

Modelling population trajectory of Kiyi (*Coregonus kiyi*) in Lake Superior using USGS bottom trawl survey data

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MODELLING POPULATION TRAJECTORY OF KIYI (COREGONUS KIYI) IN LAKE SUPERIOR
USING USGS BOTTOM TRAWL SURVEY DATA

by

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TABLE OF CONTENTS

Abstract.....	iv
Résumé	v
1 Introduction	1
2 Methods.....	1
2.1 Data.....	1
2.2 Analysis	2
3 Results.....	4
4 Discussion	9
5 References	11
Appendix.....	12
6 Meshes	12
7 Spatial Fields	13

ABSTRACT

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The Upper Great Lakes populations of Kiyi (*Coregonus kiyi*) are listed as Special Concern under Schedule 1 of the *Species At Risk Act* in Canada. A detailed analysis of trends and population size of Kiyi in Lake Superior has not been conducted. The United States Geological Survey has conducted annual bottom trawl surveys that readily capture Kiyi since 2011. A deterministic Bayesian modelling approach, Integrated Nested Laplace Approximation (INLA), is used to model population trajectory and project population size. The model identified a decline in density between the first half (2011–2014) and second half (2015–2019) of the time series; however, density increased between 2018 and 2019. Despite the declines, the lakewide population remains abundant. Lakewide projections estimated total biomass in 2019 to be 8,483 t (CI: 4,147–16,789 t) with approximately 1/3 on the Canadian side of the lake.

RÉSUMÉ

van der Lee, A.S. and Koops, M.A. 2024. Modelling population trajectory of Kiyi (*Coregonus kiyi*) in Lake Superior using USGS bottom trawl survey data. Can. Tech. Rep. Fish. Aquat. Sci. 3562 : v + 13 p.

Les populations de kiyi (*Coregonus kiyi*) du secteur supérieur des Grands Lacs ont été inscrites sur la liste des espèces préoccupantes à l'annexe 1 de la *Loi sur les espèces en péril* au Canada. Aucune analyse détaillée des tendances et de la taille de la population de kiyi dans le lac Supérieur n'a été effectuée. Depuis 2011, le United States Geological Survey (USGS) réalise des relevés annuels au chalut de fond qui permettent de capturer le kiyi. On utilise une approche de modélisation bayésienne déterministe, appelée Integrated Nested Laplace Approximation (approximation de Laplace imbriquée intégrée [INLA]), pour modéliser la trajectoire de la population et estimer sa taille. Le modèle a détecté une baisse de la densité entre la première moitié (de 2011 à 2014) et la seconde moitié (de 2015 à 2019) de la série chronologique; toutefois, la densité a augmenté entre 2018 et 2019. Malgré ces déclin, la population de l'ensemble du lac demeure abondante. Les projections à l'échelle du lac ont estimé la biomasse totale en 2019 à 8 483 t (IC : 4 147 t-16 789 t), dont environ 1/3 du côté canadien du lac.

1 INTRODUCTION

Kiyi (*Coregonus kiyi*) is one of six cisco species endemic to the Great Lakes. Kiyi once inhabited all of the Great Lakes except Lake Erie. Kiyi in Lake Ontario were identified as a separate sub-species (*C. kiyi orientalis*) from the Kiyi in Lakes Michigan, Huron and Superior (*C. kiyi kiyi*). Populations of Kiyi declined throughout the 20th century resulting in extirpation from Lakes Ontario, Michigan, and Huron. The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) assessed the sub-species as separate Designatable Units (DU). The Upper Great Lakes kiyi (*C. kiyi kiyi*) was assessed as Special Concern and Lake Ontario Kiyi was assessed as Extinct (COSEWIC 2005).

Kiyi remains common and widely distributed in Lake Superior (DFO 2012). Kiyi inhabit deep water (Gamble et al. 2011) preferring depths > 130 m (Pratt 2012). In offshore bottom trawls Kiyi represent the second most captured species by count (Vinson et al. 2018), following Deepwater Sculpin (*Myoxocephalus thompsonii*). Kiyi undertake diel vertical migrations (Hrabik et al. 2006), inhabiting deep benthic waters during the day and moving to shallow pelagic waters at night to feed on their preferred prey *Mysis diluviana* (Ahrenstorff et al. 2011).

The United States Geological Survey (USGS) conducts a nearshore and offshore bottom trawl survey in Lake Superior annually (Figure 1). The nearshore survey began sampling the whole lake in 1989 with sample locations typically < 100 m deep. The offshore survey began in 2011 with sample locations up to 315 m deep. The combined survey dataset (2011–2019) was analysed to assess the recent trends in Kiyi density in Lake Superior and estimate population size.

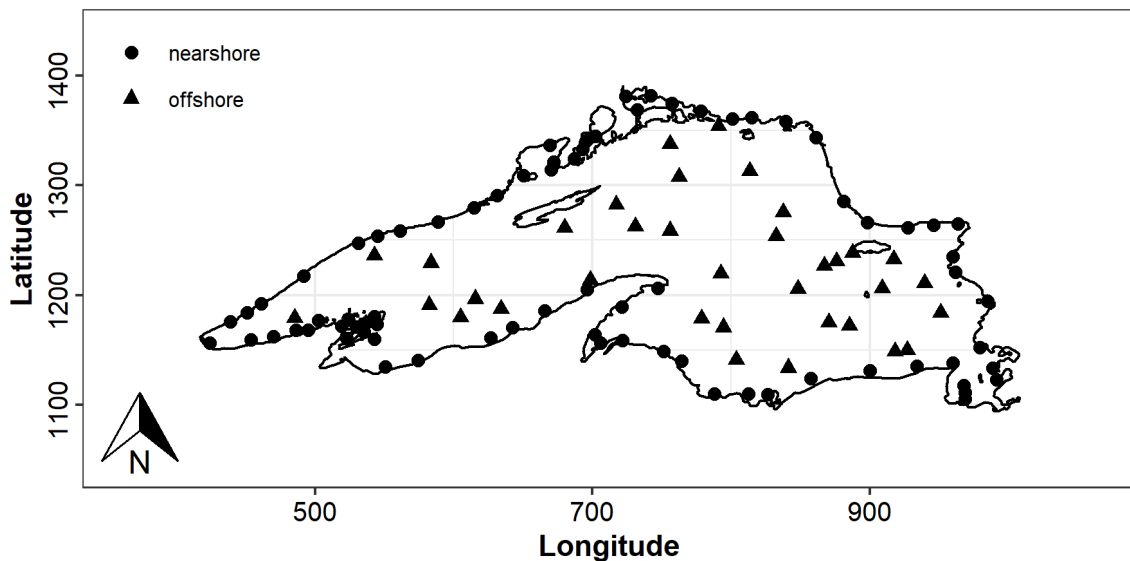


Figure 1: USGS bottom trawl survey sampling locations in 2019. Circles represent nearshore sampling locations and triangles represent offshore sampling locations.

2 METHODS

2.1 Data

The USGS conducts annual bottom trawl surveys in Lake Superior during daylight hours to assess the long-term trends in lake-wide prey fish species occurrences, relative abundance and biomass (Vinson et al. 2018). Separate surveys are conducted to sample nearshore and offshore habitat. The nearshore survey typically takes place in June and the offshore survey in July. Nearshore sampling locations are located around the perimeter of the lake with, on average, 76 sites sampled annually (range: 72–82 since 2011). In total, 687 nearshore sites were sampled between 2011 and 2019.

Nearshore trawls were conducted across depth contours. The mean of start and end depth was taken to represent depth for nearshore trawls. The average start depth for nearshore trawls was 18.3 m (range: 9.2–39.5 m) and the averaged end depth was 61.1 m (range: 11.6–144.0 m). The mean of start and end depth, used in model fitting, was 39.7 m (range: 15.2–91.8 m). Offshore sampling locations were selected using a spatially-balanced, depth-weighted probabilistic sampling design that targets depths >85 m (Vinson et al. 2018) with, on average, 35 sites sampled annually (range: 30–36). In total, 308 offshore sites were sampled between 2011 and 2019. Offshore trawls were conducted along depth contours. Mean sampling depth for offshore sites was 185.2 m (range: 87.0–315.0 m) and was consistent among years. At each sampling location, fish collections were sorted by species, counted and weighed. Density (fish/ha) and biomass (kg/ha) were estimated by dividing sample counts and weights by the area swept (ha) during the trawl.

2.2 Analysis

The data from the nearshore and offshore surveys were combined and analysed together, as such the analysis was limited to years 2011–2019. The nearshore survey represented only 1.4% of total Kiyi catch and, therefore, it was determined that the nearshore survey catch data alone would provide little insight into Kiyi abundance; Kiyi are most abundance at depths > 130 m (Pratt 2012). The nearshore data were combined with the offshore data to provide a broader range of depths sampled to allow for a more complete depth trend to be estimated and allow for lakewide density projections. The purpose of the analyses was to identify recent trends (2011–2019) in Kiyi abundance and project current population size. To analyse the data a hierarchical Bayesian approach, Integrated Nested Laplace Approximation (INLA, Rue et al. 2009), was employed. INLA used deterministic approximations to make Bayesian inferences which results in much faster computations than Markov Chain Monte Carlo (MCMC) sampling. When combined with a stochastic partial differential equation approach (SPDE, Lindgren et al. 2011) INLA can estimate Gaussian Markovian random fields (GMRF) to account for complex covariance structures common in spatial-temporal data, such as long-term survey data.

The dataset contained a large proportion of trawls where no Kiyi were caught. In the nearshore survey 39 of the 687 trawl catches (~6%) contained Kiyi and in the offshore survey 245 of the 309 trawl catches (~80%) contained Kiyi. As a result, the data were analysed using a hurdle model. Hurdle models are a two part model: a Bernoulli model for the presence-absence data; and a continuous model for the positive catch data. Biomass density (kg/ha) was used to model Kiyi catch per unit effort (CPUE). Because biomass is a continuous and positive response variable that was highly skewed (skewness = 4.7) the gamma distribution was used to model positive catches. The hurdle model, zero-altered gamma (ZAG) model, was represented by:

$$\begin{aligned}
 y_{i,t} &\sim \text{ZAG}(\mu_{i,t}, \pi_{i,t}) \\
 E(y_{i,t}) &= \pi_{i,t} \cdot \mu_{i,t} \\
 \text{var}(y_{i,t}) &= \frac{\pi_{i,t} \cdot r + \pi_{i,t} - \pi_{i,t}^2 \cdot r}{r} \cdot \mu_{i,t}^2, \\
 \text{logit}(\pi_{i,t}) &= \alpha Z_{i,t} + u_t^{01} + s_i^{01} \\
 \log(\mu_{i,t}) &= \beta X_{i,t} + u_t^{>0} + s_i^{>0}
 \end{aligned} \tag{1}$$

where, π_i represents the likelihood of occurrence, μ_i represents mean biomass density and r is the shape parameter of the gamma distribution. $Z_{i,t}$ and $X_{i,t}$ represent the potential fixed effects of intercept, depth, and time of day, and α and β represent the coefficients for the presence-absence and positive catch models respectively. All fixed effects variables were centred and scaled between 0 and 1.

The effect of year, u_t , was found to be non-linear. To allow for non-linear trends a random walk order 1 (rw1) function was applied where the effect of year t was a function of year $t - 1$, such that:

$$u_t = u_{t-1} + e_t \text{ where } e_t \sim N(0, \sigma_t^2), \quad (2)$$

The effect of depth was also found to be non-linear. Separate models were fit to determine the ideal structure. Initially, depth was incorporated as, up to, a third order polynomial to allow for non-linearity. An interaction term with time of day was included with depth to determine if Kiyi diel migrations impacted catch rate. An alternative model was fit where depth was modelled as a second order random walk (rw2) model. The advantage of the rw2 model is greater flexibility in the non-linear trend relative to the polynomial model; however, INLA requires that the random walk variable be treated as a random parameter with associated hyper-parameter σ_d . The rw2 model assumed the effect g_d on occurrence or biomass at depth d is a function of effect of depths $d - 1$ and $d - 2$, where:

$$g_d = (2 \cdot g_{d-1} - g_{d-2}) + e_d \text{ where } e_d \sim N(0, \sigma_d^2). \quad (3)$$

s_i in Equation (1) represents the correlated random effects of sampling locations. s_i is a GMRF with mean 0 and covariance matrix, Σ . The covariance matrix, Σ , incorporates the spatial variance, σ_s^2 , and correlation among locations estimated with the Matérn correlation function using SPDE ([Lindgren et al. 2011](#)). In INLA the Matérn correlation function is defined by an estimated range parameter, R , which describes the distance at which the correlation between observations drops to 0.1. The GMRF is estimated over a mesh of non-overlapping triangles covering the sampling area produced with built-in INLA functions (Figure 6.1). A random effect is estimated at each node of the mesh and the random effects are correlated with each other in all directions up to the distance R . Incorporating a spatial field into the model assumes that there are unmeasured characteristics of a particular location that would cause the presence and/or biomass at that location to be greater or less than other locations and that the effect of these unmeasured characteristics extends away from the location up to the distance R . The effect of incorporating spatial fields in the model was examined by fitting various models of different complexity. The simplest model included no spatial field like a typical generalized linear model (GLM). The second model included one spatial field for each of the Bernoulli and positive catch model components. This assumes the effect of location is constant throughout the time-series. The final model included two estimated spatial fields at defined knots (years, 2012 and 2017) in the time series. The knots years were selected such that there was equal weight applied to each field (i.e. an equal number of years were affected by each field). Each spatial field was estimated independently as a function of the weighted average of the surrounding years (e.g. the spatial field of year 2013 would be 80% influenced by field 1 and 20% influenced by field 2). This model assumes the effect of location changes through time. The best fit model was selected based on deviance information criterion (DIC).

Contrasts were used to identify the significance of changes in the occurrence and CPUE of Kiyi through time. Contrasts allow for the estimation of the difference between model outputs with the associated credible intervals (CI), demonstrating the importance of any difference. Of interest here is the change in occurrence and CPUE through time. COSEWIC uses a three generation time period to assess population change when assessing species status. The sampling data for deepwater locations in Lake Superior, where Kiyi is more likely to inhabit, were available for nine years (2011–2019), representing almost two generations for Kiyi ([COSEWIC 2005](#)). The contrasts compared the mean occurrence or CPUE between the first half (2011–2014) and second half (2015–2019) of the time series, allowing a comparison of occurrence and biomass density over approximately two generations. Using time periods will be more representative of population state than individual years as they are less influenced by catch stochasticity. The choice to compare the first half of the time series to the second half allows for determination of population change over the longest possible time frame (approximately two generations) while minimizing the influence of inter-annual stochasticity. The contrasts employed compare the difference between the time period means on the link scale from

the model fit (i.e. logit (log odds) transformed for the occurrence model and \log_e transformed for the CPUE model (Equation (2.1))). Applying the exponential function, e , to these differences gives the proportional change in the odds of capture for the presence-absence model and the proportional change in CPUE for the positive catch model. A value of 1 indicates no change in odds of capture or CPUE between the periods, a value significantly < 1 indicates a decrease in odds or CPUE between the two periods, and a value significantly > 1 indicates an increase in odds of capture or CPUE between the periods.

3 RESULTS

Total annual catch of Kiyi was greatest in 2013 and lowest in 2018 (Figure 2). Catch in 2019, however, was the largest since 2013.

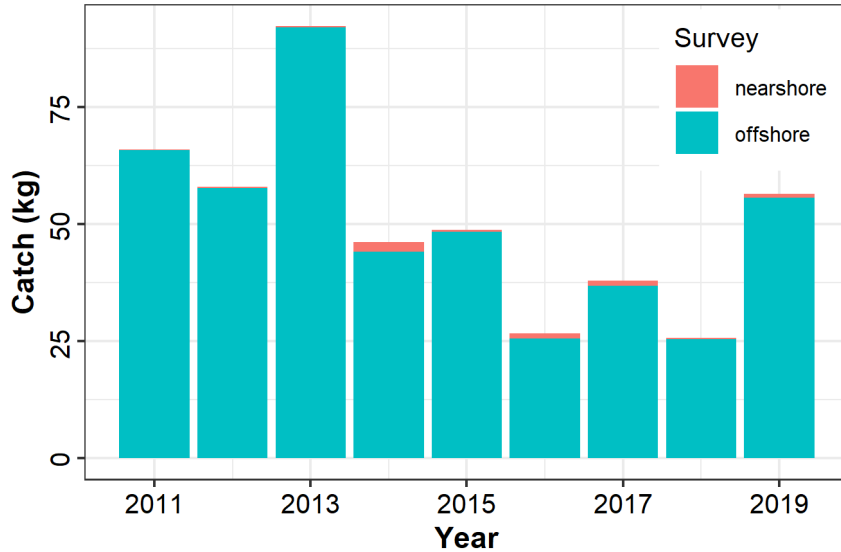


Figure 2: Total annual catch of Kiyi (kg) from USGS bottom trawl research surveys. Colour indicates catch from the nearshore (red) or offshore (blue) surveys.

Table 1: INLA hurdle model results for the USGS bottom trawl research survey data. Coefficients, fixed effects and hyper-parameters, are summarized for the presence-absence and positive catch model components. σ_y is the variance associated with the gamma distribution. σ_t is the variance associated with the temporal trend. σ_d is the variance associated with the depth trend. Range and σ_s are the hyper-parameters associated with the spatial field, correlation distance and variance.

Parameter	Presence-absence			CPUE		
	Median	LCI	UCI	Median	LCI	UCI
Intercept	1.07	0.13	2.17	-1.23	-1.58	-0.86
σ_y	NA	NA	NA	0.98	0.89	1.06
σ_d	0.01	0.01	0.03	0.01	0.00	0.02
σ_t	0.10	0.01	0.25	0.19	0.09	0.42
Range	83.18	45.59	165.76	104.29	24.25	549.28
σ_s	1.56	1.10	2.18	0.31	0.13	0.72

The best fit model (Table 1), based on DIC (Table 2), incorporated a single spatial field for the presence-absence (Figure B.1) and biomass (Figure B.2) components; the 2 spatial field model had a negligible improvement in DIC and therefore the simpler model is preferred. Depth was best fit with a rw2 model and time of day did not have an important effect on catch probability or CPUE.

Table 2: Comparison of model fit using DIC for models incorporating different random effect spatial structures (0, 1, or 2 spatial fields), depth relationships (polynomial or random walk), and sampling time of day as an interaction with depth. Preferred model fit is indicated in bold.

Model	No. of Spatial Fields	Depth Relationship	Time of Day	DIC	Δ DIC
2SF-RW	2	Random Walk	No	911.19	0.00
1SF-RW	1	Random Walk	No	911.63	0.45
1SF-poly	1	Polynomial	No	918.17	6.98
1SF-poly-time	1	Polynomial	Yes	920.01	8.82
2SF-poly	2	Polynomial	No	923.53	12.34
2SF-poly-time	2	Polynomial	Yes	925.49	14.30
GLM	0	Random Walk	No	1,009.09	97.90

Occurrence of Kiyi in bottom trawl catches has remained relatively constant since 2011 (Figure 3). Contrasts were used to compare the proportional change in the odds of capturing Kiyi in the bottom trawl survey between the second half (2015–2019) and first half (2011–2014) of the time series (Figure 4). The value of the contrast did not differ from 1 indicating that there was not an important difference.

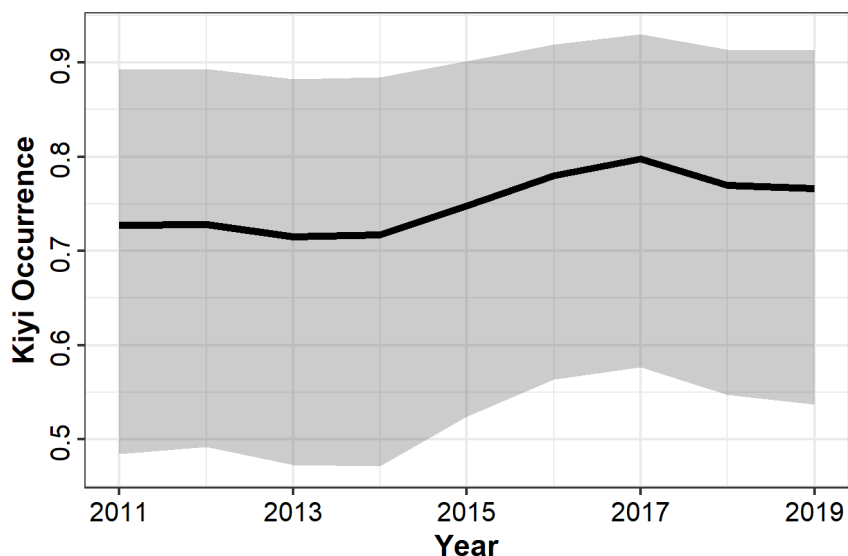


Figure 3: Temporal trend in occurrence (proportion of trawls with Kiyi caught) of Kiyi in the USGS bottom trawl research survey estimated from the INLA model. The projection is made for a 0 (mean on logit scale) depth effect, which equates to a depth of 115 m or 282 m (Figure 6).

Biomass density (kg/ha) declined between 2011 and 2018 but increased between 2018 and 2019 (Figure 5). A contrast comparing the proportional change in CPUE between the second half (2015–2019) the first half (2011–2014) of the time series indicated a significant decline (difference from 1) despite the increase in catch rate between 2018 and 2019 (Figure 7).

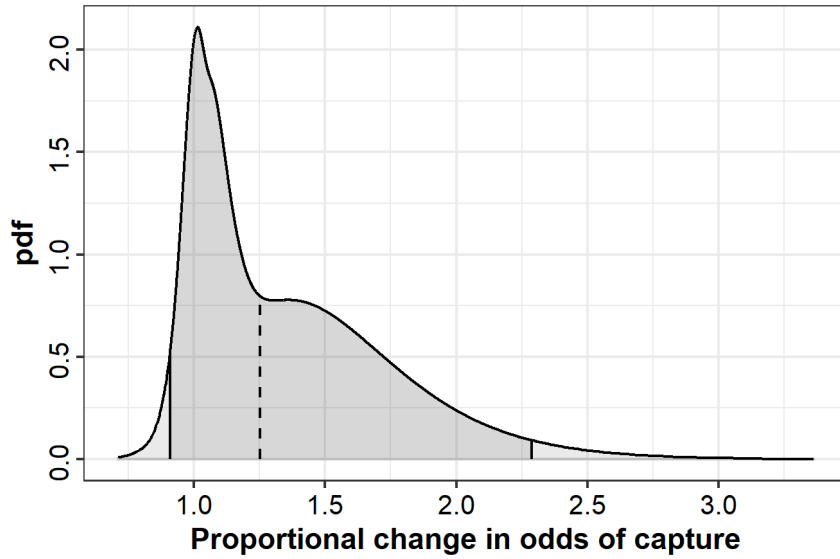


Figure 4: Posterior marginal of the contrast comparing the proportional change in the odds of capturing Kiyi in the bottom trawl survey between the second half (2015–2019) and first half (2011–2014) of the time series. A value of 1 indicates no difference in the odds of capture between the two time periods. The dashed line indicates the median.

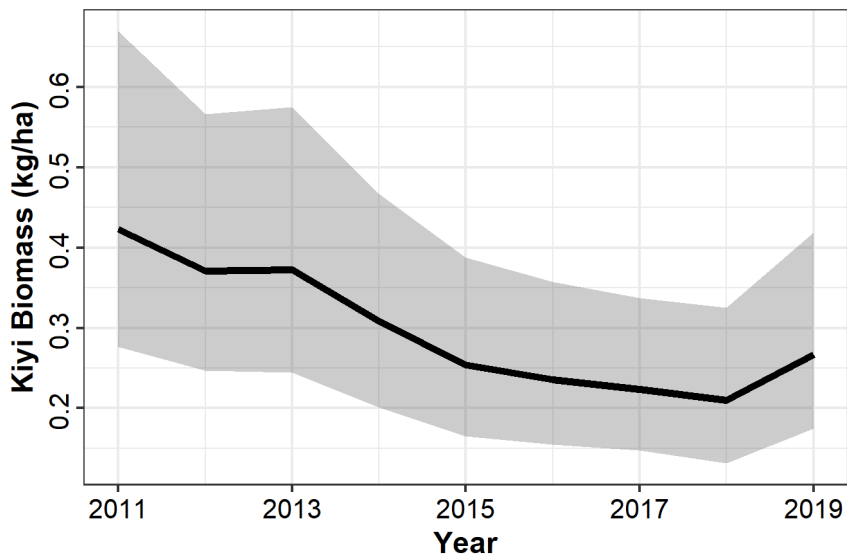


Figure 5: Temporal trends in biomass density (kg/ha) of Kiyi in the USGS bottom trawl research survey estimated from the INLA model. The projection is made for a 0 (mean on log scale) depth effect, which equates to a depth of 79 m or 251 m (Figure 8).

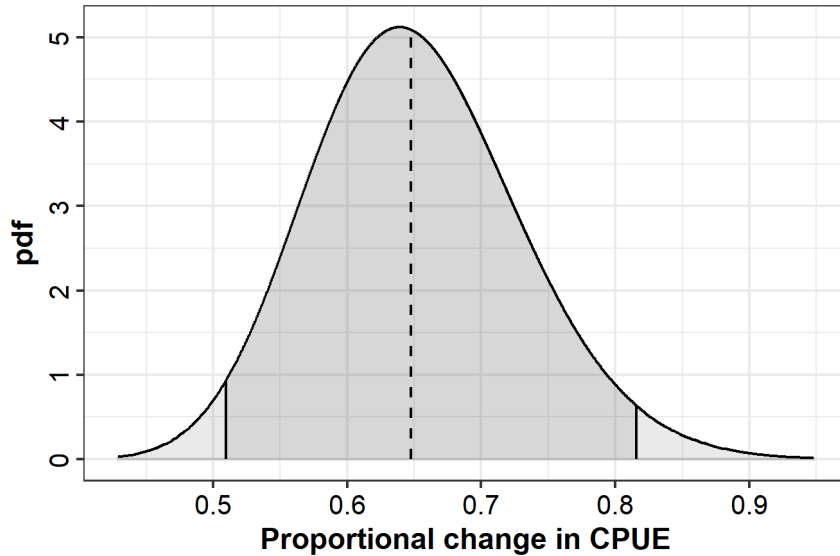


Figure 6: Posterior marginal of the contrast comparing the proportional change in the CPUE (kg/ha) of Kiyi in the bottom trawl survey between the second half (2015–2019) and first half (2011–2015) of the time series. A value of 1 indicates no difference in the CPUE between the two time periods. The dashed line indicates the median.

Depth had an important effect on occurrence (Figure 7) and CPUE (Figure 8) in the survey. Estimated occurrence was >50% at depths between 100 m and 300 m and Kiyi were ubiquitous (> 99% occurrence) at depths between 150 m and 235 m. CPUE (kg/ha) was greatest at ~ 180 m depth with a mean catch rate of 3.55 kg/ha in an average year. Mean catch rate was large (> 2 kg/ha) at depths between 145 m and 200 m. Catch rates were low (< 0.5 kg/ha) at depths < 90 m or > 240 m.

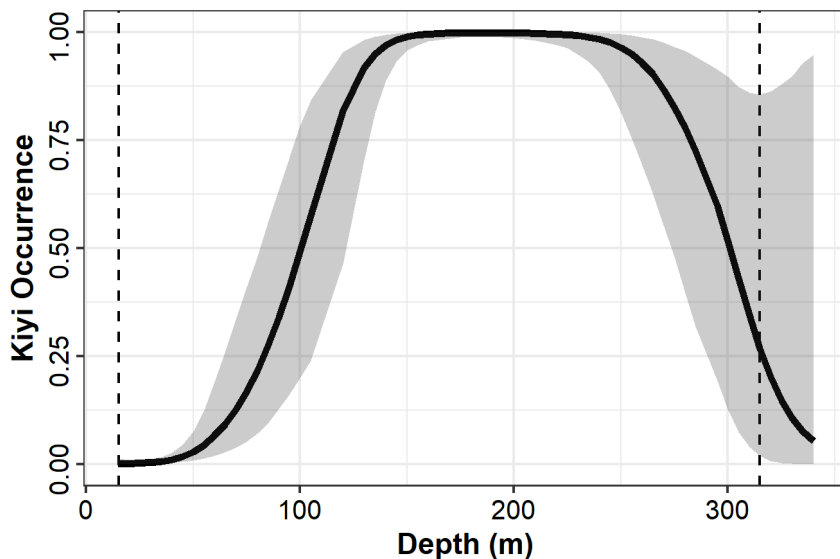


Figure 7: Trends in catch probability of Kiyi with depth (m) in the USGS bottom trawl research survey estimated from the INLA model. The solid line represents the mean estimate and the grey area represents the credibility interval. The dashed lines represent minimum and maximum sampling depths.

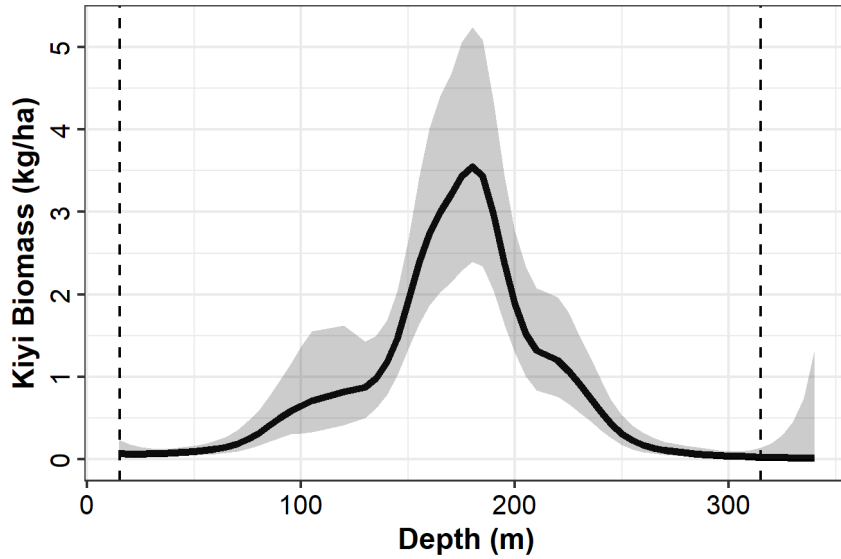


Figure 8: Trend in biomass density (kg/ha) of Kiyi with depth (m) in the USGS bottom trawl research survey estimated from the INLA model. The solid line represents the mean estimates and the grey area represents the credibility interval. The dashed lines represent minimum and maximum sampling depths.

The hurdle model was used to make projections of total Kiyi population biomass in Lake Superior (Figure 9). The credibility intervals for the estimates were broad due to parameter uncertainty and extrapolating occurrence and biomass outside of the sampled locations. The trend in population biomass followed the trend in CPUE closely. The greatest population biomass was in 2011 with a median of 13,283 t (CI: 6,530–27,014 t) and the lowest estimate was in 2018 with a median of 6,751 (CI: 3,158–13,101 t). In 2019, the estimated population biomass was 8,483 t (CI: 4,147–16,789 t). Average annual population growth rate (Table 3) was < 1 indicating a decline; however, the greatest annual growth rate estimate was between 2018 and 2019.

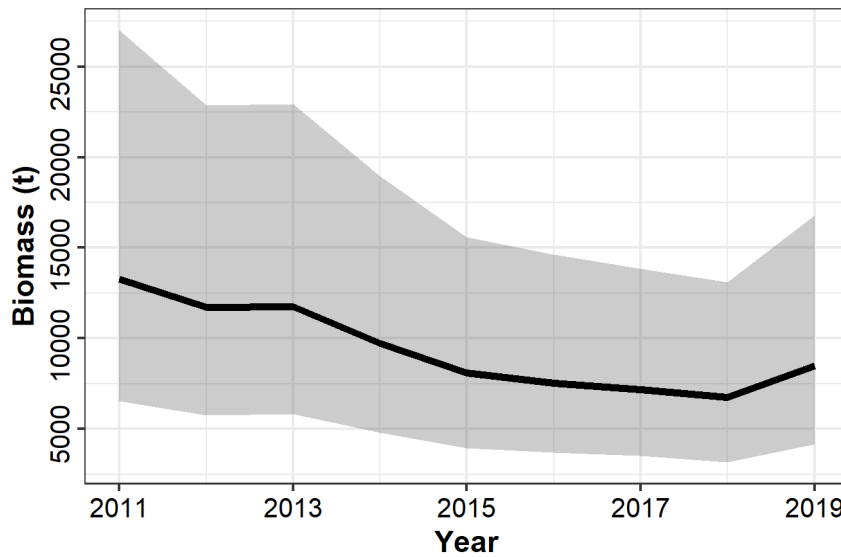


Figure 9: Projected Kiyi population biomass (t) through time estimated from the INLA model. The solid line represents median estimates and the grey area represents the credibility interval.

Table 3: Estimates of population growth rate between years and the mean over the time series. Estimated from population projections (Figure 9).

Year	Population Growth Rate
2011-2012	0.88
2012-2013	1.00
2013-2014	0.83
2014-2015	0.83
2015-2016	0.93
2016-2017	0.95
2017-2018	0.94
2018-2019	1.26
Geometric Mean	0.95

The occurrence model was used to estimate the amount of preferred habitat for Kiyi in Lake Superior by predicting where the likelihood of occurrence was $\geq 50\%$. Over the 9 year time series the mean amount of preferred habitat was 55,825 km² (CI: 40,096–65,428 km²). The projected spatial distribution of Kiyi for years 2011, 2015 and 2019 is represented in Figure 10. The projection is based on lake bathymetry and the estimated spatial field. Because the same spatial field was applied to all years of data the spatial distribution of Kiyi is assumed to be constant, however, the density (kg/ha) changes follow the temporal trends in occurrence and biomass. Greatest densities occurred in the southwest portion of the lake just northwest of the Apostle Islands. The Canadian side of the lake contained approximately 1/3 of the Kiyi population and 35% of the preferred habitat. In 2019, the population estimate on the Canadian side of the lake was 2,846 t (CI: 1,367–5,697 t) with 19,836 km² (CI: 13,716–22,554 km²) of preferred habitat.

4 DISCUSSION

Recent Kiyi abundance and population trends in Lake Superior were assessed through modelling of USGS bottom trawl survey data. Kiyi were not caught in significant numbers until the start of the offshore survey in 2011. Kiyi density declined between 2011 and 2018 but increased in 2019. The model was used to project population size to the entire lake. 2019 median population size was estimated to be to > 8,000 t, a decline from 2011 where median abundance was >13,000 t. The population growth rate over the time series was ~0.95. Few estimates of Kiyi abundance in Lake Superior exist. Ebener et al. (2008) estimated total biomass of Kiyi in the open waters of Lake Superior to be ~ 2,500 t in 2003 and 2004. These estimates were based on night time mid-water trawls and hydro-acoustic surveys. Petzold (2002; in COSEWIC 2005) estimated 2000–01 abundance of Coregonus sp. in the Canadian waters of Lake Superior at depths > 105 m from gillnet and trawl surveys at 2,211 t (90% CI: 271–4,452). This was used to project Kiyi biomass in Canadian waters at between 22 and 330 t (COSEWIC 2005). These values are considerably less than the 2019 estimate from the INLA hurdle model: 2,846 t (CI: 1,367–5,697 t). Although Kiyi population size has declined since 2011 the time series is short, only nine years, making it difficult to draw broader conclusions. Other coregonines, such as Pygmy Whitefish (*Prosopium coulterii*), in Lake Superior have shown periodic fluctuations in abundance through time (van der Lee and Koops 2020) where short-term fluctuations in population size do not necessarily reflect a long-term change. However, congener species, such as Cisco (*C. artedii*) and Bloater (*C. hoyi*), which are vulnerable to the nearshore survey, have been declining since the early 2000s, possibly due to environmental factors leading to reduced recruitment (Gorman 2019). It is possible Kiyi has been similarly impacted and that the observed short term decline is reflective of significant population change. Continued monitoring is necessary to discern if Kiyi are undergoing transient population fluctuations or a continued decline.

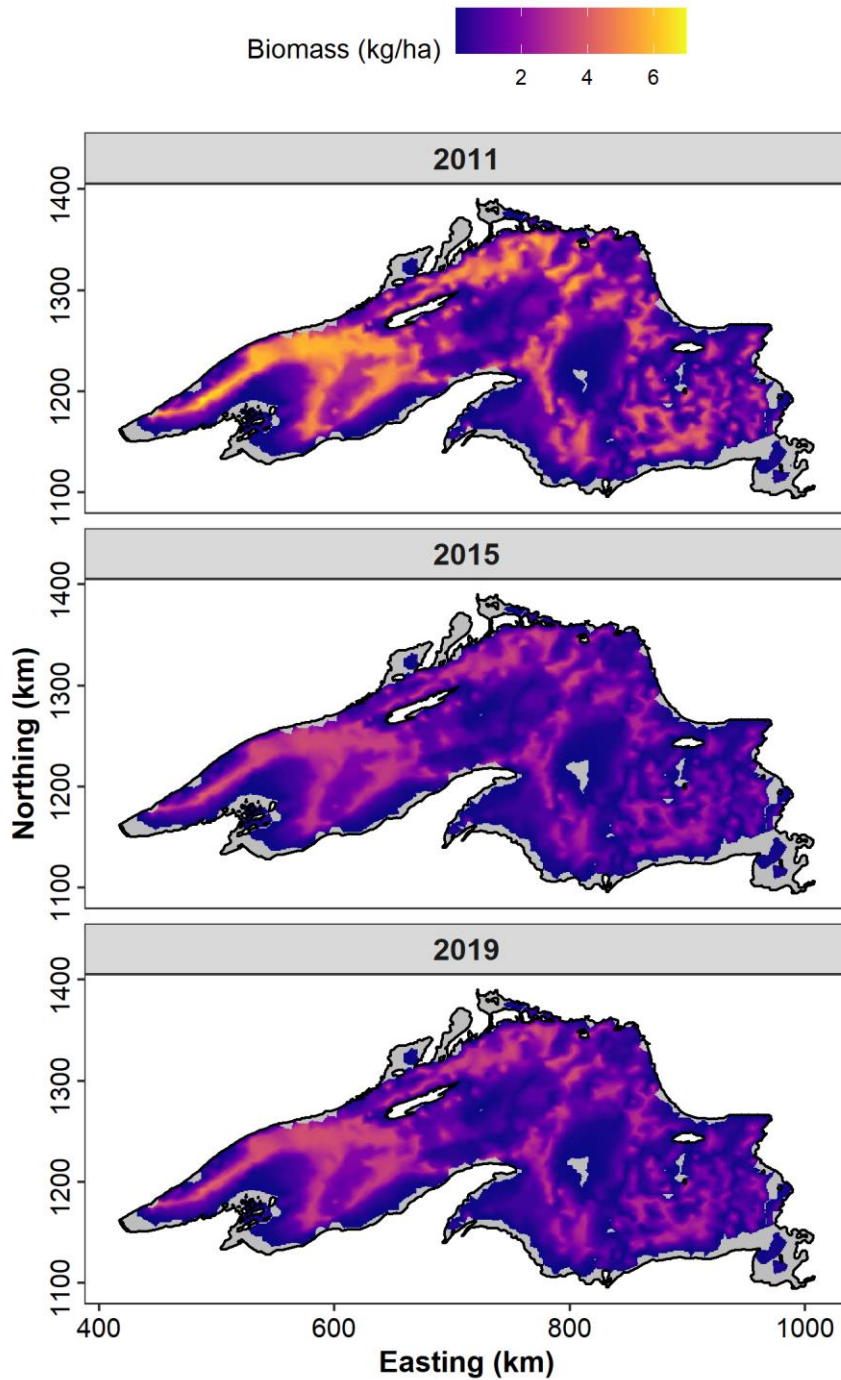


Figure 10: Projected Kiyi population size in space estimated from the INLA model.

No Canadian agency conducts monitoring of the deep-water fish community in Lake Superior. As a result, the understanding of SAR status in Lake Superior is entirely dependent on USGS survey data. Due to the Covid-19 pandemic, USGS was not permitted to survey Canadian waters in 2020 or 2021, as such, there are no data to inform Kiyi status over that time period. Establishing a Canadian monitoring program would provide knowledge of SAR species status as well as and other important members of the Lake Superior fish community.

Kiyi undertake diel vertical migrations, inhabiting demersal habitat during the day and moving to pelagic areas to feed at night (Hrabik et al. 2006). The estimate of Kiyi population trend and size were based entirely on bottom trawl sampling during daylight hours. It is likely that a portion of the population may inhabit areas away from the lake bottom which would have been missed in the surveys and not accounted for in population estimates. There was no important effect of time of day on bottom trawl catch probability or CPUE or an interaction of time of day with depth. Therefore no movement of Kiyi away from the lake bottom during the day was reflected in catch. Catchability of Kiyi with bottom trawl sampling has not been estimated. No attempt was made to account for relative catchability in model fitting. Due to the likely catchability of < 1 and potential for pelagic Kiyi whole lake biomass estimates are likely to be biased low.

Depth occupied by Kiyi in Lake Superior was identified to be between 100 and 300 m (where occurrence was > 50%). CPUE (kg/ha) was greatest at ~180 m depth with high (> 2 kg/ha) CPUE at depths between 145 m and 200 m. These results indicate a slightly deeper depth preference but are largely in agreement with previous reports (Gamble et al. 2011; Pratt 2012). An estimate of likely habitat was made from the INLA model by identifying habitat where there was a > 50% chance of capturing Kiyi. On average, 55,825 km² (CI: 40,096–65,428 km²) of habitat was available to Kiyi with 19,836 km² (CI: 13,716–22,554 km²) on the Canadian side of the lake.

In conclusion, USGS bottom trawl survey data (2011–2019) were used to model population trends and estimate population size for Kiyi in Lake Superior. The model demonstrated that Kiyi occurrence in the survey catch did not differ between the examined time periods (2011–2014 to 2015–2019) but there was a decline in biomass density in survey catches; although, as the offshore survey has only been conducted for a relatively short period of time the implications of this change cannot be discerned. The Kiyi population in Lake Superior remains large (> 8,000 t) with > 2,500 t in Canadian waters.

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APPENDIX

6 MESHES

Meshes used to estimate the INLA model

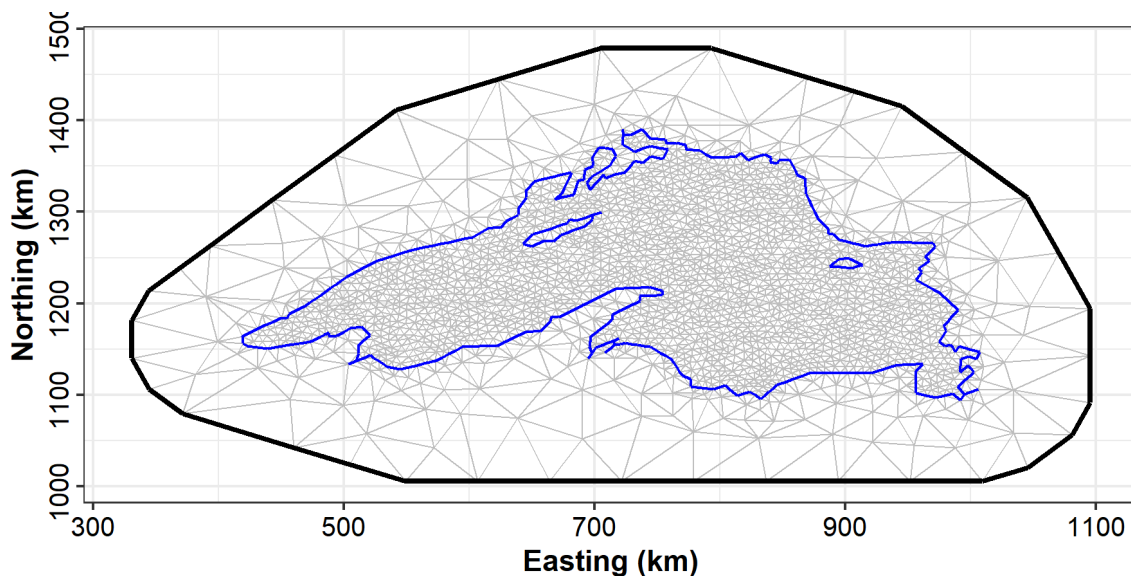


Figure A.1: Mesh of Lake Superior used to fit the INLA model.

7 SPATIAL FIELDS

Spatial random effects estimated by the INLA model.

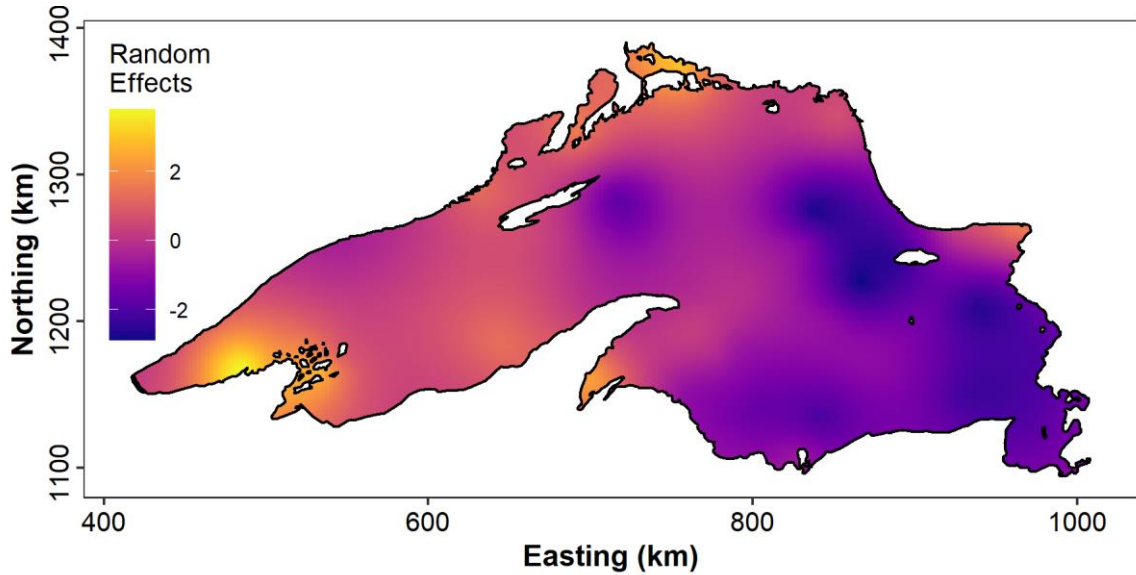


Figure B.1: Spatial field estimated for the presence-absence model from USGS bottom trawl survey data. Random effects values are on the logit scale.

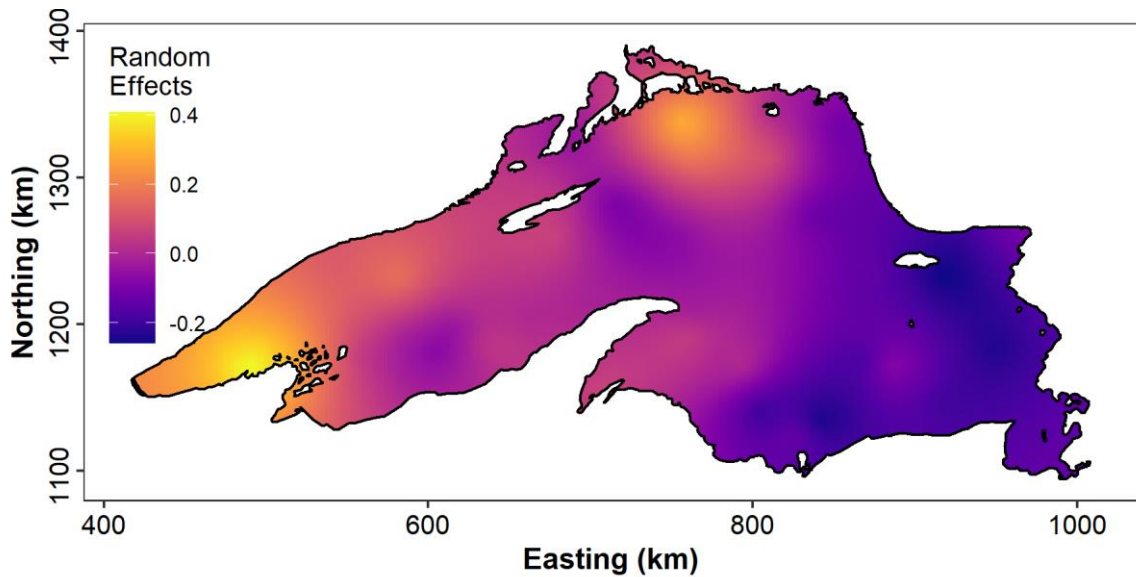


Figure B.2: Spatial field estimated for the positive catch (kg/ha) model from the USGS basin bottom trawl survey data. Random effects values are on the log scale.