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Original Research Article

An individual-based probabilistic model for simulating fisheries population dynamics

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ABSTRACT

The purpose of stock assessment is to support managers to provide intelligent decisions regarding removal from fish populations. Errors in assessment models may have devastating impacts on the population fitness and negative impacts on the economy of the resource users. Thus, accurate estimations of population size, growth rates are critical for success. Evaluating and testing the behavior and performance of stock assessment models and assessing the consequences of model mis-specification and the impact of management strategies requires an operating model that accurately describe the dynamics of the target species, and can resolve spatial and seasonal changes. In addition, the most thorough evaluations of assessment models use an operating model that takes a different form than the assessment model. This paper presents an individual-based probabilistic model used to simulate the complex dynamics of populations and their associated fisheries. Various components of population dynamics are expressed as random Bernoulli trials in the model and detailed life and fishery histories of each individual are tracked over their life span. The simulation model is designed to be flexible so it can be used for different species and fisheries. It can simulate mixing among multiple stocks and link stock-recruit relationships to environmental factors. Furthermore, the model allows for flexibility in sub-models (e.g., growth and recruitment) and model assumptions (e.g., age- or size-dependent selectivity). This model enables the user to conduct various simulation studies, including testing the performance of assessment models under different assumptions, assessing the impacts of model mis-specification and evaluating management strategies.

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1. Introduction

Fish population dynamics describe how a population changes over time as a function of growth, recruitment, mortality, immigration and emigration (Quinn & Deriso, 1999). It is the basis for understanding fish populations and associated fisheries and is the central component in stock assessment models to provide quantitative advice for fishery management (Hilborn & Walters, 1992).

Modern fisheries stock assessment models are evolving towards increasing complexity (Maunder & Punt, 2013), with capabilities to assimilate a diverse suite of data and incorporate spatial structure

(Cadurin & Secor, 2009) and the influence of environmental factors. However, the behavior and performance of these complex models need to be tested to assure a scientific basis for fishery management. As a result, extensive simulation studies have been conducted to examine the robustness of the models and incorporate various process and measurement errors, including data quality and quantity (Chen et al., 2003), mis-specifications of life history parameters (Deroba & Schueller, 2013; Punt, 2003), fishery characteristics (Cope & Punt, 2011), and violations of model assumptions (Guan, Cao, Chen, & Cieri, 2013).

Testing the sensitivity of assessment models for mis-specifications requires an operating model to predict population dynamics with known or assumed population parameters. However, most operating models are formulated identically to the population dynamic component built into the assessment model (Cope & Punt, 2011; Deroba & Schueller, 2013; Guan et al., 2013; Punt, 2003), which implicitly assumes that the dynamic processes of the population are fully understood. To avoid this problem and

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test the assessment rigorously, an alternatively structured operating model is necessary to simulate the population dynamics.

Individual-based models, which consider each individual of a population as an independent entity, have been widely used in ecology (Grimm & Railsback, 2005). The events (e.g., birth, death and predation) that occur within the simulation are at an individual rather than population level and the overall population dynamics that emerged is the sum of the individual interactions and behaviors.

The majority of individual-based models in fisheries science are developed to investigating fish behavior and fleet dynamics. They have been used to simulate the behavior of individual fish or fishermen with rules that determine their movement (Tyler & Rose, 1994; Wilson & Yan, 2009). Spatial heterogeneities in individuals and/or their environment have been added to develop spatially explicit individual-based models (Werner, Quinlan, Lough, & Lynch, 2001). However, only a few of these models have been developed for simulating fishery population dynamics. Kanaiwa, Chen, and Wilson (2008) developed an individual-based lobster simulator to simulate seasonal, sex-specific population dynamics for the American lobsters to evaluate the assessment model for that species. Further, the models that have been developed are either species-specific or focused on one particular aspect of fish life history (Kanaiwa et al., 2008).

In this paper we develop a generalized individual-based probabilistic model for simulating multi-stock fishery population dynamics. The functional component of this model is that the various aspects of the population dynamics are expressed as random Bernoulli trials and that super-individuals can be set to represent a number of homogenous individuals to reduce the computing time (Scheffer, Bavoco, DeAngelis, Rose, & Van Nes, 1995). The number of fish represented by the super-individual is a variable which depends on the number of super-individuals specified in the model. The model is able to simulate multiple stocks with unique biological parameters and multiple geographic areas can be defined to account for heterogeneity in fishing mortality or migration of fish in the various areas. Detailed life and fishery histories of each super-individual (e.g., recruitment, death, movement, growth, maturity, changes in life stage) are tracked over its life span, until death by natural or fishery-related causes. Every aspect of the population can be assessed with or without user-defined observation error.

This general type of operating model can be used to (1) test model performance under different population dynamic scenarios; (2) investigate various scientific questions related to data quantity and quality, model assumptions and model mis-specifications; and (3) evaluate management strategies. In this paper we present the details of an individual-based probabilistic model we developed. This is the first time that an individual-based probabilistic model in fisheries science is able to address these questions using a flexible model in many areas. We used the Atlantic herring and Northern shrimp populations in the Gulf of Maine as examples to illustrate the flexibility and generality of the developed model.

We intend that it will be used by as a tool to help fisheries scientist to test the appropriateness of stock assessment models and management options for fisheries. The code is written in C++, but programming knowledge is not necessary to use. All the input files are provided as text files that the C++ code can read automatically.

2. Model description

The schematic diagram of the individual-based probabilistic model is shown in Fig. 1. The basic structural unit of the population represented in the model is the super-individual which consist of a number of homogenous individuals. Detailed life and fishery history of each individual is tracked through time until it is removed

from the system by mortality or the simulation time-period has expired. Each individual has eight attributes (weight, length, age, sex, life stage, maturity condition, spatial location and stock identification) that are recorded and updated after each time step. For each time step, individuals have probabilities of dying naturally, being caught in the fishery or the fishery-independent survey, growing, maturing, changing life stage or sex and moving to another stock area (Fig. 1). Time step can be defined with a minimum resolution of one day. For each time step individual statistics are aggregated to population level outputs, including fishery and survey catch numbers by size and sex, maturity and recruitment (though individual records are also maintained).

2.1. Initial conditions

The simulated population always begins in equilibrium state, which the model identifies based on the input parameters (e.g., natural mortality, fishing mortality, growth, stock-recruit relationship) and an assumed time period for reaching equilibrium (a “burn-in” period). The best practice is to test various burn-in periods of different length to ensure the simulation has in fact reached an equilibrium state. Stock size and recruitment are then initialized in simulation year 0 using the equilibrium values.

2.2. Stock spatial structure

The model is able to simulate multiple stocks with movement among different areas (i.e., stocks can exist across multiple areas and multiple stocks may share the same area). Stocks can have unique biological parameters; for example, each stock may have its own growth parameters, natural mortality and maturity. Movement is modeled using a matrix that describes the probability of an individual moving to a given area at a given time step. Each stock may be assumed reproductively isolated (i.e., a stock-specific stock-recruit relationship) or not isolated (i.e., recruits mix throughout and stock-recruit curve is evaluated using the total spawning stock biomass).

2.3. Stock recruitment relationship

Unless recruitment by time-step is input directly into the model, a stock recruitment relationship is used. Spawning stock biomass is the biomass of all the mature individuals or matured females at the spawning time either for a given sub-stock or across the whole stock. Recruitment is related to spawning stock biomass according to a specified functional relationship. Four options for stock recruitment models are built into the simulator: (1) Ricker model (Equation (1)); (2) Beverton-Holt model (Equation (2)); (3) Re-parameterized Beverton-Holt model with parameters for average virgin spawning stock biomass (SSB_0) and steepness (τ) (Equations (3) and (4); Francis, 1992); or (4) environmental factors (e.g., sea surface temperature) can be incorporated (e.g., Richards, Fogarty, Mountain, & Taylor, 2012). The relevant equations are:

$$R = \alpha SSB e^{-\beta SSB} \quad (1)$$

$$R = \frac{\alpha SSB}{\beta + SSB} \quad (2)$$

$$\alpha = \frac{4\tau(SSB_0/SPR_0)}{5\tau - 1} \quad (3)$$

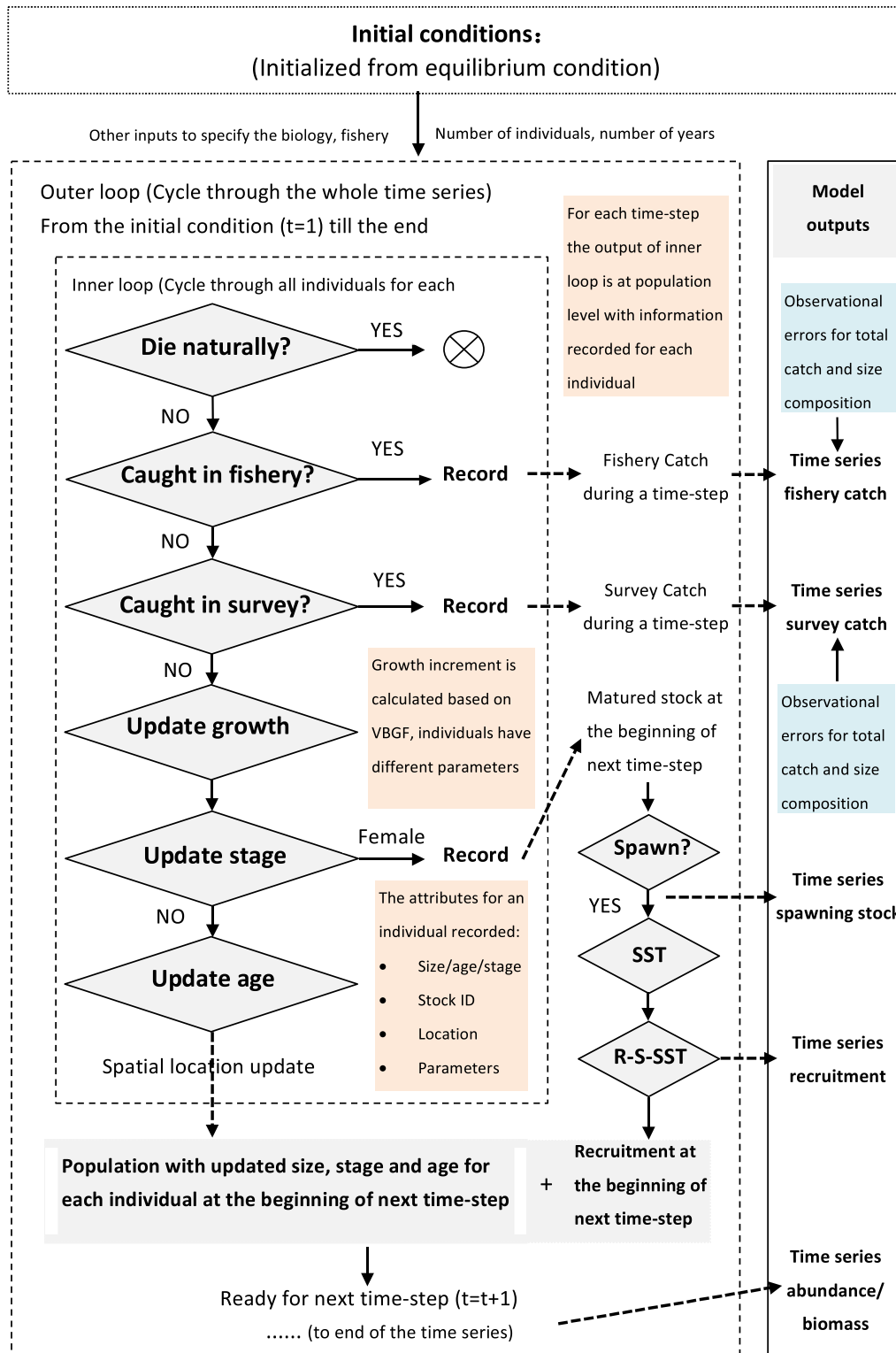


Fig. 1. Schematic diagram of the individual-based probabilistic model.

parameterized using SSB_0 and τ , SPR_0 is the spawning stock per recruit at equilibrium calculated at the end of the “burn-in” period.

$$\beta = \frac{SSB_0(1 - \tau)}{5\tau - 1} \quad (4)$$

where R is recruitment, SSB is spawning stock biomass, α and β in Eqs. (1) and (2) are parameters, α and β in Eqs. (3) and (4) are

2.4. Recruitment

Annual stock-specific recruitment can be input directly or calculated with specified error from a stock recruitment

relationship (see above). For all recruitment, the following attributes must be defined: (1) total number of recruits (can be input or obtained from a stock-recruit relationship); (4) sex ratio; (5) life stage; (6) length; (7) stock identification and (8) location. Additionally, if the model time-step is less than the recruitment time-step, the model allows annual recruitment to be partitioned into several peaks and thus individuals can recruit to the population at time steps finer than the stock-recruitment step. The user specifies the proportion of total recruits that appear at each of the smaller time-steps.

2.5. Natural mortality

Natural mortality is treated as a random event for each individual with a user-defined probability. For each individual during each time step, a random number (*Rand*) will be generated from a uniform distribution between 0 and 1, and this is compared to $1 - e^{-M}$ (the time-step probability of natural death, *P*), where *M* is the time-step-specific natural mortality for that particular individual. If $P > Rand$ then that particular individual dies and is removed from the population. Natural mortality can be defined as age- or length-dependent. All the individuals that die naturally are recorded.

2.6. Fishing mortality

Fishing mortality for time step *t*, fleet *f*, in area *h* is determined by the catchability *q*, fishing effort *E*, and fishery selectivity *S*. Fishery selectivity can be either age or size dependent. Size-dependent and age-dependent fishing mortality are formulated respectively as:

$$F_{l,t,f,h} = q_{f,t,h} E_{f,t,h} S_{l,h,f} \quad (5)$$

$$F_{a,t,f,h} = q_{f,t,h} E_{f,t,h} S_{a,h,f} \quad (6)$$

where *l* is length and *a* is age. Fishing mortality at the individual level is modeled similarly to natural mortality. A particular individual is caught by the fishery if $1 - e^{-F}$ is greater than a random number drawn from the uniform distribution between 0 and 1.

2.7. Growth

Growth is modeled as continuous process using the growth increment formula of the Von Bertalanffy growth function,

$$\Delta L = (L_{\infty} - L) (1 - e^{-K}) \quad (7)$$

where ΔL is the growth increment, L_{∞} is the average asymptotic length of individuals and *K* is the Brody growth coefficient. For each individual during a given time step, size increment can be modeled in two ways: (1) Parameters L_{∞} and *K* are randomly drawn from a multivariate normal distribution with defined means, standard deviations and a correlation between the two parameters; or (2) every individual with the same length grow an increment that is drawn randomly from a normal distribution with a specified mean and variance. The mean is obtained from the von Bertalanffy model and the variance is calculated according to the model used by Chen et al. (2003). Weight is modeled using a power function,

$$W = aL^b \quad (8)$$

where *W* is the weight, *L* is length, *a* and *b* are two user-defined parameters.

2.8. Life stage

For some species (e.g. shrimp), it is important to model changes in life stage (Alonzo et al., 2008). These can be assumed size- or age-dependent and are modeled using a normal distribution. The number of stages, along with a mean size or age per stage and associated variance must be defined by the user. The probability of a stage change *P* is the cumulative probability from the size or age distribution of the next subsequent life stage for an individual at a particular age or length. If a uniform random number *Rand* on the interval (0, 1) is larger than *P*, the individual will remain in the same life stage.

2.9. Survey

A fishery-independent survey occurs at predefined times set by the user. The probability (*P*) that an individual is recorded by survey *y* at the time when the survey is conducted is modeled as:

$$P_y = q_y S_y k \quad (9)$$

where q_y is the catchability for survey *y*, S_y is the selectivity for survey *y* (either age- or length-dependent), and *k* is a coefficient that increases the probability to ensure enough individuals are recorded in the survey for analyses outside the simulation (such as input for a stock assessment model). All the individuals recorded by surveys have their attributes logged and are not removed from the population.

3. Observational error

Fishery and survey catch are the sum of all the individuals that died from fishing mortality or were recorded in the fishery-independent survey. Since individuals have all their attributes recorded, catch is easily aggregated by time, age, length, area, stock or life history stage. Observation error can be added to catch and catch composition (i.e., age or length) data. The error of total catch is assumed to follow a log normal distribution:

$$Catch_{m,r,y,O} = Catch_{m,r,y,P} e^{\epsilon} \quad (10)$$

where $Catch_{m,r,y,O}$ is the observed catch of year *y*, month *m*, and stock *r*, $Catch_{m,r,y,P}$ is the predicted catch of year *y*, month *m*, and stock *r*, and $\epsilon \sim N(0, \log(CV^2 + 1))$. CV is the user-defined coefficient of variation. Age or length composition of catch is assumed to follow a multinomial distribution, from which random vectors are drawn to simulate the observed age or length composition. The expected probabilities for each size or age class are the true probabilities from the simulation and the number of trials used in drawing numbers from the distribution equals the effective sample size (i.e., 100) to be used.

4. Application

Two species that inhabit the northwest Atlantic, Atlantic herring (*Clupea harengus*) and Northern shrimp (*Pandalus borealis*), that have very different biological characteristics are used as examples to illustrate the model's generality and flexibility.

Atlantic herring of the Gulf of Maine/Georges Bank stock is an important pelagic fishery in the northeastern US and also a major prey item for ground fish, marine mammals, large pelagic fishes, and seabirds (Kanwit & Libby, 2009; Overholtz et al., 2004). Two stocks of herring, the Gulf of Maine (GOM) and Georges Bank (GB), and four geographic areas are defined in simulating the herring fishery population dynamics.

In this example, the two stocks move among the areas at different times of the year for feeding, spawning and overwintering (Overholtz et al., 2004; Reid et al., 1999). Catch data is separated into two gear types: fixed and mobile (Legault & Restrepo, 1998). In order to simplify the example, fishing effort is distributed homogeneously among the four areas and the two stocks share the same biological parameters. The summary of our parameterization is shown in Table 1. The values of most parameters are taken from a recent stock assessment conducted by the US National Marine Fisheries Service (Shepherd, Cieri, Powers, & Overholtz, 2009). Natural mortality, maturity, fishery and survey selectivity are assumed to be age-dependent. Stock-recruitment is modeled using the re-parameterized Beverton-Holt model and recruitment is assumed to occur at the beginning of each year. Two fishery-independent surveys conducted in spring and fall are simulated.

Northern shrimp supports an important fishery in the GOM (ASMFC, 2009). One important biological characteristic of northern shrimp is that they are hermaphrodites, maturing first as males at about 2.5 years old and transforming into females at about 3.5 years old. Most are females by the time and their carapace length reaches 22 mm (ASMFC, 2009). It is important to incorporate sex change into the assessment model (Alonzo et al., 2008). However, there is no direct evidence suggesting whether sex change is age-dependent or size-dependent. The fishery has always been seasonal in nature, peaking in late winter when egg-bearing females move into inshore waters (ASMFC, 2009).

In this example, northern shrimp in the GOM are considered as a single stock. Two seasonal fisheries (trawl and trap) are defined in the simulation. The parameter settings of the simulation come from a stock assessment report (ASMFC, 2009, Table 1). Natural mortality, maturity, and fishery and survey selectivity are assumed to be size-dependent. Annual recruitment occurs at the beginning of each year and is input directly. There is a single fishery-independent survey conducted in spring.

The simulated stage variable, abundance is multidimensional (i.e., the number of attributes associated with an individual). The abundance of herring and shrimp over time aggregated by any attribute can be easily compiled, for example stock- and stage-specific abundance by time (Fig. 2 and Fig. 3).

5. Discussion

In this paper we describe a generalized individual-based probabilistic model to simulate fishery population dynamics. The simulation methods are straightforward and can be used by modelers and fisheries biologists to examine scientific questions regarding stock assessment and management strategies.

In order to identify misleading assumptions that may be implicit in the design of a stock assessment model, it is critical to develop an operating model that has a different structure from the assessment model. The simulation discussed here is flexible and detailed and allows for various assumptions regarding the population, fishing activities and spatial structures. It is generic and thus applicable to many fisheries. In addition the resolution is high enough for most applications as it can be run for individuals on a daily time scale. These characteristics make the simulation applicable to study a range of topics related to stock assessment and management (e.g., age- and size-structured assessment model comparisons, impacts of model time steps).

Among the models developed to describe fisheries population dynamics, only few are individual-based (Kanaiwa et al., 2008). Most operating models used in simulation studies are population-based models which are identical to the assessment models they are built to examine (Deroba & Schueller, 2013; Guan et al., 2013; Punt, 2003). In addition, population-based models are either age- or length-structured and so are not resolved finely enough to determine a “true” length distribution within each age class, making comparisons between length- and age-based assessment models impossible without making assumptions regarding length error at age.

With respect to spatial components of fisheries population dynamics, most simulation models cannot incorporate multiple stocks with movement among different fishing areas. This brings substantial flexibility in modeling and enables one to examine a variety of hypotheses about spatial dynamics of populations, exploitation and management. The model can incorporate an unlimited number of sub-stocks existing within different areas. Sub-stocks can have different spatial and seasonal distributions and fishing effort can vary by area.

Another important characteristic of this model pertains to the time-step. The finest time resolution is one day. However, a daily

Table 1
Summary of simulation configurations for Atlantic herring and Northern shrimp.

Item	Herring	Shrimp
Number of stocks	2	1
Number of areas	4	1
Number of stages	1	5
Sex ratio (F/T)	0.5	1
Time horizon	1965–2011	1985–2006
Time step	Month	Month
Natural mortality	Age dependent	Size dependent
Maturity	Age dependent (logistic)	Size dependent (logistic)
Growth parameters	VBGF (multivariate normal)	VBGF (multivariate normal)
Stock-recruit	Re-parameterized B-H	Input directly
Recruitment	Normal with mean 7.2 and variance 1.5	Normal with mean 7.2 and variance 1.5
Recruitment time	Beginning of the year	Beginning of the year
Minimum age	1	1
Minimum length	4 cm	4 mm
Number of fleet	2	2
Fishery selectivity	Age dependent (by age)	Size dependent (logistic)
Fishery catchability	Constant (0.01)	Constant (0.01)
Fishing effort	Assessment report (Shepherd et al., 2009)	Assessment report (ASMFC, 2009, 2012)
Number of surveys	2	1
Survey selectivity	Age dependent (by age)	Size dependent (logistic)
Survey catchability	Constant (0.018)	Constant (0.018)
Survey time	March/September	March

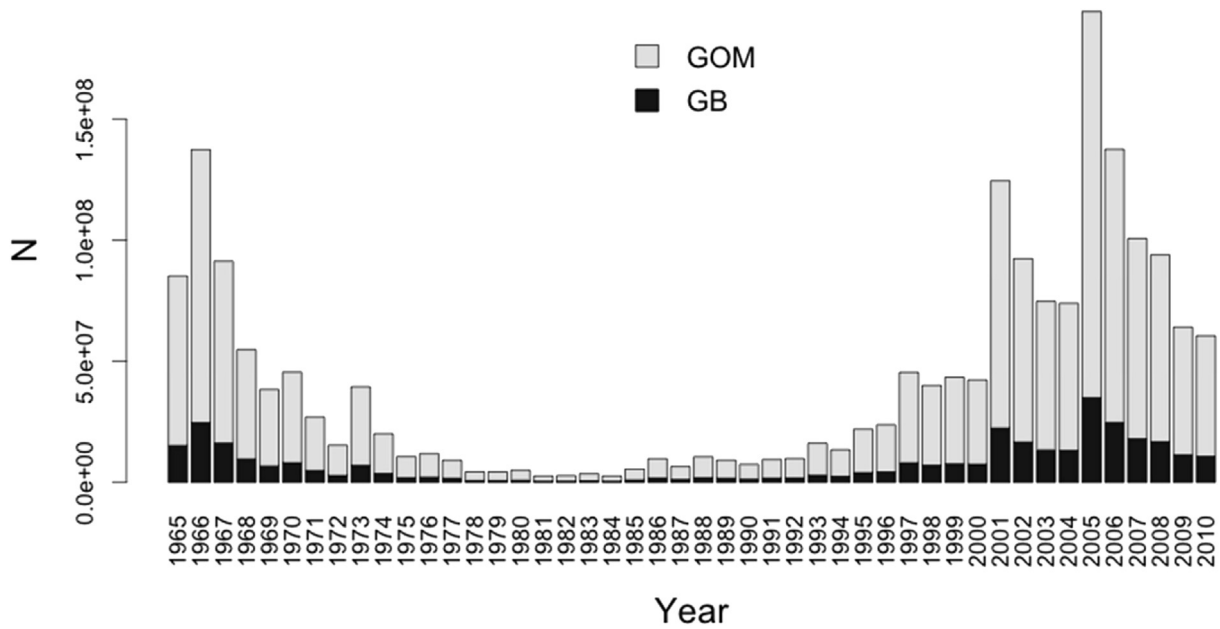


Fig. 2. Simulated Gulf of Maine and Georges Bank herring abundance over time.

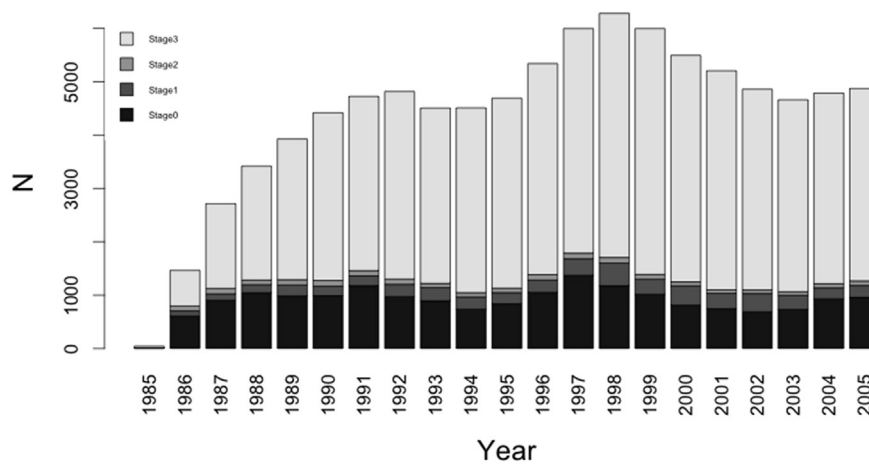


Fig. 3. Simulated stage-specific Northern shrimp abundance over time.

time-step requires substantial computing time and is not necessary in most circumstances. A monthly time-step is a good choice to reflect seasonal variations. Parameter inputs as well as processes such as growth, natural mortality can vary through time as is the case for natural populations.

We have identified a number of desirable properties of this simulation model: (1) it's generic and flexible; (2) it can output data that can be used directly to evaluate stock assessment models; (3) there is no limit on the number of sub-stocks and management areas; (4) the model is individual-based and avoids being identical to any known assessment model; and (5) environmental factors can be easily incorporated in the stock-recruit relationship. We therefore envision that this simulation model would be particularly useful in situations where retrospective patterns in the stock assessment are likely to be induced by changing climate conditions.

As noted earlier, the program will be freely available on the Internet to make simulation studies regarding stock assessment and management easier. This will enable fisheries scientists to better understand the limitations of assessment models and make

appropriate changes. Questions or comments on the code or the simulation implementation are welcome and can be directed to the corresponding author listed above.

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References

- Alonzo, S. H., Ish, T., Key, M., MacCall, A. D., & Mangel, M. (2008). The importance of incorporating protogynous sex change into stock assessments. *Bulletin of Marine Science*, 83(1), 163–179.
- ASMFC. (2009). *Assessment report for Gulf of Maine northern shrimp -2009*. ASMFC Fishery Management Report, 68 p.
- ASMFC. (2012). *Assessment report for Gulf of Maine northern shrimp -2012*. ASMFC Fishery Management Report, 81p.
- Cadrin, S. X., & Secor, D. H. (2009). Accounting for spatial population structure in stock assessment: Past, present and future. In R. J. Beamish, & B. J. Rothschild

- (Eds.), *The future of fishery science in North America* (pp. 405–426). Dordrecht: Springer.
- Chen, Y., Chen, L., & Stergiou, K. (2003b). Quantity of fisheries data and uncertainty in stock assessment. *Aquatic Science*, 65, 92–98.
- Chen, Y., Hunter, M., Vadas, R., & Beal, B. (2003a). Developing a growth-transition matrix for the stock assessment of the green sea urchin (*Strongylocentrotus droebachiensis*) off Maine. *Fishery Bulletin*, 101(4), 737–744.
- Cope, J. M., & Punt, A. E. (2011). Reconciling stock assessment and management scales under conditions of spatially varying catch histories. *Fisheries Research*, 107, 22–38.
- Deroba, J. J., & Schueller, A. M. (2013). Performance of stock assessments with misspecified age-and time-varying natural mortality. *Fisheries Research*, 146, 27–40.
- Francis, R. I. C. C. (1992). Use of risk analysis to assess fishery management strategies: A case study using orange roughy (*Hoplostethus atlanticus*) on the Chatham Rise, New Zealand. *Canadian Journal of Fisheries and Aquatic Sciences*, 49, 922–930.
- Grimm, V., & Railsback, S. F. (2005). *Individual-based modeling and ecology*. Princeton university press.
- Guan, W. J., Cao, J., Chen, Y., & Cieri, M. (2013). Impacts of population and fishery spatial structures on fishery stock assessment. *Canadian Journal of Fisheries and Aquatic Sciences*, 70(8), 1178–1189.
- Hilborn, R., & Walters, C. (1992). *Quantitative fisheries stock assessment: Choice, dynamics, and uncertainty*. N.Y: Chapman and Hall.
- Kanaiwa, M., Chen, Y., & Wilson, C. (2008). Evaluating a seasonal, sex-specific size-structured stock assessment model for the American lobster, *Homarus americanus*. *Marine and Freshwater Research*, 59(1), 41–56.
- Kanwit, J. K., & Libby, D. A. (2009). Seasonal movements of atlantic herring (*Clupea harengus*): Results from a four year tagging study conducted in the Gulf of Maine and Southern New England. *Journal of the Northwest Atlantic Fishery Science*, 40, 29–39.
- Legault, C. M., & Restrepo, V. R. (1998). *A flexible forward age-structured assessment program*. 49 pp. 246–253. ICCAT. Col. Vol. Sci. Pap.
- Maunder, M. N., & Punt, A. E. (2013). A review of integrated analysis in fisheries stock assessment. *Fisheries Research*, 142, 61–74.
- Overholtz, W. J., Jacobson, L. D., Melvin, G. D., Cieri, M., Power, M., Libby, D., et al. (2004). *Stock assessment of the Gulf of Maine - Georges Bank atlantic herring complex*, 2003. Northeast Fisheries Science Center Reference Document 04-06. Woods Hole, MA: National Marine Fisheries Service. Available from: <http://www.nefsc.noaa.gov/publications/crd/crd0406/crd0406.pdf> [accessed 22 July 2012].
- Punt, A. E. (2003). The performance of a size-structured stock assessment method in the face of spatial heterogeneity in growth. *Fisheries Research*, 65(1), 391–409.
- Quinn, T. J., & Deriso, R. B. (1999). *Quantitative fish dynamics*. New York: Qxford University Press.
- Reid, R. N., Cargnelli, L. M., Griesbach, S. J., Packer, D. B., Johnson, D. L., Zetlin, C. A., et al. (1999). *Essential fish habitat source document: Atlantic herring, Clupea harengus, life history and habitat characteristics*. NOAA Tech. Memo. NMFS-NE-126. Woods Hole, MA: U. S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northeast Region, Northeast Fisheries Science Center. Available from: <http://www.nefsc.noaa.gov/publications/tm/tm126/> [accessed 22 July 2012].
- Richards, R., Fogarty, M. J., Mountain, D. G., & Taylor, M. H. (2012). Climate change and northern shrimp recruitment variability in the Gulf of Maine. *Marine Ecology Progress Series*, 464, 167–178.
- Scheffer, M., Baveco, J. M., DeAngelis, D. L., Rose, K. A., & Van Nes, E. H. (1995). Super-individuals a simple solution for modelling large populations on an individual basis. *Ecological modelling*, 80(2), 161–170.
- Shepherd, G., Cieri, M., Powers, M., & Overholtz, W. (2009). *Transboundary resources assessment Committee: Gulf of Maine/Georges Bank atlantic herring stock assessment update*. Reference Document 2009/04. Woods Hole, Massachusetts: NOAA Fisheries, Northeast Fisheries Science Center.
- Tyler, J. A., & Rose, K. A. (1994). Individual variability and spatial heterogeneity in fish population models. *Reviews in Fish Biology and Fisheries*, 4, 91–123.
- Werner, F. E., Quinlan, J. A., Lough, R. G., & Lynch, D. R. (2001). Spatially-explicit individual based modeling of marine populations: A review of the advances in the 1990s. *Sarsia*, 86(6), 411–421.
- Wilson, J. A., & Yan, L. (2009). Self-organizing economic activity with costly information. In *Proceedings of the 11th annual conference companion on genetic and evolutionary computation conference. Late breaking papers*. ACM.