Title: Atlantic Cod as an indicator of rapid climate change

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Abstract

Atlantic cod (*Gadus morhua*) in the northwest Atlantic has become the textbook example of overfishing. However, this narrative has blinded us from the larger environmental context of this decline. Cod prefer cold and shallow habitats, environments that are also the most susceptible to rapid climate change. Cod habitat deterioration was evident well before their numerical decline, and as such, cod was a harbinger of rapid climate change. Recovery requires their habitat quality to first improve and stabilize. Calls for a cull of seals, the consensus actor causing the lack of recovery of cod, may therefore be unwise. Recovery will only occur once the variability associated with rapid climate change subsides and habitat quality improves. The timeline for this is of course unknown.

One-Sentence Summary

Was the decline of cod a harbinger of rapid climate change in the northwest Atlantic?

Introduction

The collapse of Atlantic cod (*Gadus morhua*) in the North West Atlantic during the late-1980s has become the epitome of overfishing and its consequences (Hutchings, 2000; Jackson et al., 2001; Pauly et al., 1998). Due to the strength of this conviction, a more precautionary and conservation-based approach towards natural resource exploitation evolved, with various area-based closures to fishing, a fishing moratorium upon cod, and eventually marine protected areas and reserves (Choi et al., 2005; Zwanenburg et al., 2002). But the eagerly awaited return of cod did not manifest, even after three decades of effort. Almost right from the beginning, seals were noticed to be increasing in number and that they also can eat cod. Based upon this circumstantial evidence, they were considered the cause of the lack of return

(Fu et al., 2001; Mohn and Bowen, 1996). Of course, many other factors can influence cod mortality, including continued "subsistence" fishing and bycatch (Shelton et al., 2006); cannibalism, disease, and trophic interactions or cascades causing nonlinear predation release or density-dependent or "Allee"-type effects (Frank et al., 2005; Laird et al., 2018; Puvanendran et al., 2008; Swain and Benoît, 2015; Swain and Sinclair, 2000; Walters and Kitchell, 2001) effects. However, they represent variations on a theme: predation or consumer centric hypotheses. Seals just happen to be the predator of choice given the circumstances, leading to proposals for culls to help cod recover (DFO, 2011; Laird et al., 2018; Trzcinski et al., 2006).

But what if this predation-centric mechanism is but a subplot, within a much larger story? Here we suggest this larger story is about cod habitat and how it's environment has changed over the years. Indeed, in the years immediately following the collapse, anomalous temperature events were identified as a potential cause of the collapse (Drinkwater, 2005; Steele, 1998; Zwanenburg et al., 2002). This is because temperature preferenda are a profoundly important component of the habitat of all organisms. However, the variability in bottom temperatures were found to be enormous and an anomalous event of sufficient magnitude and sustained duration was not found to support the hypothesis ((Choi et al., 2005); see Figure 1). We suggest that rejecting this approach may have been premature. A more focused question needs to be asked, one that explicitly defines cod habitat and identifies its spatiotemporal evolution.

Fortunately, an explicit, probabilistic definition of habitat is readily computed as powerful analytical approaches have now become almost routine. Computational advances, most notably, the development of INLA (Rue et al., 2009) and the advent of spatiotemporal Conditionally Autoregressive (CAR) models that can borrow information from adjacent areas and times while operating in a Bayesian context (Besag et al., 1991; Brown and Zhou, 2021; Riebler et al., 2016) permit this definition. We use this approach to describe the spatiotemporal variations of cod habitat, focusing upon the Maritimes Region of Atlantic Canada (NAFO Div. 4VWX).

Materials and Methods

Specifically, we define "habitat" as a probability: When the probability of observing cod is greater than some threshold density, we can consider the space and time sampled to be "good habitat", and those where it is less than this threshold or zero-valued to be "poor

habitat". Heuristically, we define this threshold to be the 0.05% empirical quantile of the non-zero densities of cod for a given type of sampling gear.

The binary categorization of each sampling event at an areal unit s=(1, … , a) and time unit t=(1, … , b), Y_{st}, is modeled as a *Bernoulli* process with a *logit* link function and conditional upon covariates and autocorrelated random effects in space, time and spacetime:

$$
\begin{aligned}
&Y_{st} \sim \text{Binomial}\,(\eta_{st}, \theta_{st}) \\
&\ln(\theta_{st}/(1-\theta_{st})) = x_{st}^{T}\beta_k + U_s + V_t + W_{st} \\
&\beta_k \sim \text{MVN}\,(\mu_k, \Sigma_k) \\
&U_s \sim \text{iCAR}\,(\phi_U, \sigma_U^2) \\
&V_t \sim \text{AR1}\,(\rho_V) \\
&W_{st} \sim \text{AR1}(\rho_W) \otimes \text{iCAR}\,(\phi_W, \sigma_W^2).
\end{aligned}
$$

Here, η_{st} is the vector of the number of trials and θ_{st} the vector of probabilities of success in each trial in each space and time unit; the matrix of covariates parameters β_k with a multivariate normal prior with mean μ_k and diagonal variance matrix Σ_k; the spatial autocorrelation U_s follows the iCAR (also known as a convolution model or the Besag-York-Mollié or "BYM" model in the epidemiological literature, when data are Poisson distributed) with ϕ_U the proportion of the iCAR variance, σ_U^2, attributable to spatial processes relative to nonspatial processes; the temporal error components V_t are assumed to follow a lag-1 autocorrelation process (AR1) with parameter ρ_V; and finally, the spatiotemporal errors W_{st} are modeled as a Kronecker product (⊗) of temporal AR1 and spatial iCAR processes, where time is nested in space.

For these analyses, we drew upon two high-quality bottom trawl-based research surveys conducted in the Northwest Atlantic Ocean, in the Maritimes Region of Canada. The first is an annual multispecies survey conducted by the Department of Fisheries and Oceans (DFO) from 1970 to the present ("ground fish survey"). Sampling stations were randomly allocated in depth-related strata with sample tows of approximately 1.82 to 2.73 km in length on a variety of different gears, mostly the Western IIa net. Vessel speeds ranged from 4.5 to 6.5 km/hr. Only tow-distances were availability which was used to approximate areal density using a nominal wing spread of 12.5 m.

The second data series is a survey conducted through a joint collaboration between the snow crab industry in the region and DFO, from 1999 to the present ("snow crab survey"). The survey is funded by a proactive industry as a forward-looking investment towards long-term sustainable fishing, an exemplary model of the precautionary approach to fishing. A modified

Bigouden Nephrops net designed to dig into sediments was used with sample tows of approximately 0.3 km in length and a target vessel speed of 3.7 km/h. Actual bottom contact and net configuration were monitored to provide explicit areal density estimates. The wing spreads ranged from 12 to 14 m, depending upon the substrate encountered.

Amongst the *k* covariates examined in this study were: bottom temperatures, depth, gear type, season, and a global intercept term as the overall average habitat quality. The Western IIa was used as the reference gear.

As multiple surveys with different sampling designs were used, a hybrid, Voronoi triangulation and tessellation-based solution was used. The algorithm maintains an approximately constant station density within each areal unit, a target of 30 sampling events within each areal unit and a final total number of areal units of less than 2000 units. This was a trade-off between information density and computational stability. The tesselation-based approach had the advantage of more informative areal units capable of resolving temporal trends and environmental gradients. This was critical as environmental variability has been significant in the area/time.

Further, spatial and temporal autocorrelations exist due to other unmeasured or unobservable factors and need to be parameterized and incorporated into models; they represent important sources of variation that result in more reasonable estimates of habitat quality. The model form is known as an “inseparable” space-time model, where temporal processes (AR1) are nested within spatial processes (iCAR).

All analyses were conducted with R and R-INLA with all code available online (https://github.com/jae0/aegis.survey/blob/master/inst/scripts/10_cod_habitat.R). Note that we utilize the “bym2” parametrization of the iCAR for stability and interpretability of parameter estimates (Riebler et al., 2016). Penalized Complexity (PC) priors that shrink towards a null (uninformative base model) were used for all random effects (Simpson et al., 2017). For the AR1 process, we used the "cor0" PC prior which has a base model of 0 correlation, that is, no correlation. For the spatial process ("bym2") we use the PC prior (rho=0.5, alpha=0.5). For the covariates, depth and temperature, a second order random walk process (“rw2”) was used as a smoother using 13 quantiles as discretization points. Seasonality was discretized as deciles and a cyclic “rw2” process was used. Zero-inflated variants of the binomial model were attempted but they were found to be unstable solutions. As such only the binomial results are presented.

Results and Discussions

The posterior parameter estimates were biologically informative and meaningful (Table 1). Overall, there was a 65.4% probability of observing good cod habitat in the spatial domain, from 1970 to the 2021 (intercept term). In order of importance, the factors that most influenced habitat quality for cod were: persistent random spatial effects, spatiotemporal random effects, depth, sampling gear, interannual variability, temperature and seasonal cycles. The overall temporal (inter-annual) autocorrelation across time (ρ) was high (0.945) and marginally smaller when resolved to areal units (0.909). The relative importance of neighborhood effects (ϕ) was high (0.989) when time was not resolved (0.989) and when time was resolved (0.982).

By accounting for these factors, albeit in the above admittedly simplistic model, we can begin to disentangle the *realized* thermal preferences of cod from other factors (Figure 2). In our focal spatial domain, the highest probabilities (0.65) of observing cod are from 4 to 5 °C and diminishing to a probability of less than 0.5 when temperatures are colder than 2 °C and warmer than 7 °C. But cod habitat is not defined by temperature alone. Depth is a well-known proxy for pressure, light, turbulence, substrate complexity, and overall variability of any number of other environmental factors. We find that cod has a preference for shallower environments, with the probability of finding cod dropping off to less than 0.5 beyond a depth of 150 m (Figure 3).

Clearly, cod in the Maritimes region have a preference for shallow and cooler habitats. These habitats are also the ones more susceptible to rapid climate change. Indeed, in the spatial domain of our study, the habitat quality for cod has on average, declined since a peak in the early-1980s (Figure 4). The overall average probability of finding cod habitat fell below 0.5 by the mid-1990s and currently remains at less than 0.3. The timing of the decline in numerical abundance in the early 1990s coincides with the degradation of habitat. The spatial component of the degradation of cod habitat is shown for a few key time slices in Figure 5. It is a systemic degradation of cod habitat probabilities.

The pure spatial effect (Figure 6) identifies persistently high habitat probability locations, that is, core habitat. Degradation of these core areas occurred not only due to warming (above 8°C) but also cooling (below 2 °C) in other areas (Figure 2). That is, overall climatic variability jointly operating with depth to create suboptimal habitat. Where optimal temperatures did occur, they often occurred in areas of greater depth (> 150 m; Figure 3) which did not serve to improve cod habitat.

The overall marginal effect of time (Figure 7) was similar to those of the posterior predictions (Figure 4). The variability was, however, much larger. Slightly higher magnitude marginal effects were also found in the earlier period (pre-1980). The sub-annual time trends revolved around the 0.5 level with slightly higher levels towards the end of year, when cooler bottom temperatures prevail (Figure 8). Variability in detection probability of habitat was also evident (Figure 9) with almost a doubling in the probability of detecting cod habitat from the Western IIa (historically, the primary survey gear) to the US 4 seam 3 bridle survey trawl net (the current standard). The Nephrops net used in the snow crab survey was intermediate in ability to identify cod habitat.

In summary, from this habitat perspective, fishing and seal predation along with any other mortality factor, only exacerbated the decline of cod as the preconditions necessary and sufficient for their decline were already written: spatial and temporal variability of bottom temperatures. With such habitat decline, correlated markers of a population in distress followed: reduced population size, stunted growth, early maturation, disease/parasite prevalence, declines in physiological condition (Choi et al., 2005), and most importantly, declines in the capacity to be resilient and resistant to these perturbations (Choi and Patten, 2001). Most of these latter issues have been historically blamed squarely upon fishing. There is a need to recontextualize these processes in the context of habitat change and stress. It remains to be seen if similar processes are responsible for the collapse and lack of return of cod in other areas of the northwest Atlantic. However, the large scaled nature of these climatic processes suggests that they will likely play an important role elsewhere.

Conclusions

The outcome of the collapse was a greater awareness of the ecological frailty of even historically very dominant fisheries and the general adoption of more precautionary approaches to fishery exploitation. These are all well and good. However, the real issue seems actually to have been a much more significant large-scale process: rapid climate change causing spatiotemporal variability in habitat. The premature presumption that only predator-prey interactions control cod, whether it be human, seal or other, has prevented the wider lens of rapid climate change and its influence upon cod habitat (Drinkwater, 2005) from being perceived. Indeed, the demise of cod may be better contextualized as having been an early indicator of significant environmental change. As early as the 1990s cod were suffering from the reality of significant oceanic climate variability, which we were, unfortunately, unable to appreciate in time.

If this larger narrative is correct, reversion to a cod-dominated system is, of course, possible. However, first and foremost, habitat conditions must revert to much higher probability levels. This must also last for a minimum of five years, the time to reach maturity, in order for strong year classes to form. Some minor reversion in habitat quality did occur in 2010 (Figure 4), possibly associated with extended La Nina events. However, this did not last long enough to have a significant biological effect upon cod, as they were quickly followed by a succession of extended El Nino events. Of course, predation by humans, seals and any other mortality factor also need to cooperate. But conservation and marine spatial planning measures for cod must focus upon such shallower and intermediate temperature core habitat environments. Irrespective, it must be understood that the underlying causes of these habitat changes are occurring on large time and spatial scales, via processes over which we have limited direct control. Culling cod or any other perceived predator will likely have no influence upon recovery if there is no suitable home for them to occupy. For now, we must accept that a systemic, environmentally driven hysteresis has occurred (Choi et al., 2004).

Acknowledgments:

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Competing interests: Authors declare that they have no competing interests.

Data and materials availability: All data are held in databases in Fisheries and Oceans Canada. All analytical code are available at https:://github.com/jae0/aegis.surveys/.

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Tables

Table 1. Posterior parameter mean and 95% Credible Intervals from the habitat model. σ is the posterior estimate of the standard deviation estimated for each process. ρ is the posterior temporal autocorrelation parameter and ϕ is the posterior proportion of the spatial and space-time variability associated with neighbourhood effects.

Parameter estimates	Mean	Quantile 0.025	Quantile 0.975
Intercept	0.654	0.274	0.914
σ time	0.715	0.483	1.048
σ cyclic	0.374	0.176	0.641
σ gear	0.740	0.357	1.431
σ bottom temperature	0.406	0.218	0.667
σ depth	0.793	0.377	1.540
σ space	1.383	1.235	1.521
σ space_time	1.188	1.072	1.332
ρ time	0.945	0.887	0.980
ρ space_time	0.909	0.877	0.940
ϕ space	0.989	0.970	0.998
ϕ space_time	0.982	0.952	0.997

Figures

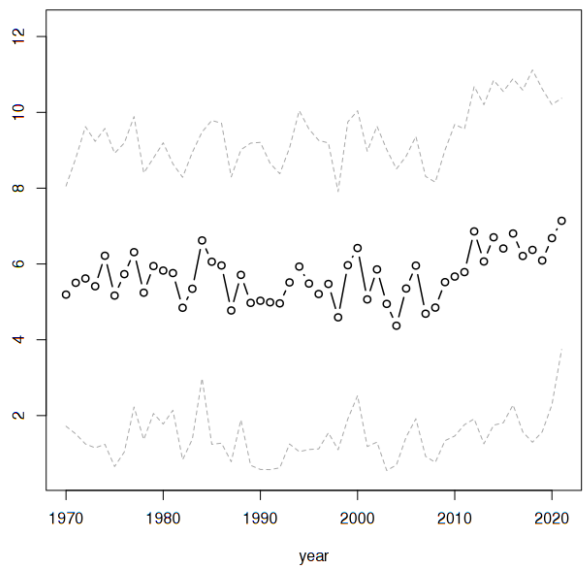

Figure 1. Predicted average (1 July) bottom temperatures in °C in the Maritimes region with 95% empirical quantiles from depths of 50 m to 400 m.

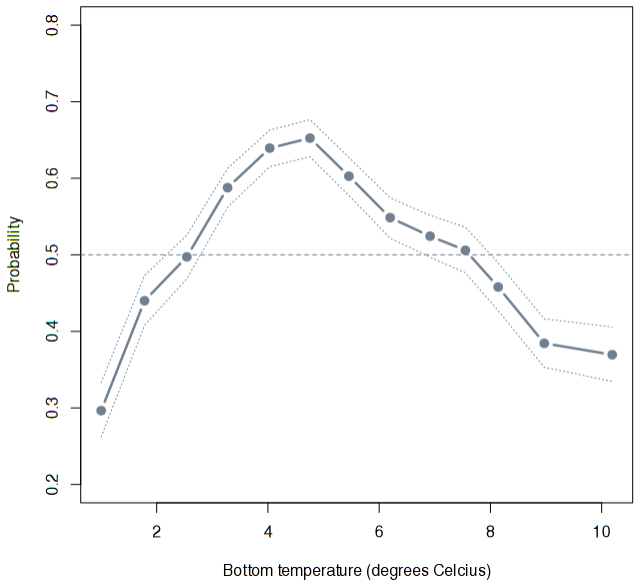

Figure 2. Posterior predicted relationship of the probability of a location being good cod habitat as a function of bottom temperature (°C), independent of depth, gear, season, and spatiotemporal autocorrelation. Stippled lines are 95% Credible Intervals.

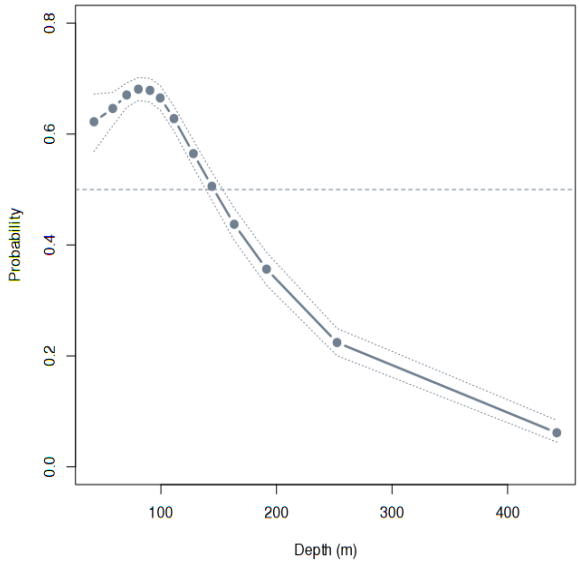

Figure 3. Posterior predicted relationship of the probability of a location being good cod habitat as a function of depth (m), independent of temperature, gear, season, and spatiotemporal autocorrelation. Stippled lines are 95% Credible Intervals.

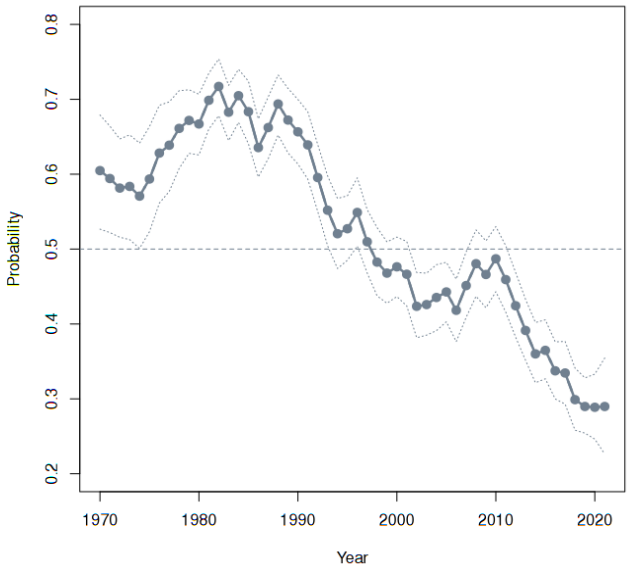

Figure 4. Posterior predicted mean cod habitat probability in the Maritime region as a function of time (i.e., combining all effects). Stippled lines are 95% Credible Intervals.

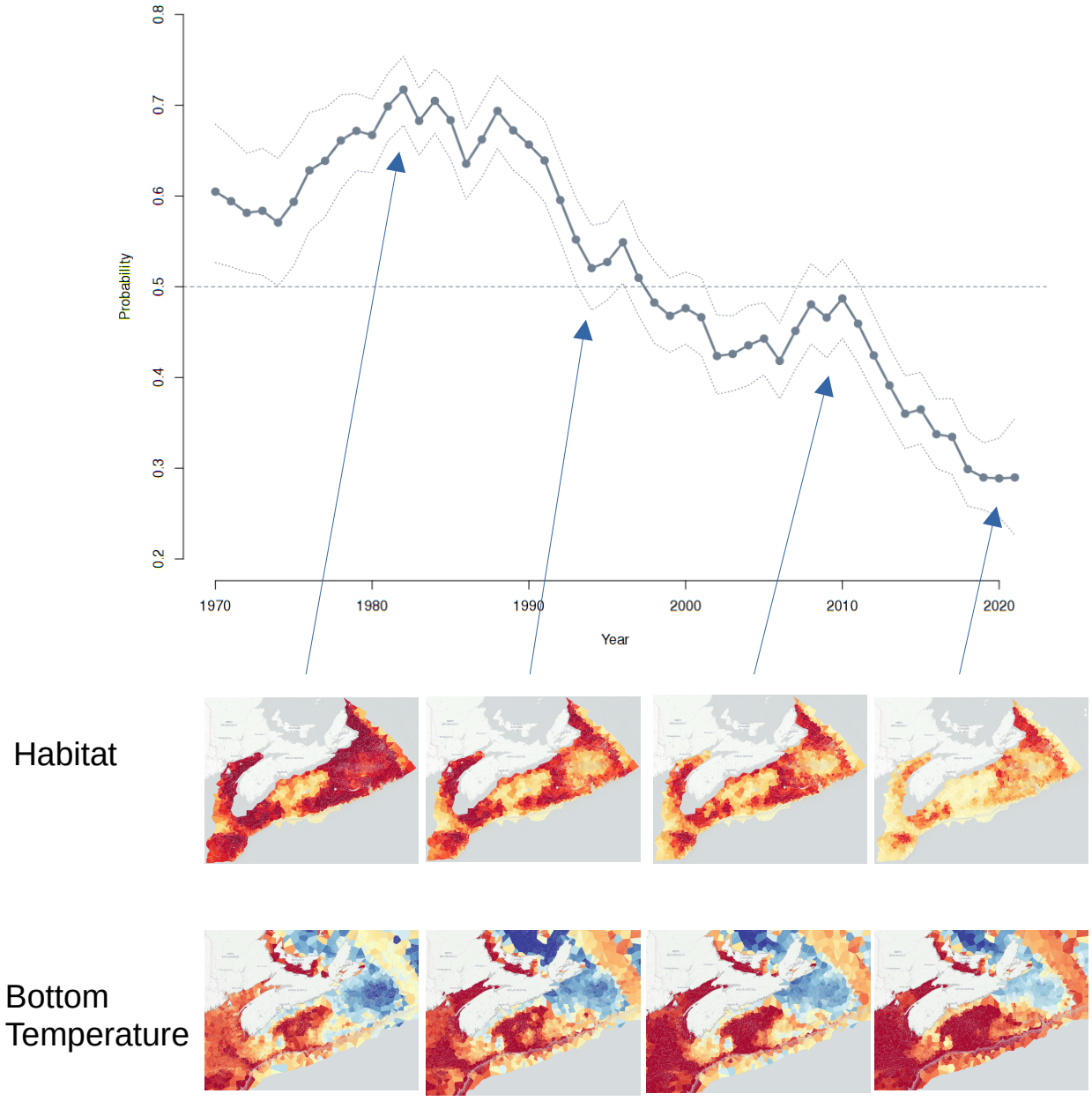

Figure 5. Spatiotemporal patterns of the posterior predicted habitat in summer, over various years. Estimates of summer bottom temperature for each time slice is also presented. Warming was evident in the post 2010 period. Colour scale for temperatures are from 1 °C (blue) to 9 °C (red).

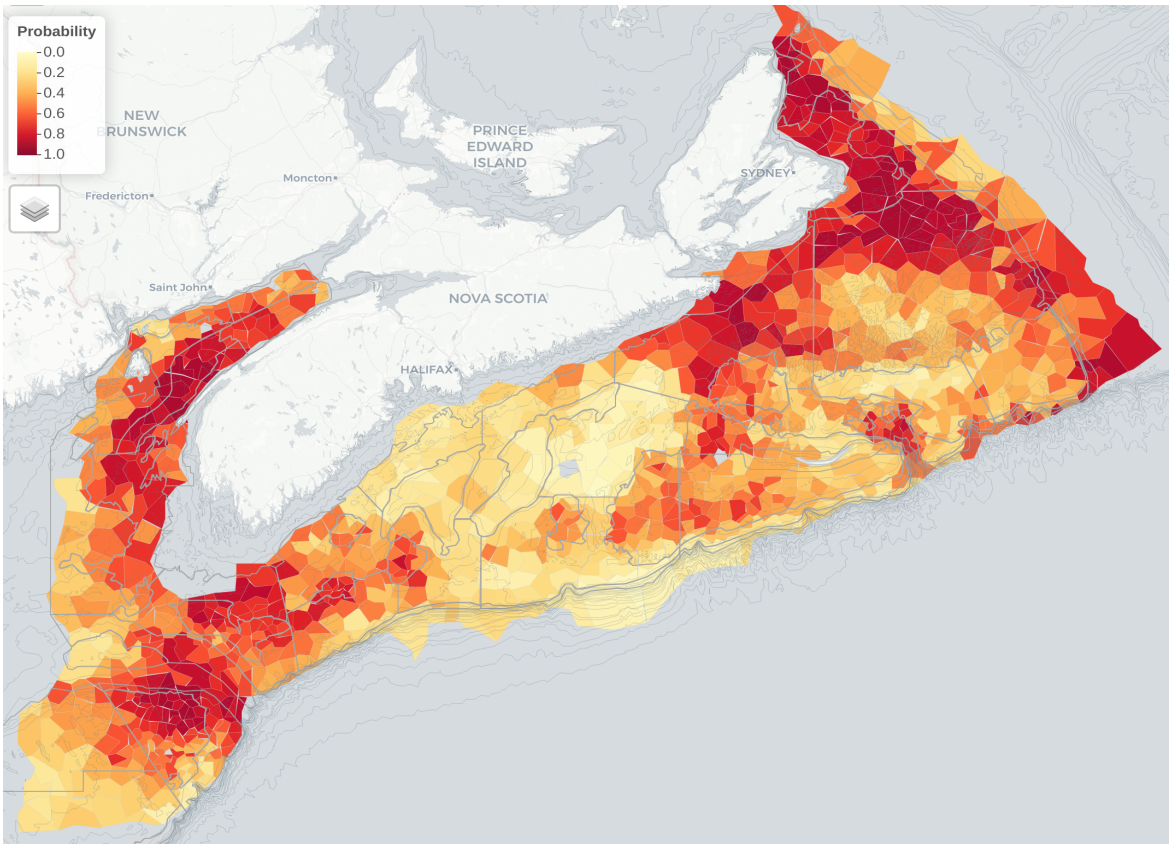

Figure 6. Posterior marginal spatial effects on cod habitat probability; that is persistent spatial patterns of habitat or core habitat areas. Overlaid are the strata used for sampling from DFO's ground fish surveys.

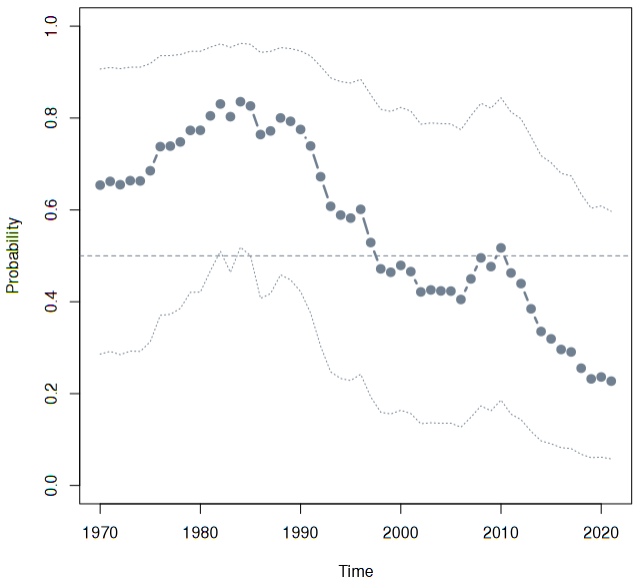

Figure 7. The posterior marginal effect of time (year) upon the probability of finding cod habitat, independent of all other factors. Note that the overall pattern is similar to the posterior predictive habitat (Figure 1). However, the 95% Credible Interval is much wider.

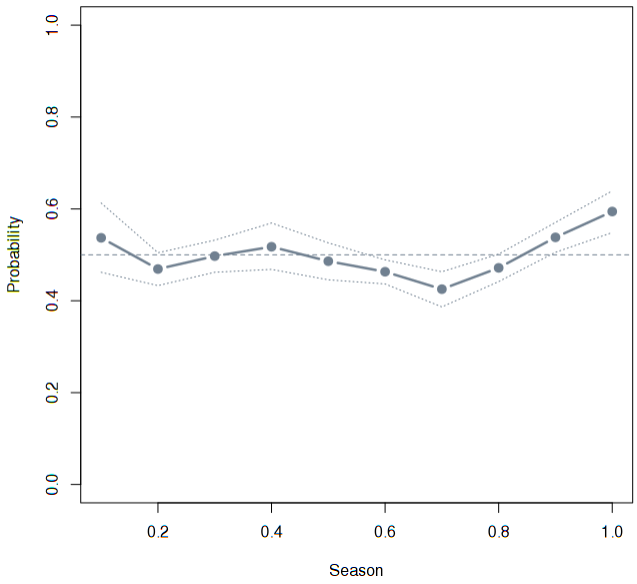

Figure 8. The posterior marginal effect of seasonality (fractional day of year) upon the probability of finding cod habitat, independent of all other factors.

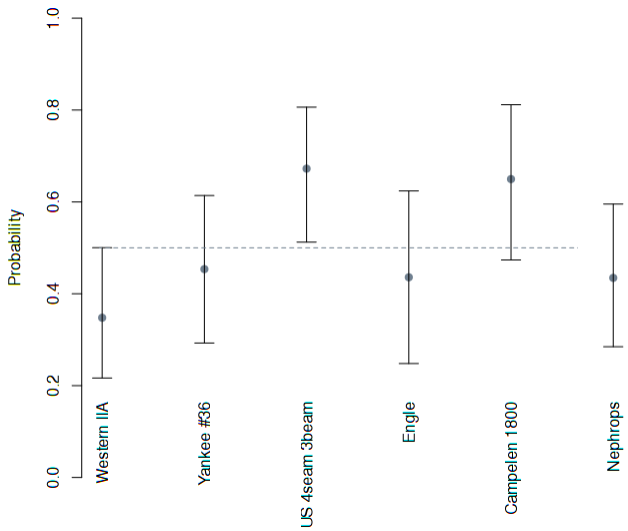

Figure 9. The posterior marginal effect of sampling gear upon the probability of finding cod habitat, independent of all other factors. Note that most have overlapping 95% Credible Intervals, though some strong differences are found between the Western IIA (most frequently used gear in the past) and the US 4 seam 3 bridle survey trawl net, the current standard.