000	1390.396	<0.0001
	OBE:Week	-0.0001	0.000	63.246	<0.0001
	closure:Week	0.034	0.007	24.170	<0.0001
	OBE:closure:Week	-0.001	0.000	26.913	<0.0001
20 km	Intercept	3.278	0.088	1414.162	<0.0001
	OBE	0.012	0.001	347.873	<0.0001
	OBE:Week	-0.0001	0.000	23.804	<0.0001
	closure:Week	0.033	0.012	7.653	0.0057
	OBE:closure:Week	-0.0005	0.000	20.463	<0.0001
10 km	Intercept	3.024	0.149	415.050	<0.0001
	OBE	0.009	0.002	24.532	<0.0001
	closure	-1.573	0.403	15.199	0.0001
	OBE:closure	0.014	0.002	31.666	<0.0001
	closure:Week	0.122	0.037	11.075	0.0009
	OBE:closure:Week	-0.001	0.000	44.269	<0.0001

Table 2.5. Vessel movement as a binomial variable (1: Move; 0: stay) predicted by relative catch rate (Δ VPUE – the current catch rate of a trawl minus the previous week’s average) modeled using a generalized additive model (GAM). Movement was defined as a distance traveled between consecutive trawls greater than the fleet wide median distance of 8.2km. Models were produced for the entire data set, including only smoothed Δ VPUE, as well as the closed and open periods alone, to include other parametric influences such as distance to line (DTL), length overall (LOA) and trawl length (hours fished). EDF is the effective degrees of freedom. Significant results are in boldface type.

Model	Parameter	Estimate	SE	z value	p-value
Full data set	Intercept	-0.005	0.015	-0.294	0.769
		EDF	χ^2		p-value
	s(Δ VPUE)	5.765	446		<0.0001
	Parameter	Estimate	SE	z value	p-value
Closed Period	Intercept	-0.896	0.174	-5.126	<0.0001
	DTL	0.003	0.001	3.858	<0.0001
	LOA	0.013	0.003	5.075	<0.0001
	Hours fished	-0.036	0.016	-2.463	0.0138
		EDF	χ^2		p-value
	s(Δ VPUE)	5.486	355.9		<0.0001
	Parameter	Estimate	SE	z value	p-value
Open Period	Intercept	-1.288	0.160	-8.056	<0.0001
	LOA	0.025	0.003	9.143	<0.0001
		EDF	χ^2		p-value
	s(Δ VPUE)	5.923	172.4		<0.0001

Table 2.6. Catch rate (VPUE) trends with distance from and along the boundary line for vessels in the East and West ‘fishing the line’ (FTL) regions, modelled a generalized additive model (GAM) with a gamma error distribution and log link, smoothed using thin plate splines. EDF is the effective degrees of freedom. Significant results are in boldface type.

Region	Year	EDF	F value	p-value
East	2005	22.95	2.721	<0.0001
	2006	13.96	2.947	<0.0001
	2007	11.14	4.85	<0.0001
	2008	10.03	2.09	0.014
West	2005	19.58	4.797	<0.0001
	2006	12.76	2.37	0.0032
	2007	5.379	1.885	0.0675
	2008	3.113	1.765	0.137

Figure 2.1. Study area. Individual trawls plotted for closure period during 2005 to 2008. East and west FTL regions in the thick lined boxes.

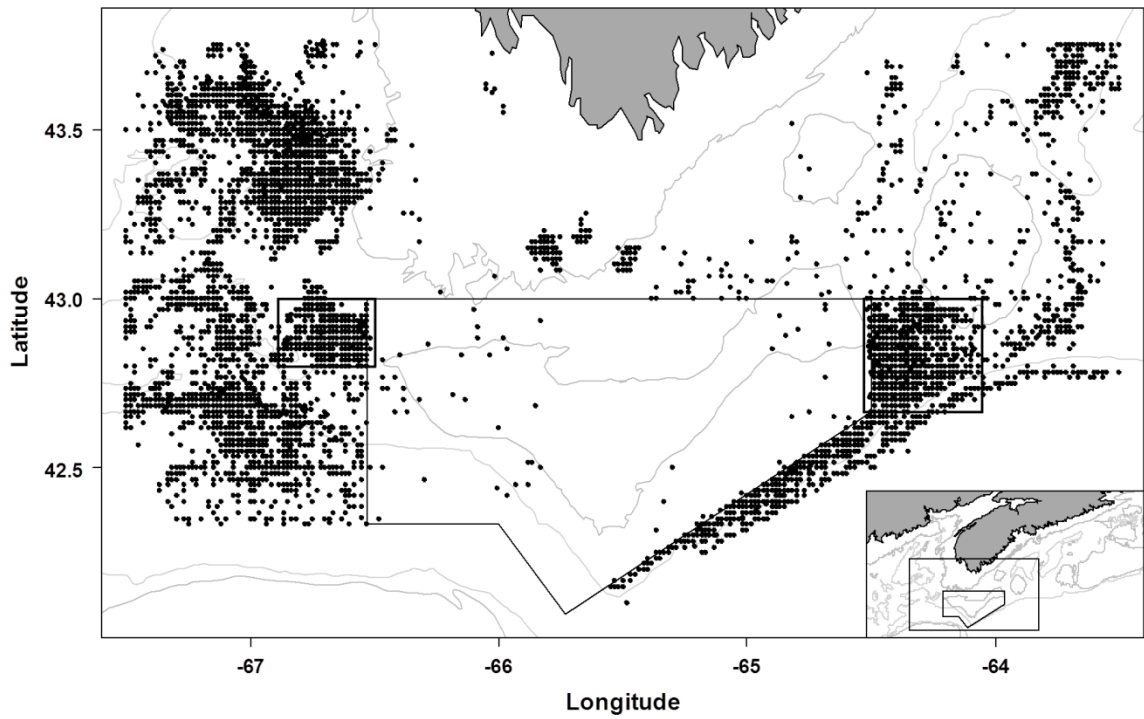


Figure 2.2. The proportion of effort (number of sets) directed towards Brown's Bank each week over the study time period, for distances: a. 30km; b. 10km from the closure boundary. The solid line is a loess smoothed curve through the data and dashed line is a 50% reference line.

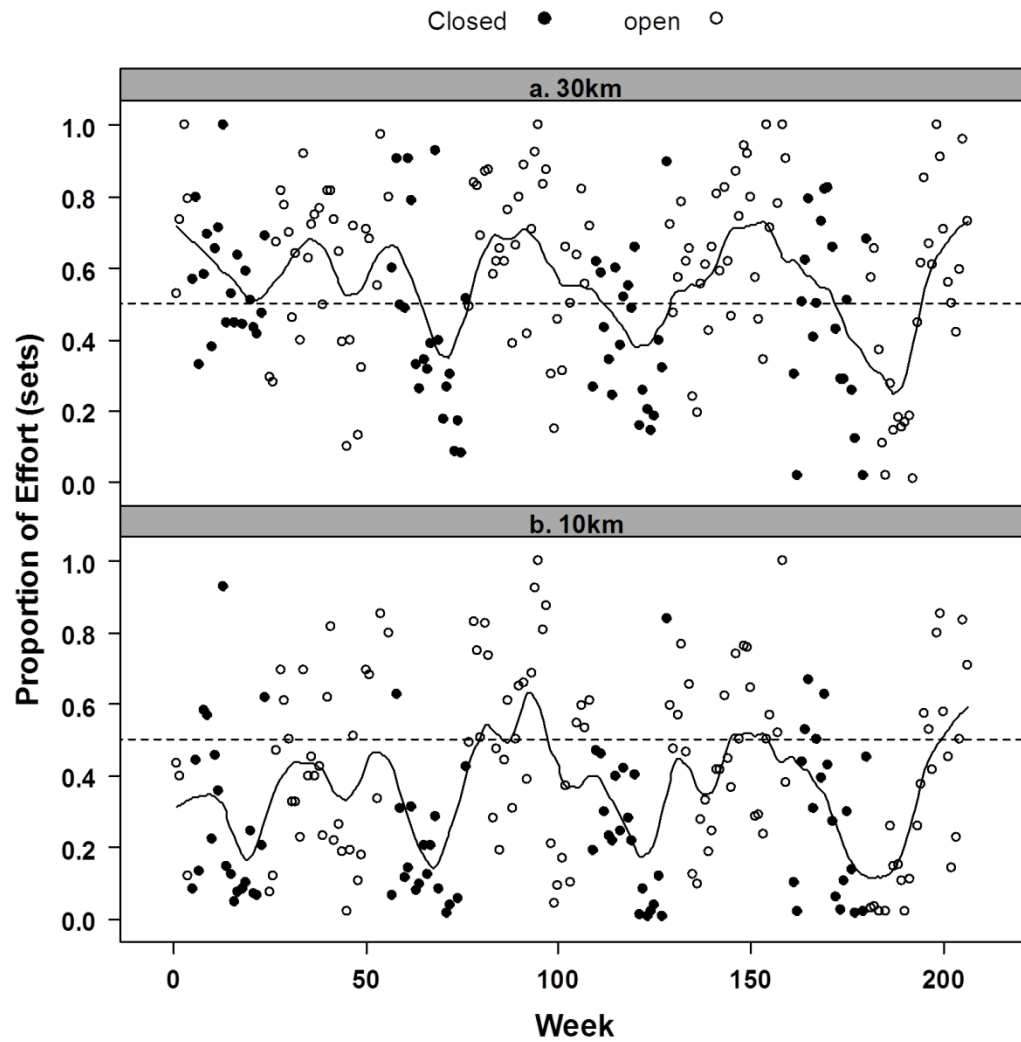


Figure 2.3. Visualization of vessel movement GAM from the entire data set with Δ VPUE (relative catch rate) as the only predictor. A move is defined as a vessel travelling a distance between the start of successive trawls greater than the fleet wide average distance (8.2km). Credibility intervals are in grey.

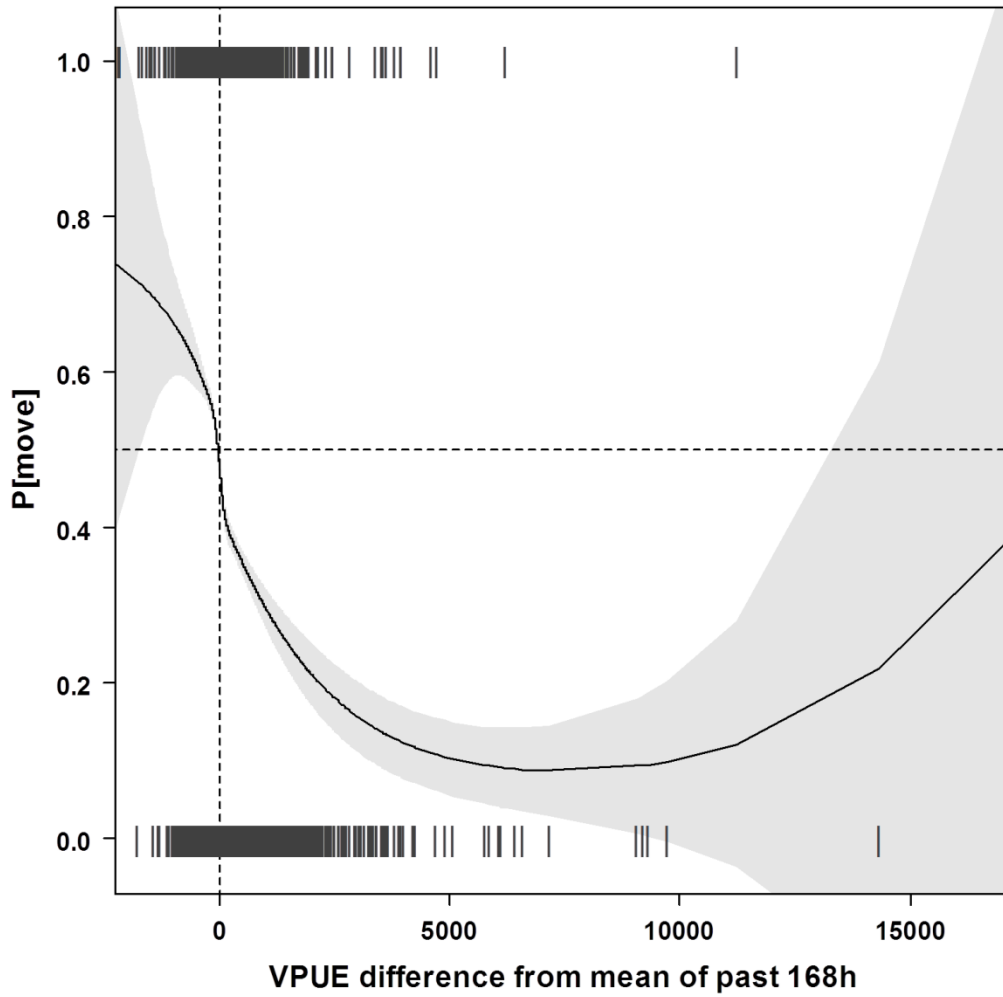


Figure 2.4. Distance from line catch rate trends for the east FTL region for years 2005:2008, each year plotted separately. Results of fitted values from GAMs of VPUE modeled against smoothed distance along and from the boundary line. Axes are in km. Circles represent trawl positions with size corresponding to the number in a given location. Black line represents the boundary line. Grey represents areas of no effort.

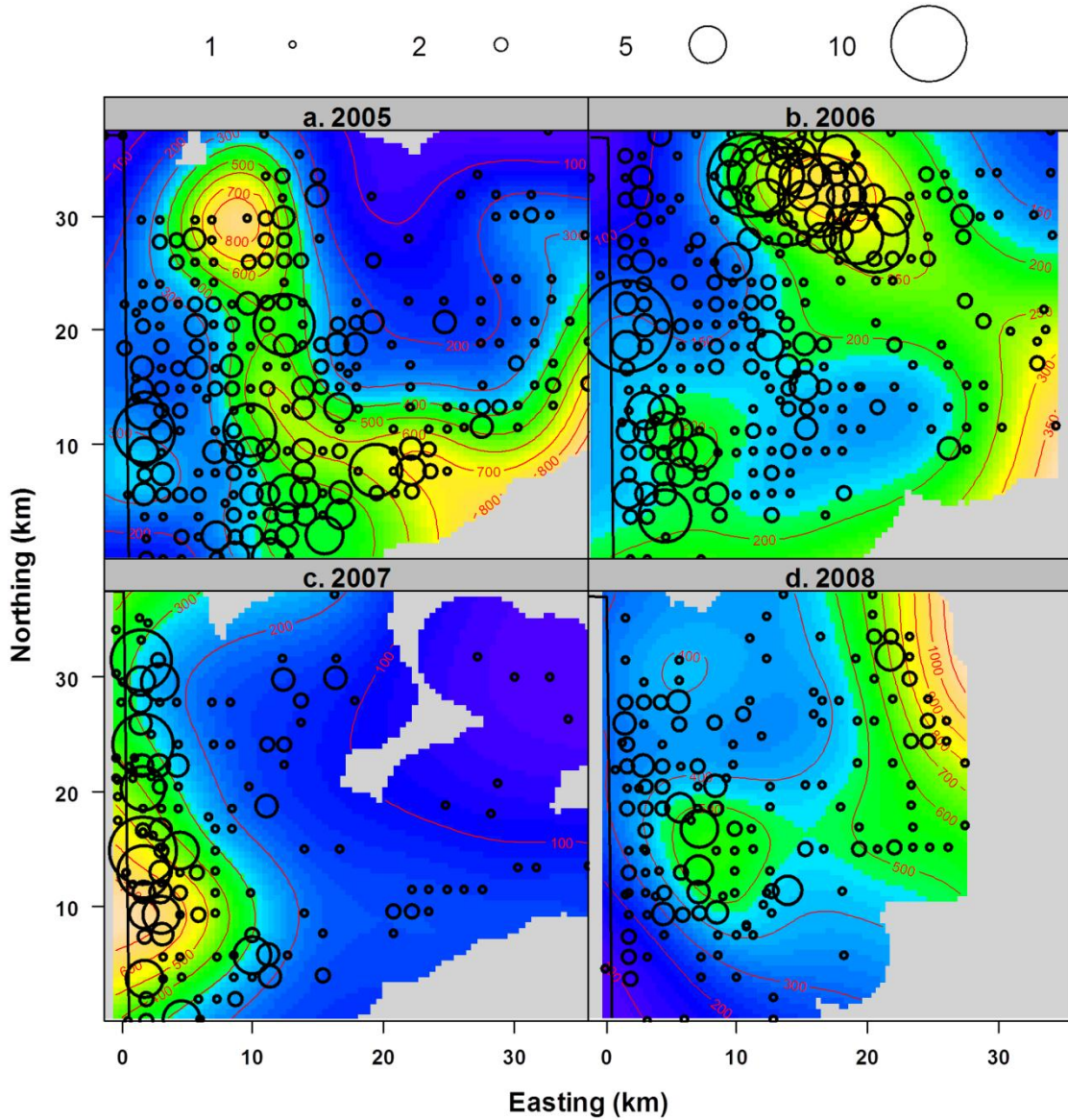
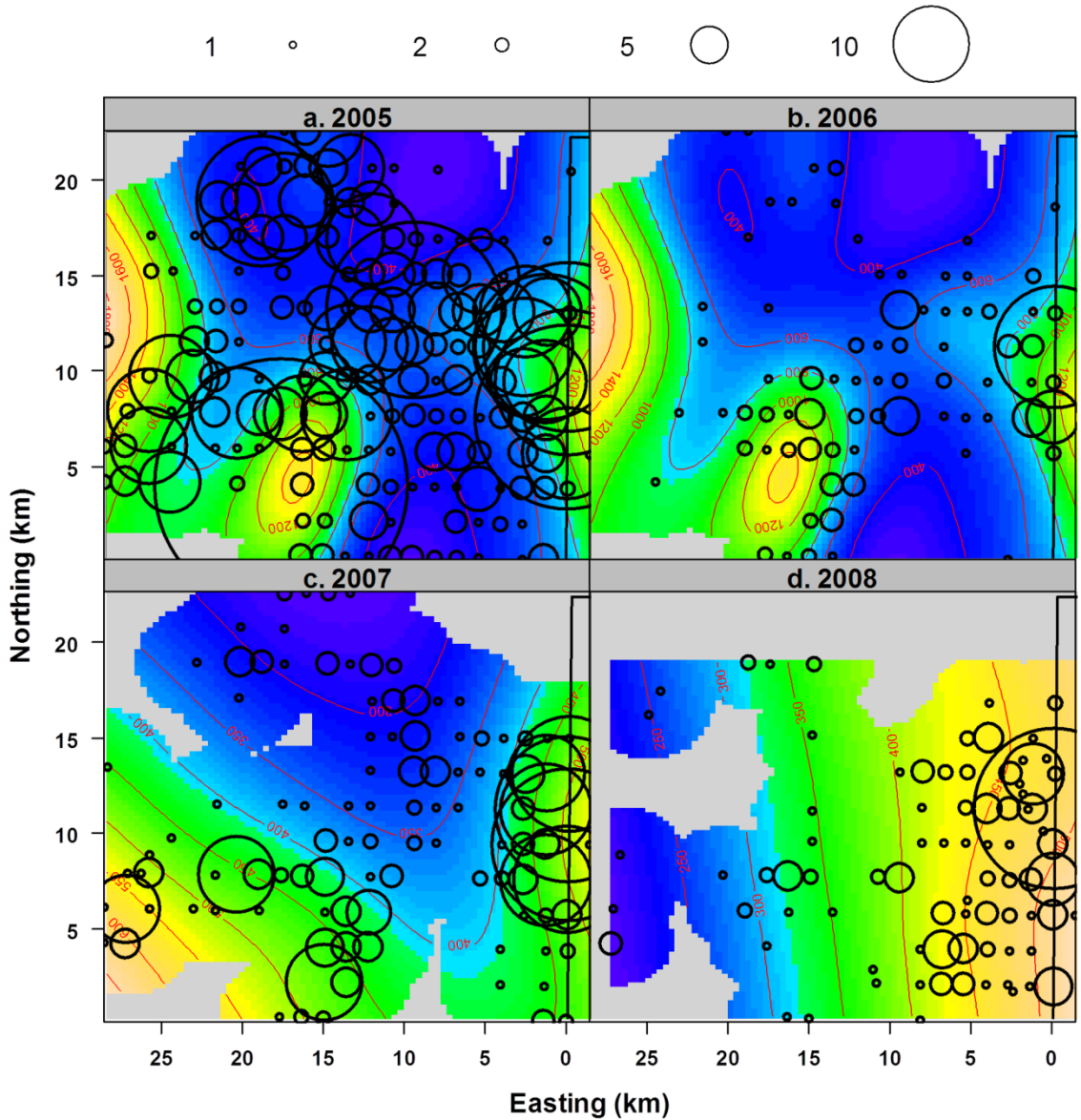


Figure 2.5. Distance from line catch rate trends for the west FTL region for years 2005:2008, each year plotted separately. Results of fitted values from GAMs of VPUE modeled against smoothed distance along and from the boundary line. Axes are in km. Circles represent trawl positions with size corresponding to the number in a given location. Black line represents the boundary line. Grey represents areas of no effort.



Chapter 3

Comparative analysis of the spatial distribution of fishing effort utilizing the ideal free distribution and discrete choice models

Abstract

The relationship between commercial catch-per-unit-effort (CPUE) and abundance has been demonstrated to often be nonlinear. Despite this, CPUE is still utilized in many fisheries models to approximate stock size. Effort distribution has been suggested as an alternative index with some finding it superior to CPUE. As a result it is vital to examine fishing effort distributions to fully understand a fishery. This study takes two approaches to investigate the effort distribution of the groundfish otter trawl fishery on the Scotian Shelf: first, through the use of the ideal free distribution (IFD) as a null model of weekly aggregate effort; and second, by development of a discrete choice model of individual location choice. The application of the IFD to the fishery was examined using a novel approach to fisheries research, isodars. Isodars represent the expected distribution of foragers between two habitats when fitness is equal. In our case, fitness was defined with relative catch rates, cost differentials and interference effects between habitats. Discrete choice models were constructed as mixed logit models, commonly used in economics, using random utility theory to give the expected probability of fishing in a particular area based on a collection of generic and individual-specific predictors. In-sample and out-of-sample predictions were made for both the IFD based on isodar models and the discrete choice models with root mean square error (RMSE) and correlation estimates used to test their performance. The isodar model consistently outperformed the mixed logit with marginally better correlation results and markedly better RMSE results. Ultimately the simpler isodar model was found to provide superior forecast to the much more detailed and complex discrete choice model.

Introduction

Historically catch-per-unit-effort (CPUE) estimates have been the basis for abundance estimates of exploited fish species, and they are still utilized within more advanced population models, such as virtual population analysis (VPA). Catch rate information can come from organized research surveys, but this is costly and often lacks temporal replication. As a result, CPUE is often derived for commercial catch and effort statistics. This becomes problematic as it requires a linear relationship between catch rate and abundance which has been demonstrated to often not be the case (Harley et al. 2001). A disruption in the relationship between CPUE and abundance can result from a number of factors. Paloheimo and Dickie (1964) found that catch rates could remain unchanged as abundance decreases due to schooling behaviour. As well, some species experience changes in spatial distribution rather than density as abundances decline (MacCall 1990), maintaining CPUE; such was the case for north Atlantic cod (*Gadus morhua*; Swain and Sinclair 1994; Rose and Kulka 1999). Fisheries targeting cryptic species with potential areas of refuge within a fishery can experience CPUE that falls faster than abundances, or hyperdepletion (Hilborn and Walters 1992). As a result of these potential relationships, it is imperative to study the spatial distribution of fishing effort to fully understand a fishery. This study examines the spatial distribution of effort from two perspectives: first analyzing the aggregate distribution of effort through the application of the ideal free distribution theory (IFD; Fretwell and Lucas 1970); and secondly, building a discrete choice model examining individual location choice within the fishery. The performance of the predictions from each model will be compared with the advantages and limitations of each respective model highlighted.

The IFD, a theory predicting the distribution of foragers among multiple foraging sites, assumes that foragers have ideal knowledge of their environment and suffer no impediments to movement between sites. This is predicted to result in foragers being distributed such that the

proportion of foragers at a given site will be equal to the proportion of resources at that site with each forager receiving equal benefit regardless of location. The IFD has frequently been considered in fisheries research having been applied to exploited species, their prey, and their harvesters and has been demonstrated to be a good first approximation of the spatial distribution of vessels in fisheries containing multiple fishers moving between distinct foraging sites (Gillis 2003). Though the assumptions of the IFD will be violated at some level in a natural system its predictions can be quite robust to such violations (Milinski and Parker 1991) or form the basis of other spatial distributions (Fretwell 1972; Abrahams 1986; Houston and McNamara 1988; Kennedy and Gray 1993).

The applicability of the IFD to a fishery is contingent on the presence of interference competition between vessels. Interference is the immediate but reversible decrease in foraging success due solely to the presence of other foragers and can be either direct or indirect (Goss-Custard 1980). Without interference competition in a system the expected distribution of foragers according to the IFD cannot be met because all foragers will target the best foraging sites and only move when prey levels fall to that of lesser sites. In a fishery, direct interference can be due to crowding of vessels, limiting a fisher's ability to manoeuvre or set gear, reducing efficiency; while indirect interference is due to prey disturbance, making them less accessible to other fishers (Gillis 2003). The presence of interference has been difficult to detect in commercial fisheries research; however, some directed studies have been successful in doing so. Abrahams and Healey (1993) detected interference by experimentally manipulating the density of three trawler vessels, finding a negative effect of density on catch rate in chinook salmon (*Oncorhynchus tshawytscha*) but a positive effect for spiny dogfish (*Squalus acanthias*) and no effect for coho salmon (*Oncorhynchus kisutch*). Gillis (1999) was able to infer the presence of interference in the silver hake (*Merluccius bilinearis*) trawl fishery from deviations in course

linearity with increased vessel density. Rijnsdrop et al. (2000a) inferred indirect interference in the Dutch beam trawl fishery after a 10% decrease in catch rate experienced by less powerful vessels during the exploitative fishing phase. Again in the same fishery Rijnsdrop et al. (2000b) took advantage of the Urk holiday, where a portion of the fleet does not fish for religious reasons for a week. They observed an increase in catch rate compared to the week prior, while there was no such change in an area unaffected by the holiday; this was attributed to interference.

In fisheries research the applicability of the IFD has been examined using a number of different analytical techniques within a variety of different fishery types. One such method regresses the angular transformed proportion of total effort for a given patch with the angular transformed proportion of total catch in that patch. If fishers are distributed according to the IFD this will result in a slope of 1 and an intercept of 0. This method has been applied to a British Columbia groundfish otter trawl fishery (Gillis et al. 1993), a Scotian Shelf Atlantic Cod fishery (Gillis and Frank 2001), a Namibian hake trawl fishery (Vogues et al. 2005), and an Anguillan artisanal fishery (Abernethy et al. 2007). Only Abernethy et al. (2007) found consistent significant deviations from the expected IFD trends. Other results suggest a correspondence with the IFD (Gillis et al. 1993), despite differing costs between foraging regions (Gillis and Frank 2001), or other IFD assumption violations (Vogues et al. 2005). Healey and Morris (1992) examined the correlation between catch rates and vessel density in the BC salmon troll fishery; finding that catch rate was independent of local vessel density suggesting fishers behave as ideal free predators. Swain and Wade (2003) also used correlation analysis between fishing effort, catch rate and abundance, as well as a second analysis developing a test statistic to examine differences between the spatial distributions of the above variables. They found that effort was more highly correlated with abundance than catch rate was and its spatial distribution was

different from abundance less often than catch rate. This is consistent with the expected IFD trends and demonstrates how effort distribution can give a superior approximation of underlying abundance in comparison to catch rate.

In this study I take a novel approach to testing the application of the IFD to a commercial fishing fleet, using isodars. Isodars are a representation of the expected distribution of foragers between two habitats when fitness is equal among foragers and between habitats. As with other expressions of the IFD, the isodar forms a distributional null hypothesis, which the observed distribution can be tested against. Isodars have been successfully applied to the spatial distributions of a variety of species including rodents (Morris 1988; 1994), salmonids (Rodriguez 1995), pike (Haugen et al. 2006), birds (Fernandez-Juricic 2001; Shochat et al. 2005) and humans (Morris and Kingston 2002). Isodars have also been extended beyond simple IFD assumptions to include the ideal despotic distribution, site-dependent habitat selection, predator-prey interactions, and multiple species (see Morris 2003 for a review). In this study, a hypothetical isodar is presented, based upon the IFD, which predicts vessel density amongst distinct fishing sites based on the relationship between density at other sites, relative catch rates, cost differences and interference.

As an alternative to evaluating fleet wide aggregate effort distribution based on a distributional null model, such as the IFD, detailed individual location choice models can be created. One such approach, utilized most frequently in economic literature, is the random utility model (RUM; McFadden 1974). This assumes individuals are selecting among a number of distinct alternatives (locations) and chooses the alternative that generates the greatest utility for that individual, with utility based on a linear combination of predictor variables. RUMs have been applied to multiple fisheries describing recreational (Bockstael and Opaluch 1983),

commercial (Holland and Sutinen 1999; 2000) and artisanal fisheries (Wilén et al. 2002). Where RUMs become particularly useful is in their ability to model the effects of potential regulatory changes such as area closures (Holland and Sutinen 1999; Hutten et al. 2004; Smith et al. 2010).

This study will investigate the spatial distribution of fishing effort of the groundfish otter trawl fleet in NAFO Division 4X (Figure 3.1). This region is subject to a seasonal area closure on Brown's Bank from February 1st to June 15th annually, where no targeted groundfish fishing is allowed to take place. I will apply both the IFD-based isodar and RUM models to periods with and without an active closure, representing different fishing opportunities. The performance of each model type will be compared using root mean square error (RMSE) and correlation estimates between observed values and predictions. This comparison will determine which model performs better and will provide insight into how best to predict the distribution of fishing effort; whether to use detailed individual choice models or simpler ecological models.

Methods

The study site and data set

Logbook data were obtained from Fisheries and Oceans Canada for the NAFO Division 4X groundfish fishery for the years 2005-2008 (Figure 3.1). Entries with missing or clearly inaccurate information were removed from the analysis. This included trawls with effort levels greater than 7 hours, excessive distances traveled between trawls in the time reported resulting in speeds greater than 25 km·h⁻¹, and trawls located in unfishable areas (e.g. off the continental slope). Catch rates were calculated as $\text{kg} \cdot \text{h}^{-1}$ and standardized using a log transformed linear model to remove the effects of year and vessel length on catch rate. All analyses were conducted in R 2.12.1 (R Development Core Team 2010).

Patch definition

The data set was split into two periods, the open period when vessels were free to fish throughout the 4X regulatory area, and the closed period where the majority of the area over Brown's Banks was closed to all targeted groundfish fishing (Figure 3.1). The closed period extended from February 1st to June 15th each year. Within each time period, the fished area was divided into spatially distinct "patches" that represent different fishing opportunities. Due to the closure limiting where fishing can take place, patches were defined for each period separately.

Patches were defined by first using kernel-smoothed intensity estimates to identify the primary areas of effort concentration. Intensity estimates were based on the point pattern distribution of trawls with the standard deviation of the Gaussian kernel intensity function set to half the median distance between trawls, 4.1km. Trawls with an intensity value below the tenth percentile were considered outside the primary areas of concentration and removed. The remaining trawls were then divided into distinct patches based on the apparent gaps that delineated clusters in the point patterns (Figure 3.1). These patches were also chosen to reflect fishing relative to Browns Bank. The level of aggregation of effort into defined patches can vary somewhat, as long as the final patches form unique choices for vessel locations. This resulted in three patches being defined for the closed periods and four during the open period. During both periods there was a concentration close to shore (the north patch), as well as one to the west of Brown's Bank (the west patch). During the closed period a third patch was located to the east of the Brown's Bank closure (the east patch). Fishing did not take place in this patch during the open period but instead there was a concentration directly on Brown's Bank (the browns patch) and an additional concentration to the south of the west patch along the boundary with NAFO Division 5Y (the south patch). In each time period there were one or two small areas of effort

concentration that could not be included in these patches and were omitted from the analysis. These areas represented alternative fishing strategies which targeted different species (winter flounder, *Pseudopleuronectes americanus*, or sliver hake, *Merluccius bilinearis*) that were not of primary interest in this study. The two concentrations excluded in the closed period represented 427 and 182 trawls respectively and in the open period the single concentration excluded represented 197 trawls. The spatstat library (Baddeley and Turner 2005) was used to generate kernel-smoothed intensity estimates. This method of patch definition was defined by the distribution of individual sets and was not reliant on arbitrary defined areas such as a grid or statistical region system.

Summaries of area usage and landed catch were calculated for each patch. Home port information was not available for each vessel; consequently the distance to each patch was calculated from West Pubnico, NS, Canada, the most common home port for trawlers in this area, to the median longitude and latitude of each patch.

Ideal free distribution

To model the IFD within this fishery I utilized the isodar approach ('iso' meaning the same and 'dar' for Darwin; Morris 1987). This is a curve that graphically represents the densities that result in equal fitness between two habitats. This assumes a declining relationship of fitness with density and a corresponding density dependence amongst habitats. Within a fishery, fitness can be represented by catch rate with the simplest IFD assumptions that catch rate equalizes between areas. For areas a and b:

$$(1) \quad C_b/f_b = C_a/f_a$$

where C is catch and f is nominal fishing effort. This is subject to the assumption that there are no cost differences between areas which will undoubtedly be violated in a natural system. Equation 1 can be modified to account for the relative difference in costs between the two patches by incorporating the component α where e^α represents a consistent ratio in profitability between patches. In addition, nonlinear effects of increasing effort on profitability, such as disproportionate interference effects, can be represented by β_m :

$$(2) \quad \frac{C_b}{f_b^{\beta_b}} = e^\alpha \times \frac{C_a}{f_a^{\beta_a}}$$

This model assumes that profitability is maintained at a constant ratio between habitats, even when the availability of prey, and resulting catch ratios, vary through time. It can be rearranged to give the habitat isodar, with fishing effort (in hours fished for this fishery) replacing the traditional density, on a logarithmic scale:

$$(3) \quad \log(f_b) = -1/\beta_b [\alpha + \log(C_a/C_b)] + \beta_a/\beta_b \times \log(f_a)$$

demonstrating a relationship between areas based on relative catches, C , differing cost effects, α , and the ratio of interference effects, β_a/β_b . This model is examined in greater detail in Gillis and van der Lee (in prep.). One limitation of the isodar in this format is that the model cannot incorporate observations with zero effort in an area. This could result from vessel avoiding habitats when fish are unavailable, or when avoiding habitats for other reasons such as local meteorological conditions. As a result, weeks with no effort or catch were excluded from the analysis on a patch by patch basis.

Isodars were created for each possible patch comparison for the open and closed period separately, using catch (as value) and effort (as hours fished) values summed weekly. The α and β_m parameters were estimated using generalized nonlinear least squares (GNLS). GNLS can

account for autocorrelation in residuals which is common in time series analysis such as this. For each isodar analysis, the correlation structure used was determined by fitting a model with a variety of correlation structures from the autoregressive-moving average (ARMA) family as well as a model with no correlation structure. The ARMA family correlation structure is a combination of the autoregressive (AR) and moving average (MA) correlation structures. Each assumes that the data are observed at evenly spaced time intervals. In an AR correlation the current observation, ε_t , is expressed as a linear function of previous observations, with lag $|t-s|$, and p correlation parameters ϕ_p plus a homoscedastic noise term ω_t (Pinheiro and Bates 2004):

$$(4) \quad \varepsilon_t = \phi_1 \varepsilon_{t-1} + \dots + \phi_p \varepsilon_{t-p} + \omega_t$$

p is termed the order of the autoregressive model which is denoted by AR(p). An MA correlation assumes the current observation is influenced by a linear function of previous i.i.d. noise terms, such that:

$$(5) \quad \varepsilon_t = \theta_1 \omega_{t-1} + \dots + \theta_q \omega_{t-q} + \omega_t$$

where q is the number of noise terms included or the order of the moving average model, denoted MA(q), and θ_q are the correlation parameters. AR and MA models can be combined to give an ARMA model:

$$(6) \quad \varepsilon_t = \sum_{i=1}^p \phi_i \varepsilon_{t-i} + \sum_{j=1}^q \theta_j \omega_{t-j} + \omega_t$$

Such a model is denoted ARMA(p,q). An ARMA model, is typically more difficult to fit to data and biologically less interpretable than an AR model. However, an ARMA(p,q) will often require fewer coefficients than a simple AR model describing the same process with p' coefficients, i.e. $p+q < p'$, and thus is preferred (Granger and Morris 1976). The p and q values were varied and refit to the isodar model. The criteria for selecting the values of p and q used in the final model

was based on minimizing AICc (Hurvich & Tsais 1989), but ensuring $p+q < p'$, otherwise the best AR(p') model was used (determined using AICc). The predicted values from the isodar then represent the expected amount of effort in a patch for a given week. This prediction was compared to the observed values using ordinary least squares (OLS) regressions where a successful model would be indicated by a slope of 1 and intercept of 0. GNLS models were estimated using the nlme library within R (Pinheiro et al. 2010).

Random Utility Model (RUM)

As an alternative to the IFD, a discrete choice random utility model (RUM) was used to model individual fisher's choice of location, on a trip by trip basis. In a RUM it is assumed that each individual will be most likely to choose the alternative that generates the highest utility. Utility for individual i and alternative j , U_{ij} , is the combination of two components: a systemic component, V_{ij} , consisting of explanatory variables and a vector of coefficients, and an unobserved random component ε_{ij} , which represents any variable contributing to the utility of a specific alternative that remains unobserved, such that:

$$(7) \quad U_{ij} = V_{ij} + \varepsilon_{ij}$$

The systemic component can consist of two kinds of variables: alternative specific x_{ij} with a generic coefficient β and individual specific z_i with an alternative specific coefficients γ_j . Generic coefficients represent the common effect of a certain variable on the overall choice probably for all alternatives while alternative specific coefficients represent the relative effects of a variable for a specific alternative in relation to a specified reference alternative. Thus, generic coefficients typically represent characteristics of the choices while the individual specific coefficients represent differences in utility among the choices due to characteristics of the chooser. This can be written as:

$$(8) \quad V_{ij} = \alpha_j + \beta x_{ij} + \gamma_j z_i$$

This combines two classic choice models, the multinomial (for individual specific) and conditional (for alternative specific) logits (Hoffman and Duncan 1988), into a single form. This combined model can be generally called multinomial logistic regression to distinguish it from the classic logistic regression whose response is a binomial variable. What is of interest is the difference between two alternatives, for example alternatives j and k :

$$(9) \quad V_{ij} - V_{ik} = (\alpha_j - \alpha_k) + \beta(x_{ij} - x_{ik}) + (\gamma_j - \gamma_k) z_i$$

This necessitates that individual coefficients (including the intercept α) be alternative specific. Additionally a coefficient for each alternative cannot be identified unless one alternative is chosen as a reference alternative and set to equal 0. As ε_j are unobserved, choice must be modeled as probabilities and the general expression of the probability of choosing alternative l is:

$$(10) \quad (P|\varepsilon_l) = P(U_l > U_1, \dots, U_l > U_j)$$

Multinomial logistic regression models are subject to a number of assumptions. Foremost it is assumed that the probability ratio of any two alternatives is independent of any other alternative. For example, given three alternatives, 1, 2 and 3, the ratio of probabilities of 1 and 2 remain the same if the characteristics of 3 are modified affecting its choice probability. This is termed the IIA or, independence of irrelevant alternative, hypothesis. Additionally the random component of utility, ε , is assumed to be independently and identically distributed (i.i.d.) with a Gumbel distribution. Given these assumptions the unconditional probabilities can be calculated from a simple logit transformation of the systemic portion V_j , of utility U_j . However the IIA hypothesis has often been shown to be violated when multinomial logistic regressions

are applied to fisheries research. This occurs when a subset of the alternatives share an unobserved characteristic that has been wrongfully attributed to the random component. With this the case a generalization of multinomial logistic regression model can be used, such as the nested (McFadden 1981) or the mixed logit models (Train 2009).

The nested logit allows for grouping of alternatives into nests, so that the IIA hypothesis is maintained within groups but not between them. This is the model used in many fisheries related discrete choice studies (Eales and Wilen 1986; Holland and Sutinen 1999; and Wilen 2002). However to be compatible with random utility maximization hypothesis each alternative must belong to one and only one group. This is not the case with the definition of patches in this study. As a result, the alternative method, the mixed logit, was utilized. A mixed logit allows for parameters to be modeled as random effects, accounting for the variability of individuals within the population. The probability that individual i chooses alternative l is then:

$$(11) \quad P_{il}|\beta_i = \frac{e^{\beta_i' x_{il}}}{e^{\sum_j \beta_i' x_{ij}}}$$

The unconditional probability is then the average conditional probability for all values of β_i . When more than one coefficient is being estimated this results in an integral with no closed form and therefore the probabilities have to be estimated through simulation. That is, R draws are made from the hypothesised distribution of β_i , the unconditional probabilities computed for each R , and averaged to give the expected unconditional probabilities (Croissant 2011).

In this study, a mixed logit model predicting the most frequently visited patch of a trip was created for the open and closed period separately, utilizing the same patch definitions as the IFD analysis to define the choice alternatives. Parameter inclusion in the final models was based on a stepwise procedure where the full model was fitted and parameters were removed if

there was a resultant improvement in AIC (Akaike 1974). The final model was the one that minimized AIC.

The primary alternative specific variables with generic coefficients that were considered for inclusion in the model were the average standardized value per unit effort (VPUE), the total number of vessel fishing, and the total number of hours fished. Each variable was from the previous week (168 hours from the start of the trawl). A week was chosen because it accounts for the temporal pattern of fishing activity observed in the data where less fishing tended to take place on the weekend. Supporting this choice model, comparisons in Chapter 2 indicated that this period best accounted for information lag based on AIC values. If there was no effort in a patch within the previous 168 hours the lagged period was extended to two weeks (336 hours) from the start of a trawl. A dummy variable was included in the model to mark when a two-week period was used to generate information; this represented old information. If there was no effort in a patch within two weeks of a trawl it was assumed that no useful information was available for the patch. In this case an additional dummy variable was entered into the model to represent the absence of information for a given patch. The number of vessels and number of hours fished in a patch are both measures of fishing effort exerted and were highly correlated, leading to collinearity issues if both were included in the final model. As a result, only the effort variable that contributed most to a lower AIC value was included in the final model.

The individual specific variables considered were, length overall, species targeting, estimated trip length (in days), and the mean fishery wide catch rate from the previous week. Targeting was determined using quantification level theory (Biseau 1998). For each species landed in the fishery, the cumulative landings of all trips, ordered from least to most, were plotted against the proportion of landings that species represented for each trip. If this resulted

in an exponential (concave) shaped curve the species was determined to be one that was targeted within the fishery. An exponential curve suggests that when that species was caught it made up a high proportion of the total landings for that trip and thus was actively targeted. A convex shaped curve suggests that that species typically represented a low proportion of a trips landing and therefore was likely a bi-catch species. Haddock (*Melanogrammus aeglefinus*), pollock (*Pollachius virens*), and redfish (*Sebastes sp.*) were found to be target species in this study. The quantification level, or the percentage of total landings a species must comprise for the trip to be deemed to be targeting that species, was set at a conservative level of 80% for each of the target species. For each target species a dummy variable was created with a 1 representing trips that targeted that species and a 0 when it was not the target species of a trip. Otherwise trips were classified as mixed-species trips, which were represented in the model by an absence of targeting. A trip length approximation was entered into the model to account for the potential relationship between distance to port and time at sea. The estimate was only approximate because time leaving port was not available in the data set. Therefore the trip length was approximated as the time for the beginning of the first trawl of a trip to the landed time. Finally, the fishery-wide mean VPUE was entered into the model as a representation of general fishery success from the previous week. This could allow for a change in behaviour if the fishery was doing particularly poorly or well in a given week. Models were constructed using the mlogit package (Croissant 2011).

Model comparison

The performance of the mixed logit and isodar models were evaluated by comparing in-sample and out-of-sample forecasts from each model to actual observed trips, following a similar approach taken by Smith (2002). The four year data set was divided into in-sample and

out-of-sample by excluding one year and using predictions of the year excluded as the out-of-sample forecasts and the years included as the in-sample forecasts. This was repeated until each year had been removed from the analysis. This produced a single estimate for each year in the out-of-sample forecasts but three estimates for each year in the in-sample forecasts which were then averaged to give a single forecast value.

The isodar produces forecasts as aggregate log transformed total hours fished in each patch while the mixed logit model produced forecasts as a probability of choosing each patch on an individual basis; as a result, the forecasts for each model had to be adjusted so that they were on the same scale. The isodar produces multiple forecasts per patch, one for each other alternative, which were averaged to give a single forecast for each patch. This result was then divided by the total amount of effort predicted each week to give the predicted proportion of effort in each patch each week, summing to 1. The mixed logit forecasts were aggregated by week to match the temporal scale of the isodar. This resulted in the predicted proportion of effort expected in each patch on a weekly basis and was comparable with the isodar forecasts. Additionally, as the isodar model cannot make predictions when effort levels were zero in a particular patch, weeks where the observed effort was zero were removed from the mixed model predictions so that the models were comparable. The accuracy of the in-sample and out-of-sample predictions was evaluated using root mean square error (RMSE) estimates and correlations between the observed and predicted values.

Results

Table 3.1 summarizes the area usage and landings for each patch. During the closed period the west patch was the most productive. It maintained the highest VPUE and contributed the most to total catch, though primarily in redfish and pollock landings. Haddock was caught

mainly in the east patch. Despite this, more effort, in hours fished, was exerted in the north patch, which was situated much closer to port.

During the open period, the south patch was the area targeted most, with the greatest number of sets and total hours fished, though it was the farthest from port. This was principally an area of haddock targeting. The west patch had the highest catch rate though it was utilized much less than any other area and was an area of redfish and pollock targeting.

Ideal free distribution

Isodar results for the closed period are summarized in Table 3.2 and the open period in Table 3.3 with predicted values plotted against observed values in Figures 3.2 and 3.3. The theoretical isodar models fit the data well once differing costs, possible interference, and autocorrelation in the residuals were taken into account. When an alternative correlation structure was necessary, an ARMA model with p and q values ranging from 0 to 3 was found to be the best fit (Table 3.2 and Table 3.3). This indicates that the amount of effort in a particular patch can be influenced by the effort levels from previous weeks. This effect, however, seems to be patch specific, with some patch comparisons showing the influence of previous effort levels going back up to three weeks, such as the east-west comparison (ARMA(3,0); Table 3.2), or having no influence from previous weeks, such as the north-east comparison (no significant ARMA; Table 3.2).

Three coefficient values within the isodar model were estimated, α and two β values (Table 3.2 and Table 3.3). The relative magnitude of α represents the desirability of the patch being predicted relative to the predicting patch. This desirability can be related to the costs that increase proportionally to fishing effort (monetary or risk), as well as other factors influencing a fisher's choice to fish in a particular patch, such as target species. An examination of α values

allows for a ranking of the desirability of patches, which from greatest to least in the closed period isodars was: north > east > west, and the open period: south > north > browns > west. This trend, in both periods, follows the reverse order of average hourly revenue observed in the fishery (Table 3.1). The β values, representing the nonlinear effects of effort on profitability, are less interpretable and were not as consistent between patch comparisons. The β_2 (predicted patch) values, however, were always greater than β_1 (observed patch) values, though this difference was often not significant, with no results being significantly different in the closed period and only occasionally different in the open period.

Mixed logit model

Discrete choice mixed logit models were developed to predict location choice of fishers on an individual level. Location choice was defined as the patch utilized most frequently over the course of a given trip. Models were created independently for the closed and opened periods. Results from the closed period model are presented in Table 3.4 and open period in Table 3.5.

The final models for the closed and open periods were similar in a number of ways but also contain marked differences. This is indicative of a fishery with strong temporal differences in effort distribution, which is undoubtedly at least partly due to the enforcement of the seasonal haddock spawning closure, leading to a redistribution of effort. Many of the primary factors relating to location choice, however, are consistent between models. Both models had a significant positive coefficient for VPUE of similar magnitude and modeled as a random effect with a log-normal distribution (Tables 3.4 and 3.5). The distributional choice was supported by AIC values comparing alternative models where VPUE was treated as a random effect with a log-normal or normal distribution. In both the closed and open models a log-normal distribution provided a much better fit with respective Δ AIC values of 409 and 28. This demonstrates that

within the population of fishers, there was variability in the magnitude of the importance of catch rate in location choice but also that it universally had a positive effect. The inclusion of the number of vessels fishing in a patch in a given week was also consistent between the two models. This was found to be a superior predictor in comparison to total hours fished during both periods based on AIC values (Δ AIC of 52 for the closed period and 43 for the open period). It was included as a random effect with a similar mean value and little difference between a normal or log-normal distribution choice on model fit; ultimately a normal distribution was chosen for the closed period model (Δ AIC: 2; Table 3.4) and log-normal was chosen for the open period (Δ AIC: 1.7; Table 3.5). Using a normal distribution to model the number of vessels in a patch as a random effect suggests that it could have had a negative effect on location choice. In this case, however, the median value for the parameter was very close to that of the open period which was modeled as a log-normal distribution and it produced positive values above the first quartile. Thus there was little negative effect. The dummy variable representing old information (when no fishing took place in a patch the previous week but did two weeks previous) was significant and negative in both models (Tables 3.4 and 3.5). This suggests a decreased likelihood of choosing a patch if the information available about its catch rate and effort levels were old. Additionally, this was found to be a fixed effect which indicates there was little variability among fishers in the influence of this variable. The dummy variable for no information available about a patch was significant and negative during the open period but not during the closed (Table 3.5). This was the expected trend for this parameter for the open period. The lack of significance during the closed period was likely due to the small number of occurrences when there was no information for a patch, 120 during the closed period compared to 667 during the open period.

The primary differences between these mixed logit models existed in the individual specific variables. For these variables the north patch was set as the reference patch to which the effects of other patches were compared. Length overall (LOA) had a similar effect during both periods; significant positive coefficients suggest that larger vessels were more likely to fish patches a greater distance from port (the east or west patch during the closed period and the west or south patch during the open period; Tables 3.4 and 3.5). Trips in which haddock was the target species also had an effect during both periods. The east patch was the area of primarily haddock targeting during the closure and during the open period the browns and south patches were utilized as haddock fishing grounds, represented by significant positive coefficients (Table 3.4 and 3.5). Other target species (pollock and redfish) could only be associated with patch choice during the closed period (Table 3.4). This was due to the temporal nature of the fishery in which there was much less targeting of these species during the open months. This made it impossible to estimate parameters for pollock and redfish targeting as models including these variables failed to converge. The primary difference between these two models however was the inclusion of a trip length parameter. This had no effect during the closed period but was highly significant and greatly affected AIC estimates during the open period (Table 3.5).

Model Comparison

The performance of the predictions of the mixed logit and isodar models were compared using root mean square error (RMSE) and correlation estimates between in-sample and out-of-sample forecasts and observed values (Table 3.6). For almost all patches the isodar model outperformed the mixed logit in both metrics for both the in-sample and out-of-sample forecasts, with the lone exception being the closed period, west patch, out-of-sample, correlation result. During the closed period, both models performed almost equally as well with

the main difference being the isodar model producing a more precise fit around the predicting line indicated by lower RMSE estimates (Figure 3.4). During the open period, however, an extra patch was defined which seemed to have more of a negative influence on the mixed logit model than it did the isodar, resulting in much higher correlation estimates for the isodar models than the mixed logit (Figure 3.5). The results of this specific comparison suggest the isodar model to be superior to the mixed logit in predicting the distribution of effort among fishing locations.

Discussion

I used two methods to model the spatial distribution of fishing effort; the first based on a fleet-wide distributional hypothesis, isodars developed from the IFD, and the second based on individual-specific location choices, modeled by a mixed logit. By use of two measures, RMSE and correlation, I found that for both in-sample and out-of-sample forecasts of the proportion of weekly aggregated effort in defined patches, the IFD model consistently outperformed the mixed logit.

The predictions of the isodar models provided a superior fit to the observed data for almost all patches in both metrics for both the in-sample and out-of-sample forecasts. The lone exception was the out-of-sample correlation comparison for the west patch during the closed period. In this instance, the mixed logit was more highly correlated with the observed data; however, the isodar provided a lower RMSE estimate. During the closed period the majority of correlation results were quite similar between the respective models and were consistently high; although the isodar model did produce better RMSE estimates in every case, yielding a tighter relationship with the observed data. The differences between the two models were more pronounced during the open period where there was an extra alternative defined. In this period the isodar produced forecasts that performed as well or better than during the closed period

while the mixed logit showed sharp declines in model prediction accuracy, especially for out-of-sample forecasts. Accuracy of predictions when utilizing discrete choice models with a large number of alternatives has proven problematic in past fisheries studies (Smith 2002; Hutten et al. 2004). This seems to be a limitation of discrete choice models that was not as prominent in the isodar model, though with a maximum of four alternatives in this study additional examples would be required to draw firm conclusions. In a similar study, Smith (2002) found an aggregate econometric model more often outperformed a discrete choice model, in this case a nested logit, using goodness-of-fit measures in comparisons of in-sample and out-of-sample forecasts with observed effort. Smith's results, however, were not as consistent as this study with some examples of the nested logit model providing superior predictions.

Both these comparisons were limited in having to aggregate the micro-behavioural model, which though necessary, did not fully represent the discrete choice-model's predictions. A discrete-choice model is most powerful when modeling the actions of individuals and thus can account for changes in behaviour due to changes in individual specific characteristics. When taking an aggregate approach, the predictions rely on the association of variables at a level greater than that of an individual and thus are unable to accurately and consistently estimate changes in choice behaviour due to changes at the individual level (Koppelman and Bhat 2006). Another potential bias in the model comparisons may have resulted from weeks with zero effort being removed from the isodar analysis. Although the same weeks were excluded from the RMSE and correlation estimates for the mixed-logit model, this information was still included in the estimation of the coefficients of the discrete-choice model. Thus, the fitted parameters of each model were not derived from exactly the same subset of the original data. The inclusion of extreme values likely decreased the performance of the mixed logit predictions but I chose to do this so that the mixed-logit model would be constructed with the most information available,

similar to the manner in which it would be applied in practice. The isodar model's performance also likely benefited from being the averaged result of multiple comparisons and that the model was constructed as a time series (Smith 2002). These however, represent advantages to the isodar approach and potential limitations of an individual-choice model.

A distinct advantage to the isodar over alternatives is its simplicity. This model is based solely on regional catch and effort data, and yet is able to account for deviations from the simple IFD due to factors such as differential costs and interference with the estimation of only three coefficients, which readily converge, and result in an excellent fit to the data. Studies have found that simpler models often outperform more complex models in fisheries research (Ludwig and Walters 1985; Adkinson 2009). The application of isodars is novel to fisheries research but it appears as effective as it has been to other biological systems. The predictions of the isodar created here differ slightly from that of the simple IFD in that costs are accounted for. Under its simple assumptions of ideal knowledge and no cost, the IFD predicts profit rates to equalize among spatially distinct patches within a fishery (Gordon 1954; Hilborn and Ledbetter 1979; Gillis 2003). These assumptions, however, particularly that of no costs, have been found to be violated in natural systems, for example, due to differing levels of risk (Hilborn and Ledbetter 1979), weather patterns (Gillis and Frank 2001), or distance from port (Gillis et al. 1993; Swain and Wade 2003). Violations such as these lead to fundamentally different expected distributions of effort, which before now were not readily included in IFD-based fisheries analyses. Differential costs were captured primarily in the desirability parameter α in the isodar model, which allowed for a ranking of patch options. Interestingly, this ranking was found to be in the reverse order of mean catch rate of the patches, a finding consistent for both periods. This suggests α to be a representation of factors influencing patch selection that are balanced against

fishing success, such as risks and more direct costs. The exact nature of these factors, however, cannot be definitively determined from these models.

Generally, β values differed from one, supporting a nonlinear relationship between effort and profitability. The relationship between β values, however, was not consistent between different patch comparisons. This is not surprising because the nonlinearities could be the result of vessel interference that may vary in intensity throughout the fishing season. Interference by definition acts instantaneously and is reversible (Gillis 2003). As a result, it is inherently difficult to detect. In this model it was expressed as a separate coefficient for each patch suggesting potentially differing magnitudes of interferences between patches. The magnitude of interference can differ between regions because of factors such as topography limiting the space available for trawling or the existence of areas of refuge for target species. Further, it will be constantly changing with changes in the density of vessels and/or prey. The confidence intervals of the β values, however, were large and often overlapping, suggesting that the evidence for differences was weak and that their values were not well estimated by the data. Finally, the tendency for the β value of the predictor to be less than that of the predicted patch, regardless of patch identity, suggests that error-in-variables bias in generalized nonlinear least squares may be influencing these results. Thus, differences in β should not be emphasized in interpretation, though the presence of nonlinear effort effects is clearly supported.

One of the primary advantages of the discrete-choice model is that it can not only account for the desirability of patches but also identify the influencing factors and provide estimates of their importance. In the models estimated in this study, catch rate, the number of vessels, and age of available information in a particular patch as well as vessel length and target species consistently influenced patch selection. All of these parameters had the kind of influence

expected *a priori* and are consistent with results from similar studies (Holland and Sutinen 1999; Hutten et al. 2004). Some results, however, were surprising. The duration of a trip (in days) had a different effect depending on what period was being analysed. Its effect was as expected during the open period with vessels taking longer trips more likely to visit patches farther away from port with the effect being amplified the farther away from port a patch was, as has been reported in other studies (Holland and Sutinen 1999; Hutten et al. 2004). During the closed period, however, no such effect was found despite similarly large difference in distance from port among patches. The time a vessel left port was not available in the data set for this study. This shouldn't have affected coefficient estimates because this detail was missing from both open and closed period's data and steam time was at least partially captured in the time taken to return to port.

Patterns such as these demonstrate the utility of a detailed model such as a discrete-choice model, which a model based on aggregate data might miss. This strength can also be a disadvantage in that the more detailed the model the more demanding it is on the available data. For example, when the parameters of interest include weather patterns (Wilén et al. 2002) or tradition (Marchal et al. 2009), the analysis may require numerous data sets from multiple sources. If certain information is not available, the parameter cannot be estimated and instead are assigned to the random component of the RUM, violating the independent and irrelevant alternative hypothesis (IIA) (Train 2009 pp. 45-50). This has been an issue in almost all applications of RUMs to fisheries research, though has not prevented useful analysis. Methodologically, the mixed logit employed here eliminates the statistical concern surrounding the violations of IIA assumption. An additional advantage to a discrete choice model over the isodar analysis used here is its ability to incorporate potential management practices into the model, such as the use of area closures (Holland and Sutinen 1999; Smith 2002). Within the

framework of a discrete-choice model, future policy decisions can be incorporated to predict the effect they will have, while the isodar model, as a time series, would have to be incorporated into a more detailed fishery model, such as those suggested by Hilborn and Walters (1987) or Gillis and Peterman (1998) to make similar predictions. An additional limitation to both models is as the number of alternatives increased, a substantial increase in the amount of data is required. For the isodar model, assigning the observed effort to more possible locations reduces the number of observations in each one. As a result, parameter estimation of β_m and α using GNLS produce poorer effort predictions. This can be even more problematic in a discrete choice model. The estimation of individual specific variables requires the estimation of $l-1$ parameters, where l is the number of alternatives, for each variable. This can quickly lead to overparameterized models which may not converge.

I have created two models to analyse the spatial distribution of fishing effort: an aggregated distributional model based on the IFD, an isodar, and a disaggregate individual-choice model, a mixed logit. The isodar model produced better in-sample and out-of-sample forecasts than did the mixed logit suggesting superior predictive performance of the aggregate model. The isodar also has the advantage of simplicity, being entirely based on simply catch and effort statistics from logbook records. The mixed logit, on the other hand, provides a detail description of the influences of location choice; however it can require much more detailed records, and as the number of alternative choices increases, the quantity of data needed increases while its performance in predicting aggregate effort distributions decreases. Ultimately, model choice will depend on the goals of the researchers and limitations of the available data.

References

- Abernethy, K.E., Allison, E.H., Molloy, P.P., and Cote, I.M. 2007. Why do fishers fish where they fish? Using the ideal free distribution to understand the behaviour of artisanal reef fishers. *Can. J. Fish. Aquat. Sci.* **64**: 1595-1604.
- Abrahams, M.V. 1986. Patch choice under perceptual constraints: a cause for departure from an ideal free distribution. *Behav. Ecol. Sociol.* **19**: 409-415.
- Abrahams, M.V., and Healey, M.C. 1993. Some consequences of variation in vessel density: a manipulative experiment. *Fish. Res.* **15**: 315-322.
- Adkinson, M.D. 2009. Drawbacks of complex models in frequentist and Bayesian approaches to natural-resource management. *Ecol. Appl.* **19**: 198-295.
- Akaike, H. 1974. A new look at statistical model identification. *IEEE Trans. Automat. Contr.* **AC-19**: 716-722.
- Baddeley, A., and Turner, R. 2005. Spatstat: an R package for analyzing spatial point patterns. *J. Stat. Softw.* **12**: 1-42. ISSN: 1548-7660.
- Biseau, A. 1998. Definition of a directed fishing effort in a mixed-species trawl fishery, and its impact on stock assessments. *Aquat. Living Resour.* **11**: 119-136.
- Bockstael, N.E., and Opaluch, J.J. 1983. Discrete modelling of supply response under uncertainty: the case of the fishery. *J. Environ. Econ. Manage.* **10**: 125-137.
- Croissant, Y. 2011. mlogit: multinomial logit model. R package version 0.2-1.

- Eales, J., and Wilen, J.E. 1986. An examination of fishing location choice in the pink shrimp fishery. *Mar. Resour. Econ.* **2**: 331-351.
- Fernandez-Juricic, E. 2001. Density-dependent habitat selection of corridors in a fragmented landscape. *Ibis* **143**: 278–287.
- Fretwell, S.D. 1972. *Populations in a seasonal environment*. Princeton University Press, Princeton.
- Fretwell, S.D., and Lucas, H.L. 1970. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheor.* **19**: 16-36.
- Gillis, D.M. 1999. Behavioral inferences from regulatory observer data: catch rate variation in the Scotian Shelf silver hake (*Merluccius bilinearis*) fishery. *Can. J. Fish. Aquat. Sci.* **56**: 288-296.
- Gillis, D.M. 2003. Ideal free distributions in fleet dynamics: a behavioural perspective on vessel movement in fisheries analysis. *Can. J. Fish. Aquat. Sci.* **81**: 177-187.
- Gillis, D.M., and Frank, K.T. 2001. Influence of environment and fleet dynamics on catch rates of eastern Scotian Shelf cod through the early 1980s. *ICES J. Mar. Sci.* **58**: 61-69
- Gillis, D.M., and R.M. Peterman. 1998. The implications of interference among fishing vessels and the ideal free distribution to the interpretation of CPUE. *Can. J. Fish. Aquat. Sci.* **55**: 37-46.

- Gillis, D.M., Peterman, R.M., and Tyler, A.V. 1993. Movement dynamics in a fishery: application of the ideal free distribution to spatial allocation of effort. *Can. J. Fish. Aquat. Sci.* **50**: 323-333.
- Gordon, H.S. 1954. The economic theory of a common property resource: the fishery. *J. Pol. Econ.* **62**: 124-142.
- Goss-Custard, J.D. 1980. Competition for food and interference among waders. *Ardea* **68**: 31-52.
- Granger, C.W.J., and Morris, M.J. 1976. Time Series modelling and interpretation. *J. R. Statist. Soc. A.* **139**: 246-257.
- Harley, S.J., Myers, R.A., and Dunn, A. 2001. Is catch-per-unit-effort proportional to abundance? *Can. J. Fish. Aquat. Sci.* **58**: 1760-1772.
- Haugen, T.O., Winfield, I.J., Vollestad, A., Fletcher, J.M., James, B.J., and Stenseth, N.C. 2006. The ideal free pike: 50 years of fitness-maximizing dispersal in Windermere. *Proc. R. Soc. B* **273**: 2917-2924.
- Healey, M.C., and Morris, J.F.T. 1992. The relationship between the dispersion of salmon fishing vessels and their catch. *Fish. Res.* **15**: 135-145.
- Hilborn, R., and Ledbetter, M. 1979. Analysis of the British Columbia salmon purse-seine fleet. *Can. J. Fish. Aquat. Sci.* **42**: 384-391.
- Hilborn, R., and Walters, C.J. 1987. A general model for simulation of stock and fleet dynamics in spatially heterogeneous fisheries. *Can. J. Fish. Aquat. Sci.* **44**: 1366-1370.

- Hilborn, R., and Walters, C.J. 1992. Quantitative fisheries stock assessment: choice, dynamics, and uncertainty. Chapman and Hall, London.
- Hoffman, S.D., and Duncan, J.D. 1988. Multinomial and conditional logit discrete-choice models in demography. *Demography* **25**: 415-427.
- Holland, D.S., and Sutinen, J.G. 1999. An empirical model of fleet dynamics in New England trawl fisheries. *Can. J. Fish. Aquat. Sci.* **56**: 253-264.
- Holland, D.S., and Sutinen, J.G. 2000. Location choice in New England fisheries: old habits die hard. *Land Econ.* **76**: 133-149.
- Houston, A.I., and McNamara, J.M. 1988. The ideal free distribution when competitive abilities differ: an approach based on statistical mechanics. *Anim. Behav.* **36**: 166-174.
- Hurvich, C.M., and Tsai, C.L. 1989. Regression and time series model selection in small sample. *Biometrika* **76**: 297-307.
- Hutton, T., Mardle, S., Pascoe, S., and Clark, R.A. 2004. Modelling fishing location choice within mixed fisheries: English North Sea beam trawlers in 2000 and 2001. *ICES Mar. Sci.* **61**: 1443-1452.
- Kennedy, M., and Grey, R.D. 1993. Can ecological theory predict the distribution of foraging animals? A critical analysis of experiments on the ideal free distribution. *Oikos* **68**: 158–166.

- Koppelman, F.S., and Bhat, C. 2006. A self instructing course in mode choice modeling: multinomial and nested logit models. U.S. Department of Transportation, Federal Transit Administration, January 31, 2006.
- Ludwig, D., and C.J. Walters. 1985. Are age-structured models appropriate for catch-effort data? *Can. J. Fish. Aquat. Sci.* **42**: 1866-1072.
- Marchal, P., Lallemand, P., and Stokes, K. 2009. The relative weight of traditions, economics, and catch plans in New Zealand fleet dynamics. *Can. J. Fish. Aquat. Sci.* **66**: 291-311.
- MacCall, A.D. 1990. Dynamic geography of marine fish populations. University of Washington Press. United States of America.
- McFadden, D. 1974. Conditional logit analysis of qualitative choice behavior. In *Frontiers in Econometrics*, pp. 105-142. Ed. by P. Zarembka. Academic Press, New York.
- McFadden, D. 1981. Econometric models of probabilistic choice. *In Structural Analysis of Discrete Data with Econometrics Applications. Edited by C. F. Manski and D. McFadden.* MIT Press, Cambridge, USA. pp. 198-272.
- Milinski, M., and Parker, G.A. 1991. Competition for resources. *In Behavioural ecology*. 3rd ed. *Edited by J.R. Krebs and N.B. Davies.* Blackwell Scientific Publications, Oxford. pp. 137-168.
- Morris D.W. 1987. Spatial scale and the cost of density-dependent habitat selection. *Evol. Ecol.* **1**: 379-388.
- Morris, D.W. 1988. Habitat-dependent population regulation and community structure. *Evol. Ecol.* **2**: 253-269.

- Morris, D.W. 1994. Habitat matching: alternatives and implications to populations and communities. *Evol. Ecol.* **8**: 387-406.
- Morris, D.W. 2003. Toward an ecological synthesis: a case for habitat selection. *Oecologia* **136**: 1-13.
- Morris, D.W., and Kingston, S.R. 2002. Predicting future threats to biodiversity from habitat selection by humans. *Evol. Ecol. Res.* **3**: 787-810.
- Paloheimo, J.E., and Dickie, L.M. 1964. Abundance and fishing success. *ICES Rapp. P.-V. Reun.* **155**: 152-162.
- Pinheiro, J.C., and Bates, D.M. 2004. *Mixed-effects models in S and S-PLUS*. Springer Science + Business Media LLC, New York, NY.
- Pinheiro, J.C., Bates, D.M., DebRoy, S., Sarkar, D., and the R Development Core Team. 2010. *Nlme: linear and nonlinear mixed effects models*. R package version 3.1-97.
- R Development Core Team. 2010. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0.
- Rijnsdorp, A.D., van Mourik Broekman, P.L., and Visser, E.G. 2000a. Competitive interactions among beam trawlers exploiting local patches of flatfish in the North Sea. *ICES J. Mar. Sci.* **57**: 894-902.
- Rijnsdorp, A.D., Dol, W., Hoyer, M., and Pastoors, M.A. 2000b. Effects of fishing power and competitive interactions on the effort allocation on the trip level of the Dutch beam trawl fleet. *ICES J. Mar. Sci.* **57**: 927-937.

- Rodríguez, M.A. 1995. Habitat-specific estimates of competition in stream salmonids: a field test of the isodar model of habitat selection. *Evol. Ecol.* **9**: 169-184.
- Rose, G.A., and Kulka, D.W. 1999. Hyperaggregation of fish and fisheries: how catch-per-unit-effort increased as the northern cod (*Gadus morhua*) declined. *Can. J. Fish. Aquat. Sci.* **56**: 118-127.
- Shochat, E., Patten, M.A., Morris, D.W., Reinking, D.L., Wolfe, D.H., and Sherrod, S.K. 2005. Ecological traps in isodars: effects of tall grass prairie management on bird nest success. *Oikos* **111**: 159-169.
- Smith, M.D. 2002. Two econometric approaches for predicting the spatial behaviour of renewable resource harvesters. *Land Econ.* **78**: 522-538.
- Smith, M.D., Lynham, J., Sanchirico, J.N., and Wilson, J.A. 2010. Political economy of marine reserves: Understanding the role of opportunity costs. *PNAS* **107**: 18300-18305.
- Swain, D.P., and Sinclair, A.F. 1994. Fish distribution and catchability: what is the appropriate measure of distribution? *Can. J. Fish. Aquat. Sci.* **51**: 1046-1054.
- Swain, D.P., and Wade, E.J. 2003. Spatial distribution of catch and effort in a fishery for snow crab (*Chionectes opilio*): test of predictions of the ideal free distribution. *Can. J. Fish. Aquat. Sci.* **60**: 897-909.
- Train, K.E. 2009. *Discrete Choice Methods with Simulation*. 2nd ed., Cambridge University Press, Cambridge, UK.

Voges, E., Gordo, A., and Field, J.G. 2005. Dynamics of the Namibian hake fleet and management connotations: application of the ideal free distribution. *Sci. Mar.* **62**: 285-293.

Wilen, J.E., Smith, M.D., Lockwood, D., and Botsford, F.W. 2002. Avoiding surprises: incorporating fisherman behavior into management models. *Bull. Mar. Sci.* **70**: 553-575.

Tables and Figures

Table 3.1. Summary data for the defined patches during the open and closed time periods within the fishery. Includes information on effort levels and catches broken down by target species (determined using quantification level).

Period	Patch	Distance from Port (km)	Number of Trawls	Hours Fished	Total Value (\$1000)	Haddock Value (\$1000)	Redfish Value (\$1000)	Pollock Value (\$1000)	Average VPUE (\$/h)
Closed	North	88.43	3249	14871	3088.35	754.73	492.82	327.93	153.09
	West	128.34	3556	10336	6842.91	67.23	2283.28	2492.02	436.71
	East	150.62	2314	8663	4431.40	3280.95	71.50	158.14	321.51
Open	North	91.35	1348	5646	1673.92	437.76	293.54	246.14	216.05
	West	139.39	651	2199	1357.34	220.90	411.22	483.37	411.97
	Browns	98.27	1928	8100	3304.31	1617.94	54.22	19.35	311.69
	South	164.70	4235	19052	6699.81	5848.08	152.97	250.75	206.07

Table 3.2. Results from isodar models for all possible patch comparisons during the closed period. This includes information on coefficients estimated using generalized nonlinear least squares, the correlation structure used, and the slope resulting from regressing the isodar predictions with observed values (a slope of 1 indicates a good fit of the isodar to the data). Standard errors of coefficients are in parentheses.

Period	Predicted Patch	Observed Patch	n	α	β_1	β_2	Correlation structure	Pred. vs obs. slope	p-value $H_0: \text{slope}=1$
Closed	East	North	53	0.238 (0.46)	1.215 (0.07)	1.470 (0.08)	ARMA(0,1)	1.047 (0.06)	0.206
	East	West	57	1.138 (0.50)	1.189 (0.09)	1.362 (0.08)	ARMA(3,0)	0.917 (0.07)	0.117
	West	North	70	0.857 (0.69)	1.304 (0.11)	1.764 (0.14)	ARMA(3,0)	1.02 (0.09)	0.410
	West	East	57	0.259 (0.26)	1.248 (0.08)	1.389 (0.10)	ARMA(3,0)	0.956 (0.09)	0.318
	North	West	70	2.479 (0.80)	1.408 (0.13)	1.696 (0.15)	ARMA(1,1)	1.080 (0.09)	0.178
	North	East	53	2.083 (0.50)	1.182 (0.07)	1.462 (0.08)	NULL	1.000 (0.05)	0.500

Table 3.3. Results from isodar models for all possible patch comparisons during the open period. This includes information on coefficients estimated using generalized nonlinear least squares, the correlation structure used, and the slope resulting from regressing the isodar predictions with observed values (a slope of 1 indicates a good fit of the isodar to the data). Standard errors of coefficients are in parentheses.

Period	Predicted Patch	Observed Patch	n	α	β_1	β_2	Correlation structure	Pred. vs obs. slope	p-value $H_0: \text{slope}=1$
Open	East	North	71	2.365 (0.89)	0.985 (0.15)	1.651 (0.16)	ARMA(1,0)	1.013 (0.10)	0.447
	East	West	46	2.507 (0.67)	1.060 (0.12)	1.598 (0.14)	ARMA(0,1)	0.983 (0.11)	0.442
	East	South	75	1.135 (0.49)	1.265 (0.08)	1.630 (0.09)	ARMA(1,0)	1.003 (0.06)	0.482
	West	North	51	2.579 (0.90)	0.706 (0.16)	1.674 (0.18)	ARMA(1,0)	1.041 (0.11)	0.361
	West	East	46	1.732 (0.82)	1.023 (0.15)	1.756 (0.19)	ARMA(0,2)	1.11 (0.13)	0.207
	West	South	44	-0.322 (0.77)	1.370 (0.12)	1.592 (0.12)	ARMA(2,0)	1.037 (0.11)	0.372
	North	West	51	3.267 (0.97)	1.028 (0.15)	1.763 (0.23)	NULL	1.00 (0.13)	0.500
	North	East	71	3.89 (0.91)	0.957 (0.12)	1.888 (0.18)	ARMA(0,3)	0.973 (0.11)	0.404
	North	South	66	0.115 (0.55)	1.366 (0.09)	1.444 (0.09)	ARMA(1,0)	0.938 (0.07)	0.183
	South	North	66	2.273 (0.54)	1.142 (0.08)	1.643 (0.09)	ARMA(1,0)	0.994 (0.05)	0.456
	South	East	75	1.623 (0.53)	1.253 (0.09)	1.551 (0.08)	NULL	1.000 (0.05)	0.500
	South	West	44	3.587 (0.89)	1.311 (0.13)	1.863 (0.17)	ARMA(1,0)	1.064 (0.10)	0.259

Table 3.4. Mixed logit results for the closed period predicting the most visited patch within an individual trip (dependent variable). Variables were models generic coefficients alternative specific coefficients with the north patch used as the reference alternative for the alternative specific coefficients. Variables that were modeled as random effects are highlighted with the distribution used in parentheses and the significance of their standard deviation included.

Variables	Coefficients	se	t-value	p-value		
Alternative specific variables with generic coefficients						
ln(VPUE)	-7.507	0.477	-15.732	<0.0001		
# of vessels	0.128	0.012	11.061	<0.0001		
Old info dummy	-1.296	0.272	-4.758	<0.0001		
Std. dev.: VPUE	1.366	0.306	4.458	<0.0001		
Std. dev.: # of vessels	0.082	0.018	4.484	<0.0001		
Individual specific variables with alternative specific coefficients						
altEAST	-3.261	0.811	-4.022	<0.0001		
altWEST	-6.849	0.772	-8.873	<0.0001		
altEAST: targetHAD	4.449	0.621	7.166	<0.0001		
altWEST: targetHAD	0.055	0.824	0.066	0.947		
altEAST: targetRED	-2.112	1.007	-2.097	0.036		
altWEST: targetRED	2.133	0.305	7.000	<0.0001		
altEAST: targetPOK	-1.153	0.893	-1.290	0.197		
altWEST: targetPOK	2.638	0.435	6.060	<0.0001		
altEAST: LOA	0.043	0.014	3.000	0.003		
altWEST: LOA	0.106	0.013	8.021	<0.0001		
Log-Likelihood	-729.95					
Mcfadden R ²	0.386					
Random effects	Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
VPUE (log-normal)	0.000	2.186e-04	5.493e-04	1.396e-03	1.380e-03	Inf
# of vessels (normal)	-Inf	0.073	0.128	0.128	0.183	Inf

Table 3.5. Mixed logit results for the open period predicting the most visited patch within an individual trip (dependent variable). Variables were models generic coefficients alternative specific coefficients with the north patch used as the reference alternative for the alternative specific coefficients. Variables that were modeled as random effects are highlighted with the distribution used in parentheses and the significance of their standard deviation included.

Variables	Coefficients	se	t-value	p-value		
Alternative specific variables with generic coefficients						
ln(VPUE)	-9.000	1.243	-7.237	<0.0001		
ln(# of vessels)	-1.814	0.164	-11.087	<0.0001		
Old info dummy	-0.927	0.218	-4.257	<0.0001		
No info dummy	-0.872	0.392	-2.227	0.0259		
Std. dev.: VPUE	-2.267	0.886	-2.559	0.0105		
Std. dev.: # of vessels	0.854	0.226	3.779	0.0001		
Std. dev.: No info dummy	1.228	0.572	2.147	0.0318		
Individual specific variables with alternative specific coefficients						
altEAST	-2.018	0.960	-2.101	0.0357		
altSOUTH	-5.327	1.042	-5.111	<0.0001		
altWEST	-8.562	1.705	-5.022	<0.0001		
altEAST: targetHAD	2.031	0.557	3.610	0.0003		
altSOUTH: targetHAD	3.451	0.522	6.609	<0.0001		
altWEST: targetHAD	-0.502	1.135	-0.444	0.6584		
altEAST: LOA	0.008	0.016	0.533	0.5938		
altSOUTH: LOA	0.047	0.016	2.867	0.0041		
altWEST: LOA	0.114	0.027	4.228	<0.0001		
altEAST: tripTime	0.422	0.117	3.611	0.0003		
altSOUTH: tripTime	0.712	0.120	5.917	<0.0001		
altWEST: tripTime	0.394	0.138	2.982	0.0043		
Log-Likelihood	-680.55					
Mcfadden R ²	0.273					
Random effects	Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
VPUE (log-normal)	0.000	2.68e-05	1.23e-04	1.161e-03	5.70e-04	Inf
# of vessels (log-normal)	0.000	9.16e-02	0.163	0.235	0.290	Inf
No info dummy (normal)	-Inf	-1.700	-0.872	-0.872	-0.044	Inf

Table 3.6. Comparison of the observed weekly proportion of effort in each patch and the predicted weekly proportion of effort in each patch from the mixed logit model and isodar model, for the closed and open periods. Predicted values are compared to observed values using root mean square error and correlations.

		Root Mean Square Error		Correlation	
		Mixed logit	Isodar	Mixed logit	Isodar
Closed Period	In Sample				
	EAST	0.135	0.048	0.831	0.893
	WEST	0.149	0.066	0.694	0.739
	NORTH	0.141	0.052	0.836	0.906
	Out of Sample				
	EAST	0.138	0.063	0.821	0.828
	WEST	0.174	0.101	0.573	0.453
	NORTH	0.163	0.082	0.754	0.798
Open Period	In Sample				
	BROWNS	0.193	0.059	0.643	0.870
	WEST	0.144	0.065	0.634	0.892
	NORTH	0.164	0.064	0.644	0.848
	SOUTH	0.176	0.054	0.682	0.940
	Out of Sample				
	BROWNS	0.225	0.066	0.543	0.835
	WEST	0.182	0.087	0.449	0.792
NORTH	0.183	0.073	0.574	0.804	
SOUTH	0.223	0.063	0.597	0.918	

Figure 3.1. Spatial point pattern of trawl positions within patches, divided by time period (top: open, bottom: closed). Thick black lines represent patch divisions (closed: north, west and east; open: north, west, browns, and south). Brown's Bank spawning closure represented by the thin line.

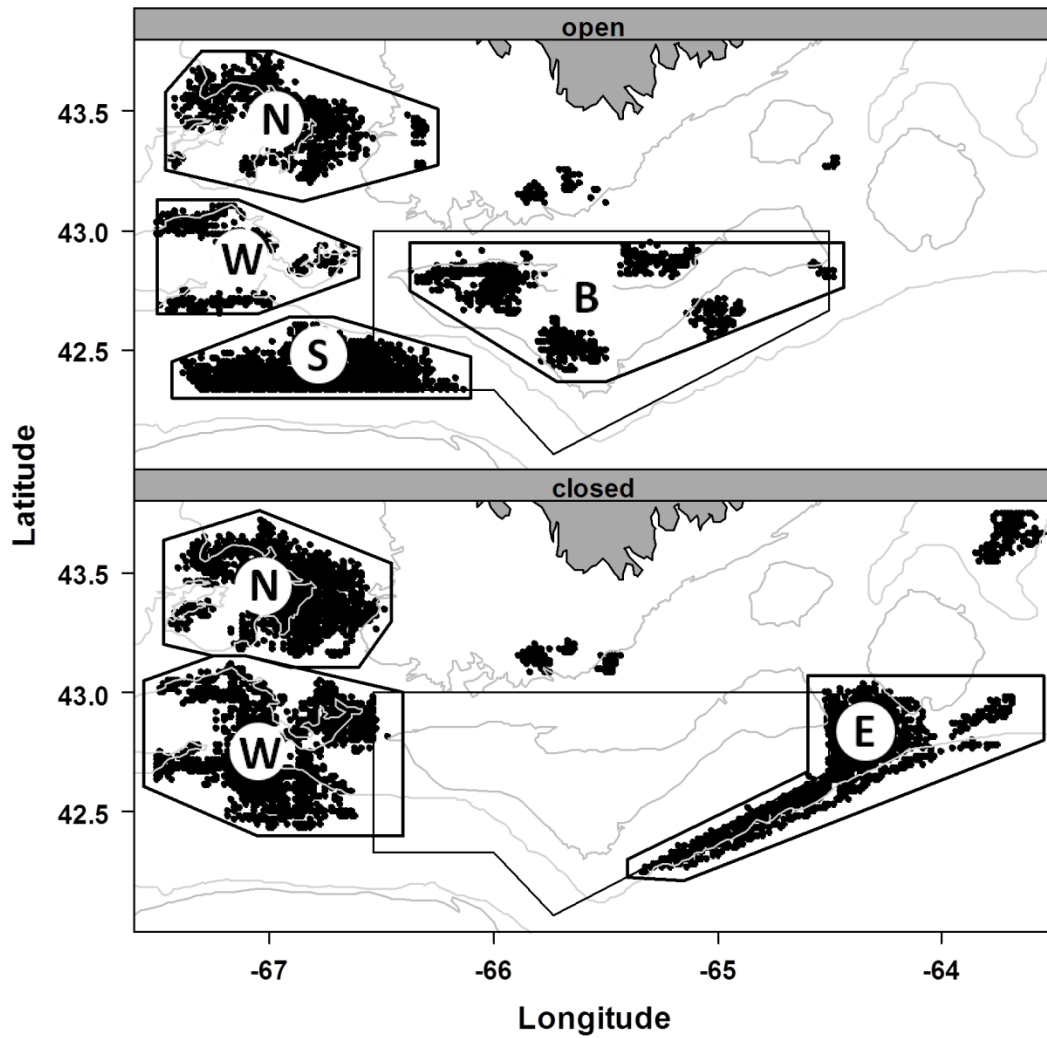


Figure 3.2. Observed log transformed effort values and the predicted isodar effort values for each patch comparison during the closed period (Predicted:Observed). Dark line is the OLS regression of the relationship and the dotted line is the slope of 1 line.

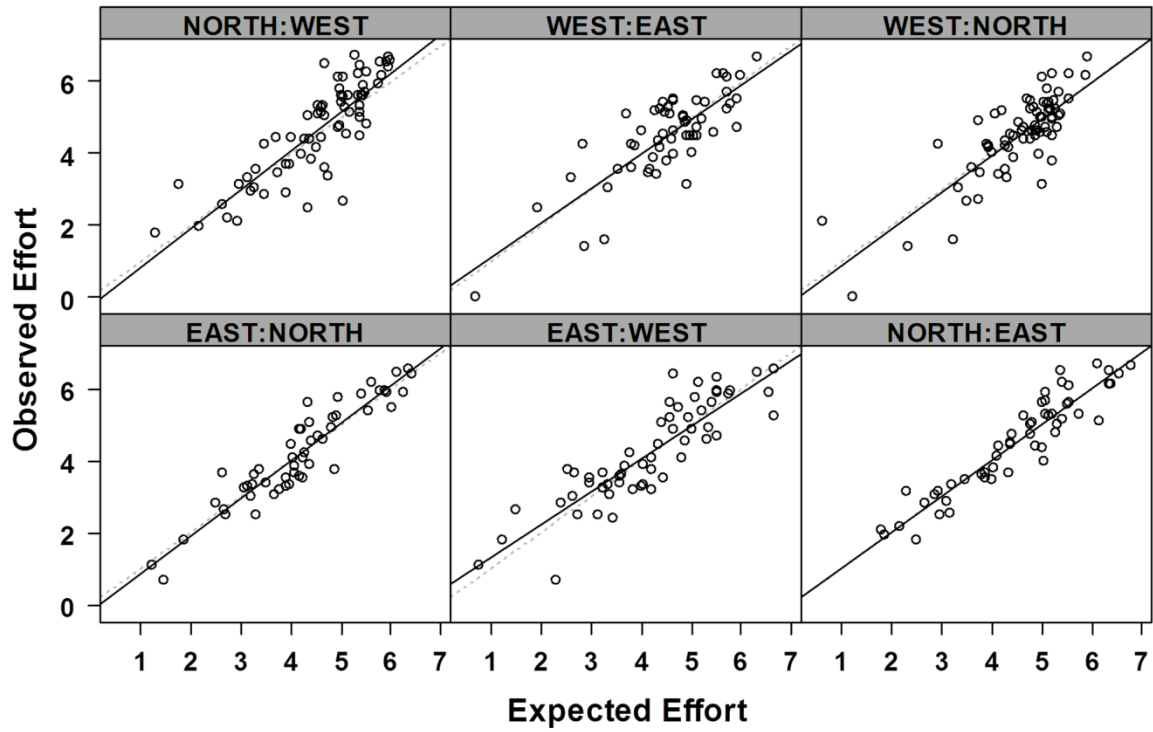


Figure 3.3. Observed log transformed effort values and the predicted isodar effort values for each patch comparison during the open period (Predicted:Observed). Dark line is the OLS regression of the relationship and the dotted line is the slope of 1 line.

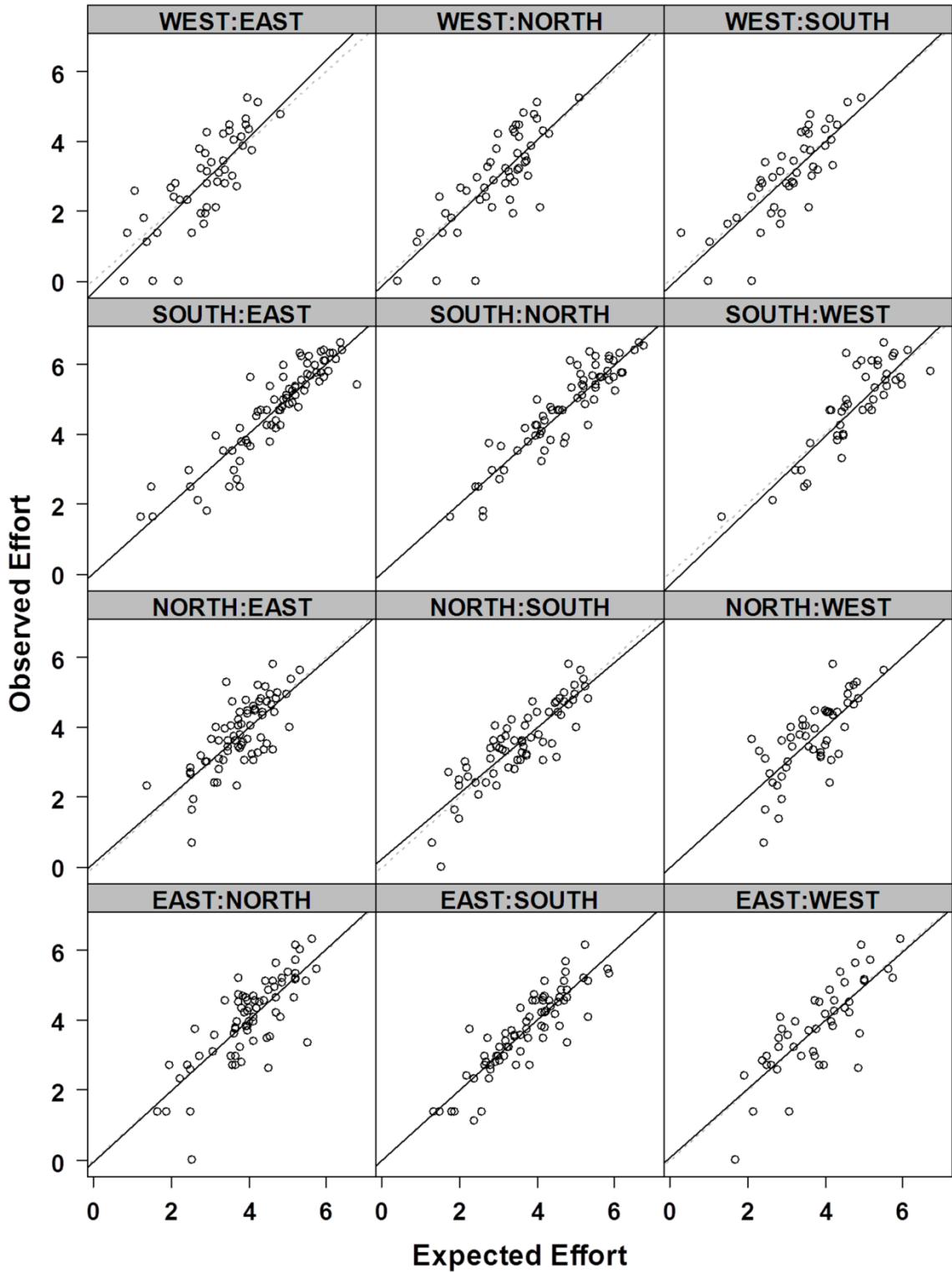


Figure 3.4. Performance of model predictions for the IFD-based isodar and mixed logit models for the closed period for both in-sample and out-of-sample forecasts.

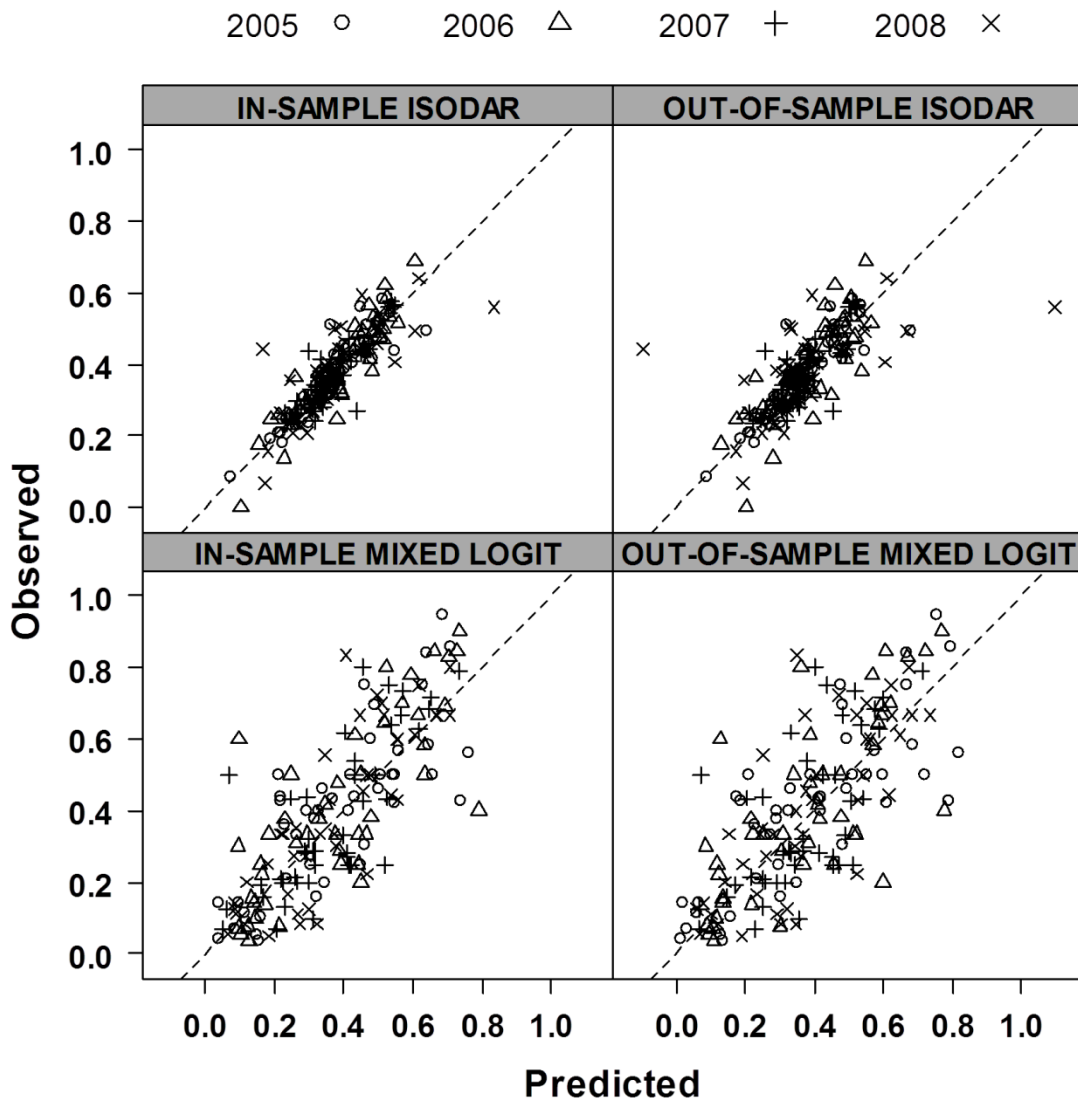
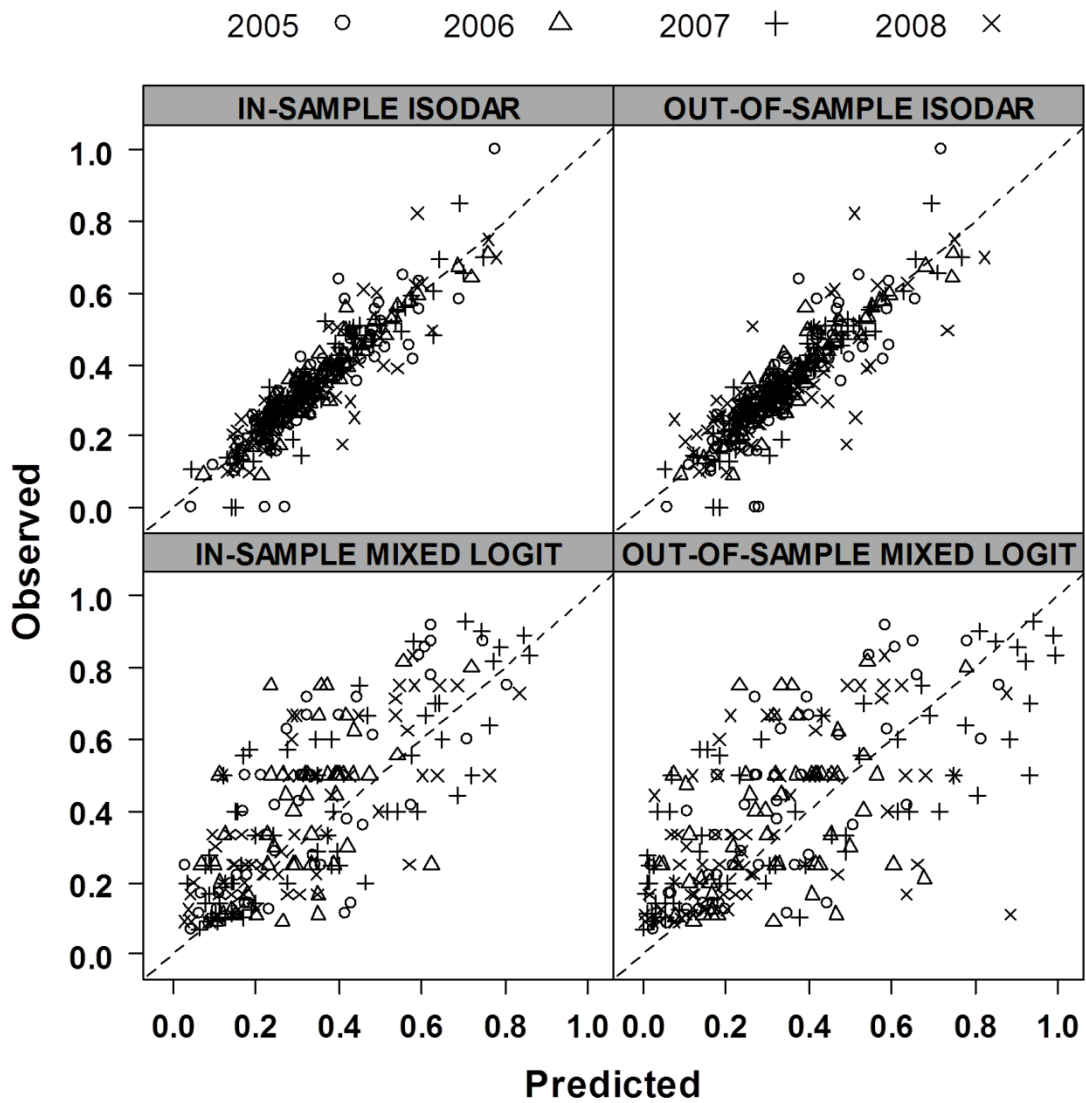


Figure 3.5. Performance of model predictions for the IFD-based isodar and mixed logit models for the open period for both in-sample and out-of-sample forecasts.



Chapter 4

General Conclusions

The focus of my MSc thesis has been the analysis of the spatial distribution of fishing effort in a region subject to a temporal area closure. This analysis has involved a variety of distinct statistical models many of which are novel to fisheries research which could be readily applied to other systems. This consisted of two primary projects. The first focused on an examination of the redistribution of fishing effort, the extent of 'fishing the line' (FTL) behaviour and resultant catch rate trends stemming from the seasonal area closure. Second was a comparative analysis of spatial distribution models, an aggregate model based on the assumptions of the ideal free distribution (IFD; Fretwell and Lucas 1970) where the fleet wide distribution of fishing effort was examined on a weekly basis utilizing isodar theory (Morris 1987), and a disaggregate model examining location selection on the individual trip level using a discrete choice model (McFadden 1974). Combined, this analysis gives a detailed depiction of how fishing effort is distributed throughout NAFO Division 4X, the impact of the closure, and factors that are relevant to the distribution of fishing effort.

In Chapter 2, the redistribution of effort was modeled using a generalized estimation equation (GEE; Liang and Zeger 1986; Zuur et al. 2009). This compared the amount of effort in an area on and around Brown's Bank to more distant areas on a weekly basis, treating the closure period as a covariate. From this, I found that though the closure caused a significant redistribution of effort, there was no change in the amount of effort directed towards the bank. This suggests that effort became concentrated at the boundaries, rather than fishers leaving the bank entirely. Studies finding effort concentrations near the boundary lines of permanent closures have been common (Roberts et al. 2001; Gell and Roberts 2002) and many studies have found a redistribution of effort due to the implementation of a seasonal closure (Holland and Sutinen 1999; Dinmore et al. 2003; Murowski et al. 2005; Poos and Rijnsdrop 2007), but there has not been previous work examining effort concentrations near the boundary of seasonal

closures such as this. Poos and Rijnsdrop (2007) noted an increase in the concentration of effort in the open area and a resultant magnified effect of interference but the position in the open area relative to the closure was not explored.

With consistent concentrations of fishing effort near the boundary of the closure established, the investigation focused on the catch rate trends of those vessels fishing directly at the boundary line, or those 'fishing the line' (FTL). This work was an extension of the methodology of Goni et al. (2006) with expected results based on the theoretical predictions of Kellner et al. (2007). Kellner et al. (2007) found distinct catch rate trends with distance from the line depending on the level of competition in the fishery and its relation to underlying effort distributions. A uniform distribution of effort led to catch rates greatest at the boundary line, a competitive fishing resulted in an IFD-distributed fishery with even catch rates throughout the fished area, and a coordinated fishery led to intense line fishing with depressed catch rates at the boundary. Goni et al. (2006) utilized a generalized additive model (GAM; Hastie and Tibshirani 1990) to examine the catch rate pattern with distance from the boundary line in a fixed gear spiny lobster fishery around a permanent closure in the Mediterranean; finding highly concentrated effort at the boundary resulting in a severe prey depression there, though this fishery was not coordinated. The analysis in this study differs from that of Goni et al. (2006) in a number of ways. Firstly, Goni et al. aggregated data from different fishing seasons into a single analysis while this analysis produced different models for each of the four years analysed. Secondly, Goni et al. aggregated all sides of the boundary into a single model producing a common trend line with side as a covariate while I produced different trend lines for aggregations in different areas along the boundary. This was necessary in my study area due to obviously different fishing patterns that resulted from different target species among the aggregations. Finally, in my analysis I employed a two-dimensional GAM which allowed the

examination of catch rate trends varying with distance away from the boundary line as well as along it. This distinction is important because the bathymetry and bottom type of the ocean floor is crucial for trawl success and can vary greatly throughout areas fished. Variable bathymetry can lead to variable density along the line. This can be readily examined in two dimensions but is it easily obscured in a one-dimensional GAM.

The results from this analysis were variable between regions and among years. In the west patch there was a tendency for catch rate to become equalized within the region in a fashion similar to that predicted by Kellner et al. (2007) in a competitive fishery and was consistent with the IFD. In contrast, the east region had significant trends with distance from and along the boundary line, where areas of high catch rate corresponded to areas of high effort whether this was at the boundary line or away from it. These results differed from those of Goni et al. (2006) in that they demonstrate marked inter-annual differences in not only how a FTL strategy was utilized within the fishery but also how it related to catch rate. These differences are likely linked to the temporal nature of the closure and the greater mobility of groundfish relative to spiny lobster. A protected resident population of groundfish (haddock or redfish) never became established on Brown's Bank, as it did for spiny lobster in the Goni et al. study, thus the closure did not create a predictable "core area" with consistent "spill over" at the closure boundaries. This study was also of a mobile gear fishery while Goni et al. examined a fixed gear fishery. This is a potential reason why the concentrations of effort near the boundary were not nearly as high as in the Goni et al. study. At higher concentration the number of interactions between vessels is likely greater in a mobile gear fishery than fixed gear leading to increased interference effects and greater impact on catch rates. Additionally, as mentioned before, bottom trawlers are limited in where they fish based on the bottom type of the ocean floor more so than fixed gear further increasing the effects of restricting the fishing area. This

study has expanded the analysis of previous studies and extended it to additional fishery types under different regulatory regimes, contributing to the knowledge of the effects closures have on the distribution and success of fishing effort. This has important implications for regulatory agencies by providing information on the outcomes these specific regulatory practices have on both the fishers and fish themselves. This includes expected effects on effort level, catch rates and what portion of the fish stock will likely be protected. Analysis such as this can be further applied to fisheries subject to closures using different gear types and targeting species with differing movement behaviours to give a more detailed depiction of the regulatory consequences in the context of alternative fishing practices.

The third chapter was a comparison of effort distribution models based on differing perspectives. This consisted of three primary components: area definitions and two spatial distribution models. The first model was an aggregated, ecological model based on the ideal free distribution (IFD) making use of isodars (Morris 1987), and the second a disaggregate, econometric model, based on individual location choice, using discrete choice models (McFadden 1974). The purpose of this project was to contribute to the greater understanding of fleet dynamics by producing replicable models describing effort distribution and comparing the performance of their predictions.

Both spatial models were contingent on fisher's use of identifiable areas, or "patches", when fishing. Historically, patch definition in spatial analysis has typically been based on pre-existing statistical management zones (Gillis et al. 1993; Holland and Sutinen 1999) or a grid system (Swain and Wade 2003; Hutten et al. 2004). These methods have appeared sufficient in past analyses but are limited in that they are often subjective or arbitrary without a basis in the actual distribution of fishing observed. Consequently, the resultant patches may not define real

fishing opportunities, define patches that are of no interest to fishers, or divide what should be a single patch into two or more patches. Each of these artefacts of patch definition could potentially result in biased parameter estimates. For example, if based on a grid or statistical area system, certain patches may be defined with little effort in them. This can lead to increased influence of the sets within these patches on coefficient estimates. If then, within a low density patch there were a few trawls with high catch rate, the average catch rate within this patch becomes inflated potentially negatively influencing the coefficient estimated for catch rate within the spatial model. Also if what should be a single patch becomes divided into two, or more, as a result of arbitrary patch divisions, a variable such as number of vessels fishing in a patch will be consistently reduced (maybe halved) for that patch, again reducing its effect within a spatial model. I have tried to avoid such problems by utilizing the data itself to define the spatial patches. I used Gaussian kernel-smoothed intensity plots to find the areas of effort concentration and divided the trawls in the top 90% of the concentration values into distinct patches. This has the advantage of being defined by the data itself with the knowledge that the results represent actual aggregations.

Even though patches were defined based upon demonstrated areas of fishing activity, there is the potential that the defined patches could have been broken up further, using finer scale intensity plots. Also, there were two small concentrations that qualified in the top 90% concentration values but could not be readily incorporated into larger patches. Subsequently, these sets were discarded from the analysis. Closure examination revealed that these areas represent targeting regions for alternative species that were not of primary concern in this study, and thus, it is assumed that their removal did not have a deleterious effect on the analysis. In the end, I feel the patches defined were an accurate portrayal of the fishing

opportunities available and that they were more accurate than the alternative patch definition options, which are more arbitrary relative to realized fishing activities.

The subsequent spatial models developed based on the defined patches examined effort distribution from alternative perspectives. The isodar model predicts weekly aggregated effort using a simple model with only three coefficients, while the discrete-choice model predicts individual level location decisions with the inclusion of many specific variables. The predictions of the models, in-sample and out-of-sample, were then compared to observed data using the goodness-of-fit measures: root mean square error (RMSE) and correlations.

The application of isodars was novel to fisheries research. Isodars relate the relative densities of distinct habitats when fitness is equal and therefore are a representation of the expected spatial distribution of foragers under the assumptions of the IFD. In their simplest form, isodars are constructed based on the declining relationship of fitness with density. In fisheries science, the fitness of a patch is usually represented by catch rate. For a variety of reasons, catch rate generally does not decline with vessel density in a measurable way (Gillis 1999), and therefore, the isodar must be derived theoretically. The parameters β_m represent the relative interference effects and variable costs from the m patches and α represents patch desirability:

$$(1) \quad \log(f_b) = -1/\beta_b [\alpha + \log(C_a/C_b)] + \beta_a/\beta_b \times \log(f_a)$$

The model in this form relaxes the assumption of equal costs of fishing in each patch, which has been found to be violated in practice (Vogues et al. 2005). This resulted in an isodar that was a good overall fit to the data producing predictions with no significant deviations from the observed data.

This, for the first time, represents a model based on the IFD that accurately described the relationship between effort levels in discrete patches in a fishery, and was reproducible among all patches and years. This has significant implications for fisheries science. An effort distribution based on the IFD suggests a breakdown in the relationship between CPUE and abundance and instead that abundance would be more highly correlated with effort. With this particular model, however, factors contributing to the α and β_m parameters also have to be taken into consideration. To further support the findings of the isodar-based model, it was important to determine how its predictions compare to alternative models of effort distribution.

The model chosen for a comparison to the isodar was a discrete choice model. The discrete choice model predicts individual location choice based on a specific multi-parameter model while the isodar gives a general distribution of effort based on few parameter estimates. I followed the procedures and initial variables for model building similar to previous studies (Holland and Sutinen 1999; Hutten et al. 2004) that were available from the data set with some additional individual-specific parameters included, which in these previous studies have not been considered (Holland and Sutinen 1999; Hutten et al. 2004). Additionally we choose to use the mixed-model perspective to account for violation of the IIA hypothesis which differs from the nested model which has been used more commonly in the primary literature (Eales and Wilen 1986; Holland and Sutinen 1999; Wilen et al. 2002). Use of a mixed model allowed parameters to vary with different individuals and did not require alternatives to be grouped into discrete nests, which was not appropriate with my patch definitions.

I used goodness-of-fit measures of in-sample and out-of-sample forecasts for both models to determine which provided better performing predictions. Consistently, the isodar model outperformed the mixed logit, though both model types produced high correlation

results. The simplicity and increased performance (especially as the number of alternatives increased) of the isodar model favoured the IFD-based isodar model but each has its own strengths. The simplicity and the aggregate nature of the isodar model make it more easily employed with commonly available fisheries data compared to the detailed econometric model. The mixed logit, however, can incorporate policy decisions into the model to forecast how they will influence fishing behaviour. One such policy decision that has been previously modeled is the use of area closures (Holland and Sutinen 1999; Hutten et al. 2004). Both of these analyses, however, have the limitation of not being able to incorporate how the closure itself will influence adjacent areas, such as through spillover, potentially biasing predictions. In the end, each model type provides an increased understanding of effort distribution within a fishery and can be useful in the study of fleet dynamics.

In the third chapter I have demonstrated a new methodology for identifying spatially distinct fishing patches not based on a uniform grid or management areas, derived an accurate and relevant IFD model using isodars, and further applied a useful econometric model to a novel fishery. Each methodology has advantages and drawbacks that can be further explored in future research. The patch selection methodology and isodars were novel to fisheries research and it will be interesting to see them applied to additional fisheries, especially those on a larger scale with a greater number of distinct patches to choose from. Further development of the isodar model is possible, with the potential of producing a single model for each patch using information from all other alternatives, instead of having to use multiple models for each patch as in this study. This will reduce the impact of zero effort observations on the model performance; though it will necessitate the development of advanced statistical procedures. Taken as a whole this analysis has contributed to the overall understanding of fleet dynamics and provided useful tools for future research.

The results of this thesis contribute to MPA and fleet dynamic research by combining the study of the specific effects a temporal closure has on 'line fishing' behaviour with the analysis of large scale spatial effort patterns. Taken together, this analysis describes, in detail, the influences on the spatial distribution of fishing effort using methodology modified from the primary literature or novel to fisheries research. All methods are readily replicable and can be used to examine the spatial distribution of fishing effort in other systems with any combination of gear type and target species.

References

- Dinmore, T.A., Duplisea, D.E., Rackham, B.D., Maxwell, D.L., and Jennings, S. 2003. Impact of a large-scale area closure on patterns of fishing disturbance and the consequences for benthic communities. *ICES J. Mar. Sci.* **60**: 371-380.
- Eales, J., and Wilen, J.E. 1986. An examination of fishing location choice in the pink shrimp fishery. *Mar. Resour. Econ.* **2**: 331-351.
- Fretwell, S.D., and Lucas, H.L. 1970. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheor.* **19**: 16-36.
- Gell, F.R., and C.M. Roberts. 2002. *The Fishery Effects of Marine Reserves and Fishery Closures*. WWF-US, 1250 24th Street, NW, Washington, DC 20037, USA.
- Gillis, D.M. 1999. Behavioral inferences from regulatory observer data: catch rate variation in the Scotian Shelf silver hake (*Merluccius bilinearis*) fishery. *Can. J. Fish. Aquat. Sci.* **56**: 288-296.

- Gillis, D.M., Peterman, R.M., and Tyler, A.V. 1993. Movement dynamics in a fishery: application of the ideal free distribution to spatial allocation of effort. *Can. J. Fish. Aquat. Sci.* **50**: 323-333.
- Goni, R., Quetglas, A., and Renones, O. 2006. Spillover of spiny lobster *Palinurus elephas* from a marine reserve to an adjoining fishery. *Mar. Ecol. Prog. Ser.* **308**: 207-219.
- Hastie, T.J., and Tibshirani, R.T. 1990. Generalized additive models. Chapman and Hall, London.
- Holland, D.S., and Sutinen, J.G. 1999. An empirical model of fleet dynamics in New England trawl fisheries. *Can. J. Fish. Aquat. Sci.* **56**: 253-264.
- Hutton, T., Mardle, S., Pascoe, S., and Clark, R.A. 2004. Modelling fishing location choice within mixed fisheries: English North Sea beam trawlers in 2000 and 2001. *ICES Mar. Sci.* **61**: 1443-1452.
- Kellner, J.B., Tetreault, I., Gaines, S.D., and Nisbet, R.M. 2007. Fishing the line near marine reserves in single and multispecies fisheries. *Ecol. Appl.* **17**: 1039-1054.
- Liang, K.Y., and Zeger, S.L. 1986. Longitudinal data analysis using generalized linear models. *Biometrika* **73**: 13-22.
- McFadden, D. 1974. Conditional logit analysis of qualitative choice behavior. *In* *Frontiers in Econometrics*. Edited by P. Zarembka. Academic Press, New York. pp. 105-142.
- Morris, D.W. 1987. Spatial scale and the cost of density-dependent habitat selection. *Evol. Ecol.* **1**: 379-388.

- Murawski, S.A., Wigley, S.E., Fogarty, M.J., Rago, P.J., and Mountain, D.G. 2005. Effort Distribution and catch patterns adjacent to temperate MPAs. *ICES J. Mar. Sci.* **62**: 1150-1167.
- Roberts, C.M., Bohnsack, J.A., Gell, F., Hawkins, J.P., and Goodridge, R. 2001. Effects on marine reserves on adjacent fisheries. *Science* **294**: 1920-1923.
- Poos, J.J., and Rijnsdorp, A.D. 2007. An “experiment” on effort allocation of fishing vessels: the role of interference competition and area specialization. *Can. J. Aquat. Sci.* **64**: 304-313.
- Swain, D.P., and Wade, E.J. 2003. Spatial distribution of catch and effort in a fishery for snow crab (*Chionectes opilio*): test of predictions of the ideal free distribution. *Can. J. Fish. Aquat. Sci.* **60**: 897-909.
- Voges, E., and Gordo, A., and Field, J.G. 2005. Dynamics of the Namibian hake fleet and management connotations: application of the ideal free distribution. *Sci. Mar.* **62**: 285-293.
- Wilens, J.E., Smith, M.D., Lockwood, D., and Botsford, F.W. 2002. Avoiding surprises: incorporating fisherman behavior into management models. *Bull. Mar. Sci.* **70**: 553-575.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., and Smith, G.M. 2009. Mixed effects models and extensions in ecology with R. Springer, New York.