A multi-stage, delay differential model of snow crab population dynamics in the Scotian Shelf of Atlantic Canada

Choi, Jae S.
Population Ecology Division
Department of Fisheries and Oceans
Bedford Institute of Oceanography
P.O. Box 1006, Dartmouth, Nova Scotia B2Y 4A2

Abstract

Snow crab (*Chionoecetes opilio*) are cold-water *stenotherms* in the northern hemisphere. As they are long-lived and have a complex life history, developing an operational model of population dynamics has been a challenge, especially in the context of human exploitation and rapid global climate change. Here we review past efforts at understanding the population dynamics of snow crab with a biomass dynamic model and the challenges of an environmentally very dynamic and heterogeneous area, the Scotian Shelf of the northwest Atlantic of Canada. We address these difficulties and propose a moderately complex model: a multi-stage, delay differential model parameterized via Bayesian techniques. Operational solutions were more stable and reasonable and permitted inference upon the intra-annual dynamics of snow crab. Further, a concept of a "Fisheries footprint", akin to fishing mortality, can be elucidated that directly addresses the conceptual impact of a fishery upon a population. The approach is promising. The model also suggests additional processes need to be accounted for that contributes to the non-"well-mixed" nature of some applications. We hypothesize that seasonal and interannual movement and spatiotemporally structured predation are key processes that require further attention. However, as computational costs are significant, these additional processes will need to be parameterized carefully.

Introduction

The life history of snow crab (*Chionoecetes opilio*) is complex. Some of the notable life history features include: sexual dimorphism with mature males being much larger than mature females; pelagic in larval stages and benthic in pre-adolescent and adult stages; semi-annual and annual molts depending upon size/age and environmental conditions; terminal molt to maturity; and live up to 15 years. They also have a narrow range of temperature preferences (Foyle et al. 1989) and demonstrate an ontogenetic shift in habitat preferences (Sainte-Marie & Lafrance 2002, Kuhn & Choi 2011). They are thought to avoid temperatures above $7^{\circ}C$, as metabolic costs have been shown to exceed metabolic gains above this temperature in laboratory studies (Foyle et al. 1989). Smaller crab and females also have differences in thermal *preferenda* (Choi et al. 2022). Further, snow crab are generally observed on soft mud bottoms; with smaller-bodied and molting crabs showing preference for more complex (boulder, cobble) substrates, presumably as they afford more shelter (Sainte-Marie & Hazel 1992, Comeau et al. 1998).

Snow crab eggs are brooded by their mothers for up to two years, depending upon ambient temperatures as well as food availability (which also depends upon temperature as it influences overall system primary and secondary production) and the health condition and maturity status of the mother (up to 27 months in primiparous females – first breeding event; and up to 24 months in multiparous females – second or possibly third breeding events; (Sainte-Marie 1993)). More rapid development of eggs (from 12 to 18 months) has been observed

in other areas (Elner & Beninger 1995, Webb et al. 2007). Over 80% of the female snow crab on the Scotian Shelf are estimated to follow an annual, possibly due to extended periods of exposure to warmer temperatures (Kuhn & Choi 2011). A primiparous female of approximately 57.4 mm carapace width produces between 35,000 to 46,000 eggs, which are extruded between February and April (Sainte-Marie 1993)). Multiparous females are thought to be more fecund, with more than 100,000 eggs being produced by each female. Eggs are hatched from April to June when larvae are released. This pelagic larval stage lasts for three to five months (zoea stages 1 and 2) during which snow crab feed upon zooplankton. Pelagic stages seem to have highest abundance in October and so may begin settling in January (Choi et al. 2005b). Thereafter, they settle closer to the bottom in their megalopa stage. Very little is known of survival rates at these early life stages, but these also are thought to depend highly upon temperature (Sainte-Marie & Lafrance 2002).

Every known population of snow crab is also exploited by humans, primarily for consumption. They are also used as fertilizer, bait in other fisheries and for the glucosamine polysaccharide derived from chitin, known as chitosan. Chitosan is widely used in medicine as an agent to slow bleeding from wounds (Zhang et al. 2015, Moghadas et al. 2016), agriculturally as natural fungicides and bactericides (Linden & Stoner 2007), plastic replacement (Tampieri et al. 2003) and even as a battery electrolyte (Poosapati et al. 2021).

As they are fully exploited, it is imperative that this exploitation is conducted in a responsible and sustainable manner. In North America, the largest of males (> 95 mm carapace width; CW) are preferentially captured due to their higher meat-yield and consumer preferences. This represents a built-in, market-driven, protection for the female reproductive component that never reaches such sizes and smaller immature crab. This represents protection that spans up to 10 years of age or more, from larval release (Figure 1), and has been critical in keeping the snow crab populations from being over-exploited. However, extreme exploitation of mature males can have long-term consequences in terms of reduced reproductive success of females; loss of dominance by invasion of habitat by competitors (Choi et al. 2005b) and potentially even genetic/phenotypic selection for reduced size at maturity (Comeau & Conan 1992).

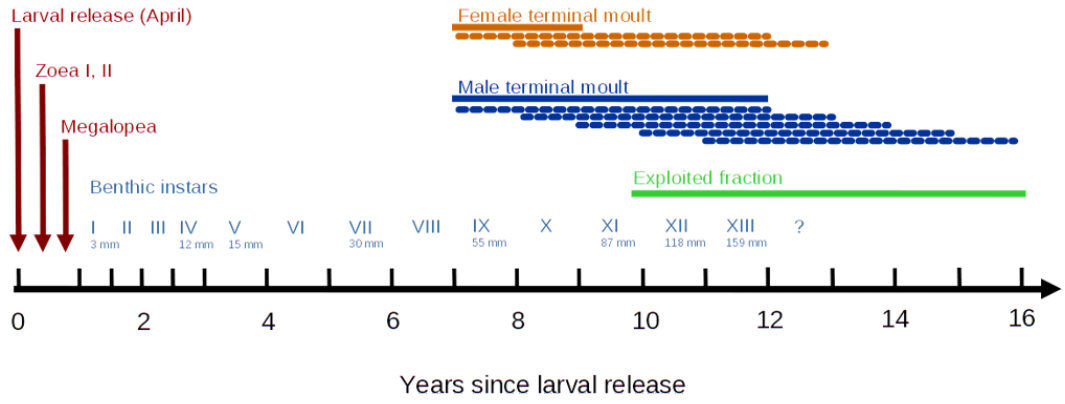

Figure 1. Life history patterns of snow crab and approximate timing of the main life history stages of snow crab and size measured as carapace width (CW) and instar (Roman numerals). Size and timings are specific to the area of study and likely vary with regional environmental conditions, food availability and genetic variability.

This complex life history also renders them a challenge to sample, understand, model and predict. This is especially the case in a population-dynamic context, compounded by their narrow environmental preferences operating in a region of highly variable ocean climate. Sampling in an unbiased manner under such conditions is particularly difficult as the random stratified sampling (i.e., spatial) that is usually adopted to account for such variability, fail to do so due to the large dynamic (i.e., spatiotemporal) structures operating on scales comparable to the domain. The additional factors of global rapid climate change and human exploitation of crab by fishers with knowledge of their environment and the species aggregation patterns enable them to target their efforts in time and space, making this understanding even more difficult (Choi et al. 2022). Here we will briefly review a few of the historical attempts to address these issues and propose an alternative approach that can address some of the key challenges. Namely, this is accomplished by having a two-stage process: the first process addresses the estimation problem, specifically, biases induced by differential spatiotemporal variability in habitat for differing life stages which upon aggregation across space, permits an index of abundance comparable across time (years); and then a secondary process that uses this temporally intercomparable index to address observation error across sex and stage-structure and infer population dynamics. This examination is conducted in the Scotian Shelf of the northwest Atlantic of Canada where the variability of ocean climate is known to be high (Choi et al. 2004, Drinkwater 2005) and where we also have a consistently sampled population since the late 1990s (Figure 2).

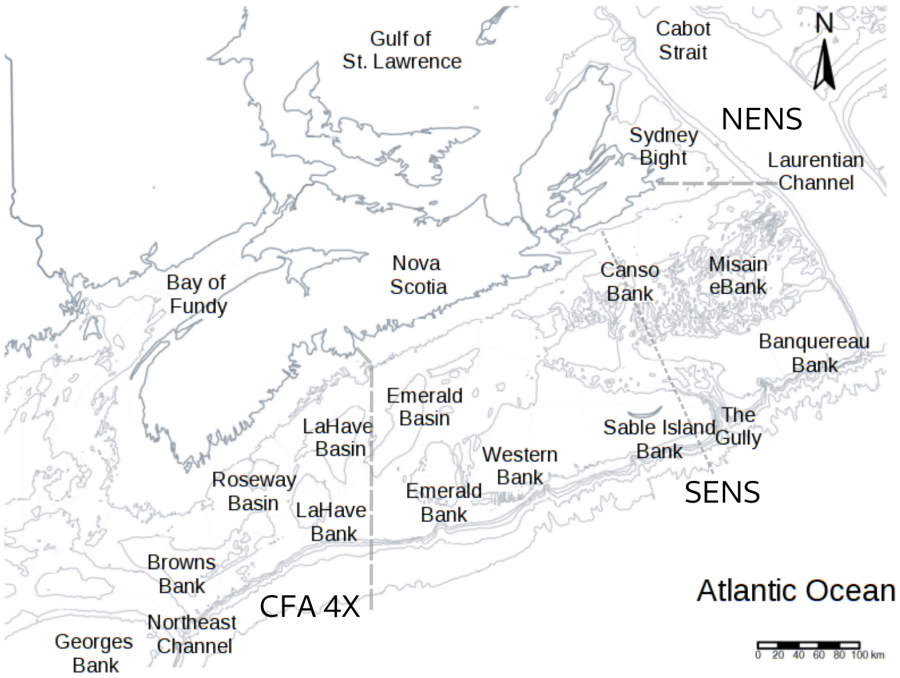

Figure 2. The area of interest in the Scotian Shelf of the northwest Atlantic Ocean (Canada, NAFO Div. 4VWX). Shown are isobaths and some of the major bathymetric features in the area. This area is at the confluence of the Gulf Stream from the south and south east along the

shelf edge, Labrador Current and St. Lawrence outflow from the north and north east, as well as a nearshore Nova Scotia current, running from the northeast. It is hydro-dynamically very complex due to mixing of cold, low salinity water from the north with the warm saline water from the south. Shown also are the managed Crab Fishing Areas (CFAs; divided by dashed lines): NENS, SENS, 4X. SENS is further subdivided (dotted line) into 23 (northwest) and 24 (southeast).

Data

Data collection and subsequent index modeling are described in (Choi et al. 2022). This study focuses upon the period from 1999 to 2021. Importantly, no survey was conducted in 2020 due to Covid-19 related uncertainties. The index generation method being Bayesian, imputes these estimates, but variability attached to this year is large and this is propagated into Model 2, but not Model 1 (below). This is because Model 1 is a simple baseline model with minimal assumptions.

Area of study

In the area of study, the continental shelf of the northwest Atlantic Ocean known as the Scotian Shelf (Nova Scotia, Canada; Figure 2), snow crab are exposed to high bottom temperature variability due to the confluence of a number of oceanic currents: the warm Gulf Stream, the cold Labrador current, low salinity outflow from the St. Lawrence river and the cold coastal Nova Scotia current. In this region, snow crab are generally observed between depths of 50 to 300 m and between temperatures of $-1\ to\ 11^{\circ}C$ (Choi 2011). As the focal area is thermally complex, their spatial distributions can fluctuate seasonally and annually.

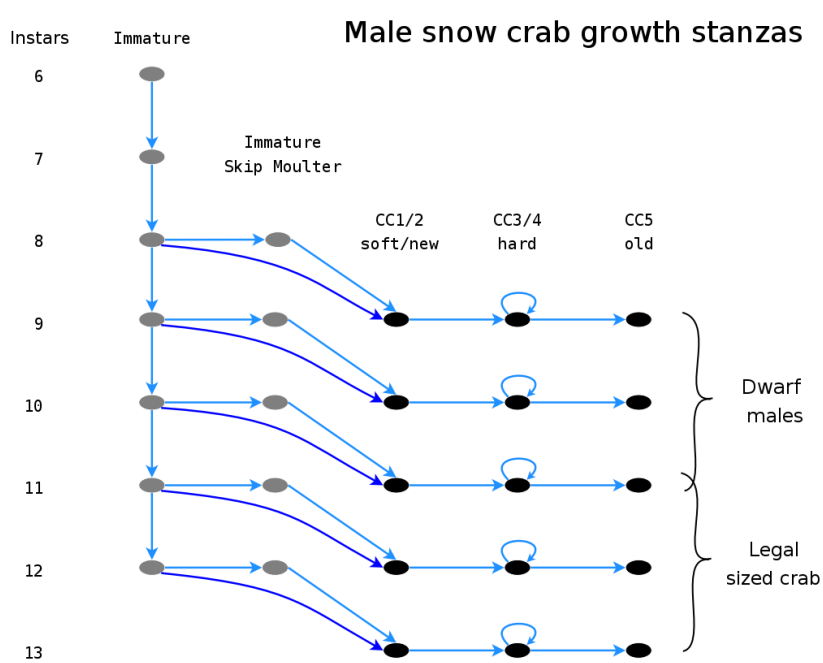

Figure 3. The growth stanzas of the male component and decision paths to maturity and terminal moult. Black ellipses indicate terminally molted animals.

There have only been a small number of attempts at modeling the dynamics of snow crab populations. Being long-lived, sexually dimorphic, deep water, benthic organisms, usually living far offshore, they are not easily surveyed. Snow crabs have a complex life history that spans up to 14 years from planktonic to benthic stages. They molt 2 times a year in the early stages and then approximately annually by instar 5 (about 15 mm CW) and can even skip molts when living conditions are poor. This life history complexity causes complexity in their dynamics and spatial distributions. Most population assessments approach abundance estimation as a fishery- or survey-based relative index of a narrow segment of the population (the fishable component). When modeled, these empirical estimates of abundance are assumed to be known without bias.

Further, aging of snow crab is not possible due to a lack of retention of calcified body parts through molts. This has encouraged adoption of size-based models (Siddeek et al. 2009, Cadigan et al. 2017, Ianelli et al. 2022), often with strong and questionable assumptions. For example, Siddeek et al. (2009) assume the male fishable component is the spawning stock biomass, though of course it is the females that are the reproductive component and completely unexploited. Similarly, Choi and Zisserson (2011) implicitly assumes that the fishable biomass regenerates itself by application of a biomass dynamics model. Importantly, sex and size-selectivity of sampling gear are almost always assumed to be a constant or some smooth monotonic function of body size, and so static across time and space. These are significant and biologically problematic assumptions. The problems associated with the interplay between snow crab life history and behavior and our inability to observe them without bias due to sampling design being non-random with respects to the environmental factors controlling their distribution and abundance, and the sampling machinery (mesh size, trawls that cannot access rugose areas) that can only observe a small fraction of the population, are fundamental issues shared with all other attempts at assessment.

Biological models

The *phenomenological* single component model of Verhulst which was first used to describe Belgium's population growth is well understood (Verhulst 1845, Bacaër 2011; Appendix 1, 2):

$$\frac{dN}{dt} = rN\,(1 - \frac{N}{K}). \qquad \text{(eq. 1)}$$

It is parameterized by an intrinsic rate of increase (r) representing the maximum exponential rate of increase and carrying capacity (K) the upper threshold. When numerical abundance $N \to 0$, the loss term also $\frac{N}{K} \to 0$, and so $\frac{dN}{dt} \to rN$. When $N \to K$, then $\frac{N}{K} \to 1$ and so the loss rate approaches rN and the overall rate of change approaches zero ($\frac{dN}{dt} \to 0$).

Parenthetically, this can be simplified further by dividing both sides by K to give: $\frac{dN}{dt}/K = rN(1 - r\frac{N}{K})\,/\,K$. By focussing upon $n = \frac{N}{K}$ as a non-dimensional number ranging from (0,1), this becomes:

$$\frac{dn}{dt} = rn(1 - n). \qquad \text{(eq. 2)}$$

For parameter estimation/inference, this form (eq. 2) is useful as it is simpler and the magnitudes of variables are mostly similar, with the exception of K. This renders beneficial properties to numerical optimization procedures. Parenthetically, this form can be simplified even further by scaling time by r to give: $\frac{dn}{d\tau} = n(1 - n)$, where $\tau = t/r$.

The sigmoid nature of the equation has rendered it a frequently encountered model that shows versatility in phenomenologically describing population dynamics. Its discrete form is particularly common in fisheries settings (Schaefer 1954, Meyer & Millar 1999) and has also been used to describe snow crab dynamics in the area of study (Choi and Zisserson 2011). The focus is usually upon biomass B and its normalized value, $b = BK^{-1}$, rather than numerical abundance:

$$b_{t+1} = b_t + \Delta b_t,$$

$$\Delta b_t = rb_t(1 - b_t) - Fishing_t K^{-1}.$$

Here, $Fishing_t$ is scaled by K to make it non-dimensional and also in the interval (0,1); it is usually treated as an external factor (perturbation), measured without error. Of course, there is usually observation error and/or illegal removals that will get absorbed as a biological process; in this case by elevating the intrinsic rate of increase to compensate for the additional losses. This will have an effect of creating bias and uncertainty in related parameters and reference points (see below) as well. Note also that the discretization to an annual basis is a significant assumption as the time span is large relative to the processes of most biota. This has the effect of averaging out sub-annual dynamics. This means temporal aliasing or discretization errors and censoring are introduced which ultimately increases process and observation errors (see subannual dynamics, below).

From this *phenomenological* view, the minimal parameters required to estimate biological reference points, and the relative distance a system is from such reference points help delimit the status of a population (Schaefer 1954, Meyer & Millar 1999). Values such as Maximum sustainable yield ($MSY = rK/4$) and the fishing mortality associated with such a yield ($FMSY = r/2$) are commonly used to help define some consistent landmarks of scale for use as management reference points to guide the implementation of consistent "Precautionary Approach"
for fishery exploitation.

Many approaches exist to estimate these model parameters. Currently, Maximum Likelihood (ML) approaches dominate due to their computational speed. However, it has been the author's experience that they do not navigate and optimize very high-dimensional parameter spaces reliably, especially in the delay differential equation models that we explore. This renders their utility in an operational setting, minimally useful. The related Maximum A-Posteriori (MAP) solutions, where using the same optimization techniques but with the addition of prior-like constraints can result in marginally more stable results, but it has been the author's experience that they still have tremendous difficulty with high dimensional parameter spaces and the associated numerous local optima/multiple equilibria.

The operationally most viable approach encountered so far has been Bayesian inference, where informative priors for these parameters are explicit and variance propagation of index variables can be accomplished by using them as priors to respective likelihood error terms. They facilitate parameter estimates that are stable and credible, given some latent process

and observation models (Meyer & Millar 1999). Previously, JAGS (Just Another Gibbs Sampler; Plummer (2003)) and STAN (Stan Development Team 2022) were used to compute the posteriors via MCMC (Choi & Zisserson 2011). The latter uses the more efficient NUTS sampler which significantly speeds up the estimation process of these discrete difference equation models. Presently, we use Julia (Bezanson et al. 2017) and the supporting "Turing" library (Ge et al. 2018) for parameter inference and the "DifferentialEquations" library (Rackauckas & Nie 2017) for modeling delay differential equation models; they demonstrate orders of magnitude greater efficiency and flexibility to model such problems, relative to basic MCMC procedures due to use of automatic differentiation and heavily optimized solution engines.

The estimation approach was to use the biomass dynamics (*phenomenological*) model discretized to an annual basis (eq. 3) the latent (real but unobserved) biomass was assumed to have a model "process" error with recursive Gaussian error structure (standard deviation) σ_p (Bolker 2008):

$$b_{t+1} \sim N\left(b_t + r\, b_t\,(1 - b_t) - Fishing_t K^{-1}, \sigma_p\right). \qquad \text{(eq. 3)}$$

The following marginally informative priors were assumed:

$r \sim N(1.0,\ 0.1)$, and
$K \sim N(\kappa,\ 0.1 \cdot \kappa)$.

The prior mean of the carrying capacity ($\kappa = [5.0, 60, 1.25]$, in kt, for the northern (N), southern (S), and area 4X, respectively) were based upon historical analyses with other analytical procedures (Choi et al. 2005b, Choi & Zisserson 2007, Choi 2011). It is further assumed that the real unobservable (latent) process b is sampled with error (observation standard deviation σ_o). The observation model in most fishery applications is a simple multiplicative factor, known as a "catchability" coefficient q, such that:

$q \sim N(1.0, 0.1)$,
$$Y_t \sim N\left(qKb_t, \sigma_o\right). \qquad \text{(eq. 4)}$$

This means that the observed biomass index Y are some constant fraction of the true abundance b_t, across all sampling time (years, season) and locations. This observation model (eq. 4) in tandem with the recursive logistic process model (eq. 3), we will refer to it as, "**Model 1**" (Choi & Zisserson 2011).

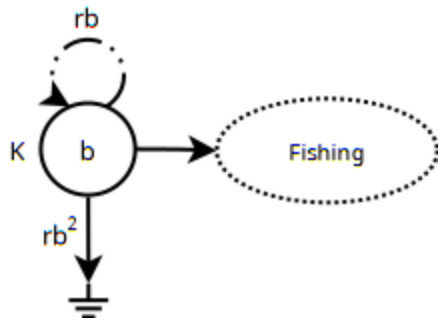

Figure 4. A graphical representation of Model 1 (simple logistic; eq. 1). Here, $b = BK^{-1}$ is a non-dimensional number that ranges from (0, 1) that represents the biomass B after being scaled to K. The loop rb identifies the growth rate and the loss term rb^2 identifies the quadratic increase in "mortality" as $b \to 1$. Fishing is also scaled to K, such that: $\frac{db}{dt} = rb - rb \cdot b - f = birth - death - fishing$; such that total mortality = death + fishing.

From the graphical representation of the processes of Model 1 (Figure 4), one can immediately see that there is no input term from outside of the system: it is a simple *phenomenological* self-loop model with two outputs (death and fishing). The term rb can be referred to as the (net) "birth process" (Gillespie 1992, Qian & Bishop 2010, Albert 2016), and represents a first order processes that increases b (via birth, growth, enhanced survival, improved food availability, immigration, strong year class strength, etc.), through the single (static) parameter r. The mechanism is not identified and is implied to be some internal recycling of b. In reality, there are biological mechanisms involved and associated parameters that are not-static and non-stationary (in first and second order; across time and space). Growth in biomass or increase in numbers is seasonal and pulsed, due to the molting process and body mass increases, that progress at variable rates depending upon time of year and environmental variability. Across years, there are strong and weak year classes due to match-mismatch type processes (Cushing 1969, Durant et al. 2007), and so also pulsed. These simple models cannot address these more realistic dynamics and so we obtain instead, an average state, with poor resolution of peaks and troughs and so parameter estimates that are likely to be in error.

The strength of **Model 1** is simplicity; but this simplicity is also a weakness. As the biomass dynamics model is phenomenological; it is heuristic, without mechanism. For example, fishable biomass "creates" fishable biomass at a maximum exponential rate (r) to a limit of K. In reality, fishable biomass being mature male snow crab, does not produce more mature male snow crab; instead, it is the female mature population that creates the eggs and broods them to larvae, some fraction of which eventually mature into the fishable component. The rate of increase in biomass is not a simple exponential rate; instead, a certain number of fishable crab die from various causes (predation, disease, competitive fighting), a certain number of recruits terminally molt to a size in the fishable range to increase their numbers, they grow in weight as they eat, some fraction move in and out of a given area, and some are fished; these rates are not constant in time nor space. Fundamentally it is a numerical process. So Model 1 from the perspective of "biomass dynamics" is less than satisfactory in terms of biological realism. However, in the heuristic perspective, it implies that the biomass in one year is related to the biomass in the previous year within some constraints, constraints that are only diffusely/indirectly related to the "real" mechanistic processes represented by individual-individual interactions. As such, they can be seen as a temporal autoregressive model.

These constraints unfortunately result in a model that is sometimes not responsive enough to large fluctuations in dynamics caused by intrinsic and/or extrinsic factors. For example, due to the pulse-like dynamics observed since the late 1990s, no recruits entered fishable components for a number of years, even though their abundance was low (Choi 2011). Model 1 expected recruitment simply because biomass was low. This was an erroneous expectation given the low numbers of pre-recruits for an extended period of time, nor the extremes of bottom temperature and associated shifts in their distributions nor the increase in abundance of predators that followed which reduced the strength of recruitment. Model 1 is too simple to express the expectations of such highly nonlinear pulse-like dynamics and interactions with environment and predators. In another example, there was an extreme warming event in 2021 that significantly altered and constricted the spatial distribution of snow crab (Choi et al. 2022). Again a simple model such as Model 1, with static expectations of environmental conditions are not able to account for such effects.

In an attempt to *begin* addressing these issues, we entertain **Model 2** (Figure 5) which resolves some size groups, sex and maturity and permits time-varying viable habitat area. Model 2 is, therefore, an intermediately complex, marginally more structural and mechanistic (*ontological*) model relative to Model 1 (Appendix 1).

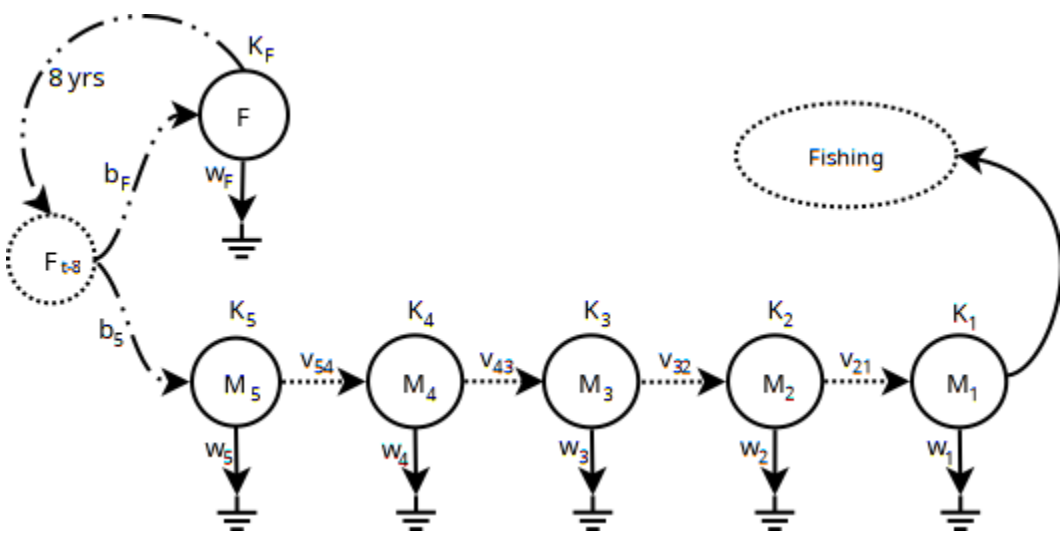

Figure 5. Graphical structure of the six-component Model 2 of snow crab with associated numerical flows. F indicates mature females, determined from size range and morphometric maturity. Associated with each component is a carrying capacity (K_i), and a death rate w_i, and molt rates v_{ij}; and birth/survival rates b_i. F_{t-8} is the state of mature females F from 8 years prior. Fishing is considered an external, deterministic sink imposed by external factors.

There is approximately an 8+ year period that is required for females F_{t-8} to produce the next

generation of instar 9 females and males, denoted by F_t and $M_{5,t}$, respectively. They represent crabs in the range of approximately 40 to 60 mm CW. The “birth” rates represent a combination of egg production and larval survival to instar 9+. If the population is stable, “birth” rates are expected to be similar in magnitude to overall death rates. Note that “stage” is defined based upon size-sex-morphometric traits and so misclassification is likely. The error in such knife-edge stage determinations can be substantial if growth and maturity schedules vary significantly. It is assumed, here, that in the aggregate, this has been stable in the survey record (1999 to 2021). This may of course be incorrect if persistent size/stage/age related mortality occurs due to exploitation/predation patterns and/or directional environmental change such as climate warming or food availability shifts.

Some fraction of instar 9 males transition to instar 10 (M_4), and then 11 (M_3) to 12 (M_2) and 13+ (M_1); each transition rate parameterized by v, with numeric indices identifying the instar pairs. Due to the knife edge-cut of stages, there will be misclassification issues which will be absorbed by these transition rates. For example, a small fraction of instar 11 crab (M_3) will be large enough to be considered a fishable size (>95mm CW); but most will molt into instar 12 (M_2); this would result in a reduced molt transition rate. M_2 will represent a composite group of most crab that have entered fishable size but are still immature. Some fraction of this group will mature into the fishable component in the next year; the fractional nature will result in a smaller molt transition rate. Others will continue to molt to instar 13 and higher; for our purposes, all morphologically mature males of fishable size will be considered M_1 and so it represents a range of different ages. This is especially the case as terminally molted crab can live for up to another 5 years; this aggregation will effectively decrease mortality rate of the group.

Survey sampling and estimation of instar 9 to 13+ (40 mm to 130+ mm CW) is reasonably informative. Earlier instars tend to have more divergent habitat preferences relative to those of the fishable component and are also known to be poorly/erratically sampled due to their being small enough to be significantly affected by sampling mesh size. This is because the snow crab surveys are primarily optimized for sampling the fishable component (> 95 mm CW), both in terms of mesh size and choices of sampling location. The utility of these additional compartments is that they also permit more stable parameter estimation and forward projections that are biologically more reasonable (mechanistic). The challenge is to keep track of much more information due to the increased realism and computational limits. Each state variable $U = (M_1, M_2, M_3, M_4, M_5, F)$, is scaled by their respective carrying capacity K_i, such that they are non-dimensional numbers:

$$u_i = (U_1 K_1^{-1}, U_2 K_2^{-1}, U_3 K_3^{-1}, U_4 K_4^{-1}, U_5 K_5^{-1}, U_6 K_6^{-1}).$$

Thus, for example, in the molt transition process from $i = 2$ to $j = 1$, the instantaneous rate is:

$$v_{21} u_{2,t-1} a_{21} = v_{21} (U_{2,t-1} K_2^{-1}) \; K_2 K_1^{-1} = v_{21} U_{2,t-1} K_1^{-1}.$$

The multiplier $a_{21} = K_2 K_1^{-1}$ is required to convert normalized density of category 2 to that of category 1 via the ratio of the respective normalizing constants, K_i.

As with Model 1, first order birth/survival rates b_i are assumed:

$$\beta_i = b_i u_i.$$

So far, most of the core model has been the same as Model 1, only applied to more components with some appropriate time lags. Where Model 2 diverges from Model 1 is by decomposing mortality into two components: the first component is a simple background mortality parameterized as a first order decay ($\omega_i u_{i,t}$); the second component is mortality associated with fluctuations of viable habitat, parameterized as in the logistic equation as a second order process $\psi_i \frac{U_{i,t}}{K_{i,t} H_{it}} \cdot U_{i,t}$. Note the congruence to the $r\frac{N}{K} \cdot N$ loss term of Model 1 (see Fig. 4, eq. 1), such that upon normalization to u, we obtain:

$$w_{i,t} = \omega_i u_{i,t} + \psi_i \frac{u_{i,t}}{H_{i,t}} \cdot u_{i,t}.$$

Here, $H = V/max(V)$, represents the viable habitat surface area (V) normalized to a maximum value of 1, where the maximum is defined in the reference/focal time period. This modifies the carrying capacity proportionately and so KH can be seen as the "effective carrying capacity", adjusting for viable habitat fluctuations. The assumption here is that when viable habitat area declines by some fraction H, so too does the effective carrying capacity (linearly).

The inclusion of predator-prey and other ecological processes are therefore straightforward extensions as additional terms in this type of model formalism and well understood in the literature (Lotka 1920, Bertalanffy 1950, Pianka 1970, Wangersky 1978). Such extensions are planned for future research and evaluation.

The full set of delay differential equations are, therefore:

$$\begin{aligned}
du_1/dt &= v_{21} u_{2,t-1} a_{21} & & - w_{1,t} - Landings_t K_{1,t}^{-1} \\
du_2/dt &= v_{32} u_{3,t-1} a_{32} & - v_{21} u_{2,t-1} & - w_{2,t} \\
du_3/dt &= v_{43} u_{4,t-1} a_{43} & - v_{32} u_{3,t-1} & - w_{3,t} \\
du_4/dt &= v_{54} u_{5,t-1} a_{54} & - v_{43} u_{4,t-1} & - w_{4,t} \\
du_5/dt &= b_5 \; u_{6,t-8} a_{56} & - v_{54} u_{5,t-1} & - w_{5,t} \\
du_6/dt &= b_6 \; u_{6,t-8} & & - w_{6,t}
\end{aligned}$$

Model 2 is, therefore, a more structured extension of Model 1 that brings to bear additional information available about the abundance of other size and sex classes and transition rates between them, and variations in viable habitat surface area dependent mortality rates.

Fishery landings were converted to number based upon annual average weight of the fishable component estimated from surveys and discretized to a two week time step within each year.

The latter was to avoid strong discontinuities which facilitates differential equation modeling and parameter inference. Survey-based indices of numerical abundance were estimated using a Hurdle process, where probability of observation and the numerical abundance of positive-valued observations were modeled as an extension of small-area analysis (Conditional AutoRegressive Models in space and time; see methods in Choi et al. 2022, Choi 2022). Modeled average weights, also analyzed using the same small-area space-time analyses were used to convert numbers back to biomass to make comparisons with Model 1.

In Model 1, the meaning of q is clear: a survey catches only some (fixed) fraction of the true abundance. This is a reasonable first approximation. However, what is implied is: first, this fraction is unchanging, applying equally in high abundance and low abundance years and areas, whether they are in the mating or molting season or not. Ignored are issues such as differential net saturation, aggregation behavior, even when bottom temperatures can force aggregation and dispersal away from or into other areas. The second issue implied by q is that when a survey fails to capture snow crab, that there truly is no snow crab in the area: an observation of zero is a true zero. *This is clearly false*. Visual observation of trawl operation through video monitoring have shown that crabs are missed: when they are in a slight depression, when they are close to protruding rocks or on bedrock, when bottom topography is complex or simply by the gear jumping off of the bottom due to tidal currents. That is, sampling gear is biased. Furthermore, it is not just sampling gear that is problematic. Survey design is biased: in design, each areal unit is expected to be homogeneous in space AND time. External factors being factored out such as bottom temperatures, food availability and predation, aggregation behavior are not homogeneous, no matter how well designed a sampling design may be. Further, there is the notion of “trawlable bottom”: some areas cannot be sampled without tearing or losing nets. These areas are of course not sampled and only habitats that are easier to sample will be used and consequently, over represented. Though allocation may be “random” in design and theory, in application, it is at best, “almost random” and depending upon bottom type, usually biased.

As such, the observation model is also more complex in Model 2. The assumption of zero values in survey abundance indicating a true zero is a very strong assumption. This is especially tenuous when it is known that surveys sample many size classes very poorly. The observation model of Model 2 is, therefore, a simple linear regression. Of course, higher order terms and other covariates can and should enter into the observation model to account for potential survey and behavior induced bias, as is often done for catch rate analyses. In the case of snow crab assessment, this is mostly accomplished in the (statistical) abundance index model using CARSTM (Choi et al. 2022).

However, some additional freedom is given in the observation model in that the prior for the intercept term c_i was informed by μ_i, the fraction of the minimum observed value relative to the maximum value.

$m_i \sim N(1.0, 0.1)$,

$c_i \sim N\left(\mu_i, 0.1\right)$, and

$y_{ti} \sim N\left(m_i n_{ti} + c_i, \sigma_{ti}\right)$.

Here, $y_{ti} = Y_{ti}/max(Y_i)$, constrains abundance to the interval (0, 1) and helps to confer better numerical properties (faster and more stable optimization, integration) in that variables are of similar magnitudes.

Additionally, the variability of the observations was propagated into Model 2 by assuming that the coefficient of variation of observations were modal estimates of the observation model using a Lognormal (LN) prior with a mode of log(CV) specific to each component and survey time and a SD of 0.25 (=128% error on the normal scale). This works well as y_{ti} are already normalized to (0,1):

$$\sigma_{ti_} \sim LN(\,log(CV_{ti})\,,\ 0.25).$$

The other priors used for the Model 2 are also informative based upon expected biological constraints and some very wide distributions for the variance components to provide well mixed posterior samples as determined by Effective Sample Size (given autocorrelation in samples within chains) and "Rhat" (convergence criterion across chains):

$$K \sim LN(\,log(\kappa),\ 0.25),$$
$$b \sim LN(\,log(10),\ 0.5),$$
$$d \sim LN(\,log(0.22),\ 0.25),$$
$$\psi \sim LN(\,log(0.49),\ 0.5),$$
$$v \sim LN(\,log(1.46),\ 0.5)\ .$$

Fixed reference points analogous to the concepts of MSY and FMSY are not readily identifiable in Model 2 as "production" is dependent upon multiple system components each of which have externally imposed effective habitat viability trends and related mortalities and fishing mortalities (perturbations). It is, however, possible to compute a related concept, which we will call the "*fisheries footprint*"; it is computed as the difference in trajectories between the system state estimated for the fishable component with and without fishing. The biological parameters are estimated under conditions of fishing activity. In the absence of fishing, these parameters may be expected to be different, especially when fishing activity is extreme. In some cases, maturity and growth schedules can shift (Zwanenburg et al. 2002, Choi et al. 2004, 2005a). The assumption here is that extreme fishing activity has not occurred with sufficient pressure nor time to generate phenotypic or genotypic change. The difference in predicted trajectories between the fished and unfished conditions, therefore, provides a crude, first order estimate of the impact of fishing, without assumptions (other than the model parameters are appropriate). This fisheries footprint is placed on a relative scale from 0 to 1, by normalizing with the expected unfished abundance. As such, the *fisheries footprint* identifies the fraction of potential biomass that was reduced by fishery exploitation.

Results and Discussions

A first estimate of potential recruitment (M_2) and mature female abundance (F, Figure 6) shows that Model 2 has difficulty tracking these components. However, peaks and troughs are identified and they seem to be coherent across areas. The lack of concordance with the observations suggest that other, as yet unmodeled processes need to be better modeled. The most likely missing processes include movement (inshore-offshore, shallow-deep) as well as predation, as the areas of study are not "well mixed" and show spatiotemporal structure. The latter suggests smaller areal units might be useful than the three we used in this study.

Estimates of fishable biomass are shown for each region for each model in Figure 7. In NENS, the discrete Model 1 showed two troughs in (pre-fishery) abundance in 2005 and 2017. The surveyed index after adjustment for the observation model tends to be lower relative to the pre-fishery abundance, which is consistent with the removal of biomass during the fishing season. The exception to this pattern was in the late 2013 and 2019 when strong recruitment was also observed. Model 2 shows a similar pattern of fall fishable biomass, though with a reduced magnitude. The post 2019 period showed significant divergence relative to the survey index and especially in 2020 when no surveys were completed due to Covid-19 related disruptions. SENS also demonstrated a similar periodicity to NENS in both models (Figure 7). Model 2 suggests a dampened time series, attributable to the dynamics of the recruitment being estimated to be very smooth (Figure 6). In Area 4X, Model 1 suggests an important decline following a peak in 2010. Model 2 suggests a similar trajectory, though one that is much more variable. This area is subject to crab movement from the adjoining area as well as spatial aggregation due to extreme temperature conditions, elevated mortality from other predators and disease. Model 2 also suggests abundance that is much lower than the very optimistic expectations of Model 1.

It is important to note that Model 1 will project an increase in abundance, even if recruitment does not exist. It will only project a decline if abundance is above carrying capacity. This structural expectation is of course unrealistic. Model 2, which accounts for recruitment, navigates this problem a little more sensibly. It projects for 4X, a decline, even in the absence of fishing. In SENS, abundance is projected to increase slightly in the absence of fishing. Only NENS was projected to have a rapid increase in abundance (Figure 7).

Another observation is that abundance may be overestimated by Model 1. For example, in 4X where we have supporting information of very high natural mortality rates associated with predation and environmental variability, through the loss of strong year classes, abundance estimates are extremely optimistic. The same issues also exist for N-ENS, where strong adolescent crab year classes seem to disappear at a rate faster than might be expected, possibly due to predation. By extension, S-ENS also likely exhibits overly optimistic time trends, given the very strong year classes diminishing rapidly before entry into the fishable component. As a result of this potential overestimation of abundance, fishing mortality estimates by Model 1 may in fact be overly low. Model 2's solutions seem more reasonable given the supporting information known of the different areas. The overall relative shapes of abundance and fishing mortality are, however, similar (Figure 8).

The continuous form of Model 2 also permits us to infer the subannual dynamics of the snow crab. The saw tooth pattern of abundance (Figure 7) suggests that during the fishing season, the rate of exploitation far surpasses the slower rate of growth of the fishable component. It also identifies how important temporal aliasing might be if observations of landings or survey sample times are not properly accounted for. The fishery footprint across the different areas (Figure 9) indicates that they are very similar to fishing mortality in overall form (as they should be, as the numerator, catch are the same). The former is on a scale that is the same as abundance and so simpler to understand than the exponential scale of an instantaneous rate. *Fishery footprint* also has a reasonably direct relationship to a question that is often asked in applied situations: "How much of an effect is fishing activity having?" In the case of the areas studied, the fishery footprint has declined to conservative and manageable levels since the mid-2000's. SENS, in particular, has been consistently sustainable in the historical record. In the presence of strong environmental variability, it will be necessary to continue to maintain a small fisheries footprint such that the species does not undergo extreme changes in abundance as has been the case for Atlantic cod.

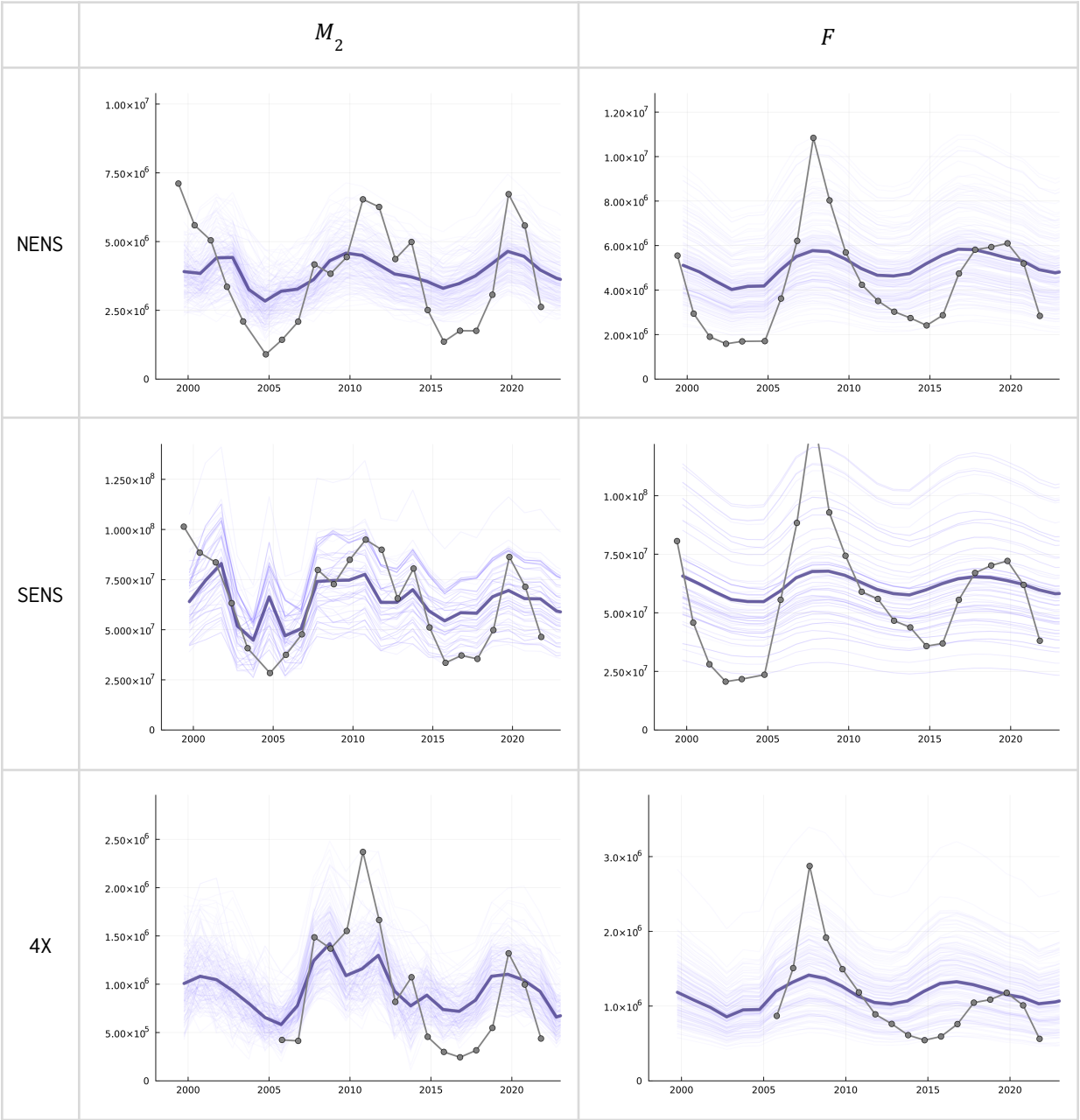

Figure 6. Model 2 posterior numerical abundance for M_2 (recruits) and F (mature female). Overlaid (gray) are survey abundance estimates (post-fishery, except prior to 2004) after correction for observation models.

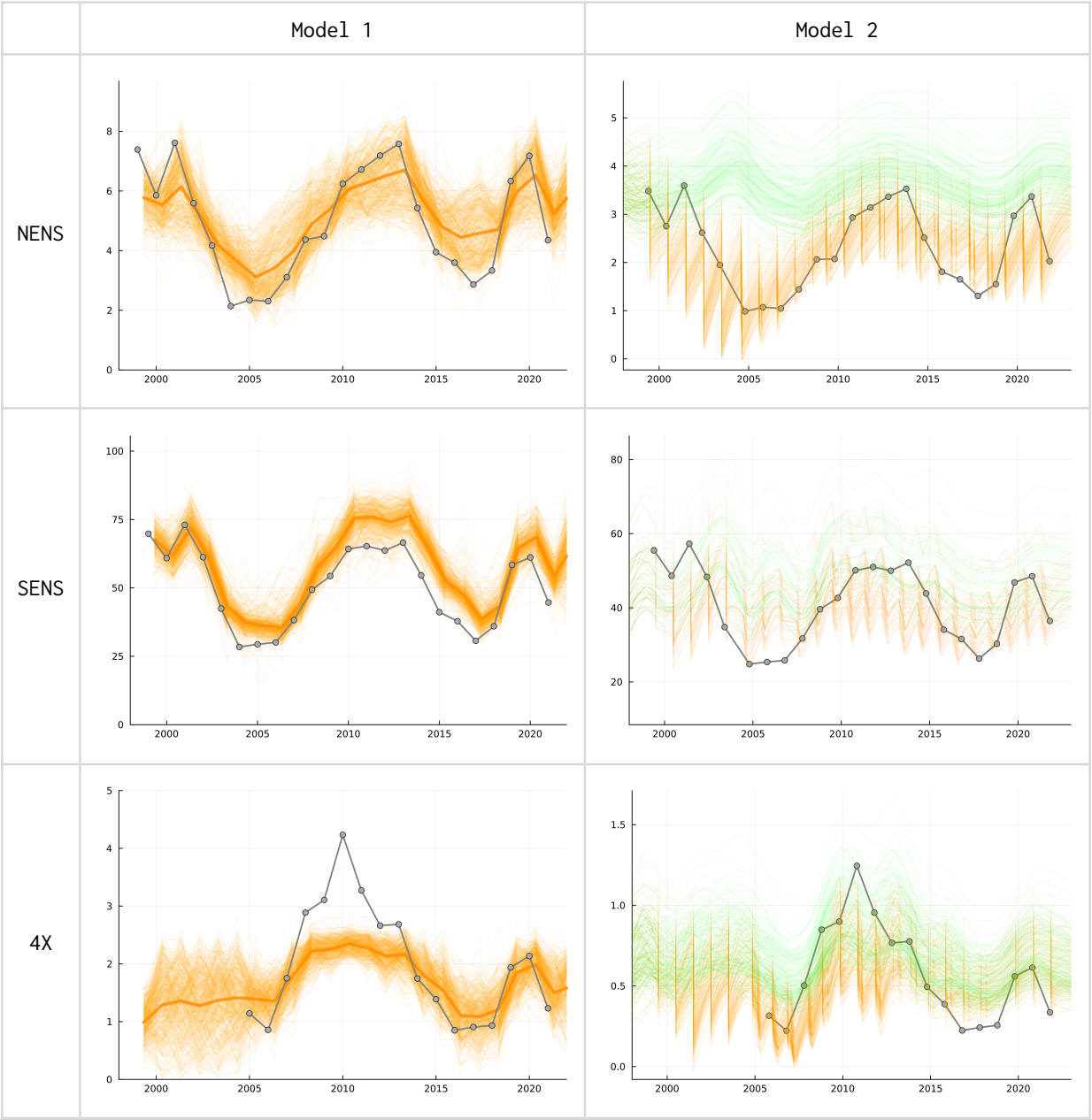

Figure 7. Posterior median biomass (dark orange) for each area of study and model. Posterior realizations (n=200) of dynamics are shown to demonstrate distributional range. For Model 1 (left), “pre-fishery” fishable biomass are shown. For Model 2, the posterior distributions of fishable biomass are shown in green. Overlaid (gray) in both are survey abundance estimates (post-fishery, except prior to 2004) after correction for their respective observation models. Overlaid in green are posterior samples of abundance trajectories expected had there been no fisheries exploitation (green).

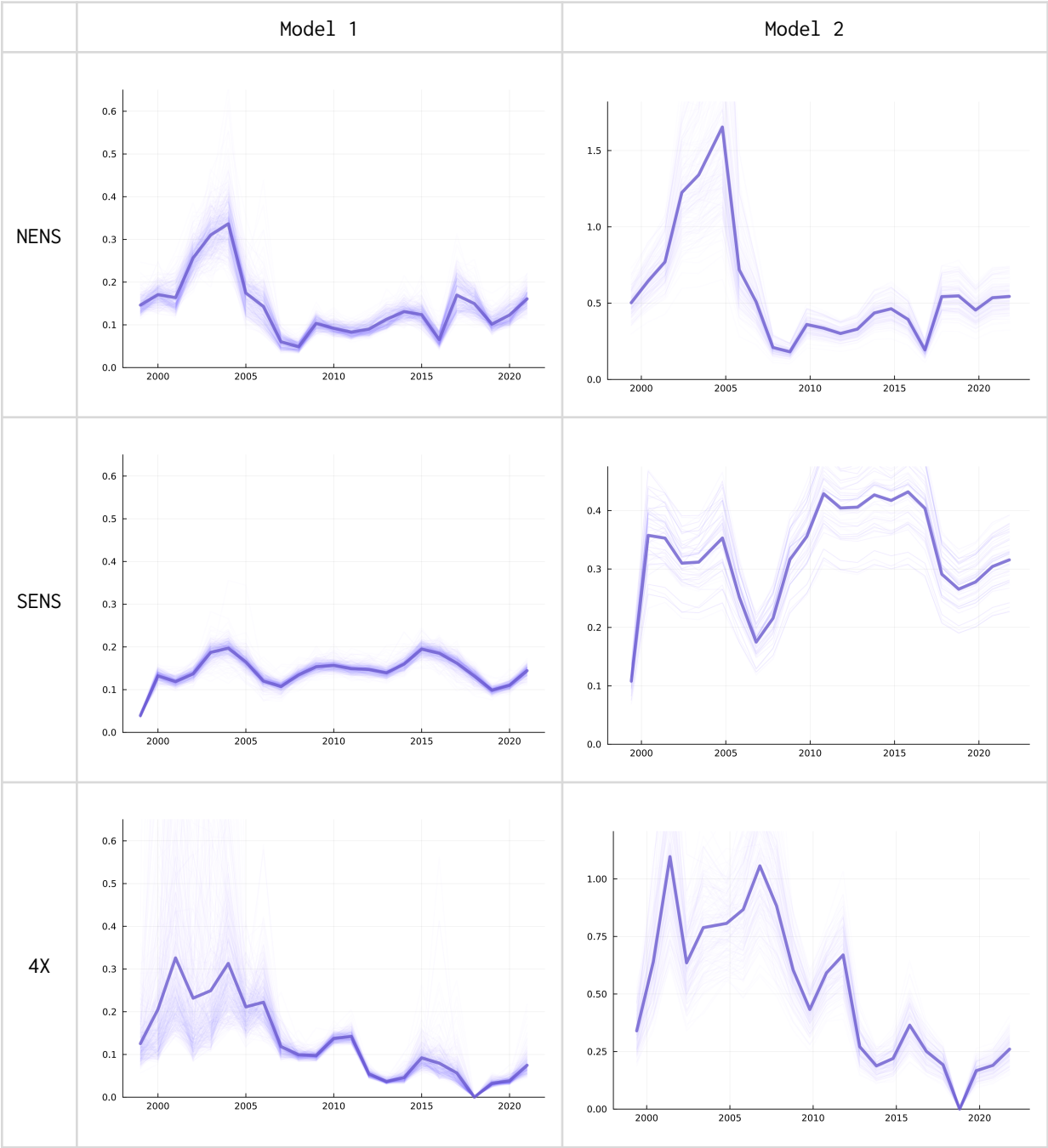

Figure 8. Instantaneous fishing mortality estimated from Models 1 and 2 across time. The overall patterns of fishing mortality are similar across models. However, the overall magnitudes are much higher in Model 2. Fishing in 4X was closed in 2018 due to low abundance estimates and warm environmental conditions.

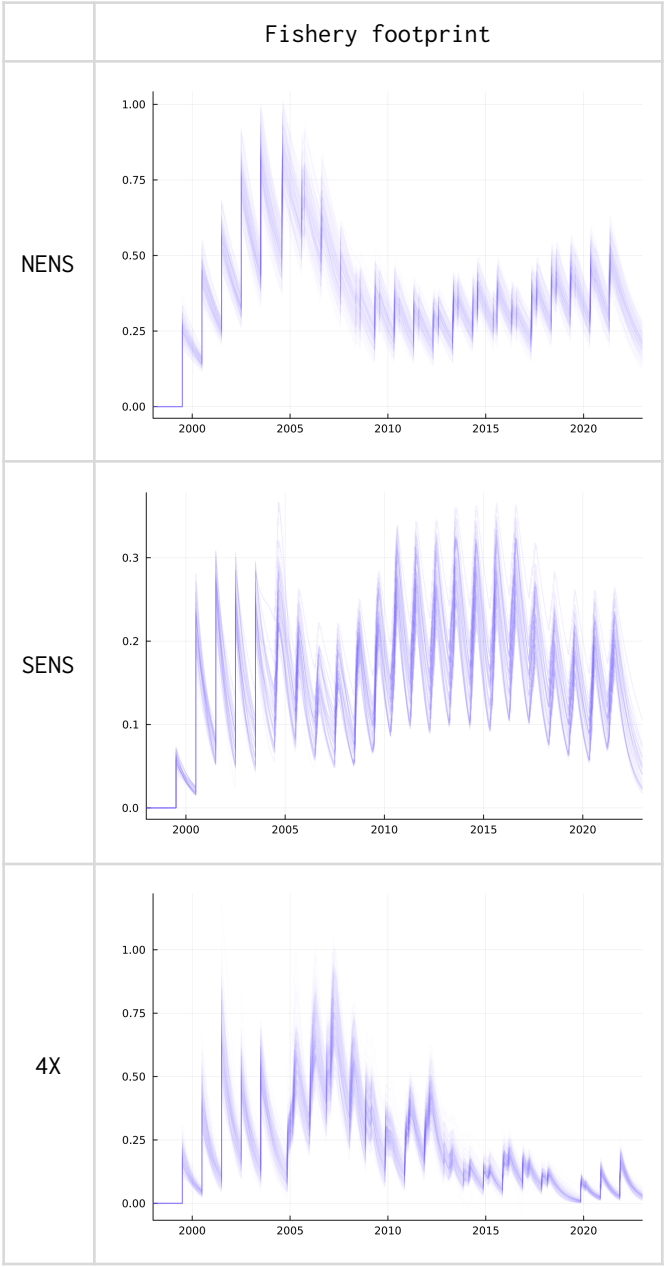

Figure 9. Posterior realizations (n=200) of Fisheries footprint for each area of study derived from Model 2

Conclusions

In studies of exploited marine animal populations, most models focus upon age structure (Quinn 2003). Most also tend to be temporally discrete (annual) difference equation models. This is largely due to the annual nature of exploitation, and data assimilation, survey and assessment cycles and historically due to limitations to computational capacity. With such discretizations, come various approximations and assumptions and ultimately potential error or bias from temporal (and spatial) aliasing. Space is treated as an externality or more usually, completely ignored, though of course, advection-diffusion differential equation models are readily formulated.

The continuous approach that we developed in this study addresses mechanisms in a structured manner. The additional model complexity succeeds in providing a similar and perhaps more reasonable understanding of snow crab population dynamics than the classical biomass dynamics model. It also permits a promising way forward towards describing the footprint of a fishery measured relative to potential abundance in the absence of fishing. It also identifies that there are difficulties that need to be addressed: most notably the non-"well-mixed" nature of the areas studied show spatial and temporal structures that require further parameterization and development.

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Appendix 1. Model continuum

Population dynamics can be studied in many ways. Arguably, the simplest is to see it as a single component such as the total number of individuals, as in the logistic equation (eq. 1). Such single component models have a long tradition (Verhulst 1845, McKendrick & Pai 1912, Pearl & Reed 1920, Lotka 1925, Bacaër 2011). This we will refer to as a *phenomenological* perspective in that it abstracts a multitude of processes and interactions into very few externally facing parameters and one state variable (population size). Often used for such cases, the logistic model specifies dynamics with two parameters: a maximum specific rate of change, and some upper limit. Their utility and properties are well known and used in many domains.

Discriminating subcomponents of a population, as we did in Model 2, such as sex, age or size groups, phenotype and genotypes, one can follow increasingly more refined components over time and space. This we will refer to as an aggregate "mean-field", "*mechanistic*" perspective. For example, ecophysiological models characterize the average aggregate level processes under the assumption that individual-level metabolic rates (e.g., per capita rates of consumption, egestion, excretion, respiration, predation, somatic, gonadal growth, etc.) are relevant to aggregate level estimates to create mass-balance, mean-field type models (Kitchell et al. 1974, Boudreau & Dickie 1992, Bundy 2004).

When this discrimination extends to each individual with equally unique rules of interactions for every individual, these models are known as *individual-based* perspective. They too are simple, but this simplicity is in the types of interactions rather than the number of components. The interactions are biologically recognizable mechanisms: this individual grew 10 cm, this individual died at 9.25 years, this individual reproduced and gave birth to 2 females, and this individual moved 10.5 km to find good habitat. Some individuals will grow faster and this has consequences upon other aspects of their interactions with other organisms and reproduction and death.

Though simple in concept, the application of *individual-based* models is actually quite difficult in that the rules need to be carefully constructed to describe correlated mean processes and also the variability between individuals. The rules thus tend to be probabilistic and context dependent. The rules can be modified to explore "what if" scenarios via stochastic simulation and eventually aggregated to offer insights on dynamic and spatial control measures. They tend to be most expressive when the number of individuals are low and stochastic effects become significant and observable (e.g., a countable population of whales). But estimating these rules is a challenge due to the open-ended and contingent manner in which they apply to a particular set of environmental conditions, in a particular population, with a particular phylogenetic history, surrounded by predators and prey that are themselves also subject to their own particularities. Their open-endedness means that some other factor may have been missed or misrepresented and so inferences are difficult to generalize beyond the model domain.

Mechanistic models with some intermediate number of subcomponents, therefore, represent a reasoned balance between number of components and number of interactions. Their focus is upon the manner in which the mean (and sometimes the variability) changes with time, usually specified by differential equations. Identifying informative subcomponents is dependent upon the peculiarities of a particular system (species or population) that permit useful abstraction or simplifying assumptions. The drawback of these models is that they still require a lot of information and skill to parameterize them, information that is usually not available or observable, causing assumptions to be made that are not always justified.

Appendix 2. Logistic model

Verhulst's original formulation of the logistic equation was used to model Belgium's population growth (Verhulst 1845, Bacaër 2011). His arguments alluded to Malthusian geometric (exponential) growth with some upper limit. The intrinsic rate of increase (r) representing the exponential rate of increase while carrying capacity (K) represented this limit. Subsequently (McKendrick & Pai 1912) used it for bacterial growth and then (Pearl & Reed 1920, Lotka 1925) used it for the US population. It continues to be used today in numerous fields due to its underlying sigmoid shape (Beverton & Holt 1957, Pianka 1970, Bohner & Chieochan 2013).

Lotka (1925) recognized that the logistic equation can more simply be seen as a 2nd order Taylor series approximation of any general function $\frac{dN}{dt} = G(N)$, evaluated at N=0 and $O(N^h)$ are higher order terms greater of power h>2:

$$\frac{dN}{dt} = rN - (rK^{-1})\,N^2 + O(N^h).$$

Pianka (1970 Fig. 9.5) suggested a slightly different perspective on the logistic equation. He begins with birth and death rates that are linear functions of abundance: $\beta = \beta_0 - eN$, and $\delta = \delta_0 + fN$. At equilibrium, K, $\beta = \delta$ due to the intersection of the lines, which gives $\beta_0 - eK = \delta_0 + fK$, and so:

$$r_0 = \beta_0 - \delta_0 = (e - f)\,K.$$

Away from equilibrium, after some algebra, we obtain the logistic equation:

$$\frac{dN}{dt} = rN = ((\beta_0 - eN) - (\delta_0 + fN))\,N = r_0 N - r_0 N^2.$$

Interestingly, the sigmoid Beverton-Holt difference equation has also been shown to be related to the logistic equation (Beverton & Holt 1957, Bohner & Chieochan 2013):

$$n_{t+1} = \frac{\nu K n_t}{K_t + (\nu - 1) n_t}.$$

It is discrete in time and also sigmoid in shape with asymptotic limit (carrying capacity that varies with time) $K_t > 0$ and growth rate $\nu > 1$, for number $n_t > 0$. If we define: $r = (\nu - 1)/\nu$ then $\nu = 1/(1 - r)$, then substitution and solving for n_t and then Δn_t gives: $\Delta n_t = r n_{t+1}(K_t - n_{t+1})/(K_t - r n_{t+1})$, which simplifies further to the discrete logistic difference equation: $\Delta n_t = r n_{t+1}(1 - n_t/K_t)$. In the limit as $\Delta t \to 0$, this becomes the differential form of the logistic equation: $dn/dt = rn(1 - n/K_t)$.

Finally, another similar model, the "logistic discrete map", could be used for parameter estimation. The "discrete logistic map" is often represented as a Euler approximation of the logistic differential equation, $\frac{dZ}{dt} = r\,Z\,(1 - Z\,K^{-1})$. Normalization of Z to $z = Z/K$ allows simplification to: $\frac{dz}{dt} = r\,z(1 - z)$. The Euler approximation for a small increment of time $\tau_{t+1} = \tau_t + \Delta\tau$, z in the next time interval is estimated as: $z_{t+1} = z_t + \Delta\tau \cdot \frac{dz}{dt}|_{z_t}$, which upon substitution of the differential equation and simplification gives: $z_{t+1} = (1 + \Delta\tau\,r)\,z_t - \Delta\tau\,r\,z_t^{\,2}$. The identities: $\rho = 1 + \Delta\tau\,r$, and $n_t = \frac{\Delta\tau\,r\,z_t}{\rho}$, help to simplify further: $n_{t+1} = \frac{\Delta\tau\,r\,z_{t+1}}{\rho}$. Substitution of the identity of z_{t+1} to gives: $n_{t+1} = \frac{\Delta\tau\,r\,((1+\Delta\tau\,r)\,z_t - \Delta\tau\,r\,z_t^{\,2})}{\rho} = \rho\,n_t(1 - n_t)$. Note that ρ is $1 + rescaled(r)$, where recalled means it is a fractional change relative to the previous *time step*. Similarly, n are rescaled values of z, more meaningful with a time step of Δt. Importantly, this derivation is for infinitesimal changes in time. If the increment in time is relatively large, such as $\Delta t = 1\ year$, as it is commonly used in fisheries applications, the "infinitesimal" change assumption is not biologically reasonable.