Determining the Habitat Occupancy of Young of Year Arctic Grayling (*Thymallus arcticus*) in Sub-Arctic tundra Streams While Accounting for Imperfect Detection

by

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Author's Declaration

Abstract

I developed multi-state, multi season occupancy models to determine how a number of interacting ecological variables influence the occurrence of young-of-year (YOY) Arctic Grayling (*Thymallus arcticus*) in nine streams on the sub-Arctic tundra. The model was developed and parameterized such that three different ‘states’ of occupancy were investigated (i.e., not occupied, somewhat occupied, and highly occupied), and temporal replication allowed me to account for uncertainty associated with imperfect detection; a common limitation of quantitative species-habitat-use studies. Depth and velocity decreased the probability of occupancy, and the effects were similar to previous Barrenland research. Stream Slope, Overhanging Cover, and Distance to Overwintering Habitat played a major role in explaining YOY Arctic Grayling habitat occupancy; while habitat complexity also was an important determinant. Electrofishing was more efficient at detecting YOY Arctic Grayling in somewhat occupied stream segments, while survey method is unimportant for detecting YOY in highly occupied stream segments. Also, detection efficiency varied between model seasons, and decreased with depth. By accounting for imperfect detection, my research improves the accuracy of occupancy estimates, and enhances our understanding of the habitat requirements of YOY Arctic Grayling in lake outlet streams of the sub-Arctic tundra. This should provide researchers and managers with a greater understanding of the habitats that YOY Arctic Grayling use, and enable researchers, resource managers, and regulators to track shifts in habitat use by YOY Arctic Grayling as climate change and growing industrial presence continue to shape the Canadian North.

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List of Abbreviations and Symbols

YOY	Young of Year Arctic Grayling
DOC	Dissolved Organic Carbon
S	Seasonal parameterization for occupancy estimates
Slope	Stream Segment Slope: Drop in elevation per meter of horizontal distance
D2OW	Distance to overwintering habitat: measured run-of-river distance to the nearest lake suitable for overwintering
GOHV	Good overhanging vegetation: Binary covariate representing >50% stream cover provided by overhanging riparian vegetation
H'/5	Habitat complexity: Shannon-Weiner diversity index used to compare habitat type within each stream segment (i.e., run, riffle, pool, cascade, and shallow water pond)
D	Mean segment depth: measured along thalweg at four equi-distant points within each stream segment
D_1	Mean segment depth in the first model-season
$D_{1,2,3,4}$	Season-specific mean segment depth
DSQ	Mean segment depth squared
V	Mean segment velocity: measured along thalweg at four equi-distant points within each stream segment
$V_{1,}$	Mean segment velocity in the first model-season
$V_{1,2,3,4}$	Season-specific mean segment velocity
VSQ	Mean segment velocity squared
CoeffV	Flow heterogeneity: coefficient of variation of velocity within each stream segment
Q	Stream-level discharge
$Q_{1,2,3,4}$	Season-specific discharge
Repeat	Repeat survey bias: covariate to test if the occupancy state of the first survey influenced the occupancy state of subsequent surveys
Method	Survey Method: covariate to test the relative detection efficiency between electrofishing+visual and visual-only methods
AIC	Aikake Information Criterion
AICc	Aikake Information Criterion with correction for small sample size
ΔAICc	Difference in AIC scores between the a particular model and the top ranked model

w_i	Akaike weight
QAICc	Quasi-likelihood estimation parameter with correction for small sample size
$\hat{C}$	Variance inflation factor
X^2	Chi-square statistic
CPUE	Catch per unit effort: expressed as number of fish detected per 300 seconds of survey effort
$\varphi^{[1]}$	Probability a stream segment is somewhat occupied
$\varphi^{[2]}$	Probability a stream segment is highly occupied
ψ	Probability a stream segment is occupied ($\psi = \varphi^{[1]} + \varphi^{[2]}$)
R	Probability a stream segment is in the high occupancy state, given that the segment is occupied ($R = \varphi^{[2]}/\psi$).
δ	State-uncertainty estimate: probability of correctly classifying a highly occupied segment, given that the segment is occupied
p1	Probability of detecting a single fish when the segment is somewhat occupied
p2	Probability of detecting a single fish when the segment is highly occupied

“*There’s love in this world for everyone,*

Every rascal and son of a gun.”

- Michael Marra

Chapter 1: General Introduction

ARCTIC GRAYLING BIOLOGY

Distribution and Basic Ecology

Arctic Grayling are a stenothermic, iteroparous, cold-water salmonid species that is valued by both Aboriginal and sport fishers (Tack 1974; Berkes 1990; Renner & Huntington 2014). Like many salmonids, Arctic Grayling require many habitats to complete their life history (Schlosser 1991; Roussel & Bardonnet 1997). In North America, Arctic Grayling occupy lakes, streams, and rivers in all three northern territories (mainland) and in Alaska, and in northern drainages in the four provinces moving west from Manitoba (Sawatzky *et al.* 2007; Stewart *et al.* 2007). This vast geographic range varies greatly in geomorphology and ecological/seasonal processes. To find suitable habitat, Arctic Grayling demonstrate a correspondingly plastic life history (Fausch *et al.* 2002); some populations employ a resident (lacustrine) life history whereas others are migratory (fluvial or adfluvial) (Tack 1980; Kaya 1991; Nykänen *et al.* 2004b).

Despite plasticity in life history, Arctic Grayling, are sensitive to habitat disturbance and exploitation (Buhl & Hamilton 1991). Historically, Arctic Grayling occupied watersheds as far south as Michigan and the Upper Missouri basin of Montana and Idaho (Northcote 1995). Arctic Grayling in Michigan were not able to persist in the face of heavy development and angling pressure, and were extirpated from the area during the 1930s (Hubbs & Lagler 1958). An isolated population still exists in the Upper Missouri Basin of Montana and Idaho, and is maintained as a catch and release sport fishery (Lohr *et al.* 1996; Lamothe & Magee 2004).

It is believed that Arctic Grayling first colonized North America during the mid to late Pliocene (3-5 Million years ago), via the Bering Land-bridge. This was followed by several other colonization events throughout the Pleistocene (Stamford & Taylor 2004). The greatest diversity of the genus *Thymallus* occurs in Eurasia, the suspected origin of the genus (Scott & Crossman 1973), but Arctic Grayling are the only species within the genus that occurs in North America (Armstrong 1986;

Ahrenstorff *et al.* 2012). There are two known populations of Arctic Grayling in Asia; one in the Lake Bakail area of sourthern Siberia, and the other in the Amur basin of east Asia (Knizhin *et al.* 2008). Whether or not the Asian populations represent the source population for lineages in North America, or represent a biological artifact from potential "back migrations" is uncertain (Stamford & Taylor 2004; Weiss *et al.* 2006).

Life History

Arctic Grayling are easily distinguished from other salmonid species by their sail-like dorsal fin, their silver and mauve body colouration, and a striking array of iridescent colours displayed on their fin rays (Warner 1955). The intensity of the body colouration and the overall size of the dorsal fin signal social dominance and play a key role in mating success for male Arctic Grayling (Bishop 1971; Beauchamp 1990). Arctic Grayling are smaller than other salmonids, with an average weight and length of 400 grams and 350 mm, respectively (Craig & Poulin 1975).

Depending on the length of the open water season, Arctic Grayling reach sexual maturity between 3-6 years of age, and their lifespan varies from 10-20 years (Tripp & McCart 1974; DeCicco & Brown 2006). After reaching maturity, Arctic Grayling employ an iteroparous reproductive strategy and undergo a spawning migration every spring for the duration of their life (Tack 1980). In tundra streams, where dramatic climactic events can sometimes decimate entire year classes, an iteroparous reproductive strategy likely confers a fitness advantage (Armstrong 1986); Arctic Grayling spread out their egg production over many years, thereby dampening the effect of environmental stochasticity on productivity, and enabling individual fish to build up energy stores to survive the winter months(Buzby & Deegan 2004).

Arctic Grayling require spawning habitat that is vastly different from the habitat where they feed and overwinter. When possible, they select shallow, fast-flowing stream reaches where temperatures rise quickly in spring; this allows increased rates of metabolism and egg development (Craig & Poulin 1975; Luecke & MacKinnon 2008). Because eggs are extremely vulnerable to dislodgement by high flow or flash flood events, passing through the 8 to 29 day incubation period as fast as possible greatly enhances chance of survival (Deegan *et al.* 1999). Spawning and incubation occurs mainly over coarse sand, and un-embedded pea-sized gravel (Warner 1955; Tack 1973). Once hatched, alevins spend 3-4 days within the substrate while absorbing the yolk sack. They then emerge as fry and seek shallow, calm water (Deegan *et al.* 2005). Later, young-of-the-year (YOY) Arctic Grayling move into areas with stronger flow to exploit greater drift feeding opportunities (Jones & Tonn 2004b).

For optimal growth and energy storage rates YOY require stream rearing habitat with complex stream morphology and ample invertebrate drift feed with velocities below 0.8m/s, and temperatures between 12-16ºC. YOY Arctic Grayling that have accumulated energy stores in the form of triglycerides are more likely to survive the extended sub-Arctic winters (Driedger *et al.* 2011; Heim *et al.* 2014). Once feeding, spawning, or overwintering habitats are established, Arctic Grayling show strong inter-annual site-fidelity for the rest of their life history (Buzby & Deegan 2000). However, how the site-fidelity behaviour of Arctic Grayling respond in watersheds with significant shifts in habitat suitability has not been clearly established.

Arctic Grayling are opportunistic generalist feeders, feeding on a variety of benthic and pelagic invertebrates, terrestrial invertebrates, forage fish, and small mammals (Rawson 1950; Bishop 1967; De Bruyn & McCart 1974). Ontogenetic shifts in Arctic Grayling diet, linked to changes in gape size, require rearing habitat to support a large diversity of prey types (Haugen & Rygg 1996). After yolk sac reabsorption, the initial diet of Arctic Grayling mainly consists of zooplankton (Schmidt & O'Brien 1982). Three to five days later, YOY begin selectively feeding on chironomid and simuliid larvae, and appear to avoid feeding on the far more abundant microcrustacea (Jones et al. 2003). This selective feeding behaviour aligns with the optimal foraging theory that predicts predators will focus on prey with higher energy gains rather than what is most available (Werner *et al.* 1983). Larger prey species, such as Acrididae and Coleoptera become an important energy source as Arctic Grayling mature (Jones *et al.* 2003a).

Timing of Migrations

Because overwintering, spawning, and rearing habitats are not typically available in the same stream or lake, Arctic Grayling commonly adopt fluvivial or adfluvial behaviour to meet their life history requirements (West *et al.* 1992; Buzby & Deegan 2000). The migratory circuit for Arctic Grayling typically involves annual movements between overwintering, spawning, and feeding habitats (Armstrong 1986; West *et al.* 1992). However, the timing and extent of these movements depend on seasonal ice dynamics and the proximity of suitable habitat for each life history event (Tack 1980). Results from previous research indicate that northern populations of Arctic Grayling begin spawning migrations as soon as water begins to flow in spring, and that spawning typically occurs between mid-May and mid-June in relatively fast-flowing tributary, lake inlet, or lake outlet streams (Warner 1955; Bishop 1971; Beauchamp 1990). Migration timing is dependent on stream temperature, day length, and net stream discharge, with behavioural thermoregulation and rheotaxis being the main contributors for the initiation of spawning migrations (Kaya 1989; Northcote 1995).

Most mature Arctic Grayling appear to return to lakes or larger rivers soon after spawning (Jessop & Lilley 1975; Northcote 1995), but there is anecdotal evidence of late stream residency by adults in Barrenland systems (Buzby & Deegan 2000; personal observations). If Arctic Grayling can find ample food and cover in their overwintering habitat, it may be more beneficial to individual fitness to migrate back to overwintering habitat relatively early and face the increased predation risks in deeper waters versus the stranding risks of remaining in shallow streams (De Beers Canada 2010d). This is particularly true in Barrenland streams as discharges decrease quickly after freshet, which effectively decreases the functional connectivity of stream habitat (Baki *et al.* 2012). Researchers believe that Arctic Grayling are able to assess when stream characteristics become unfavourable (e.g., forage availability, temperature, and flow) and emigrate from these regions to return to overwintering lakes (Hughes 2000). Thus, if habitat suitability remains favorable, it is not unreasonable to assume that Arctic Grayling would use streams opportunistically, with an added advantage that streams can provide temporary refuge from large fish predators.

As predation risks to YOY Arctic Grayling are greater than their mature counterparts, the YOY exploit the relative refuge of their natal streams for the length of the open-water season (Buzby & Deegan 2000). In autumn, declining discharge further reduces surface water connectivity in these shallow rearing streams and frazil ice begins to develop; eventually the streams freeze to the bottom (Brown *et al.* 2011; Heim *et al.* 2015). To avoid stranding and/or ice-related mortality, YOY Arctic Grayling migrate to lakes, deep pools, or groundwater-fed streams and rivers to overwinter (Armstrong 1986; Deegan *et al.* 1999; Huusko *et al.* 2007; Heim *et al.* 2014).

BARRENLAND POPULATIONS OF ARCTIC GRAYLING

Life History

To understand the life cycle of Barrenland populations of Arctic Grayling, one must first understand the geomorphology and ecological process that influence the fish's ability to complete their life cycle. With mean annual precipitation between 265 and 290 mm, the Barrenlands are a "wet desert". While continuous permafrost holds the water table close to the land surface, arid conditions promote a rapid drop in stream water levels after spring freshet, rendering many Barrenland streams ephemeral by the end of the summer (Woo & Mielko 2007). This, along with rapid ice formation in streams and shallow lakes in fall, forces Arctic Grayling to take on a fluvial-adfluvial migratory life history (Huusko *et al.* 2007) in the chain lake systems that are common to the northern Barrenlands (Stewart *et al.* 2007).

As described above, Barrenland populations of Arctic Grayling spawn and feed in streams that experience rapid shifts in discharge. As such, they are at a relatively high risk of stranding (Woo & Mielko 2007). Finding suitable overwintering habitat presents another challenge; Barrenland Arctic Grayling must select a lake that is deep enough to sustain under-ice water with enough dissolved oxygen throughout the winter (West *et al.* 1992). Ice thickness in the Barrenlands extends to 2.5 meters, freezing many lakes and streams to the bottom. Suitable overwintering habitat is thus scarce and sporadic (Cott *et al.* 2008). The availability of overwintering habitat, and the distance and functional connectivity between suitable overwintering and spawning habitats, likely have a profound effect on the fitness, productivity, and distribution of Barrenland populations of Arctic Grayling (Nykänen *et al.* 2004b; Lesack & Marsh 2010; Baki *et al.* 2012).

Barrenland streams are well suited to YOY Arctic Grayling development, as they warm to between 12-16ºC within two weeks after freshet (Jones *et al.* 2003b; De Beers Canada 2010b). However, the precipitation-associated spikes in stream velocity in Barrenland streams may cause dislodgment of YOY and increase mortality rates (Deegan *et al.* 1999). Sustained rain or thaw events often result in flash flooding (Marsh *et al.* 2008), and YOY Arctic Grayling that are not strong enough to hold their stream position may be swept downstream to unsuitable habitat where they are exposed to predators (Deegan *et al.* 1999). In some years, flash flood events in bog-type systems have caused complete year class failures in Arctic Grayling (Tack 1973).

Timing and extent of migrations

Each year, Arctic Grayling move between three major habitat types: spawning sites, feeding sites, and overwintering habitat. However, the timing and extent of migratory life history of Arctic Grayling is influenced by regional geomorphology, ecological processes, and habitat heterogeneity (Northcote 1995). In mountain stream systems, Arctic Grayling often migrate over 100 km upstream each May to reach suitable spawning habitat (West *et al.* 1992). However, as many Barrenland streams are poorly sorted and thus have high habitat heterogeneity, it is possible that Arctic Grayling in the Barrenland region do not have to travel as far to find suitable spawning habitat (Jones *et al.* 2003b). The complexity, intermittency, and variable water temperatures in Barrenland streams likely restrict the timing and extent of Arctic Grayling movement patterns and habitat use, but these relationships have not been studied extensively (Jones & Tonn 2004b).

The movement patterns of European Grayling (*Thymallus thymallus*) are also influenced by regional differences in the ecological composition of watersheds (Parkinson *et al.* 1999; Nykänen *et al.* 2004a; Bass *et al.* 2014). Fluvial European Grayling in Finland have been observed to migrate up to 37 km to find suitable spawning and summer feeding habitat, but the majority of migrations remain between

0 and 15 km (Zakharchenko 1973; Nykänen *et al.* 2004a). Lacustrine or fluvial-adfluvial European Grayling adults in the sub-Arctic lakes of Norway use spawning and feeding sites only briefly in the spring (Bass *et al.* 2014). Adults return to overwintering lakes for the rest of the open-water period because the stream systems are too shallow; seasonal drops in flow limit the profitability of stream habitat (Bass *et al.* 2014). Similar factors (i.e., water depth, discharge) may influence the distribution and habitat use of adfluvial Arctic Grayling in the Kennady Lake area.

Water depths, velocities, and stream substrates occupied during summer feeding by adult Grayling is also similar between European Grayling in stream systems in northern Europe, and North American Arctic Grayling populations (i.e., >0.4 m/s, 0.8-1.2 m, and primarily boulder substrate, respectively; Mallet *et al.* 2000; Nykänen *et al.* 2001). Mature European Grayling tend to show strong site fidelity to summer feeding positions, with seasonal home ranges less than 75 m, even when changes due to flow or temperature influence the profitability of this habitat (Nykänen *et al.* 2001; Nykänen *et al.* 2004b). Interestingly, in streams where water depths are within the European Grayling's preferred summer range (0.8 to 1.2m; Nykänen *et al.* 2004b), the fish tend not to associate with overhead cover when avian predators are abundant. Instead they rely upon schooling, depth as cover, and fleeing to nearby lakes to evade predators. Other salmonids tend to rely heavily on cover to prevent avian-predation (Fraser & Huntingford 1986). While there may be some transferability of findings on European Grayling to North American Arctic Grayling, there is still a need for further characterize movement patterns and habitat use in the Canadian Arctic. Furthermore, the majority of studies on European Grayling have focused on montane and boreal stream reaches close to human populations. Thus, there remains a great deal of uncertainty as to how Arctic Grayling use habitat features on the Barrenland tundra.

There is limited information on Arctic Grayling migration patterns in the Barrenlands. Qualitative analysis of three tagged Arctic Grayling adults in the Kennady Lake watershed in 2005 revealed that all three Grayling moved from the outlet (spawning) stream back to overwintering habitat shortly after spawning (i.e., mid- to late-June; De Beers Canada 2010e). During the remainder of the open-water season, these fish moved between various basins of a large Barrenland lake. In another study of adult Arctic Grayling, tagged individuals in tundra streams in the Northwest Territories moved through a fish pass in a constructed choke-pool fish, but would not use gabion-style stepped pool-weir passes (Cahill *et al.* 2015). Results from studies on YOY indicate that these fish are first detected in Barrenland streams ~3 weeks after eggs are deposited, which usually occurs between mid- to late-June (Stewart *et al.* 2007). YOY tend to occupy shallow, slow-flowing stream habitats in early summer and faster, deeper midstream habitats in later summer (De Bruyn & McCart 1974; Lee 1985; Jones & Tonn 2004b). Migrations to winter lake habitats occur between mid-August and mid-September, and are undertaken to avoid mortality resulting from rapid ice formation and decreasing stream discharge (Armstrong 1986; Huusko *et al.* 2007; Heim *et al.* 2015)

IMPETUS FOR STUDY

The main impetus for this study is to improve understanding of YOY Arctic Grayling life history in sub-Arctic Barrenland watersheds. My research is driven by two imperatives: the mitigation of industrial impacts, and a contribution to the scientific knowledge base. Results from my M.Sc. thesis will contribute to the development of a statistically robust baseline dataset that can be used in future years to determine how habitat use by YOY Arctic Grayling changes in response to changes in habitat suitability. This will allow industrial managers and government regulators to construct adaptive management and monitoring plans as the north begins to open up to resource extraction and development. We still know very little about the habitat-use patterns of YOY Arctic Grayling.

Because the literature on this subject is so sparse, it is difficult to make substantiated claims on the effects of regional differences in stream morphology, overwintering habitat availability, flow dynamics and overhanging cover on the distribution and occupancy of YOY Arctic Grayling. To my knowledge, only one prior study has attempted to characterize the habitat-use patterns of YOY Arctic Grayling in the sub-Arctic tundra system (Jones & Tonn 2004b). Jones and Tonn (2004b) characterized resource use in two streams, one artificial and one natural, limiting the applicability of the study's findings. I had the opportunity to fill in knowledge gaps by studying YOY Arctic Grayling habitat use across a greater spatial range. This allowed me to explore habitat covariates that may not have been available in the previous study (e.g., distance to overwintering habitat, stream slope, and overhanging riparian cover).

To maximize the inferential power of this study, I used a habitat occupancy modeling approach (MacKenzie *et al.* 2003), and expanded the spatial scale from two streams to nine without compromising the resolution of quantifiable habitat characteristics.

OCCUPANCY MODELS

Model Structure

Occupancy models are a recently-developed statistical method for representing the presence or absence of a species on a landscape as it relates to environmental covariates (MacKenzie *et al.* 2006). Unlike previous presence/absence models, occupancy models explicitly account for imperfect detection, whereas previous models assumed perfect detection efficiency (i.e., if a species is present, it was detected 100% of the time; Williams *et al.* 2002; Martin *et al.* 2005). Failure to account for imperfect detection has the potential to bias model outputs, and can mislead conservation authorities and environmental managers as to the true status of their study populations (MacKenzie 2005). This is especially true when varying site or survey covariates (e.g., cover, flow dynamics, or predation risk) influence detectability (Bayley & Peterson 2001; Nichols & Karanth 2002). To illustrate, if results of a model indicate that the removal of low-lying brush results in increased presence of certain mouse species, is this increase in habitat occupancy due to an actual increase in presence of that mouse species, or an increase in detectability? Without accounting for imperfect detection, it would be impossible to provide evidence that supports or denounces either hypothesis. Occupancy modeling offers a solution to this problem by including repeat surveys of sampling units (temporal or spatial) in an area of interest as part of the experimental design; these repeat surveys are performed during a time when overall occupancy (i.e., species is present or species is absent) of a given sampling unit is not expected to change (Rota *et al.* 2009). In occupancy modeling terms, this static occupancy state represents the assumption of 'closure' (i.e., closed to changes in occupancy). Inferences gained from estimating probability of detection are then used to better estimate probability of occupancy (MacKenzie *et al.* 2006).

To design an occupancy model study, researchers begin by identifying an area of interest—the area of a landscape where we are interested in finding out where habitat is used and not used. The area of interest is then split into discrete survey units (MacKenzie *et al.* 2006). The size of survey units is driven by both practical and biological considerations (Hines *et al.* 2010); biologically, the units must be large enough so that the assumption of 'closure' is met (MacKenzie *et al.* 2002). The unit must also be small enough that environmental covariates that influence the occupancy of a species can be well-characterized. Logistics often constrain the number of units a researcher is able to visit during each sampling period, so an *a priori* set of sampling units is decided upon for repeat surveys using power analysis (Field *et al.* 2005; Guillera-Arroita & Lahoz-Monfort 2012). Next, data on hypothesis-driven landscape characteristics are recorded for each survey unit (e.g., temperature, habitat type, water depth). These environmental covariates fall into two categories: occupancy-specific and detection-specific (MacKenzie *et al.* 2002). Occupancy-specific covariates are gathered to test their effect on habitat occupancy, and must be a constant or average value across all sampling surveys (e.g., average water depth at a given unit of stream during three sampling surveys in July and August). In contrast, detection-specific covariate data are gathered to test for effects on detection efficiency (e.g., time of day, cloud cover, etc), and these may vary between each survey (Pellet & Schmidt 2005).

There is a trade-off in the design of occupancy model-based studies; samplers must choose between increasing the number of repeat surveys or increasing the number of sites visited. Optimization decisions are based on *a priori* knowledge on the detectability of the study species, as well as the scale at which the researcher wants to make inferences. Once data are gathered, models are run in the software PRESENCE (MacKenzie *et al.* 2002) to determine the probability of species occupancy and detection based on the data (downloadable from http://www.proteus.co.nz).

Once the researcher has specified hypotheses related to probability of occupancy and detection, model sets are created, tested, and ranked using Akaike's Information Criterion (AIC). Following the principle of parsimony, AIC uses log likelihoods and degrees of freedom to find models that account for as much of the variation as possible, with the fewest number of parameters (Burnham & Anderson 1998; MacKenzie & Bailey 2004).

Model Assumptions

The main assumptions of occupancy models include closure, survey independence, accurate species identification, and no unmodelled heterogeneity. Again, closure means that survey sites that are occupied remain occupied and sites that are unoccupied remain unoccupied for the duration of the user-defined sampling season (Rota *et al.* 2009). Survey independence means that repeated temporal surveys do not influence the study species' detectability and the presence or absence in following surveys (MacKenzie & Royle 2005; Canessa *et al.* 2015). Accurate species identification means that species are not misidentified to give either a false absence or a false presence. Finally, no unmodelled heterogeneity requires that all variation in occupancy and detection efficiency is accounted for by environmental covariates. This final assumption is not possible to fulfill, but efforts should be made in the hypothesis-generating process to identify all possible influencing factors and include them in the model (Dorazio *et al.* 2006)

Benefits of Occupancy Models

By accounting for imperfect detection and relying on presence absence data, occupancy models confer several other advantages over previous presence/absence model types (Dextrase *et al.* 2014). These advantages include an improved transferability of results between study sites and years by accounting for spatio-temporal variation in detectability, reduced sampling time by relying on incidence data, and an *a priori* ability to explicitly evaluate sampling design (power analysis) with regard to temporal replication versus spatial coverage (Guillera-Arroita & Lahoz-Monfort 2012; Dextrase *et al.* 2014). In the Arctic, where the cost of research is exponentially higher than in southern regions, and where we still have vast tracts of unstudied and uncharacterized habitat, these model improvements are highly prized efficiencies.

Since occupancy models characterize areas that are occupied as well as areas that are unoccupied, they may allow us to monitor changes in species distribution that previous "presence-only" type data sets could directly address. With presence-only models (e.g. mark-recapture), true species absences cannot be differentiated from false absences (i.e., the species is there, but we cannot detect it), and habitat characteristics associated with species' absence are not investigated (MacKenzie & Bailey 2004). Occupancy models, with their presence/absence data and detection efficiency estimations, enable a more complete characterization of species' distribution and habitat use. Thus, these models also possess more reliable predictive and monitoring power (MacKenzie 2006; Bailey *et al.* 2014).

Limitations of Occupancy Models

While having many benefits, occupancy models also possess a few limitations, especially when it comes to dealing with abundance; presence/absence data do not yield inferences on relative abundance. Instead, researchers are encouraged to model changes in species distribution to monitor populations. Recent developments in multi-state occupancy models can, however, be used to develop semi-quantitative inferences on coarse abundance states (e.g., high, low, medium abundance; Nichols *et al.* 2007; Jensen & Vokoun 2013). Multi-state models are employed in this thesis.

Improvements to Current Understandings

By exploiting the advantages of recently-developed occupancy models, I can improve upon previous studies of habitat use by YOY Arctic Grayling in Barrenland streams. Relative to the most detailed previous work (Jones & Tonn 2004b), I increased the spatial and temporal scale of sampling, estimated probability of detection with repeat surveys, and collected habitat variables in areas where the species was absent as well as present. I also quantified the detection efficiency (for YOY Arctic Grayling) of two common sampling methods - electrofishing and visual surveys - in hopes of optimizing sampling efforts for future monitoring programs. This study will act as a useful baseline for future long term studies. Multi-season and multi-year monitoring programs function well with occupancy models, because accounting for imperfect detection improves the transferability of findings and researchers can relate changes in habitat variables to changes in immigration and extinction rates between years or seasons (Fausch *et al.* 2002; MacKenzie *et al.* 2003).

In summary, occupancy models offer a lot of advantages over previous presence/absence and presence-only models of species' distribution and habitat use. Occupancy models can be used in the establishment of large-scale monitoring programs (e.g., Ferraz *et al.* 2007; Pavlacky *et al.* 2012), and may be especially useful in remote northern environments, where it is vitally important to optimize the efficiency of sampling designs. As we refine sampling techniques based on *a priori* data, it is possible to establish highly reliable and statistically robust model sets that can be used by environmental managers and other decision makers to monitor and conserve populations. Furthermore, these models increase our understanding of species distribution, and provide the opportunity to evaluate changes in species distribution as it relates to anthropogenic disturbances such as industrial activity and climate change (Rockstrom *et al.* 2009).

LOCAL IMPLICATIONS

The reason for studying the life history of Arctic Grayling in the Barrenlands was provided by regulators and industrial managers involved with the development of a new open-pit diamond mine development in the Northwest Territories: Gahcho Kué. To access diamond-bearing kimberlite bodies, found beneath lake basins, the proposed open-pit mining development will isolate, fish-out, and drain a section of Kennady Lake (Figure 1.1). As Kennady Lake is a headwater lake, these changes will significantly alter watershed morphology, seasonal flow regimes, and the functional connectivity downstream of Kennady Lake.

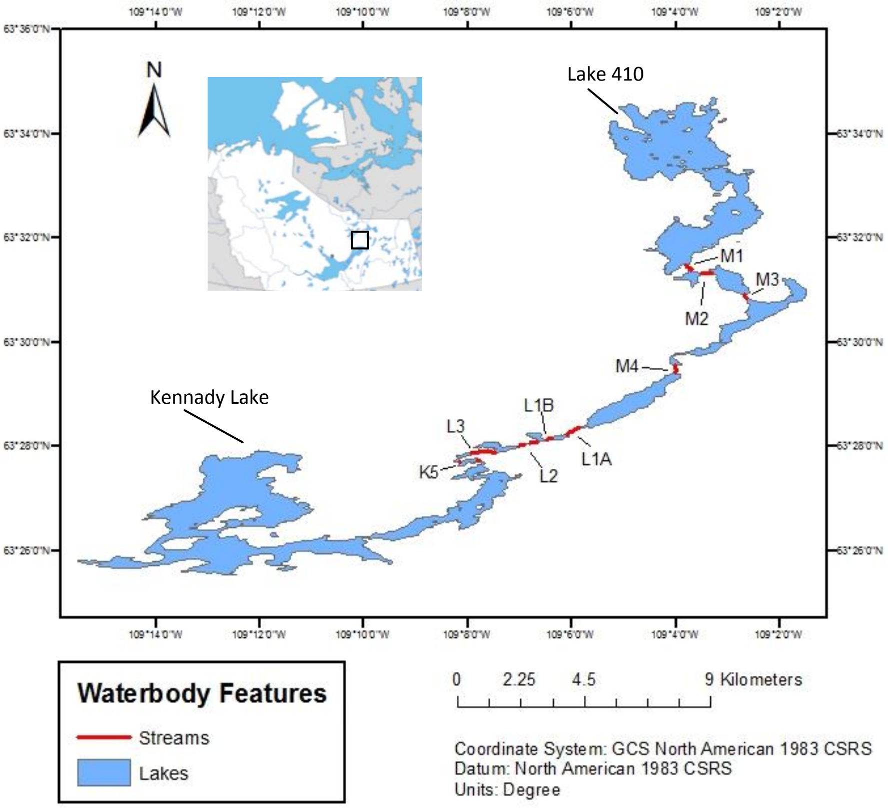

Figure 1.1. Map of study area.

In 2013, the *Fisheries Act* was amended to remove protection to fish habitat, and instead focus on protecting recreational, commercial, and aboriginal fisheries. While Arctic Grayling are an important recreational and aboriginal fishery, and would continue to be protected under the version of the *Fisheries Act* (2013), the recent changes do not apply to the Gahcho Kué diamond mine development, as initial stages for this project began in the mid-1990s. Instead, this study site is regulated by the rules and guidelines in the previous iteration of the *Fisheries Act* (1985) that states the occurrence of harmful alteration, disruption, and destruction (HADD) to fish and fish habitat be prevented. The *Fisheries Act* dictates that management resources be focused on reducing harmful impacts to fish and fish habitat, and when possible ensuring No Net Loss (NNL) of the productive capacity of the fishery (Department of

Fisheries and Oceans 1985). Productive capacity, here, can be defined as “maximum natural capability of habitats to produce healthy fish… or to support or produce aquatic organisms upon which fish depend”.

In this project, a portion of the resources devoted to NNL is being used (as directed by Fisheries and Oceans Canada) to fund independent research in the development area. The hope is that shifting the focus toward independent research will help to remove any uncertainty regarding the impact of the mining activity, fill in knowledge gaps on northern fishes, and provide scientifically defensible information to advise habitat management and monitoring programs. My research focuses on describing the habitat use of YOY Arctic Grayling; Arctic Grayling use both Kennady Lake and the adjacent lakes and streams for spawning, rearing, and overwintering.

STUDY AREA

The Kennady Lake drainage system is located approximately 280 km north northeast of Yellowknife (ca. 63°26'15 N, 109°11'51 W) (Figure 1.1). Kennady Lake is a headwater lake approximately 20km north of the treeline, within the sub-Arctic Tundra Shield ecozone (Ecosystem Classification Group 2012). Commonly known as the “wet desert”, the sub-Arctic Tundra is characterized by a low Arctic climate; with average annual precipitation levels between 260 and 275 mm. Shrub tundra dominates the landscape with scattered black spruce and dwarf birch groves populating lake shores and other sheltered areas. The sub-Arctic tundra ecozone is a low-relief bedrock plain covered with blankets of hummocky glacial till made up of granite derived Brunisols and organic Cryosols (Ecosystem Classification Group 2012). Permafrost is continuous in the area, except under deeper lakes (i.e. Kennady Lake) where large open taliks exist and connect with deep groundwater flow nearly 300 meters below land surface (De Beers Canada 2010a). Formed because continuous permafrost holds water to the surface, the Kennady Lake watershed is made up of a series of several small, shallow lakes (other than Kennady Lake depths vary between 1-8 meters) connected by short outlet streams (lengths vary btw. 60-400m) that make a chain-lake structure in the low lying areas.

Kennady Lake is a headwater lake within the Lockhart Drainage system. It flows north to join the Lockhart River system at Aylmer Lake, then curls back south in a clockwise fashion. The Lockhart River drops approximately 200m in elevation before draining into Great Slave Lake. From there, water mixes with several other drainage systems, and follows the Mackenzie River north to the Arctic Ocean.

My main study area, the Kennady Lake watershed, consists of a series of nine connected lakes and lake-outlet streams flowing north from Kennady Lake (i.e. Kennady Lake and the L and M lakes and streams) (Figure 1.2). This set of lakes and streams, along with the N-system directly west of Kennady Lake, have been identified as likely candidates to be impacted by the diamond mine development once flow diversion commences. Flow will be diverted from Kennady Lake watershed into the N watershed, so the N watershed will experience yearly flow rates that exceed the natural variation of the system. The L and M water bodies will likely experience flow rates lower than natural variation once mining production begins. However, the N watershed joins the Kennady Lake watershed at Lake 410 (Figure 1.1), and the flow regime of the combined drainages is expected to return to natural variation as it flows through the P watershed to Kirk Lake.

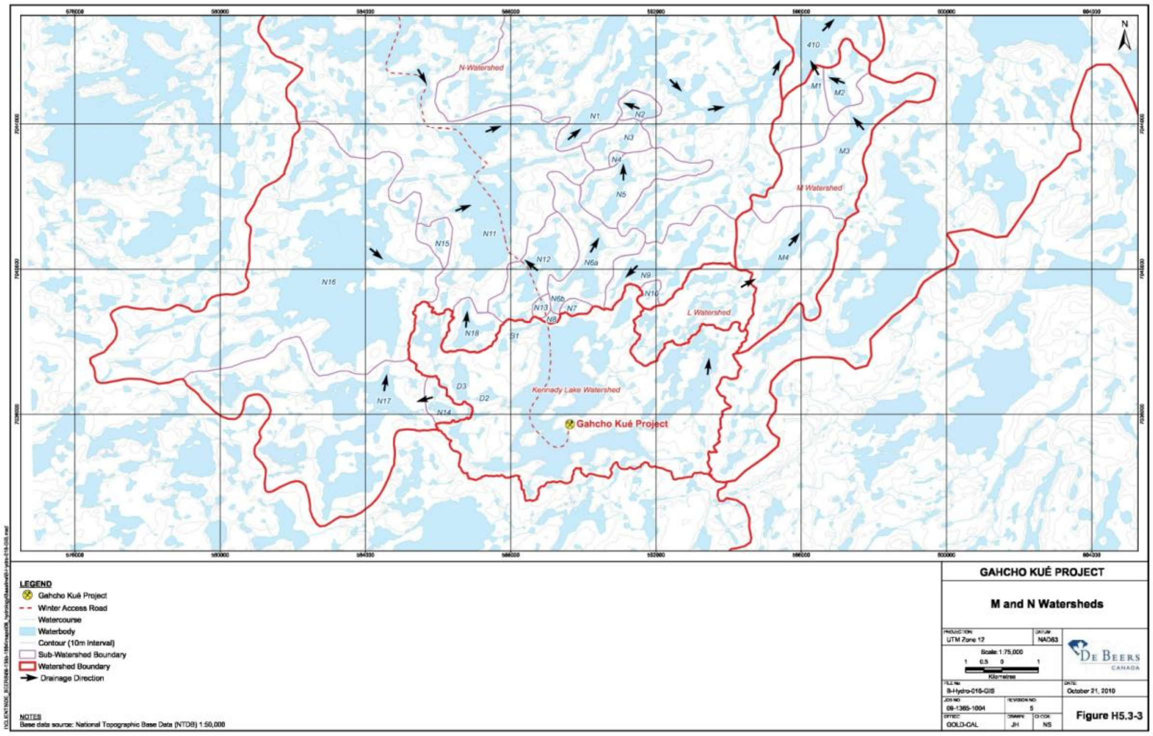

Figure 1.2 Map of study area and surrounding watershed (De Beers Canada 2010b).

With a surface area of 11.8 km^2 and a maximum depth of 18 meters, Kennady Lake is the largest and deepest lake in the study area. Kennady Lake is oligotrophic, with characteristically low nutrient levels (4-6mg/L DOC, 0.3-9mg/L PO_4^{3-}, 0.005mg/L NO_3^-) , specific conductivity (9-25µS/cm), hardness (0.5-7mg/L), and total alkalinity (1-30 mg/L); and these oligotrophic characteristics are consistent throughout the drainage system (De Beers Canada 2010c). Nine fish species inhabit Kennady Lake: Northern Pike (*Esox lucius*), Lake Trout (*Salvelinus namaycushi*), Arctic Grayling (*Thymallus arcticus*), Round Whitefish (*Prosopium cylindraceum*), Burbot (*Lota lota*), Longnose Sucker (*Catostomus catostomus*), Slimy Sculpin (*Cottus cognatus*), Lake Chub (*Couesius plumbeus*), and Ninespine Stickleback (*Pungitius pungitius*).

Ice dynamics in the region play an in important role in nutrient dispersal, functional connectivity, and the life history of aquatic species. Ice formation begins in late September as temperatures fall below freezing, and remain below zero until mid to late May (De Beers Canada 2010b). As mean monthly temperatures between December and March are below -20ºC, lake ice thickens rapidly throughout the winter. Lake ice thickness reaches a maximum extent of 2m by April (De Beers Canada 2010b). Since the ice is so thick, many of the smaller lakes in this study system likely do not provide suitable overwintering habitat due to their shallow depth (often < 5 m), thick ice (often exceeding 2 m in thickness), and corresponding lack of oxic bottom waters (Clilverd *et al.* 2009; unpublished data). Ice-off occurs nearly a month and a half after the initiation of spring thaw (late June).

In mid to late May, the snow pack melts and the streams begin to thaw. The connective channels between lake outlets are quickly re-established, but persistent lake ice cover influences the temperature of the connecting streams thereby, influencing the physiology and life history of the species that use these corridors for spawning and feeding. All nine fish species present in the Kennady Lake drainage use the connective streams to fulfill some aspects of their life history (De Beers Canada 2010d).

Stream temperatures during the open-water season range from 1ºC to 20ºC. Undercut banks, sedge tussocks (*Eriphora spp.*), dwarf birch (*Betula nana*), willow (*Salix spp.)* and small, isolated black spruce (*Picea mariana*) provide cover for fish along lake and stream margins, whereas large boulders, bur-reed (*Sparganium hyperboreum*), and mare's tail (*Hippuris vulgaris*) provide patches of instream cover. The streams are often braided, or multi-channeled, and the streambed is poorly-sorted and dominated by boulders. Streams vary in length from ~100 to 400 m, and are generally shallow (average depth 0.01-1 m) and wide (range 4-80 m, bankfull width in June)

As continuous permafrost holds water to the surface, precipitation or meltwater are quickly funneled into low lying areas. This results in sharp fluctuations in stream discharge after precipitation events (Woo 2012). However, arid summer conditions promote rapid evaporation and drawn down rates, so some stream segments become impassable to fish (Golder Associates 2012). In some years, increased autumn precipitation levels increase stream discharge enough to reestablish functional connectivity just prior to freeze up (De Beers Canada 2010b).

THESIS OBJECTIVES

The objective of my thesis is to increase understanding of YOY Arctic Grayling life history in a sub-Arctic Tundra stream setting. I use multi-state, multi-season occupancy models to clearly discern patterns in Arctic Grayling habitat occupancy and detection efficiency. My results lend insight into Arctic Grayling life history that is part descriptive and part hypothesis testing.

Objectives:

a. Relate occupancy of Arctic Grayling in sub-Arctic Tundra streams to a suite of habitat variables.
b. Account for imperfect detection, and relate environmental covariates to non-random variation in detection probabilities.
c. Compare two sampling method for detecting YOY Arctic Grayling in sub-Arctic Tundra streams: electrofishing and visual.

RELEVANCE

Business, political, and aboriginal leaders have elected to extract resources from this pristine watershed. By learning more about the life history of Arctic Grayling, we can alter, refine, and improve current best-practice management procedures related to water management and fish habitat management. Furthermore, by conducting these studies in advance of watershed alteration we can construct a baseline to which future data can be compared (Lapointe *et al.* 2014). These comparisons can be used to evaluate the effectiveness of highly experimental management practices, and suggest alterations should managers and conservation authorities see fit. Finally, by applying the latest advancements in statistical modeling to a pristine and unique system like Kennady Lake, we contribute to the development and calibration of these methods.

By learning as much as we can about the species that reside beyond the direct footprint of mining development, and take actions—through management, mitigation, or reclamation efforts—we can lessen the negative effects derived from significant alterations made to the watershed. Federal government regulators, DeBeers Canada, and the University of Waterloo have made a commitment to explore the complex interactions of the species in this area with their environment; with a particular focus on Arctic Grayling. Arctic Grayling are a good indicator of alterations to stream productivity as their life history requirements depend on their ability to access the full extent and heterogeneity of this sub-Arctic Tundra watershed.

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Chapter 2: Habitat Occupancy of Young of Year Arctic Grayling (*Thymallus arcticus*)

INTRODUCTION

The Arctic is currently experiencing a period of rapid change in climate and hydrology (Stieglitz *et al.* 1999). Over the next 100 years, researchers predict an increase in atmospheric temperatures, precipitation, and snow depth along with a thawing of the permafrost layer (Prowse *et al.* 2011). These hydrologic and cryospheric changes, combined with ever-growing industrial development in the north, are having, and will continue to have, a profound effect on Arctic and sub-Arctic lotic ecosystems, and will likely result in increased stream temperatures, and increased functional connectivity (Rouse *et al.* 1997; Woo & Mielko 2007; Quinton *et al.* 2011; Connon *et al.* 2014). Unfortunately, climate- and industry-induced changes are outpacing the capacity for regulatory bodies to meaningfully assess and mitigate impacts (Schindler 2001), which is of paramount concern because many Arctic and sub-Arctic freshwater ecosystems provide subsistence resources for local peoples (Berkes 1990; Miltenberger & Strahl 2014).

Changes in climate and hydrology are predicted to affect habitat use and distribution in northern fishes (Reist *et al.* 2006a; Reist *et al.* 2006b). Changes in nutrient availability, hydrologic dynamics, fish metabolic rates, interspecific competition, and predation are predicted to constrain the regional/sub-continental dispersal and distribution for some northern fishes, while aiding in the proliferation of others (Reist *et al.* 2006b). It is likely that fishes with a migratory life history and those that use a variety of freshwater habitats are particularly vulnerable to climate-induced changes in hydrology, but scientists are unsure of the inferential reliability of large scale trends and hypotheses when predicting effects in specific catchment systems; especially in remote, poorly-studied ecosystems such as sub-Arctic tundra chain lake systems (Reist *et al.* 2006a). To address uncertainties in regional habitat-use, scientists often construct mathematical models that relate the distribution and abundance of organisms to an array of biotic and abiotic explanatory variables (Elton 1927; Railsback *et al.* 1999; Krebs 2015).

In the Canadian north, habitat-use models must address a unique set of challenges that include a large degree of spatiotemporal variation in hydrology and climate, and limited surveying capacity due to the high cost of research and harsh climate. As spatiotemporal variation in climate and hydrology influence the detectability of target species, there is a great deal of uncertainty regarding the transferability research findings to predict regional patterns in species distribution and habitat use; attributable to the understudied nature of these systems (Lapointe *et al.* 2014). To address these issues, scientists tend to deploy habitat-use models that include multiple spatial scales (Fausch *et al.* 2002; Hershey *et al.* 2006) The majority of these models, however, do not account for imperfect detection, nor address how detection efficiency may vary over gradients of space and time (and we know that habitat use patterns of organisms and detectability vary in space and time; Morris 1987; Boulinier *et al.* 1998). Models that do not account for detection efficiency may introduce a degree of uncertainty for habitat-use estimates and bias the effects of environmental covariates (Moilanen 2002; Tyre *et al.* 2003). This uncertainty is derived from not knowing whether non-detection arises from a site not being occupied (true absence) or from the organism of interest being present at a site but not detected (false absence) (MacKenzie *et al.* 2002).

Occupancy modeling, the study of the proportion of area, patches or sample units that are occupied by a species or set of species of interest, improves upon traditional habitat use models (e.g., resource selection functions; Boyce & McDonald 1999; MacKenzie 2005) by explicitly assessing the probability of detection as well as probability of habitat occupancy (MacKenzie *et al.* 2006; Haynes *et al.* 2013). By accounting for imperfect detection, occupancy models offer a more reliable estimate of habitat-use and the relative effects of environmental covariates. Furthermore, by relying entirely on incidence data in their simplest form, occupancy models can substantially reduce the amount of time spent surveying and thereby the overall cost of surveys (MacKenzie *et al.* 2006). The importance of these advantages cannot be overstated in logistically challenging and understudied Arctic and sub-Arctic freshwater ecosystems; a more affordable and less time-consuming option for conducting reliable sampling and monitoring is of interest to many stakeholders (Neil Mochnacz, Fisheries and Oceans

Canada, Winnipeg, pers. comm; Mike Palmer, Cumulative Impacts Monitoring Program, Gov't of the Northwest Territories, Yellowknife, pers. communication).

Occupancy modeling relies on the use of 'presence-absence' data collected for a 'population' of spatial replicates on a given landscape (MacKenzie *et al.* 2002). Incidence data are used to elucidate relationships between species distribution and patterns in environmental covariates (MacKenzie *et al.* 2006). To account for imperfect detection, occupancy modeling requires that repeat surveys occur within each of the studied spatial replicates (MacKenzie 2005). Detection probability can be related to environmental and sampling covariates (e.g., stream depth, method) within occupancy model frameworks (Royle & Nichols 2003). This is extremely valuable when conducting exploratory research in uncharacterized ecosystems as results can be used to optimize sampling methods.

The simplest implementation of occupancy models is a two-state model (i.e., the species is either present or absent; MacKenzie *et al.* 2006). While results provide insightful information on species distribution and species-habitat relationships, results do not allow investigators to differentiate between habitats that only support a few individuals and those that support many individuals (Nichols *et al.* 2008). For fine-scale projects designed to monitor and protect species in areas vulnerable to a specific anthropogenic disturbance, the relative importance of occupied habitat in two or more states (e.g., highly occupied vs. somewhat occupied) can provide information that is crucial to the development of evidence-based management and policy (Nichols *et al.* 2007). Studies that use an index of relative abundance to delineate between different occupancy states have had success in identifying relative importance of occupied habitat for rare and endangered species (Martin *et al.* 2010; Jensen & Vokoun 2013; Tempel & Gutiérrez 2013). The assumption made with a multi-state model (e.g., none/some/many) is that higher organism abundance within a habitat patch indicates that the patch has a greater quantity or quality of resources important to individual fitness within the species of interest (Freckleton *et al.* 2006).

Arctic Grayling (*Thymallus arcticus* Pallas 1776) are a migratory freshwater salmonid fish species that is distributed over much of the western Canadian Arctic and sub-Arctic. Because Arctic Grayling are a valuable subsistence fish for northern peoples, and connect lentic and lotic food webs via their migratory behaviour, considerable effort has been made to understand their general ecology (De Bruyn & McCart 1974; Baker 1976; Beauchamp 1990). Young of the Year (YOY) Arctic Grayling are often found in seasonally available lake outlet streams in Barrenland systems (Jones & Tonn 2004b). In these habitats, relatively high invertebrate production outweighs the energetic demands created by changing stream hydrology and temperature, and allows for the rapid growth and lipid storage that is essential for YOY to survive winter (Jones *et al.* 2003a; Deegan *et al.* 2005; Heim *et al.* 2014). However, the YOY life history stage is vulnerable to changes in flow regimes (Deegan *et al.* 2005).

The species-habitat interactions for certain environmental covariates have been well characterized for YOY Arctic Grayling. For instance, several studies have shown that YOY Arctic Grayling occur in stream sections where the average velocity is between 15 and 25 $cm \cdot s^{-1}$ (Jones & Tonn 2004b; Deegan *et al.* 2005). Furthermore, it is well known that YOY leave stream rearing habitat for overwintering grounds in response to discharge and temperature conditions (<0.1 m3/s and <10ºC, respectively, in streams in northern Alaska; Heim *et al.* 2015). It is not currently known, however, how stream segment slope and distance to overwintering habitat influence the habitat occupancy of YOY Arctic (e.g., Deegan *et al.* 1999; Jones & Tonn 2004b). Furthermore, patchy ecological covariates such as overhanging riparian cover have not been well characterized in previous models of habitat use by YOY Arctic Grayling because of the limited spatial scale of these studies (Jones & Tonn 2004b). Overhanging riparian cover is important to consider, because the vegetation provides visual isolation from aerial predation, minimizes temperature fluctuations and lowers the average temperature of the water, and provides additional drift feed via an increased deposition rate of terrestrial invertebrates (Hawkins *et al.* 1982; Wesche *et al.* 1987; Moore & Gregory 1989). Finally, previous studies of habitat use in YOY Arctic Grayling have not quantified detection efficiency; that is, how probable it is that YOY Arctic Grayling are detected when they are present in a survey unit (Deegan *et al.* 1999; Jones & Tonn 2004b). Thus, it is unknown how detectability changes with changing hydrology or with different survey methods. A common sampling technique that researchers use to maximize efficiency when sampling stream fishes is backpack electrofishing (Albanese *et al.* 2011). However, due to low electrical conductivity in many streams in northern Canada, the effective range of the electrofisher may be highly reduced (De Beers Canada 2010c; Golder Associates 2012). Conversely, extremely low turbidity in Barrenland streams may improve the relative efficiency of visual detection methods.

To lend further insight into how YOY Arctic Grayling use seasonal Barrenland stream environments and determine how to best monitor them in these remote environments, I applied multi-season, multistate occupancy modeling techniques to a series of lake-outlet streams in the sub-Arctic Tundra Shield. Multiple sample-seasons (early July, late July, August, September) were used to assess how temporal variation in hydrology through the open-water season affected occupancy, detection, and environmental covariate effect estimates. Multiple occupancy states were used as a coarse assessment of relative abundance (i.e., highly occupied, somewhat occupied, not occupied) to determine the overall probability of occupancy (ψ) and, in stream segments that were occupied, the probability that the stream segment was highly occupied *(R).*High probability that a segment was highly occupied was used as an indication of greater relative habitat quality. A variety of ecological data were collected to maximize inference, and detection efficiency was compared between model-seasons using two common survey techniques (visual, and electrofishing+visual).

Based on previous research results and the known ecology and life history of YOY Arctic Grayling, I hypothesized that probability of occupancy of YOY Arctic Grayling would 1) decrease with increases in distance to overwintering habitat and discharge; 2) increase with increases in overhead cover, stream slope, habitat complexity, and flow heterogeneity; and 3) reach a maximum at depths and velocities similar to those found in Jones and Tonn's study (2004b). Because YOY Arctic Grayling are cryptically coloured and water obscures visual detection, I hypothesized that the probability of detection of YOY Arctic Grayling was inversely related to water depth and overhanging riparian cover and greater for electrofishing+visual surveys relative to visual surveys.

Results from this study provide researchers, regulators, and industry with: 1) an *in situ* demonstration of how accounting for imperfect detection when temporal variation biases detection can improve the accuracy of habitat occupancy estimates, lending support to occupancy models as a standardized model framework to be used in Arctic and sub-Arctic freshwater systems; 2) a scientifically-defensible way determine the optimal sampling method for detecting YOY Arctic Grayling; and 3) the means to determine how the local distribution and abundance state of YOY Arctic Grayling is influenced by multiple interacting environmental covariates.

MATERIALS AND METHODS

STUDY AREA

The 16.5 km^2 study area is located approximately 280 km northeast of Yellowknife, NT, in the headwaters of the Lockhart drainage system (63º 26'N, 109º 12'W). Specifically, the study area begins at the outlet of Kennady Lake, a small yet relatively deep headwater lake (9 km^2 and 18 m max depth, respectively), and continues 9 kilometers downstream through a network of small, shallow lakes that are connected by short outlet streams that vary in length (btw. 60-400 m) (i.e., Barrenland chain-lake system; Figure 2.1). Situated in the transition zone between the Taiga Shield and Sub-Arctic Tundra Shield ecozones, 20km north of the treeline, the region is characterized by low topographic relief, continuous permafrost, and a semi-arid climate (260 – 275 mm average annual precipitation). The mean annual temperature is approximately -6.6°C, with a summer maxima of 34.3°C and a winter minima of -53.5°C (Environment Canada 2000). This series of lakes and streams was selected for study because this part of the watershed will be directly affected by mining-associated water removal that occurs in Kennady Lake as part of development of the Gahcho Kue diamond mine (water removal began in the spring of 2015).

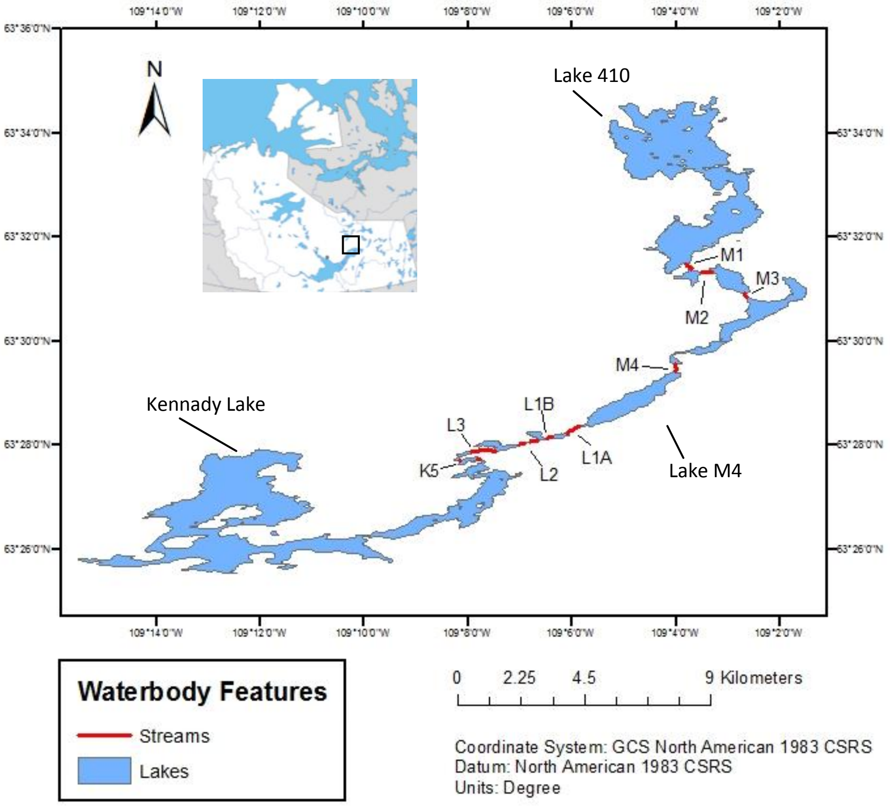

Figure 2.1. Map of the study streams

In this study system, freshet begins in late May with flash flooding caused by runoff that remains above the continuous permafrost layer (De Beers Canada 2010b). As nearly 50% of annual precipitation falls in the winter as snow, stream flows are typically highest in early spring and lessen as the summer persists. In areas of continuous permafrost such as this, downstream flow and high levels of evaporation, driven by semi-arid conditions, cause significant drawdown on the water table (De Beers Canada 2010b; Baki *et al.* 2012). Thus, many of the lakes in the region lose surface flow connectivity via streams prior to freeze up in late September (Golder Associates 2012).

As the study area is located 20 km above the tree line, riparian vegetation generally occurs in one of two groupings: i) a mix of sedge tussocks (*Eriphora spp.*) and grasses that typically inhabit low lying and inundated areas; and, ii) a combination of low shrub tundra (*e.g.*, dwarf birch (*Betula nana*) and willow (*Salix spp*.) that typically inhabit areas where wind cover is sufficient and where channelization staves off inundation (Ecosystem Classification Group 2012). Banks are often undercut, and stream temperatures range between 1 and 20ºC; stream temperatures are largely influenced by the epilimnetic temperature of upstream lakes and permafrost runoff (De Beers Canada 2010b; Quinton *et al.* 2011).

Stream beds are poorly-sorted, and comprised primarily of glacier-derived boulder till (Ecosystem Classification Group 2012). This more-uniform streambed, higher temperatures relative to the surrounding lakes, and declining surface flow connectivity throughout the summer exclude some large-bodied fishes, such as Lake Trout (*Salvelinus namaycushi*) and Northern Pike (*Esox lucius*) (Tack 1980; Stewart *et al.* 2007; De Beers Canada 2010d). Nutrient levels (4-6 mg/L DOC, 0.3-9mg/L PO_4^{3-}, 0.005 mg/L NO_3^-) specific conductivity (9-25 µS/cm), hardness (0.5-7 mg/L), and total alkalinity (1-30 mg/L) are relatively low throughout the study system (De Beers Canada 2010c), whereas dissolved oxygen concentrations (9-12mg/L) are at or near saturation throughout the open-water season (De Beers Canada 2010c).

Nine species of fish reside within the study area. Round Whitefish (*Prosopium cylindraceum*) and Lake Trout are present in the greatest relative abundance in the lake habitats (De Beers Canada 2010d). The focal species for this study, Arctic Grayling, is the most abundant species in seasonally available stream habitats (De Beers Canada 2010d). Other species present in the study area include Burbot (*Lota lota*), Northern Pike, Longnose sucker (*Catostomus catostomus*), Ninespine Stickleback (*Pungitius pungitius*), Slimy Sculpin (*Cottus cognatus*), and Lake Chub (*Couesius plumbeus*) (De Beers Canada 2010d). Since many of the shallow lakes in the region freeze to the bottom during the winter, only a few lakes with sufficiently deep basins offer year-round habitat for fish populations. Kennady Lake, Lake M4, and Lake 410 are the only lakes within our study area with confirmed year-round populations of fish (De Beers Canada 2010d; unpublished telemetry data).

SAMPLING DESIGN

Sampling Structure and Definitions

A multi-state, multi-season occupancy model was used to examine the probability of habitat occupancy at different survey periods within the 2014 single open-water season. In occupancy modeling, imperfect detection is accounted for via direct estimation of detection efficiency using temporal or spatial replicates within a season (Guillera-Arroita *et al.* 2010). A 'season' is defined as a survey period where the occupancy state of a study segment remains unchanged (e.g., 'occupied' or 'unoccupied') (MacKenzie *et al.* 2006). From this point forward, I will refer to this definition of season as 'model season'. To track changes in habitat occupancy throughout the open water season, occupancy surveys fell into four model-seasons that were conducted at equally dispersed intervals between July 11th and September 3rd (Table 2.1). Model-seasons were limited to approximately five days to satisfy our assumption of closure; because YOY Arctic Grayling show strong site fidelity to rearing sites as long as flow and foraging conditions remain consistent the five day time limit seemed reasonable (Stewart *et al.* 2007). The 'state' in multi-state occupancy models refers to a category of occupancy that remains unchanged for the duration of the model season (e.g., relative abundance or breeding status; Nichols *et al.* 2007). In this study, there were three occupancy states that I describe in more detail below – unoccupied, overall occupancy, and conditionally high occupancy.

Table 2.1. Summary of model-season start and end dates. Occupancy state closure assumed within model seasons.

Model-Season	Start Date	End Date
1	July 10, 2014	July 15, 2014
2	July 30, 2014	August 4, 2014
3	August 13, 2014	August 17, 2014
4	August 28, 2014	September 2, 2014

There is approximately 2 km of stream habitat in the 9km-long study area (Figure 2.1). As stream habitat is the focal point of this study, streams were broken up into 30 meters segments, with 67 stream segments in total. Segment boundaries were drawn perpendicular to the segment's longitudinal midline, and all segments shared upstream and downstream boundaries with neighbouring segments (inlet/outlet segments excepted). The rationale for selecting 30 meters as the uniform length for sampling segments was based on both the scale of the research questions and the basic dispersal biology of YOY Arctic Grayling (De Bruyn & McCart 1974; Armstrong 1986). I selected this fine-scale segment size because I was interested in how YOY Arctic Grayling use habitat throughout the summer open-water period in a relatively small geographic area. This required detailed data collection on a suite of habitat variables, while also allowing for the inclusion of meso-landscape components such as distance to overwintering habitat. The 30 meter segment size was also likely to meet the assumption of occupancy state 'closure'; that is, that overall occupancy of a particular stream segment did not change within a model season; previous research has shown that YOY Arctic Grayling that find stream sections with suitable drift feed, flow dynamics, and cover tend to hold their position for extended periods of time (Jones & Tonn 2004b; Stewart *et al.* 2007; Rota *et al.* 2009).

In each model-season, two occupancy surveys (one electrofishing+ visual, one visual) were conducted on each of the 67 stream segments, for a total of 8 surveys. Ten occupancy-specific covariates (covariates that relate to the probability that a stream segment is occupied), and five detection-specific covariates (covariates that relate to the probability of detection) were investigated (Table 2.2 and Table 2.3). For occupancy-specific covariates that remained constant (e.g., stream segment slope) throughout the entire study period, data were collected from June 10th to June 16th, 2014. For occupancy-specific and detection-specific covariates that changed throughout the study period (e.g., discharge), data were collected immediately following occupancy surveys in each model season (Table 2.1).

Table 2.2. Description of covariates used to model probability of occupancy

Occupancy-Specific Covariates	Abbrev.	Units/ Category	Data type	Description
Included in final model set				
Habitat Complexity	(H'/5)	Index 0-1	Continuous	Shannon-Weiner diversity index used to compare habitat type within each stream segment. Habitat type was characterized using a modified Rosgen classification system to aggregate habitat type into the five following habitat types: Run, Riffle, Cascade, Pool, Shallow Water. To limit the range of diversity index between 0 and 1, the data was standardized by dividing it all by 5.
Good Overhanging Vegetation	(GOHV)	(Y/N)	Binary	Stream segments with more than 50% of the stream bank covered with overhanging vegetation thick enough to obstruct view of the stream below were characterized as having GOHV
Distance to overwintering habitat	(D2OW)	(m)	Continuous	Run-of-River distance from the centroid of each stream segment to the nearest lake suitable for overwintering
Stream Segment Slope	(Slope)	degrees	Ordinal	Stream slope of each stream segment, measured in degrees.
Discharge	(Q)	m^3/s	Continuous	Average discharge as measured at one transect per stream using flowtracker flowmeter. The same discharge measurement is then applied to all stream segments within their respective stream and model-season
Mean Segment Depth	(D)	(m)	Continuous	Mean segment depth as measured along thalweg at four equi-distant points within each stream segment
Mean Segment Velocity	(V)	(m/s)	Continuous	Mean segment velocity taken from four mid-column (0.6) measurements at four equi-distant points within each stream segment
Eventually excluded from final model set				
Mean Segment Depth Squared	(DSQ)	(m)	Continuous	Mean segment depth squared, to test parabolic relationship with occupancy
Mean Segment Velocity Squared	(VSQ)	(m)	Continuous	Mean segment velocity squared, to test parabolic relationship with occupancy
Segment-Level Flow Heterogeneity	(CoeffV)	Proportion [0-1]	Continuous	Coefficient of variation of velocity within each stream segment. Taken to characterize the variations in depth experience within each sampling unit.

Table 2.3. Description of covariates used to model probability of detection.

Detection-**Specific Covariates**	**Abbrev.**	**Units/ category**	**Data type**	**Description**
Included in final model set				
Survey Method	(Method)		Binary	A binary variable containing two survey methods: (0) Survey conducted using visual detection methods, and (1) Survey conducted using electrofishing+visual methods
Mean Segment Depth	(D)	(m)	Continuous	Mean segment depth as measured along thalweg at four equi-distant points within each stream segment
Eventually excluded from final model set				
Mean Segment Depth Squared	(DSQ)	(m)	Continuous	Mean segment depth squared, to test parabolic relationship with occupancy
Repeat Survey Effect	(Repeat)		Binary	Within model-season covariate to test if the occupancy state of the first survey influenced the occupancy state of subsequent surveys
Good Overhanging Vegetation	(GOHV)		Binary	Stream segments with more than 50% of the stream bank covered with overhanging vegetation thick enough to obstruct view of the stream below were characterized as having GOHV

Occupancy Survey Methods

Occupancy surveys were conducted by moving upstream from the downstream end of each stream. Upon detection of a YOY Arctic Grayling, the recorder noted its presence, and tallies were kept to enumerate fish captured in each stream segment. Due to logistical considerations, all surveys were conducted with replacement (e.g., fish were not removed from the stream after capture), and a block net was not used at the upstream boundary of the stream segment. To ensure that fish observed at or near the segment boundary did not bias the occupancy status of the adjacent stream segment, their positions were noted and fish observed in the same location in the following survey were not included in tallies. Polarized lenses were worn at all times during surveys.

Visual surveys were conducted using longitudinal passes. As most streams were quite wide (i.e., 30m ± 14SD), the stream was split lengthwise into two halves and two field technicians each surveyed half of the segment. To reduce disturbance on the fishes and prevent them from fleeing the stream segment, passes were made using slow methodical steps, when possible on above-water substrate, with pauses to scan 180 degrees for fish. In wider stream segments, several passes were needed to survey the entire segment. Survey effort was recorded in seconds.

Electrofishing surveys were conducted using a Smith-Root LR-20B backpack electrofisher with a six inch anode ring to shock between tightly-packed boulder substrate. One hour after the visual survey, the field crew started again at the downstream end of the stream and both the electrofisher operator and the netter moved upstream using a zig-zag pattern to detect fish, making sure to sample mid-stream and streamside micro-habitat evenly (Figure 2.2)(Cowx & Lamarque 1990). Low conductivity limited the effective range of the electrofisher (Beaumont *et al.* 2006). To get an average amperage output of 0.20A, the electrofisher was set to maximum voltage output (Voltage – 990 V; Duty Cycle – 50; Frequency – 35). Even so, the maximum effective range of the electrofisher was likely no greater than 2 meters. Fish caught by the electrofisher or seen outside the effective range of the electrofisher were counted as detections. This effectively meant we had two detection methods: i) visual only; ii) electrofisher+visual. Survey effort was recorded in seconds.

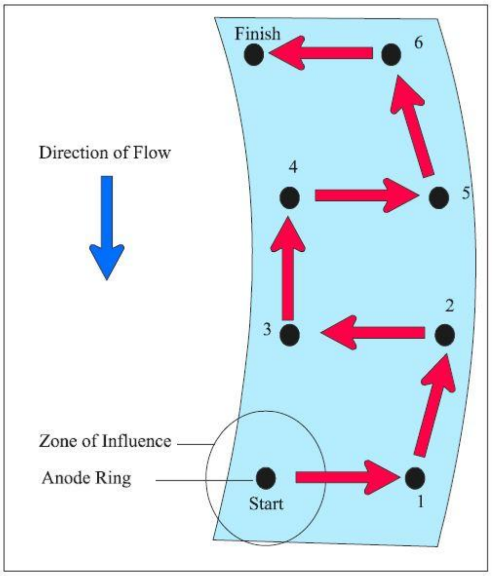

Figure 2.2. Diagram of survey path taken during electrofishing+visual surveys (SFCC 2007)

Collection of Covariate Data

I categorized occupancy-specific covariates—those used to model the probability of the three different occupancy states—into four categories: stream morphology, distance to overwintering habitat, flow dynamics, and biotic habitat characteristics (Dunham & Rieman 1999). Stream morphology covariates that were assessed for each model-season included stream segment slope, and meso-habitat complexity. Stream slope, reported in degrees, was measured as the change in elevation from the upstream to downstream end of each segment (m) (using a clinometer) divided by the segment length. I calculated meso-habitat complexity using the Shannon-Weiner Diversity index to analyze percent habitat type data. Habitat type was aggregated and grouped into five categories (run, riffle, pool, cascade, and shallow water) using the Rosgen classification system (Rosgen 1994). In each stream segment, visual assessments were used to determine the percentage composition of habitat type, and all percentages summed to 100 percent. The diversity index was then standardized by dividing the number by the total number of available habitats (i.e., five), to reflect habitat complexity on a range of 0 to 1. Distance to overwintering habitat was calculated by measuring the distance between the stream segment centroid and the nearest lake where Arctic Grayling overwintering has been confirmed (i.e., Kennady Lake, Lake M4, Lake 410) (De Beers Canada 2010d; unpublished data).

Flow dynamic covariates that were assessed during each model-season included mean segment depth, mean segment velocity, segment-level flow heterogeneity, and stream-level discharge. Mean segment velocity and depth were measured using a Hach FH950 handheld flow meter mounted on a wading rod; four measurements were taken along the thalweg at equi-distant points between the segment boundaries. Velocity measurements were taken at the mid-point of the stream (0.6 of depth below the surface). Segment-level flow heterogeneity was determined by calculating the coefficient of variation from the four velocity measurements used to calculate mean segment velocity (Sabo *et al.* 1996). Stream-level discharge was calculated using the United States Geological Survey mid-section method (adapted from Buchanan & Somers 1969). Measurement intervals were spaced to include a minimum of 20 points per cross-section (measurement intervals varied from 0.25-0.75m depending on stream width). Discharge locations were fixed in each stream, and measurements were taken in each stream and all model-seasons; the same discharge value was assigned to all points within a stream.

Overhanging riparian cover, a biotic covariate, was determined using a visual estimation of the percentage of stream that was shaded by either riparian vegetation or geomorphic features (Nielsen & Johnson 1983). When the percentage of overhanging cover exceeded 50%, the stream segment was classified as having good overhanging vegetation (GOHV) (Figure 2.3)(Nielsen & Johnson 1983).

Figure 2.3. Photographs that illustrate stream segments with good overhanging vegetation (left) and stream segments without good overhanging vegetation (right). Photograph on left was taken in stream L1a on June 14th, 2014. Photograph on right was taken in stream M4 on June 10th, 2014).

Survey-specific covariates, used to model probability of detection, included survey method (i.e., ‘electrofishing + visual’ or visual), mean segment depth (described above), repeat survey bias, and overhanging vegetation (described above). Visual and electrofishing +visual surveys were recorded as: 0 = Visual Survey and 1 = ‘electrofishing + visual’ survey. To address the possibility of repeat sampling bias, I included a binary sampling covariate that equaled 0 if there were no previous detections and 1 for all surveys after YOY had been detected (pers. communication, D. Mackenzie).

All data were examined for outliers and for violations of normality using Shapiro-Wilk tests, and log(x+1) and square-root transformations were applied when necessary to achieve normality. Continuous covariates were standardized by calculating z-scores.

STATISTICAL ANALYSIS

Parameterization of model

To elucidate patterns in YOY Arctic Grayling habitat occupancy, I used a multi-state, multi-season parameterization of the occupancy modeling framework (Nichols *et al.* 2007). This meant that occupancy fell into three occupancy states—unoccupied (1-probability of occupancy), somewhat occupied ($\varphi^{[1]}$), and highly occupied ($\varphi^{[2]}$). My objective was to determine the probability of overall occupancy and the probability that a stream segment was highly occupied. Thus, occupancy parameters were defined in the following way: ψ represents the probability of occupancy in either occupied state ($\psi = \varphi^{[1]} + \varphi^{[2]}$), and R represents the probability that a stream segment was highly occupied, given that the stream segment was already occupied (i.e., a conditional probability, $R = \varphi^{[2]}/\psi$). To account for non-random variation in the probability that a segment was either occupied (ψ) or highly occupied (R), environmental covariates were fitted to parameter estimates using logit-link regressions. Models were then ranked using AIC methods (Burnham & Anderson 1998; MacKenzie *et al.* 2006). Regression coefficients were estimated and communicated the magnitude and direction of the environmental covariates' influence on both occupancy parameters. A negative covariate coefficient associated with the probability that a segment was occupied (ψ) indicated a greater probability that the stream segment was unoccupied for every unit of covariate increase (Nichols *et al.* 2007). A negative covariate coefficient associated with the probability that a stream segment was highly occupied (R) indicated a greater probability that the stream segment was somewhat occupied for every unit of covariate increase (Nichols *et al.* 2007).

To delineate between occupancy states, I used catch per unit effort (CPUE) data. CPUE was calculated as the number of fish captured during 300 seconds of effort for both visual and 'electrofishing+visual' survey methods. I examined frequency histograms of the CPUE data—where frequency data were binned as single unit increases in CPUE (fish/300s effort)—and selected a delineation point for the separation of two occupancy states at an evident break in the frequency data (e.g., Jensen & Vokoun 2013).

To account for imperfect detection, multi-state, multi-season occupancy models must consider how detection probabilities vary among occupancy states (Nichols *et al.* 2007). Models account for the probability of detection for segments that are truly somewhat occupied (*p1*), the probability of detection for segments that are truly highly occupied (*p2*), and state-uncertainty (δ) (i.e., the probability of correctly categorizing segments that were highly occupied, given that they were occupied) (MacKenzie *et al.* 2009). In other words, *p1* represents the probability of observing a single fish in stream segments that are somewhat occupied, *p2* represents the probability of observing a single fish in stream segments that are highly occupied, and 1-δ represents the probability of only observing a few individuals when there are actually many more. The probability of observing at least one fish in segments that were somewhat occupied (*p1*) was allowed to vary between model seasons, while the probability of correctly categorizing stream segments with high abundance (δ), and the probability of observing at least one fish in stream segments that were highly occupied (*p2*) were held constant for all seasons. Environmental covariates were also fitted to detection estimates to help explain non-random variance (Nichols *et al.* 2007).

I evaluated the entire set of environmental covariates for collinearity using Pearson Correlations executed in R (RStudio Team 2015). When covariates were highly correlated (i.e., $|x| \geq 0.70$, $p \leq 0.05$; Berry & Feldman 1985), the covariate that was least likely to be nested in another covariate effect was removed from further analysis. Covariates related to stream morphology and distance to overwintering habitat were least likely to be nested in another covariate effect, followed by covariates related to flow dynamics and biotic processes. To demonstrate, in other model design structures that I explored but were not included in this study (i.e., stream-level occupancy models using spatial replicates) temperature was removed from further analysis because it was highly correlated with discharge and stream slope ($x= 0.79$, $p \leq 0.05$ and $x= -0.78$, $p \leq 0.05$; respectively). This choice was made because slope and discharge have an influence on stream temperature whereas temperature does not influence stream slope and discharge.

Occupancy-specific covariate specifications

Two variations of the depth covariate were included in the *a priori* model set: mean segment depth in the first model season (D_1) and mean segment depth that varied by model-season ($D_{1,2,3,4}$; a.k.a season-specific depth). Mean segment depth in the first model season (D_1) was included to examine whether high early season depths had a threshold effect on YOY Arctic Grayling habitat occupancy, while mean segment depth for each model season was included to examine whether the relationship between depth and habitat occupancy states was maintained throughout the open water season. To test if the effect of depth on YOY Arctic Grayling occupancy was quadratic (e.g., Jones & Tonn 2004b), I included a mean segment depth-squared covariate for both D_1 and $D_{1,2,3,4}$. Similar to depth, I tested two variations of the velocity covariate: mean segment velocity in the first model-season (V_1), and mean segment velocity that varied by model-season ($V_{1,2,3,4}$; aka season-specific velocity). As peak flow typically occurs soon after freshet, I included V_1 to determine whether increasing velocity had a threshold effect on YOY Arctic Grayling habitat occupancy—as evidenced by lower probability of occupancy at higher velocities in other studies (Jones & Tonn 2004b). Season-specific velocity ($V_{1,2,3,4}$) was included to determine if velocity experience throughout the open water season had an effect on YOY Arctic Grayling habitat occupancy. Finally, stream-level discharge in each model seasons ($Q_{1,2,3,4}$) was related to occupancy states of YOY Arctic Grayling.

Detection-specific covariate specifications

I included survey method as a covariate to test the relative detection efficiency between the two detection methods: visual and electrofishing+visual. To determine whether the two detection methods were best analyzed separately or used as temporal replicates in the same model, I ran the two detection methods in separate single season models and compared the results. If environmental covariates were similarly ranked, that would indicate that survey method was not selecting behaviourally distinct subpopulations of YOY, and that it would be acceptable to run detection methods as temporal replicates in multi-state, multi season models (Graves et al. 2012). While detailed further in the results, final models to determine effects of environmental covariates were run with both visual and 'electrofishing+visual' survey methods used as temporal replicates in the multi-state, multi-season model parameterization. Detection efficiency was still modeled for each method, however.

Model Selection and Goodness of Fit Testing

I constructed an *a priori* model set and used Akaike's Information Criterion (AIC) methods to compare and rank competing models in the program PRESENCE (Ver. 9.7) (Burnham & Anderson 1998). Using multiple competing hypotheses enabled me to make inferences on which combination of environmental covariates best approximated the full reality of occupancy and detection (Table 2.2 and 2.3) (Chamberlin 1965; Anderson 2008). Furthermore, I used Akaike model weights to account for model selection uncertainty (i.e., how certain I was that the model selected was the best approximation of biological reality) (Burnham & Anderson 2002). Models were evaluated using their AIC_c values (Hurvich & Tsai 1989), which includes a second-order bias correction for smaller sample sizes (small *n* relative to the number of model parameters, *K*) in order to reduce the chances of overfitting. AIC_c has a somewhat larger penalty term on including extra parameters than AIC, but AIC_c converges on AIC as sample size increases, thus there is negligible disadvantage to using AIC_c (Burnham & Anderson 2004).

It is important in all modeling exercises to demonstrate that a fitted model adequately describes the observed data. AIC assumes that the candidate model set contains at least one model that fits the data adequately; AIC is used to select the best model, but this is no assurance that the selected model is a good model, and substantial lack of fit can lead to inaccurate inferences (Burnham & Anderson 1998). It is common to find overdispersion in binomial estimates of biological populations because of lack of independence in the data due to animal behaviors such as schooling (Eberhardt 1978). While the estimates of model parameters remain unbiased in the presence of overdispersion, the variance estimate from the sample will be too small, thus the data appears to be more dispersed than is expected under the model (White *et al.* 2001).

Goodness-of-fit testing in AIC typically requires the identification of a global model, in which there is a maximum number of relevant parameters (without covariates) based on knowledge of the system; this model should best fit the data (Burnham & Anderson 2002). All other models having fewer parameters would be derived from this model, and would be considered special cases of the global model, thus it is only necessary to assess the goodness of fit of the global model. From this global model, overdispersed variance can be detected by calculating a variance inflation factor (c) from a modified (MacKenzie & Bailey 2004) parametric bootstrapped goodness-of-fit chi-square statistic (X^2) using:

$$\hat{c} = X^2_{\mathrm{Obs}}/\bar{X}^2_{\mathrm{B}}$$

where X^2_{Obs} is the chi-squared test statistic for the observed data and $\bar{X}^2_{\mathrm{B}}$ is the average of the chi squared test statistics obtained from parametric bootstrapping of the data (n=199). If the global model is an adequate description of the data, then $\hat{c}$ should be approximately 1. Serious deviations from $\hat{c}=1$, require use of the Quasi-likelihood estimation parameter (QAICc; Wedderburn 1974); this provides a correction and allows for overdispersion in model selection. However, at present there is no agreed-upon method for testing the goodness-of-fit in multi-state, multi-season occupancy models (pers. communication, D. MacKenzie). Thus, I undertook a modified testing procedure to indirectly assess the goodness of fit of both the most complex (global) model and the top-ranked model. I calculated QAICc for the model set at multiple arbitrary values of $\hat{c}$, to see how this affected the relative ranking of candidate models. Values of $\hat{c}$ were increased by increments of 0.25 and ranged from 1-2. By adjusting $\hat{c}$ to higher values, suggestive of a lack of fit of the models, the model selection becomes more conservative, which tends to favour models with less covariates. If overdispersion exists within the model set, the relative weightings and order of the candidate models change with small changes in $\hat{c}$, and the data is likely too sparse for robust modeling. If the best models continue to be ranked at the top of the candidate model set, this lends some measure of confidence that the best models are a reasonable fit for the data (White & Burnham 1999; Cooch 2012).

Relative Predictive Value of Covariates and the Removal of 'Pretending' Covariates

To provide a formal representation of relative strength of evidence provided by each environmental covariate (independent variables) to explain occupancy and detection parameters (dependent variables), I calculated evidence ratios and ranked them from largest to smallest (Burnham & Anderson 2002). Evidence ratios were calculated by dividing the summed Akaike weights of a particular covariate by its inverse. Environmental covariates with the largest evidence ratios had greater predictive value for a particular occupancy or detection parameter (Burnham & Anderson 2002). Environmental covariates with evidence ratios <1 were identified as 'pretending' variables and removed from further analyses (e.g.,Wylie *et al.* 2010; Dextrase *et al.* 2014). Pretending variables add no predictive value to models within the *a priori* set, and increase the AIC_c scores through the parameter penalty term (Anderson 2008).

Model averaging

Typically, exploratory multivariate research is unable to identify a single best approximating model (i.e., a model with an Akaike weight >0.9; Burnham & Anderson 2002). When no best approximating model exists, it indicates that there is model selection uncertainty among the candidate models (i.e., uncertainty regarding which of top ranked models is the best approximating model in reality; Burnham & Anderson 2002). However, model averaging is computationally difficult with large model sets, so researchers often use a sub-set of models from the candidate set (e.g.,Whittingham *et al.* 2005; Long *et al.* 2011). There are several suggestions on how to select a sub-set of models for model averaging. Richards (2005) suggested that models with ΔAIC >6 should be excluded from further analysis. He also suggested that models that have a ΔAIC<2 are, practically speaking, as good as the best approximate model. The concept behind Richard's (2005) assertion and the method I used to select a sub-set of models for model-averaging is called a 95% confidence set (Burnham & Anderson 2002). Within the selected 95% confidence model sub-set, there is 95% certainty that the best approximating model has been selected. I determined which models should be included in the 95% confidence set by summing Akaike weights from the models after pretending variables were removed, from largest to smallest, and making a cut-off point once the cumulative model weights reached 0.95 (Burnham & Anderson 2002). The 95% threshold is arbitrary, but it is commonly used among researchers and is derived from the frequentist approach.

Multimodel Inference

Once the appropriate model sub-set was selected, I used model-averaging to determine model-weighted estimates for occupancy (i.e., ψ and R) and detection ($p1$, $p2$, and δ) parameters for each model-season. Next, I isolated the model-weighted effect of individual environmental covariates on model-season estimates of occupancy and detection. Standard errors and confidence intervals for covariate parameter estimates were calculated using the delta method (Cooch 2012; Falke *et al.* 2012). Because the stream segments covered the entire study area, a finite population correction to adjust standard errors was merited (Levy 1998). Finite population correction adjustments were calculated for isolated covariate effects when delta method calculations were applied (Cooch 2012). However, the adjustments were not applied to model-averaged estimates of occupancy and detection parameters, so the reported standard errors are conservative (pers. communications, D. Mackenzie).

RESULTS

GENERAL FINDINGS

Young-of-Year Detections

Each of the 67, 30-m stream segments was surveyed a total of 8 times throughout the open water season (4 paired visual and electrofishing+visual surveys). A total of 999 YOY Arctic Grayling were observed during the course of the study using electrofishing + visual surveys, and 929 fish were detected during the course of the study using visual only surveys (Table 2.4). The number of fish detected declined through the study; more fish were detected in model season 1 than in model-seasons 2, 3, or 4 (Table 2.4 and Table 2.5). Fish were most abundant in stream L1A, and least abundant in streams M1, M2, and M3 (Table 2.5).

Table 2.4. Method-specific mean, range, and total number of fish detected in each model season.

Model Season	Mean (±SD) number of fish detected per stream segment		Range of number of fish detected per stream segment		Total number of fish detected for all stream segments	
	Visual	Electro + visual	Visual	Electro + visual	Visual	Electro + visual
Season 1	7.93±20.3	8.66±18.7	0-109	0-97	531	580
Season 2	3.91±9.51	4.31±7.09	0-51	0-41	262	289
Season 3	1.85±3.46	1.31±2.32	0-17	0-10	124	88
Season 4	0.18±0.67	0.63±2.17	0-4	0-16	12	42
TOTAL					**929**	**999**

Table 2.5. Number of fish detected in each stream in each model season (summed across multiple stream segments per stream).

	Model-Season 1		**Model-Season 2**		**Model-Season 3**		**Model-Season 4**		
Stream	Visual	Electro + visual	Visual	Electro + visual	Visual	Electro + visual	Visual	Electro + visual	Total
K5	0	5	3	5	1	2	0	0	16
L3	101	121	9	14	5	3	2	3	258
L2	15	15	23	23	21	21	2	2	122
L1B	99	70	1	8	3	3	0	1	185
L1A	320	357	184	168	60	41	5	26	1161
M4	2	10	56	70	42	18	4	10	212
M3	1	2	0	0	0	0	0	0	3
M2	0	0	0	1	0	0	0	0	1
M1	0	0	0	0	0	0	0	0	0
TOTAL	538	580	276	289	132	88	13	42	

Determining Occupancy States

As described in the methods, data were binned into “occupancy state” categories. Frequency of CPUE was plotted to assess if there were natural breakpoints in the data. A break was apparent between 5 and 6 fish per 300 seconds (Figure 2.4), thus the three occupancy states were set as follows: unoccupied was $\mathrm{CPUE}=0$, somewhat occupied ($\varphi^{[1]}$) was $0<\mathrm{CPUE}<6$, and highly occupied ($\varphi^{[2]}$) was $\mathrm{CPUE} \geq 6$.

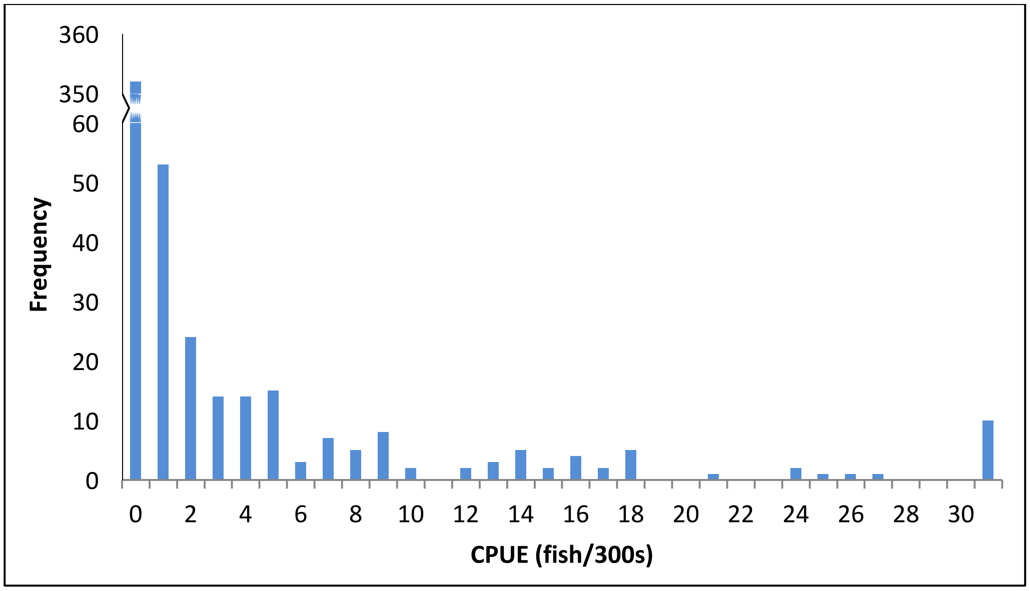

Figure 2.4. Frequency of catch per unit effort (CPUE) data for each survey occasion (summed across all surveys and all model seasons). CPUE was calculated as the number of fish observed per 300 seconds of effort within a single survey. Bin 0-1 contains both non-detection data (i.e., 0 CPUE) and surveys where less than 1 fish was observed per 300 seconds effort (e.g., one fish observed for 500 seconds of effort). *N* = 536 surveys.

Summary of Ecological Covariates

Summary data for stream habitat variables are presented in Tables 2.6 and 2.7. Average discharge, velocity, and depth were highest in model-season 1 and lowest in model-season 4 (Table 2.6). The number of segments with lost surface connectivity was lowest in the first two model-seasons and highest in the final model-season (Table 2.7). Good overhanging vegetation was present in approximately 40% of stream segments, and the majority of stream segments had a stream slope of 1 degree or less (Table 2.7). Run habitat accounted for approximately 73% of meso-habitat across the studied stream segments, such that increasing habitat complexity indicated an increase in the frequency of riffle, cascade, pool, or shallow water pond habitat (Table 2.6). Boulder substrate was the dominant substrate type in approximately 84% of stream segments (Table 2.7). Bankfull width in the pre-survey period ranged from 4 to 80 meters wide. All streams and stream segments were well-oxygenated throughout the sampling period (minimum dissolved oxygen concentration was 9 mg/L) with near-neutral pH and low specific conductivity (Table 2.6). Water temperature varied from 8.6 - 22.4°C, and distance to overwintering habitat varied from 0 to 1.65 km (Table 2.6).

Table 2.6. Mean, standard deviation, and range of continuous habitat variables used in models.

	Mean±SD	**Range**
Bankfull Width (m) (June)	29.4±14.28	4-80.25
% Run	73.19±27.45	0-100
% Riffle	9.1±9.69	0-50
%Pool	4.64±7.13	0-40
% Pond	8.73±24.24	0-100
% Cascade	3.8±13.57	0-75
% Undercut Banks	14.72±12.16	0-75
Temperature model season 1 (T1; °C)	16.6±1.6	14.2-18.8
Temperature model season 2 (T2; °C)	19±2.5	15.7-22.4
Temperature model season 3 (T3; °C)	15.8±2	12.4-18.7
Temperature model season 4 (T4; °C)	10.1±1.2	8.6-11.8
Dissolved oxygen model season 1 (DO1; mg/L)	10±0.7	9-11
Dissolved oxygen model season 2 (DO2; mg/L)	9.6±0.5	9-10
Dissolved oxygen model season 3 (DO3; mg/L)	9.4±0.4	9-10
Dissolved oxygen model season 4 (DO4; mg/L)	9.2±0.4	9-10
pH model season 1 (pH1; pH)	7±0.1	6.85-7.16
pH model season 2 (pH2; pH)	7.2±0.2	6.85-7.45
pH model season 3 (pH3; pH)	6.9±0.2	6.59-7.28
pH model season 4 (pH4; pH)	6.7±0.1	6.45-6.8
Specific conductivity model season 1 (SPC1; µS/cm)	13.9±0.6	12.9-14.8
Specific conductivity model season 2 (SPC2; µS/cm)	14.3±0.5	13.8-15.3
Specific conductivity model season 3 (SPC3; µS/cm)	14.5±0.8	13.4-15.9
Specific conductivity model season 4 (SPC4; µS/cm)	14.6±0.9	13.4-16.3
Discharge model season 1 (Q1; m3/s)	0.21±0.04	0.15-0.31
Discharge model season 2(Q2; m3/s)	0.09±0.02	0.06-0.12
Discharge model season 3 (Q3; m3/s)	0.06±0.02	0.03-0.1
Discharge model season 4 (Q4; m3/s)	0.03±0.02	0.01-0.05
Mean segment depth model season 1 (D1; m)	0.38±0.19	0.12-1
Mean segment depth model season 2 (D2; m)	0.32±0.22	0.09-1
Mean segment depth model season 3 (D3; m)	0.31±0.23	0.073-1
Mean segment depth model season 4 (D4; m)	0.28±0.21	0.01-1
Mean segment velocity model season 1 (V1; m/s)	0.13±0.1	0.01-0.55
Mean segment velocity model season 2 (V2; m/s)	0.09±0.067	0.0075-0.38
Mean segment velocity model season 3 (V3; m/s)	0.075±0.063	0.0075-0.4175
Mean segment velocity model season 4 (V4; m/s)	0.043±0.042	0.0025-0.2675
H'/5	0.29±0.08	0.2-0.48
Distance to overwintering habitat (D2OW; m)	458.43±437.25	0-1645

Table 2.7. Median, mode, range, and sum of non-continuous habitat variables used in models.

	Median	Mode	Range	Total
Stream segment slope (degrees)	1	1	0-4	
Good overhanging vegetation (y/n)	0	0	0-1	
Dominant substrate score*	4	4	1-4	
No. of segments with lost surface water connectivity (model-season 1)	-	-	-	0
No. of segments with lost surface water connectivity (model-season 1)	-	-	-	0
No. of segments with lost surface water connectivity (model-season 1)	-	-	-	1
No. of segments with lost surface water connectivity (model-season 1)	-	-	-	10

*Dominant substrate score is a numerical representation of the dominant substrate type where 1= fines, 2=gravel, 3=cobble, 4=boulder, and 5=bedrock (Vancouver Island University 2014).

MODEL PREPARATION

Model Structure and AIC Corrections

To determine whether it was appropriate to use the two detection methods (i.e., electrofishing+visual and visual only) as repeat surveys within model-seasons to increase the precision of detection and occupancy estimates, I separated occupancy data by survey method and ran each set in single-season, multi-state models. The influence of environmental covariates on the probability of occupancy and detection (derived from summed model weights) was similar (similarly ranked) in both ‘electrofishing+visual’ and visual-only models, with differences highlighted in grey (Tables 2.8 and 2.9). This indicated that using detection methods as repeat surveys in the main model (to establish effects of covariates on probability of occupancy states) should not introduce undue bias to model selection. Meaning, the conclusions I am drawing from using the two survey methods as repeat surveys is not method dependent.

As model sets were too complex to directly assess the fit of the model (see Methods), I used the manual $\hat{c}$ adjustment procedure for indirect goodness-of-fit assessment. I found that both the top model and the global (most complex) model retained high AIC weights (w_i), providing evidence that the models were not overdispersed, and as such, that QAICc adjustment was not necessary for model ranking.

Table 2.8. Model statistics for the single-season, multistate models using visual detection surveys.

Model	AICc	ΔAICc	AIC wgt	Model Likelihood	no.Par.	-2*LogLike
ψ(.),*R*(GOHV),*p1*(.),*p2*(.),*δ*(.)	412.38	0	0.912	1	6	398.98
ψ(Q),*R*(.),*p1*(.),*p2*(.),*δ*(.)	418.37	5.99	0.0456	0.05	6	404.97
ψ(.),*R*(H'/5),*p1*(.),*p2*(.),*δ*(.)	419.86	7.48	0.0217	0.0238	6	406.46
ψ(.),*R*(V),*p1*(.),*p2*(.),*δ*(.)	421.09	8.71	0.0117	0.0128	6	407.69
ψ(D2OW),*R*(.),*p1*(.),*p2*(.),*δ*(.)	423.36	10.98	0.0038	0.0041	6	409.96
ψ(.),*R*(D2OW),*p1*(.),*p2*(.),*δ*(.)	425.45	13.07	0.0013	0.0015	6	412.05
ψ(.),*R*(.),*p1*(Depth),*p2*(.),*δ*(.)	426.29	13.91	0.0009	0.001	6	412.89
ψ(Slope),*R*(.),*p1*(.),*p2*(.),*δ*(.)	427.23	14.85	0.0005	0.0006	6	413.83
ψ(V),*R*(.),*p1*(.),*p2*(.),*δ*(.)	427.25	14.87	0.0005	0.0006	6	413.85
ψ(H'/5),*R*(.),*p1*(.),*p2*(.),*δ*(.)	427.33	14.95	0.0005	0.0006	6	413.93
ψ(D),*R*(.),*p1*(.),*p2*(.),*δ*(.)	427.46	15.08	0.0005	0.0005	6	414.06
ψ(.),*R*(.),*p1*(.),*p2*(.),*δ*(.)	428.45	16.07	0.0003	0.0003	5	417.47
ψ(.),*R*(.),*p1*(D,DSQ),*p2*(.),*δ*(.)	428.79	16.41	0.0002	0.0003	7	412.89
ψ(.),*R*(.),*p1*(GOHV),*p2*(.),*δ*(.)	428.86	16.48	0.0002	0.0003	6	415.46
ψ(D,DSQ),*R*(.),*p1*(.),*p2*(.),*δ*(.)	429.96	17.58	0.0001	0.0002	7	414.06

Table 2.9. Model statistics for the single-season, multistate models using electrofishing+visual detection surveys. Covariate rankings that diverge from visual survey model are highlighted in grey.

Model	AICc	ΔAICc	AIC wgt	Model Likelihood	no.Par.	-2*LogLike	Visual Ranking
ψ(.),*R*(GOHV),*p1*(.),*p2*(.),*δ*(.)	436.05	0	0.9871	1	6	422.65	1
ψ(Q),*R*(.),*p1*(.),*p2*(.),*δ*(.)	445.57	9.52	0.0085	0.0086	6	432.17	2
ψ(.),*R*(V),*p1*(.),*p2*(.),*δ*(.)	448.74	12.69	0.0017	0.0018	6	435.34	4
ψ(V),*R*(.),*p1*(.),*p2*(.),*δ*(.)	450.5	14.45	0.0007	0.0007	6	437.1	9
ψ(.),*R*(H'/5),*p1*(.),*p2*(.),*δ*(.)	450.81	14.76	0.0006	0.0006	6	437.41	3
ψ(.),*R*(.),*p1*(D),*p2*(.),*δ*(.)	451.22	15.17	0.0005	0.0005	6	437.82	7
ψ(Slope),*R*(.),*p1*(.),*p2*(.),*δ*(.)	452.72	16.67	0.0002	0.0002	6	439.32	8
ψ(Depth),*R*(.),*p1*(.),*p2*(.),*δ*(.)	453.35	17.3	0.0002	0.0002	6	439.95	11
ψ(.),*R*(.),*p1*(D,DSQ),*p2*(.),*δ*(.)	453.72	17.67	0.0001	0.0001	7	437.82	13
ψ(H'/5),*R*(.),*p1*(.),*p2*(.),*δ*(.)	454.52	18.47	0.0001	0.0001	6	441.12	10
ψ(.),*R*(D2OW),*p1*(.),*p2*(.),*δ*(.)	455.49	19.44	0.0001	0.0001	6	442.09	6
ψ(D2OW),*R*(.),*p1*(.),*p2*(.),*δ*(.)	455.81	19.76	0.0001	0.0001	6	442.41	5
ψ(D,DSQ),*R*(.),*p1*(.),*p2*(.),*δ*(.)	455.85	19.8	0	0.0001	7	439.95	15
ψ(.),*R*(.),*p1*(.),*p2*(.),*δ*(.)	455.92	19.87	0	0	5	444.94	12
ψ(.),*R*(.),*p1*(GOHV),*p2*(.),*δ*(.)	458.06	22.01	0	0	6	444.66	14

'Pretending' Covariates, Covariate Ranking, and the 95% Confidence Model Set

No covariates were removed from the modeling analysis based on correlation alone, as none of the *a priori* set of explanatory covariates of probability of occupancy and/or detection had Pearson correlation values greater than 0.70 (Appendix A; Tables A1 and A2). To ensure that 'pretending' covariates were not lending false inference to my model set, covariates were ranked using evidence ratios and those with evidence ratios <1 were removed from further analysis (Table 2.10 and 2.11; highlighted in grey) (MacKenzie 2006; Dextrase *et al.* 2014). This set of models did not include the following covariates on: 1) ψ – (the probability a segment is occupied; $\psi = \varphi^{[1]} + \varphi^{[2]}$): good overhanging vegetation, velocity-squared, season-specific depth, depth squared, variance of segment velocity; 2) R (conditional probability that a segment is highly occupied, given it is at least somewhat occupied; $R = \varphi^{[2]} / \psi$): stream segment slope, first model-season depth, season-specific depth, season-specific velocity, velocity-squared, depth-squared, discharge, variance of segment velocity; 3) δ (probability that a highly occupied stream segment is correctly identified): all survey-specific covariates; 4) *p1* (the probability that at least one fish was observed in stream segments that are somewhat occupied): repeat survey bias, good overhanging vegetation, depth squared ; and, 5) *p2* (probability that at least one fish was observed in stream segments that are at a highly occupied): all survey specific covariates (Table 2.10 and 2.11).

Summed AIC weights were used to determine the relative explanatory power of fitted covariates on occupancy and detection parameters, with 1 being the strongest evidence (Table 2.10). Covariates that had the strongest effect on the probability that a stream segment was occupied (ψ), from strongest to weakest, included: stream segment slope, distance to overwintering habitat, discharge, mean segment depth in the first model season, and mean segment velocity in the first model season (each having summed Akaike weights >0.95; Table 2.10). There was also strong evidence that habitat complexity (H'/5) was related to the probability that a stream segment was occupied, with a summed Akaike weight of 0.91. Covariates that were most strongly related to the conditional probability that a stream segment was highly occupied (R), from strongest to weakest, included: good overhanging vegetation, distance to overwintering habitat, and habitat complexity (total Akaike weight >0.98). There was moderate evidence that velocity in the first model-season was related to the conditional probability that a segment was highly occupied (Σw_{v1}= 0.72). Sample method was the most important covariate (Σw_{Method}= 0.95) and stream depth was moderately important (Σw_{sdepth}= 0.80) in determining the probability of detecting a fish in stream segments that were somewhat occupied ($\varphi^{[1]}$) (Table 2.10). Models that included a combination of these environmental covariates but were beyond the cumulative Akaike weight of 0.95 were removed from further analysis to form the 95% confidence set; highlighted in grey (Tables 2.11 and 2.12). As described in the methods, using criteria outlined in (Burnham & Anderson 2002), a 95% confidence set represents 95% certainty that the model-averaged model set is the best approximating model (Table 2.12). A description of occupancy-specific and detection-specific environmental covariates used in *a priori* model set was provided in Tables 2.2 and 2.3 (Methods).

Table 2.10. Evidence ratios and summed model weights of the covariates included in the *a priori* model set. Evidence ratios are calculated by taking the quotient of the covariate summed model weight and its inverse, where the two sum to 1 (i.e., summed model weight/(1-summed model weight). Covariates with an evidence ratio less than one were considered 'pretending' variables and were removed from further analysis; highlighted in grey.

Parameter	Covariate	Evidence Ratio	Summed Model Weight
R	GOHV	3332	0.9997
ψ	Slope	1999	0.9995
R	D2OW	832	0.9988
ψ	D2OW	416	0.9976
ψ	Q	356	0.9972
ψ	D1	103	0.9904
R	H'/5	51	0.9806
ψ	V1	24	0.9599
$p1$	Method	19	0.9495
ψ	H'/5	10	0.9086
$p1$	Depth	4	0.7962
R	V1	3	0.7212
δ	Method	0.38	0.2732
ψ	Velocity Squared	0.29	0.2341
$p1$	Depth Squared	0.29	0.2243
δ	Repeat	0.02	0.0167
$p1$	Repeat	0.002	0.0018
ψ	Depth Squared	<0.01	<0.001
R	Depth Squared	<0.01	<0.001
R	Velocity Squared	<0.01	<0.001

Table 2.11. *A priori* model set. Models that contain ‘pretending’ variables or were ranked outside the 95% confidence set were removed from further analysis; highlighted in grey.

Model	AICc	ΔAICc	wgt	Likelihood	*K*	-2*LogLik
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV),*δ*(.),*p1*(Method,Depth),*p2*(.)	685.60	0.00	0.1020	1.0000	25	603.89
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,V1,H'/5,GOHV),*δ*(.),*p1*(Method,Depth),*p2*(.)	686.19	0.59	0.0759	0.7445	26	599.09
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV),*δ*(.),*p1*(Method,Depth,DSQ),*p2*(.)	686.23	0.63	0.0744	0.7298	26	599.13
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,V1,H'/5,GOHV),*δ*(.),*p1*(Method),*p2*(.)	686.59	0.99	0.0622	0.6096	25	604.88
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV),*δ*(.),*p1*(*R*epeat,Depth),*p2*(.)	686.81	1.21	0.0557	0.5461	25	605.1
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV),*δ*(Method),*p1*(Method,Depth),*p2*(.)	687.01	1.41	0.0504	0.4941	26	599.91
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,D(1-4),V1,H'/5,GOHV),*δ*(.),*p1*(Method,Depth),*p2*(.)	687.25	1.65	0.0447	0.4382	27	594.48
ψψ(S,D2OW,V1,CoeffVD1,Q,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV),*δ*(.),*p1*(Method,Depth),*p2*(.)	687.58	1.98	0.0379	0.3716	26	600.48
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV),*δ*(*R*epeat),*p1*(Method,Depth),*p2*(.)	687.64	2.04	0.0368	0.3606	26	600.54
ψψ(S,D2OW,V1,D1,VSQ1,Q,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV),*δ*(.),*p1*(Method,Depth),*p2*(.)	687.82	2.22	0.0336	0.3296	26	600.72
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV),*δ*(.),*p1*(Method,Depth),*p2*(Method)	687.84	2.24	0.0333	0.3263	26	600.74
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV),*δ*(.),*p1*(Method,Depth),*p2*(depth)	688.09	2.49	0.0294	0.2879	26	600.99
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,V(1-4),VSQ,H'/5,GOHV),*δ*(.),*p1*(Method,Depth),*p2*(.)	688.38	2.78	0.0254	0.2491	27	595.61
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV),*δ*(Depth),*p1*(Method,Depth),*p2*(.)	688.55	2.95	0.0233	0.2288	26	601.45
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,H'/5,Q,GOHV),*δ*(.),*p1*(Method,Depth),*p2*(.)	689.21	3.61	0.0168	0.1645	26	602.11
ψψ(S,D2OW,D1,Q,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV),*δ*(.),*p1*(Method,Depth),*p2*(.)	689.28	3.68	0.0162	0.1588	24	612.71
ψψ(S,D2OW,D1,Q,H'/5,Slope),*R*(S,D2OW,V1,H'/5,GOHV),*δ*(.),*p1*(Method,Depth),*p2*(.)	689.29	3.69	0.0161	0.1580	25	607.58
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV),*δ*(.),*p1*(,Depth,DSQ),*p2*(.)	689.30	3.70	0.0160	0.1572	25	607.59
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV),*δ*(.),*p1*(Method,Depth,*R*epeat),*p2*(.)	689.30	3.70	0.0160	0.1572	26	602.2
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,V(1-4),H'/5,GOHV),*δ*(.),*p1*(Method,Depth),*p2*(.)	689.52	3.92	0.0144	0.1409	26	602.42
ψψ(S,D2OW,V1,D1,DSQ,Q,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV),*δ*(.),*p1*(Method,Depth),*p2*(.)	689.61	4.01	0.0137	0.1347	26	602.51
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,V1,H'/5,GOHV),*δ*(.),*p1*(Depth),*p2*(.)	689.72	4.12	0.0130	0.1275	25	608.01
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,D1,H'/5,GOHV),*δ*(.),*p1*(Method,Depth),*p2*(.)	689.79	4.19	0.0126	0.1231	26	602.69
ψψ(S,D2OW,V(1-4,D1,Q,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV),*δ*(.),*p1*(Method,Depth),*p2*(.)	689.86	4.26	0.0121	0.1188	25	608.15
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV),*δ*(.),*p1*(.),*p2*(.)	690.28	4.68	0.0098	0.0963	23	618.61
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV),*δ*(.),*p1*(Method,GOHV),*p2*(.)	690.40	4.80	0.0093	0.0907	25	608.69
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV),*δ*(.),*p1*(Method,*R*epeat),*p2*(.)	690.48	4.88	0.0089	0.0872	25	608.77
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope,GOHV),*R*(S,D2OW,H'/5,GOHV),*δ*(.),*p1*(Method,Depth),*p2*(.)	690.62	5.02	0.0083	0.0813	26	603.52
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV,Slope),*δ*(.),*p1*(Method,Depth),*p2*(.)	690.64	5.04	0.0082	0.0805	26	603.54
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV),*δ*(.),*p1*(Method,Depth),*p2*(GOHV)	690.71	5.11	0.0079	0.0777	26	603.61
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV),*δ*(.),*p1*(Method,Depth,gohv),*p2*(.)	690.72	5.12	0.0079	0.0773	26	603.62
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV),*δ*(GOHV),*p1*(Method,Depth),*p2*(.)	690.96	5.36	0.0070	0.0686	26	603.86
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,V1,VSQ,H'/5,GOHV),*δ*(.),*p1*(Method,Depth),*p2*(.)	691.25	5.65	0.0060	0.0593	27	598.48
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,D(1-4),DSQ,H'/5,GOHV),*δ*(.),*p1*(Method,Depth),*p2*(.)	691.33	5.73	0.0058	0.0570	27	598.56
ψψ(S,D2OW,CoeffV,D1,Q,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV),*δ*(.),*p1*(Method,Depth),*p2*(.)	691.43	5.83	0.0055	0.0542	25	609.72
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,V1,CoeffV,H'/5,GOHV),*δ*(.),*p1*(Method,Depth),*p2*(.)	691.49	5.89	0.0054	0.0526	27	598.72
ψψ(S,D2OW,V1,Q,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV),*δ*(.),*p1*(Method,Depth),*p2*(.)	691.67	6.07	0.0049	0.0481	24	615.1
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV),*δ*(Method,*R*epeat),*p1*(Method,Depth),*p2*(.)	692.14	6.54	0.0039	0.0380	27	599.37
ψψ(S,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV),*δ*(.),*p1*(Method,Depth),*p2*(.)	692.99	7.39	0.0025	0.0248	24	616.42
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV),*δ*(.),*p1*(GOHV,Depth),*p2*(.)	693.63	8.03	0.0018	0.0180	25	611.92
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV),*δ*(.),*p1*(Method,Depth),*p2*(Depth,DSQ)	693.70	8.10	0.0018	0.0174	27	600.93
ψψ(S,D2OW,V1,VSQ1,Q,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV),*δ*(.),*p1*(Method,Depth),*p2*(.)	693.72	8.12	0.0018	0.0172	25	612.01
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV),*δ*(Depth,DSQ),*p1*(Method,Depth),*p2*(.)	694.22	8.62	0.0014	0.0134	27	601.45
ψψ(S,D2OW,V(1-4),CoeffV,D1,Q,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV),*δ*(.),*p1*(Method,Depth),*p2*(.)	694.56	8.96	0.0012	0.0113	26	607.46
ψψ(S,D2OW,V(1-4),VSQ,D1,Q,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV),*δ*(.),*p1*(Method,Depth),*p2*(.)	695.13	9.53	0.0009	0.0085	26	608.03
ψψ(S,D2OW,V1,D(1-4),DSQ,Q,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV),*δ*(.),*p1*(Method,Depth),*p2*(.)	695.77	10.17	0.0006	0.0062	26	608.67
ψψ(S,D2OW,V1,D(1-4),Q,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV),*δ*(.),*p1*(Method,Depth),*p2*(.)	696.23	10.63	0.0005	0.0049	25	614.52
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,H'/5,GOHV),*δ*(.),*p1*(Method,Depth),*p2*(.)	696.80	11.20	0.0004	0.0037	24	620.23
ψψ(S,D2OW,V1,D1,H'/5,Slope),*R*(S,D2OW,H'/5,GOHV),*δ*(.),*p1*(Method,Depth),*p2*(.)	697.48	11.88	0.0003	0.0026	24	620.91
ψψ(S,D2OW,V1,D1,Q,H'/5),*R*(S,D2OW,H'/5,GOHV),*δ*(.),*p1*(Method,Depth),*p2*(.)	699.79	14.19	0.0001	0.0008	24	623.22
ψψ(S,D2OW,V1,D1,Q,H'/5,GOHV),*R*(S,D2OW,H'/5,GOHV),*δ*(.),*p1*(Method,Depth),*p2*(.)	702.18	16.58	0.0000	0.0003	25	620.47
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,H'/5,Slope),*δ*(.),*p1*(Method,Depth),*p2*(.)	718.59	32.99	0.0000	0.0000	25	636.88
ψψ(S,D2OW,V1,D1,Q,H'/5,Slope),*R*(S,D2OW,H'/5),*δ*(.),*p1*(Method,Depth),*p2*(.)	719.21	33.61	0.0000	0.0000	24	642.64

Table 2.12. Model statistics for the 6 models that formed the 95% confidence set.

Model	AICc	ΔAICc	K	$-2l$	w_i
ψ (S,D2OW,V1,D1,Q,H'/5,Slope),R(S,D2OW,H'/5,GOHV),δ(.),$p1$(Method,Depth),$p2$(.)	685.60	0.00	25	603.89	0.37
ψ (S,D2OW,V1,D1,Q,H'/5,Slope),R(S,D2OW,V1,H'/5,GOHV),δ(.),$p1$(Method,Depth),$p2$(.)	686.19	0.59	26	599.09	0.27
ψ (S,D2OW,V1,D1,Q,H'/5,Slope),R(S,D2OW,V1,H'/5,GOHV),δ(.),$p1$(Method),$p2$(.)	686.59	0.99	25	604.88	0.22
ψ (S,D2OW,D1,Q,H'/5,Slope),R(S,D2OW,V1,H'/5,GOHV),δ(.),$p1$(Method,Depth),$p2$(.)	689.29	3.69	25	607.58	0.06
ψ (S,D2OW,V1,D1,Q,H'/5,Slope),R(S,D2OW,V1,H'/5,GOHV),δ(.),$p1$(Depth),$p2$(.)	689.72	4.12	25	608.01	0.05
ψ (S,D2OW,V1,D1,Q,H'/5,Slope),R(S,D2OW,H'/5,GOHV),δ(.),$p1$(.),$p2$(.)	690.28	4.68	23	618.61	0.04

Estimates for Model-Season Occupancy and Imperfect Detection

Model selection statistics indicated that model ψ(D2OW,V1,D1,Q,H,Slope), R(D2OW,H,GOHV), δ(.), $p1$(Method, Depth), and $p2$(.) provided the best description of the data (w_1= 0.37) (Table 2.12). However, the global model and a model omitting depth fitted for detection a stream segment that was somewhat occupied ($p1$) were also well-supported (w_2= 0.27, and w_3= 0.22) (Table 2.12). To account for model selection uncertainty, model-averaging was applied to all models in the 95% confidence set (Table 2.12); full results of model-averaging are available in Appendix B.

The model averaged detection probability for state uncertainty between occupied states (δ) was δ=0.59, SE= 0.06 for all four model seasons (Table 2.13); thus there was a 60% probability that a stream segment was correctly classified as being highly occupied (given that it was occupied). Model-averaged probabilities of detecting a single fish in stream segments that were occupied varied considerably across model seasons, with the greatest detection efficiency occurring in season three ($p1_{\text{season 1}} = 0.547 \pm 0.13$ SD, $p1_{\text{season 2}} = 0.30 \pm 0.11$ SD, $p1_{\text{season 3}} = 0.755 \pm 0.11$ SD, $p1_{\text{season 4}} = 0.246 \pm 0.10$ SD) (Table 2.13). The model-averaged probability of detecting a single fish in stream segments that were highly occupied ($p2$) was near perfect ($p2$=0.98, SE=0.02) (Table 2.13).

After adjusting for non-detection, probability of occupancy for stream segments that were occupied (ψ) was relatively high in the first two model seasons (ψ_1=0.60± SD=0.36 and ψ_2=0.89±

SD=0.16), whereas occupancy estimates decreased slightly in model season 3 and stayed relatively constant through model season 4 (ψ_3=0.43± SD=0.33 and ψ_4=0.47± SD=0.33) (Table 2.13). These occupancy values are greater than naïve occupancy estimates (where probability of detection is not taken into account), which were approximately 0.55 in model-season 1, 0.60 in model-season 2, 0.41 in model-season 3, and 0.22 in model-season 4) (Table 2.13).

The conditional probability that a stream segment was highly occupied, *R*, was similar for the first two seasons (R_1=0.35± SD= 0.31 and R_2=0.32± SD=0.32), whereas the conditional probability of highly occupied stream segments decreased in seasons 3 and 4 (R_3=0.24± SD=0.28 and 0.05 ± SD=0.12) (Table 2.13). The adjusted (for imperfect detection) probability estimates for highly occupied stream segments were less than naïve estimates (naïve occupancy estimate approximately 0.4 in season 1, 0.4 in season 2, 0.39 in season 3, and 0.08 in season 4), but the difference between naïve and derived occupancy estimates was not as great for stream segments that were highly occupied as it was for overall occupancy (Table 2.13).

Table 2.13. Naïve and model-averaged estimates of probability that stream segments were occupied (ψ; psi), and highly occupied (R). Model-averaged estimates of seasonal detection probabilities for occupied stream segments ($p1_{\text{seasons1-4}}$), as well as probability that stream segments were correctly classified as highly occupied (δ), and probability that at least one fish was detected in highly occupied stream segments ($p2$).

Seasonal Occupancy and Detection	**Naïve Estimates**	**Model-Avg-Est**	**SD**
ψ(model season 1)(avg. all stream segments)	0.55	0.604	0.358
ψ (model season 2)(avg. all stream segments)	0.60	0.898	0.163
ψ (model season 3)(avg. all stream segments)	0.41	0.432	0.337
ψ (model season 4)(avg. all stream segments)	0.22	0.477	0.331
R(model season 1)(avg. all stream segments)	0.4	0.359	0.314
R (model season 2)(avg. all stream segments)	0.4	0.328	0.328
R (model season 3)(avg. all stream segments)	0.39	0.242	0.286
R (model season 4)(avg. all stream segments)	0.08	0.0586	0.121
δ (.)	-	0.594	0.0598*
$p1$(model season 1)(avg. all stream segments)	-	0.547	0.126
$p1$(model season 2)(avg. all stream segments)	-	0.299	0.109
$p1$(model season 3)(avg. all stream segments)	-	0.755	0.112
$p1$(model season 4)(avg. all stream segments)	-	0.246	0.0953
$p2$(.)	-	0.984	0.0160*

* Both δ and $p2$ detection parameters were held constant for all model seasons, and were not associated with any ecological covariates. The variance term reported is the standard error as calculated by the delta method.

EFFECTS OF ENVIRONMENTAL COVARIATES

Beta coefficients

Table 2.14a and 2.14b provide a summary of the Beta regression coefficients (on the logit scale) for model-season specific parameter intercepts (Table 2.14a) and environmental covariates (Table 2.14b). For season-specific occupancy and detection parameters in Table 2.14a, Beta coefficients represent the baseline occupancy or detection upon which the additive effects of environmental covariates are summed to determine occupancy or detection estimates (e.g., *p1* in model-season 1 = -0.08(1) + 0.85(Method) + -0.4(Depth)). A Beta value of 0.00 is equivalent to 50% occupancy or detection on the probability scale. For continuous covariates in Table 2.14b, Beta coefficients represent the relative magnitude and direction of the standardized effect over one standard deviation increase in the covariate value. For binary and ordinal data, Beta coefficients represent the relative magnitude and direction of effect for every unit of increase. This approach is particularly useful when covariates are measured in different units. However, since data must be transformed from the logit scale to the probability scale using the delta method, model-averaged Beta coefficiencts should be considered a preliminary evaluation of the magnitude and direction of covariate effects (MacKenzie *et al.* 2006; Greene 2012).

Table 2.14a. Summary of model-averaged Beta estimates for model-season intercepts (β_0) prior to being converted onto the probability scale with corrections to standard errors applied

Parameter	Model Season	β estimate	SE
ψ	1	6.29	0.81
ψ	2	3.18	0.86
ψ	3	-1.76	0.27
ψ	4	-2.76	0.69
R	1	-2.54	0.35
R	2	-3.28	0.39
R	3	-4.07	0.51
R	4	-6.61	0.67
p1	1	-0.08	0.19
p1	2	-1.37	0.21
p1	3	0.76	0.26
p1	4	-1.74	0.32
p2	All	4.11	0.5
δ	All	0.38	0.12

Table 2.14b. Summary of model-averaged Beta estimates (β_1) for fitted covariates prior to being converted onto the probability scale with corrections to standard errors applied.

Parameter	Covariate	β estimate	SE
R	GOHV	3.82	0.39
ψ	Q	-2.71	0.39
ψ	$D_{season1}$	-2.2	0.4
ψ	Slope	1.89	0.34
R	D2OW	-1.63	0.24
ψ	D2OW	-1.4	0.21
ψ	V1	-1.25	0.21
p1	Method	0.85	0.34
R	H'/5	0.78	0.35
ψ	H'/5	0.69	0.21
R	$V_{season1}$	-0.64	0.7
p1	Depth	-0.4	0.46

Probability a segment is occupied (ψ) – In the first model season, increasing water depth, velocity of the stream segment, and stream-scale discharge all had a negative influence on the probability that a stream segment was occupied (Figures 2.5 to 2.7).

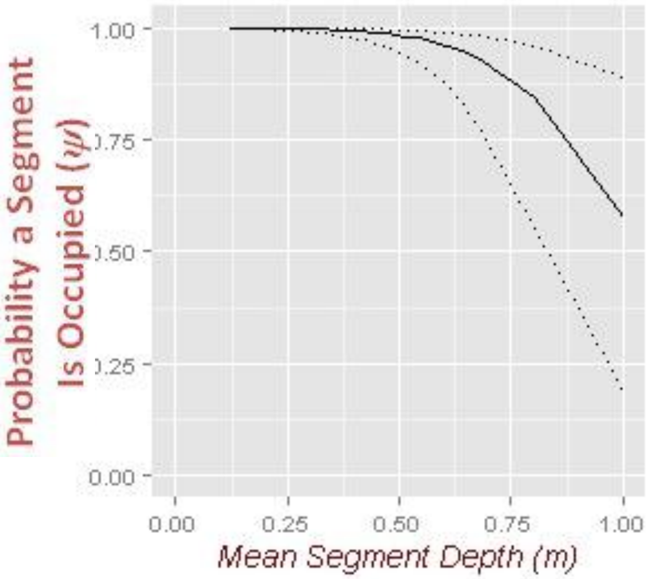

Figure 2.5. Model-averaged effect of mean segment depth (m) on the probability a stream segment is occupied (ψ) in the first model-season. Dotted lines represent 95% confidence intervals.

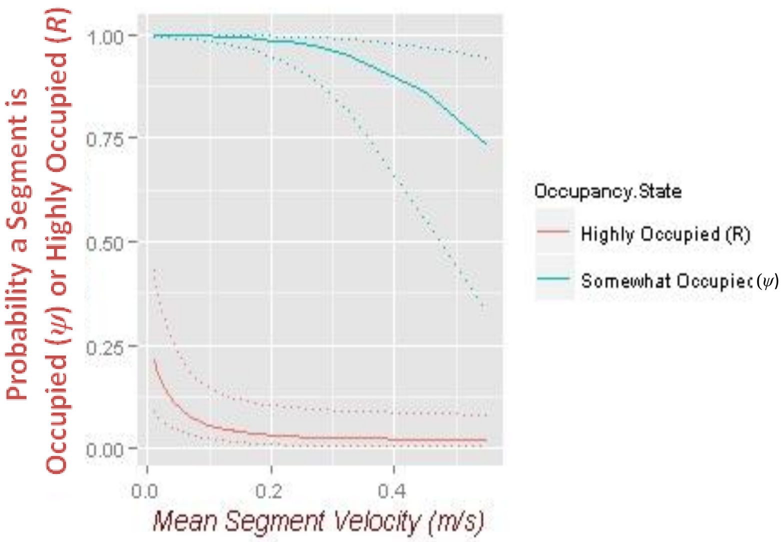

Figure 2.6. Model-averaged effects of mean segment velocity (m/s) on the probability a stream segment is occupied (*ψ*) and conditionally highly occupied (*R*) in the first model-season. Dotted lines represent 95% confidence intervals.

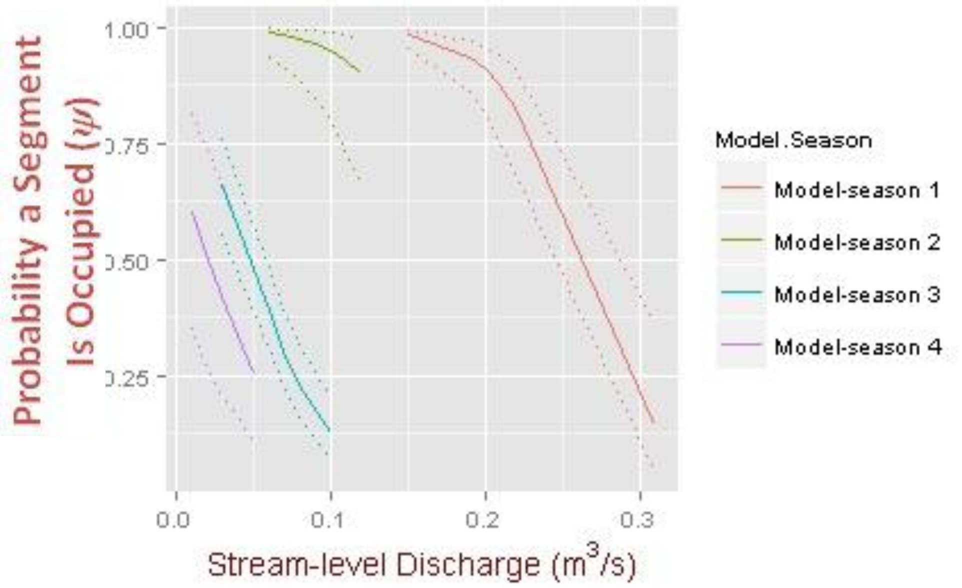

Figure 2.7. Model averaged effects of stream-level discharge (m^3/s) on the probability a stream segment was occupied (*ψ*) in each of the four model seasons. Dotted lines represent 95% confidence intervals.

In model seasons 2, 3, and 4, stream segment slope and distance to overwintering habitat had the greatest effect on the probability a stream segment was occupied (Figures 2.8 and 2.9). Habitat complexity and stream discharge were also key determinants of a stream segment being occupied (Figures 2.7 and 2.10). Stream segment slope and habitat complexity had a positive influence on the stream segments being occupied, whereas distance to overwintering habitat and stream-level discharge had a negative influence on the stream segment being occupied (Figures 2.7 to 2.10). In model seasons 3 and 4, the greatest decline in probability that a stream segment was occupied (ψ) occurred in the first 500m from an overwintering lake (Figure 2.9). As overall discharge decreased across model seasons, so too did the overall probability of occupancy (Figure 2.7).

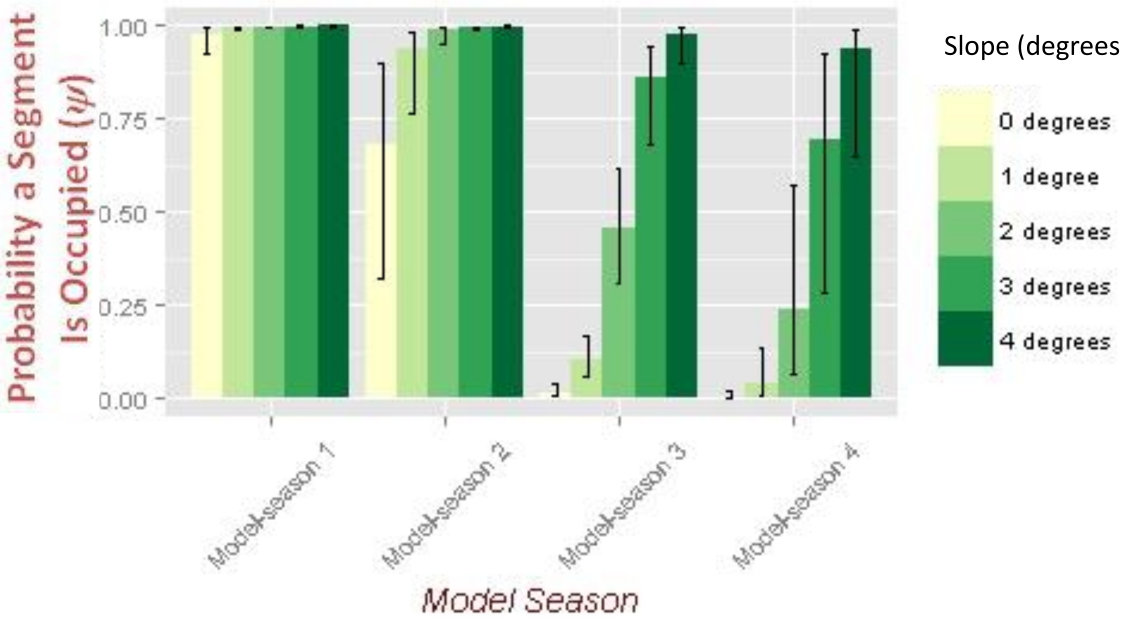

Figure 2.8. Model-averaged effects of stream segment slope (degrees) on the probability a stream segment is occupied (ψ) in each of the four model seasons. Error bars represent 95% confidence intervals.

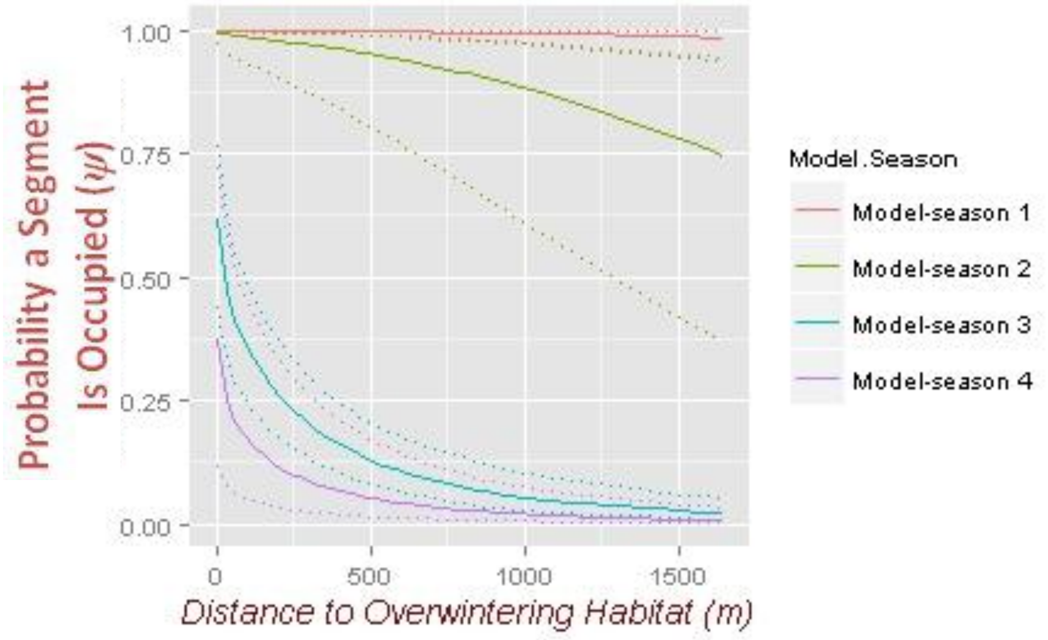

Figure 2.9. Model-averaged effects of distance to overwintering habitat (m) on the probability that a stream segment was occupied (*ψ*) in each of the four model seasons. Dotted lines represent 95% confidence intervals.

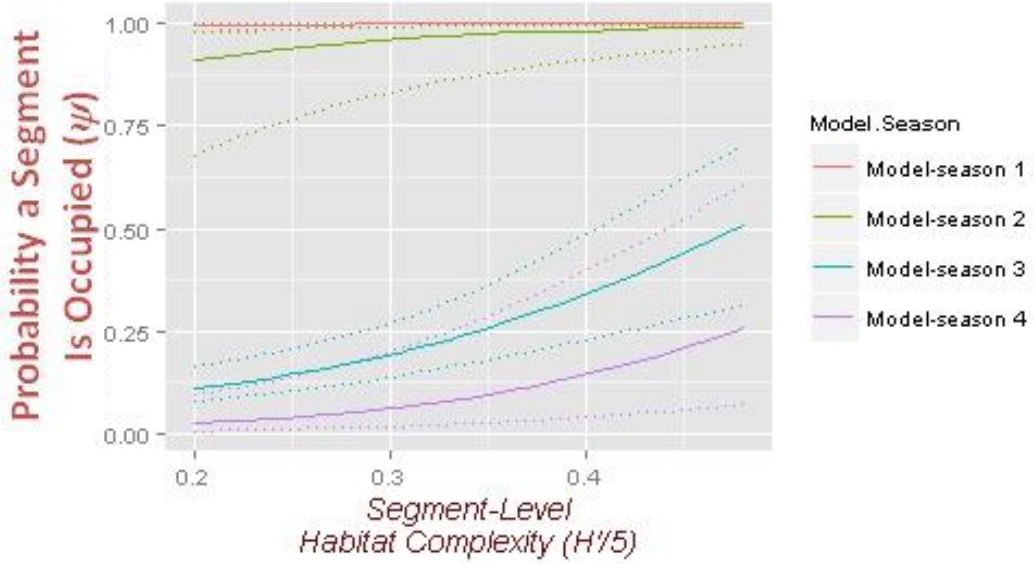

Figure 2.10. Model-averaged effects of habitat complexity (*H'/5*) on the probability a stream segment was occupied (*ψ*) in each of the four model-seasons. Dotted lines represent 95% confidence intervals.

Conditional probability that a segment was highly occupied (R) – In model seasons 1, 2, and 3, good overhanging vegetation and distance to overwintering habitat had the greatest effect on the probability that stream segments were highly occupied, given the segment was occupied; these effects were relatively less strong in model-season 4 when high occurrence was generally low (Figures 2.11 and 2.12). In general, stream segments with more overhanging vegetation and higher habitat complexity were more likely to be highly occupied (Figures 2.11 and 2.13). Similar to the effect of distance to overwintering habitat on a segment being occupied, increasing distance to overwintering habitat (range 0-1645 m) also had a negative effect on the conditional probability of a segment being highly occupied; with the greatest decline in highly occupied segments observed within the first 200m from overwintering habitat (Figure 2.12). Habitat complexity had a moderately positive effect on the conditional probability that a stream segment was highly occupied (Figure 2.13). The weakest covariate of conditional probability of high occupancy in the 95% model set was mean segment velocity in the first model-season (Figure 2.6); this effect was negative.

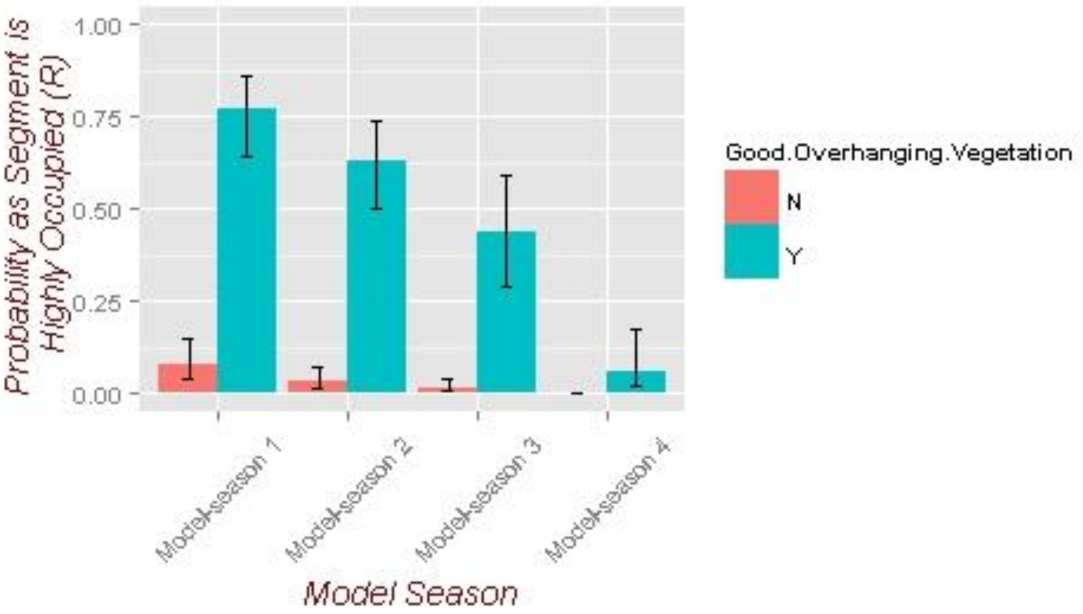

Figure 2.11. Model-averaged effects of good overhanging vegetation on the conditional probability that a stream segment was highly occupied, given the segment was already occupied (*R*) in each of the four model seasons. Error bars represent 95% confidence intervals.

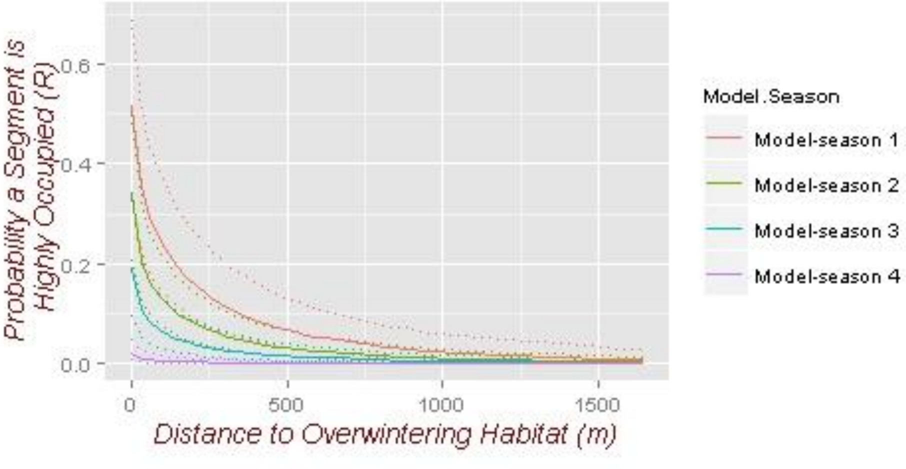

Figure 2.12. Model-averaged effects of distance to overwintering habitat (m) on the conditional probability that a stream segment was highly occupied, given the segment was already occupied (*R*) in each of the four model-seasons. Dotted lines represent 95% confidence intervals.

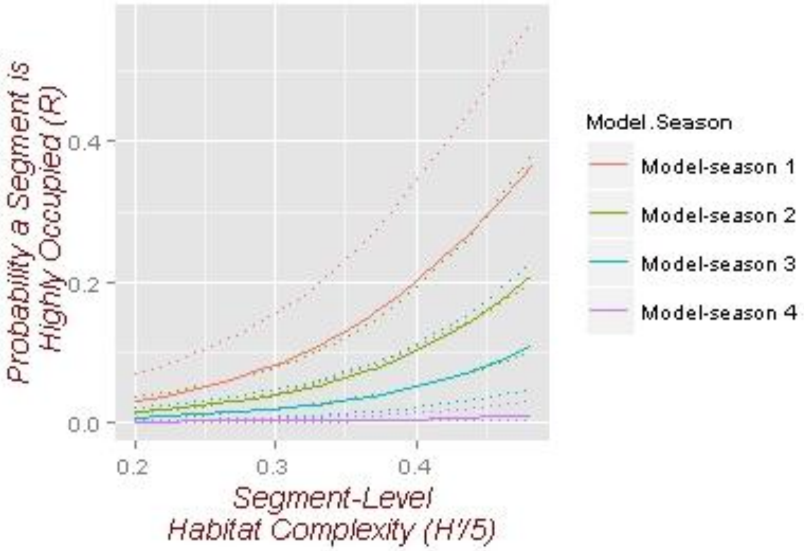

Figure 2.13. Model-averaged effects of habitat complexity (*H'/5*) on the conditional probability that a stream segment was highly occupied, given the segment was already occupied (*R*) in each of the four model-seasons. Dotted lines represent 95% confidence intervals.

Detection efficiency – In stream segments that were somewhat occupied ($\varphi^{[1]}$), detection probabilities (*p1*) were affected by survey method and mean segment depth. The probability of detection in stream segments was higher using the electrofishing+visual method (Figure 2.14) and declined with mean segment depth (Figure 2.15). Depth and other habitat covariates did not influence the detection of fish when stream segments were highly occupied (*p2*), and did not explain any uncertainty in the probability of correctly classifying highly occupied segments (δ; state uncertainty). There was a marked increase in detection efficiency between model-seasons 2 and 3, however the model structure does not account for inter-season variability in detection.

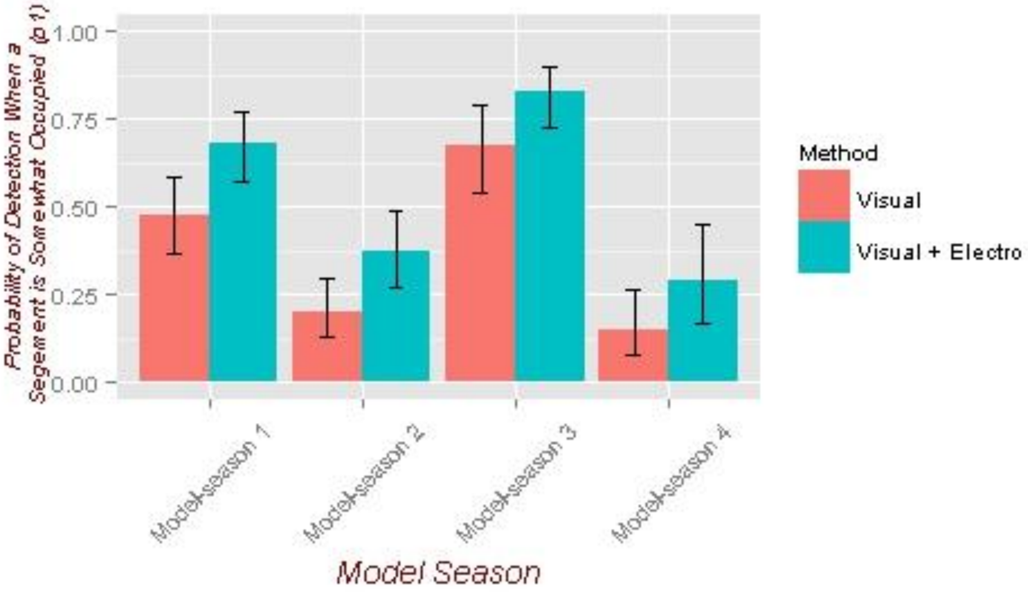

Figure 2.14. Model-averaged effects of mean segment depth (m) on the probability of detection for stream segments that are somewhat occupied (*p1*) in each of the four model-seasons. Dotted lines represent 95% confidence intervals.

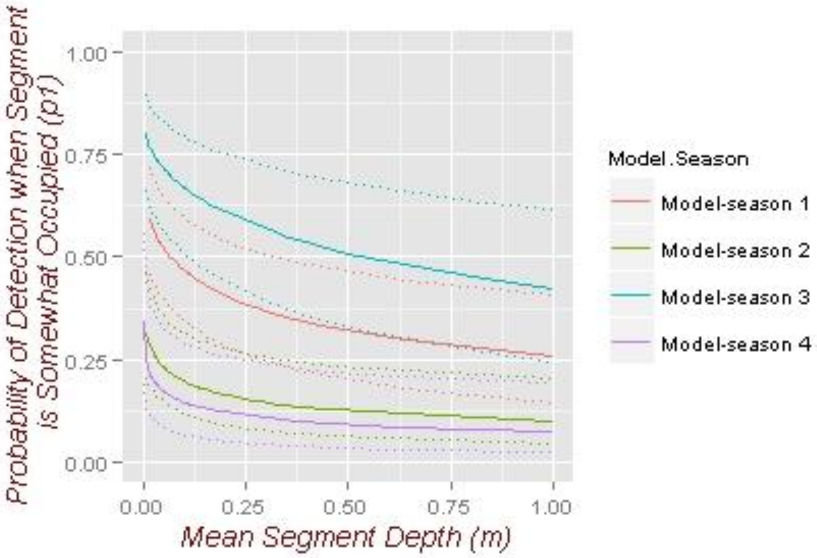

Figure 2.15. Model-averaged effects of mean segment depth (m) on the probability of detection for stream segments that are somewhat occupied (*p1*) in each of the four model-seasons. Dotted lines represent 95% confidence intervals.

DISCUSSION

DETECTION

Ecologists have long accepted imperfect detection as an unavoidable limitation of quantitative habitat-use studies of animals, which obscures our understanding of the actual distribution and abundance of a species (MacKenzie *et al.* 2006). Imperfect detection may also obscure the relative importance of the ecological components associated with a species' distribution, and the magnitude of their effect (Guillera-Arroita *et al.* 2010; Dextrase *et al.* 2014). In the present study, lower detection efficiencies in the second and fourth survey periods could have led to incorrect conclusions had I used naïve occupancy estimates alone, given that I estimate that the overall occupancy of stream segments (ψ) by YOY was only 75% of the actual proportion of occupied stream segments.

Imperfect detection also played an important role in correctly determining occupancy states of coarse abundance. Detection efficiencies in this study were similar with those of another study using CPUE to distinguish multiple abundance states (Jensen & Vokoun 2013). The probability of correctly classifying highly occupied segments as such (δ) was approximately 60% across all four survey periods, but was not affected by environmental covariates included in our *a priori* model set, likely as a result of the difficult nature of observing cryptically-coloured species like YOY Arctic Grayling.

Survey method affected detection probabilities for segments that were somewhat occupied (*p1*). As expected, detection efficiency increased when using the combined electrofishing+visual survey method over the visual-only method. The increase in detection using electrofishing+visual relative to visual-only surveys was smaller than observed in other studies (Albanese *et al.* 2011; Rodtka *et al.* 2015). On average, electrofishing+visual surveys resulted in a 1.5 times greater chance of detecting YOY Arctic Grayling in segments that were somewhat occupied over visual-only detection methods alone. This muted effect is likely best explained by low conductivity (14.32 ± SD 0.76 µS/cm) throughout the study system. Sub-Arctic tundra streams have low conductivity in general, so the decision to use electrofishing+visual surveys versus visual-only surveys would depend on the cost of sampling in these remote areas with or without an electrofisher, and how often surveyors can visit the site to conduct the repeat surveys necessary to account for imperfect detection. So if you are planning a study or monitoring program on the habitat occupancy of YOY Arctic Grayling, and you are interested in knowing where there are a few fish as well as many fish – you'll need to use an electrofisher in Barrenland streams.

The probability of detecting a fish in sites that are highly occupied (*p2*) was near perfect, detecting a fish 98% of the time when sites were highly occupied, and no habitat or method covariates were related to the probability of detection. This means, that when there is relatively high CPUE, it doesn't matter what method you use – electrofishing or visual – or how deep the water is - you are still going to detect at least one fish in these sites. In other words, where there are lots of fish and occupancy is high, visual detection methods are as good as electrofishing without the suffering and it costs less too. This is useful to researchers and managers concerned with optimizing sampling protocols that identify the best habitats for YOY Arctic Grayling.

Increasing stream depth had a negative effect on the probability of detecting YOY Arctic Grayling in stream segments that were somewhat occupied (*p1*) whereas increasing amounts of obscuring, overhanging riparian vegetation did not affect detection probabilities. Depth is used as cover by many fish species, including Grayling (e.g., Wesche *et al.* 1987; Groce *et al.* 2012). My results indicate that probability of detection decreased with increasing depth, and that deeper, more lentic habitats, such as shallow water ponds, may be more easily misclassified as being unoccupied. This is likely due to decreasing efficacy of both visual and electofishing sampling methods in deeper habitats. As good overhanging cover was an important determinant of segments that were highly occupied, the lack of effect of overhanging cover on the probability of detection given the segment was somewhat occupied ($p1$) could have been limited by the number of segments where both the lower occupancy state and good overhanging vegetation occurred.

There was a general trend in probability of detection across the survey periods, with marked increase in detection efficiency observed between the second and third survey periods. However, transitions in detection probabilities are implicit within the model structure, and it was not possible to use environmental covariates to explain this increase in detection efficiency. One possible explanation for the observed increase in detectability is that declining discharge improves detectability. Along with a decline in mean segment depth, declines in discharge cause a lateral contraction of stream habitat (personal observations), and may have a concentrating effect on YOY Arctic Grayling. It is also possible, that as YOY grew and their swimming capability improved that they became easier to detect. The drop in detection efficiency in the fourth survey period was likely due expected declines in YOY numbers, due to either increased mortality or emigration to overwintering habitat, and the use of interstitial flow as habitat.

OCCUPANCY

The occurrence of YOY Arctic Grayling in this study depended on numerous interacting ecological variables, such as water depth, velocity, and discharge, stream slope, habitat complexity, distance to overwintering habitat, and the availability of sufficient overhanging riparian vegetation. The relative magnitude of these effects varied by the state of occupancy, where psi (ψ) represented the probability of a stream segment being occupied (either somewhat or highly occupied), and (R) represented the conditional probability that a stream segment was highly occupied (given occupancy was established).

Effects of stream morphology

In all but the first survey period, the slope of the stream segment was an important determinant for all occupied stream segments (ψ). The lack of effect in the first survey period is likely due to an interaction with mean segment velocity and stream slope. In the latter three survey periods, I observed YOY Arctic Grayling more frequently in the higher slope stream segments (i.e., stream slopes between 2-4°). This is somewhat unexpected as stream segment slope was moderately correlated with mean segment velocity ($x = 0.50$, $p<0.01$; Appendix A), and velocity had a negative effect on occupancy. However, Barrenland streams stream morphology differs from what would be expected across a similar range of slopes in better-sorted, alluvial stream systems (Montgomery & Buffington 1997; Robert 2014). In this study system, the streambed is predominantly composed of poorly-sorted boulder and cobble substrate, producing a uniform ‘steep and shallow rapid’ morphology. This uniform stream morphology may improve the suitability of higher slope stream segments to YOY Arctic Grayling by providing ample velocity refugia in the form of quiet pockets of water immediately behind larger rocks and boulders. These pockets could improve the ability of YOY Arctic Grayling to conserve energy, while the surrounding turbulence confers several advantages, such as cover from predators. Aquatic predators, such Northern Pike (*Esox lucius*) are excluded from shallow and turbulent environments due to their larger, non-streamline morphology (Inskip 1982).

Higher sloped stream segments with higher velocity water also tend to have greater macro-invertebrate drift (Ciborowski *et al.* 1977). Barrenland YOY Arctic Grayling have been found to feed primarily upon stream invertebrates such as midge and blackfly larvae (Chironomidae and Simuliidae; Jones *et al.* 2003a), the latter of which almost exclusively inhabit flow over boulders directly upstream of the same velocity refugia that YOY use (Sommerman *et al.* 1955). I posit that stream segment slope is a proximate environmental factor that influences many other habitat features that ultimately affect the survival of YOY. Thus, it is important to understand the effects of other environmental variables that scale with slope such as water velocity, streambed morphology, refugia from predators, and availability of food sources.

Increasing habitat complexity (i.e., the diversity of meso-habitat – run, riffle, pool, cascade, and shallow water) had a positive influence on the probability that a stream segment was occupied (ψ) in most model-seasons. Additionally, increasing habitat complexity had a greater effect on the conditional probability that a segment was highly occupied (R). As the lack of suitable stream habitat is a well described limitation to fish populations (Minns *et al.* 2011), an increase in the probability of occupancy for both occupancy states was expected; increased stream complexity tends to lead to greater resiliency of the stream community to flash flooding events, and provides a variety of cover and foraging opportunities (Lonzarich & Quinn 1995; Anlauf-Dunn *et al.* 2014). Hence, maintenance of habitat complexity in these Barrenland streams is an important consideration for resource managers and regulators implementing impact mitigation strategies (Jones & Tonn 2004a).

Effects of distance to overwintering habitat

Increasing distance to overwintering habitat had a negative effect on the probability of a stream segment was occupied by YOY Arctic Grayling, with the conditional probability of a segment being highly occupied (*R*) decreasing more sharply than overall occupancy. In August and September a few fish are occupying sites as far away as 500m from overwintering habitat, but most fish are less than 200m from overwintering habitat. This is consistent with findings from descriptive studies of Arctic Grayling (Craig 1989). Furthermore, both Hershey et al. (2006) and Haynes et al. (2014) found that the distance to the nearest lake had a negative influence on mature Arctic Grayling presence. However, neither study examined the effect of distance to the nearest lake on the occurrence of YOY Arctic Grayling. The negative relationship between distance to overwintering habitat and occupancy is not surprising in this study system. The streams in this system lose surface water connectivity as the open-water season progresses, and many of the smaller lakes in this study system were likely not suitable overwintering habitat due to their shallow depth (often < 5 m), thick ice (often exceeding 2 m in thickness), and corresponding lack of oxic bottom waters (Clilverd *et al.* 2009; unpublished data).

As Arctic Grayling are known to migrate many kilometers to overwintering habitat (West *et al.* 1992; Bradford *et al.* 2008), and exhibit site-fidelity to natal spawning grounds (Buzby & Deegan 2000), I posit that distance to overwintering habitat limits the occupancy of Arctic Grayling differently for each life stage. Distance to overwintering habitat may limit the ability of mature Arctic Grayling to reach suitable spawning grounds, but also limit the ability of streams to provide passage to overwintering habitat at the end of the YOY rearing season. Thus, stream segments that are most likely to be occupied by YOY Arctic Grayling must meet the criteria of being physically connected to overwintering habitat at the beginning and end of the open-water season, and secondarily, provide better-than-average rearing habitat.

Effects of stream flow and depth

During the first survey period, higher stream velocities led to a linear decrease in the probability that a stream segment was either occupied (ψ) or highly occupied (R) by YOY Arctic Grayling, with the conditional probability that a segment was highly occupied (R) decreasing more sharply than overall occupancy. There are likely a few fish occupying sites up to approximately 0.3-0.4 m/s, but that there are more fish in sites with very slow velocities (<0.1 m/s). Water velocity becomes unimportant to habitat occupancy in the latter three survey periods, likely because of three converging factors, the improved swimming capabilities of YOY, more flow that is available within range, and the considerable velocity refuge provided by the poorly sorted boulder-dominated streams (Kratt & Smith 1977; Deegan *et al.* 2005). Jones and Tonn (2004) also found that YOY Arctic Grayling associated with water velocities below 0.1m/s, and that the effect of velocity was unimportant to YOY habitat-use later on in the season. Due to differences in available velocities, it is possible that the linear relationship we observed between velocity and occupancy is the result of sampling only one side of the range that is found in Jones and Tonn's study (2004). Because of this, the extra covariate required to characterize quadratic relationships did not carry enough explanatory weight in the AIC model rankings. It is possible that velocity measurements, taken 60% of depth from the bottom of the thalweg, do not accurately represent swimming experience of YOY Arctic Grayling. Stream-bottom or snoutdepth measurements may have provided a more accurate representation of velocity experience for YOY Arctic Grayling.

Deeper water in stream segments also led to a linear decrease in the probability of stream segments being occupied (ψ) in the first survey period, with highest probability of YOY occupancy occurring at sites with depths less than half a meter. Depth becomes unimportant to YOY habitat occupancy in the latter three survey periods as YOY spread out to use deep water pond habitat (pers. observations). Jones and Tonn (2004) also found that early season YOY habitat use was restricted to shallow water depths. One explanation for this is that it is possible that recently-emerged YOY avoid deeper habitats because these habitats are more likely to house fish predators, but this requires further investigation.

Unlike Jones and Tonn (2004b) who modeled an optimum (i.e., quadratic function) for both water velocity and depth of approximately 0.5 m/s and 0.60 m, respectively, at which small YOY were most abundant, I observed a linearly decreasing relationship between YOY occupancy and both water velocity and depth. In the present study, the range of velocity observed was 0.01-0.55 m/s, and the range of depth was 0.12-1m, but segments with velocity and depth values in the middle of those ranges were underrepresented in sampling. Therefore, it is likely that the effect of velocity and depth were modeled as a negative linear effect because velocity and depth optima present in Jones and Tonn's (2004b) study were unavailable to sample. It is also possible that this reflects an AIC variable penalization effect. AIC is a parsimonious model selection process that favours the simplest models over those having marginally useful additional terms. A quadratic function in a model necessitates the inclusion of two terms for a single variable (the mean^2 + mean, as in the equation of a quadratic function). Based on the available range of water velocity data and depth in this study, the quadratic function could have modeled the data marginally better than the linear function, but was ranked as worse by AIC due to the penalization for the extra term. It is likely that the real effect of water velocity and depth on YOY Arctic Grayling occupancy is in fact still that of an environmental optimum (quadratic), but further research is required.

Increasing stream discharge had a negative effect on the probability that stream segments were occupied for all four survey periods. This was particularly true during the first survey, likely due to a combination of depth and velocity exceeding the natural optima (Ford 1995; Jones & Tonn 2004b; Deegan *et al.* 2005). The magnitude and persistence of the effect of discharge on occupancy through the subsequent three survey periods was likely driven by one of the streams in our study system (Stream M1). Discharge rates in the M1 stream segments were approximately 1.5 times greater than the average discharge of all other streams, and no YOY Arctic Grayling detections in Stream M1, in any of the four survey periods.

A qualitative assessment of discharge and habitat occupancy revealed that the probability a segment was occupied began to decline when average survey period discharge dropped below 0.1 m^3/s. A qualitative assessment of the Kennady Lake drainage system suggested a similar relationship between stream discharge and YOY Arctic Grayling occurrence (Golder Associates 2012). However, transitions in occupancy states are implicit within the current model structure. Thus, it was not possible to use environmental covariates to explain this decrease in overall occupancy. Although it is beyond the scope of this study, the influence of discharge on colonization and local extinction dynamics could be addressed with only a slight adjustment in model design. It is thought that declines in discharge may act as a cue to YOY and juvenile Arctic Grayling to depart from productive stream habitats to overwintering grounds (Deegan *et al.* 1999; Heim *et al.* 2015), so it would also be interesting to examine which aspect of discharge (measured as the water velocity x depth x width) is the strongest driver of occupancy. Although it was not measured, it appeared that as discharge decreased, there was an exponential decrease in bankfull width of the stream segment relative to mean segment depth (personal observation). As such, it is possible that stream width is the strongest driver of occupancy. This would explain the discrepancy between the apparent lack of importance of velocity and depth in the 2nd-4th survey periods, while discharge remained an important variable for describing probability that a segment was occupied (ψ) throughout the summer of 2014.

It is important to note that in 2014, the year of this study, precipitation levels were 34% lower than the 50-year average; 2014 was the 2nd driest year since 1948 (Environment Canada 2014). The lighter snowpack and shortage of summer rain reduced the magnitude of the spring freshet discharge, and my data indicate that the study streams had far less sustained flow throughout the open-water season than in previous recent years (De Beers Canada 2010b; Golder Associates 2012). These conditions resulted in lower than average water depths and velocity throughout the open water season, and likely promoted earlier development of barriers to fish movement. These conditions could also have resulted in a stronger-than-usual effect of distance to overwintering habitat on probability of occupancy; more data collected over a range of years with differing hydrological conditions would be required to investigate this.

Effects of riparian vegetation

Increasing amounts of overhanging vegetation (GOHV) increased the probability that stream segments were highly occupied (CPUE≥6). This is consistent with the findings of Jones and Tonn (2004b), who found that YOY Arctic Grayling selected habitat with greater overhanging vegetation. While the link between visual isolation and YOY Arctic Grayling occurrence is not a new finding (e.g.,McClure & Gould 1991), this study more fully quantifies the importance of overhead cover for YOY Arctic Grayling in Barrenland streams, as I sampled stream reaches that ranged from 0% to 100% cover. As there is considerable regional variation in the quantity of overhanging riparian cover available on the sub-Arctic tundra (partially related to the distance from the treeline; Ecosystem Classification Group 2012), the relative importance of overhanging vegetation found in Jones and Tonn's (2004) more northerly study may not be apply to streams in my study system (i.e., 100km vs. 20km to treeline, respectively).

Riparian vegetation that overhangs a stream obscures the stream from visual predators, deposits terrestrially-derived invertebrates and leaf litter, and regulates and stabilizes in-stream temperature (Hawkins *et al.* 1982; Beschta 1997; Wipfli 1997; Richardson *et al.* 2010). Refuge from predators may be particularly important in higher latitudes with 24 hours of daylight during the earliest, most vulnerable stages of rearing. These refugia allow YOY to spend less energy on evasive behaviour, experience reduced mortality rates, and focus more energy on feeding to build up lipid reserves that are important to overwintering survival (Maddock *et al.* 2013). It is also possible that mature Arctic Grayling seek out reaches with good overhanging vegetative cover during spawning. Arctic Grayling are iteroparous, spawning each year upon reaching maturity; thus, refuge from aerial predation during spawning may be an important component for survival and fecundity.

Overhead riparian cover may also subsidize aquatic invertebrate food resources with greater amounts of terrestrial macro-invertebrates. In many freshwater systems, riparian vegetation may be the dominant source of invertebrate resources for fish (Mason & Macdonald 1982; Wipfli 1997). In nutrient-poor, Barrenland systems, this terrestrial subsidization may provide more than half of the energy needed by fish in order to survive to maturity (Allan et al. 2003). Jones et al. (2003) found that terrestrially-derived invertebrates were of relatively limited availability and rarely found in YOY Arctic Grayling diet. However, a lack of extensive overhanging vegetation in their study (estimated 20-30% in photos accompanying publication) limits extrapolation to the present study which had up to 100% vegetation cover. Further research using stomach content analysis, stable isotopes, and relative abundance of macro-invertebrates would be required to characterize sources of macro-invertebrate in YOY Arctic Grayling diet.

The presence of greater quantities of overhanging cover in my study system relative to Jones and Tonn (2004b) study system could also help to explain the difference in habitat use as related to stream segment depth. Visual isolation may allow YOY Arctic Grayling to abandon certain evasive behaviours, such as occupying deeper stream segments, to occupy stream reaches with shallower depths, but greater cover and food availability (De Bruyn & McCart 1974; Deegan *et al.* 2005).

Temporal trends in stream occupancy

Temporal trends were evident in the occupancy of stream segments by YOY Arctic Grayling. Occupancy was highest in mid-to late-July (during the first round of surveys), and decreased through the summer to the lowest occupancy observed during the fourth round of surveys (September). At the end of the season, the exceptionally low occupancy of YOY Arctic Grayling in stream segments likely reflects both the progressive loss of YOY from declining survival as well as the successful winter migration of some portion of the remaining YOY (Jones

& Tonn 2004b). Migrations of YOY were not tracked in this study, thus it is not possible to separate these two factors affecting occupancy, and as such, it is not prudent to assume that YOY occupancy of the stream segments during the fourth survey (September) entirely reflects the effects of mortality or suitability of environmental conditions.

Assuming that some of the decline in occupancy through the four surveys represents successful migrations to overwintering habitats, it appears that YOY began departing for overwintering habitat in early- to mid-August—as discharges in the Kennady Lake drainage system fell below 0.1 m^3/s. However, extinction and colonization rates need to be modeled before I can make this claim with certainty. The timing of this emigration is notable when one considers that YOY have the potential to amass approximately 0.8 g/day by feeding in these outlet streams (Heim *et al.* 2014). Since similar patterns in the timing of apparent emigration and declines in both discharge and habitat-use were also observed in Jones and Tonn (2004b), it would appear that the availability of stream rearing habitat on the Barrenlands is constrained by discharge-related declines in habitat quantity and surface-water connectivity. Consequently, YOY likely spent less time in these productive outlet streams than could be expected in years with more precipitation.

LIMITATIONS, IMPLICATIONS, AND FUTURE RESEARCH

As the survey methods in this study involved sampling adjacent segments within each stream, it is unlikely that spatial independence between stream segments was achieved (this is a common problem in stream studies). If this is true, then the spatial correlation is unaccounted for in the current model, and as such, the results may have overestimated the effect of environmental covariates (Dale & Fortin 2014); current research outside the scope of my thesis is investigating this possibility. However, it could be possible to account for spatial correlation by adding a confounding factor covariate to our model set. Several other factors could have influenced occupancy or detection, including the presence of potential predators of YOY Arctic Grayling (mainly Northern pike; *Esox lucius*), inter-annual variation in climate and hydrology, and lower-trophic productivity. These variables could play a role in distribution of YOY Arctic Grayling, and may be sources of uncertainty unaccounted for in this model.

Relatively little is known about the Arctic Grayling residing in the sub-Arctic tundra shield, thus the study of YOY Arctic Grayling should be extended into a multi-year program, in order to gain better understanding of inter-annual variability in abundance. As evidenced by the success of the long term ecological research network (LTER) located in the foothills region of the North Slope of Alaska, multi-year studies are also able to provide valuable information regarding spatio-temporal variation of habitat use (Hobbie & Kling 2014). Multi-year studies can help identify the relative importance of habitat features in the face of varying climate, precipitation, stochastic events (i.e. fire), industrial development, and changing year-class dynamics (Franklin 1989; Minns 2001). From there, models should be integrated into a network of regional studies on habitat occupancy to better inform decision-makers who wish to maintain the productivity and resilience of these freshwater systems (Lapointe *et al.* 2014). By understanding the regional nuances of freshwater habitat-use by Arctic Grayling, we will be better equipped to track shifts in habitat use as climate change and growing industrial presence continue to shape the Canadian North.

By examining previously uncharacterized environmental covariates such as stream slope, habitat complexity, distance to overwintering habitat, and the availability of sufficient overhanging riparian vegetation, my study improves the current knowledge base on the occurrence of YOY Arctic Grayling in Barrenland (Jones & Tonn 2004b; Deegan *et al.* 2005). Since environmental covariates such as water depth, velocity, and discharge have similar effects on YOY Arctic Grayling in Jones and Tonn's (2004) study, we may be able to expand the inference of these findings to predict YOY occurrence in other Barrenland streams. Conservation efforts for populations of Barrenland Arctic Grayling should focus on protecting and mitigating effects on these crucial habitat characteristics to maintain suitable habitat for this valued fish species. Where resources for conservation and management are limited, special consideration should be given to preserving lakes with overwintering habitat and higher sloped streams with overhanging cover that are in close proximity to these lakes.

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Chapter 3: General Discussion

SUMMARY OF RESULTS

To my knowledge, this is the first attempt to quantify imperfect detection in habitat use models for young-of-year (YOY) Arctic Grayling (*Thymallus arcticus*). Prior to this, studies have simply accepted occurrence or non-occurrence as an accurate representation of habitat-use and non-use (Jones & Tonn 2004b; Hershey *et al.* 2006). My findings clearly demonstrate the benefits of accounting for imperfect detection in habitat-use models. With detection probabilities for stream segments that were somewhat occupied as low as 0.25 in some survey periods (i.e., there was a 25% chance that YOY were detected in segments where 0<CPUE>6), it appears that imperfect detection, if unaccounted for, has the potential to bias estimates of YOY Arctic Grayling habitat occupancy. So by accounting for imperfect detection, the model increases the accuracy of occupancy estimates that would normally go unaccounted for in other model designs (MacKenzie *et al.* 2009).

Occupancy models also allowed me to account for non-random variation in detection efficiency (Guillera-Arroita *et al.* 2010). Both survey-method and mean segment depth were important determinants of the probability of detection for stream segments that were somewhat occupied (*p1*); while environmental covariates were unimportant in determining the probability of accurately differentiating between high and low occupancy states (δ) and for segments that were highly occupied (*p2*). Now, if you want to design the most efficient sampling program for these fish at this site, sample in mid-July when YOY Arctic Grayling are most abundant. If you are interested in where all the fish are, use an electrofisher. If you are interested in where most of the fish are, visual surveys are fine.

Furthermore, my findings demonstrate the effect of numerous interacting environmental covariates on the habitat occupancy of YOY Arctic Grayling in sub-Arctic tundra streams, and demonstrate how these effects change through the open-water season. During the first survey period, water velocity, depth and discharge led to a decrease in the probability of overall occupancy (ψ). As flow dynamics often limit habitat-use by YOY Arctic Grayling by exceeding thresholds necessary for maintaining a net energetic gain in these streams (Deegan *et al.* 1999; Jones & Tonn 2004b), the influence of flow dynamics on the probability of occupancy for YOY Arctic Grayling was expected and largely agrees with other studies in Arctic and sub-Arctic regions (Deegan *et al.* 1999; Jones & Tonn 2004b; Heim *et al.* 2015). While the maximum thresholds for water depth, velocity, and discharge were identified by their linear relationship with habitat occupancy, further testing in this system is required to better characterize the quadratic relationship between YOY Arctic Grayling habitat occupancy and flow. Although not captured in this model structure, declines in discharge over time were associated with a decline in overall occupancy, and appear to indicate that habitat area diminishes with seasonal flow.

In the latter three survey periods, increasing stream slope and habitat complexity led to a higher probability of overall occupancy (ψ) whereas increasing distance to overwintering habitat decreased the probability that a stream segment was occupied. Covariates such as these provided a novel understanding regarding the habitat occupancy of YOY Arctic Grayling in Barrenland Arctic stream systems and demonstrated the relative influence of broader scale environmental components (i.e., distance to overwintering habitat) on local habitat conditions. This also suggests that results are very case specific. Limited spatial coverage and regional differences in environmental conditions (e.g., proportion of overhanging vegetation, stream slope, and distance to overwintering habitat) offer an explanation for why these factors have not previously been characterized in habitat-use studies of YOY Arctic Grayling (Deegan *et al.* 1999; Jones & Tonn 2004b).

The effects of water velocity, habitat complexity, and distance to overwintering habitat were accentuated when predicting the conditional probability that a stream segment was highly occupied (R), while the presence overhanging riparian cover was also a crucial determinant of highly occupied segments. Visual isolation and increased terrestrial invertebrate drift offer possible explanations as to why YOY Arctic Grayling occupy habitat with overhanging riparian cover (McClure & Gould 1991; Wipfli 1997), but further examination of the lower-trophic productivity in this study system is required.

Based on my findings, I believe that occupancy models provide the necessary framework to: 1) account for imperfect detection and determine which environmental covariates are influencing detection efficiency; 2) compare the relative detection efficiency of electrofishing and visual survey methods in Barrenland streams; and 3) determine how environmental covariates influence YOY Arctic Grayling habitat occupancy in Barrenland streams.

LIMITATIONS OF CURRENT MODEL PARAMETERIZATION

There are two areas of uncertainty in my current model parameterization that need to be addressed. First, the standardization of fish counts for each survey method (by seconds of effort) may introduce bias into results. The current from electrofishing may result in YOY Arctic Grayling hiding from electric shock, or, alternatively fish may be drawn in by the electric field to a greater extent than might be expected using visual observations for the same given effort (Bovee & Cochnauer 1977; Heggenes *et al.* 1990). To determine the suitability of standardizing both survey methods by the same unit of effort (time), I conducted a *post-hoc* paired t-test on CPUE abundance estimates. I found that there was no significant difference between the two detection methods for a given unit of effort (t_{267}= 1.97, p = 0.39). Thus, in this study system, the unit of effort was reasonably equivalent between the two methods. This equivalency could be attributable to the low conductivity of Barrenland streams, where the effective range of the electrofisher was approximately 2 meters. Two meters is well within the effective range of visual observations, and allowed detection of YOY Arctic Grayling that were fleeing the electric field. Based on these findings, it appears that no undue method bias was introduced by combining survey method CPUE data when delineating between the abundance categories used in multi-state occupancy models.

Second, detection efficiencies could vary between habitat types, and may introduce Type I error into estimates of habitat occupancy. To account for the effects of habitat type on occupancy estimates, fisheries surveyors typically use a stratified habitat approach when searching for fish (Hankin 1984; Buckland *et al.* 2005). The relative amounts of mesohabitat such as runs, riffles, pools, cascades, or pond habitat in a stream section are estimated and each of these is searched for a corresponding proportion of the total effort. However, I chose a timed, standardized path search, because this is the survey method utilized most often by government monitoring programs, and has several advantages. It does not require repeated identification and estimation of mesohabitat types/proportions which can be highly susceptible to operator bias, particularly in an area such as the Gahcho Kue mine site where there are inconsistent habitat unit boundaries. Additionally, these barrenland streams are much more poorly sorted, with mesohabitats that are less defined than in a typical southern stream system. Since occupancy models require repeat surveys of each sampling unit, this kind of standardized method can be easily implemented year after year. So to account for the effect of Type I error due to habitat type on occupancy estimates, habitat complexity (i.e., the diversity of mesohabitat type) should be run as a covariate in any state estimate of occupancy (as was done in this study). That said, a timed, standardized path search could also lead to greater Type II error rates (false absences) which might have biased the probability of detecting YOY Arctic Grayling in either of the visual and electrofishing methods. Thus, it is possible that my estimates of detection efficiency may be conservative. This could result in an inflation of the imperfect detection parameter, which may have serious consequences if Arctic Grayling were to become more rare and imperiled in this area. This means that if habitat complexity is not included as a predictive covariate for imperfect detection estimates, then detection estimates may underestimate the number of occupied segments when there are several habitat types and few fish. A further study comparing the capture efficiency of each method to a removal survey would aid in quantifying the probability of bias.

FUTURE RESEARCH

Several questions arose during my study that could either be addressed using already-gathered data in alternate parameterizations of occupancy models (e.g., local extinction and colonization rates, effects of predator occurrence, spatial correlation between stream segments) (MacKenzie *et al.* 2003; Zipkin *et al.* 2010; Graves *et al.* 2012), and still others that would require changes to the sampling structure in future (MacKenzie *et al.* 2006). Potential areas to explore include the effect of inter-annual variation in flow regimes on the relative importance of environmental covariates, and watershed- and region-specific effects on YOY Arctic Grayling habitat occupancy (Nichols *et al.* 2008). The latter could be addressed by expanding sampling schemes to examine habitat occupancy of YOY Arctic Grayling at different spatial scales (i.e., segment-level, stream-level, and drainage-level) in drainage systems that are representative of the different ecozones in the Arctic and sub-Arctic (e.g.,Dextrase *et al.* 2014).

LOCAL IMPLICATIONS

This study expanded the spatial coverage of previous YOY Arctic Grayling habitat-use studies in sub-Arctic tundra streams, and is the first to quantify imperfect detection; this improves the performance of predictive models in response to spatiotemporal variation in detectability (Guillera-Arroita *et al.* 2010). Furthermore, as habitat-use studies on YOY Arctic Grayling are sparse, this study adds to the body of research on Arctic Grayling in general and contributes significant information on region-specific habitat-use in chain-lake systems like those found in the sub-Arctic tundra.

Development plans in the Kennady Lake drainage system include a series of stream flow manipulations in our study streams (Golder Associates 2012). Since this study was conducted prior to disturbance, it has the potential to serve as a baseline for the before-after assessment of YOY Arctic Grayling habitat occupancy. Furthermore, my findings can be used to develop mitigative or preventative management strategies by setting flow thresholds specific to the Kennady Lake drainage. For instance, one way to maintain the functional connectivity between rearing and overwintering habitats in this drainage system would be to use the findings from this study to recommend base-flow amounts, flow maxima, and seasonal flow regimes. These thresholds, if followed, could prevent YOY dislodgement from flushing flows and stranding due to low baseline flows or rapid drops in discharge (Deegan *et al.* 1999). Furthermore, as stream slope and dense overhanging vegetation had the greatest effect on overall and high occupancy, respectively, I recommend that the preservation of riparian vegetation in high sloped streams be set as a priority for those who wish to maintain rearing habitat for YOY Arctic Grayling; especially these habitat components are found in close proximity to overwintering habitat.

IMPLICATIONS BEYOND THE STUDY SYSTEM

My findings have implications for the conservation of YOY Arctic Grayling in sub-Arctic Tundra streams, and demonstrate the general applicability of occupancy models in the vast and understudied northern freshwater systems. Again, in streams where flow regimes are unaltered, the conservation of YOY Arctic Grayling rearing habitat can be facilitated by preserving riparian zone cover, with a particular focus on higher slope streams in close proximity to overwintering habitat. Real-world applications of these findings could involve the creation of policy or water license stipulations that mandate scientifically-defensible stream buffer zones to those applying for development project approvals that involve the use or alteration of freshwater ecosystems (e.g., ice road portages, water withdrawals, resource exploration, and mining activity).

More generally, my study provides another example where accounting for imperfect detection improves the accuracy occupancy estimates as well as the relative effect of environmental covariates. This improves researcher ability to compare results between regions where spatiotemporal variation in stream morphology, flow, and overhanging cover can influence the detectability of study species. (MacKenzie 2005; Dextrase *et al.* 2014). Moreover, my findings demonstrate the ability of occupancy models simultaneously determine patterns in occurrence as it relates to environmental covariates and compare the relative efficiency of survey methods. This allows researchers to adapt and optimize sampling protocols based on *in situ* evaluations of detection efficiency and decreases their reliance on findings that may not be relevant to their particular study system. These benefits make occupancy models an attractive candidate for expansion into long-term, systematic monitoring programs across Arctic and sub-Arctic freshwater ecosystems. By selecting watersheds that are representative of the various geomorphic, hydrological, and biological conditions within the Arctic, researchers can use occupancy models to track and manage shifts in species distribution and habitat occupancy (Lapointe *et al.* 2014). From there, systematic reviews could be conducted to provide resource managers with objective, quantitatively-based evidence to support the best possible decision making (Lapointe *et al.* 2014).

The Northwest Territories is unique in that they have produced several forward-thinking pieces of legislation in recent years dealing with freshwater ecosystems; both "Northern Voices, Northern Waters" and the Alberta Trans-boundary water agreement communicate an in-depth appreciation of the complex and intertwined nature of various ecological variables and their role in maintaining long-term ecosystem health (Miltenberger & Strahl 2014). These policies clearly outline ecosystem-based management approaches that aim to preserve the integrity of freshwater ecosystems, and enable sharing the benefits of healthy ecosystems with their entire populous. Intrinsically, it is our values that shape decision-making priorities at all levels of governance. The aforementioned policies communicate a commitment to fairness, environmental stewardship, scientific-objectivity, and long-term prosperity. I believe that models like the one presented in this thesis will empower decision-makers with the evidence necessary to follow through on implicit values communicated in their policies and legislation.

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Appendix A: Autocorrelation Testing

Table A.1. Pearson's Correlation data for environmental covariates related to the probability of occupancy state.

	Discharge m-s 1	Discharge m-s 2	Discharge m-s 3	Discharge m-s 4	Velocity m-s 1	Velocity m-s 2	Velocity m-s 3	Velocity m-s 4	CoeffV m-s 1	CoeffV m-s 2	CoeffV m-s 3	CoeffV m-s 4	Depth m-s 1	Depth m-s 2	Depth m-s 3	Depth m-s 4	DSQ m-s 1	DSQ m-s 2	DSQ m-s 3	DSQ m-s 4	Gradient	D2OW	Diversity	GOHV
Discharge m-s 1	1.00																							
Discharge m-s 2	0.39	1.00																						
Discharge m-s 3	0.51	0.60	1.00																					
Discharge m-s 4	0.38	0.55	0.55	1.00																				
Velocity m-s 1	0.01	-0.05	-0.04	-0.15	1.00																			
Velocity m-s 2	-0.03	0.16	0.06	-0.01	0.86	1.00																		
Velocity m-s 3	-0.04	0.02	-0.01	-0.14	0.83	0.88	1.00																	
Velocity m-s 4	0.07	0.07	0.06	-0.03	0.77	0.80	0.85	1.00																
CoeffV m-s 1	-0.05	0.09	-0.02	-0.20	0.11	0.17	0.16	0.06	1.00															
CoeffV m-s 2	-0.03	-0.08	-0.07	-0.25	0.10	0.15	0.09	0.00	0.64	1.00														
CoeffV m-s 3	-0.22	-0.05	-0.15	-0.25	0.18	0.18	0.24	0.05	0.48	0.56	1.00													
CoeffV m-s 4	-0.11	-0.15	-0.19	-0.20	0.08	0.09	0.16	0.13	0.30	0.19	0.31	1.00												
Depth m-s 1	0.14	0.22	0.14	0.05	-0.42	-0.41	-0.33	-0.22	-0.06	0.03	-0.09	-0.21	1.00											
Depth m-s 2	0.07	0.21	0.14	0.05	-0.42	-0.45	-0.37	-0.28	-0.08	-0.03	-0.07	-0.26	0.93	1.00										
Depth m-s 3	0.14	0.29	0.19	0.06	-0.42	-0.44	-0.38	-0.27	-0.03	0.02	-0.01	-0.18	0.87	0.90	1.00									
Depth m-s 4	0.19	0.24	0.17	0.15	-0.46	-0.48	-0.44	-0.35	-0.15	-0.10	-0.13	-0.28	0.86	0.92	0.88	1.00								
DSQ m-s 1	0.12	0.26	0.15	0.10	-0.47	-0.45	-0.38	-0.27	-0.10	-0.05	-0.16	-0.26	0.99	0.94	0.88	0.89	1.00							
DSQ m-s 2	0.06	0.23	0.14	0.09	-0.47	-0.48	-0.41	-0.31	-0.14	-0.12	-0.15	-0.31	0.92	0.99	0.90	0.93	0.95	1.00						
DSQ m-s 3	0.10	0.31	0.18	0.10	-0.46	-0.46	-0.40	-0.29	-0.08	-0.07	-0.07	-0.21	0.84	0.88	0.99	0.86	0.87	0.90	1.00					
DSQ m-s 4	0.14	0.26	0.17	0.19	-0.50	-0.50	-0.46	-0.37	-0.22	-0.18	-0.20	-0.36	0.86	0.92	0.87	0.98	0.91	0.95	0.88	1.00				
Gradient	-0.03	0.02	0.18	-0.11	0.54	0.46	0.52	0.51	-0.05	-0.20	0.02	0.16	-0.21	-0.25	-0.30	-0.31	-0.22	-0.26	-0.30	-0.29	1.00			
D2OW	-0.23	0.03	-0.16	0.29	-0.22	-0.15	-0.15	-0.16	-0.31	-0.40	-0.17	-0.07	-0.02	0.06	-0.11	0.09	0.03	0.10	-0.06	0.13	0.00	1.00		
Diversity	-0.02	-0.16	-0.20	-0.26	0.41	0.37	0.42	0.35	0.24	0.35	0.34	0.20	0.03	-0.02	-0.06	-0.06	-0.03	-0.06	-0.10	-0.11	0.31	-0.04	1.00	
GOHV	-0.36	-0.07	0.02	-0.16	0.48	0.36	0.36	0.36	-0.09	-0.12	0.10	0.04	-0.26	-0.26	-0.31	-0.34	-0.28	-0.28	-0.30	-0.32	0.48	0.09	0.22	1.00

Table A.2. Pearson's Correlation data for environmental covariates related to the probability of detection

	Depth	DSQ	Method	GOHV	Repeat
Depth	1.00				
DSQ	0.98	1.00			
Method	0.00	0.00	1.00		
GOHV	-0.29	-0.29	0.00	1.00	
Repeat	-0.09	-0.09	0.30	-0.02	1.00

APPENDIX B: MODEL-AVERAGED ESTIMATES OF OCCUPANCY AND DETECTION PARAMETERS BY STREAM SEGMENT

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PRESENCE AIC FILE:c:\users\admin\documents\my
project\data\occupancy\presencet𝑅ials\presenceanalysis\altmodels.pa3

nsegments=67 nsrvys=8 nmods=6
ψ
ψ(model-season 1)(segment   1) model-avg-est:  0.3078 se=  0.1622 K5-1
ψ(model-season 1)(segment   2) model-avg-est:  0.3394 se=  0.2377 K5-2
ψ(model-season 1)(segment   3) model-avg-est:  0.1677 se=  0.1181 K5-3
ψ(model-season 1)(segment   4) model-avg-est:  0.8444 se=  0.1141 K5-4
ψ(model-season 1)(segment   5) model-avg-est:  0.9616 se=  0.0428 L3-1
ψ(model-season 1)(segment   6) model-avg-est:  0.9817 se=  0.0236 L3-2
ψ(model-season 1)(segment   7) model-avg-est:  0.9898 se=  0.0156 L3-3
ψ(model-season 1)(segment   8) model-avg-est:  0.9758 se=  0.0316 L3-4
ψ(model-season 1)(segment   9) model-avg-est:  0.9949 se=  0.0071 L3-5
ψ(model-season 1)(segment  10) model-avg-est:  0.9944 se=  0.0074 L3-6
ψ(model-season 1)(segment  11) model-avg-est:  0.9003 se=  0.0809 L3-7
ψ(model-season 1)(segment  12) model-avg-est:  0.9400 se=  0.0597 L3-8
ψ(model-season 1)(segment  13) model-avg-est:  0.8723 se=  0.0843 L3-9
ψ(model-season 1)(segment  14) model-avg-est:  0.5297 se=  0.2176 L3-10
ψ(model-season 1)(segment  15) model-avg-est:  0.4382 se=  0.2012 L3-11
ψ(model-season 1)(segment  16) model-avg-est:  0.2556 se=  0.2123 L3-12
ψ(model-season 1)(segment  17) model-avg-est:  0.8965 se=  0.0840 L3-13
ψ(model-season 1)(segment  18) model-avg-est:  0.8026 se=  0.2349 L2-1
ψ(model-season 1)(segment  19) model-avg-est:  0.9248 se=  0.1585 L2-2
ψ(model-season 1)(segment  20) model-avg-est:  0.1437 se=  0.1310 L2-3
ψ(model-season 1)(segment  21) model-avg-est:  0.6020 se=  0.3240 L2-4
ψ(model-season 1)(segment  22) model-avg-est:  0.0011 se=  0.0021 L2-5
ψ(model-season 1)(segment  23) model-avg-est:  0.0079 se=  0.0142 L2-6
ψ(model-season 1)(segment  24) model-avg-est:  0.0075 se=  0.0136 L2-7
ψ(model-season 1)(segment  25) model-avg-est:  0.9485 se=  0.0709 L2-8
ψ(model-season 1)(segment  26) model-avg-est:  0.4886 se=  0.5593 L2-9
ψ(model-season 1)(segment  27) model-avg-est:  0.8531 se=  0.1232 L2-10
ψ(model-season 1)(segment  28) model-avg-est:  0.8704 se=  0.1075 L1B-1
ψ(model-season 1)(segment  29) model-avg-est:  0.9218 se=  0.0777 L1B-2
ψ(model-season 1)(segment  30) model-avg-est:  0.6158 se=  0.1407 L1B-3
ψ(model-season 1)(segment  31) model-avg-est:  0.9986 se=  0.0024 L1A-1
ψ(model-season 1)(segment  32) model-avg-est:  0.6843 se=  0.2781 L1A-2
ψ(model-season 1)(segment  33) model-avg-est:  0.9909 se=  0.0118 L1A-3
ψ(model-season 1)(segment  34) model-avg-est:  0.3068 se=  0.1770 L1A-4
ψ(model-season 1)(segment  35) model-avg-est:  0.5780 se=  0.4222 L1A-5
ψ(model-season 1)(segment  36) model-avg-est:  0.9998 se=  0.0004 L1A-6
ψ(model-season 1)(segment  37) model-avg-est:  0.9983 se=  0.0030 L1A-7
ψ(model-season 1)(segment  38) model-avg-est:  0.9955 se=  0.0061 L1A-8
ψ(model-season 1)(segment  39) model-avg-est:  0.4724 se=  0.1800 L1A-9
ψ(model-season 1)(segment  40) model-avg-est:  0.8972 se=  0.0666 L1A-10
ψ(model-season 1)(segment  41) model-avg-est:  0.9659 se=  0.0396 M4-1
ψ(model-season 1)(segment  42) model-avg-est:  0.9668 se=  0.0369 M4-2
ψ(model-season 1)(segment  43) model-avg-est:  0.8901 se=  0.0883 M4-3
ψ(model-season 1)(segment  44) model-avg-est:  0.9602 se=  0.0379 M4-4
ψ(model-season 1)(segment  45) model-avg-est:  0.7589 se=  0.1453 M4-5
ψ(model-season 1)(segment  46) model-avg-est:  0.9044 se=  0.0679 M4-6
ψ(model-season 1)(segment  47) model-avg-est:  0.6673 se=  0.1586 M4-7
ψ(model-season 1)(segment  48) model-avg-est:  0.7997 se=  0.0989 M4-8
ψ(model-season 1)(segment  49) model-avg-est:  0.8429 se=  0.1338 M4-9
ψ(model-season 1)(segment  50) model-avg-est:  0.9163 se=  0.0654 M4-10
ψ(model-season 1)(segment  51) model-avg-est:  0.7488 se=  0.2263 M3-1
ψ(model-season 1)(segment  52) model-avg-est:  0.6875 se=  0.1927 M3-2
ψ(model-season 1)(segment  53) model-avg-est:  0.2347 se=  0.1360 M3-3
ψ(model-season 1)(segment  54) model-avg-est:  0.1901 se=  0.1812 M3-4
ψ(model-season 1)(segment  55) model-avg-est:  0.3776 se=  0.2789 M3-5
ψ(model-season 1)(segment  56) model-avg-est:  0.7930 se=  0.1666 M2-1
ψ(model-season 1)(segment  57) model-avg-est:  0.3143 se=  0.1199 M2-2
ψ(model-season 1)(segment  58) model-avg-est:  0.0680 se=  0.0939 M2-3
ψ(model-season 1)(segment  59) model-avg-est:  0.0865 se=  0.0998 M2-4
ψ(model-season 1)(segment  60) model-avg-est:  0.1068 se=  0.2618 M2-5
ψ(model-season 1)(segment  61) model-avg-est:  0.1722 se=  0.0850 M2-6
ψ(model-season 1)(segment  62) model-avg-est:  0.1775 se=  0.1840 M1-1
ψ(model-season 1)(segment  63) model-avg-est:  0.1359 se=  0.1494 M1-2
ψ(model-season 1)(segment  64) model-avg-est:  0.1069 se=  0.1161 M1-3
ψ(model-season 1)(segment  65) model-avg-est:  0.0191 se=  0.0243 M1-4
ψ(model-season 1)(segment  66) model-avg-est:  0.0570 se=  0.0662 M1-5
ψ(model-season 1)(segment  67) model-avg-est:  0.0052 se=  0.0069 M1-6
ψ(model-season 1)(avg.allsegments) model-avg-est:   0.6038 sd=  0.3583

Ψ (model-season 2)(segment   1) model-avg-est:  0.9441 se=  0.0835 K5-1
Ψ (model-season 2)(segment   2) model-avg-est:  0.9349 se=  0.1079 K5-2
Ψ (model-season 2)(segment   3) model-avg-est:  0.8466 se=  0.2065 K5-3
Ψ (model-season 2)(segment   4) model-avg-est:  0.9726 se=  0.0443 K5-4
Ψ (model-season 2)(segment   5) model-avg-est:  0.9352 se=  0.0962 L3-1
Ψ (model-season 2)(segment   6) model-avg-est:  0.9252 se=  0.1091 L3-2
Ψ (model-season 2)(segment   7) model-avg-est:  0.8994 se=  0.1424 L3-3
Ψ (model-season 2)(segment   8) model-avg-est:  0.9053 se=  0.1347 L3-4
Ψ (model-season 2)(segment   9) model-avg-est:  0.9784 se=  0.0355 L3-5
Ψ (model-season 2)(segment  10) model-avg-est:  0.9933 se=  0.0119 L3-6
Ψ (model-season 2)(segment  11) model-avg-est:  0.9347 se=  0.0960 L3-7
Ψ (model-season 2)(segment  12) model-avg-est:  0.9892 se=  0.0192 L3-8
Ψ (model-season 2)(segment  13) model-avg-est:  0.9715 se=  0.0448 L3-9
Ψ (model-season 2)(segment  14) model-avg-est:  0.8432 se=  0.2123 L3-10
Ψ (model-season 2)(segment  15) model-avg-est:  0.7347 se=  0.3067 L3-11
Ψ (model-season 2)(segment  16) model-avg-est:  0.8269 se=  0.2260 L3-12
Ψ (model-season 2)(segment  17) model-avg-est:  0.9520 se=  0.0725 L3-13
Ψ (model-season 2)(segment  18) model-avg-est:  0.6489 se=  0.3558 L2-1
Ψ (model-season 2)(segment  19) model-avg-est:  0.6362 se=  0.3622 L2-2
Ψ (model-season 2)(segment  20) model-avg-est:  0.1888 se=  0.2450 L2-3
Ψ (model-season 2)(segment  21) model-avg-est:  0.7839 se=  0.2710 L2-4
Ψ (model-season 2)(segment  22) model-avg-est:  0.1731 se=  0.2302 L2-5
Ψ (model-season 2)(segment  23) model-avg-est:  0.5858 se=  0.3827 L2-6
Ψ (model-season 2)(segment  24) model-avg-est:  0.5734 se=  0.3867 L2-7
Ψ (model-season 2)(segment  25) model-avg-est:  0.9998 se=  0.0006 L2-8
Ψ (model-season 2)(segment  26) model-avg-est:  0.9985 se=  0.0032 L2-9
Ψ (model-season 2)(segment  27) model-avg-est:  0.9901 se=  0.0192 L2-10
Ψ (model-season 2)(segment  28) model-avg-est:  0.8657 se=  0.1798 L1B-1
Ψ (model-season 2)(segment  29) model-avg-est:  0.9288 se=  0.1059 L1B-2
Ψ (model-season 2)(segment  30) model-avg-est:  0.8514 se=  0.1962 L1B-3
Ψ (model-season 2)(segment  31) model-avg-est:  1.0000 se=  0.0000 L1A-1
Ψ (model-season 2)(segment  32) model-avg-est:  0.9990 se=  0.0021 L1A-2
Ψ (model-season 2)(segment  33) model-avg-est:  0.9976 se=  0.0045 L1A-3
Ψ (model-season 2)(segment  34) model-avg-est:  0.9320 se=  0.1023 L1A-4
Ψ (model-season 2)(segment  35) model-avg-est:  0.9831 se=  0.0274 L1A-5
Ψ (model-season 2)(segment  36) model-avg-est:  1.0000 se=  0.0002 L1A-6
Ψ (model-season 2)(segment  37) model-avg-est:  1.0000 se=  0.0002 L1A-7
Ψ (model-season 2)(segment  38) model-avg-est:  0.9996 se=  0.0008 L1A-8
Ψ (model-season 2)(segment  39) model-avg-est:  0.8314 se=  0.2215 L1A-9
Ψ (model-season 2)(segment  40) model-avg-est:  0.9976 se=  0.0045 L1A-10
Ψ (model-season 2)(segment  41) model-avg-est:  0.9922 se=  0.0135 M4-1
Ψ (model-season 2)(segment  42) model-avg-est:  0.9938 se=  0.0109 M4-2
Ψ (model-season 2)(segment  43) model-avg-est:  0.9890 se=  0.0185 M4-3
Ψ (model-season 2)(segment  42) model-avg-est:  0.9938 se=  0.0109 M4-2
Ψ (model-season 2)(segment  43) model-avg-est:  0.9890 se=  0.0185 M4-3
Ψ (model-season 2)(segment  44) model-avg-est:  0.9981 se=  0.0037 M4-4
Ψ (model-season 2)(segment  45) model-avg-est:  0.9840 se=  0.0265 M4-5
Ψ (model-season 2)(segment  46) model-avg-est:  0.9956 se=  0.0078 M4-6
Ψ (model-season 2)(segment  47) model-avg-est:  0.9967 se=  0.0060 M4-7
Ψ (model-season 2)(segment  48) model-avg-est:  0.9960 se=  0.0072 M4-8
Ψ (model-season 2)(segment  49) model-avg-est:  0.9990 se=  0.0020 M4-9
Ψ (model-season 2)(segment  50) model-avg-est:  0.9994 se=  0.0012 M4-10
Ψ (model-season 2)(segment  51) model-avg-est:  0.8905 se=  0.1692 M3-1
Ψ (model-season 2)(segment  52) model-avg-est:  0.9876 se=  0.0231 M3-2
Ψ (model-season 2)(segment  53) model-avg-est:  0.8172 se=  0.2560 M3-3
Ψ (model-season 2)(segment  54) model-avg-est:  0.8680 se=  0.1995 M3-4
Ψ (model-season 2)(segment  55) model-avg-est:  0.9206 se=  0.1322 M3-5
Ψ (model-season 2)(segment  56) model-avg-est:  0.9290 se=  0.1027 M2-1
Ψ (model-season 2)(segment  57) model-avg-est:  0.9397 se=  0.0889 M2-2
Ψ (model-season 2)(segment  58) model-avg-est:  0.9194 se=  0.1154 M2-3
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Ψ (model-season 2)(segment  59) model-avg-est:  0.9308 se=  0.1009 M2-4
Ψ (model-season 2)(segment  60) model-avg-est:  0.9441 se=  0.0840 M2-5
Ψ (model-season 2)(segment  61) model-avg-est:  0.9214 se=  0.1136 M2-6
Ψ (model-season 2)(segment  62) model-avg-est:  0.9867 se=  0.0222 M1-1
Ψ (model-season 2)(segment  63) model-avg-est:  0.9858 se=  0.0233 M1-2
Ψ (model-season 2)(segment  64) model-avg-est:  0.9771 se=  0.0363 M1-3
Ψ (model-season 2)(segment  65) model-avg-est:  0.9650 se=  0.0537 M1-4
Ψ (model-season 2)(segment  66) model-avg-est:  0.9507 se=  0.0737 M1-5
Ψ (model-season 2)(segment  67) model-avg-est:  0.7020 se=  0.3211 M1-6
Ψ (model-season 2)(avg.all segments) model-avg-est:  0.8975 sd=  0.1632

Ψ (model-season 3)(segment   1) model-avg-est:  0.5445 se=  0.1123 K5-1
Ψ (model-season 3)(segment   2) model-avg-est:  0.5072 se=  0.2342 K5-2
Ψ (model-season 3)(segment   3) model-avg-est:  0.2787 se=  0.1394 K5-3
Ψ (model-season 3)(segment   4) model-avg-est:  0.7166 se=  0.1417 K5-4
Ψ (model-season 3)(segment   5) model-avg-est:  0.1858 se=  0.0682 L3-1
Ψ (model-season 3)(segment   6) model-avg-est:  0.1631 se=  0.0646 L3-2
Ψ (model-season 3)(segment   7) model-avg-est:  0.1228 se=  0.0603 L3-3
Ψ (model-season 3)(segment   8) model-avg-est:  0.1303 se=  0.0624 L3-4
Ψ (model-season 3)(segment   9) model-avg-est:  0.4223 se=  0.1182 L3-5
Ψ (model-season 3)(segment  10) model-avg-est:  0.7083 se=  0.1281 L3-6
Ψ (model-season 3)(segment  11) model-avg-est:  0.1838 se=  0.0712 L3-7
Ψ (model-season 3)(segment  12) model-avg-est:  0.5954 se=  0.1715 L3-8
Ψ (model-season 3)(segment  13) model-avg-est:  0.3523 se=  0.0845 L3-9
Ψ (model-season 3)(segment  14) model-avg-est:  0.0783 se=  0.0534 L3-10
Ψ (model-season 3)(segment  15) model-avg-est:  0.0416 se=  0.0306 L3-11
Ψ (model-season 3)(segment  16) model-avg-est:  0.0700 se=  0.0468 L3-12
Ψ (model-season 3)(segment  17) model-avg-est:  0.2381 se=  0.0915 L3-13
Ψ (model-season 3)(segment  18) model-avg-est:  0.0567 se=  0.0356 L2-1
Ψ (model-season 3)(segment  19) model-avg-est:  0.0538 se=  0.0344 L2-2
Ψ (model-season 3)(segment  20) model-avg-est:  0.0075 se=  0.0076 L2-3
Ψ (model-season 3)(segment  21) model-avg-est:  0.1067 se=  0.0546 L2-4
Ψ (model-season 3)(segment  22) model-avg-est:  0.0068 se=  0.0069 L2-5
Ψ (model-season 3)(segment  23) model-avg-est:  0.0439 se=  0.0301 L2-6
Ψ (model-season 3)(segment  24) model-avg-est:  0.0418 se=  0.0292 L2-7
Ψ (model-season 3)(segment  25) model-avg-est:  0.9935 se=  0.0101 L2-8
Ψ (model-season 3)(segment  26) model-avg-est:  0.9613 se=  0.0462 L2-9
Ψ (model-season 3)(segment  27) model-avg-est:  0.7783 se=  0.1659 L2-10
Ψ (model-season 3)(segment  28) model-avg-est:  0.3107 se=  0.1001 L1B-1
Ψ (model-season 3)(segment  29) model-avg-est:  0.4806 se=  0.1151 L1B-2
Ψ (model-season 3)(segment  30) model-avg-est:  0.2858 se=  0.0982 L1B-3
Ψ (model-season 3)(segment  31) model-avg-est:  0.9988 se=  0.0022 L1A-1
Ψ (model-season 3)(segment  32) model-avg-est:  0.9175 se=  0.0697 L1A-2
Ψ (model-season 3)(segment  33) model-avg-est:  0.8269 se=  0.1223 L1A-3
Ψ (model-season 3)(segment  34) model-avg-est:  0.1302 se=  0.0853 L1A-4
Ψ (model-season 3)(segment  35) model-avg-est:  0.3903 se=  0.1084 L1A-5
Ψ (model-season 3)(segment  36) model-avg-est:  0.9947 se=  0.0088 L1A-6
Ψ (model-season 3)(segment  37) model-avg-est:  0.9945 se=  0.0090 L1A-7
Ψ (model-season 3)(segment  38) model-avg-est:  0.9689 se=  0.0365 L1A-8
Ψ (model-season 3)(segment  39) model-avg-est:  0.0507 se=  0.0367 L1A-9
Ψ (model-season 3)(segment  40) model-avg-est:  0.8275 se=  0.1085 L1A-10
Ψ (model-season 3)(segment  41) model-avg-est:  0.7497 se=  0.0965 M4-1
Ψ (model-season 3)(segment  42) model-avg-est:  0.7901 se=  0.0908 M4-2
Ψ (model-season 3)(segment  43) model-avg-est:  0.6768 se=  0.1089 M4-3
Ψ (model-season 3)(segment  44) model-avg-est:  0.9266 se=  0.0579 M4-4
Ψ (model-season 3)(segment  45) model-avg-est:  0.5880 se=  0.1467 M4-5
Ψ (model-season 3)(segment  46) model-avg-est:  0.8425 se=  0.0787 M4-6
Ψ (model-season 3)(segment  47) model-avg-est:  0.8767 se=  0.0695 M4-7
Ψ (model-season 3)(segment  48) model-avg-est:  0.8541 se=  0.0783 M4-8
Ψ (model-season 3)(segment  49) model-avg-est:  0.9606 se=  0.0346 M4-9
Ψ (model-season 3)(segment  50) model-avg-est:  0.9766 se=  0.0233 M4-10
Ψ (model-season 3)(segment  51) model-avg-est:  0.1145 se=  0.0794 M3-1
Ψ (model-season 3)(segment  52) model-avg-est:  0.5647 se=  0.1892 M3-2
Ψ (model-season 3)(segment  53) model-avg-est:  0.0657 se=  0.0496 M3-3
Ψ (model-season 3)(segment  54) model-avg-est:  0.0944 se=  0.0694 M3-4
Ψ (model-season 3)(segment  55) model-avg-est:  0.1568 se=  0.1163 M3-5
Ψ (model-season 3)(segment  56) model-avg-est:  0.3035 se=  0.0885 M2-1
Ψ (model-season 3)(segment  57) model-avg-est:  0.3425 se=  0.0875 M2-2
Ψ (model-season 3)(segment  58) model-avg-est:  0.2750 se=  0.0853 M2-3
Ψ (model-season 3)(segment  59) model-avg-est:  0.3101 se=  0.0860 M2-4
Ψ (model-season 3)(segment  60) model-avg-est:  0.3616 se=  0.0932 M2-5
Ψ (model-season 3)(segment  61) model-avg-est:  0.2812 se=  0.0846 M2-6
Ψ (model-season 3)(segment  62) model-avg-est:  0.3611 se=  0.1703 M1-1
Ψ (model-season 3)(segment  63) model-avg-est:  0.3463 se=  0.1410 M1-2
Ψ (model-season 3)(segment  64) model-avg-est:  0.2430 se=  0.1092 M1-3
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Ψ (model-season 3)(segment  65) model-avg-est:  0.1712 se=  0.0854 M1-4
Ψ (model-season 3)(segment  66) model-avg-est:  0.1256 se=  0.0691 M1-5
Ψ (model-season 3)(segment  67) model-avg-est:  0.0170 se=  0.0148 M1-6
Ψ (model-season 3)(avg.all segments) model-avg-est:  0.4320 sd=  0.3369

Ψ (model-season 4)(segment   1) model-avg-est:  0.6634 se=  0.2860 K5-1
Ψ (model-season 4)(segment   2) model-avg-est:  0.6290 se=  0.3291 K5-2
Ψ (model-season 4)(segment   3) model-avg-est:  0.3906 se=  0.2907 K5-3
Ψ (model-season 4)(segment   4) model-avg-est:  0.8055 se=  0.2288 K5-4
Ψ (model-season 4)(segment   5) model-avg-est:  0.2069 se=  0.1797 L3-1
Ψ (model-season 4)(segment   6) model-avg-est:  0.1822 se=  0.1639 L3-2
Ψ (model-season 4)(segment   7) model-avg-est:  0.1377 se=  0.1340 L3-3
Ψ (model-season 4)(segment   8) model-avg-est:  0.1460 se=  0.1410 L3-4
Ψ (model-season 4)(segment   9) model-avg-est:  0.4546 se=  0.2953 L3-5
Ψ (model-season 4)(segment  10) model-avg-est:  0.7326 se=  0.2841 L3-6
Ψ (model-season 4)(segment  11) model-avg-est:  0.2047 se=  0.1833 L3-7
Ψ (model-season 4)(segment  12) model-avg-est:  0.6254 se=  0.3466 L3-8
Ψ (model-season 4)(segment  13) model-avg-est:  0.3831 se=  0.2706 L3-9
Ψ (model-season 4)(segment  14) model-avg-est:  0.0883 se=  0.0887 L3-10
Ψ (model-season 4)(segment  15) model-avg-est:  0.0468 se=  0.0494 L3-11
Ψ (model-season 4)(segment  16) model-avg-est:  0.0789 se=  0.0795 L3-12
Ψ (model-season 4)(segment  17) model-avg-est:  0.2630 se=  0.2290 L3-13
Ψ (model-season 4)(segment  18) model-avg-est:  0.0449 se=  0.0499 L2-1
Ψ (model-season 4)(segment  19) model-avg-est:  0.0426 se=  0.0475 L2-2
Ψ (model-season 4)(segment  20) model-avg-est:  0.0058 se=  0.0071 L2-3
Ψ (model-season 4)(segment  21) model-avg-est:  0.0858 se=  0.0884 L2-4
Ψ (model-season 4)(segment  22) model-avg-est:  0.0052 se=  0.0065 L2-5
Ψ (model-season 4)(segment  23) model-avg-est:  0.0346 se=  0.0393 L2-6
Ψ (model-season 4)(segment  24) model-avg-est:  0.0329 se=  0.0375 L2-7
Ψ (model-season 4)(segment  25) model-avg-est:  0.9912 se=  0.0185 L2-8
Ψ (model-season 4)(segment  26) model-avg-est:  0.9492 se=  0.0913 L2-9
Ψ (model-season 4)(segment  27) model-avg-est:  0.7309 se=  0.3190 L2-10
Ψ (model-season 4)(segment  28) model-avg-est:  0.2615 se=  0.2137 L1B-1
Ψ (model-season 4)(segment  29) model-avg-est:  0.4206 se=  0.2778 L1B-2
Ψ (model-season 4)(segment  30) model-avg-est:  0.2392 se=  0.2002 L1B-3
Ψ (model-season 4)(segment  31) model-avg-est:  0.9997 se=  0.0006 L1A-1
Ψ (model-season 4)(segment  32) model-avg-est:  0.9818 se=  0.0296 L1A-2
Ψ (model-season 4)(segment  33) model-avg-est:  0.9591 se=  0.0638 L1A-3
Ψ (model-season 4)(segment  34) model-avg-est:  0.4329 se=  0.2975 L1A-4
Ψ (model-season 4)(segment  35) model-avg-est:  0.7637 se=  0.2315 L1A-5
Ψ (model-season 4)(segment  36) model-avg-est:  0.9989 se=  0.0026 L1A-6
Ψ (model-season 4)(segment  37) model-avg-est:  0.9988 se=  0.0026 L1A-7
Ψ (model-season 4)(segment  38) model-avg-est:  0.9933 se=  0.0123 L1A-8
Ψ (model-season 4)(segment  39) model-avg-est:  0.2138 se=  0.1878 L1A-9
Ψ (model-season 4)(segment  40) model-avg-est:  0.9592 se=  0.0598 L1A-10
Ψ (model-season 4)(segment  41) model-avg-est:  0.6995 se=  0.2579 M4-1
Ψ (model-season 4)(segment  42) model-avg-est:  0.7448 se=  0.2379 M4-2
Ψ (model-season 4)(segment  43) model-avg-est:  0.6203 se=  0.2866 M4-3
Ψ (model-season 4)(segment  44) model-avg-est:  0.9062 se=  0.1216 M4-4
Ψ (model-season 4)(segment  45) model-avg-est:  0.5275 se=  0.3139 M4-5
Ψ (model-season 4)(segment  46) model-avg-est:  0.8053 se=  0.2039 M4-6
Ψ (model-season 4)(segment  47) model-avg-est:  0.8457 se=  0.1742 M4-7
Ψ (model-season 4)(segment  48) model-avg-est:  0.8190 se=  0.1978 M4-8
Ψ (model-season 4)(segment  49) model-avg-est:  0.9489 se=  0.0727 M4-9
Ψ (model-season 4)(segment  50) model-avg-est:  0.9693 se=  0.0470 M4-10
Ψ (model-season 4)(segment  51) model-avg-est:  0.1288 se=  0.1299 M3-1
Ψ (model-season 4)(segment  52) model-avg-est:  0.5954 se=  0.3363 M3-2
Ψ (model-season 4)(segment  53) model-avg-est:  0.0742 se=  0.0790 M3-3
Ψ (model-season 4)(segment  54) model-avg-est:  0.1064 se=  0.1106 M3-4
Ψ (model-season 4)(segment  55) model-avg-est:  0.1757 se=  0.1784 M3-5
Ψ (model-season 4)(segment  56) model-avg-est:  0.4196 se=  0.2792 M2-1
Ψ (model-season 4)(segment  57) model-avg-est:  0.4634 se=  0.2840 M2-2
Ψ (model-season 4)(segment  58) model-avg-est:  0.3863 se=  0.2686 M2-3
Ψ (model-season 4)(segment  59) model-avg-est:  0.4271 se=  0.2765 M2-4
Ψ (model-season 4)(segment  60) model-avg-est:  0.4841 se=  0.2849 M2-5
Ψ (model-season 4)(segment  61) model-avg-est:  0.3937 se=  0.2674 M2-6
Ψ (model-season 4)(segment  62) model-avg-est:  0.5761 se=  0.3550 M1-1
Ψ (model-season 4)(segment  63) model-avg-est:  0.5603 se=  0.3353 M1-2
Ψ (model-season 4)(segment  64) model-avg-est:  0.4366 se=  0.3193 M1-3
Ψ (model-season 4)(segment  65) model-avg-est:  0.3331 se=  0.2798 M1-4
Ψ (model-season 4)(segment  66) model-avg-est:  0.2578 se=  0.2371 M1-5
Ψ (model-season 4)(segment  67) model-avg-est:  0.0399 se=  0.0443 M1-6
Ψ (model-season 4)(avg.all segments) model-avg-est:  0.4766 sd=  0.3310

R(model-season 1)(segment   1) model-avg-est:  0.1319 se=  0.0767 K5-1
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R(model-season 1)(segment   2) model-avg-est:   0.7194 se=  0.2553 K5-2
R(model-season 1)(segment   3) model-avg-est:   0.4502 se=  0.2129 K5-3
R(model-season 1)(segment   4) model-avg-est:   0.3230 se=  0.1590 K5-4
R(model-season 1)(segment   5) model-avg-est:   0.4621 se=  0.1455 L3-1
R(model-season 1)(segment   6) model-avg-est:   0.4973 se=  0.1538 L3-2
R(model-season 1)(segment   7) model-avg-est:   0.0188 se=  0.0175 L3-3
R(model-season 1)(segment   8) model-avg-est:   0.0316 se=  0.0301 L3-4
R(model-season 1)(segment   9) model-avg-est:   0.1756 se=  0.1485 L3-5
R(model-season 1)(segment  10) model-avg-est:   0.5367 se=  0.1610 L3-6
R(model-season 1)(segment  11) model-avg-est:   0.5109 se=  0.1535 L3-7
R(model-season 1)(segment  12) model-avg-est:   0.3949 se=  0.1953 L3-8
R(model-season 1)(segment  13) model-avg-est:   0.7267 se=  0.1111 L3-9
R(model-season 1)(segment  14) model-avg-est:   0.7905 se=  0.1016 L3-10
R(model-season 1)(segment  15) model-avg-est:   0.7332 se=  0.1869 L3-11
R(model-season 1)(segment  16) model-avg-est:   0.0656 se=  0.0419 L3-12
R(model-season 1)(segment  17) model-avg-est:   0.0475 se=  0.0361 L3-13
R(model-season 1)(segment  18) model-avg-est:   0.0120 se=  0.0125 L2-1
R(model-season 1)(segment  19) model-avg-est:   0.0170 se=  0.0186 L2-2
R(model-season 1)(segment  20) model-avg-est:   0.0084 se=  0.0090 L2-3
R(model-season 1)(segment  21) model-avg-est:   0.0588 se=  0.0660 L2-4
R(model-season 1)(segment  22) model-avg-est:   0.0354 se=  0.0487 L2-5
R(model-season 1)(segment  23) model-avg-est:   0.0335 se=  0.0463 L2-6
R(model-season 1)(segment  24) model-avg-est:   0.0317 se=  0.0442 L2-7
R(model-season 1)(segment  25) model-avg-est:   0.3949 se=  0.5503 L2-8
R(model-season 1)(segment  26) model-avg-est:   0.3613 se=  0.6607 L2-9
R(model-season 1)(segment  27) model-avg-est:   0.6899 se=  0.1791 L2-10
R(model-season 1)(segment  28) model-avg-est:   0.5130 se=  0.1493 L1B-1
R(model-season 1)(segment  29) model-avg-est:   0.6276 se=  0.1323 L1B-2
R(model-season 1)(segment  30) model-avg-est:   0.5041 se=  0.1609 L1B-3
R(model-season 1)(segment  31) model-avg-est:   0.9086 se=  0.1170 L1A-1
R(model-season 1)(segment  32) model-avg-est:   0.8476 se=  0.1823 L1A-2
R(model-season 1)(segment  33) model-avg-est:   0.8583 se=  0.1006 L1A-3
R(model-season 1)(segment  34) model-avg-est:   0.4415 se=  0.2722 L1A-4
R(model-season 1)(segment  35) model-avg-est:   0.4514 se=  0.4781 L1A-5
R(model-season 1)(segment  36) model-avg-est:   0.8485 se=  0.0887 L1A-6
R(model-season 1)(segment  37) model-avg-est:   0.8479 se=  0.0857 L1A-7
R(model-season 1)(segment  38) model-avg-est:   0.9028 se=  0.0639 L1A-8
R(model-season 1)(segment  39) model-avg-est:   0.8595 se=  0.0863 L1A-9
R(model-season 1)(segment  40) model-avg-est:   0.8503 se=  0.0902 L1A-10
R(model-season 1)(segment  41) model-avg-est:   0.1755 se=  0.1059 M4-1
R(model-season 1)(segment  42) model-avg-est:   0.1405 se=  0.0751 M4-2
R(model-season 1)(segment  43) model-avg-est:   0.1115 se=  0.0665 M4-3
R(model-season 1)(segment  44) model-avg-est:   0.4013 se=  0.1820 M4-4
R(model-season 1)(segment  45) model-avg-est:   0.0525 se=  0.0388 M4-5
R(model-season 1)(segment  46) model-avg-est:   0.1820 se=  0.0958 M4-6
R(model-season 1)(segment  47) model-avg-est:   0.9085 se=  0.0686 M4-7
R(model-season 1)(segment  48) model-avg-est:   0.2168 se=  0.1074 M4-8
R(model-season 1)(segment  49) model-avg-est:   0.9576 se=  0.0477 M4-9
R(model-season 1)(segment  50) model-avg-est:   0.6874 se=  0.2031 M4-10
R(model-season 1)(segment  51) model-avg-est:   0.0154 se=  0.0183 M3-1
R(model-season 1)(segment  52) model-avg-est:   0.4168 se=  0.2700 M3-2
R(model-season 1)(segment  53) model-avg-est:   0.2376 se=  0.2071 M3-3
R(model-season 1)(segment  54) model-avg-est:   0.0304 se=  0.0436 M3-4
R(model-season 1)(segment  55) model-avg-est:   0.0453 se=  0.0619 M3-5
R(model-season 1)(segment  56) model-avg-est:   0.6197 se=  0.1419 M2-1
R(model-season 1)(segment  57) model-avg-est:   0.0566 se=  0.0408 M2-2
R(model-season 1)(segment  58) model-avg-est:   0.0169 se=  0.0158 M2-3
R(model-season 1)(segment  59) model-avg-est:   0.0214 se=  0.0189 M2-4
R(model-season 1)(segment  60) model-avg-est:   0.0208 se=  0.0195 M2-5
R(model-season 1)(segment  61) model-avg-est:   0.0299 se=  0.0236 M2-6
R(model-season 1)(segment  62) model-avg-est:   0.2752 se=  0.1627 M1-1
R(model-season 1)(segment  63) model-avg-est:   0.2008 se=  0.1462 M1-2
R(model-season 1)(segment  64) model-avg-est:   0.1416 se=  0.0916 M1-3
R(model-season 1)(segment  65) model-avg-est:   0.1665 se=  0.0968 M1-4
R(model-season 1)(segment  66) model-avg-est:   0.1225 se=  0.0801 M1-5
R(model-season 1)(segment  67) model-avg-est:   0.1010 se=  0.0668 M1-6
R(model-season 1)(avg.all segments) model-avg-est:   0.3593 sd=  0.3138

R (model-season 2)(segment   1) model-avg-est:   0.1119 se=  0.0621 K5-1
R (model-season 2)(segment   2) model-avg-est:   0.5053 se=  0.1966 K5-2
R (model-season 2)(segment   3) model-avg-est:   0.2522 se=  0.1173 K5-3
R (model-season 2)(segment   4) model-avg-est:   0.2337 se=  0.1327 K5-4
R (model-season 2)(segment   5) model-avg-est:   0.4526 se=  0.1392 L3-1
R (model-season 2)(segment   6) model-avg-est:   0.4088 se=  0.1408 L3-2
R (model-season 2)(segment   7) model-avg-est:   0.0104 se=  0.0103 L3-3
R (model-season 2)(segment   8) model-avg-est:   0.0113 se=  0.0109 L3-4
R (model-season 2)(segment   9) model-avg-est:   0.0646 se=  0.0448 L3-5
R (model-season 2)(segment  10) model-avg-est:   0.5613 se=  0.1319 L3-6
R (model-season 2)(segment  11) model-avg-est:   0.4513 se=  0.1468 L3-7
R (model-season 2)(segment  12) model-avg-est:   0.4201 se=  0.1535 L3-8
R (model-season 2)(segment  13) model-avg-est:   0.6929 se=  0.1141 L3-9
R (model-season 2)(segment  14) model-avg-est:   0.7228 se=  0.1089 L3-10
R (model-season 2)(segment  15) model-avg-est:   0.5469 se=  0.1464 L3-11
R (model-season 2)(segment  16) model-avg-est:   0.0480 se=  0.0321 L3-12
R (model-season 2)(segment  17) model-avg-est:   0.0263 se=  0.0212 L3-13
R (model-season 2)(segment  18) model-avg-est:   0.0060 se=  0.0067 L2-1
R (model-season 2)(segment  19) model-avg-est:   0.0057 se=  0.0064 L2-2
R (model-season 2)(segment  20) model-avg-est:   0.0053 se=  0.0061 L2-3
R (model-season 2)(segment  21) model-avg-est:   0.0130 se=  0.0127 L2-4
R (model-season 2)(segment  22) model-avg-est:   0.0047 se=  0.0055 L2-5
R (model-season 2)(segment  23) model-avg-est:   0.0044 se=  0.0052 L2-6
R (model-season 2)(segment  24) model-avg-est:   0.0042 se=  0.0050 L2-7
R (model-season 2)(segment  25) model-avg-est:   0.7190 se=  0.1743 L2-8
R (model-season 2)(segment  26) model-avg-est:   0.7402 se=  0.1747 L2-9
R (model-season 2)(segment  27) model-avg-est:   0.7403 se=  0.1787 L2-10
R (model-season 2)(segment  28) model-avg-est:   0.4341 se=  0.1410 L1B-1
R (model-season 2)(segment  29) model-avg-est:   0.6346 se=  0.1287 L1B-2
R (model-season 2)(segment  30) model-avg-est:   0.4004 se=  0.1405 L1B-3
R (model-season 2)(segment  31) model-avg-est:   0.9710 se=  0.0282 L1A-1
R (model-season 2)(segment  32) model-avg-est:   0.9475 se=  0.0422 L1A-2
R (model-season 2)(segment  33) model-avg-est:   0.8713 se=  0.0805 L1A-3
R (model-season 2)(segment  34) model-avg-est:   0.2097 se=  0.0996 L1A-4
R (model-season 2)(segment  35) model-avg-est:   0.1259 se=  0.0664 L1A-5
R (model-season 2)(segment  36) model-avg-est:   0.8445 se=  0.0832 L1A-6
R (model-season 2)(segment  37) model-avg-est:   0.8386 se=  0.0838 L1A-7
R (model-season 2)(segment  38) model-avg-est:   0.8593 se=  0.0768 L1A-8
R (model-season 2)(segment  39) model-avg-est:   0.7844 se=  0.0974 L1A-9
R (model-season 2)(segment  40) model-avg-est:   0.8690 se=  0.0749 L1A-10
R (model-season 2)(segment  41) model-avg-est:   0.0885 se=  0.0518 M4-1
R (model-season 2)(segment  42) model-avg-est:   0.1122 se=  0.0625 M4-2
R (model-season 2)(segment  43) model-avg-est:   0.0613 se=  0.0386 M4-3
R (model-season 2)(segment  44) model-avg-est:   0.3367 se=  0.1682 M4-4
R (model-season 2)(segment  45) model-avg-est:   0.0412 se=  0.0305 M4-5
R (model-season 2)(segment  46) model-avg-est:   0.1605 se=  0.0803 M4-6
R (model-season 2)(segment  47) model-avg-est:   0.9233 se=  0.0534 M4-7
R (model-season 2)(segment  48) model-avg-est:   0.1764 se=  0.0879 M4-8
R (model-season 2)(segment  49) model-avg-est:   0.9803 se=  0.0204 M4-9
R (model-season 2)(segment  50) model-avg-est:   0.6732 se=  0.1894 M4-10
R (model-season 2)(segment  51) model-avg-est:   0.0060 se=  0.0073 M3-1
R (model-season 2)(segment  52) model-avg-est:   0.2840 se=  0.1771 M3-2
R (model-season 2)(segment  53) model-avg-est:   0.1201 se=  0.0944 M3-3
R (model-season 2)(segment  54) model-avg-est:   0.0046 se=  0.0060 M3-4
R (model-season 2)(segment  55) model-avg-est:   0.0090 se=  0.0111 M3-5
R (model-season 2)(segment  56) model-avg-est:   0.5330 se=  0.1387 M2-1
R (model-season 2)(segment  57) model-avg-est:   0.0299 se=  0.0228 M2-2
R (model-season 2)(segment  58) model-avg-est:   0.0210 se=  0.0175 M2-3
R (model-season 2)(segment  59) model-avg-est:   0.0253 se=  0.0202 M2-4
R (model-season 2)(segment  60) model-avg-est:   0.0325 se=  0.0249 M2-5
R (model-season 2)(segment  61) model-avg-est:   0.0216 se=  0.0180 M2-6
R (model-season 2)(segment  62) model-avg-est:   0.2337 se=  0.1327 M1-1
R (model-season 2)(segment  63) model-avg-est:   0.2169 se=  0.1057 M1-2
R (model-season 2)(segment  64) model-avg-est:   0.1351 se=  0.0730 M1-3
R (model-season 2)(segment  65) model-avg-est:   0.0864 se=  0.0523 M1-4
R (model-season 2)(segment  66) model-avg-est:   0.0587 se=  0.0395 M1-5
R (model-season 2)(segment  67) model-avg-est:   0.0505 se=  0.0348 M1-6
R (model-season 2)(avg.all segments) model-avg-est:   0.3280 sd=  0.3276

R (model-season 3)(segment   1) model-avg-est:   0.0549 se=  0.0434 K5-1
R (model-season 3)(segment   2) model-avg-est:   0.3175 se=  0.1751 K5-2
R (model-season 3)(segment   3) model-avg-est:   0.1343 se=  0.0899 K5-3
R (model-season 3)(segment   4) model-avg-est:   0.1241 se=  0.0978 K5-4
R (model-season 3)(segment   5) model-avg-est:   0.2734 se=  0.1416 L3-1
R (model-season 3)(segment   6) model-avg-est:   0.2394 se=  0.1370 L3-2
R (model-season 3)(segment   7) model-avg-est:   0.0048 se=  0.0060 L3-3
R (model-season 3)(segment   8) model-avg-est:   0.0052 se=  0.0064 L3-4
R (model-season 3)(segment   9) model-avg-est:   0.0305 se=  0.0273 L3-5
R (model-season 3)(segment  10) model-avg-est:   0.3680 se=  0.1551 L3-6
R (model-season 3)(segment  11) model-avg-est:   0.2726 se=  0.1519 L3-7
R (model-season 3)(segment  12) model-avg-est:   0.2483 se=  0.1516 L3-8
R (model-season 3)(segment  13) model-avg-est:   0.5067 se=  0.1540 L3-9
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R (model-season 3)(segment  14) model-avg-est:  0.5429 se=  0.1515 L3-10
R (model-season 3)(segment  15) model-avg-est:  0.3547 se=  0.1711 L3-11
R (model-season 3)(segment  16) model-avg-est:  0.0226 se=  0.0207 L3-12
R (model-season 3)(segment  17) model-avg-est:  0.0123 se=  0.0131 L3-13
R (model-season 3)(segment  18) model-avg-est:  0.0028 se=  0.0038 L2-1
R (model-season 3)(segment  19) model-avg-est:  0.0026 se=  0.0036 L2-2
R (model-season 3)(segment  20) model-avg-est:  0.0025 se=  0.0034 L2-3
R (model-season 3)(segment  21) model-avg-est:  0.0060 se=  0.0072 L2-4
R (model-season 3)(segment  22) model-avg-est:  0.0022 se=  0.0030 L2-5
R (model-season 3)(segment  23) model-avg-est:  0.0020 se=  0.0029 L2-6
R (model-season 3)(segment  24) model-avg-est:  0.0019 se=  0.0028 L2-7
R (model-season 3)(segment  25) model-avg-est:  0.5422 se=  0.2069 L2-8
R (model-season 3)(segment  26) model-avg-est:  0.5693 se=  0.2136 L2-9
R (model-season 3)(segment  27) model-avg-est:  0.5697 se=  0.2183 L2-10
R (model-season 3)(segment  28) model-avg-est:  0.2588 se=  0.1421 L1B-1
R (model-season 3)(segment  29) model-avg-est:  0.4420 se=  0.1547 L1B-2
R (model-season 3)(segment  30) model-avg-est:  0.2331 se=  0.1350 L1B-3
R (model-season 3)(segment  31) model-avg-est:  0.9382 se=  0.0537 L1A-1
R (model-season 3)(segment  32) model-avg-est:  0.8914 se=  0.0763 L1A-2
R (model-season 3)(segment  33) model-avg-est:  0.7546 se=  0.1380 L1A-3
R (model-season 3)(segment  34) model-avg-est:  0.1084 se=  0.0731 L1A-4
R (model-season 3)(segment  35) model-avg-est:  0.0621 se=  0.0468 L1A-5
R (model-season 3)(segment  36) model-avg-est:  0.7119 se=  0.1342 L1A-6
R (model-season 3)(segment  37) model-avg-est:  0.7029 se=  0.1329 L1A-7
R (model-season 3)(segment  38) model-avg-est:  0.7357 se=  0.1214 L1A-8
R (model-season 3)(segment  39) model-avg-est:  0.6235 se=  0.1462 L1A-9
R (model-season 3)(segment  40) model-avg-est:  0.7519 se=  0.1165 L1A-10
R (model-season 3)(segment  41) model-avg-est:  0.0426 se=  0.0343 M4-1
R (model-season 3)(segment  42) model-avg-est:  0.0546 se=  0.0420 M4-2
R (model-season 3)(segment  43) model-avg-est:  0.0292 se=  0.0255 M4-3
R (model-season 3)(segment  44) model-avg-est:  0.1877 se=  0.1229 M4-4
R (model-season 3)(segment  45) model-avg-est:  0.0195 se=  0.0194 M4-5
R (model-season 3)(segment  46) model-avg-est:  0.0806 se=  0.0574 M4-6
R (model-season 3)(segment  47) model-avg-est:  0.8458 se=  0.0921 M4-7
R (model-season 3)(segment  48) model-avg-est:  0.0897 se=  0.0642 M4-8
R (model-season 3)(segment  49) model-avg-est:  0.9580 se=  0.0376 M4-9
R (model-season 3)(segment  50) model-avg-est:  0.4842 se=  0.2172 M4-10
R (model-season 3)(segment  51) model-avg-est:  0.0027 se=  0.0039 M3-1
R (model-season 3)(segment  52) model-avg-est:  0.1528 se=  0.1222 M3-2
R (model-season 3)(segment  53) model-avg-est:  0.0582 se=  0.0581 M3-3
R (model-season 3)(segment  54) model-avg-est:  0.0021 se=  0.0031 M3-4
R (model-season 3)(segment  55) model-avg-est:  0.0041 se=  0.0058 M3-5
R (model-season 3)(segment  56) model-avg-est:  0.3419 se=  0.1594 M2-1
R (model-season 3)(segment  57) model-avg-est:  0.0139 se=  0.0140 M2-2
R (model-season 3)(segment  58) model-avg-est:  0.0098 se=  0.0105 M2-3
R (model-season 3)(segment  59) model-avg-est:  0.0118 se=  0.0122 M2-4
R (model-season 3)(segment  60) model-avg-est:  0.0152 se=  0.0151 M2-5
R (model-season 3)(segment  61) model-avg-est:  0.0100 se=  0.0107 M2-6
R (model-season 3)(segment  62) model-avg-est:  0.1241 se=  0.0978 M1-1
R (model-season 3)(segment  63) model-avg-est:  0.1132 se=  0.0793 M1-2
R (model-season 3)(segment  64) model-avg-est:  0.0672 se=  0.0519 M1-3
R (model-season 3)(segment  65) model-avg-est:  0.0418 se=  0.0355 M1-4
R (model-season 3)(segment  66) model-avg-est:  0.0280 se=  0.0259 M1-5
R (model-season 3)(segment  67) model-avg-est:  0.0240 se=  0.0226 M1-6
R (model-season 3)(avg.all segments) model-avg-est:  0.2424 sd=  0.2861

R (model-season 4)(segment   1) model-avg-est:  0.0046 se=  0.0050 K5-1
R (model-season 4)(segment   2) model-avg-est:  0.0354 se=  0.0346 K5-2
R (model-season 4)(segment   3) model-avg-est:  0.0122 se=  0.0120 K5-3
R (model-season 4)(segment   4) model-avg-est:  0.0112 se=  0.0117 K5-4
R (model-season 4)(segment   5) model-avg-est:  0.0288 se=  0.0270 L3-1
R (model-season 4)(segment   6) model-avg-est:  0.0242 se=  0.0236 L3-2
R (model-season 4)(segment   7) model-avg-est:  0.0004 se=  0.0006 L3-3
R (model-season 4)(segment   8) model-avg-est:  0.0004 se=  0.0006 L3-4
R (model-season 4)(segment   9) model-avg-est:  0.0025 se=  0.0030 L3-5
R (model-season 4)(segment  10) model-avg-est:  0.0439 se=  0.0380 L3-6
R (model-season 4)(segment  11) model-avg-est:  0.0287 se=  0.0276 L3-7
R (model-season 4)(segment  12) model-avg-est:  0.0255 se=  0.0254 L3-8
R (model-season 4)(segment  13) model-avg-est:  0.0749 se=  0.0582 L3-9
R (model-season 4)(segment  14) model-avg-est:  0.0856 se=  0.0647 L3-10
R (model-season 4)(segment  15) model-avg-est:  0.0417 se=  0.0378 L3-11
R (model-season 4)(segment  16) model-avg-est:  0.0018 se=  0.0023 L3-12
R (model-season 4)(segment  17) model-avg-est:  0.0010 se=  0.0013 L3-13
R (model-season 4)(segment  18) model-avg-est:  0.0002 se=  0.0004 L2-1
R (model-season 4)(segment  19) model-avg-est:  0.0002 se=  0.0003 L2-2
R (model-season 4)(segment  20) model-avg-est:  0.0002 se=  0.0003 L2-3
R (model-season 4)(segment  21) model-avg-est:  0.0005 se=  0.0007 L2-4
R (model-season 4)(segment  22) model-avg-est:  0.0002 se=  0.0003 L2-5
R (model-season 4)(segment  23) model-avg-est:  0.0002 se=  0.0003 L2-6
R (model-season 4)(segment  24) model-avg-est:  0.0001 se=  0.0002 L2-7
R (model-season 4)(segment  25) model-avg-est:  0.0871 se=  0.0809 L2-8
R (model-season 4)(segment  26) model-avg-est:  0.0966 se=  0.0911 L2-9
R (model-season 4)(segment  27) model-avg-est:  0.0969 se=  0.0926 L2-10
R (model-season 4)(segment  28) model-avg-est:  0.0268 se=  0.0257 L1B-1
R (model-season 4)(segment  29) model-avg-est:  0.0588 se=  0.0483 L1B-2
R (model-season 4)(segment  30) model-avg-est:  0.0234 se=  0.0229 L1B-3
R (model-season 4)(segment  31) model-avg-est:  0.5457 se=  0.2371 L1A-1
R (model-season 4)(segment  32) model-avg-est:  0.3932 se=  0.2040 L1A-2
R (model-season 4)(segment  33) model-avg-est:  0.1960 se=  0.1348 L1A-3
R (model-season 4)(segment  34) model-avg-est:  0.0095 se=  0.0096 L1A-4
R (model-season 4)(segment  35) model-avg-est:  0.0052 se=  0.0056 L1A-5
R (model-season 4)(segment  36) model-avg-est:  0.1631 se=  0.1100 L1A-6
R (model-season 4)(segment  37) model-avg-est:  0.1572 se=  0.1058 L1A-7
R (model-season 4)(segment  38) model-avg-est:  0.1799 se=  0.1162 L1A-8
R (model-season 4)(segment  39) model-avg-est:  0.1155 se=  0.0828 L1A-9
R (model-season 4)(segment  40) model-avg-est:  0.1930 se=  0.1235 L1A-10
R (model-season 4)(segment  41) model-avg-est:  0.0035 se=  0.0039 M4-1
R (model-season 4)(segment  42) model-avg-est:  0.0045 se=  0.0050 M4-2
R (model-season 4)(segment  43) model-avg-est:  0.0024 se=  0.0028 M4-3
R (model-season 4)(segment  44) model-avg-est:  0.0179 se=  0.0185 M4-4
R (model-season 4)(segment  45) model-avg-est:  0.0016 se=  0.0020 M4-5
R (model-season 4)(segment  46) model-avg-est:  0.0069 se=  0.0072 M4-6
R (model-season 4)(segment  47) model-avg-est:  0.3018 se=  0.1704 M4-7
R (model-season 4)(segment  48) model-avg-est:  0.0078 se=  0.0080 M4-8
R (model-season 4)(segment  49) model-avg-est:  0.6426 se=  0.2198 M4-9
R (model-season 4)(segment  50) model-avg-est:  0.0695 se=  0.0649 M4-10
R (model-season 4)(segment  51) model-avg-est:  0.0002 se=  0.0004 M3-1
R (model-season 4)(segment  52) model-avg-est:  0.0141 se=  0.0164 M3-2
R (model-season 4)(segment  53) model-avg-est:  0.0048 se=  0.0064 M3-3
R (model-season 4)(segment  54) model-avg-est:  0.0002 se=  0.0003 M3-4
R (model-season 4)(segment  55) model-avg-est:  0.0003 se=  0.0005 M3-5
R (model-season 4)(segment  56) model-avg-est:  0.0394 se=  0.0353 M2-1
R (model-season 4)(segment  57) model-avg-est:  0.0011 se=  0.0015 M2-2
R (model-season 4)(segment  58) model-avg-est:  0.0008 se=  0.0011 M2-3
R (model-season 4)(segment  59) model-avg-est:  0.0009 se=  0.0013 M2-4
R (model-season 4)(segment  60) model-avg-est:  0.0012 se=  0.0016 M2-5
R (model-season 4)(segment  61) model-avg-est:  0.0008 se=  0.0011 M2-6
R (model-season 4)(segment  62) model-avg-est:  0.0112 se=  0.0117 M1-1
R (model-season 4)(segment  63) model-avg-est:  0.0100 se=  0.0101 M1-2
R (model-season 4)(segment  64) model-avg-est:  0.0057 se=  0.0061 M1-3
R (model-season 4)(segment  65) model-avg-est:  0.0034 se=  0.0039 M1-4
R (model-season 4)(segment  66) model-avg-est:  0.0023 se=  0.0028 M1-5
R (model-season 4)(segment  67) model-avg-est:  0.0019 se=  0.0024 M1-6
R (model-season 4)(avg.all segments) model-avg-est:  0.0586 sd=  0.1205
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Detection

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p1(model-season 1)(survey-1)(segment   1) model-avg-est:  0.3786 se=  0.1743 K5-1
p1(model-season 1)(survey-1)(segment   2) model-avg-est:  0.3288 se=  0.2162 K5-2
p1(model-season 1)(survey-1)(segment   3) model-avg-est:  0.3390 se=  0.2069 K5-3
p1(model-season 1)(survey-1)(segment   4) model-avg-est:  0.4294 se=  0.1429 K5-4
p1(model-season 1)(survey-1)(segment   5) model-avg-est:  0.5420 se=  0.1225 L3-1
p1(model-season 1)(survey-1)(segment   6) model-avg-est:  0.5557 se=  0.1248 L3-2
p1(model-season 1)(survey-1)(segment   7) model-avg-est:  0.5775 se=  0.1305 L3-3
p1(model-season 1)(survey-1)(segment   8) model-avg-est:  0.5043 se=  0.1215 L3-4
p1(model-season 1)(survey-1)(segment   9) model-avg-est:  0.5043 se=  0.1215 L3-5
p1(model-season 1)(survey-1)(segment  10) model-avg-est:  0.5354 se=  0.1218 L3-6
p1(model-season 1)(survey-1)(segment  11) model-avg-est:  0.4789 se=  0.1252 L3-7
p1(model-season 1)(survey-1)(segment  12) model-avg-est:  0.4506 se=  0.1337 L3-8
p1(model-season 1)(survey-1)(segment  13) model-avg-est:  0.4340 se=  0.1407 L3-9
p1(model-season 1)(survey-1)(segment  14) model-avg-est:  0.4184 se=  0.1486 L3-10
p1(model-season 1)(survey-1)(segment  15) model-avg-est:  0.3898 se=  0.1662 L3-11
p1(model-season 1)(survey-1)(segment  16) model-avg-est:  0.3768 se=  0.1756 L3-12
p1(model-season 1)(survey-1)(segment  17) model-avg-est:  0.4294 se=  0.1429 L3-13
p1(model-season 1)(survey-1)(segment  18) model-avg-est:  0.5664 se=  0.1273 L2-1
p1(model-season 1)(survey-1)(segment  19) model-avg-est:  0.5930 se=  0.1359 L2-2
p1(model-season 1)(survey-1)(segment  20) model-avg-est:  0.5354 se=  0.1218 L2-3
p1(model-season 1)(survey-1)(segment  21) model-avg-est:  0.4363 se=  0.1396 L2-4
p1(model-season 1)(survey-1)(segment  22) model-avg-est:  0.2575 se=  0.2915 L2-5
p1(model-season 1)(survey-1)(segment  23) model-avg-est:  0.2575 se=  0.2915 L2-6
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p1(model-season 1)(survey-1)(segment  24) model-avg-est:  0.2575 se=  0.2915 L2-7
p1(model-season 1)(survey-1)(segment  25) model-avg-est:  0.4683 se=  0.1279 L2-8
p1(model-season 1)(survey-1)(segment  26) model-avg-est:  0.4555 se=  0.1319 L2-9
p1(model-season 1)(survey-1)(segment  27) model-avg-est:  0.4816 se=  0.1247 L2-10
p1(model-season 1)(survey-1)(segment  28) model-avg-est:  0.5289 se=  0.1213 L1B-1
p1(model-season 1)(survey-1)(segment  29) model-avg-est:  0.5522 se=  0.1242 L1B-2
p1(model-season 1)(survey-1)(segment  30) model-avg-est:  0.4605 se=  0.1302 L1B-3
p1(model-season 1)(survey-1)(segment  31) model-avg-est:  0.4482 se=  0.1346 L1A-1
p1(model-season 1)(survey-1)(segment  32) model-avg-est:  0.3947 se=  0.1630 L1A-2
p1(model-season 1)(survey-1)(segment  33) model-avg-est:  0.5321 se=  0.1215 L1A-3
p1(model-season 1)(survey-1)(segment  34) model-avg-est:  0.3482 se=  0.1987 L1A-4
p1(model-season 1)(survey-1)(segment  35) model-avg-est:  0.2969 se=  0.2480 L1A-5
p1(model-season 1)(survey-1)(segment  36) model-avg-est:  0.5289 se=  0.1213 L1A-6
p1(model-season 1)(survey-1)(segment  37) model-avg-est:  0.4272 se=  0.1440 L1A-7
p1(model-season 1)(survey-1)(segment  38) model-avg-est:  0.4363 se=  0.1396 L1A-8
p1(model-season 1)(survey-1)(segment  39) model-avg-est:  0.4631 se=  0.1294 L1A-9
p1(model-season 1)(survey-1)(segment  40) model-avg-est:  0.4250 se=  0.1451 L1A-10
p1(model-season 1)(survey-1)(segment  41) model-avg-est:  0.5073 se=  0.1213 M4-1
p1(model-season 1)(survey-1)(segment  42) model-avg-est:  0.5387 se=  0.1221 M4-2
p1(model-season 1)(survey-1)(segment  43) model-avg-est:  0.4735 se=  0.1265 M4-3
p1(model-season 1)(survey-1)(segment  44) model-avg-est:  0.4735 se=  0.1265 M4-4
p1(model-season 1)(survey-1)(segment  45) model-avg-est:  0.4816 se=  0.1247 M4-5
p1(model-season 1)(survey-1)(segment  46) model-avg-est:  0.4816 se=  0.1247 M4-6
p1(model-season 1)(survey-1)(segment  47) model-avg-est:  0.4272 se=  0.1440 M4-7
p1(model-season 1)(survey-1)(segment  48) model-avg-est:  0.4294 se=  0.1429 M4-8
p1(model-season 1)(survey-1)(segment  49) model-avg-est:  0.4581 se=  0.1310 M4-9
p1(model-season 1)(survey-1)(segment  50) model-avg-est:  0.4037 se=  0.1572 M4-10
p1(model-season 1)(survey-1)(segment  51) model-avg-est:  0.5043 se=  0.1215 M3-1
p1(model-season 1)(survey-1)(segment  52) model-avg-est:  0.4099 se=  0.1534 M3-2
p1(model-season 1)(survey-1)(segment  53) model-avg-est:  0.4363 se=  0.1396 M3-3
p1(model-season 1)(survey-1)(segment  54) model-avg-est:  0.3497 se=  0.1974 M3-4
p1(model-season 1)(survey-1)(segment  55) model-avg-est:  0.3786 se=  0.1743 M3-5
p1(model-season 1)(survey-1)(segment  56) model-avg-est:  0.5354 se=  0.1218 M2-1
p1(model-season 1)(survey-1)(segment  57) model-avg-est:  0.4078 se=  0.1547 M2-2
p1(model-season 1)(survey-1)(segment  58) model-avg-est:  0.4272 se=  0.1440 M2-3
p1(model-season 1)(survey-1)(segment  59) model-avg-est:  0.4228 se=  0.1463 M2-4
p1(model-season 1)(survey-1)(segment  60) model-avg-est:  0.4735 se=  0.1265 M2-5
p1(model-season 1)(survey-1)(segment  61) model-avg-est:  0.4120 se=  0.1522 M2-6
p1(model-season 1)(survey-1)(segment  62) model-avg-est:  0.4735 se=  0.1265 M1-1
p1(model-season 1)(survey-1)(segment  63) model-avg-est:  0.4956 se=  0.1223 M1-2
p1(model-season 1)(survey-1)(segment  64) model-avg-est:  0.4899 se=  0.1231 M1-3
p1(model-season 1)(survey-1)(segment  65) model-avg-est:  0.3697 se=  0.1810 M1-4
p1(model-season 1)(survey-1)(segment  66) model-avg-est:  0.4272 se=  0.1440 M1-5
p1(model-season 1)(survey-1)(segment  67) model-avg-est:  0.4184 se=  0.1486 M1-6
p1(model-season 1)(survey-2)(segment   1) model-avg-est:  0.5840 se=  0.1565 K5-1
p1(model-season 1)(survey-2)(segment   2) model-avg-est:  0.5249 se=  0.2021 K5-2
p1(model-season 1)(survey-2)(segment   3) model-avg-est:  0.5377 se=  0.1912 K5-3
p1(model-season 1)(survey-2)(segment   4) model-avg-est:  0.6371 se=  0.1289 K5-4
p1(model-season 1)(survey-2)(segment   5) model-avg-est:  0.7343 se=  0.1184 L3-1
p1(model-season 1)(survey-2)(segment   6) model-avg-est:  0.7445 se=  0.1204 L3-2
p1(model-season 1)(survey-2)(segment   7) model-avg-est:  0.7603 se=  0.1248 L3-3
p1(model-season 1)(survey-2)(segment   8) model-avg-est:  0.7045 se=  0.1157 L3-4
p1(model-season 1)(survey-2)(segment   9) model-avg-est:  0.7045 se=  0.1157 L3-5
p1(model-season 1)(survey-2)(segment  10) model-avg-est:  0.7292 se=  0.1175 L3-6
p1(model-season 1)(survey-2)(segment  11) model-avg-est:  0.6829 se=  0.1171 L3-7
p1(model-season 1)(survey-2)(segment  12) model-avg-est:  0.6573 se=  0.1222 L3-8
p1(model-season 1)(survey-2)(segment  13) model-avg-est:  0.6415 se=  0.1273 L3-9
p1(model-season 1)(survey-2)(segment  14) model-avg-est:  0.6261 se=  0.1335 L3-10
p1(model-season 1)(survey-2)(segment  15) model-avg-est:  0.5964 se=  0.1489 L3-11
p1(model-season 1)(survey-2)(segment  16) model-avg-est:  0.5820 se=  0.1578 L3-12
p1(model-season 1)(survey-2)(segment  17) model-avg-est:  0.6371 se=  0.1289 L3-13
p1(model-season 1)(survey-2)(segment  18) model-avg-est:  0.7524 se=  0.1224 L2-1
p1(model-season 1)(survey-2)(segment  19) model-avg-est:  0.7711 se=  0.1284 L2-2
p1(model-season 1)(survey-2)(segment  20) model-avg-est:  0.7292 se=  0.1175 L2-3
p1(model-season 1)(survey-2)(segment  21) model-avg-est:  0.6438 se=  0.1265 L2-4
p1(model-season 1)(survey-2)(segment  22) model-avg-est:  0.4247 se=  0.3072 L2-5
p1(model-season 1)(survey-2)(segment  23) model-avg-est:  0.4247 se=  0.3072 L2-6
p1(model-season 1)(survey-2)(segment  24) model-avg-est:  0.4247 se=  0.3072 L2-7
p1(model-season 1)(survey-2)(segment  25) model-avg-est:  0.6735 se=  0.1186 L2-8
p1(model-season 1)(survey-2)(segment  26) model-avg-est:  0.6619 se=  0.1211 L2-9
p1(model-season 1)(survey-2)(segment  27) model-avg-est:  0.6852 se=  0.1168 L2-10
p1(model-season 1)(survey-2)(segment  28) model-avg-est:  0.7242 se=  0.1169 L1B-1
p1(model-season 1)(survey-2)(segment  29) model-avg-est:  0.7420 se=  0.1198 L1B-2
p1(model-season 1)(survey-2)(segment  30) model-avg-est:  0.6665 se=  0.1200 L1B-3
p1(model-season 1)(survey-2)(segment  31) model-avg-est:  0.6551 se=  0.1229 L1A-1
p1(model-season 1)(survey-2)(segment  32) model-avg-est:  0.6016 se=  0.1459 L1A-2
p1(model-season 1)(survey-2)(segment  33) model-avg-est:  0.7267 se=  0.1172 L1A-3
p1(model-season 1)(survey-2)(segment  34) model-avg-est:  0.5488 se=  0.1820 L1A-4
p1(model-season 1)(survey-2)(segment  35) model-avg-est:  0.4827 se=  0.2428 L1A-5
p1(model-season 1)(survey-2)(segment  36) model-avg-est:  0.7242 se=  0.1169 L1A-6
p1(model-season 1)(survey-2)(segment  37) model-avg-est:  0.6349 se=  0.1298 L1A-7
p1(model-season 1)(survey-2)(segment  38) model-avg-est:  0.6438 se=  0.1265 L1A-8
p1(model-season 1)(survey-2)(segment  39) model-avg-est:  0.6688 se=  0.1195 L1A-9
p1(model-season 1)(survey-2)(segment  40) model-avg-est:  0.6327 se=  0.1307 L1A-10
p1(model-season 1)(survey-2)(segment  41) model-avg-est:  0.7069 se=  0.1157 M4-1
p1(model-season 1)(survey-2)(segment  42) model-avg-est:  0.7317 se=  0.1179 M4-2
p1(model-season 1)(survey-2)(segment  43) model-avg-est:  0.6781 se=  0.1178 M4-3
p1(model-season 1)(survey-2)(segment  44) model-avg-est:  0.6781 se=  0.1178 M4-4
p1(model-season 1)(survey-2)(segment  45) model-avg-est:  0.6852 se=  0.1168 M4-5
p1(model-season 1)(survey-2)(segment  46) model-avg-est:  0.6852 se=  0.1168 M4-6
p1(model-season 1)(survey-2)(segment  47) model-avg-est:  0.6349 se=  0.1298 M4-7
p1(model-season 1)(survey-2)(segment  48) model-avg-est:  0.6371 se=  0.1289 M4-8
p1(model-season 1)(survey-2)(segment  49) model-avg-est:  0.6642 se=  0.1205 M4-9
p1(model-season 1)(survey-2)(segment  50) model-avg-est:  0.6110 se=  0.1407 M4-10
p1(model-season 1)(survey-2)(segment  51) model-avg-est:  0.7045 se=  0.1157 M3-1
p1(model-season 1)(survey-2)(segment  52) model-avg-est:  0.6175 se=  0.1375 M3-2
p1(model-season 1)(survey-2)(segment  53) model-avg-est:  0.6438 se=  0.1265 M3-3
p1(model-season 1)(survey-2)(segment  54) model-avg-est:  0.5507 se=  0.1805 M3-4
p1(model-season 1)(survey-2)(segment  55) model-avg-est:  0.5840 se=  0.1565 M3-5
p1(model-season 1)(survey-2)(segment  56) model-avg-est:  0.7292 se=  0.1175 M2-1
p1(model-season 1)(survey-2)(segment  57) model-avg-est:  0.6153 se=  0.1386 M2-2
p1(model-season 1)(survey-2)(segment  58) model-avg-est:  0.6349 se=  0.1298 M2-3
p1(model-season 1)(survey-2)(segment  59) model-avg-est:  0.6305 se=  0.1316 M2-4
p1(model-season 1)(survey-2)(segment  60) model-avg-est:  0.6781 se=  0.1178 M2-5
p1(model-season 1)(survey-2)(segment  61) model-avg-est:  0.6196 se=  0.1365 M2-6
p1(model-season 1)(survey-2)(segment  62) model-avg-est:  0.6781 se=  0.1178 M1-1
p1(model-season 1)(survey-2)(segment  63) model-avg-est:  0.6972 se=  0.1159 M1-2
p1(model-season 1)(survey-2)(segment  64) model-avg-est:  0.6924 se=  0.1162 M1-3
p1(model-season 1)(survey-2)(segment  65) model-avg-est:  0.5740 se=  0.1632 M1-4
p1(model-season 1)(survey-2)(segment  66) model-avg-est:  0.6349 se=  0.1298 M1-5
p1(model-season 1)(survey-2)(segment  67) model-avg-est:  0.6261 se=  0.1335 M1-6
p1(model-season 1)(all-surveys)(avg.all segments) model-avg-est:   0.0.5469 sd=  0.1260

p1(model-season 2)(survey-1)(segment   1) model-avg-est:  0.1917 se=  0.0977 K5-1
p1(model-season 2)(survey-1)(segment   2) model-avg-est:  0.1410 se=  0.1100 K5-2
p1(model-season 2)(survey-1)(segment   3) model-avg-est:  0.1389 se=  0.1108 K5-3
p1(model-season 2)(survey-1)(segment   4) model-avg-est:  0.2189 se=  0.0975 K5-4
p1(model-season 2)(survey-1)(segment   5) model-avg-est:  0.3018 se=  0.1267 L3-1
p1(model-season 2)(survey-1)(segment   6) model-avg-est:  0.3144 se=  0.1346 L3-2
p1(model-season 2)(survey-1)(segment   7) model-avg-est:  0.2673 se=  0.1093 L3-3
p1(model-season 2)(survey-1)(segment   8) model-avg-est:  0.2833 se=  0.1165 L3-4
p1(model-season 2)(survey-1)(segment   9) model-avg-est:  0.2614 se=  0.1071 L3-5
p1(model-season 2)(survey-1)(segment  10) model-avg-est:  0.2010 se=  0.0971 L3-6
p1(model-season 2)(survey-1)(segment  11) model-avg-est:  0.2405 se=  0.1009 L3-7
p1(model-season 2)(survey-1)(segment  12) model-avg-est:  0.2209 se=  0.0977 L3-8
p1(model-season 2)(survey-1)(segment  13) model-avg-est:  0.2027 se=  0.0970 L3-9
p1(model-season 2)(survey-1)(segment  14) model-avg-est:  0.1572 se=  0.1046 L3-10
p1(model-season 2)(survey-1)(segment  15) model-avg-est:  0.1860 se=  0.0983 L3-11
p1(model-season 2)(survey-1)(segment  16) model-avg-est:  0.1278 se=  0.1151 L3-12
p1(model-season 2)(survey-1)(segment  17) model-avg-est:  0.2209 se=  0.0977 L3-13
p1(model-season 2)(survey-1)(segment  18) model-avg-est:  0.2643 se=  0.1082 L2-1
p1(model-season 2)(survey-1)(segment  19) model-avg-est:  0.2940 se=  0.1222 L2-2
p1(model-season 2)(survey-1)(segment  20) model-avg-est:  0.2673 se=  0.1093 L2-3
p1(model-season 2)(survey-1)(segment  21) model-avg-est:  0.2405 se=  0.1009 L2-4
p1(model-season 2)(survey-1)(segment  22) model-avg-est:  0.1004 se=  0.1268 L2-5
p1(model-season 2)(survey-1)(segment  23) model-avg-est:  0.1004 se=  0.1268 L2-6
p1(model-season 2)(survey-1)(segment  24) model-avg-est:  0.1004 se=  0.1268 L2-7
p1(model-season 2)(survey-1)(segment  25) model-avg-est:  0.2336 se=  0.0995 L2-8
p1(model-season 2)(survey-1)(segment  26) model-avg-est:  0.2314 se=  0.0991 L2-9
p1(model-season 2)(survey-1)(segment  27) model-avg-est:  0.2270 se=  0.0985 L2-10
p1(model-season 2)(survey-1)(segment  28) model-avg-est:  0.2766 se=  0.1134 L1B-1
p1(model-season 2)(survey-1)(segment  29) model-avg-est:  0.3018 se=  0.1267 L1B-2
p1(model-season 2)(survey-1)(segment  30) model-avg-est:  0.2314 se=  0.0991 L1B-3
p1(model-season 2)(survey-1)(segment  31) model-avg-est:  0.2209 se=  0.0977 L1A-1
p1(model-season 2)(survey-1)(segment  32) model-avg-est:  0.1874 se=  0.0982 L1A-2
p1(model-season 2)(survey-1)(segment  33) model-avg-est:  0.2505 se=  0.1035 L1A-3
p1(model-season 2)(survey-1)(segment  34) model-avg-est:  0.1361 se=  0.1118 L1A-4
p1(model-season 2)(survey-1)(segment  35) model-avg-est:  0.1004 se=  0.1268 L1A-5
p1(model-season 2)(survey-1)(segment  36) model-avg-est:  0.2643 se=  0.1082 L1A-6
p1(model-season 2)(survey-1)(segment  37) model-avg-est:  0.2209 se=  0.0977 L1A-7
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p1(model-season 2)(survey-1)(segment  38) model-avg-est:  0.2405 se=  0.1009 L1A-8
p1(model-season 2)(survey-1)(segment  39) model-avg-est:  0.2336 se=  0.0995 L1A-9
p1(model-season 2)(survey-1)(segment  40) model-avg-est:  0.1833 se=  0.0987 L1A-10
p1(model-season 2)(survey-1)(segment  41) model-avg-est:  0.2628 se=  0.1077 M4-1
p1(model-season 2)(survey-1)(segment  42) model-avg-est:  0.2868 se=  0.1183 M4-2
p1(model-season 2)(survey-1)(segment  43) model-avg-est:  0.2531 se=  0.1043 M4-3
p1(model-season 2)(survey-1)(segment  44) model-avg-est:  0.2643 se=  0.1082 M4-4
p1(model-season 2)(survey-1)(segment  45) model-avg-est:  0.2479 se=  0.1028 M4-5
p1(model-season 2)(survey-1)(segment  46) model-avg-est:  0.2505 se=  0.1035 M4-6
p1(model-season 2)(survey-1)(segment  47) model-avg-est:  0.2336 se=  0.0995 M4-7
p1(model-season 2)(survey-1)(segment  48) model-avg-est:  0.1994 se=  0.0971 M4-8
p1(model-season 2)(survey-1)(segment  49) model-avg-est:  0.1978 se=  0.0972 M4-9
p1(model-season 2)(survey-1)(segment  50) model-avg-est:  0.1819 se=  0.0990 M4-10
p1(model-season 2)(survey-1)(segment  51) model-avg-est:  0.2673 se=  0.1093 M3-1
p1(model-season 2)(survey-1)(segment  52) model-avg-est:  0.1860 se=  0.0983 M3-2
p1(model-season 2)(survey-1)(segment  53) model-avg-est:  0.1903 se=  0.0978 M3-3
p1(model-season 2)(survey-1)(segment  54) model-avg-est:  0.1474 se=  0.1077 M3-4
p1(model-season 2)(survey-1)(segment  55) model-avg-est:  0.1508 se=  0.1066 M3-5
p1(model-season 2)(survey-1)(segment  56) model-avg-est:  0.2614 se=  0.1071 M2-1
p1(model-season 2)(survey-1)(segment  57) model-avg-est:  0.1819 se=  0.0990 M2-2
p1(model-season 2)(survey-1)(segment  58) model-avg-est:  0.1697 se=  0.1013 M2-3
p1(model-season 2)(survey-1)(segment  59) model-avg-est:  0.1621 se=  0.1032 M2-4
p1(model-season 2)(survey-1)(segment  60) model-avg-est:  0.2151 se=  0.0973 M2-5
p1(model-season 2)(survey-1)(segment  61) model-avg-est:  0.1781 se=  0.0996 M2-6
p1(model-season 2)(survey-1)(segment  62) model-avg-est:  0.2673 se=  0.1093 M1-1
p1(model-season 2)(survey-1)(segment  63) model-avg-est:  0.2454 se=  0.1021 M1-2
p1(model-season 2)(survey-1)(segment  64) model-avg-est:  0.2586 se=  0.1061 M1-3
p1(model-season 2)(survey-1)(segment  65) model-avg-est:  0.1631 se=  0.1029 M1-4
p1(model-season 2)(survey-1)(segment  66) model-avg-est:  0.2027 se=  0.0970 M1-5
p1(model-season 2)(survey-1)(segment  67) model-avg-est:  0.1994 se=  0.0971 M1-6
p1(model-season 2)(survey-2)(segment   1) model-avg-est:  0.3557 se=  0.1187 K5-1
p1(model-season 2)(survey-2)(segment   2) model-avg-est:  0.2711 se=  0.1436 K5-2
p1(model-season 2)(survey-2)(segment   3) model-avg-est:  0.2671 se=  0.1455 K5-3
p1(model-season 2)(survey-2)(segment   4) model-avg-est:  0.3961 se=  0.1196 K5-4
p1(model-season 2)(survey-2)(segment   5) model-avg-est:  0.5015 se=  0.1654 L3-1
p1(model-season 2)(survey-2)(segment   6) model-avg-est:  0.5156 se=  0.1759 L3-2
p1(model-season 2)(survey-2)(segment   7) model-avg-est:  0.4605 se=  0.1403 L3-3
p1(model-season 2)(survey-2)(segment   8) model-avg-est:  0.4800 se=  0.1512 L3-4
p1(model-season 2)(survey-2)(segment   9) model-avg-est:  0.4531 se=  0.1368 L3-5
p1(model-season 2)(survey-2)(segment  10) model-avg-est:  0.3699 se=  0.1180 L3-6
p1(model-season 2)(survey-2)(segment  11) model-avg-est:  0.4259 se=  0.1263 L3-7
p1(model-season 2)(survey-2)(segment  12) model-avg-est:  0.3989 se=  0.1200 L3-8
p1(model-season 2)(survey-2)(segment  13) model-avg-est:  0.3724 se=  0.1180 L3-9
p1(model-season 2)(survey-2)(segment  14) model-avg-est:  0.2995 se=  0.1317 L3-10
p1(model-season 2)(survey-2)(segment  15) model-avg-est:  0.3468 se=  0.1197 L3-11
p1(model-season 2)(survey-2)(segment  16) model-avg-est:  0.2466 se=  0.1561 L3-12
p1(model-season 2)(survey-2)(segment  17) model-avg-est:  0.3989 se=  0.1200 L3-13
p1(model-season 2)(survey-2)(segment  18) model-avg-est:  0.4567 se=  0.1385 L2-1
p1(model-season 2)(survey-2)(segment  19) model-avg-est:  0.4926 se=  0.1592 L2-2
p1(model-season 2)(survey-2)(segment  20) model-avg-est:  0.4605 se=  0.1403 L2-3
p1(model-season 2)(survey-2)(segment  21) model-avg-est:  0.4259 se=  0.1263 L2-4
p1(model-season 2)(survey-2)(segment  22) model-avg-est:  0.1927 se=  0.1885 L2-5
p1(model-season 2)(survey-2)(segment  23) model-avg-est:  0.1927 se=  0.1885 L2-6
p1(model-season 2)(survey-2)(segment  24) model-avg-est:  0.1927 se=  0.1885 L2-7
p1(model-season 2)(survey-2)(segment  25) model-avg-est:  0.4165 se=  0.1236 L2-8
p1(model-season 2)(survey-2)(segment  26) model-avg-est:  0.4135 se=  0.1229 L2-9
p1(model-season 2)(survey-2)(segment  27) model-avg-est:  0.4075 se=  0.1216 L2-10
p1(model-season 2)(survey-2)(segment  28) model-avg-est:  0.4720 se=  0.1465 L1B-1
p1(model-season 2)(survey-2)(segment  29) model-avg-est:  0.5015 se=  0.1654 L1B-2
p1(model-season 2)(survey-2)(segment  30) model-avg-est:  0.4135 se=  0.1229 L1B-3
p1(model-season 2)(survey-2)(segment  31) model-avg-est:  0.3989 se=  0.1200 L1A-1
p1(model-season 2)(survey-2)(segment  32) model-avg-est:  0.3490 se=  0.1194 L1A-2
p1(model-season 2)(survey-2)(segment  33) model-avg-est:  0.4391 se=  0.1309 L1A-3
p1(model-season 2)(survey-2)(segment  34) model-avg-est:  0.2620 se=  0.1481 L1A-4
p1(model-season 2)(survey-2)(segment  35) model-avg-est:  0.1927 se=  0.1885 L1A-5
p1(model-season 2)(survey-2)(segment  36) model-avg-est:  0.4567 se=  0.1385 L1A-6
p1(model-season 2)(survey-2)(segment  37) model-avg-est:  0.3989 se=  0.1200 L1A-7
p1(model-season 2)(survey-2)(segment  38) model-avg-est:  0.4259 se=  0.1263 L1A-8
p1(model-season 2)(survey-2)(segment  39) model-avg-est:  0.4165 se=  0.1236 L1A-9
p1(model-season 2)(survey-2)(segment  40) model-avg-est:  0.3425 se=  0.1203 L1A-10
p1(model-season 2)(survey-2)(segment  41) model-avg-est:  0.4549 se=  0.1377 M4-1
p1(model-season 2)(survey-2)(segment  42) model-avg-est:  0.4841 se=  0.1537 M4-2
p1(model-season 2)(survey-2)(segment  43) model-avg-est:  0.4425 se=  0.1322 M4-3
p1(model-season 2)(survey-2)(segment  44) model-avg-est:  0.4567 se=  0.1385 M4-4
p1(model-season 2)(survey-2)(segment  45) model-avg-est:  0.4357 se=  0.1296 M4-5
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p1(model-season 2)(survey-2)(segment  46) model-avg-est:  0.4391 se=  0.1309 M4-6
p1(model-season 2)(survey-2)(segment  47) model-avg-est:  0.4165 se=  0.1236 M4-7
p1(model-season 2)(survey-2)(segment  48) model-avg-est:  0.3675 se=  0.1180 M4-8
p1(model-season 2)(survey-2)(segment  49) model-avg-est:  0.3651 se=  0.1181 M4-9
p1(model-season 2)(survey-2)(segment  50) model-avg-est:  0.3404 se=  0.1207 M4-10
p1(model-season 2)(survey-2)(segment  51) model-avg-est:  0.4605 se=  0.1403 M3-1
p1(model-season 2)(survey-2)(segment  52) model-avg-est:  0.3468 se=  0.1197 M3-2
p1(model-season 2)(survey-2)(segment  53) model-avg-est:  0.3535 se=  0.1189 M3-3
p1(model-season 2)(survey-2)(segment  54) model-avg-est:  0.2824 se=  0.1385 M3-4
p1(model-season 2)(survey-2)(segment  55) model-avg-est:  0.2884 se=  0.1360 M3-5
p1(model-season 2)(survey-2)(segment  56) model-avg-est:  0.4531 se=  0.1368 M2-1
p1(model-season 2)(survey-2)(segment  57) model-avg-est:  0.3404 se=  0.1207 M2-2
p1(model-season 2)(survey-2)(segment  58) model-avg-est:  0.3206 se=  0.1250 M2-3
p1(model-season 2)(survey-2)(segment  59) model-avg-est:  0.3079 se=  0.1288 M2-4
p1(model-season 2)(survey-2)(segment  60) model-avg-est:  0.3906 se=  0.1190 M2-5
p1(model-season 2)(survey-2)(segment  61) model-avg-est:  0.3342 se=  0.1218 M2-6
p1(model-season 2)(survey-2)(segment  62) model-avg-est:  0.4605 se=  0.1403 M1-1
p1(model-season 2)(survey-2)(segment  63) model-avg-est:  0.4324 se=  0.1284 M1-2
p1(model-season 2)(survey-2)(segment  64) model-avg-est:  0.4495 se=  0.1352 M1-3
p1(model-season 2)(survey-2)(segment  65) model-avg-est:  0.3097 se=  0.1282 M1-4
p1(model-season 2)(survey-2)(segment  66) model-avg-est:  0.3724 se=  0.1180 M1-5
p1(model-season 2)(survey-2)(segment  67) model-avg-est:  0.3675 se=  0.1180 M1-6
p1(model-season 2)(all-surveys)(avg.all segments) model-avg-est:  0.0.2997 sd=  0.1090

p1(model-season 3)(survey-1)(segment   1) model-avg-est:  0.6916 se=  0.1281 K5-1
p1(model-season 3)(survey-1)(segment   2) model-avg-est:  0.5649 se=  0.2285 K5-2
p1(model-season 3)(survey-1)(segment   3) model-avg-est:  0.5493 se=  0.2457 K5-3
p1(model-season 3)(survey-1)(segment   4) model-avg-est:  0.4452 se=  0.3832 K5-4
p1(model-season 3)(survey-1)(segment   5) model-avg-est:  0.7990 se=  0.1063 L3-1
p1(model-season 3)(survey-1)(segment   6) model-avg-est:  0.7974 se=  0.1062 L3-2
p1(model-season 3)(survey-1)(segment   7) model-avg-est:  0.7822 se=  0.1060 L3-3
p1(model-season 3)(survey-1)(segment   8) model-avg-est:  0.7593 se=  0.1077 L3-4
p1(model-season 3)(survey-1)(segment   9) model-avg-est:  0.7430 se=  0.1104 L3-5
p1(model-season 3)(survey-1)(segment  10) model-avg-est:  0.7430 se=  0.1104 L3-6
p1(model-season 3)(survey-1)(segment  11) model-avg-est:  0.7593 se=  0.1077 L3-7
p1(model-season 3)(survey-1)(segment  12) model-avg-est:  0.7016 se=  0.1236 L3-8
p1(model-season 3)(survey-1)(segment  13) model-avg-est:  0.6866 se=  0.1306 L3-9
p1(model-season 3)(survey-1)(segment  14) model-avg-est:  0.5093 se=  0.2943 L3-10
p1(model-season 3)(survey-1)(segment  15) model-avg-est:  0.7142 se=  0.1186 L3-11
p1(model-season 3)(survey-1)(segment  16) model-avg-est:  0.5417 se=  0.2545 L3-12
p1(model-season 3)(survey-1)(segment  17) model-avg-est:  0.7091 se=  0.1206 L3-13
p1(model-season 3)(survey-1)(segment  18) model-avg-est:  0.7649 se=  0.1070 L2-1
p1(model-season 3)(survey-1)(segment  19) model-avg-est:  0.7649 se=  0.1070 L2-2
p1(model-season 3)(survey-1)(segment  20) model-avg-est:  0.7764 se=  0.1062 L2-3
p1(model-season 3)(survey-1)(segment  21) model-avg-est:  0.7245 se=  0.1152 L2-4
p1(model-season 3)(survey-1)(segment  22) model-avg-est:  0.4210 se=  0.4196 L2-5
p1(model-season 3)(survey-1)(segment  23) model-avg-est:  0.4210 se=  0.4196 L2-6
p1(model-season 3)(survey-1)(segment  24) model-avg-est:  0.4210 se=  0.4196 L2-7
p1(model-season 3)(survey-1)(segment  25) model-avg-est:  0.7566 se=  0.1081 L2-8
p1(model-season 3)(survey-1)(segment  26) model-avg-est:  0.7511 se=  0.1089 L2-9
p1(model-season 3)(survey-1)(segment  27) model-avg-est:  0.7245 se=  0.1152 L2-10
p1(model-season 3)(survey-1)(segment  28) model-avg-est:  0.7734 se=  0.1064 L1B-1
p1(model-season 3)(survey-1)(segment  29) model-avg-est:  0.7792 se=  0.1061 L1B-2
p1(model-season 3)(survey-1)(segment  30) model-avg-est:  0.7297 se=  0.1137 L1B-3
p1(model-season 3)(survey-1)(segment  31) model-avg-est:  0.6990 se=  0.1247 L1A-1
p1(model-season 3)(survey-1)(segment  32) model-avg-est:  0.6509 se=  0.1520 L1A-2
p1(model-season 3)(survey-1)(segment  33) model-avg-est:  0.6965 se=  0.1258 L1A-3
p1(model-season 3)(survey-1)(segment  34) model-avg-est:  0.5474 se=  0.2479 L1A-4
p1(model-season 3)(survey-1)(segment  35) model-avg-est:  0.4210 se=  0.4196 L1A-5
p1(model-season 3)(survey-1)(segment  36) model-avg-est:  0.7635 se=  0.1072 L1A-6
p1(model-season 3)(survey-1)(segment  37) model-avg-est:  0.7297 se=  0.1137 L1A-7
p1(model-season 3)(survey-1)(segment  38) model-avg-est:  0.7538 se=  0.1084 L1A-8
p1(model-season 3)(survey-1)(segment  39) model-avg-est:  0.7040 se=  0.1226 L1A-9
p1(model-season 3)(survey-1)(segment  40) model-avg-est:  0.6721 se=  0.1385 L1A-10
p1(model-season 3)(survey-1)(segment  41) model-avg-est:  0.7142 se=  0.1186 M4-1
p1(model-season 3)(survey-1)(segment  42) model-avg-est:  0.7851 se=  0.1060 M4-2
p1(model-season 3)(survey-1)(segment  43) model-avg-est:  0.7376 se=  0.1116 M4-3
p1(model-season 3)(survey-1)(segment  44) model-avg-est:  0.7593 se=  0.1077 M4-4
p1(model-season 3)(survey-1)(segment  45) model-avg-est:  0.7511 se=  0.1089 M4-5
p1(model-season 3)(survey-1)(segment  46) model-avg-est:  0.7350 se=  0.1123 M4-6
p1(model-season 3)(survey-1)(segment  47) model-avg-est:  0.7193 se=  0.1169 M4-7
p1(model-season 3)(survey-1)(segment  48) model-avg-est:  0.6990 se=  0.1247 M4-8
p1(model-season 3)(survey-1)(segment  49) model-avg-est:  0.6793 se=  0.1344 M4-9
p1(model-season 3)(survey-1)(segment  50) model-avg-est:  0.6579 se=  0.1473 M4-10
p1(model-season 3)(survey-1)(segment  51) model-avg-est:  0.7430 se=  0.1104 M3-1
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p1(model-season 3)(survey-1)(segment  52) model-avg-est:  0.6626 se=  0.1442 M3-2
p1(model-season 3)(survey-1)(segment  53) model-avg-est:  0.7016 se=  0.1236 M3-3
p1(model-season 3)(survey-1)(segment  54) model-avg-est:  0.6440 se=  0.1569 M3-4
p1(model-season 3)(survey-1)(segment  55) model-avg-est:  0.6236 se=  0.1725 M3-5
p1(model-season 3)(survey-1)(segment  56) model-avg-est:  0.7457 se=  0.1099 M2-1
p1(model-season 3)(survey-1)(segment  57) model-avg-est:  0.6818 se=  0.1331 M2-2
p1(model-season 3)(survey-1)(segment  58) model-avg-est:  0.6793 se=  0.1344 M2-3
p1(model-season 3)(survey-1)(segment  59) model-avg-est:  0.6697 se=  0.1399 M2-4
p1(model-season 3)(survey-1)(segment  60) model-avg-est:  0.6649 se=  0.1428 M2-5
p1(model-season 3)(survey-1)(segment  61) model-avg-est:  0.6486 se=  0.1536 M2-6
p1(model-season 3)(survey-1)(segment  62) model-avg-est:  0.7167 se=  0.1177 M1-1
p1(model-season 3)(survey-1)(segment  63) model-avg-est:  0.7193 se=  0.1169 M1-2
p1(model-season 3)(survey-1)(segment  64) model-avg-est:  0.7116 se=  0.1196 M1-3
p1(model-season 3)(survey-1)(segment  65) model-avg-est:  0.6214 se=  0.1743 M1-4
p1(model-season 3)(survey-1)(segment  66) model-avg-est:  0.6602 se=  0.1458 M1-5
p1(model-season 3)(survey-1)(segment  67) model-avg-est:  0.6673 se=  0.1413 M1-6
p1(model-season 3)(survey-2)(segment   1) model-avg-est:  0.8398 se=  0.0871 K5-1
p1(model-season 3)(survey-2)(segment   2) model-avg-est:  0.7488 se=  0.1551 K5-2
p1(model-season 3)(survey-2)(segment   3) model-avg-est:  0.7358 se=  0.1683 K5-3
p1(model-season 3)(survey-2)(segment   4) model-avg-est:  0.6362 se=  0.2917 K5-4
p1(model-season 3)(survey-2)(segment   5) model-avg-est:  0.9013 se=  0.0707 L3-1
p1(model-season 3)(survey-2)(segment   6) model-avg-est:  0.9005 se=  0.0708 L3-2
p1(model-season 3)(survey-2)(segment   7) model-avg-est:  0.8925 se=  0.0716 L3-3
p1(model-season 3)(survey-2)(segment   8) model-avg-est:  0.8800 se=  0.0735 L3-4
p1(model-season 3)(survey-2)(segment   9) model-avg-est:  0.8707 se=  0.0757 L3-5
p1(model-season 3)(survey-2)(segment  10) model-avg-est:  0.8707 se=  0.0757 L3-6
p1(model-season 3)(survey-2)(segment  11) model-avg-est:  0.8800 se=  0.0735 L3-7
p1(model-season 3)(survey-2)(segment  12) model-avg-est:  0.8460 se=  0.0842 L3-8
p1(model-season 3)(survey-2)(segment  13) model-avg-est:  0.8367 se=  0.0885 L3-9
p1(model-season 3)(survey-2)(segment  14) model-avg-est:  0.7004 se=  0.2080 L3-10
p1(model-season 3)(survey-2)(segment  15) model-avg-est:  0.8538 se=  0.0811 L3-11
p1(model-season 3)(survey-2)(segment  16) model-avg-est:  0.7294 se=  0.1751 L3-12
p1(model-season 3)(survey-2)(segment  17) model-avg-est:  0.8507 se=  0.0823 L3-13
p1(model-season 3)(survey-2)(segment  18) model-avg-est:  0.8831 se=  0.0730 L2-1
p1(model-season 3)(survey-2)(segment  19) model-avg-est:  0.8831 se=  0.0730 L2-2
p1(model-season 3)(survey-2)(segment  20) model-avg-est:  0.8893 se=  0.0720 L2-3
p1(model-season 3)(survey-2)(segment  21) model-avg-est:  0.8600 se=  0.0789 L2-4
p1(model-season 3)(survey-2)(segment  22) model-avg-est:  0.6092 se=  0.3304 L2-5
p1(model-season 3)(survey-2)(segment  23) model-avg-est:  0.6092 se=  0.3304 L2-6
p1(model-season 3)(survey-2)(segment  24) model-avg-est:  0.6092 se=  0.3304 L2-7
p1(model-season 3)(survey-2)(segment  25) model-avg-est:  0.8784 se=  0.0739 L2-8
p1(model-season 3)(survey-2)(segment  26) model-avg-est:  0.8753 se=  0.0746 L2-9
p1(model-season 3)(survey-2)(segment  27) model-avg-est:  0.8600 se=  0.0789 L2-10
p1(model-season 3)(survey-2)(segment  28) model-avg-est:  0.8878 se=  0.0722 L1B-1
p1(model-season 3)(survey-2)(segment  29) model-avg-est:  0.8909 se=  0.0718 L1B-2
p1(model-season 3)(survey-2)(segment  30) model-avg-est:  0.8630 se=  0.0779 L1B-3
p1(model-season 3)(survey-2)(segment  31) model-avg-est:  0.8445 se=  0.0849 L1A-1
p1(model-season 3)(survey-2)(segment  32) model-avg-est:  0.8131 se=  0.1020 L1A-2
p1(model-season 3)(survey-2)(segment  33) model-avg-est:  0.8429 se=  0.0856 L1A-3
p1(model-season 3)(survey-2)(segment  34) model-avg-est:  0.7342 se=  0.1700 L1A-4
p1(model-season 3)(survey-2)(segment  35) model-avg-est:  0.6092 se=  0.3304 L1A-5
p1(model-season 3)(survey-2)(segment  36) model-avg-est:  0.8823 se=  0.0731 L1A-6
p1(model-season 3)(survey-2)(segment  37) model-avg-est:  0.8630 se=  0.0779 L1A-7
p1(model-season 3)(survey-2)(segment  38) model-avg-est:  0.8769 se=  0.0742 L1A-8
p1(model-season 3)(survey-2)(segment  39) model-avg-est:  0.8476 se=  0.0836 L1A-9
p1(model-season 3)(survey-2)(segment  40) model-avg-est:  0.8273 se=  0.0935 L1A-10
p1(model-season 3)(survey-2)(segment  41) model-avg-est:  0.8538 se=  0.0811 M4-1
p1(model-season 3)(survey-2)(segment  42) model-avg-est:  0.8941 se=  0.0714 M4-2
p1(model-season 3)(survey-2)(segment  43) model-avg-est:  0.8677 se=  0.0765 M4-3
p1(model-season 3)(survey-2)(segment  44) model-avg-est:  0.8800 se=  0.0735 M4-4
p1(model-season 3)(survey-2)(segment  45) model-avg-est:  0.8753 se=  0.0746 M4-5
p1(model-season 3)(survey-2)(segment  46) model-avg-est:  0.8661 se=  0.0770 M4-6
p1(model-season 3)(survey-2)(segment  47) model-avg-est:  0.8569 se=  0.0800 M4-7
p1(model-season 3)(survey-2)(segment  48) model-avg-est:  0.8445 se=  0.0849 M4-8
p1(model-season 3)(survey-2)(segment  49) model-avg-est:  0.8320 se=  0.0909 M4-9
p1(model-season 3)(survey-2)(segment  50) model-avg-est:  0.8178 se=  0.0991 M4-10
p1(model-season 3)(survey-2)(segment  51) model-avg-est:  0.8707 se=  0.0757 M3-1
p1(model-season 3)(survey-2)(segment  52) model-avg-est:  0.8210 se=  0.0971 M3-2
p1(model-season 3)(survey-2)(segment  53) model-avg-est:  0.8460 se=  0.0842 M3-3
p1(model-season 3)(survey-2)(segment  54) model-avg-est:  0.8083 se=  0.1052 M3-4
p1(model-season 3)(survey-2)(segment  55) model-avg-est:  0.7940 se=  0.1155 M3-5
p1(model-season 3)(survey-2)(segment  56) model-avg-est:  0.8723 se=  0.0753 M2-1
p1(model-season 3)(survey-2)(segment  57) model-avg-est:  0.8336 se=  0.0901 M2-2
p1(model-season 3)(survey-2)(segment  58) model-avg-est:  0.8320 se=  0.0909 M2-3
p1(model-season 3)(survey-2)(segment  59) model-avg-est:  0.8257 se=  0.0944 M2-4
p1(model-season 3)(survey-2)(segment  60) model-avg-est:  0.8226 se=  0.0962 M2-5
p1(model-season 3)(survey-2)(segment  61) model-avg-est:  0.8115 se=  0.1031 M2-6
p1(model-season 3)(survey-2)(segment  62) model-avg-est:  0.8553 se=  0.0806 M1-1
p1(model-season 3)(survey-2)(segment  63) model-avg-est:  0.8569 se=  0.0800 M1-2
p1(model-season 3)(survey-2)(segment  64) model-avg-est:  0.8522 se=  0.0817 M1-3
p1(model-season 3)(survey-2)(segment  65) model-avg-est:  0.7924 se=  0.1167 M1-4
p1(model-season 3)(survey-2)(segment  66) model-avg-est:  0.8194 se=  0.0981 M1-5
p1(model-season 3)(survey-2)(segment  67) model-avg-est:  0.8242 se=  0.0953 M1-6
p1(model-season 3)(all-surveys)(avg.all segments) model-avg-est:   0.7551 sd=  0.0.1122

p1(model-season 4)(survey-1)(segment   1) model-avg-est:  0.1794 se=  0.1075 K5-1
p1(model-season 4)(survey-1)(segment   2) model-avg-est:  0.1015 se=  0.1005 K5-2
p1(model-season 4)(survey-1)(segment   3) model-avg-est:  0.1410 se=  0.1000 K5-3
p1(model-season 4)(survey-1)(segment   4) model-avg-est:  0.1794 se=  0.1075 K5-4
p1(model-season 4)(survey-1)(segment   5) model-avg-est:  0.3417 se=  0.2259 L3-1
p1(model-season 4)(survey-1)(segment   6) model-avg-est:  0.2559 se=  0.1473 L3-2
p1(model-season 4)(survey-1)(segment   7) model-avg-est:  0.2057 se=  0.1175 L3-3
p1(model-season 4)(survey-1)(segment   8) model-avg-est:  0.1937 se=  0.1125 L3-4
p1(model-season 4)(survey-1)(segment   9) model-avg-est:  0.2007 se=  0.1153 L3-5
p1(model-season 4)(survey-1)(segment  10) model-avg-est:  0.2057 se=  0.1175 L3-6
p1(model-season 4)(survey-1)(segment  11) model-avg-est:  0.2083 se=  0.1188 L3-7
p1(model-season 4)(survey-1)(segment  12) model-avg-est:  0.1758 se=  0.1064 L3-8
p1(model-season 4)(survey-1)(segment  13) model-avg-est:  0.1454 se=  0.1005 L3-9
p1(model-season 4)(survey-1)(segment  14) model-avg-est:  0.1241 se=  0.0993 L3-10
p1(model-season 4)(survey-1)(segment  15) model-avg-est:  0.1873 se=  0.1101 L3-11
p1(model-season 4)(survey-1)(segment  16) model-avg-est:  0.0957 se=  0.1010 L3-12
p1(model-season 4)(survey-1)(segment  17) model-avg-est:  0.1852 se=  0.1094 L3-13
p1(model-season 4)(survey-1)(segment  18) model-avg-est:  0.1873 se=  0.1101 L2-1
p1(model-season 4)(survey-1)(segment  19) model-avg-est:  0.2110 se=  0.1200 L2-2
p1(model-season 4)(survey-1)(segment  20) model-avg-est:  0.1758 se=  0.1064 L2-3
p1(model-season 4)(survey-1)(segment  21) model-avg-est:  0.2007 se=  0.1153 L2-4
p1(model-season 4)(survey-1)(segment  22) model-avg-est:  0.0767 se=  0.1030 L2-5
p1(model-season 4)(survey-1)(segment  23) model-avg-est:  0.0767 se=  0.1030 L2-6
p1(model-season 4)(survey-1)(segment  24) model-avg-est:  0.0767 se=  0.1030 L2-7
p1(model-season 4)(survey-1)(segment  25) model-avg-est:  0.1852 se=  0.1094 L2-8
p1(model-season 4)(survey-1)(segment  26) model-avg-est:  0.2007 se=  0.1153 L2-9
p1(model-season 4)(survey-1)(segment  27) model-avg-est:  0.1852 se=  0.1094 L2-10
p1(model-season 4)(survey-1)(segment  28) model-avg-est:  0.1915 se=  0.1116 L1B-1
p1(model-season 4)(survey-1)(segment  29) model-avg-est:  0.2110 se=  0.1200 L1B-2
p1(model-season 4)(survey-1)(segment  30) model-avg-est:  0.1740 se=  0.1059 L1B-3
p1(model-season 4)(survey-1)(segment  31) model-avg-est:  0.1555 se=  0.1018 L1A-1
p1(model-season 4)(survey-1)(segment  32) model-avg-est:  0.1529 se=  0.1014 L1A-2
p1(model-season 4)(survey-1)(segment  33) model-avg-est:  0.2007 se=  0.1153 L1A-3
p1(model-season 4)(survey-1)(segment  34) model-avg-est:  0.1249 se=  0.0993 L1A-4
p1(model-season 4)(survey-1)(segment  35) model-avg-est:  0.0874 se=  0.1019 L1A-5
p1(model-season 4)(survey-1)(segment  36) model-avg-est:  0.2494 se=  0.1427 L1A-6
p1(model-season 4)(survey-1)(segment  37) model-avg-est:  0.2032 se=  0.1164 L1A-7
p1(model-season 4)(survey-1)(segment  38) model-avg-est:  0.2007 se=  0.1153 L1A-8
p1(model-season 4)(survey-1)(segment  39) model-avg-est:  0.1657 se=  0.1039 L1A-9
p1(model-season 4)(survey-1)(segment  40) model-avg-est:  0.1432 se=  0.1002 L1A-10
p1(model-season 4)(survey-1)(segment  41) model-avg-est:  0.1723 se=  0.1055 M4-1
p1(model-season 4)(survey-1)(segment  42) model-avg-est:  0.2007 se=  0.1153 M4-2
p1(model-season 4)(survey-1)(segment  43) model-avg-est:  0.2138 se=  0.1214 M4-3
p1(model-season 4)(survey-1)(segment  44) model-avg-est:  0.1983 se=  0.1143 M4-4
p1(model-season 4)(survey-1)(segment  45) model-avg-est:  0.2166 se=  0.1229 M4-5
p1(model-season 4)(survey-1)(segment  46) model-avg-est:  0.1915 se=  0.1116 M4-6
p1(model-season 4)(survey-1)(segment  47) model-avg-est:  0.1960 se=  0.1134 M4-7
p1(model-season 4)(survey-1)(segment  48) model-avg-est:  0.1583 se=  0.1024 M4-8
p1(model-season 4)(survey-1)(segment  49) model-avg-est:  0.1705 se=  0.1050 M4-9
p1(model-season 4)(survey-1)(segment  50) model-avg-est:  0.1542 se=  0.1016 M4-10
p1(model-season 4)(survey-1)(segment  51) model-avg-est:  0.1873 se=  0.1101 M3-1
p1(model-season 4)(survey-1)(segment  52) model-avg-est:  0.1410 se=  0.1000 M3-2
p1(model-season 4)(survey-1)(segment  53) model-avg-est:  0.1503 se=  0.1011 M3-3
p1(model-season 4)(survey-1)(segment  54) model-avg-est:  0.1283 se=  0.0994 M3-4
p1(model-season 4)(survey-1)(segment  55) model-avg-est:  0.1225 se=  0.0994 M3-5
p1(model-season 4)(survey-1)(segment  56) model-avg-est:  0.1915 se=  0.1116 M2-1
p1(model-season 4)(survey-1)(segment  57) model-avg-est:  0.1338 se=  0.0995 M2-2
p1(model-season 4)(survey-1)(segment  58) model-avg-est:  0.1399 se=  0.0999 M2-3
p1(model-season 4)(survey-1)(segment  59) model-avg-est:  0.1627 se=  0.1032 M2-4
p1(model-season 4)(survey-1)(segment  60) model-avg-est:  0.1627 se=  0.1032 M2-5
p1(model-season 4)(survey-1)(segment  61) model-avg-est:  0.1420 se=  0.1001 M2-6
p1(model-season 4)(survey-1)(segment  62) model-avg-est:  0.1673 se=  0.1042 M1-1
p1(model-season 4)(survey-1)(segment  63) model-avg-est:  0.1937 se=  0.1125 M1-2
p1(model-season 4)(survey-1)(segment  64) model-avg-est:  0.1657 se=  0.1039 M1-3
p1(model-season 4)(survey-1)(segment  65) model-avg-est:  0.1275 se=  0.0994 M1-4
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p1(model-season 4)(survey-1)(segment  66) model-avg-est:   0.1555 se=  0.1018 M1-5
p1(model-season 4)(survey-1)(segment  67) model-avg-est:   0.1399 se=  0.0999 M1-6
p1(model-season 4)(survey-2)(segment   1) model-avg-est:   0.3388 se=  0.1642 K5-1
p1(model-season 4)(survey-2)(segment   2) model-avg-est:   0.2021 se=  0.1601 K5-2
p1(model-season 4)(survey-2)(segment   3) model-avg-est:   0.2756 se=  0.1530 K5-3
p1(model-season 4)(survey-2)(segment   4) model-avg-est:   0.3388 se=  0.1642 K5-4
p1(model-season 4)(survey-2)(segment   5) model-avg-est:   0.5406 se=  0.3119 L3-1
p1(model-season 4)(survey-2)(segment   6) model-avg-est:   0.4449 se=  0.2220 L3-2
p1(model-season 4)(survey-2)(segment   7) model-avg-est:   0.3779 se=  0.1799 L3-3
p1(model-season 4)(survey-2)(segment   8) model-avg-est:   0.3605 se=  0.1721 L3-4
p1(model-season 4)(survey-2)(segment   9) model-avg-est:   0.3707 se=  0.1765 L3-5
p1(model-season 4)(survey-2)(segment  10) model-avg-est:   0.3779 se=  0.1799 L3-6
p1(model-season 4)(survey-2)(segment  11) model-avg-est:   0.3816 se=  0.1817 L3-7
p1(model-season 4)(survey-2)(segment  12) model-avg-est:   0.3331 se=  0.1624 L3-8
p1(model-season 4)(survey-2)(segment  13) model-avg-est:   0.2834 se=  0.1534 L3-9
p1(model-season 4)(survey-2)(segment  14) model-avg-est:   0.2454 se=  0.1535 L3-10
p1(model-season 4)(survey-2)(segment  15) model-avg-est:   0.3508 se=  0.1683 L3-11
p1(model-season 4)(survey-2)(segment  16) model-avg-est:   0.1905 se=  0.1628 L3-12
p1(model-season 4)(survey-2)(segment  17) model-avg-est:   0.3477 se=  0.1671 L3-13
p1(model-season 4)(survey-2)(segment  18) model-avg-est:   0.3508 se=  0.1683 L2-1
p1(model-season 4)(survey-2)(segment  19) model-avg-est:   0.3854 se=  0.1836 L2-2
p1(model-season 4)(survey-2)(segment  20) model-avg-est:   0.3331 se=  0.1624 L2-3
p1(model-season 4)(survey-2)(segment  21) model-avg-est:   0.3707 se=  0.1765 L2-4
p1(model-season 4)(survey-2)(segment  22) model-avg-est:   0.1507 se=  0.1736 L2-5
p1(model-season 4)(survey-2)(segment  23) model-avg-est:   0.1507 se=  0.1736 L2-6
p1(model-season 4)(survey-2)(segment  24) model-avg-est:   0.1507 se=  0.1736 L2-7
p1(model-season 4)(survey-2)(segment  25) model-avg-est:   0.3477 se=  0.1671 L2-8
p1(model-season 4)(survey-2)(segment  26) model-avg-est:   0.3707 se=  0.1765 L2-9
p1(model-season 4)(survey-2)(segment  27) model-avg-est:   0.3477 se=  0.1671 L2-10
p1(model-season 4)(survey-2)(segment  28) model-avg-est:   0.3572 se=  0.1707 L1B-1
p1(model-season 4)(survey-2)(segment  29) model-avg-est:   0.3854 se=  0.1836 L1B-2
p1(model-season 4)(survey-2)(segment  30) model-avg-est:   0.3303 se=  0.1616 L1B-3
p1(model-season 4)(survey-2)(segment  31) model-avg-est:   0.3004 se=  0.1553 L1A-1
p1(model-season 4)(survey-2)(segment  32) model-avg-est:   0.2960 se=  0.1547 L1A-2
p1(model-season 4)(survey-2)(segment  33) model-avg-est:   0.3707 se=  0.1765 L1A-3
p1(model-season 4)(survey-2)(segment  34) model-avg-est:   0.2469 se=  0.1534 L1A-4
p1(model-season 4)(survey-2)(segment  35) model-avg-est:   0.1734 se=  0.1672 L1A-5
p1(model-season 4)(survey-2)(segment  36) model-avg-est:   0.4368 se=  0.2160 L1A-6
p1(model-season 4)(survey-2)(segment  37) model-avg-est:   0.3742 se=  0.1781 L1A-7
p1(model-season 4)(survey-2)(segment  38) model-avg-est:   0.3707 se=  0.1765 L1A-8
p1(model-season 4)(survey-2)(segment  39) model-avg-est:   0.3171 se=  0.1583 L1A-9
p1(model-season 4)(survey-2)(segment  40) model-avg-est:   0.2794 se=  0.1531 L1A-10
p1(model-season 4)(survey-2)(segment  41) model-avg-est:   0.3276 se=  0.1609 M4-1
p1(model-season 4)(survey-2)(segment  42) model-avg-est:   0.3707 se=  0.1765 M4-2
p1(model-season 4)(survey-2)(segment  43) model-avg-est:   0.3893 se=  0.1857 M4-3
p1(model-season 4)(survey-2)(segment  44) model-avg-est:   0.3672 se=  0.1749 M4-4
p1(model-season 4)(survey-2)(segment  45) model-avg-est:   0.3933 se=  0.1879 M4-5
p1(model-season 4)(survey-2)(segment  46) model-avg-est:   0.3572 se=  0.1707 M4-6
p1(model-season 4)(survey-2)(segment  47) model-avg-est:   0.3638 se=  0.1734 M4-7
p1(model-season 4)(survey-2)(segment  48) model-avg-est:   0.3050 se=  0.1560 M4-8
p1(model-season 4)(survey-2)(segment  49) model-avg-est:   0.3249 se=  0.1602 M4-9
p1(model-season 4)(survey-2)(segment  50) model-avg-est:   0.2982 se=  0.1550 M4-10
p1(model-season 4)(survey-2)(segment  51) model-avg-est:   0.3508 se=  0.1683 M3-1
p1(model-season 4)(survey-2)(segment  52) model-avg-est:   0.2756 se=  0.1530 M3-2
p1(model-season 4)(survey-2)(segment  53) model-avg-est:   0.2916 se=  0.1542 M3-3
p1(model-season 4)(survey-2)(segment  54) model-avg-est:   0.2530 se=  0.1530 M3-4
p1(model-season 4)(survey-2)(segment  55) model-avg-est:   0.2424 se=  0.1538 M3-5
p1(model-season 4)(survey-2)(segment  56) model-avg-est:   0.3572 se=  0.1707 M2-1
p1(model-season 4)(survey-2)(segment  57) model-avg-est:   0.2630 se=  0.1528 M2-2
p1(model-season 4)(survey-2)(segment  58) model-avg-est:   0.2737 se=  0.1529 M2-3
p1(model-season 4)(survey-2)(segment  59) model-avg-est:   0.3121 se=  0.1573 M2-4
p1(model-season 4)(survey-2)(segment  60) model-avg-est:   0.3121 se=  0.1573 M2-5
p1(model-season 4)(survey-2)(segment  61) model-avg-est:   0.2775 se=  0.1531 M2-6
p1(model-season 4)(survey-2)(segment  62) model-avg-est:   0.3197 se=  0.1589 M1-1
p1(model-season 4)(survey-2)(segment  63) model-avg-est:   0.3605 se=  0.1721 M1-2
p1(model-season 4)(survey-2)(segment  64) model-avg-est:   0.3171 se=  0.1583 M1-3
p1(model-season 4)(survey-2)(segment  65) model-avg-est:   0.2515 se=  0.1531 M1-4
p1(model-season 4)(survey-2)(segment  66) model-avg-est:   0.3004 se=  0.1553 M1-5
p1(model-season 4)(survey-2)(segment  67) model-avg-est:   0.2737 se=  0.1529 M1-6
p1(model-season 4) (all-surveys) (avg.all segments) model-avg-est:   0.2458 sd=  0.0953

δ (all model-seasons)(all-surveys) model-avg-est:   0.5936 se=  0.0598
p2(all model-season 1)(all-surveys) model-avg-est:   0.9835 se=  0.0160
```