Update to: Lake Superior Pygmy Whitefish (*Prosopium coulterii*) population trends, habitat characteristics, and abundance

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UPDATE TO: LAKE SUPERIOR PYGMY WHITEFISH (*PROSOPIUM COULTERII*) POPULATION TRENDS, HABITAT CHARACTERISTICS, AND ABUNDANCE

by

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ABSTRACT

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Populations of Pygmy Whitefish (*Prosopium coulterii*) in Lake Superior were assessed as Threatened by the Committee on the Status of Endangered Wildlife in Canada. van der Lee and Koops (2020, CSAS Res Doc 2020/074) preformed an analysis of the United States Geological Survey's bottom trawl research survey data (1989–2018) to estimate the temporal trend in catch-per-unit-effort (CPUE; kg/ha) and estimate lake-wide population size. An update to the analysis is provided to include data from 2019 and provide a direct estimate of the extent of the decline in CPUE over three generations. There was a slight increase in CPUE between 2018 and 2019, potentially reflecting the historic trends of periodic fluctuations through time; however, additional observations from future years are needed to confirm continued periodicity. There was a significant decrease in CPUE from the period of 2003–2006 to 2016–2019 (approximately three generations). The average estimate of the decrease was approximately 40%. There was a > 75% probability that the decreased exceeded 30% and ~ 25% probability that the decreased exceeded 50%. The median estimate of the whole-lake population size, however, was 98 t with approximately 80% of the populations occupying the Canadian side of Lake Superior.

RÉSUMÉ

van der Lee, A.S., Drake, D.A.R. and Koops, M.A. 2024. Update to: Lake Superior Pygmy Whitefish (*Prosopium coulterii*) population trends, habitat characteristics, and abundance. Can. Tech. Rep. Fish. Aquat. Sci. 3607: v + 15 p.

Les populations de corégone pygmée (*Prosopium coulterii*) du lac Supérieur ont été évaluées par le Comité sur la situation des espèces en péril au Canada (COSEPAC) comme étant menacées.
En 2020, van der Lee et Koops (doc. de rech. du SCAS 2020/074) ont effectué une analyse des données des relevés au chalut de fond du United States Geological Survey (1989-2018) pour estimer la tendance temporelle des captures par unité d'effort (CPUE; kg/ha) et pour estimer la taille de la population à l'échelle du lac. On a effectué une mise à jour de l'analyse afin d'inclure les données de 2019 et de fournir une estimation directe de l'ampleur du déclin des CPUE sur trois générations. Une légère augmentation des CPUE a été observée entre 2018 et 2019, reflétant potentiellement les tendances historiques des fluctuations périodiques au fil du temps; cependant, des observations supplémentaires pour les années à venir sont nécessaires pour confirmer la continuité de la périodicité. Une baisse significative des CPUE a été observée entre 2003-2006 et 2016-2019 (environ trois générations). L'estimation moyenne de la diminution était d'environ 40 %. Il y avait > 75 % de probabilité que la diminution dépasse 30 % et ~ 25 % de probabilité que la diminution dépasse 50 %. L'estimation médiane de la taille de la population de l'ensemble du lac était cependant de 98 t, avec environ 80 % des populations occupant le côté canadien du lac Supérieur.

1 INTRODUCTION

Pygmy Whitefish (*Prosopium coulterii*, PWF) is a small whitefish with a highly discontinuous distribution throughout North America (COSEWIC 2016). The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) identified seven designatable units (DU) for the species. The Great Lakes - Upper St. Lawrence populations, consisting of populations in Lake Superior, were assessed as Threatened on the basis of a 48% decline in catch rate estimated from the United States Geological Survey (USGS) nearshore bottom trawl research survey between 2000 and 2016.

USGS conducts annual bottom trawl surveys in Lake Superior to assess the status and trends of the prey fish community (Figure 1). Two surveys are conducted annually, the nearshore and offshore surveys. The nearshore survey samples shallower (< 100 m) locations around the perimeter of the lake and has been sampling locations on the Canadian side of the lake since 1989. The offshore survey began in 2011 to sample deeper locations (up to 315 m).

van der Lee and Koops (2020) conducted an analysis of the USGS bottom trawl data, using advanced statistical techniques, to identify temporal and spatial trends in catch-per-unit-effort (CPUE) and occurrence and estimate whole-lake population size based on data up to 2018. The analysis revealed that rather than a continuous decline in CPUE, the population has experienced periodic fluctuations; however, the 2018 CPUE estimate was the lowest of the 30 year time series. The whole-lake population estimate for 2018 was ~ 68 t. The analysis is updated here to include data from the 2019 survey and make direct comparisons in CPUE between years to estimate the extent and significance of any potential declines.

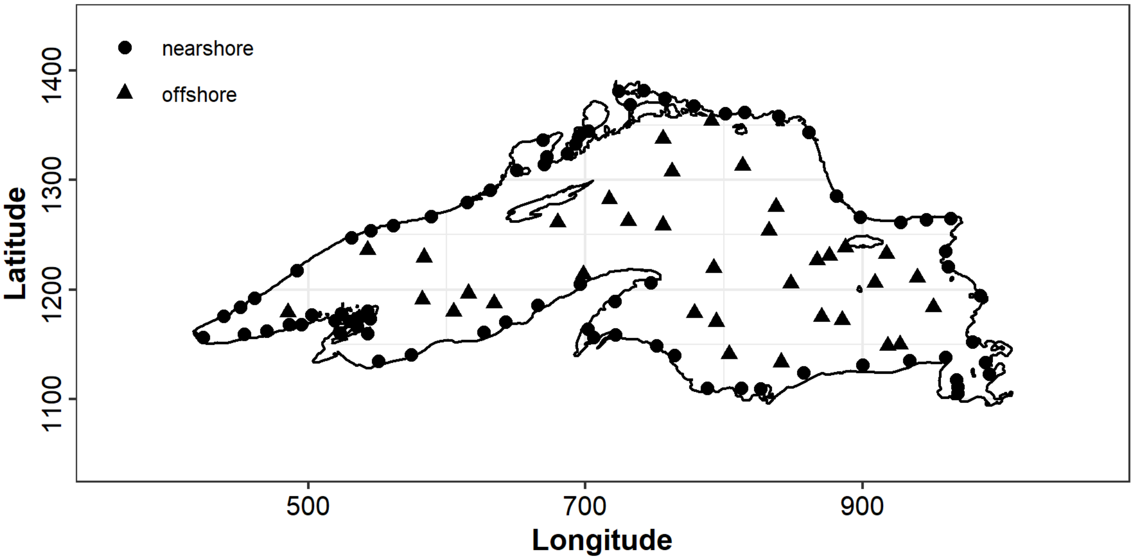

Figure 1: USGS bottom trawl survey sampling locations in 2019. Circles represent nearshore sampling locations and triangles represent offshore sampling locations.

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 occurrence, 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, 77 sites sampled annually (range: 52–87 since 1989). In total, 2391 nearshore sites were sampled between 1989 and 2019 with 975 capturing PWF. Nearshore trawls were conducted across depth contours. Depth was recorded at the start and end of each trawl. For use in analysis, depth was represented with the average of the recorded start and end depths for nearshore trawls. The mean start depth for nearshore trawls was 18.5 m (range: 8.9–62) and the mean end depth was 63.8 m (range: 11.6–144.0). The mean of average trawl depth, used in model fitting, was 41.1 m (range: 15.2–91.8). 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, 34 sites sampled annually (range: 30–36). In total, 308 offshore sites were sampled between 2011 and 2019 with 40 capturing PWF. Offshore trawls were conducted along depth contours. Mean sampling depth for offshore sites was 185.2 m (range: 87.0 – 315.0). At each sampling location, fish collections were sorted by species, counted and weighed. Density (count/ha) and biomass density (kg/ha) were estimated by dividing sample counts and weights by the area fished (ha) during the trawl.

2.2 *Analysis*

The analysis followed van der Lee and Koops (2020) with two models created. The first model included only the nearshore survey data to identify the long-term trends in occurrence of PWF in trawl catches and biomass CPUE (kg/ha) and will hereafter be referred to as the long-term trend model. The second model included the nearshore and offshore data from 2011 to 2019 to estimate whole lake population size and will hereafter be referred to as the population model. To analyse the data a hierarchical Bayesian approach, Integrated Nested Laplace Approximation (INLA, Rue et al. 2009), was employed. INLA uses 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 datasets contained a large proportion of trawls where no PWF were caught. As a result, the data were analysed using hurdle models. A hurdle model is 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 PWF CPUE. Because CPUE is a continuous and positive response variable the gamma distribution was used to model positive catches. The hurdle model, zero-altered gamma (ZAG) model, was represented by:

$$\begin{aligned} y_{i,t} &\sim \mathrm{ZAG}\left(\mu_{i,t}, \pi_{i,t}\right) \\ E\left(y_{i,t}\right) &= \pi_{i,t} \cdot \mu_{i,t} \\ var\left(y_{i,t}\right) &= \frac{\pi_{i,t} \cdot r + \pi_{i,t} - \pi_{i,t}^{2} \cdot r}{r} \cdot \mu_{i,t}^{2} \quad , \\ \mathrm{logit}\left(\pi_{i,t}\right) &= Z_{i,t} + u_{t}^{01} + s_{i}^{01} \\ \log\left(\mu_{i,t}\right) &= X_{i,t} + u_{t}^{>0} + s_{i}^{>0} \end{aligned} \qquad (1)$$

where, π_i represents the likelihood of occurrence, μ_i represent mean CPUE and r is the shape parameter of the gamma distribution. $Z_{i,t}$ and $X_{i,t}$ represent the fixed effects. For the long-term trend model the only fixed effect included was the intercept. For the population model depth as a second order polynomial was also included as a fixed effect as it has previously been identified as an important covariate (van der Lee and Koops 2020). All fixed effects variables were centred and scaled.

The effect of year, u_t, was assumed 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:

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

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 spatial 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 there are unmeasured characteristics of a particular location that would cause the presence and/or abundance 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 models included multiple spatial fields estimated at pre-defined knots (approximately every 5 years) in the time series. Including multiple spatial fields allows for some variation in the spatial distribution of PWF though time. The fields were assumed to be correlated with an auto-regressive order 1 (AR1) structure, with estimated correlation parameter ρ. The spatial field for each sampled year is calculated as the weighted average of the spatial fields at surrounding knots.

Contrasts were used to identify the significance of changes in the occurrence and CPUE of PWF through time estimated from the long-term model. 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 was the change in occurrence and CPUE through time. COSEWIC has identified thresholds for levels of decline as criteria for status assessment of wildlife species (COSEWIC 2015). Criteria A1 identifies a wildlife species as Threatened if it has experienced a decline of > 50% over 10 years or three generations (whichever is longer) if the reductions have ceased and are reversible. Criteria A2 identifies a wildlife species as Threatened if it has experienced a decline of > 30% over 10 years or three generations (whichever is longer) if the reductions are ongoing and may not be reversible. Generation time for PWF in Lake Superior was estimated as 4.3 years (van der Lee and Koops 2021). Therefore, of interest was the change over an approximately 13 year period. With contrasts, comparisons can be made between time periods (multiple year averages) as well as individual years. Time periods will typically be more representative of population state than individual years as they are less influenced by inter-annual variation in environmental conditions or catchability. As well, annual peaks and troughs in CPUE may over-emphasize differences across time. A focus on longer time periods in comparisons will diminish this effect and provide greater evidence of a sustained change in the system. Here, time periods of 4 years (approximately 1 generation) were compared. Therefore the average occurrence and CPUE between the final four years of the time series, 2016–2019, were compared to a four year period that occurred 13 years previously, 2003–2006. 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 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 of capture or CPUE between the two periods, and a value significantly > 1 indicates an increase in odds of capture or CPUE between the periods. The likelihood of 30% and 50% declines are computed to compare against COSEWIC criterion A1 and A2.

3 RESULTS

Total annual catch of PWF has fluctuated through time (Figure 2). Greatest total catch was in 1994. Catch has been below the 1989-2019 average in recent years (2014–2019); however, catch increased between 2018 and 2019.

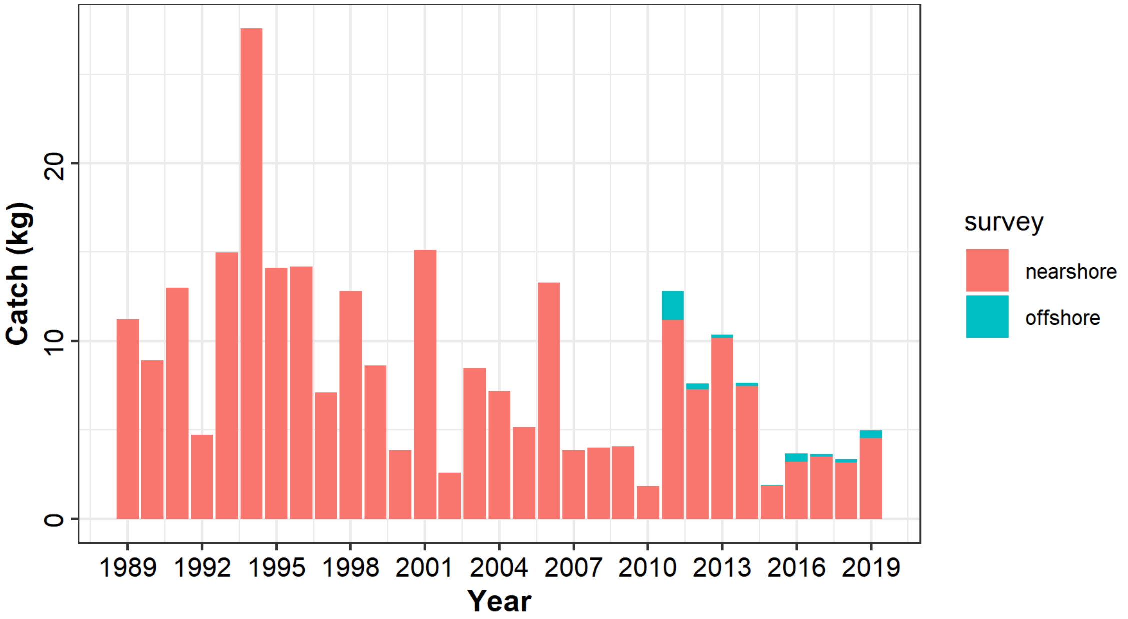

Figure 2: Total annual catch of Pygmy Whitefish (kg) from USGS bottom trawl research surveys. Colour indicates survey, nearshore or offshore.

Table 1: Long-term trend model results. The INLA hurdle model applied to the nearshore USGS bottom trawl research survey data. Coefficients, fixed effects and hyper-parameters, are summarized for the presence-absence and positive catch model components. r is the shape parameter of the gamma distribution. σ_t is the variance associated with the temporal trend. $Range$, σ_s, ρ are the hyper-parameters associated with the spatial field, correlation distance, variance and correlation among spatial fields. NA indicates not applicable as as the shape term does not apply to the binomial distribution. LCI and UCI represent the lower and upper credible intervals repectively.

	Presence-absence			**CPUE**		
Parameter	Median	LCI	UCI	Median	LCI	UCI
$Intercept$	-0.91	-1.98	0.07	-3.75	-4.32	-3.21
r	NA	NA	NA	1.06	0.97	1.16
σ_t	0.11	0.03	0.31	0.19	0.11	0.34
$Range$	93.01	64.72	133.21	55.07	40.78	76.39
σ_s	2.92	2.29	3.70	1.68	1.41	2.01
ρ	0.97	0.93	0.99	0.91	0.85	0.95

A hurdle model fit to the USGS nearshore bottom trawl survey data was used to identify the long-term temporal trends in PWF occurrence and CPUE (Table 1). The model incorporated multiple spatial fields for the presence-absence (Figure B.1) and CPUE (Figure B.2) model components, which allows for temporal variation in the spatial distribution; however, the correlation between fields was high (>90%, Table 1) indicating little change in the spatial distributions. There was no evident trend in model residuals and the hurdle approach produced an adequate proportion of 0s indicating potentially adequate model fit.

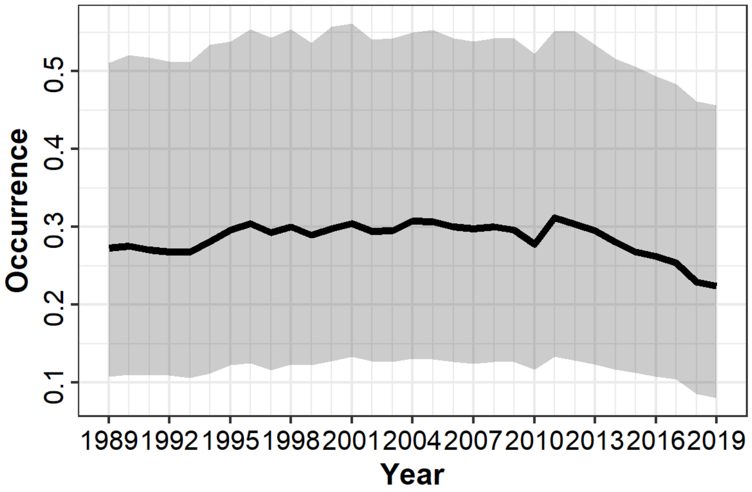

Figure 3: Long-term temporal trend in occurrence of PWF (proportion of trawls with PWF catch) in the nearshore USGS bottom trawl research survey estimated from the INLA model.

Occurrence of PWF in nearshore bottom trawl catches has remained relatively stable since 1989 (Figure 3). Contrasts were used to compare the proportional change in the odds of capture between 2003–2006 and 2016–2019 (Figure 4). The time periods are approximately one generation in length and reflect the change over approximately three generations. The contrast indicate a non-significant (upper CI > 1) decrease in occurrence between the two time periods.

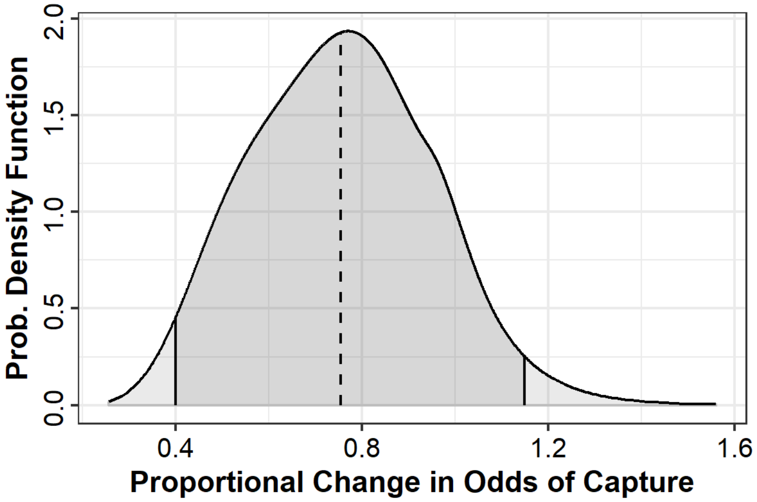

Figure 4: Posterior marginal distribution of the contrast examining the odds of capturing PWF in 2016–2019 as a proportion of the odds of capturing PWF in 2003–2006 in the USGS Lake Superior nearshore bottom trawl survey. The years selected are approximately three generations apart and represent approximately one generation of time. Values < 1 indicate a decline from the 2003–2006 period to the 2016-2019 period, while values > 1 indicate an increase from the 2003–2006 period to the 2016–2019 period. The dashed line indicates the median.

The temporal trend in average CPUE (kg/ha; Figure 5) indicates periodic fluctuations. In recent years, since 2014, CPUE has been below the long-term average with a slight increase between 2018 and 2019. A contrast comparing the proportional change in CPUE between 2003–2006 and 2016–2019 indicates that there has been a significant decrease (Figure 6). The median value of the contrast was 0.585 (mean: 0.645). The value indicates the mean CPUE for 2016-2019 as a proportion of the CPUE in 2003–2006. As well, the upper CI was < 1 indicating an important difference between the two time periods. This indicates that there was an approximately 40% decrease in CPUE between the two periods. Figure 7 provides a representation of the probability that the recent decline in CPUE exceeded COSEWIC's listing criterion A. There was a 77.2% likelihood that CPUE decreased by at least 30% and a 26.1% likelihood that CPUE decreased by at least 50% (Figure 7). The 2019 data may be an indication that CPUE is increasing and following the periodic fluctuations observed historically; however, more years of data are needed to infer a trend.

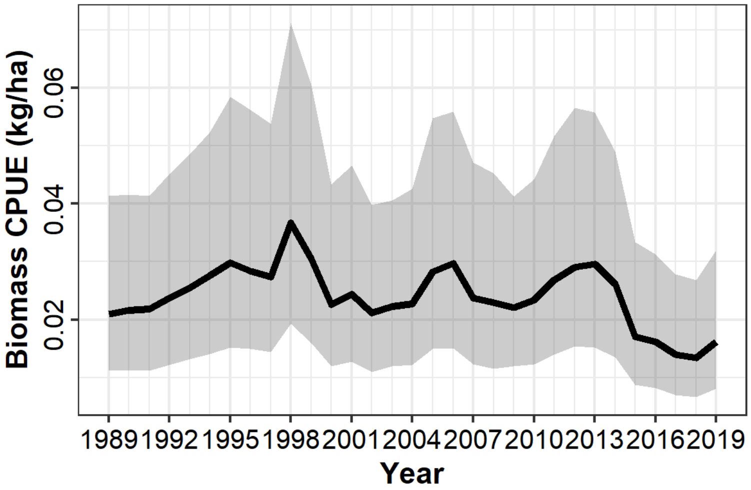

Figure 5: Long-term temporal trends in PWF biomass CPUE (kg/ha) in the nearshore USGS bottom trawl research survey estimated from the INLA model.

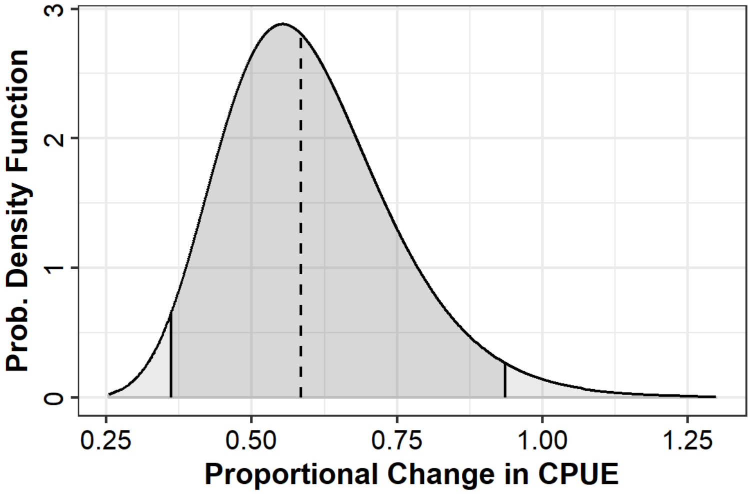

Figure 6: Posterior marginal distribution of the contrast examining PWF CPUE in 2016–2019 as a proportion of PWF CPUE in 2003–2006 in the USGS Lake Superior nearshore bottom trawl survey. The years selected are approximately three generations apart and represent approximately one generation of time. Values < 1 indicate a decline from the 2003–2006 period to the 2016–2019 period, while values > 1 indicate an increase from the 2003–2006 period to the 2016–2019 period. The dashed line indicates the median.

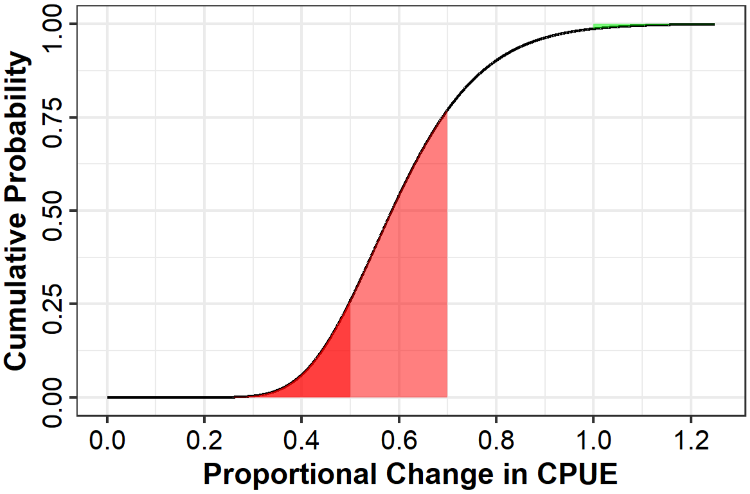

Figure 7: Cumulative probability function of the proportional change in CPUE (kg/ha) in the nearshore bottom trawl survey between years 2003–2006 and 2016-2019. The x-axis is the estimated proportional change in CPUE between the two time periods with values < 1 indicating a decline. The y-axis is the likelihood that a change of that magnitude has occurred. The dark red area represent the probability of at least a 50% decline (26.1%), the light red area represents the probability of at least a 30% decline (77.2%) and the green area represents the probability of increase between the two time periods (1.3%).

A hurdle model fit to USGS nearshore and offshore bottom trawl survey data since 2011 was used to estimate lake-wide population size (Table 2). The model incorporated multiple spatial fields for the presence-absence (Figure 4) and CPUE (Figure 5) model components, which allows for temporal variation in the spatial distribution. In addition, depth as a second order polynomial was included as a fixed effect. There was no evident trend in model residuals and the hurdle approach produced an adequate proportion of 0s indicating potentially adequate model fit.

Table 2: Population model results. The INLA hurdle model applied to the nearshore and offshore USGS bottom trawl research survey data since 2011. Coefficients, fixed effects and hyper-parameters, are summarized for the presence-absence and positive catch model components. r is shape parameters of the gamma distribution. σ_t is the variance associated with the temporal trend. $Range$, σ_s, ρ are the hyper-parameters associated with the spatial field, correlation distance, variance and correlation among spatial fields. NA indicates not applicable as the shape term does not apply to the binomial distribution. LCI and UCI represent the lower and upper credible intervals respectively.

	Presence-absence			**CPUE**		
Parameter	Median	LCI	UCI	Median	LCI	UCI
$Intercept$	1.07	0.16	1.92	-2.94	-3.60	-2.30
$Depth$	-0.33	-1.07	0.36	-0.02	-0.69	0.66
$Depth^2$	-4.74	-6.19	-3.45	-2.89	-4.08	-1.63
r	NA	NA	NA	1.08	0.92	1.27
σ_t	0.24	0.11	0.50	0.28	0.14	0.52
$Range$	63.38	40.54	100.93	41.29	27.46	61.85
σ_s	1.65	1.24	2.18	1.48	1.22	1.80
ρ	0.97	0.82	1.00	0.74	0.40	0.91

Depth had an important effect on occurrence and CPUE in the survey (Table 2). Estimated occurrence was > 50% at depths between 48 m and 115 m and CPUE peaked at 86 m.

The population model was used to make projections of total PWF population size in Lake Superior (Figure 8). The credible intervals for population estimates were broad due to parameter uncertainty and extrapolating occurrence and CPUE outside of the sampled locations. The trend in population size followed the trend in CPUE closely. The greatest projected population size was in 2011 with a median of 224.1 t (CI: 26.1–2358.2 t) and the lowest population projection estimate was in 2018 with a median of 69.7 t (CI: 6.8–788.9 t). In 2019, the projected population size was 97.6 t (CI: 9.6–1076.1 t).

The projected spatial distribution of PWF for years 2011, 2015 and 2019 is represented in (Figure 9). The projection is based on lake bathymetry and the estimated spatial field. Greatest densities occurred in the northeast portion of the lake around Michipicoten Island. The Canadian side of the lake contained on average 79.4% of the PWF population and 51.9% of the likely occupied (> 50% probability of occurrence) habitat. In 2019, the population estimate on the Canadian side of the lake was 76.7 t (CI: 8–767 t) with 4762 km^2 (CI: 471–10552 km^2) of likely occupied habitat.

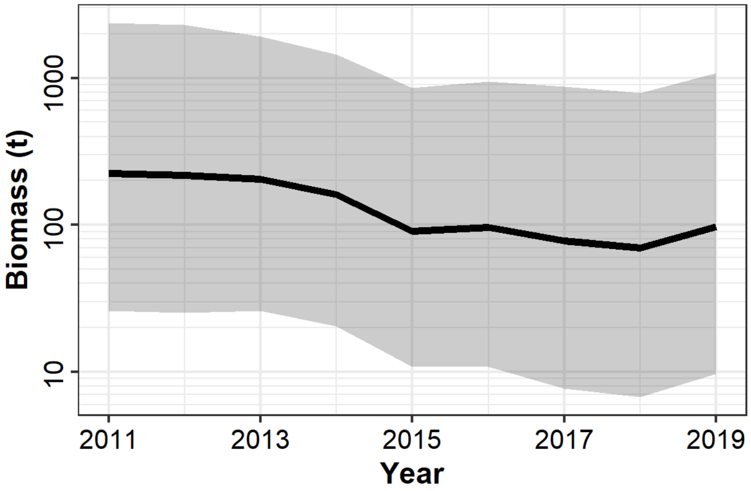

Figure 8: PWF population size (log_{10} transformed) through time estimated from the INLA model. The solid line represents median estimates and the grey area represents the credible interval.

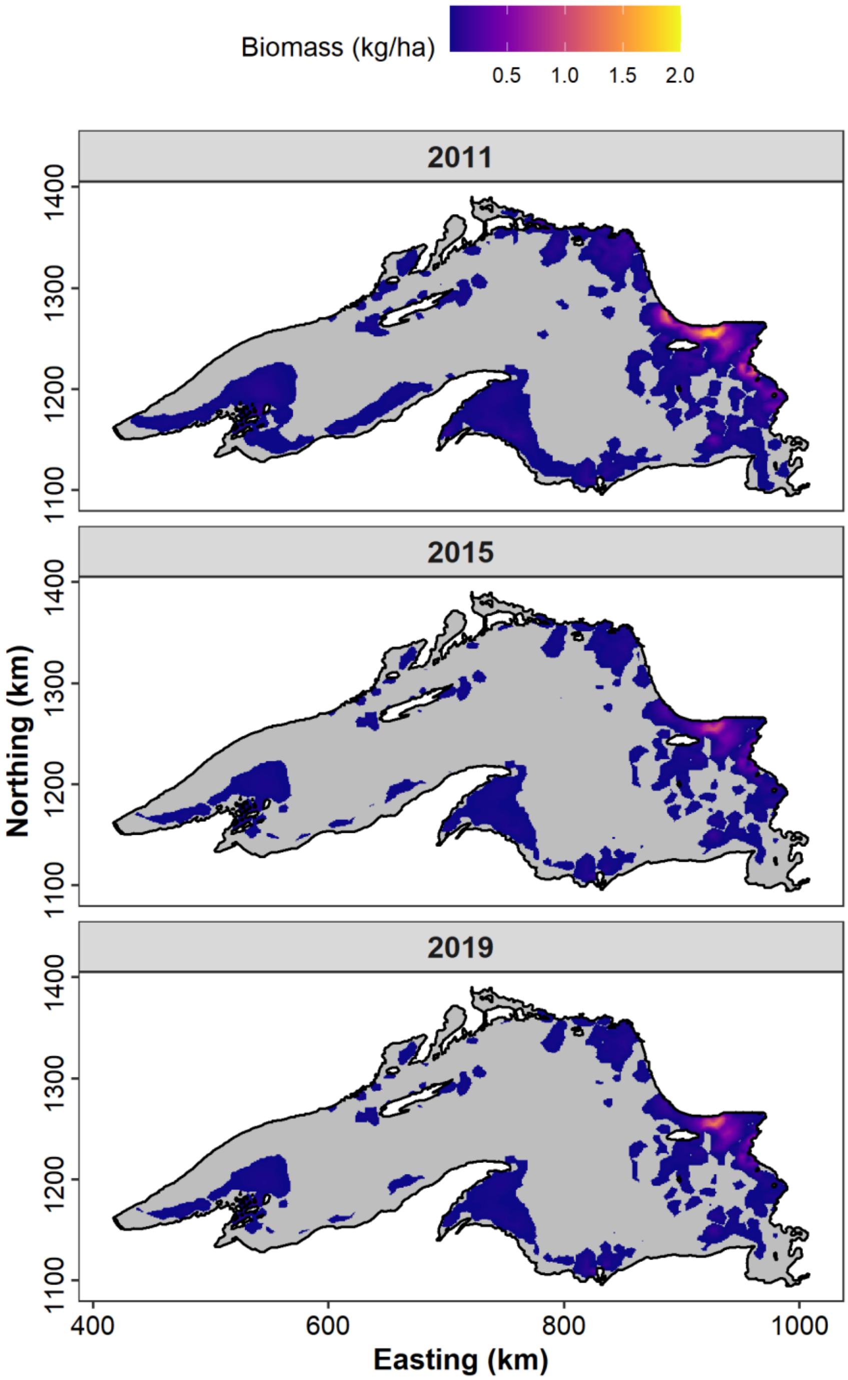

Figure 9: Projected PWF population size in space estimated from population model.

4 DISCUSSION

An update is provided to van der Lee and Koops (2020) to include survey data from 2019 and contrasts were added to assess the level of decline experienced by PWF in Lake Superior over the previous 3 generations. The results of the analysis still indicate that PWF occurrence in the catch has remained relatively constant throughout the time series (Figure 3) and that CPUE has fluctuated periodically (Figure 5). In recent years, 2014–2019, CPUE was at the lowest point in the 31 year time series.

A comparison of CPUE between 2016–2019 and 2003–2006 was made to determine the level of decline over approximately three generations with generation time taken to be 4.3 years (van der Lee and Koops 2021). The decline in catch rate over three generations was significant with an average estimate of approximately 40%. The probability that the decline has been > 30% was > 75% and the probability that the decline has been > 50% was 26%. The increase in CPUE between 2018 and 2019 and the historic pattern suggest that the decline may not be ongoing; however, further observations are needed to confirm this trend. In addition, the cause of the decline to a 30 year low is not clear. It is not evident that PWF in Lake Superior is subject to any significant anthropocentric threats (Andrews et al. 2021). Other coregonines have experienced recruitment failures in recent years (Vinson et al. 2018) and it is possible PWF has as well. The population size, however, remains robust. Lake-wide projections provide a median estimate of population size of almost 100 t for 2019, although with a large amount of uncertainty. Approximately 80% of the population resides on the Canadian side of Lake Superior. Population modelling has indicated that the minimum viable population size (population large enough to have a < 1% chance of extinction over 100 years) was only 75 kg (van der Lee and Koops 2021) indicating that PWF in Lake Superior likely have a low risk of extirpation in the near-term.

5 REFERENCES

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APPENDIX

6 MESHES

Mesh used to estimate the INLA model

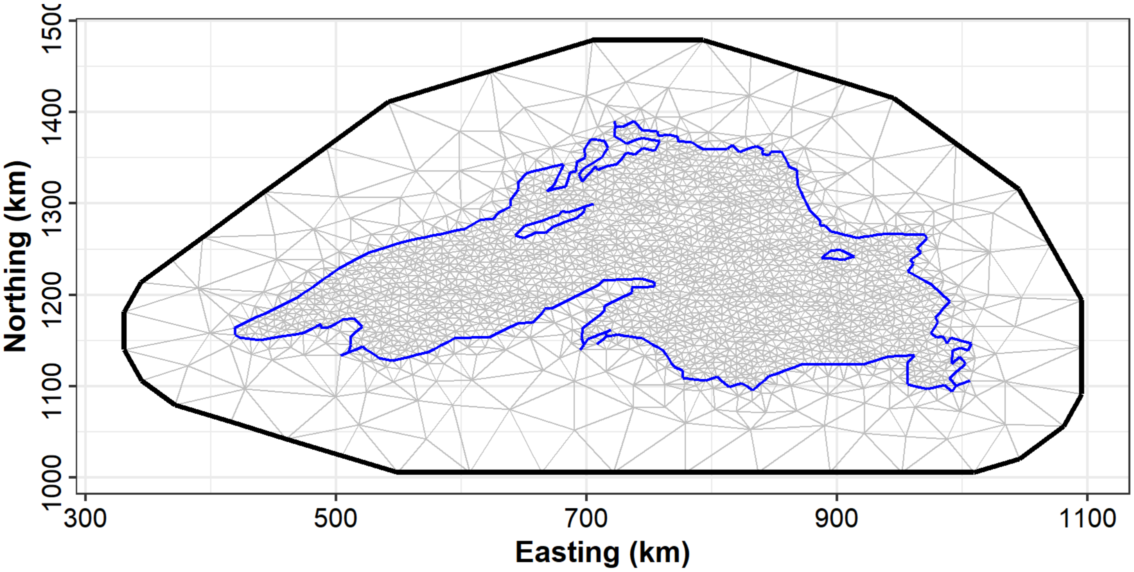

Figure A.1: Mesh of Lake Superior used to fit the INLA model.

7 SPATIAL FIELDS

Spatial random effects estimated by the INLA model.

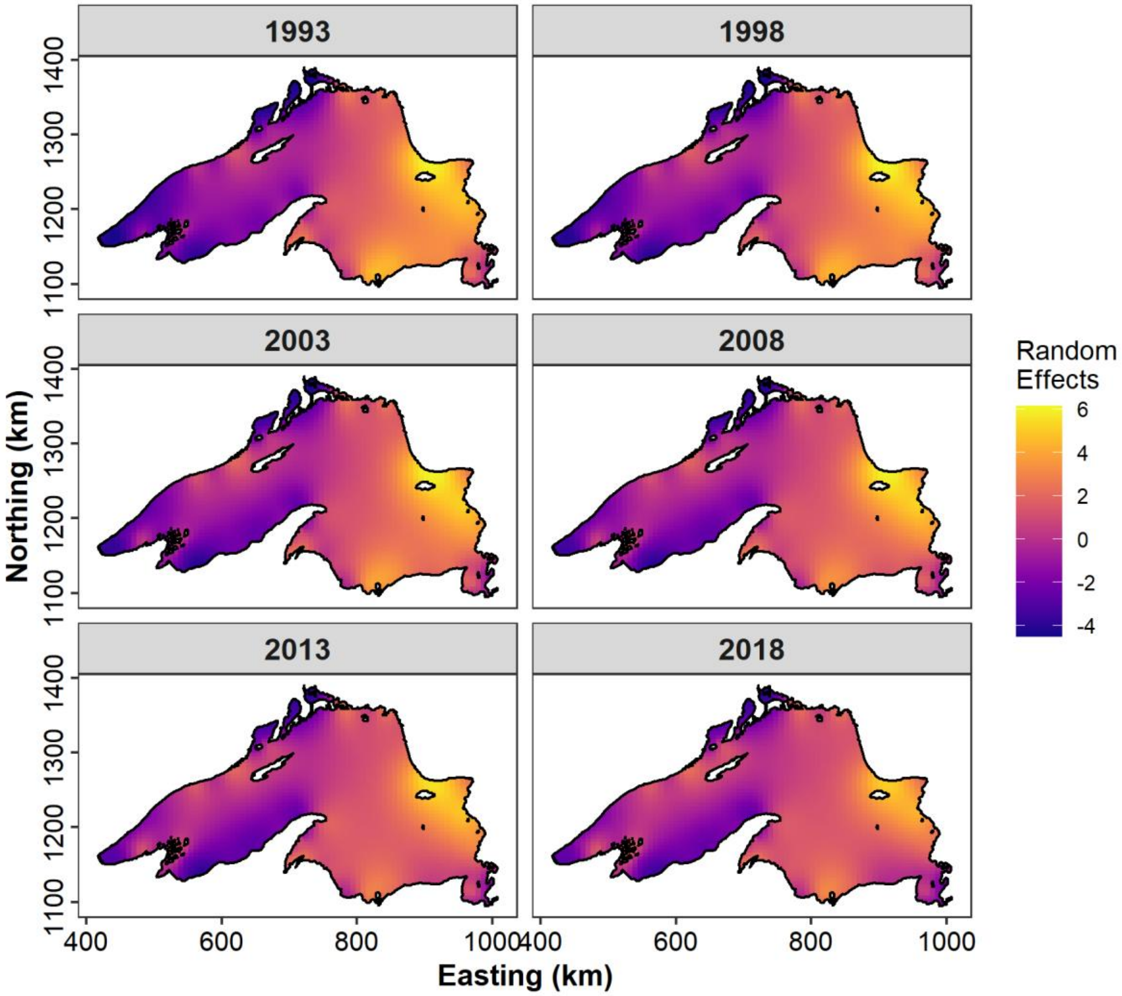

Figure B.1: Long-term model spatial field estimated for the presence-absence model from USGS bottom trawl survey data. Random effects values are on the logit scale.

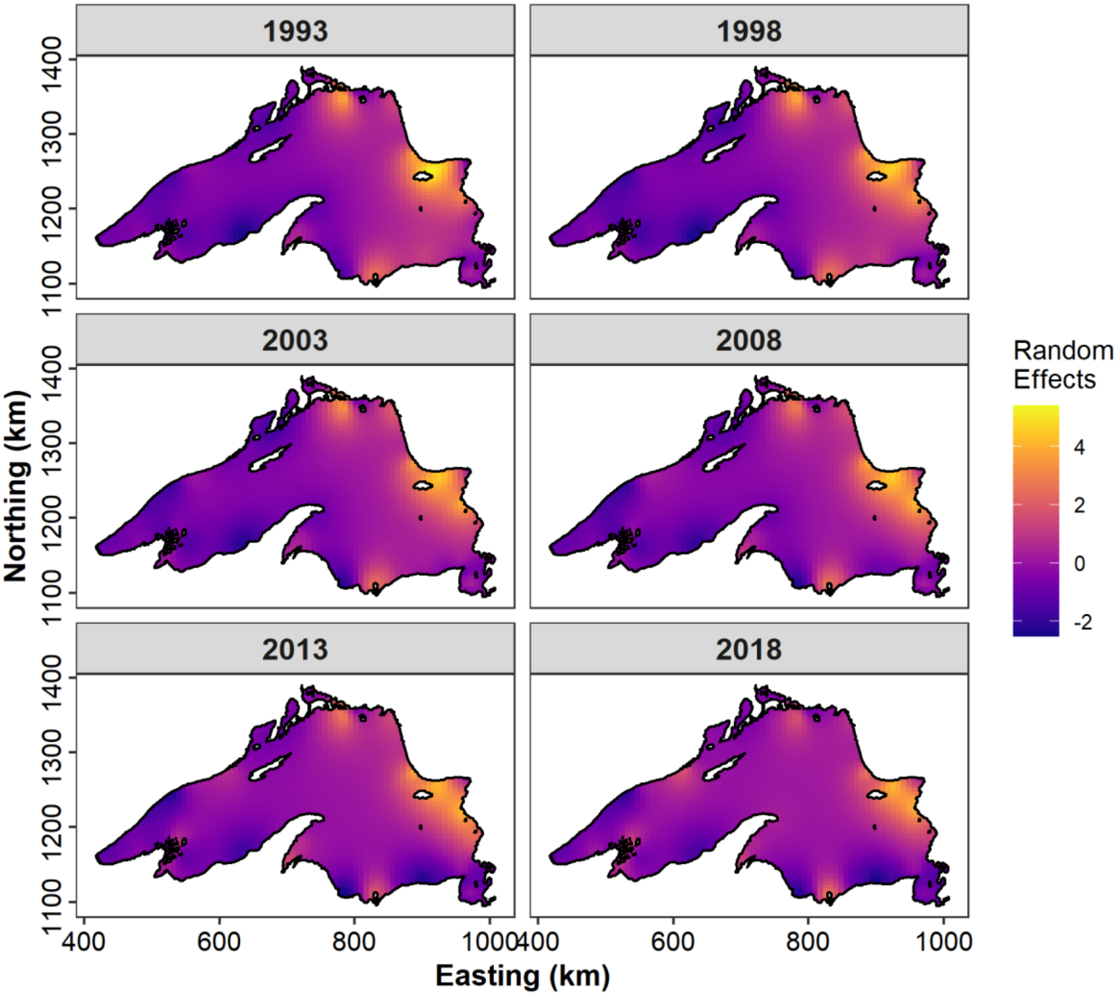

Figure B.2: Long-term model spatial field estimated for the CPUE (kg/ha) model from the USGS bottom trawl survey data. Random effects values are on the log scale.

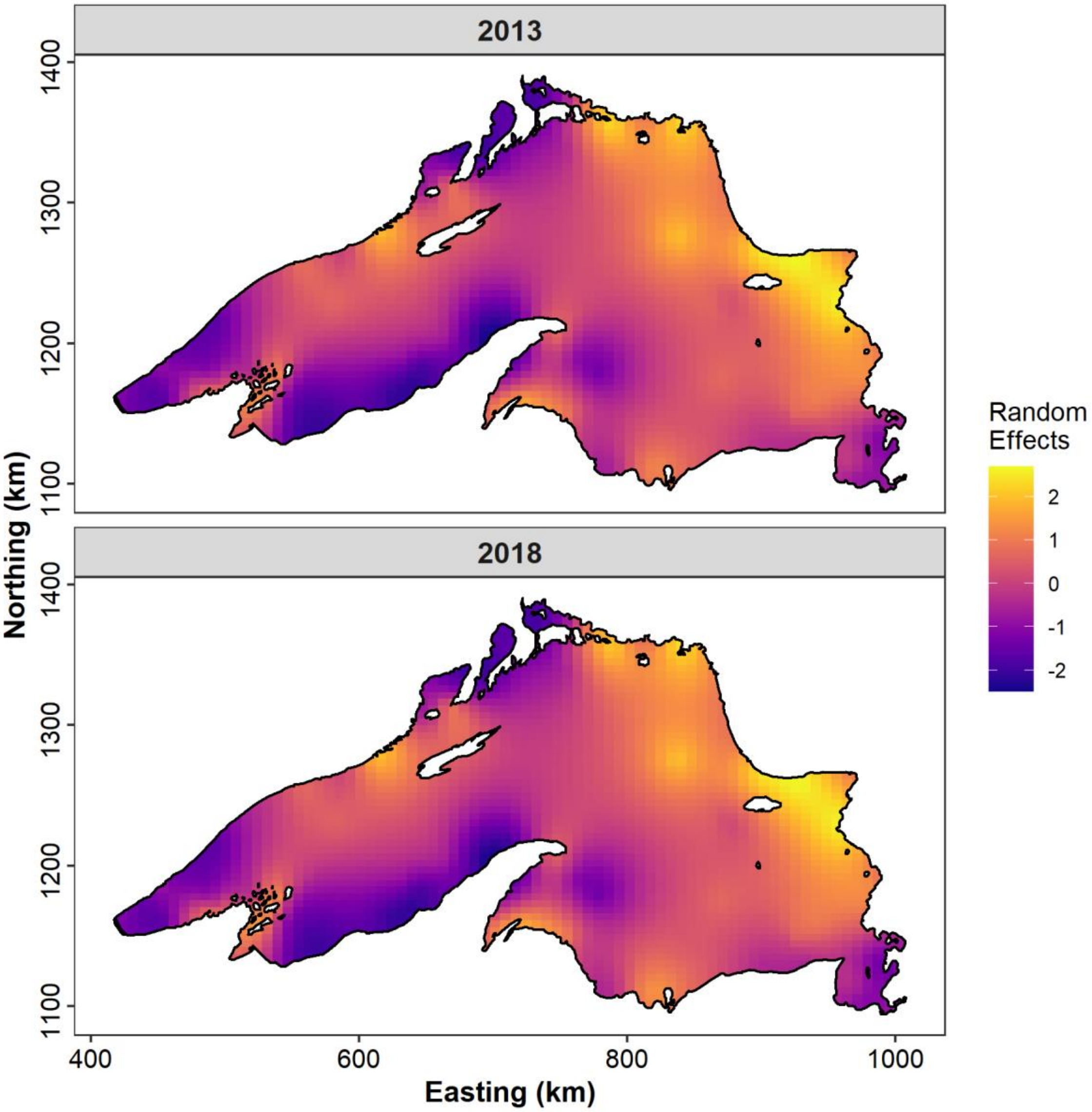

Figure B.3: Population model spatial field estimated for the presence-absence model from USGS bottom trawl survey data. Random effects values are on the logit scale.

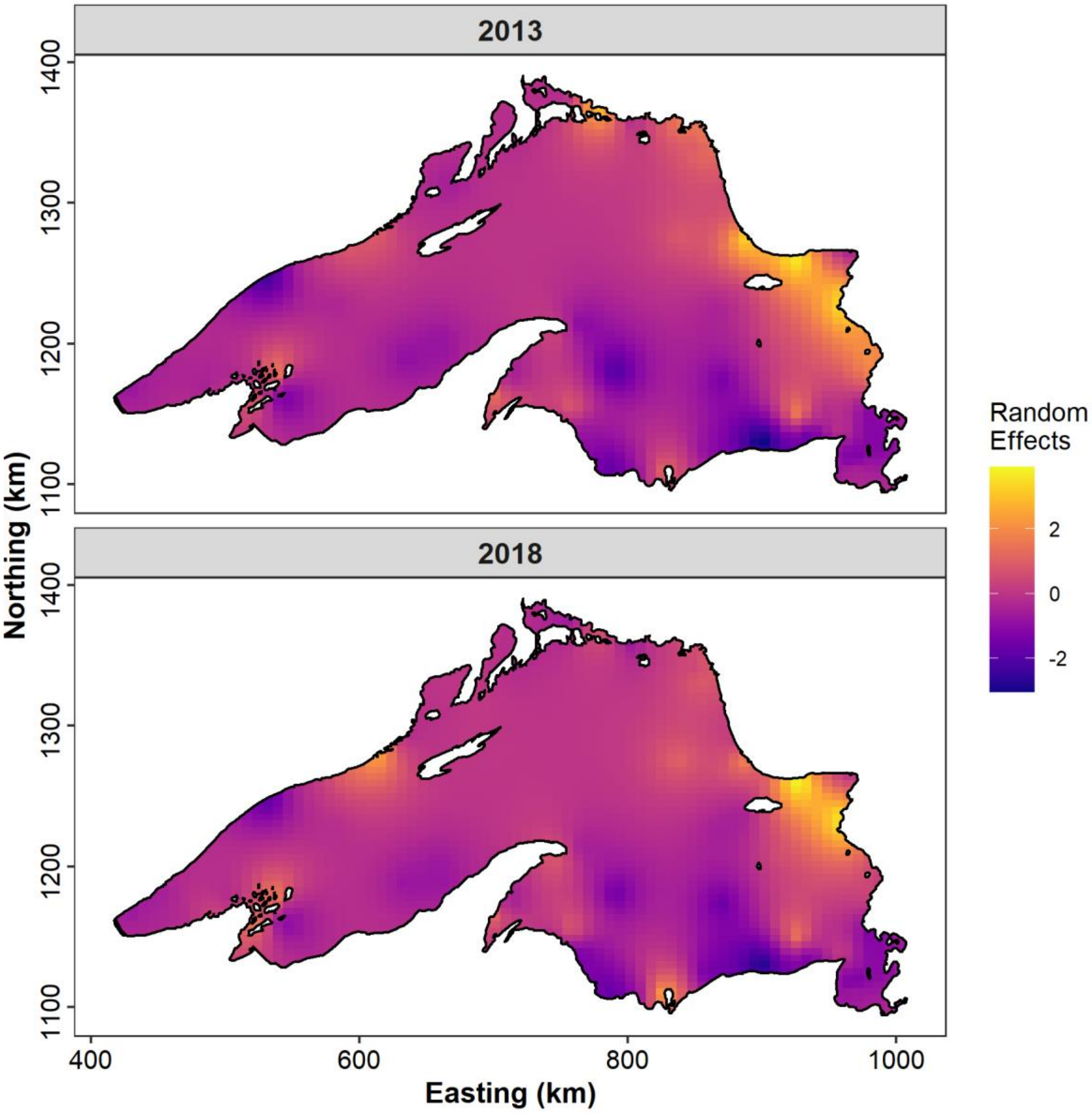

Figure B.4: Population model spatial field estimated for the CPUE (kg/ha) model from the USGS bottom trawl survey data. Random effects values are on the log scale.