

An Examination of Predator Habitat Usage: Movement
Analysis in a Marine Fishery and Freshwater Fish

by
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Abstract

This thesis investigates the influence of predator movements upon habitat selection and foraging success. It deals with two very distinct datasets one from a marine system, the snow crab (*Chionoecetes opilio*) fishery, and the second from a freshwater system, an experimental rainbow trout (*Oncorhynchus mykiss*) aquaculture operation. Deriving a standardized measure of catch from logbook data is important because catch per unit effort (CPUE) is used in fisheries analysis to estimate abundance, but in some cases CPUE is a biased estimate. For the snow crab fishery, a relative abundance measure was developed using fisher movements and logbook data that reflected commercially available biomass and produced an improved relative abundance estimate. Results from the aquaculture dataset indicate that escaped farmed rainbow trout continue to use the cage site when waste feed is available, while native lake trout do not interact with the cage. Once access to waste feed is removed, both lake trout and escaped rainbow trout do not use the cage site. This thesis uses methods to identify patterns and behaviours using movement tracks to increase our understanding of predator habitat usage.

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Chapter 1: Introduction

My MSc thesis consists of two primary research projects. The first project investigates vessel movement in the snow crab (*Chionoecetes opilio*) fishery in the Gulf of St. Lawrence and the second project examines escaped rainbow trout (*Oncorhynchus mykiss*) movement from a commercial aquaculture operation at the Experimental Lakes Area (ELA). The major theme of my thesis is to quantify and interpret movement patterns in two distinct data sets, one from a marine and the other from a freshwater environment.

Movement, or sometimes lack thereof, can influence population dynamics through various processes such as foraging, breeding and habitat selection. With the exception of sessile organisms, movement is a key feature that enables animals to survive. The topic of animal movement is covered in many areas such as conservation and island biogeography (Quammen 1996), fisheries analysis (Bertrand et al. 2007), individual animal tracking (Jonsen et al. 2003) and hidden Markov models to identify behaviours of tagged animals (Franke et al. 2004). Typically, due to the availability of information, humans can make informed decisions concerning their environment, but these decisions are still affected by risks and rewards. Many of the different activities that organisms perform can be visually identified, but problems arise when trying to identify behaviours when direct observation is not possible. To interpret data from remote sensing, quantitative models of animal movement and space utilization must be developed.

Early work on animal movement was concentrated on areas such as net displacement (Kareiva and Shigesada 1983), fractal dimensions (Dicke and Burrough 1988), home range analysis (Anderson 1982) and angular data (Cain 1989). More recent

techniques have been developed such as Levy flights (Viswanathan et al. 1999), state space models (Jonsen et al. 2003) and memory effects (Gautestad 2011) to improve our understanding and analytical abilities in the field of animal movement. Early work was restricted because of limits in computing power and available methods, but developments of new hardware, software and programming languages (R, MATLAB, Python, etc.) has led to the expansion of available methods for researchers.

Along with the more recent techniques, new methods for tracking animal movements have also been developed. Remote sensing technology has increased the ability of researchers to record positions of animals in greater detail (Jonsen et al. 2005). Satellite tags and acoustic tags have become more pivotal in tracking studies in the last decade, with use in studies of both avian and non-avian animals. Tracking animal movement paths has been used to characterize the movement paths of many species such as leatherback turtles (*Dermochelys coriacea*) (Hughes et al. 1998), green turtles (*Chelonia mydas*) (Luschi et al. 1996), woodland caribou (*Rangifer tarandus*) (Franke et al. 2004), bluefin tuna (*Thunnus thynnus*) (Block et al. 1998), Belugas (*Delphinapterus leucas*) (Richard et al. 1998) and whale sharks (*Rhincodon typus*) (Gifford et al. 2007). However satellite tracking is not restricted to animal tracking as the entire Peruvian industrial fishing fleet is equipped with a vessel monitoring system (VMS) (Bertrand et al. 2005).

Satellite, ARGOS, archival and harmonic radar tags allow researchers to follow marine and terrestrial animals over large distances where previous methods failed. These methods however all come with inherent errors which must be corrected before data processing (Jonsen et al. 2003). Telemetry technology has great implications for

monitoring aquatic organisms in their natural environment. In the early stages, biotelemetry positions were recorded manually over time (manual tracking), recent advances in telemetry technology allows for automated tracking (Blanchfield et al. 2005). Further upgrades in biotelemetry now allows remote sensing of multiple organisms simultaneously and removes the burden of time consuming and expensive data collection.

The availability of high resolution data showing the spatial and temporal resolution of foragers gives insights into behaviours across long distances and time periods. This kind of data has revealed fine scale information about behaviours such as foraging and feeding as well as habitat use, migration and dispersal (Giuggioli and Bartumeus 2010). Foraging behavior can be divided into two major states; (1) searching and (2) feeding (or collecting). Searching behavior can be classified as long steps and linear movements with small, occasional turning angles and fast constant velocity. There may be a transition to feeding behavior when prey densities increase and this is characterized by short steps, decreased travel rate and increased turning frequency and angle (Benichou et al. 2005, Jonsen et al. 2007, Mills et al. 2007). A fishing vessel does not feed, but instead has a state classified as effort (fishing), incorporating similar behaviours as previously described for feeding.

The foraging success of fishing vessels is commonly calculated by the size of their catch, with higher catch rates associated with increased success. Within the field of fisheries analysis, it is important to develop indices that represent the success of fishers. Catch per unit effort (CPUE) is one of the most widely used and most important statistics in fisheries analysis. This fact is due to the assumption that CPUE is assumed to be proportional to abundance (Kimura 1981). Catch rates can not only be used to estimate

stock size, but also may give information about reproduction, growth and the size structure of the stock (Hilborn and Walters 1992). Unfortunately CPUE does not always accurately reflect stock size and it is in these fisheries where the interpretation of CPUE must be further developed.

Forager's attempt to maximize energy input through a combination of habitat selection, avoiding stress, movement and environmental interactions. These interactions include a combination of factors such as temperature, light, predation risk and food availability which can display significant spatial variation. Food patch quality varies spatially and temporally and thus it may be difficult to locate the optimal food patches. When a rich patch is encountered, energy gain should be maximized and therefore foraging effort is expected to be concentrated on these areas. This assumption does not strictly hold true however as patch use is not solely dependent on resource availability, there are trade-offs between resource availability and safety (Moenting and Morris 2006). For example, minnow movement was found to be restricted in the presence of a predator in complex habitats, but in simple habitats minnows formed larger shoal sizes and there was no change in movement (Orpwood et al. 2008). Snow crabs may be able to find sanctuary in areas that are unfishable (rocky, uneven ground) to vessels, resulting in a proportion of the population that cannot be exploited. In this situation, classical CPUE would not represent the true abundance of the population. The previous cases may lead to predators foraging near boundaries of habitats and thus habitat edges may be very important in maximizing energy gain.

Habitat selection is incorporated in the concept of an animal's home range. Home range can be defined as the area used by an individual in everyday activities for foraging,

mating and caring for young. A more probabilistic definition is based upon the bivariate probability density function which gives the probability of finding an animal at a particular location. This is termed as the “utilization distribution”, or UD. This is a useful definition because the UD describes the use of space and not the use of resources (Anderson 1982). Since the UD only gives information about space use, identifying the behaviours will also be important. Behaviours can be inferred from the speed, step lengths and turning frequencies and angles of an individual’s movement pathway. Habitat use and activity of animals can be identified by investigating a series of positions recorded over time. Home ranges can be calculated by the kernel density estimator method and this method has shown to be a good estimator of space use and can effectively highlight areas of concentrated activity. This method could result in two or more unconnected areas for an individual (Worton 1987).

This master’s thesis will investigate movement patterns in a marine fishery and freshwater fish. The first project will examine how vessel movement patterns relate to catch rates and using hidden Markov models to create a new standardized abundance estimate. The second project will investigate the behaviour of rainbow trout after they have escaped from an aquaculture farm during periods of operation and post-operation. The first project will show how vessel movement patterns can be used to develop a fishery dependent index of abundance in a fixed gear fishery and the second project will give insight into rainbow trout behaviour once they disperse from the cage site and no longer have access to waste feed.

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Chapter 2: Using hidden Markov models to identify
vessel activities in the snow crab (*Chionoecetes*
opilio) fixed gear fishery and its application to catch
estimation

Introduction

Increasing commercial catches and the demands of growing human populations adds new urgency to the development of more accurate and accessible stock assessments. An important statistic in fisheries analysis has always been catch per unit effort (CPUE) due to the assumption that CPUE is proportional to abundance (Kimura 1981). Unfortunately many researchers have found that this is not the case. Harley et al. (2001) found that in 70% of the cases examined CPUE was likely to remain high while abundance declined. This indicates that while CPUE can be useful measure of abundance, new measures must be developed in order to assess populations where traditional CPUE does not accurately reflect stock size.

The broad array of commercial fishing methods can be classified as either mobile or fixed gear. Mobile gear fisheries include methods such as purse seining, bottom trawling and Danish seining. Their method of fishing involves deploying a net at reduced speeds. These speeds vary among fisheries, but for fishers in Galicia (NW Spain) the speeds can range from 1.5 to 2.1 knots for pair trawlers or 3.2 to 4.5 knots for single trawlers (Vazquez-Rowe et al. 2010), the silver hake (*Merluccius bilinearis*) fishery on the Scotian Shelf displays mean trawling speeds of 3.4 knots (Gillis 1999), while Dutch beam trawlers, which typically target groundfish, maintain trawling speeds of 4 to 5 knots (Rijnsdorp et al. 2000). Fixed gear fisheries use traps, gillnets, and longlines to catch their target species. In a fixed gear fishery vessels typically travel at reduced speed to set their gear. They then leave the area and later return to collect the catch after letting the gear soak for periods ranging from less than an hour to several days. A recent strategy employed by fisheries managers requires the implementation of vessel monitoring

systems (VMS). These systems use satellites for positioning and data retrieval. In some cases entire fleets have been equipped with VMS which transmit vessel position at regular intervals (Vermard et al. 2010, Bertrand et al. 2007). The spatial distribution of fishers provides researchers and managers information on the spatial distribution of both effort and fish, and allows the detection of vessels encroaching into marine protected areas (Peel and Good 2011). Inferring behaviours from movement pathways can be challenging because positions are recorded at discrete time intervals and provide no information about fishing activities. In a study performed by Bez et al. (2011) looking at fishing activity of tuna purse seiners, where the targeted species were yellowfin tuna (*Thunnus albacares*), skipjack (*Katsuwonus pelamis*), and bigeye tuna (*Thunnus obesus*), VMS records were used to identify activities using speed and turning angles between successive positions. A VMS can be a very powerful tool for measuring effort, but the detection time associated with a VMS, usually 1-2 hours, can introduce compounding factors into the interpretation of effort. Vermard et al. (2010) analyzed VMS records collected from pelagic trawlers in the Bay of Biscay and used a hidden Markov model (HMM) to infer behavioural state changes when the VMS detection frequency was not synchronous with switching instant. Due to the detection frequency of a VMS, records are not associated with specific behaviours and thus we must rely on physical factors (speed, turning angles) to identify changes in behaviour (Peel and Good 2011).

The analysis of vessel movements follows that of natural foragers and reflects the spatial distribution of target species (Bertrand et al. 2005). Ecologists have long been interested in modeling behaviours from movement pathways. New techniques designed to interpret animal movements have been developed to study dispersal, foraging,

behaviour, and memory (Viswanathan 2010, Giuggioli and Bartumeus 2010). The increased use, as well as miniaturization of satellite and acoustic receivers, has led to the collection of vast databases of animal movement. The variance in detection time and resolution has created complex data structures, biological mechanisms and statistical properties (Jonsen et al. 2005). Individual animal movements are indicative of not only spatial distribution, but also behavioural responses to the environment (Gurarie et al. 2009). Similarly, Peel and Good (2011) successfully applied a HMM based on vessel movement to classify fishing activities in three coastal trawl fisheries near Queensland, Australia.

The Gulf of St. Lawrence snow crab (*Chionoecetes opilio*) fishery is one of the most economically important species in Eastern Canada. In 2006, 2007 and 2008 the value of landings for the Gulf of St. Lawrence region exceeded \$71 million, \$110 million and \$92 million respectively. The economic importance of this species has led to increased interest in conservation and fishing management strategies (Biron et al. 2008). The snow crab fishery has existed since the 1960's and occurs in several zones, with the largest fishery located in zone 12 (Figure 2-1). This fishery opens in early spring and lasts about 10-12 weeks. Legal landings are exclusively hard shelled male snow crabs with a carapace width of 95 mm or greater (Swain and Wade 2003).

In this paper, I initially estimate the activities of vessels using HMMs based upon VMS records. In a HMM, the states are not directly observable and the classification of a finite number of hidden states can be made according to the observed distribution of the observations (Patterson et al. 2009). HMMs can be thought of as a generalization of mixture models, where each state is not independent, but rather related to each other by a

Markov process. Secondly, I will relate the HMM parameter estimates and logbook information to develop a fishery dependent measure of abundance. I will investigate differences in movement patterns in years with different biomass estimates and use logbook information to investigate movement patterns for varying catch rates. Finally I will introduce a novel method for estimating abundance in a fishery using a generalized linear model (GLM), HMM parameters estimates and logbook information.

Materials and Methods

The fishery

My study focuses on the Gulf of St. Lawrence snow crab fishery (Zone 12, Figure 2-1). Vessels from ports in New Brunswick, PEI, Quebec and Nova Scotia participate in this fishery. Within the fleet there are distinct fish harvesters which are classified as Traditional, New Access and First Nations. Traditional fishers, who have a permanent allocation within the fishery, are composed of two groups. Traditional midshore fishers have a maximum allocation of 150 traps, while traditional inshore fishers from PEI are allowed 75 traps. New access and First Nations fishers with quotas up to 50 t are entitled to 75 traps while fishers who receive quotas over 50 t are allowed 150 traps (Gillis et al. 2006; <http://www.dfo-mpo.gc.ca/decisions/fm-2012-gp/atl-021-eng.htm>, May 4, 2012). All vessels within the fishery are fitted with a VMS that records time, position and speed. The VMS delivers high resolution data, recording positions at 15 minute intervals throughout the season.

The snow crab fishery is a fixed gear fishery deploying traps by two different modes: initial sets and replacing traps at the same location after removing the catch (resets). Initial sets occur when fishers arrive at a new area. In this case vessels travel

rather quickly (~4-7 knots) through the water as the traps can be set in the water as soon as they are baited. When fishers return to previously set traps they haul each trap onto the vessel. After the trap contents are emptied onto the sorting table the captain has two options (1) reset the traps in the same location or (2) relocate them in an attempt to increase catch rates. During retrieval, vessels travel at slower speeds (~1-4 knots) to allow sufficient time for sorting catch and re-baiting of traps. Movement among sites and to or from port occurs at higher speeds, with unset traps secured on deck and the catch sorted and stowed in the hold, though some final sorting may occur.

The dataset

The data collected for this study spans three fishing seasons from years 2006-2008. The VMS database includes each registered position (latitude and longitude), a unique vessel identifier, a unique trip identification number, landing and the vessels' homeport. A separate logbook database provided records by trip that included catch information, number of traps used and the date and time of the beginning (hail out) and end (hail in) of the trip.

Data manipulations

All data manipulations and subsequent analysis were done using the R statistical language (R Development Core Team 2011). To begin, I applied a three step pre-processing algorithm to filter the raw data. I first matched the date and time when a vessel left port and when the ship returned to port using logbook information. Visual inspection of these initial trips showed that the hail out and hail in times were insufficient to properly define individual trips due to multiple VMS detections while still anchored at

port. Therefore, I defined each unique fishing trip by limiting each trip to start and end within a 5 kilometer (3 mile) radius of a port. A second filtering step was able to successfully identify and remove multiple entries for a vessel docked at port. Turchin (1998) classifies trajectories that are sampled at regular time intervals as “steps”, but this process artificially breaks a single activity into several observations. Such steps do not correspond to unique behavioral events, which are referred to as movement legs. To reduce autocorrelation I followed methods developed by Bertrand et al. (2007) to transform the steps into moves by choosing a threshold to identify significant changes of direction and used 10° as a suitable threshold to identify changes in behavioral events. Thus when vessels had turning angles less than 10° between successive steps, these steps were combined to form a movement leg. After the pre-processing algorithm the dataset included 757, 996 and 1033 unique fishing trips and 32 163, 39 750 and 49 571 data points in 2006, 2007 and 2008 respectively.

The distance travelled during a move was calculated from latitudes and longitudes using the haversine formula (Sinnot 1984). Speeds were calculated for each move by taking the distance traveled between point A and point B divided by the time difference. The methods for calculating bearing and distances are shown in Appendix I.

Continuous time Markov processes

The vessel activities during different movement legs were represented as a continuous time Markov model with transitions between all states allowed. A multi-state model can be used to describe how an individual changes between k number of states $S = \{1, 2, \dots, k\}$. Assuming that an individual is able to freely change back and forth between k

number of states through continuous time, a $k \times k$ transitional intensity matrix (Q matrix) is defined as:

$$(1) \quad q_{rs}(t, z(t)) = \lim_{\delta t \rightarrow 0} P(S(t + \delta t) = s \mid S(t) = r) / \delta t$$

where q_{rs} is the instantaneous rate of change from state r to state s . The rows of the Q matrix sum to zero, the diagonal entries are defined by $q_{rr} = -\sum_{s \neq r} q_{rs}$, and the off-diagonal entries can be any non-negative number (Saint-Pierre et al. 2003, Jackson 2011). Alternatively, the P matrix contains discrete time switching probabilities which correspond to the same state transitions as the Q matrix. The P matrix can be calculated using the matrix exponential (Spencer and Susko 2005):

$$(2) \quad P(t) = e^{Qt} = \sum_{m=0}^{\infty} \frac{(Qt)^m}{m!}$$

where e is the base of natural logarithms. The P matrix corresponds to the Q matrix of a continuous time Markov model when making predictions at evenly-spaced points in time.

HMMs also provide other insights into the modeled processes. The time spent in each state (sojourn time) in a time-homogenous Markov model is exponentially distributed with mean $-1/q_{rr}$. Finally, a P_{next} matrix can be constructed that defines the probability of transition from r to s regardless of time elapsed. The diagonal entries of the P_{next} matrix are equal to zero.

Development of hidden Markov models

HMMs were developed using the *msm* package for R (Jackson 2011). The models were fit to the snow crab fleet based upon the calculated speed of the movement legs in order to identify different behaviours. The distributions used to represent emissions from the hidden states within the models were the normal distribution, the Weibull distribution and the t-distribution. Other distributions such as uniform and gamma were tried, but the models did not converge to solution, nor did they appear to reflect the observed distributions well. Modifications to the software were required to support the t-distribution (see Appendix I). In order to examine the possible speed distributions for each hidden state, quantile plots were examined using the *car* package (Fox and Weisberg 2011). The number of hidden states was initially inferred by visual inspection and tests comparing the fits of alternative HMMs suggested the possibility of either two or three underlying states. Therefore I compared a simple two state HMM (fast and slow speeds) to a more complex three state model (fast, intermediate and slow speeds). The *mixtools* package for R (Benaglia et al. 2009) was used to provide initial estimates of the speeds for each hypothesized state, assuming normality. The values calculated using the *mixtools* package were used as the initial estimates of the emission distributions in the *msm* package. Using the *msm* package, I developed this initial two state model with two normal distributions and then I applied a two state model with one normal distribution and one Weibull distribution. The initial values of the two Weibull parameters, shape and scale, were estimated using the *lmom* package (Hosking 2009), these parameters were estimated when the speed distribution predicted from the HMM were non-normal. To account for an additional behaviour, a three state model was developed using normal,

Weibull, and t distributions. The two state models classified observations into two groups, based upon speed (labeled slow and fast), while the three state models classified three speed groupings: slow, intermediate and fast. I interpreted slow and intermediate speeds with fishing activities, with slow speeds simultaneously associated with retrieving and resetting traps, intermediate speeds with initial sets, and fast speeds with movements among fishing sites or to and from port (steaming). In the two state model, the slow speed classification included both the setting and the retrieving and resetting behaviours.

Covariates

In the application of a HMM to VMS data in the snow crab fishery, the impact of CPUE (kg/trap) and year were examined by fitting them as covariates within the HMM (Jackson 2011). This allowed me to determine if hidden state transitions varied with local fishing success or among the years examined.

Generalized linear models

The effect of vessel characteristics and movements on catch per trip was examined with generalized linear models (GLMs). There are three components incorporated into a GLM; (1) the random component, (2) the systematic component and (3) the link function. The random component identifies the distribution of the response variable Y , with independent observations (y_1, \dots, y_n) . The systematic component represents the linear predictors in a model. Let x_{ij} denote the value of predictor j ($j=1, 2, \dots, k$) for subject i , then:

$$(3) \quad \eta_i = \beta_0 + \beta_1 X_i + \cdots + \beta_k X_k$$

This combination of variables is referred to as the linear predictor (Agresti 2002). The predictors may be continuous or categorical and any interactions between may also be included (Quinn and Keough 2001). The third component of a GLM is the link function which connects the random and systematic components (Agresti 2002). The basic purpose of the link function is to transform the data into a linear relationship and can be written as:

$$(4) \quad g(\mu) = \beta_0 + \beta_1 X_1 + \cdots + \beta_k X_k$$

It is important to note that the link function is applied to the expected values and not used to transform the original observations. This can be expressed as:

$$(5) \quad Y \sim \text{Distribution}(\mu, \theta), \quad \mu = g^{-1}(\beta_0 + \beta_1 X_1 + \cdots + \beta_k X_k)$$

where $\text{Distribution}()$ is the pattern of deviations around the expected values of Y , θ represents the parameters of this distribution and g^{-1} indicates the inverse of the link function. The Gamma distribution was chosen because the variance of the response variables increased with the mean.

The link function used in the GLM was the inverse linear polynomial and had the form:

$$(6) \quad \frac{1}{y} = a + b \frac{1}{x}$$

Taking the reciprocal gives:

$$(7) \quad y = \frac{x}{b + ax}$$

The inverse linear polynomial link was chosen over others based upon the distribution of the residuals and due to the fact that it is effective at representing a variety of functional forms (linear, asymptotic, exponential decay) (Crawley 2002). Parameter estimates were performed using the `glm()` function in the R statistical programming environment (R Development Core Team 2011).

Results

Vessel movement patterns: Hidden Markov model

A visual inspection of the observed distribution of VMS speed estimates (Figures 2-2 and 2-3) suggested that there could be either two or three distinct underlying states. To select between them the best fit two and three state HMMs were compared.

The two state HMM effectively classified observed speeds into two groups with fishing behaviours classified by a Weibull distribution and steaming behaviour classified by a normal distribution (Figure 2-2). The two state models identified two distinct states which are referred to as fishing (slow) and steaming (fast) based upon the reduction in speed required to set or retrieve traps.

A three state HMM was used to partition the former fishing state into trap "setting" and "retrieval" (where retrieval may involve resetting traps at the same location). Table 2-2 lists the parameter estimates of the emission distributions of three state HMM that were obtained using the msm package. To begin, a simple model with three normal distributions (N–N–N) was used, which was compared to alternative models that could also use t-distributions. The final model used normal distributions to define fishing and relocating and a t-distribution to describe steaming behaviour (N-N-t). Both the initial and final models converged to an optimal solution (Table 2-2). Figure 2-3 depicts the distribution of states predicted by the N-N-t distributions. In this model retrieving and steaming behaviours are similar to the two state models, but with the intermediate speeds classified as setting behavior. I examined both AIC and BIC as criteria to select the most strongly supported model for further analysis (Table 2-3). The model chosen as superior by both AIC and BIC was the three state N-N-t model and this model was used for further analysis of covariates. The movement characteristic speed was used to define each of the behavioural states. These states of “retrieving”, “setting” and “steaming” were estimated with means of 1.59, 5.43 and 9.56 knots respectively

The final model was formally defined by the instantaneous rate of change between states (Q matrix, Table 2-4), but was also represented by the transition probabilities (P matrix, Table 2-5), sojourn times (Table 2-6), and the most probable future state transition (P_{next} , Table 2-7).

Year as a covariate

Changes among years were examined by using year as a covariate within the HMM. The behavioral states of “retrieving”, “setting” and “steaming” were estimated

with means of 1.72, 6.11 and 9.60 knots respectively. The sojourn times, showing the average time spend in each state over the course of the study were estimated from the HMM. Figure 2-4 shows the sojourn times while “retrieving”, “setting” and “steaming” for the years 2006-2008, with the observed steaming times of 3.57 ± 0.11 hours in 2006, 2.89 ± 0.05 hours in 2007 and 2.34 ± 0.06 hours in 2008. Setting times also decreased as years progressed with an average sojourn time of 1.73 ± 0.05 hours in 2006, 1.52 ± 0.03 hours in 2007 and 1.34 ± 0.03 hours in 2008. In contrast the time to retrieve traps was not influenced by the interannual variation abundance of snow crabs.

The state changes over a 15 minute time interval show significant changes at a 5% confidence level for all interannual transitions except for two events, when continuing to set traps and when transitioning from setting to retrieving (Figure 2-5). Figure 2-5 shows that there is a high probability of remaining in the same state after a 15 minute interval for all states over each year. Similar patterns are revealed by the instantaneous transition rates shown in Figure 2-6.

The probabilities of entering a different state other than the current state were calculated for all states as well as all years. Switching from the retrieving or steaming state showed no significant changes over the period of the study. Switching from a setting state showed significant differences between seasons with the probability of switching from setting to retrieving decreased over time and switching from setting to steaming increased over the same period (Figure 2-7).

CPUE as a covariate

Changes in behaviour with local fishing success were examined by using CPUE as a covariate within the HMM. The behavioural states of “retrieving”, “setting” and “steaming” were readily estimated with means of 1.73, 5.62 and 9.55 knots respectively. The sojourns times related to CPUE are displayed in Figure 2-8. Steaming times increase with increasing CPUE, retrieving and setting times show little change with increasing CPUE. The P matrix values (Figure 2-9) show little to no changes in behaviours from when switching from retrieving or steaming states, but as CPUE increases, the probability of changing from setting to retrieving increases to the point where it is as likely as remaining in a setting state.

Vessel movement and fishing success: Generalized linear model

Using estimates obtained from the HMM described in the HMM section above as well as logbook information, a GLM was developed to define each year using parameters shown in Table 2-8. The form of the relationship between a trip’s catch and the variables found to be statistically significant at the 5% level are shown in Table 2-8 for each period. In 2006 only two variables 1/traps ($p < 0.001$) and time steaming ($p < 0.001$) had significant influences. In 2007 only one variable (1/time soaking, $p = 0.387$) was not found to be significant. Finally, in 2008 all of the variables were found to be highly significant ($p < 0.001$) except the intercept which was weakly significant ($p = 0.0351$).

Over the course of this study, there were changes to the overall biomass of the commercial snow crab and these changes are shown in Table 2-9. Over the period of 3 years the estimated commercial biomass available to the fleet decreased from 74,285 t to

52,564 t (DFO 2012). Though the quota decreased each year, CPUE (kg/trap) was similar in 2006 and 2007, but then dropped off dramatically in 2008. The start of the crab fishing season varied from year to year, as did the CPUE throughout the seasons (Figure 2-10). The initial catch rates among years showed a negative trend as time increased, with higher biomass years showing increased catch rates at the beginning of each respective season and then becoming more similar among years as the seasons progressed.

The GLM was used to estimate an expected catch for a trip in each study year based upon a “typical trip”. To estimate a typical trip, the median values of the variables used to fit the GLM were used to define the typical effort employed by fishers during a trip. The following are used to define the measures of effort for a typical trip: number of traps (73), trap soak time (72 hours), time setting (2.64 hours) and time steaming (6.72 hours) were used to predict catch per trip (Table 2-9). The GLM predicted catch per trip to decline in each year of study, there was no significant difference from 2006 to 2007, while 2008 was significantly different from the other two years of study. The estimated commercial biomass followed the same pattern as the predicted catch per trip.

The complexity of the inverse polynomial link function prevents simple interpretation of the parameters. To more clearly define the relationships, catch was estimated from the GLM for each predictor over the range of their observed values. Figure 2-11 illustrates the relationship between catch and each predictor used in the GLM with other predictors held at their typical trip values. Time setting shows a slightly negative relationship with catch while time steaming shows a positive relationship. The soak time reaches an asymptote around 12 hours suggesting that longer soak times do not increase catch while number of traps has a highly positive relationship with catch.

Discussion

The analysis from this study led to the development of a fishery dependent relative measure of abundance which reflected annual available biomass within the snow crab fishery more closely than the current CPUE measure (kg/trap). In order to estimate fishers' activities, a three state HMM was developed to identify behaviours within a fixed gear fishery. The three state HMM successfully described vessel behaviours in the Gulf of St. Lawrence snow crab fishery. From this model three distinct states of retrieving, setting and steaming were inferred based on the continuous distribution of observed vessel speeds. HMM classifications allowed the estimation of time spent in each state during a trip which led to new behavioural variables for the prediction of fishing success. These predictors combined with current effort measures to provide a new abundance index that can explicitly incorporate fish harvester behaviour into assessment methodology using data collected during the normal prosecution of the fishery.

Observer data has been increasingly used to verify behaviours in mobile gear fisheries. Mills et al. (2007) developed rules to identify fishing and steaming behaviours using observer data for a beam trawler fishery in the North Sea. From vessel speed observations they were able to define the upper and lower boundaries for individual vessel actions. Though they were able to isolate behaviours very well, they found that the frequency of detections from the VMS was lower than required to identify all behaviours during a fishing trip. Previous studies using VMS data to identify fishing grounds, fishing effort or apply management strategies have had detection intervals of one hour or more (Bertrand et al. 2007, Mills et al. 2007, Peel and Good 2011). The high frequency rate of

detection (15 minute intervals) in the snow crab fishery allowed me to identify behaviours that other studies may have missed due to lower temporal resolution.

VMS records provide additional detailed information on fishing activities where observer data may be limited or unavailable. VMS records can define fishing grounds (Jennings and Lee 2012), effort distribution (Bertrand et al. 2008) and can be linked to logbook data to examine independent effort data across an entire fleet (Gerritsen and Lordan 2011). For example, Mullowney and Dawe (2009) used VMS data to develop indices of commercial fishery performance in the Newfoundland and Labrador snow crab fishery. Fishing activity was defined directly by speed between successive VMS readings using thresholds based on the experience of the observers. However, the relationship between speed and activity, including the number of activities, were defined a priori rather than objectively from the data. HMMs increase the utility of VMS data by allowing the detailed inference of fishing activities without the need for an onboard observer. Hypothesized activity models (number of states or alternative distributions of observations) can be compared based upon information theoretic criteria (AIC, BIC, etc.). Ideally these inferences should be compared to directly observed vessel behaviours. Unfortunately, in this study onboard observer data was not available to validate the HMM. However, its utility in predicting catch per trip supports its potential for further research.

The significance of year as a covariate in the HMM provides insight into behavioural variation among the seasons studied. Due to changes in snow crab abundance over the course of the study, we would expect changes to CPUE, measured as kg/trap. Variation in CPUE could also be compounded by the uncertain location of the target

species, with unpredictability increasing as the fishing season progresses (Gillis et al. 2006). Years of high abundance were associated with increased vessel steaming times. These increased steaming times suggest that vessels were travelling further away from port, possibly to more abundant areas (Sampson 1992). More distant fishing is usually more costly, due to increased fuel consumption, longer times at sea and exposure to more risk (ie. storms, breakdowns, accidents) (Sampson 1991). Distant trips would require higher payoffs (CPUE) to balance these costs. During the low abundance year (2008), steaming times and CPUE both decreased. The lower abundance of snow crab appeared to alter fishers behaviour in a way that kept vessels in closer proximity to port. Fishers seemed less willing to impart riskier ventures when the chance of a large payoff declined.

Increased steaming times were associated with higher catches, but variability in catch rates and the increased risk of more distant fishing trips prevented fishers from exploiting higher density sites. Using CPUE as a covariate with effort represented as number of traps, I was able to examine the relationships between fishing behaviours and catch rates. Steaming time showed the greatest change with increasing CPUE, with setting and retrieving times showing little change. Catch rates of 110 kg/trap show steaming times almost 3 times longer than when catch was 30 kg/trap (Figure 2-8). This reinforces the idea that as local populations become overexploited and density decreases, fishers are forced to exploit new locations. Venturing to relatively unexploited patches is costly because patch densities become uncertain and operating costs increase. Daw (2008) examined the relationship between catch and distance travelled in the lobster fishery around the Corn Islands and found that exploiting more distant sites can lead to

higher catch rates as well as higher revenues. These incentives do not always lead to fishers using these more distant fishing grounds however due to variability of catch rates.

The snow crab fishery is another example where simple CPUE may not reflect abundance (Harley et al. 2001, Maunder et al. 2006). Instead of using the classical CPUE (kg/trap) to standardize catch, my four component measure of effort incorporated vessel activities, which may change in response to the distribution and abundance of crab. This model estimates catch for a typical trip (median predictor values) that could more accurately reflect target species abundance on a yearly basis. In my data, the fishery independent abundance estimates support the greater accuracy of my model, but additional years will be required to fully test this proposition. However, the ongoing collection of detailed, georeferenced effort data make this both possible here, and expandable to other commercial fisheries.

The nonlinear relationship between soaktime and catch suggests gear saturation occurs quickly and there is little advantage in terms of catch for fishers to leave their traps unchecked for prolonged periods of time. However, other factors may contribute to the extended soak times observed such as storms, injuries, illness, gear failure, and logistic considerations while in port. As generally expected, I observed a positive relationship between number of traps and catch. However, this trend was highly variable, likely due to differences in local densities around each trap, possible changes in substrate and other environmental factors along the length of a string of traps and throughout the Gulf of St. Lawrence. The types of traps used may also affect catch rate within the fishery. Hebert et al. (2001) conducted a study comparing catchability between three different traps, they found that conical and pyramidal traps caught larger male snow crabs

compared to rectangular traps if soak times were 24 hours. Although conical traps caught larger snow crabs than rectangular traps, CPUE between trap types did not differ significantly. Dufour (1984) tested catch rates between three types of traps at differing soak times and found that conical traps outperformed rectangular traps at longer soak times. These results could impact the estimates from the GLM only if different styles of traps were used, though this was not noted in the logbook records.

Using a combination of fishers' activities and logbook data I was able to develop a fishery dependent relative measure of abundance. By utilizing fishers' behaviours and logbook data I produced a standard trip in which to compare interannual differences in expected catch rates. Hidden Markov models allowed me to identify three unique fishing behaviours in a fixed gear fishery. Future studies should focus on applying HMMs and logbook data to additional years of data in order to further develop the measure of relative abundance. My analyses have shown that HMMs can produce credible representations of fishing activity from VMS data and these activity estimates can be used to improve catch predictions using a GLM. These models provide fisheries scientists and managers with an alternative index of abundance, based upon regularly collected information, which can be used to reflect variation within seasons in addition to the survey data that currently estimates variation between seasons.

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Tables

Table 2-1: The mean and standard deviation of speeds (knots) to which each hidden state was assigned for the two-state models. The 95% confidence interval is given in parentheses. “Norm” indicates that a normal distribution was used and “Weib” indicates that a Weibull distribution was used.

Model	Fishing		Steaming	
	Mean	SD	Mean	SD
two state [Norm, Norm]	3.443 (0.038)	2.555 (0.031)	9.465 (0.033)	1.290 (0.029)
two state [Norm, Weib]	3.459 (0.038)	2.604 (0.029)	9.284 (0.040)	1.544 (0.022)

Table 2-2: The mean and standard deviation of speeds (knots) to which each hidden state was assigned for the three-state models. The distributions used are displayed in the model column. The 95% confidence interval is given in parentheses. *No confidence interval due to degrees of freedom being kept fixed during analysis.

Model	Retrieving		Setting		Steaming	
	<i>Mean</i>	SD	Mean	SD	Mean	SD
three state [N-N-N]	1.8 (0.029)	1.17 (0.21)	6.192 (0.155)	2.373 (0.079)	9.581 (0.038)	1.784 (0.028)
three state [N-N-t]	1.596 (0.028)	1.139 (0.02)	5.431 (0.139)	2.484 (0.067)	9.557 (0.023)	2.44*

Table 2-3: Summary of hidden Markov model comparisons using AIC and BIC. Distributions used are represented by N = normal distribution, W = Weibull distribution, t = t-distribution.

Number of hidden states (k)	Model	df	AIC	BIC
k=2	N-N	6	571 018.8	571 076.9
	N-W	6	577 071.5	577 129.6
k=3	N-N-N	12	527 797.3	527 913.5
	t-N-N	12	506 271.3	506 387.5

Table 2-4: Instantaneous transition (Q) matrix for the 3 state (t – N – N) hidden Markov model with the 95% CI in parentheses. The “from” state is represented by the rows and the “to” state is represented by the columns.

		<i>To</i>		
		Steaming	Setting	Retrieving
<i>From</i>	Steaming	-0.391 (-0.404, -0.377)	0.287 (0.274, 0.300)	0.104 (0.096, 0.112)
	Setting	0.492 (0.468, 0.52)	-1.8 (-1.869, -1.731)	1.308 (1.246, 1.366)
	Retrieving	0.030 (0.026, 0.036)	0.634 (0.61, 0.658)	-0.665 (-0.688, -0.641)

Table 2-5: Transition probability (P) matrix for a 3 state (t –N – N) hidden Markov model using a time interval of 15 minutes with the 95% CI in parentheses. The “from” state is represented by the rows and the “to” state is represented by the columns.

		<i>To</i>		
		Steaming	Setting	Retrieving
<i>From</i>	Steaming	0.911 (0.908, 0.914)	0.057 (0.055, 0.059)	0.032 (0.031, 0.034)
	Setting	0.096 (0.091, 0.1)	0.659 (0.649, 0.669)	0.245 (0.236, 0.254)
	Retrieving	0.015 (0.013, 0.016)	0.118 (0.115, 0.122)	0.867 (0.863, 0.871)

Table 2-6: State specific sojourn times (in hours) showing the average amount of time spent in each state in the 3 state (t – N – N) hidden Markov model.

	Estimates	SE	Lower	Upper
Steaming	2.559	0.043	2.478	2.652
Setting	0.556	0.011	0.532	0.577
Retrieving	1.505	0.028	1.449	1.559

Table 2-7: Shows the probability (pnext matrix) of entering the next state given the current state for the 3 state (t –N – N) hidden Markov model. The 95% confidence intervals are shown in parentheses.

		<i>To</i>		
		Steaming	Setting	Retrieving
<i>From</i>	Steaming	0	0.735 (0.715, 0.756)	0.265 (0.244, 0.285)
	Setting	0.273 (0.262, 0.285)	0	0.727 (0.715, 0.739)
	Retrieving	0.046 (0.038, 0.054)	0.954 (0.946, 0.962)	0

Table 2-8: Catch models by trip among years for the snow crab fishery. GLMs used the gamma distribution and inverse link function. The 95% confidence intervals for each variable are shown in parentheses. P values that are significant at the 5% level are shown in bold.

Year	Variable	Coefficient Estimates	p-value
(a) 2006 (n = 1192)			
	Intercept	-9.13×10^{-6} (-2.25×10^{-5} , 4.27×10^{-6})	0.182
	1/Traps	1.67×10^{-2} (1.59×10^{-2} , 1.75×10^{-2})	<0.001
	1/Time Soaking	9.63×10^{-5} (-8.5×10^{-5} , 2.78×10^{-4})	0.298
	Time Steaming	-1.25×10^{-6} (-1.87×10^{-6} , -6.41×10^{-7})	<0.001
	Time Setting	1.44×10^{-7} (-9.28×10^{-7} , 1.22×10^{-6})	0.793
(b) 2007 (n = 1554)			
	Intercept	-2.19×10^{-5} (-3.34×10^{-5} , -1.06×10^{-5})	<0.001
	1/ Traps	1.85×10^{-2} (1.78×10^{-2} , 1.92×10^{-2})	<0.001
	1/Time Soaking	-6.5×10^{-5} (-2.12×10^{-4} , 8.23×10^{-5})	0.387
	Time Steaming	-1.82×10^{-6} (-2.4×10^{-6} , -1.24×10^{-6})	<0.001
	Time Setting	1.45×10^{-6} (5.89×10^{-7} , 2.31×10^{-6})	<0.001
(c) 2008 (n = 1553)			
	Intercept	-1.49×10^{-5} (-2.87×10^{-5} , -1.05×10^{-6})	0.0351
	1/ Traps	2.03×10^{-2} (1.94×10^{-2} , 2.11×10^{-2})	<0.001
	1/Time Soaking	4.69×10^{-4} (2.25×10^{-4} , 7.13×10^{-4})	<0.001
	Time Steaming	-2.09×10^{-6} (-2.76×10^{-6} , -1.42×10^{-6})	<0.001
	Time Setting	2.09×10^{-6} (1.12×10^{-6} , 3.06×10^{-6})	<0.001

Table 2-9: Quota, fishing effort, catch and predicted catch per trip for the snow crab fishery in area 12. The 95% confidence intervals are shown in parentheses. Quota, CPUE and commercial biomass were obtained from DFO (2012).

	2006	2007	2008
Quota (t)	25 869	23 207	20 900
CPUE (kg/trap-haul)	64.4	65.7	56.4
Commercial Biomass (t)	74 285	66 660	52 564
	(66 192 - 83 087)	(60 183-79 638)	(46 658 - 59 006)
Model Prediction	4704.1	4506	3831.6
(Catch per trip (kg))	(4566.3 - 4850.4)	(4399.6 - 4617.6)	(3733.6 - 3934.9)

Figures

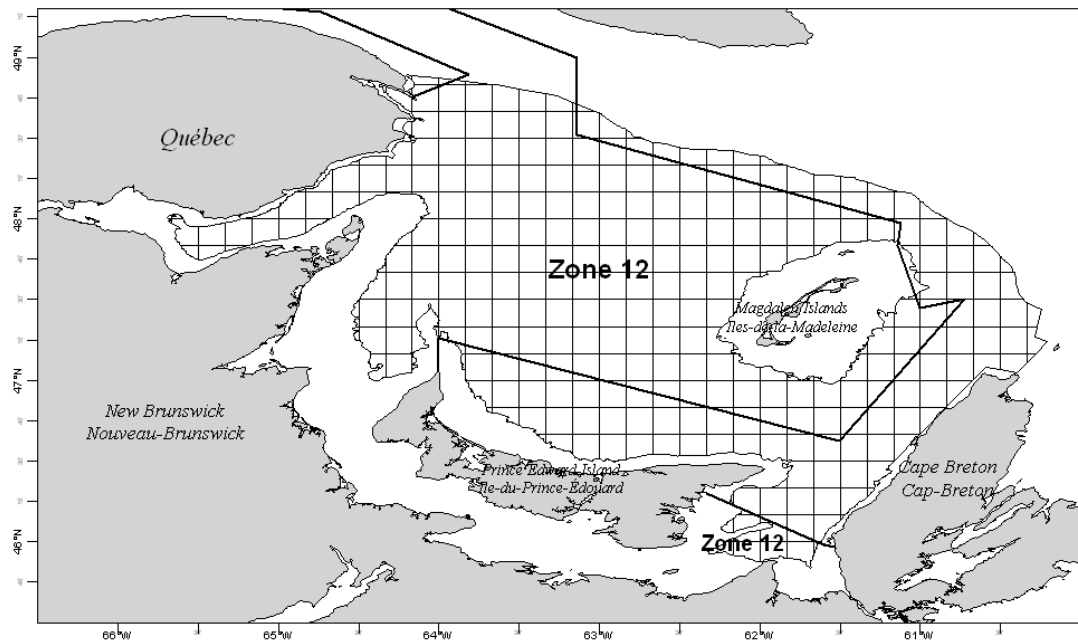


Figure 2-1: Fishable area in zone 12 for the snow crab fishery (*Chionoecetes opilio*) fishery in the Gulf of St. Lawrence. This fishery is located on the eastern seaboard in Canada, with the grid representing the sampling area for the pre-season survey.

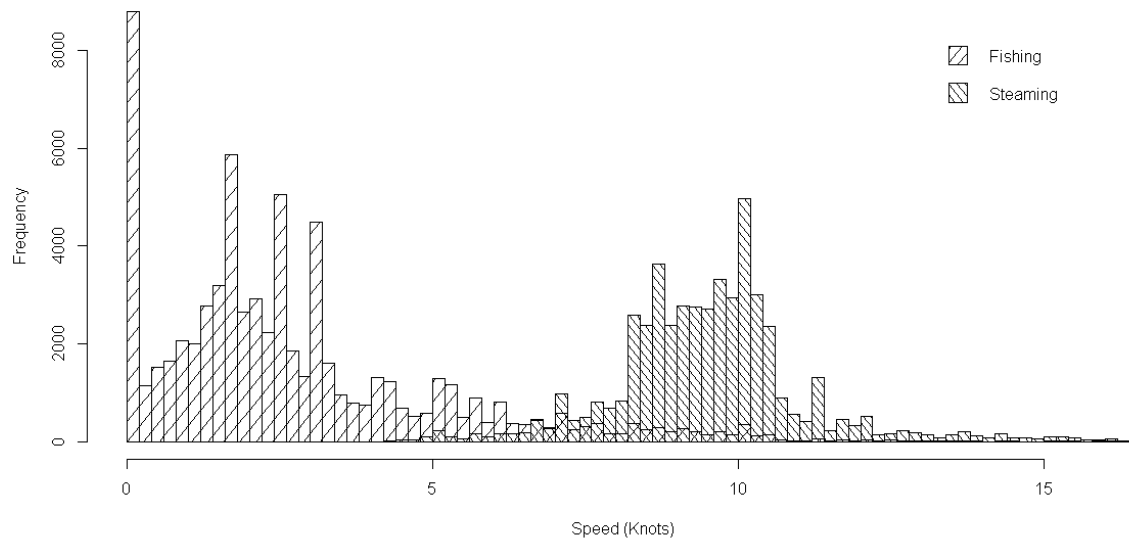


Figure 2-2: Two state HMM using normal distributions to describe both the fishing and steaming states. Fishing activities are represented by slower speeds and steaming activities are represented by faster speeds.

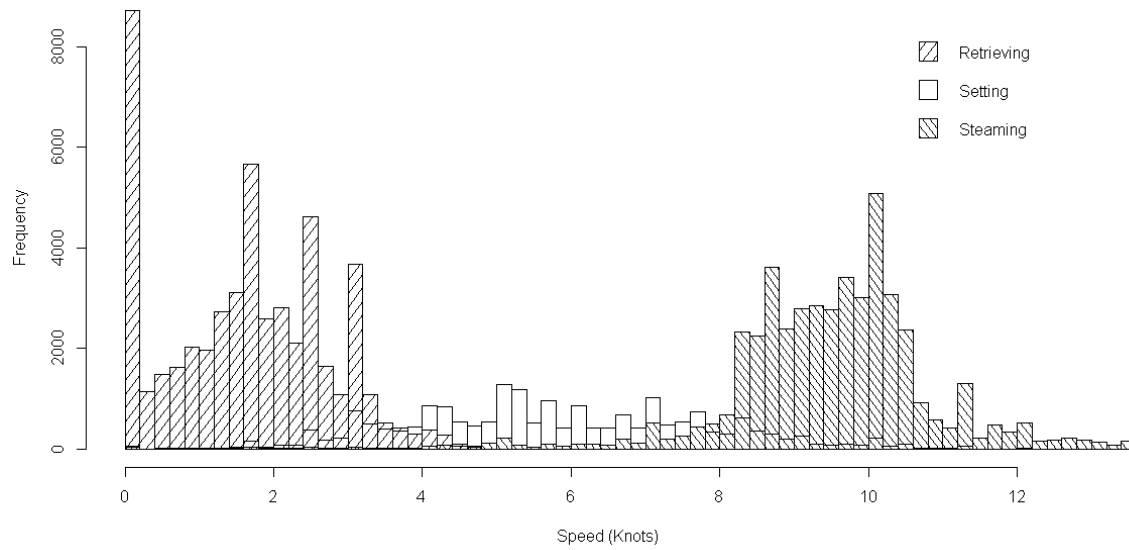


Figure 2-3: Three state HMM using normal distributions for the retrieving and setting states and a t-distribution for the steaming state.

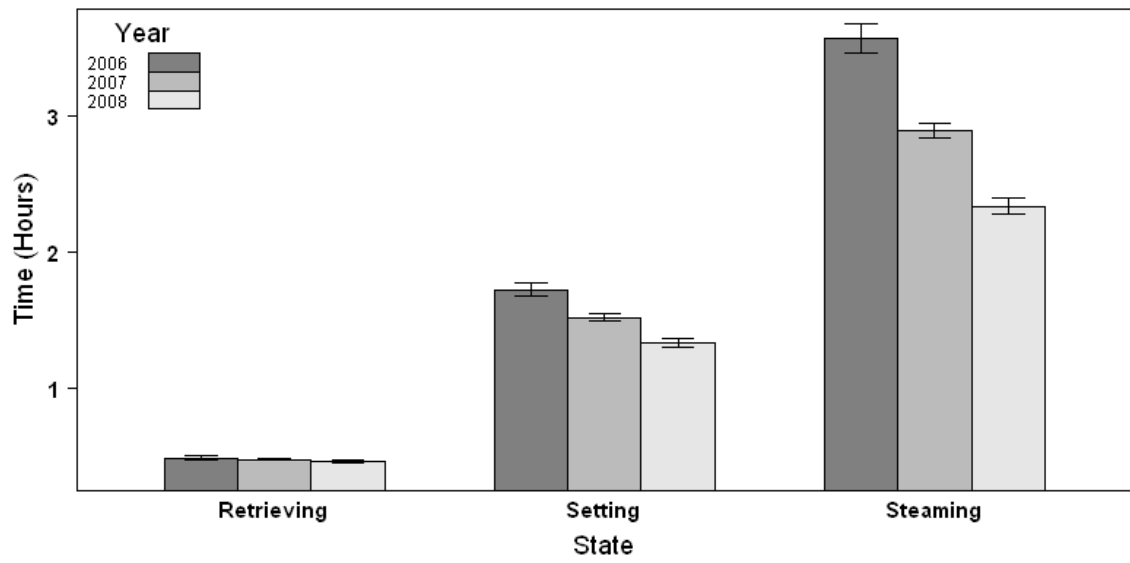


Figure 2-4: The sojourn times for a vessel staying in a particular state for each year of the study. The 95% CI for the means are shown.

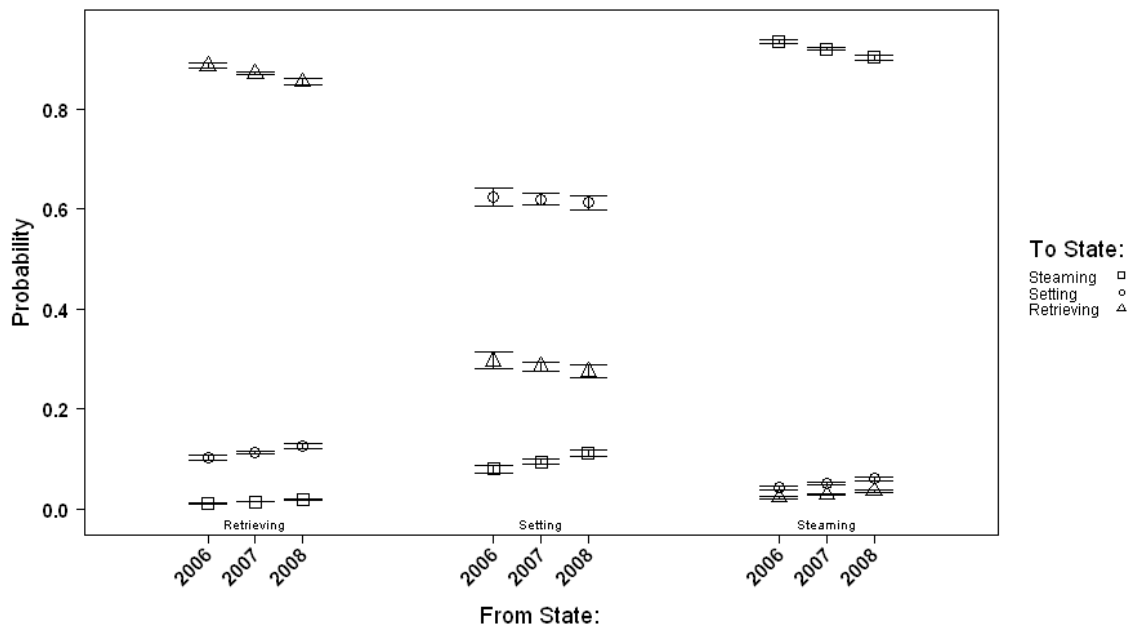


Figure 2-5: State specific probability of entering another state based on the current state over a 15 minute interval. The x axis displays the “from” state and the symbols represent the “to” state with differences shown between years for all “from” states.

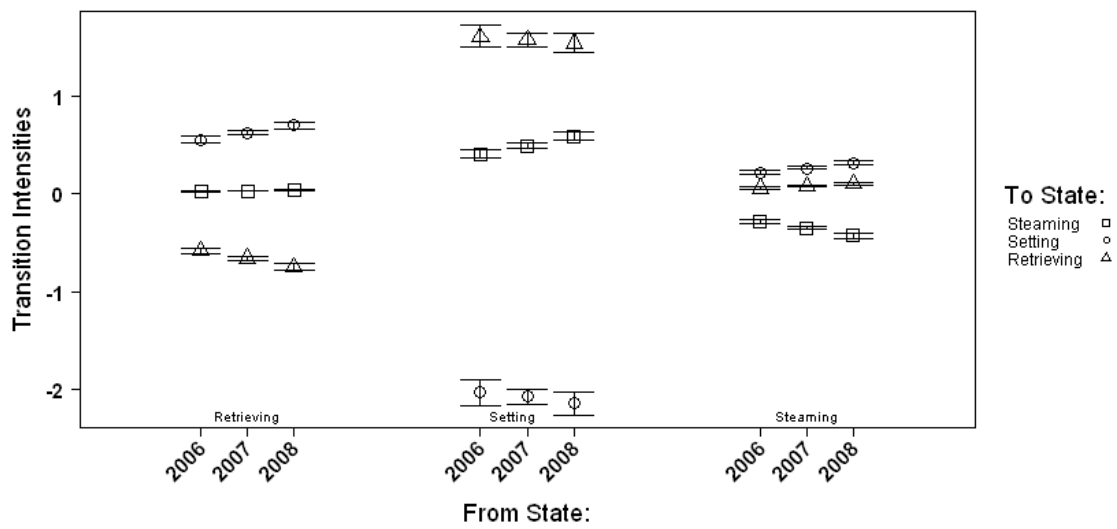


Figure 2-6: State specific Q matrix values over each year of study showing the transition intensities between states. The x axis displays the “from” state and the symbols represent the “to” state and differences shown between years for all “from” states.

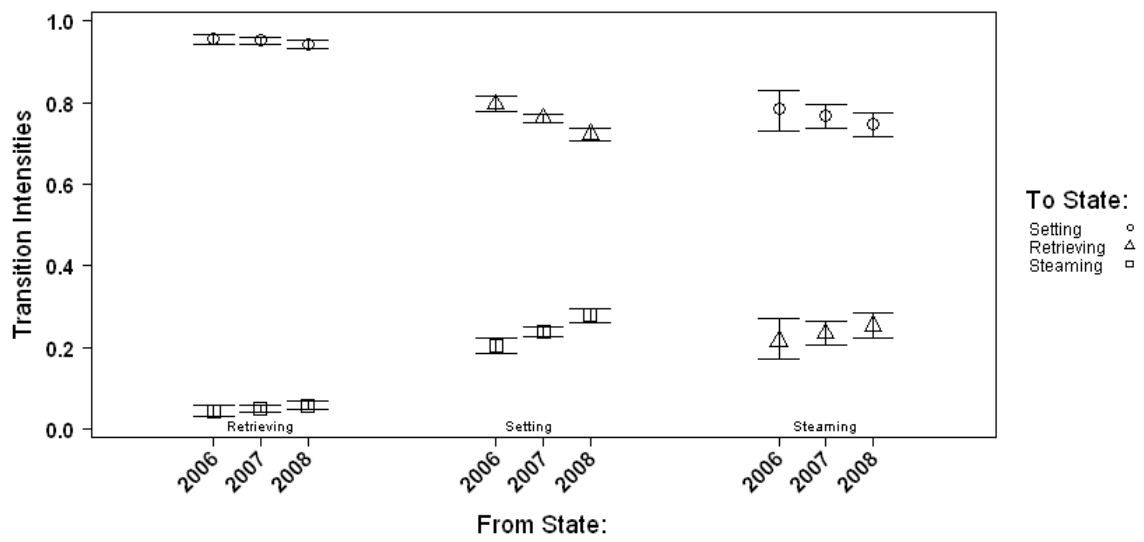


Figure 2-7: The probability of entering a different state, given the current state over the 3 years of study. The values on the x-axis show the “from” state while the symbols represent the “to” state.

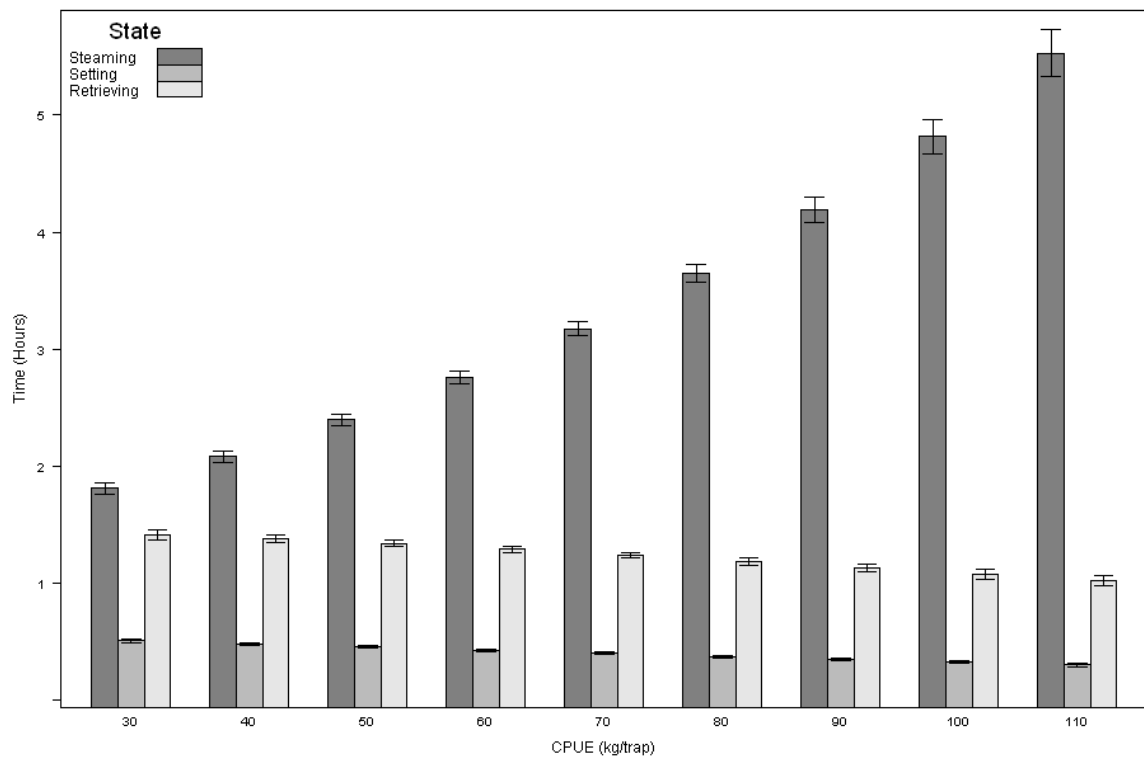


Figure 2-8: The sojourn times for each hidden state across a wide range of catch rates. The catch rates shown on the graph contain 90% of the observed catch records over the period of study.

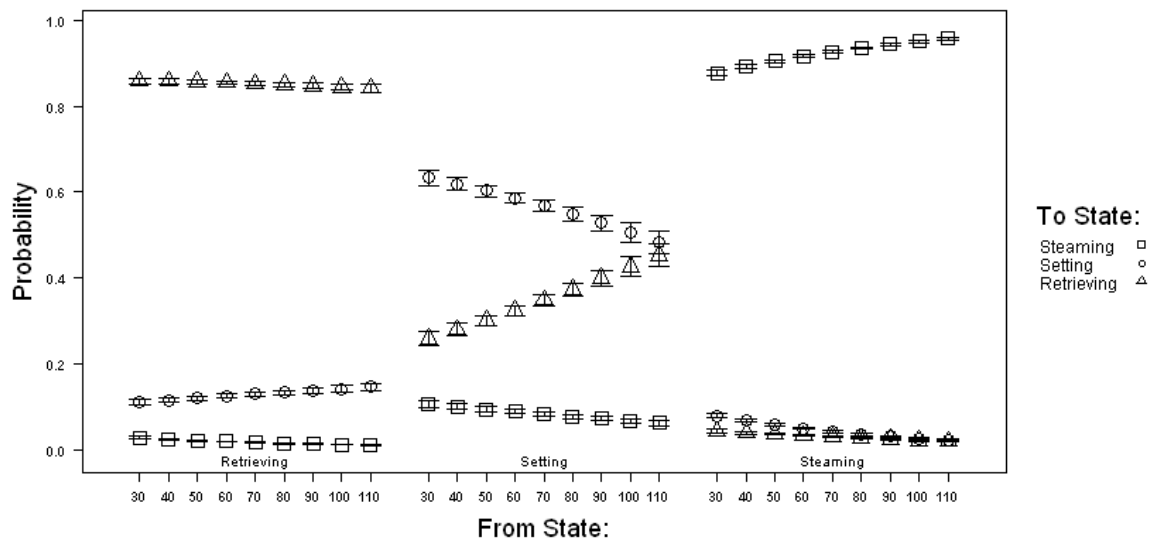


Figure 2-9: The probability of entering the next state given the current state, as well as the catch rate.

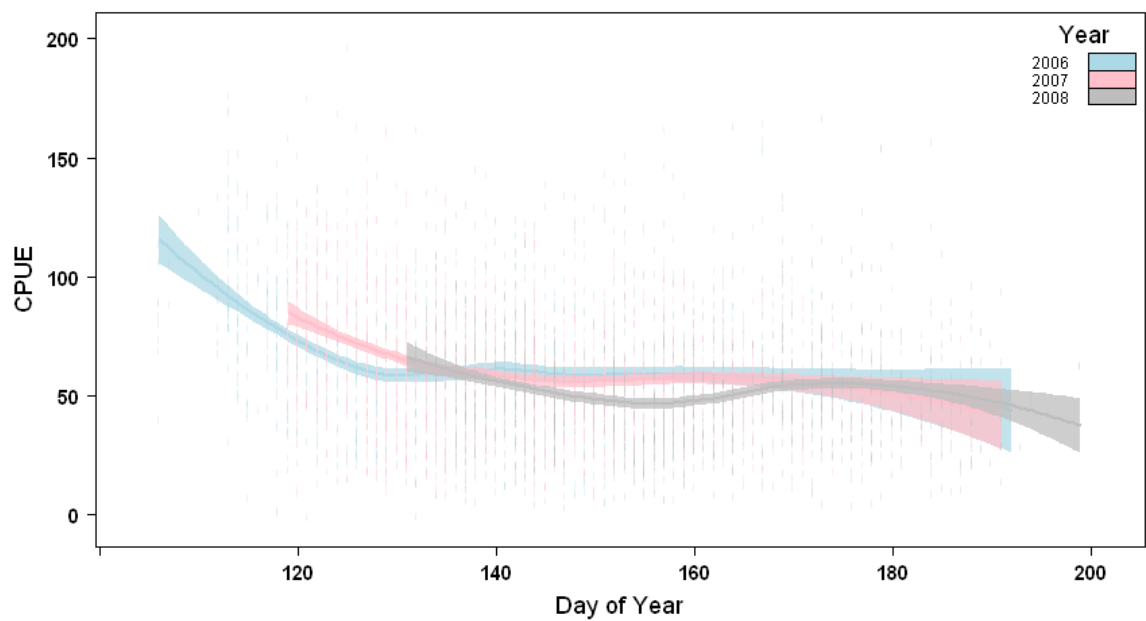


Figure 2-10: Catch rates throughout each individual season as season length progresses. Means are plotted using a loess line with the 95% CI shown by the shaded regions around each line.

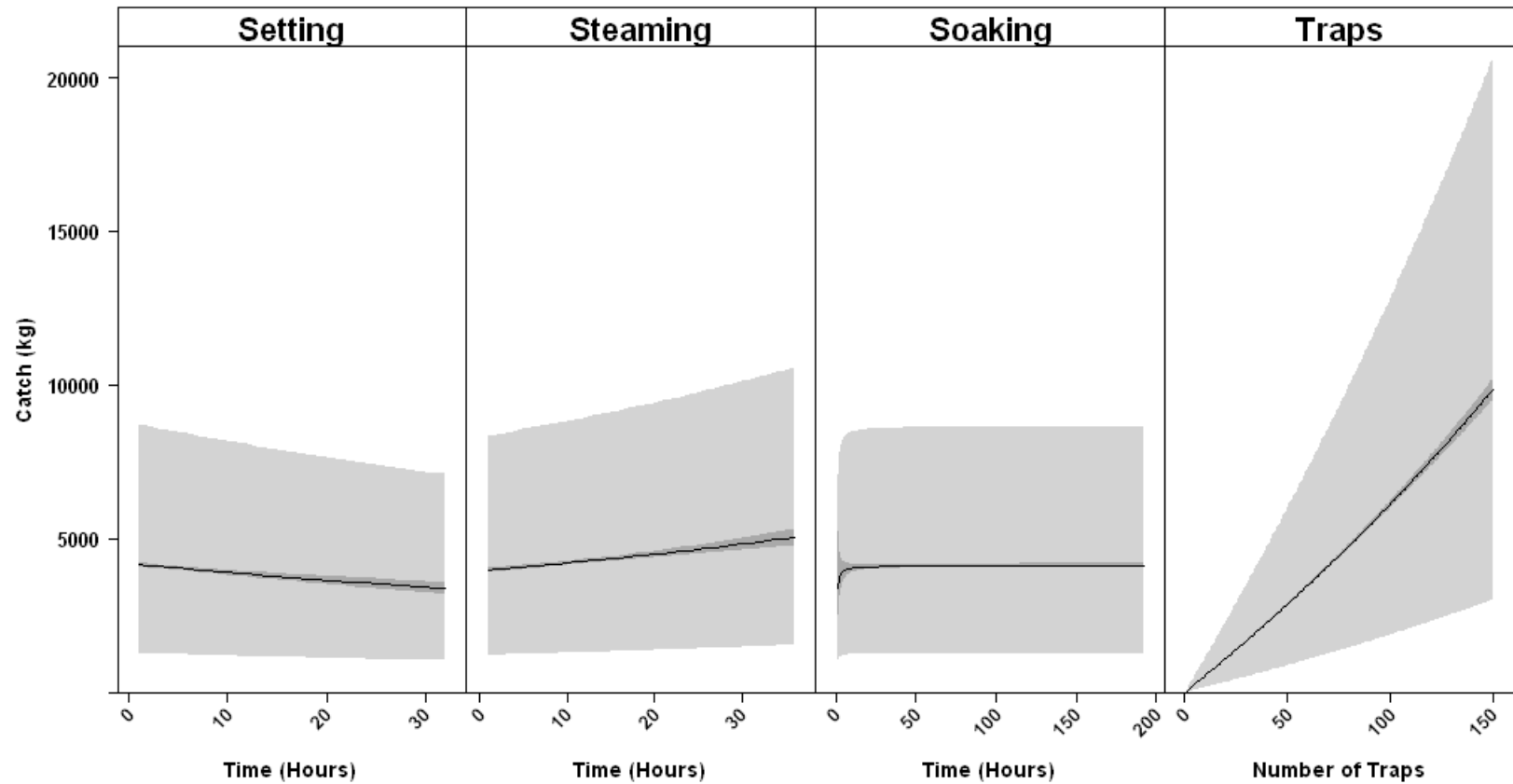


Figure 2-11: Catch predicted for each response variable in the GLM. Responses are modeled using typical values for each measure of effort (as previously described in Table 10). The black line depicts the mean predicted catch over the range of observed values, the dark grey line is the 95% confidence interval of the mean and the lightly shaded grey region is the 95% prediction interval.

Chapter 3: Pre- and post-dispersal habitat use by
escaped rainbow trout (*Oncorhynchus mykiss*) from
an experimental freshwater aquaculture facility

Introduction

In Canada, rainbow trout (*Oncorhynchus mykiss*) open pen aquaculture production is a multimillion dollar industry, with approximately 3 800 tonnes (~\$15.7 million) produced in Ontario fish farms in 2006. The total annual contribution that aquaculture made to the Ontario economy was estimated to be \$55 – 60 million in 2006 (Moccia and Bevan 2007). The environmental impacts of the aquaculture industry are under close observation and continued scrutiny from government and public agencies, be it through the release of solid and dissolved wastes (Azevado et al. 2011) or large scale escapes of farmed fish (Naylor et al. 2005). Escape events from aquaculture cages are referred to as acute or chronic. Chronic escapes are a continuous, slow process, while an acute loss results in a large scale loss of fish over a short amount of time (Bridger and Garber 2002). The potential for escapes from aquaculture cages present serious challenges for farm owners, law makers and the public. Escaped farm fish have the ability to negatively affect wild fish populations through high propagule pressure, competition and interbreeding (Gross 1998, Naylor et al. 2005, Consuegra et al. 2011). After an escape event, farmed fish are known to disperse away from the cage site and thus have the opportunity to interact with native fish or wild conspecifics (Fiske and Lund 1999).

Habitat use of ectotherms is known to be strongly tied to temperature due to physiological and bioenergetic performance (Rodnick et al. 2004). North-temperate lakes, especially small lakes like those found at the Experimental Lakes Area (ELA), are subject to summer stratification. During this time the thermocline depth increases as temperatures rise throughout the spring and summer causing a decrease in lake trout habitat. The

optimal habitat for lake trout can be defined by a combination of temperature ($<15^{\circ}\text{C}$) and oxygen ($>4\text{ mg/L}$) (Plumb and Blanchfield 2009), while rainbow trout have a higher thermal tolerance with an upper lethal temperature above 24°C (Bear et al. 2007). During the stratified period lake trout do not have access to high energy littoral prey species and are mainly restricted to pelagic prey items. However, rainbow trout are able to access littoral regions during the stratified period and therefore are able to exploit the resources in these areas.

Space use is commonly associated with resource availability, especially the relationship between home range size and resource distribution (Mitchell and Powell 2007). Home range size as a result of limiting resources has previously been discussed in home range studies for black bears (*Ursus americanus*) (Lindzey and Meslow 1977, Mitchell and Powell 2007), Shiras moose (*Alces alces shirasi*) (Baigas et al. 2010) and roe deer (*Capreolus capreolus*) (Said et al. 2005). Food especially is considered a density dependent entity, with patches located independent of each other which causes predators to actively search for abundant patches and compete for resources. Predators encounter food within these patches, but must travel between patches to exploit their resources. As soon as a predator encounters a patch and begins foraging, the prey density and the predator's foraging efficiency decreases in that patch as time spent increases (Charnov 1976). In the presence of a continued food source (the cage site), it would be expected that the spatial distribution of foragers would be concentrated near this location.

Escaped rainbow trout have the ability to not only negatively impact the environment through predator-prey interactions or habitat degradation, but they may also damage native fish stocks by preying on eggs during spawning seasons. The objective of

this study is to compare the movement patterns and habitat use of farmed rainbow trout released from an experimental aquaculture operation and native lake trout in the same lake. Specifically, I want to quantify potential habitat interactions between species. I will examine interspecific (rainbow trout and lake trout) differences in attraction to an aquaculture cage, during and post-operation (simulating dispersal from the cage site) as well as variation in interspecific habitat overlap throughout the study. A better understanding of escapee movements will help with recapture efforts and predicting ecological impacts.

Methods

Study Area

All field work was conducted at the ELA, located in Northwestern Ontario (Figure 3-1). It consists of 58 small glacial relict lakes and their watersheds set aside for research purposes (Cleugh and Hauser 1971). The ELA aquaculture experiment was in operation from 2003-2007 with two years of background research and two years of ecosystem recovery observations. The study site was Lake 375 which is a small (23 ha) double basin lake with max depths of 17 and 26 m in the north and south basins respectively (Figure 3-2). A large steel frame was built to suspend a fish cage measuring approximately 10 m \times 10 m \times 10 m in the north basin of Lake 375 and the base of the cage hung approximately 5 m above the lake bottom. Each year the cage was stocked with roughly 10 000 female rainbow trout fingerlings weighing less than 200 g. The rainbow trout were hand fed twice daily in the morning and evening, usually 2 hours after sunrise and 2 hours before sunset (Blanchfield et al. 2009, Rooney and Podemski 2009).

Each fall from 2003 to 2007 rainbow trout were surgically implanted with pressure-sensing acoustic transmitters and released into Lake 375 to simulate an escape scenario. Lake trout have been tagged in Lake 375 since 2002. The surgical tagging procedure is described in more detail by Blanchfield et al. (2009). The acoustic transmitters in the fish were detected by two RAPT systems where one system was positioned in the north basin and the other in the south basin in Lake 375 (Figure 3-2). The RAPT systems consisted of a triad of moored buoys which received signals from tags and recorded four dimensions of information: latitude, longitude, depth and time simultaneously throughout the open water season. The buoys received signals from the implanted receivers and then transmitted their information to a nearby onshore receiving station where a computer calculated fish positions over time. More information about the RAPT system is available from Blanchfield et al. (2005).

Dataset and Manipulations

The data collected for this study spans four open water seasons from years 2006-2009. An experimental aquaculture operation was in effect in 2006 and 2007, followed by two years of ecosystem recovery in 2008 and 2009. All data manipulations and subsequent analysis were done using the R statistical programming language (R Development Core Team 2012). A method to spatially correct telemetry positions was developed using stationary tags deployed at various locations within the lake. This method was used to correct the biases associated with the telemetry system using a geostatistical method, specifically Kriging (Journel and Huijbregts 1978) using the geoR package in R. Methods and results for the spatial correction of stationary tag trials and

fish positions are shown in Appendix II. Kriged positions are used for all subsequent spatial analyses.

Behaviour and Space Use

The spatial distribution of tagged fish was analyzed using the kernel method in the adehabitatHR package (Calenge 2006). The kernel method calculates a utilization distribution (UD) giving the probability density that an individual is found at a certain point in space (Worton 1987). I focused on core area use (50% of UD) to compare habitat size among each species over each year of study. Core area estimates were restricted from extending outside of the lake to reduce over estimation of habitat usage.

Using the fixed kernel estimates, a utilization distribution overlap index (UDOI) was calculated to assess the amount of habitat overlap shown by each fish species in the lake in each year and season. Fieberg and Kochanny (2005) reviewed different methods of analyzing space use sharing and concluded that the UDOI is the most appropriate index for quantifying overlap. The UDOI is a generalization of Hurlbert's (1978) E/E_{uniform} statistic and has the form:

$$(1) \quad UDOI = A_{1,2} \iint_{-\infty-\infty}^{\infty\infty} UD_1(x,y) \times UD_2(x,y) dx dy$$

This measure is a product of the two UD's, where they equal the joint distribution of the two animals' UD's under the assumption that they use space independently of one another. $A_{1,2}$ is the area of overlap between the two animals' home range. The UDOI can range in value from zero (no overlap) to 1 (if both UD's are uniformly distributed and

have 100% overlap). The UDOI value can be >1 if the UD's are not uniformly distributed and show a high degree of overlap. In general, UDOI values <1 indicate less space use sharing than would be expected from overlapping uniform distributions while UDOI values >1 indicate more space use sharing than would be expected from overlapping uniform distributions. The UDOI calculates overlap in two dimensions, but fish occupy a three dimensional space within lakes, therefore during periods of stratification when fish may occupy different thermal habitats, the UDOI does not discern between depth distributions. I used a randomization test procedure to statistically compare mean UDOI values among each species to test interspecific habitat overlap and cage overlap. First I compared the difference (D_1) in means for each group, then randomly allocated samples to each group and calculated D_2 . I repeated the random allocation 10 000 times to generate a randomization distribution. Finally I calculated a p-value from the randomization distribution and D_1 to test whether the overlap index could have arisen from a random process (Manly 1997).

To measure space use around the cage, a square buffer of 25 m was defined around the cage site (Figure 3-2). Fish presence around the cage site was measured two ways. First, the mean number of detections per minute within the buffer was calculated for each individually tagged fish over each open water season over the course of each day. Secondly, a Near Cage Habitat (NCH) was created by simulating a uniform UD within the area of the buffer. The NCH was used to calculate UDOI values between the cage and fish species in the lake.

As part of the long term monitoring program, temperature and dissolved oxygen (DO) measurements during the open water season were taken at two week intervals and 1

m depth intervals over the deepest part of the lake using a portable temperature and DO meter. In the metalimnion, where temperature change was $>1^{\circ}\text{C}/\text{m}$, the sampling interval was every 0.25 m. During the ice covered periods sampling was performed twice, usually in early January and late March. Due to physiological constraints imposed by environmental variables upon lake trout during the stratified period, temperature and oxygen measurements can be used to define habitat requirements.

Results

Habitat use

During the open water seasons, rainbow trout generally occupied warmer water habitats compared to lake trout, especially during the stratified periods. Rainbow trout showed the greatest depth overlap with lake trout in 2006, displaying continuous overlap for the entire open water season (Figure 3-3). During the rest of this study, there was some vertical overlap, but there were also periods of clear depth separation. As temperature and oxygen became depleted during the summer months (June – September) lake trout habitat became confined until fall turnover except in 2009. During the final year of study, lake trout depth distribution did not become limited by an oxygen limitation (Figure 3-3).

Yearly open water core area sizes for individual rainbow trout ranged from 0.29 to 4.50 ha and from 0.22 to 4.03 ha for individual lake trout. Mean core area size did not vary significantly among years for rainbow trout, but mean core area size for lake trout declined each year from 2006-2008 and then increased again in 2009 (Figure 3-4). Lake trout maximum seasonal depth decreased each year from 2006 to 2008, followed by a drastic depth shift in 2009 where lake trout reached a maximum depth of about 10 m in

early September before moving into the upper few meters of the water column for fall spawning. In contrast, rainbow trout maximum depth decreased throughout the study (Figure 3-5). Lake trout exhibited seasonal depth changes each year that coincided with changes in surface water temperatures. During the spring and summer months, as air and water temperatures increased, lake trout were forced to continually seek colder depths in Lake 375 (Figure 3-5) due to temperature and oxygen constraints (Plumb and Blanchfield 2009). In 2006, rainbow trout mean depth increased as the season progressed and then decreased rapidly during fall turnover. In 2007 and 2008, rainbow trout maximum depth peaked in August and didn't reach the maximum depth observed in 2006. In the final study year rainbow trout depth did not change throughout the open water season, with rainbow trout remaining in the upper 1-2 meters of the water column for the entire open water season.

In 2006 and 2007, when the commercial production of rainbow trout was ongoing, the core areas of rainbow trout show considerable overlap with the cage site during the fall and summer, while in 2008 and 2009, after production ceased, their spatial distribution does not display the same affinity to the cage site. In all 4 years of study, lake trout show considerable attraction to a near shore area in the north basin as well as to the east shore between the RAPT systems (Figure 3-6). In 2008 neither species has any core areas in the south basin of the lake.

Affinity to cage site

Presence of acoustically tagged fish at the cage site was measured by number of detections within the 25 m buffer around the cage site. Rainbow trout were attracted to the cage in 2006 and 2007 although presence at the cage site was not consistent

throughout all hours of the day, but rather detections displayed a diurnal pattern (Figure 3-7). In the two years of ecosystem recovery, rainbow trout did not display the same attraction to the cage site and were rarely detected there. Lake trout on the other hand showed no affinity to the cage site during periods of production or ecosystem recovery. Lake trout were rarely detected (<2 detections/day) at the cage site. This indicates no attraction to the cage site (Figure 3-7).

Measuring cage use by comparing space use by each species to the NCH, rainbow trout spent more time around the cage when it was in production than did lake trout (Table 3-1). In the summer of 2006 the UD of individual rainbow trout overlapped with the NCH more than lake trout (randomization test, $P < 0.006$) as well as in the fall of 2006 (randomization test, $P < 0.015$). A similar trend was seen in 2007 when rainbow trout overlap with the cage was significantly higher in both the summer (randomization test, $P < 0.041$) and fall (randomization test, $P < 0.0065$). When production ceased, there was no significant difference in cage space use between the two species.

Interspecific interactions

During times of cage production, the rainbow trout overlap with conspecifics had UDOI values ranging from 0.99 – 2.7 which means overlapping uniform distributions (0.99) to highly concentrated overlapping habitat use (2.7). Alternatively, rainbow trout overlap with lake trout during this same period showed relatively low overlap indices of 0.36 – 0.56 (Table 3-2). In each year and season during cage production, intraspecific rainbow trout overlap was significantly higher than the interspecific overlap revealing similar attraction to the cage site by individuals and attraction to each other. During the post-production phase there were significant differences in spatial overlap in the summer

of 2008 (randomization test, $P < 0.001$) and fall of 2009 (randomization test, $P < 0.05$). However, there was no evidence for interspecific differences in spatial overlap during the fall of 2008 and summer of 2009.

Discussion

At some point in each year of this study, trout displayed interspecific overlap at a known spawning shoal. This may be a case where escapees may have a negative effect on native fish by eating their eggs and reducing recruitment for following years. Rainbow trout remain one of the highest potential invaders due to their introduction in many countries for sport fishing and their value to the aquaculture industry (Fausch 2007). Global aquaculture production has increased rapidly, especially for salmonids (FAO 2012), increasing the potential for large scale escapes. Though the likelihood of escaped salmonids establishing a naturally producing population is considered to be minimal (Soto et al. 2006, Podemski and Blanchfield 2006), the competition effect of escapees on native species in lieu of successful reproduction should be a concern for producers and the public. In order to minimize risk to the ecosystem, steps should be taken to reduce the potential impacts such as construction of fish barriers to reduce dispersal or choosing fishless lakes as potential sites for fish farms.

Changes in food abundance and quality during the stratified period may have driven the reduction in observed habitat use by lake trout, but not affected rainbow trout. Vander Zanden and Rasmussen (1996) reported that lake trout diets typically consisted of pelagic forage fish, but Lake 375 lacks pelagic forage fish which alters the food web and places more importance on a freshwater shrimp, *Mysis diluviana* (previously *M. relicta*). *Mysis* have similar habitat preferences to those of lake trout and their abundance declined

throughout this study (Paterson et al. 2011). The disappearance of *Mysis*, a major food source for lake trout during the stratified period, along with reduced available habitat likely led to their reduced core areas observed in 2007 and 2008. Changes in food availability and habitat usage may have been driven by water temperature and oxygen limitations throughout that time due to the fact that Lake 375 did not undergo a full turnover in the fall of 2007 or the spring of 2008. Heightened anoxic levels in the lake diminished the available habitat for *Mysis* to avoid predators in dark, cold, well oxygenated waters increasing their predation risk from trout. The higher thermal tolerance of rainbow trout allowed them access to high energy littoral minnows for longer periods than cold-water dependent fish. Access to this food source reduces their energetic stress and allows them to meet their metabolic demands. Escaped rainbow trout may not forage as efficiently as wild fish because they have been known to mistake indigestible materials as food pellets (Rikardsen and Sandring 2006).

While the aquaculture cage was in production escaped rainbow trout displayed an attraction to the cage site, but not after. Post-production, rainbow trout were not detected at the cage site, but rather their spatial distribution shows that littoral regions in the north basin became more important. The crepuscular activity of rainbow trout at the cage site suggests that they exploit the cage site during feeding times when they have access to waste feed. The diets of escaped rainbow may not have been significantly altered due to the presence of continued waste feed during the open water seasons in 2006 and 2007. The waste feed is not only available to fish however, as excess feed can accumulate on the sediments and become available to invertebrates (Ramos et. al. 2008, Kullman et al. 2009). Instead of actively pursuing live prey, rainbow trout could have minimized

energetic output and directed more energy to lipid storage rather than protein storage, as lipids are an easily mobilized energy reserve and can be used during times of low food quality or abundance (Rikardsen and Elliot 2000). In addition, rainbow trout conspecific associations may partly be due to the fact that for the first year of their lives they were reared in high concentrations and perhaps they habituated to high conspecific densities and actively sought out other fish. Johnston et al. (2010) indicate that salmonid cage culture in Lake Huron attracted wild fish, but results from my experiment suggest the opposite in that wild lake trout were not attracted to the cage site. Other studies have also reported wild fish attraction to cages sites (Dempster et al. 2002, Fernandez-Jover et al. 2008). The differences in attraction to the cage site may be due to behavioural and habitat preferences of the study species.

The strength of using applying the UDOI methodology in fish biology has been shown in two ways, (1) using it to measure attraction to an area of interest and (2) interspecific overlap of top predators in a lake. The UDOI could have major implications for management decisions based on assessing interactions among individuals and site fidelity (Fieberg and Kochanny 2005). The utility of the UDOI as an estimator of site fidelity has been shown in this study. Previous uses of the UDOI have studied sexual segregation and water source use by bighorn sheep (*Ovis Canadensis*) (Whiting et al. 2010), spatial overlap between Eastern Rockhopper Penguins (*Eudyptes filholi*) and Northern Rockhopper Penguins (*E. moseleyi*) (Thiebot 2012) and breeding affiliations in sandhill cranes (*Grus canadensis*) (Krapu et al. 2011). The study performed by Whiting et al. (2011) could further quantify water source importance by simulating uniform UD's around each water source and measuring bighorn overlap with each area to determine

which sources are highly used for future conservation implications. Some other areas that could benefit from this methodology include testing if coral reef remediation is successful, off-shore structure impacts on fish and animal behaviour and prediction of disease spread.

Monitoring the environmental impacts of escaped farmed fish should receive increased effort due to the high likelihood of farmed fish escaping enclosures. The relatively small size of Lake 375 made it an excellent system to contrast the movements of escapees when a commercial aquaculture facility was in operation and after operations ceased. My results suggest that in the case of farmed fish escapes, recapture efforts should focus on areas near the cage sites during feeding times. Future studies should focus on studying systems where larger commercial aquaculture cages are in use and monitor the movements of more native fish species and their attraction to the cage site. The high thermal tolerances and invasive threat of rainbow trout should be a concern for managers when aquaculture facilities are being planned in lakes where rainbow trout are not native due to the effects they can have on the structure of the food web (zooplankton, benthic invertebrates) and spawning success of native fish (eating eggs and young of year fish).

In addition to biological concerns, my work provides significant methodological refinements to the use of fish telemetry data. I introduced a new method to measure space sharing of mobile fish with an immobile aquaculture cage using a technique that focuses on an organism's use of space and related these estimates to the availability of resources. Additionally, studies should focus on lifespans and fecundity of escapees to monitor the

potential environmental impacts to native fish stocks, zooplankton and invertebrate populations and diversity.

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Tables

Table 3-1 – UDOI values for aquaculture operation in Lake 375 with each species in the summer and fall. Sample sizes are shown in parentheses and P values significant at the 5% level are shown in bold.

Year	Season	Production	Lake trout	Rainbow trout	P value
2006		Yes			
	Summer		0.0749 (11)	0.311 (18)	0.005
	Fall		0.0149 (9)	0.49 (13)	0.0149
2007		Yes			
	Summer		0.0409 (10)	0.227 (19)	0.0409
	Fall		0.00424 (8)	0.358 (15)	0.0064
2008		No			
	Summer		0.0774 (9)	0.0882 (12)	0.283
	Fall		0.00545 (9)	0.0459 (7)	0.0537
2009		No			
	Summer		0.0494 (10)	0.0475 (4)	0.465
	Fall		0.00597 (10)	0.0102 (3)	0.193

Table 3-2 – UDOI values for rainbow trout overlap with lake trout in each year and season. Sample sizes are shown in parentheses and P values significant at the 5% level are shown in bold.

Year	Season	Lake trout	Rainbow trout	P value
2006	Summer	0.423 (11)	1.065 (18)	1.48×10^{-3}
	Fall	0.409 (9)	2.668 (13)	6.92×10^{-6}
2007	Summer	0.564 (10)	0.991 (19)	2.42×10^{-3}
	Fall	0.362 (8)	1.238 (15)	1.13×10^{-3}
2008	Summer	0.675 (9)	1.128 (12)	4.34×10^{-5}
	Fall	0.55 (9)	0.587 (7)	0.4002
2009	Summer	0.606 (10)	0.656 (4)	0.314
	Fall	0.315 (10)	0.186 (4)	4.34×10^{-2}

Figures



Figure 3-1: Map of Canada showing location of the Experimental Lakes Area in northwestern Ontario.

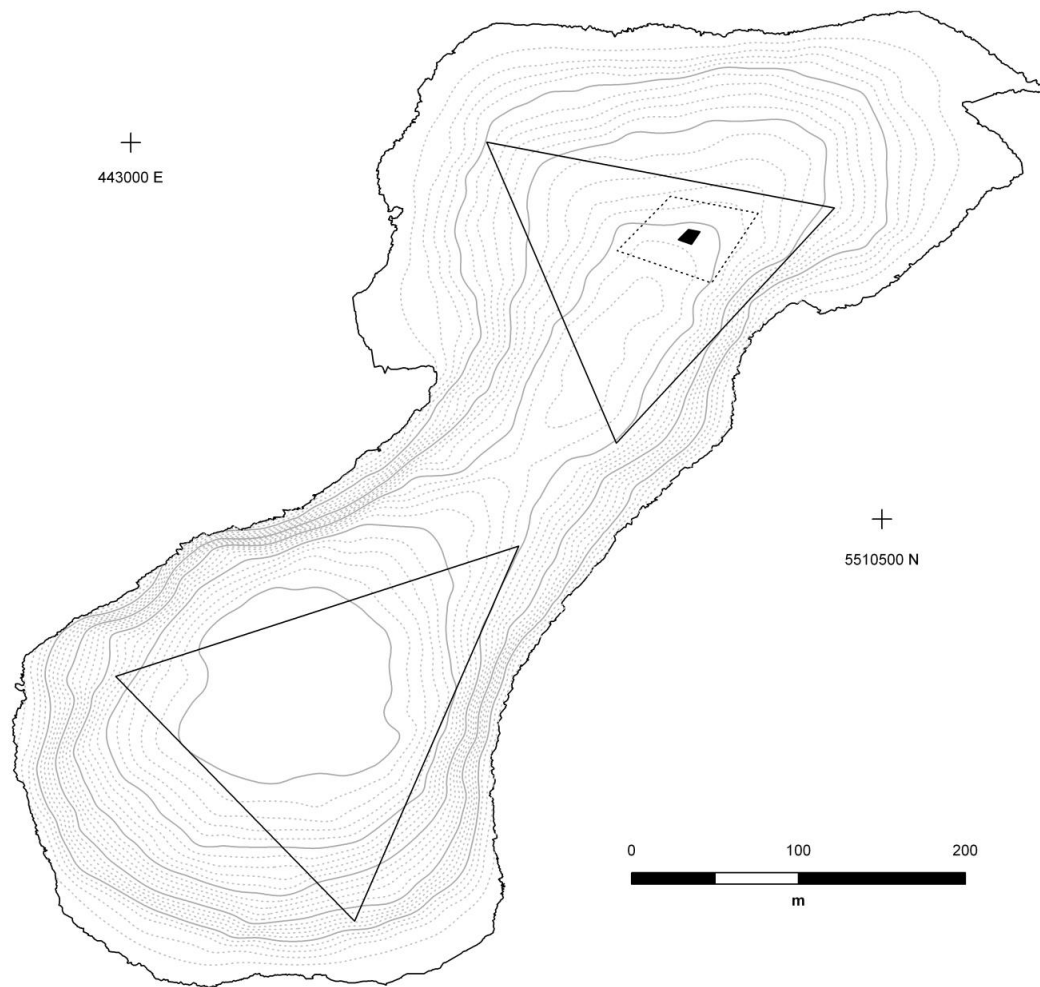


Figure 3-2: Bathymetric map of Lake 375 showing positions of the two VRAP systems (triangles) with individual buoys located at the points of the triangles. Location of cage (filled box) shown in north basin and 25m buffer around the cage (dashed black line). Depth contours are shown in grey (dashed), with 5m intervals shown as solid grey lines. Lake 375 is located in UTM zone 15.

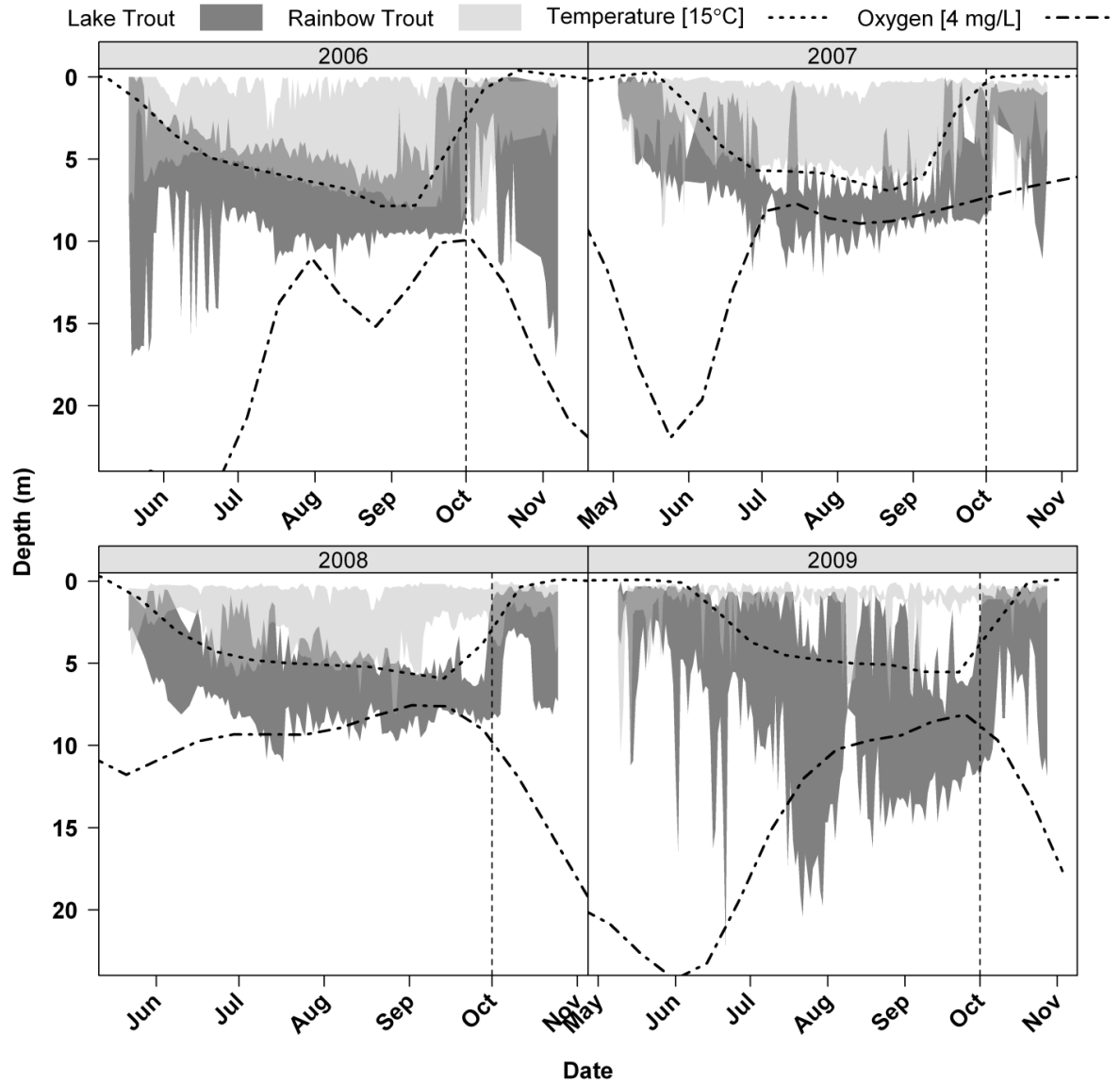


Figure 3-3: Daily occupied vertical habitat for acoustically tagged lake trout and rainbow trout in Lake 375 (shading represents the 2.5th to 97.5th percentiles of all occupied depths). Depths are plotted by calendar date for 2006-2009. The 15°C temperature and 4 mg/L oxygen boundaries are also shown. The vertical black line shows the cut-off for the spring and fall seasons.

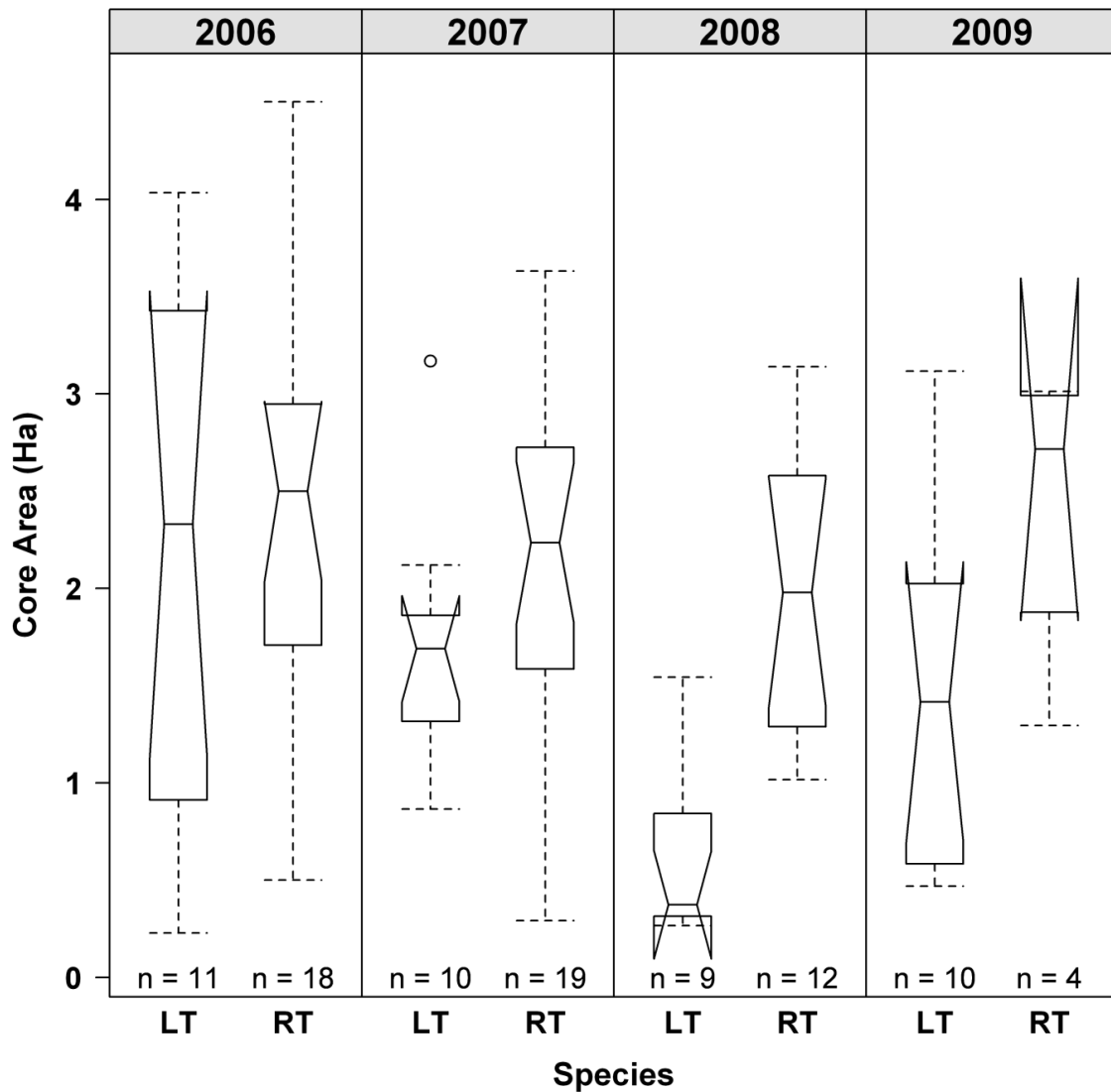


Figure 3-4: Differences in core area sizes between lake trout and rainbow trout among years. The size of the boxes represent the 50% of the observations, the umbrellas show data within 1.5 times the interquartile range and outliers displayed as points. The notches represent the 95% confidence interval of the median.

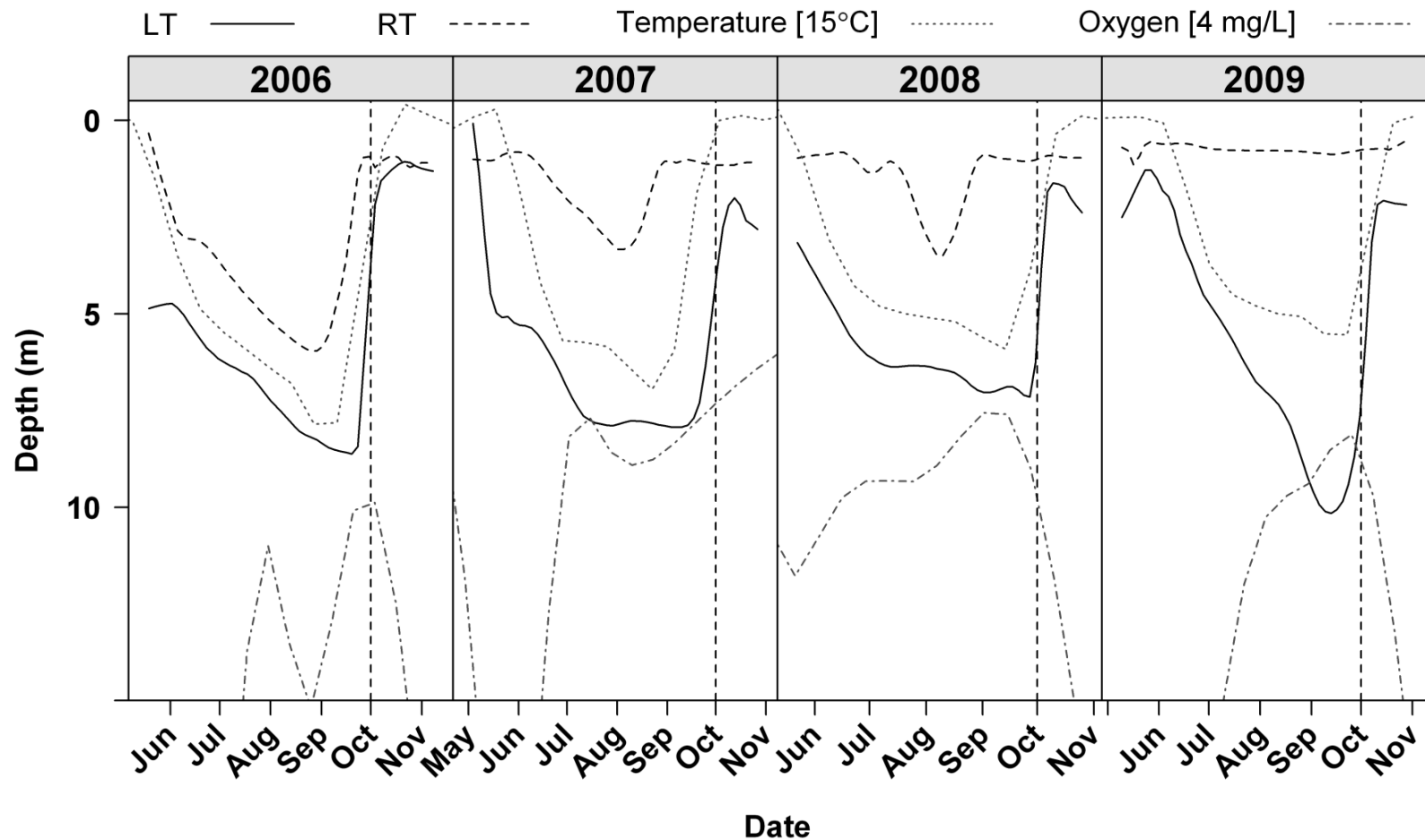


Figure 3-5: Differences in mean depth distribution between species throughout the open water seasons from 2006-2009. The upper temperature (15°C) and lower oxygen (4 mg/L) limitations for lake trout are displayed to represent usable area for lake trout in each year. Lake trout are represented by LT, while rainbow trout are represented by RT in the legend. The vertical black line shows the cut-off for the spring and fall seasons.

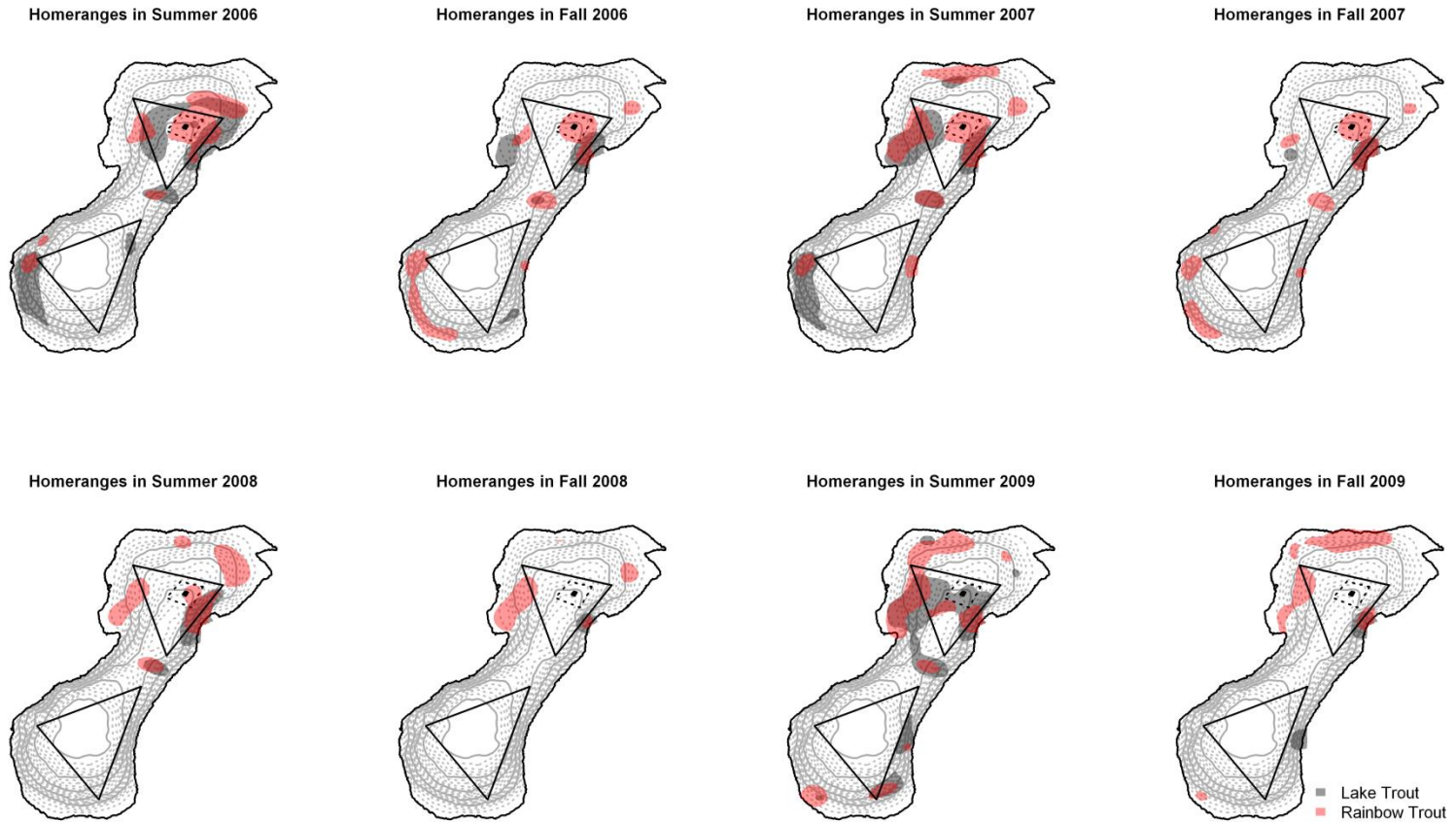


Figure 3-6: Spatial distribution of core areas displayed by each species in Lake 375. Rainbow trout core areas are shown in grey and lake trout core areas are shown in black. The position of the north and south VRAP systems are shown by the triangles, the 25 m buffer around the cage is shown by the dotted line and the cage site is the black square.

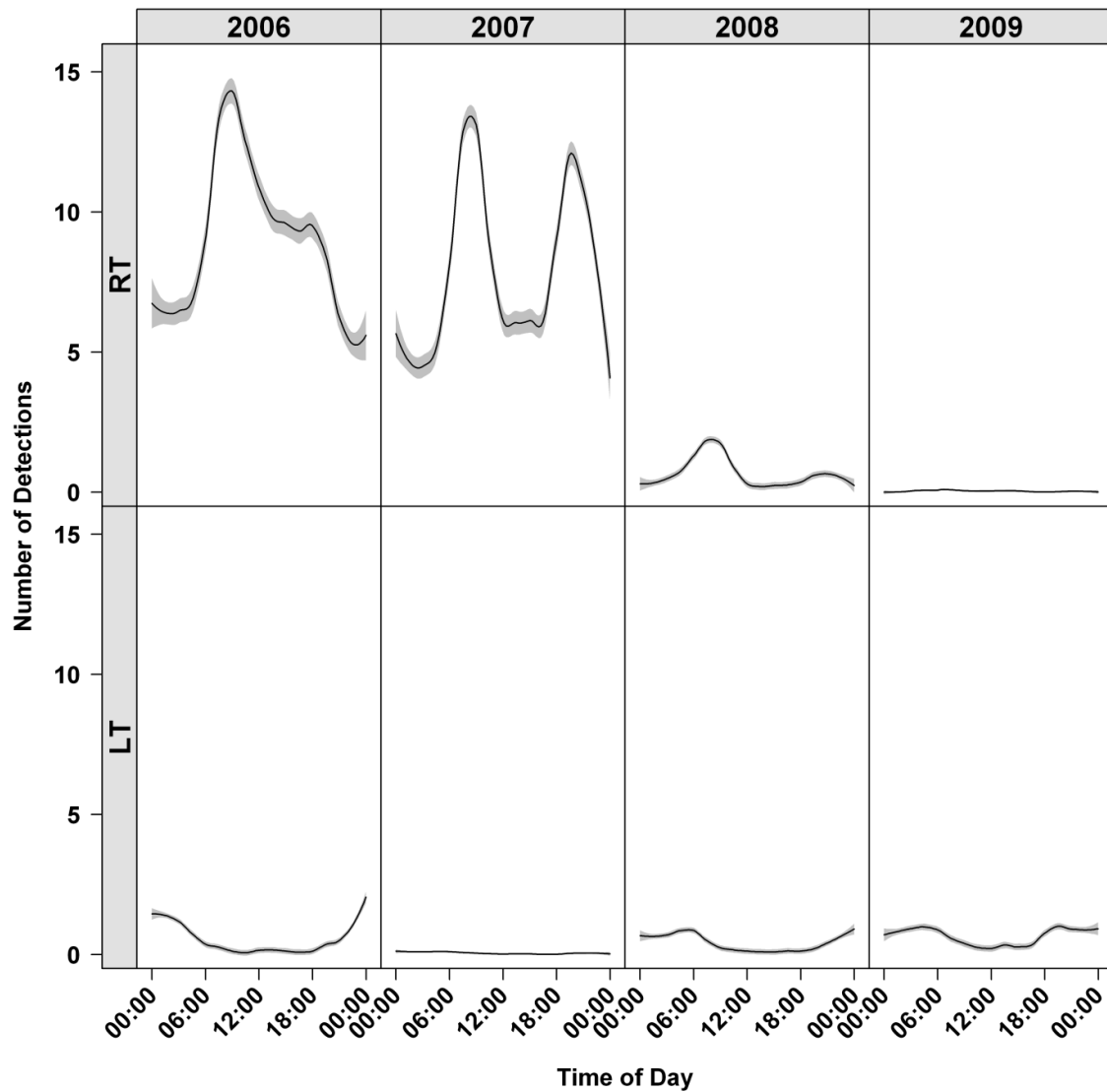


Figure 3-7: Mean number of detections within the 25 m buffer around the cage site over the course of a day from 00:00 to 23:59. Detections were calculated by mean number per minute while the RAPT systems were operational. Grey regions represent the 95% confidence interval around the mean.

Chapter IV: Conclusion

The overall theme of my MSc thesis was the analysis of forager movements and consisted of two primary projects. The first focused on snow crab fishing vessel movements in the Gulf of St. Lawrence by defining their behaviours based on speed distributions using hidden Markov models (HMM) and relating these movements to fishing success, measured by catch rate. The second project dealt with escaped rainbow trout movements in a small glacial relict lake and the relationship of these movements to both the aquaculture operations and native fish habitat during production and post-production. Though the study systems differed, the general underlying ecological concepts about movement applied to both.

In Chapter II, catch rate was modeled by a combination of vessel movement metrics and number of traps set during an individual fishing trip using a generalized linear model (GLM; Nelder and Mead 1972) to develop a model to predict catch using available fisheries data. The purpose of this project was to develop a new estimate of standardized catch which more closely reflected the natural variations displayed by the snow crab population from year to year. Commercial biomass, as estimated from a yearly DFO trawl survey showed that the classical measure of catch-per-unit-effort (CPUE) (kg/trap) did not follow the commercial abundance estimates from the trawl survey thus required a new measure to represent abundance. Combining trip catch records with HMM estimates, provided the framework for variables in a GLM which was used to predict catch based on a typical trip (effort) displayed by the fishermen and produced an estimate for yearly crab abundance that more closely reflected the pattern estimated by the trawl survey than the classical CPUE measure.

My novel application of HMMs to vessel movements in a fixed gear fishery provides distinct advantages in behavioural classification. Previous studies have applied HMMs to a wide variety of systems from free ranging woodland caribou (*Rangifer tarandus*) (Franke et al. 2004) to determining vessel activity in the Queensland trawl fishery (Peel and Good 2011). Unlike the study performed by Peel and Good (2011) which looked at mobile gear, the snow crab fishery uses fixed gear which adds complexity to the interpretation of behaviours due to differences in observed speeds during different fishing activities (relocating and resetting traps). Identifying behaviours from movement pathways has always caused problems for biologists (Turchin 1998), but using a technique such as HMMs can explicitly define behaviours as long as the sampling resolution is adequate. Within the framework of a HMM, in order to identify the hidden states one must choose the appropriate distributions. Since the models are described within a statistical framework it is simple to implement goodness-of-fit tests (AIC or BIC) and model diagnostics to measure the strength of the models (Peel and Good 2011). Another advantage gained by using HMMs is that states can be identified using continuous distributions instead of distinct cutoffs. The ability to analyze and classify behavioural states exhibited by snow crab fishers has long been of interest to fisheries managers, but until now they have been unable to successfully develop a model (E. Wade, personal communication). In this study I was able to identify three distinct behaviours of fishers using vessel monitoring system (VMS) records. The observed vessel speeds when performing distinct behaviours allowed me to use continuous distributions in the HMM to identify each behaviour and how long a vessel remained in

each state during individual trips. Future studies should involve onboard observers to verify the speeds used during fishing trips to their respective behaviour.

Standardized CPUE measures are critical to monitoring population fluctuations of marine fish. Absolute population estimates of fish stocks cannot be quantified because most populations are not directly observable, instead standardized abundance measures are used to monitor and track changes in abundance (Hilborn and Walters 1992). GLMs have developed into one of the most common methods used for standardizing catch and effort data (Maunder and Punt 2004), while Gavaris (1980) seems to be one of the first to use GLMs in this manner. In his early study, only categorical explanatory variables were used to model catch and they were applied to the natural logarithm of CPUE so that catch rate would meet the classical assumptions of generalized linear models.

Catch rates can vary in a fishery from year to year and the efficiency of a fishing fleet is also constantly changing. There are three possible scenarios when using catch rate to estimate abundance, these being hyperstability, hyperdepletion and proportionality (Hilborn and Walters, 1992). The sustainability of a fishery is one of the most important aspects in determining whether it can continue to be profitable over the long term, therefore changes in stock abundance are needed to monitor the population and predict future catches (Stocker and Fournier, 1984). Recently, GLMs have been used to estimate abundance for highly migratory species such as Pacific bigeye tuna (*Thunnus obesus*) (Bigelow et al. 2002), blue marlin (*Makaira nigricans*) (Hinton and Nakano 1996) and yellowfin tuna (*Thunnus albacares*) (Langley et al. 2005). In the past, GLMs have been used in management decisions regarding stock assessments. The GLM input into the annual South African rock lobster (*Palinurus gilchristi*) assessment is the most important

component, which is based on an age-structured production model (Groeneveld 2003). In Chapter II, the variables used in the GLM represented various measures of effort displayed by individual fishermen to quantify the success of the entire fleet in each fishing season. Using median values of effort expressed by fishermen within the fleet, I was able to predict the catch for a single trip in each year that represented the overall abundance. Though the GLM output did not produce an absolute population estimate it did produce an index that represented the total available biomass to fishers. Further development of this model could include variables such as discards and weights of soft-shell and immature snow crab per trap to predict future biomass.

The application of HMMs to vessel movement contributes to the developing fleet dynamics literature. Fleet dynamics can be broadly defined as changes that relate to the fishing capacity of a group of vessels and their fishing activities, which include the intensity of their fishing effort and spatial distribution through time. Two main areas that have dominated the literature are models that focus on individual behaviour and models that explain the behaviour of individuals in groups (reviewed in van Putten et al. 2012). Using expected utility theory, one expects decision makers (fishers) to make a decision that maximizes profit and minimizes costs (van Putten et al. 2012). These decisions typically involve many factors such as distance to fishing site, fuel costs, market prices, risk assessment, competition from other fishers and information exchange.

The snow crab fishery has the advantage of a thorough pre-season survey, which is conducted yearly, usually in the summer or fall prior to the next fishing season. This survey serves two purposes, the first is to regulate the fishery and minimize over-exploitation risk and the second is to provide fishers with information on crab abundance

and location. Finding profitable fishing sites is the utmost concern for fishers, but the importance of the pre-season survey decreases as the season progresses and fishers must employ new tactics to target abundant snow crab patches (Gillis et al. 2006). One of these tactics involves setting more than a single string of traps during a fishing trip to explore new areas to achieve higher catch rates as local prey density declines and it may also possibly reduce competition between fishers, though further work would needed to be done to confirm this.

In the third chapter I have demonstrated new methodology for the spatial correction of acoustically tagged fish using a stationary tag trial data and measures of spatial overlap using the utilization distribution overlap index (UDOI). The methodologies implemented in this project can be further explored in future research. Measuring two dimensional habitat overlap using the UDOI proved easy to apply to this ecological dataset and it would be interesting to see how it performs in other aquatic studies. The application of simulating a uniform distribution of space use for the cage site should be further explored and applied to future aquaculture studies, as this method provides a comparison of habitat overlap between an individual and its space use around an inanimate object of interest to researchers. As a whole, this project has contributed to aquaculture research and the fate of escapees as time in the wild increases.

The biological implications of large scale escapes usually receive the most interest, but these escape events also have economic consequences as well. Farm operators can sustain significant financial losses in the result of large scale escapes and unless the cause of the escape was negligence, other factors are usually to blame (storms, sabotage, etc.). Recapture efforts should focus on important questions such as how long

do escaped fish remain at the cage site and when are they most likely to be located there. I found that rainbow trout only remained near the aquaculture cage when the operation was active, and chiefly at feeding times. My findings suggest that recapture efforts should begin immediately after an escape event and should be focused during feeding times to increase the likelihood of success. If recapture efforts are delayed for some reason and rainbow trout disperse from the cage site, the chances for successful recapture efforts diminish rapidly because of the uncertainty of where efforts should be concentrated. A confounding factor may be the size of the study system, with a relatively small lake used, the escaped fish could only disperse less than 1 km from the cage site. This element removes the dispersal element during cage production, but it still produces evidence for cage attraction.

Both of my studies are centered in the theories of foraging ecology. Typically, the success of an individual is judged by its breeding success, though in order to breed, animals must consume resources from the environment (foraging ecology or predator prey interactions) (Morris 2003). A similar definition can be used for fishers, but their success comes from the size of their catch or their profitability throughout a season. The more foraging success an individual achieves over their lifetime, we would expect a greater advantage over its competitors. For fish, this typically means greater breeding potential, speed or fitness, while for fishers it could mean equipment upgrades to increase their advantage over other fishers or increased catch rates. Unfortunately, food patches are a density dependent entity, with patches located independent of each other which causes predators to actively search for abundant patches and compete for resources. Predators encounter food within these patches, but must travel between patches to exploit

their resources. As soon as a predator encounters a patch and begins foraging, the prey density decreases, as does the predator's foraging efficiency as time increases (Charnov 1976). Foraging behaviour is not a random activity in this study as results obtained in Chapter III show that rainbow trout attraction to the cage site shows that even organisms with less developed cognitive abilities can also alter their behaviour to maximize foraging efficiency. The patterns in trout distributions associated with the increased food availability at the cage site suggest that different species do not use the same resource patch and therefore probably target different prey items.

This thesis has produced novel methodology for application of ecological foraging theory in fisheries and aquaculture. I have shown that using fishers behaviours combined with traditional measures of effort produces an index of abundance that more closely reflects exploitable biomass in the snow crab fishery. This first study can be further developed to be included in methods of stock assessment in other fisheries where obtaining accurate estimates are difficult or impossible to implement quotas and guidelines to ensure sustainable fisheries. The increasing availability of VMS data create a high potential for this methodology to be further used to increase our understanding of fleet and stock dynamics. In the second project I was able to quantify overlap indices of escaped rainbow trout to an aquaculture cage and other fish using acoustic telemetry. This project showed the significance of the presence of the cage as an area of interest to escapees while food was available and then how rainbow trout did not use the cage site when waste feed was not available. My work clearly demonstrates the potential of the interdisciplinary application of general ecological principles to specific problems in fisheries and aquaculture.

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Appendix I

Distance Calculation

In order to calculate the turning angles and distances between successive locations I had to compute the bearing of each step. The bearings were calculated using the following formulas described by Bullock (2007), two quantities, S and C must first be calculated using the following equations:

$$(1) \quad S = \cos\varphi_B \sin\Delta L$$

$$(2) \quad C = \cos\varphi_A \sin\varphi_B - \sin\varphi_A \cos\varphi_B \cos\Delta L$$

where φ denotes latitude and ΔL denotes differences in longitudes. Point A will have latitude φ_A and longitude L_A , and point B will have latitude φ_B and longitude L_B . The bearing β of B from A is calculated from the following equation:

$$(3) \quad \beta = \text{atan2}(S, C)$$

The distances were calculated using the haversine. The basis for choosing this method is because of its ability to accurately estimate distance even when two points are in very close proximity to one another. The haversine is able to accurately estimate distances because the algorithm avoids the inverse cosine function (Kotwicki *et al.*, 2011). As described by Sinnot (1984), the haversine can be calculated as follows:

$$(4) \quad hav\alpha = \sin^2(\alpha/2)$$

The distance between two points can be found using the following formulas as described by Sinnot (1984) and Bullock (2007):

$$(5) \quad hav\theta = hav\Delta\phi + \cos\phi_A \cos\phi_B hav\Delta L$$

$$(6) \quad \theta = 2\sin^{-1}(\sqrt{hav})$$

$$(7) \quad D = R\theta$$

where $\Delta\phi$ is the difference in latitudes, θ is the angular distance in radians, $hav\theta$ is the square of half the chord length between the points and R is the radius of the earth. R is taken to be equal to 6371.00 km as published by Haynes (2011).

Modifications to the msm Library

The msm package was already able to fit normal and Weibull distributions, but not t distributions. The package maintainer provided the source code for the msm package and we were able to add a t distribution into the msm function. The degrees of freedom within the t distributions were kept fixed during analysis to prevent the distribution from wavering.

Maximum Likelihood Estimation and Model Comparison

The method of maximum likelihood used for model optimization is described by Nelder and Mead (1965). This is the default method used in the *msm* package. Model comparison was done by using Akaike's information criterion (AIC) and Bayesian information criterion (BIC). The AIC method is originally described by Akaike (1973) and measures the quality of fit of a model by applying criteria from information theory. AIC is computed as:

$$(8) \quad AIC = (-2) \text{ maximum log likelihood} + 2p$$

where p is the number of parameters in the model. This equation accounts for the increase in likelihood expected with increases in the number of parameters regardless of the true accuracy of the model. BIC is calculated in a similar way to AIC, but it also adds a penalty for sample size (n). BIC is computed as:

$$(9) \quad BIC = (-2) \text{ maximum log likelihood} + p * \ln(n)$$

When comparing models, the model that minimizes the value of AIC or BIC is chosen as superior to the other models being tested (Ward 2008). A model was said to converge when the optimization reached a global maximum rather than a local maximum over the likelihood surface (Jackson 2011). The AIC and BIC values were compared between models that converged to an optimal solution to select the best model for further analysis.

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Appendix II – Spatial Correction using Kriging

Positioning Error and Correction

In order to test the accuracy and precision of the RAPT system, stationary tag trials were performed in the fall of 2005. In total there were 17 different test locations using 3 different tags (Figure II-1). One location between the two RAPT systems suffered from an echo effect that caused positions from this station to be very erratic with sequential positions located across the entire lake and was dropped from further analysis. To predict the spatial error of the stationary tag trials the easting and northing error were calculated at each station and a geostatistical technique called Kriging was used (Journel and Huijbregts 1978). This technique incorporates spatial autocorrelation modeled from the tag trials through a variogram (Figure II-2a and II-2c). A Gaussian theoretical variogram was used to represent both the northing and easting errors, as they provided the best relocations in relation to the location of the stationary tags. Easting and northing errors were interpolated from a $10\text{ m} \times 10\text{ m}$ grid of estimates calculated from the Kriging model (Figure II-2b and II-2d).

Spatial Correction

Although the RAPT system was able to detect the stationary tags at all locations, the systems' accuracy was low. Fortunately, the precision of the system was fairly high, allowing the use of kriging to correct the spatial locations of the stationary tags. In the north and south basins of Lake 375, many of the points were 'pulled' in towards the centre of their respective triads, but in some cases the RAPT system 'pushed' points outwards and the resulting positions would have been located on land. Many of the

stationary tag locations were located near shore where some of the most biologically important behaviours (e.g. spawning, feeding on minnows) occur. The interpolated values for the tag trials (Figure II-1) show that kriging effectively corrected the RAPT positions at all remaining stations. The northing error estimated from the stationary tag trials ranged from -9.8 – 171.1 m (where negative values represent positioning points south of their actual position and positive values north of their actual position) and the easting errors ranged from -60.6 – 61.7 m (where negative values represent positioning points west of their actual position and positive values east of their actual position). The absolute error range of the stationary tag trials ranged from 2.64 – 170.3 m.

Uncorrected positions of acoustically tagged fish recorded in Lake 375 over the four years of study are shown in figure II-3a. There are two problem areas in Lake 375, the first is located at the north end of the lake and the second is located on the west side of the lake in the south basin. In these areas, the RAPT system consistently positioned fish outside of the lake, causing problems for interpreting biologically relevant behaviour. Including these positions in further analysis could bias results by inaccurately representing fish core area size. Removing them could also remove records of important behaviours. Using information developed from the stationary tag trials, a correction was applied to the fish positions in order to relocate detections to their assumed positions. The Kriged fish positions shown in Figure II-3b display much more affinity to the depth contours of the lake. I examined the validity of calculated positions according to 2 criteria; (1) whether a fish was above or below the sediment at its spatial coordinates and (2) whether the fish was positioned within the lake. Before the correction was applied, there were 40,073 (14.53%) positions below the sediment at their calculated position and

29,386 (10.65%) positions outside of the lake shoreline. Post-correction these values both decreased, with 30,404 (11.03%) positions below the sediment and 6,510 (2.36%) outside the shoreline. These remaining points outside of the shoreline were removed from further analysis, resulting in 269,261 locations for further analysis.

Literature Cited

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Figures

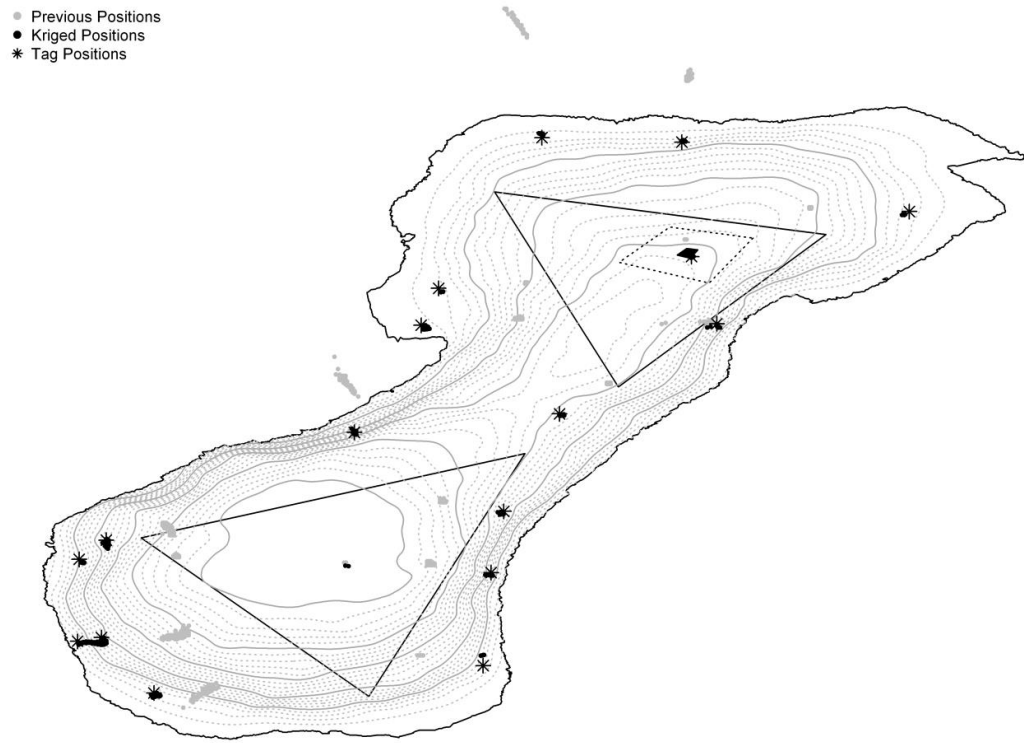


Figure II-1: Map of Lake 375 showing stationary tag trial positions, pre-processing positions and post-processing positions.

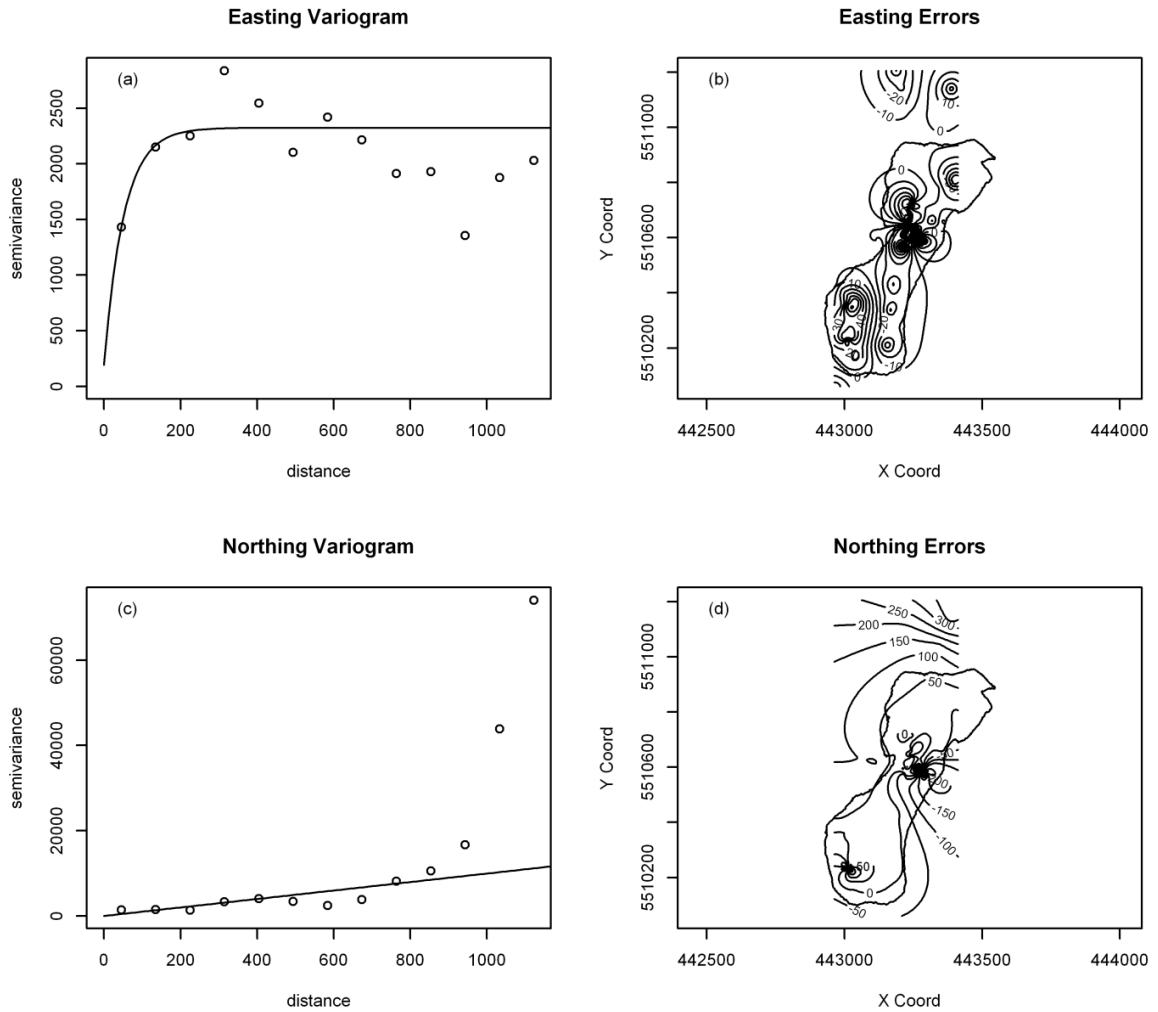


Figure II-2: Empirical variograms used to describe the error structure in Lake 375. The easting variogram is shown in II-2a and the northing variogram in II-2c. The error estimates of the easting (II-2b) and northing (II-2d) error estimates from the stationary tag trials.

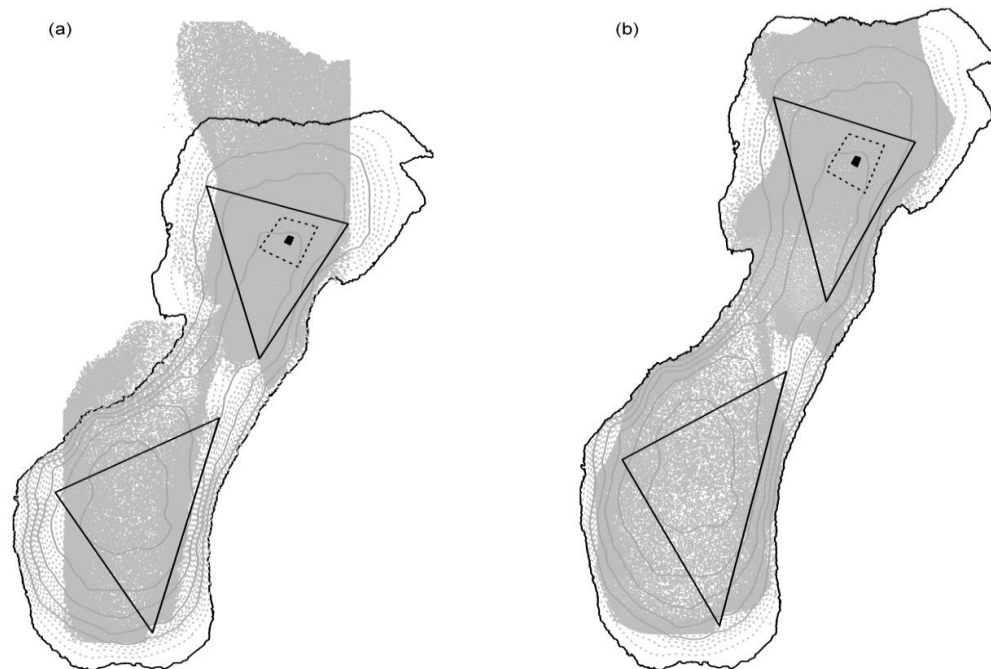


Figure II-3: Positions of fish by the RAPT system in Lake 375. Fish positions in Lake 375 before kriging was applied (II-3a) and post correction positions (II-3b). Location of cage (filled box) shown in north basin and 25m buffer around the cage (dashed black line). Depth contours are shown in grey (dashed), with 5m intervals shown as solid grey lines. Fish positions are represented by grey points.