



Abstract—Crustacean species are socioeconomically and ecologically crucial across the world. For crustaceans, as ectotherms, anthropogenic climate change threatens to significantly alter key life history characteristics, such as size at maturity and growth rate. Because crustaceans are difficult to age, length data are used in assessments of crustacean stocks; however, climate-induced changes in maturation and growth can greatly influence the performance of size-structured stock assessment models. We coupled individual-based and size-structured models for American lobster (*Homarus americanus*) off northeastern North America in the Gulf of Maine—to conduct a novel sensitivity analysis of the effects of maturity and growth-related input parameters on model outputs. For this analysis, we used a bottom-up approach (with parameters shifted independently) and a top-down approach (with parameters shifted jointly as they were predicted to be influenced by climate change). We found that our American lobster stock assessment model is resilient to relatively extreme shifts in biological input parameters. For size-structured modeling in assessments of crustacean stocks, we recommend the expansion of sensitivity analyses to include evaluation of the influence of climate-driven changes on input parameters based on time-varying life history traits.

Manuscript submitted 21 February 2022.
Manuscript accepted 23 August 2022.
Fish. Bull. 120:240–251 (2022).
Online publication date: 21 September 2022.
doi: 10.7755/FB.120.3-4.5

The views and opinions expressed or implied in this article are those of the author (or authors) and do not necessarily reflect the position of the National Marine Fisheries Service, NOAA.

Climate-driven changes in growth and size at maturity of Gulf of Maine lobster stocks: implications for stock assessment models

Cameron T. Hodgdon (contact author)^{1,2}

Noah S. Khalsa²

Mackenzie D. Mazur³

Yong Chen²

Email address for contact author: cameron.hodgdon@maine.edu

¹ School of Marine Sciences
University of Maine
5741 Libby Hall, Room 221
Orono, Maine 04469

² School of Marine and Atmospheric Sciences
Stony Brook University
Stony Brook, New York 11790

³ Pacific Biological Station
Fisheries and Oceans Canada
3190 Hammond Bay Road
Nanaimo, British Columbia V9T6N7, Canada

Anthropogenic climate change is transforming many marine ecosystems through warming waters, ocean acidification, freshening, and deoxygenation (Brander, 2010; Doney et al., 2012; Gattuso et al., 2018; Doney et al., 2020). Perturbations to the abiotic environment, in particular to temperature, are especially influential on marine ectotherms because they do not physiologically regulate their body temperature (Huey et al., 1993; Madeira et al., 2012); rather, their body temperature is driven by the environment. As a consequence, temperature directly influences individual and population-level biological processes of crustacean species, such as metabolism, recruitment, reproduction, growth, size at maturity, and natural mortality (Madeira et al., 2012), which have significant implications for assessment and management of crustacean fisheries (Audzijonyte et al., 2016). Typically, in data-rich crustacean stock assessments, size-structured models are used (Punt et al., 2013), and the outputs of such models can be influenced by environmentally driven variability in input parameters

based on size-related life history characteristics, such as growth and size at maturity. Therefore, it is important to quantify how climate-driven shifts in key life history characteristics will influence crustacean stocks and will manifest in assessment models used for guiding future management decisions.

The American lobster (*Homarus americanus*) is an ecologically and socioeconomically vital crustacean species in the northwestern Atlantic Ocean (Le Bris et al., 2018), and the biology of this species is directly influenced by temperature. American lobster, like many crustaceans, grow through a series of molts, also known as ecdysis. During ecdysis, the old carapace is replaced with a new, larger one (Herrick, 1911). Molting typically occurs annually in adult American lobster, although it can happen more than once or be skipped entirely depending on the size, age, and maturity of the individual (Herrick, 1911; Aiken and Waddy, 1976; Aiken, 1977; Comeau and Savoie, 2001). Although the physiology of individual American lobster is known to influence growth processes, temperature is

a primary abiotic driver of growth changes in this species. Rising temperatures have been shown to increase molting frequency and decrease molting increment, the length a lobster grows in a given molting event (Aiken, 1977). Additionally, in several studies, rising temperatures were found to contribute to reduced sizes at maturities for American lobster (Little and Watson, 2003, 2005; Le Bris et al., 2017; Waller et al., 2021). Indeed, climate-driven changes in these life history characteristics can likely affect results from the size-structured stock assessment model currently used for management of American lobster (ASMFC, 2020).

Understanding the effect that climate-driven shifts in input parameters for life history characteristics have on stock assessment model outputs is critical for future model development and fisheries management. In a recent study, incorporating temperature-driven recruitment was found to improve the performance of a size-structured stock assessment model for American lobster (Tanaka et al., 2019). When simulating the effects of pooling multiple populations of red rock lobster (*Jasus edwardsii*) with varying growth rates, the performance of a size-structured stock assessment model was not reduced (Punt, 2003), indicating that accounting for different growth rates of assessed populations may not be consequential for estimating reference points. If pooling population data of red rock lobster had reduced model performance, it may have indicated a need to further consider the importance of variable growth in future assessments of the population. In contrast, other research results indicate that failing to account for the plasticity of growth in fisheries stock assessment models can lead to deviations of more than 30% in outputs, critically altering the calculation of reference points (Lorenzen, 2016). Indeed, depending on the species biology and stock assessment model design, changes in growth can have inconsistent effects on model outputs.

Typically, sensitivity analyses can evaluate whether uncertainties in model assumptions, input data sources, and biological parameters have an effect on reference points or other model outputs (Maunder and Punt, 2013; Maunder and Piner, 2015). However, in these analyses, adjustments to inputs usually are considered only on their own, rather than in combination (Lehuta et al., 2010; Saltelli et al., 2019), and these analyses seldom involve testing model sensitivity to inputs that are based on life history traits and developed outside of the assessment model, such as growth transition matrices. Given the potential for dissimilar consequences of changing life history characteristics for stock assessment model outputs and the yet unrealized but possible shifts in crustacean growth in the future, it is important to evaluate the sensitivity of size-structured stock assessment models on a case-by-case basis.

In our study, we conducted a novel sensitivity analysis of a length-structured stock assessment model for American lobster by using an individual-based simulation model to evaluate the sensitivity of the model to shifts in growth-related life history input parameters, specifically molting probability, molt increment probability, and size at maturity. In a series of sensitivity analyses, we used classical bottom-up methods in which each parameter was shifted

independently, and we used a top-down approach in which parameters were jointly shifted under the driving mechanism of climate change. We used both approaches to ascertain at what point shifts in these input parameters could result in a significant change in the stock status time series estimated with the length-structured stock assessment model, relative to a historical baseline. Our overarching goal for this study was to determine the extent of the influence that climate change has on the reliability and robustness of outputs from the stock assessment model used for American lobster in the Gulf of Maine.

Materials and methods

Shifting growth and size at maturity

Seasonal growth matrices in this study were calculated by using an individual-based lobster simulator model (IBLS) first developed by Chen et al. (2005) and later expanded by Chang (2015) and Mazur et al. (2018). This model simulates individual lobster from recruitment to mortality by sending each lobster through random Bernoulli trials representative of life history and fishery parameters derived from prior field research and modeling (Chen et al., 2005; Chang, 2015; Mazur et al., 2018). This seasonal probabilistic model is used to simulate lobster fishery dynamics to capture complex fishery-dependent and fishery-independent processes (Chen et al., 2005; Zhang et al., 2011) and has historically been used to test the performance of the American lobster stock assessment model (Chen et al., 2005). The model creates individual lobster records over a given time series that include sex, size bin, carapace length (CL), maturity, and mortality, allowing calculation of population abundance, spawning stock biomass, and landings (Mazur et al., 2018). A full explanation of this model can be found in Mazur et al. (2018).

The IBLS can be used to create seasonal growth matrices by simulating lobster with total absence of fishery-dependent and fishery-independent mortality as well as recruitment. Effectively, the abundance of lobster remains constant over the simulated time series, but the biomass changes exclusively because of input of data on growth of the animals. At each step, a lobster is in 1 of 35 size bins (in increments of 5 mm, from 53 mm CL to ≥ 223 mm CL). The simulation was run long enough that every lobster ended up in the final size bin at the end of the time series. Every growth instance for every lobster for a given season over the entire time series is marked in a matrix with the size bin before the molting event on the x -axis and the size bin after the molting event on the y -axis, and the matrix is scaled so that the sum of each row is effectively 1. This simulation creates a probabilistic growth matrix in which each row is a function of size change for a given lobster of that size class. This process is done 4 times, once for each season: winter (January–March), spring (April–June), summer (July–September), and fall (October–December).

The growth inputs to the IBLS are 2 independent factors: molting probability and probability for different molt

increments. Molting probability is the probability of a lobster molting in a particular time step dependent on the CL, maturation status of the individual, and how many seasons it has gone without molting (Fig. 1). Molt increment probability is the probability of a lobster growing a certain size (1–20 mm CL in 1-mm-CL bins) because of a molting event and is dependent on the CL of the individual (Fig. 1). The input data for these parameters in the base case of the IBLs came from the stock assessment conducted in 2015 (ASMFC, 2015).

Because of climate change, American lobster are expected to molt more frequently but grow less per molt (ASMFC, 2015). To simulate these effects on overall growth, both molting probability (P_M) and molt increment probability (P_{MI}) were manipulated in the IBLs. Molting probability was increased by shifting left in relation to seasons since the prior molt (Fig. 1) and was described by the following equations:

$$P_M = \frac{yas + b_1}{k_{CL}}, \quad (1)$$

$$yas = \begin{cases} 1, \dots, k_{CL} & \text{if immature} \\ 2, \dots, k_{CL} & \text{if mature; and} \end{cases} \quad (2)$$

$$k_{CL} = 1 + e^{-8.08127 + 0.076535CL}, \quad (3)$$

where yas = time spent (in units of the time step of the model; in this case, the unit is seasons) at current size of an individual lobster;

k_{CL} = the longest time a lobster of a given CL (in millimeters) could feasibly go before molting (NEFSC, 1996; ASMFC¹); and

b_1 = the shifting parameter.

Therefore, a b_1 of 1 would represent a shift of 1 season, increasing the overall probability of molting in comparison to the unshifted probability.

Average size increase per molt was lowered by shifting molt increment probability left in relation to the size increase per molt (Fig. 1), described by using the equations below:

$$P_{MI} = N(\overline{\Delta L_L} - b_2, \sigma^2), \quad (4)$$

$$\overline{\Delta L_L} = \begin{cases} 1.2236 + 0.1294L & \text{for males with } L < 95; \\ 1.2236 + (0.1294 \times 95) & \text{for males with } L \geq 95; \\ 1.2288 + 0.1285L & \text{for females with } L < 82; \text{ and} \\ 1.2288 + (0.1285 \times 82) & \text{for females with } L \geq 82, \end{cases} \quad (5)$$

where N = the normal distribution truncated by upper and lower boundary probabilities of 0.975 and

0.025, respectively, with standard deviation (σ) being equal to 2.1 (ASMFC²);

L = the current length (in millimeters);

ΔL_L = the change in length (in millimeters), given L and sex; and

b_2 = the shifting parameter.

Therefore, a b_2 of 1 would represent a shift of 1 mm, decreasing the overall size increment change during a given molt.

To maintain some biological realism, shifts of molting probability and molt increment probability were paired, and the corresponding growth matrices reflect possible effects from climate change. Two paired shifts were used in this study. The first paired shift, hereafter referred to as $G1$, was a leftward shift of molting probability by 1 year and of molt increment probability by 1 size bin ($b_1=b_2=1$) (Fig. 1). The second paired shift, hereafter referred to as $G2$, was a leftward shift of molting probability by 2 seasons and of molt increment probability by 2 size bins ($b_1=b_2=2$) (Fig. 1).

Probabilistic size at maturity (P_{SAM}) in the IBLs is calculated with the below equation:

$$P_{SAM} = \frac{1}{1 + e^{-0.3 \times (CL - L_{50})}}, \quad (6)$$

where P_{SAM} = the probability of maturity of an individual lobster of a given CL (in millimeters); and

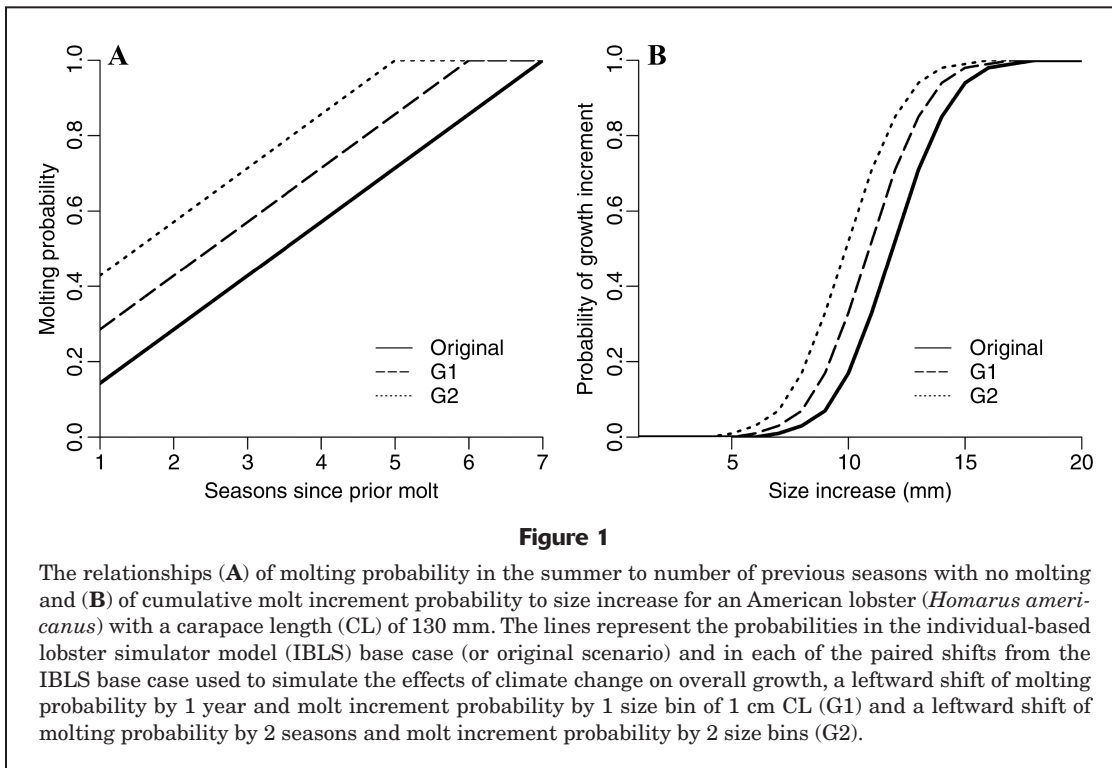
L_{50} = the predefined CL (in millimeters) at 50% maturity.

The parameter L_{50} was set to 90.81 mm CL for the IBLs base case (ASMFC, 2015). Given that size at maturity for American lobster is expected to decrease 2.8 mm CL per 1°C rise in bottom temperature (Le Bris et al., 2017) and that current projections of bottom temperature for the Gulf of Maine are for an increase up to 2°C by 2050 and up to 4°C by 2100 (IPCC, 2019; Brickman et al., 2021), the L_{50} values of 85.21 and 79.61 mm CL were additionally tested in this study. These lengths are not considered projected values of size at maturity, but rather they are the L_{50} values needed in calculations to provide reasonable levels of change from historical data for the sensitivity analyses.

The IBLs were used to generate a total of 7 sets of growth matrices in this study (with 4 matrices in each set corresponding to seasons) (Table 1). The first set (the IBLs base case) was calculated with the original (unshifted) molt probability and molt increment probability paired with the original L_{50} value of 90.81 mm. The next 4 sets of matrices were calculated under IBLs scenarios 2–5, with shifts of either growth ($G1$ or $G2$) or L_{50} (85.21 or 79.61 mm CL), and the last 2 sets were calculated under IBLs scenarios 6 and 7, with paired shifts of both growth and L_{50} ($G1$ and 85.21 mm CL or $G2$ and 79.21 mm CL). Scenarios

¹ ASMFC (Atlantic States Marine Fisheries Commission). 2000. American lobster stock assessment report for peer review. Atl. States Mar. Fish. Comm., Stock Assess. Rep. 00-01 (Suppl.), 334 p. ASMFC, Arlington, VA. [Available from [website](#).]

² ASMFC (Atlantic States Marine Fisheries Commission). 2006. American lobster stock assessment report for peer review. Atl. States Mar. Fish. Comm., Stock Assess. Rep. 06-03 (Suppl.), 175 p. ASMFC, Boston, MA. [Available from [website](#).]

**Table 1**

Individual-based lobster simulator (IBLS) scenarios for American lobster (*Homarus americanus*) in the Gulf of Maine. The parameters of the scenarios are a paired set of shifts in molting probability and molt increment probability for the growth dynamic and the predefined carapace length at 50% maturity (L_{50}) for each scenario. The IBLS base case or original scenario includes input data from the American lobster benchmark stock assessment conducted by the Atlantic States Marine Fisheries Commission in 2015. The paired shifts in growth factors are a leftward shift of molting probability by 1 year and molt increment probability by 1 size bin (G1) and a leftward shift of molting probability by 2 seasons and molt increment probability by 2 size bins (G2).

Parameter	IBLS scenario						
	1	2	3	4	5	6	7
Growth dynamic	Original	G1	G2	Original	Original	G1	G2
L_{50} (mm)	90.81	90.81	90.81	85.21	79.61	85.21	79.61

2–5 were used to observe effects from specific parameters, whereas scenarios 6–7 were meant to provide outputs that are more biologically realistic and expected given the predicted relationships between climate change and the life history traits on which these parameters are based. Additionally, an analysis of time-varying growth and size-at-maturity parameters was conducted. Results of this analysis can be found in [Supplementary Figure 1](#).

Stock assessment and sensitivity analyses

The University of Maine Lobster Stock Assessment Model (UMM) was initially developed by Chen et al. (2005) and

expanded in ASMFC (2015) and Tanaka et al. (2019). It is a seasonal, sex-specific, length-structured assessment model for American lobster in the Gulf of Maine, Georges Bank, and Southern New England. It was designed with input from the Atlantic States Marine Fisheries Commission with the intent that it would be used for future lobster stock assessments. The population dynamics equation of the UMM is as follows:

$$N_{t,s} = \left(N_{t,s-1} \times G_s \times e^{-F_{t,s} + M_s} \right) + R_{t,s}, \quad (7)$$

where $N_{t,s}$ = a vector of the number of lobster in each size bin in year t and season s ;

G = the seasonal growth transition matrix;
 F = the seasonal fishing mortality;
 M = the seasonal natural mortality; and
 R = recruitment abundance for each size bin
 (Chen et al., 2005).

A list of all data used in the UMM consistently across scenarios can be found in Table 2. For more detailed descriptions of this model, see Chen et al. (2005) and Tanaka et al. (2019).

In the base case of the UMM, the original growth matrices and size at maturity of 90.81 mm CL from the IBLS base case were used as input data. Growth transition matrices and size-at-maturity data from the other 6 IBLS scenarios were individually input into the UMM, for a total of 7 scenarios including the UMM base case (all growth matrices used are provided in the [Supplementary Material](#)). For each scenario, biological reference points (BRPs) were calculated for output reference abundance (individuals larger than 53 mm CL) by using the methods outlined in ASMFC (2015): the target was calculated as the 75th percentile of reference abundance over the time series, and the threshold was calculated as the 25th percentile of reference abundance over the time series (ASMFC, 2015). It is important to note that the reference time series for these calculations used by the Atlantic States Marine Fisheries Commission was for the period of 1982–2003, but in this study, we used data from a reference period

of 1984–2003 because of data input limitations. These BRPs allowed determination of historical fishery status over time, meaning simply the reference abundance of a given year in relation to the predefined BRPs (below the 25th percentile, between the 25th and 75th percentile, or above the 75th percentile). By using these reference points, terminal-year stock status was compared between all UMM runs in this study. However, for all sensitivity analyses in this study, historical fishery statuses over the entire time series were compared between each UMM scenario and the UMM base case.

Scenarios 6 and 7 in the IBLS were designed to represent small and large future climate effects, respectively. These effects on growth and size at maturity are plausible given climate projections (IPCC, 2019; Brickman et al., 2021), but it is unknown if these changes are large enough to affect stock status from what it would be under the UMM base case. To this end, a sensitivity analysis was conducted for scenarios 6 and 7 to examine whether stock status differed in consecutive years between the scenario and the UMM base case.

In the sensitivity analyses, IBLS scenarios representative of smaller and smaller incremental shifts in growth and size at maturity were added to determine the level of sensitivity (the breaking point), and those new growth matrices and sizes at maturity from these analyses were used in the UMM. For example, if historical fishery statuses from the UMM in which outputs from IBLS

Table 2

Settings and data that were consistent across scenarios used in the University of Maine Lobster Stock Assessment Model for American lobster (*Homarus americanus*) in the Gulf of Maine. IBLS=individual-based lobster simulator model; SSB/R=spawning stock biomass divided by the number of recruits to the stock; MEDMR=Maine Department of Marine Resources; MADMF=Massachusetts Division of Marine Fisheries; NHFGD=New Hampshire Fish and Game Department; NEFSC=NOAA Northeast Fisheries Science Center.

Setting or data category	Description
Period for time series	1984–2013
No. of seasons	4 (each a 3-month time block, same as IBLS)
No. of sexes	1 (data averaged across males and females)
Size range	53–223 mm carapace length
Size bin length	5 mm carapace length
Initial conditions	First-year size composition from survey data
Recruitment size	53–73 mm carapace length
SSB/R relationship	None
No. of commercial fleets	1
Commercial fleet selectivity at size	Double logistic
Survey data sources	MEDMR Ventless Trap Survey (2006–2012) Spring MEDMR/NHFGD inshore bottom-trawl survey (2001–2013) Fall MEDMR/NHFGD inshore bottom-trawl survey (2000–2013) Spring MADMF bottom-trawl survey (1984–2013) Fall MADMF bottom-trawl survey (1984–2013) Spring NEFSC bottom-trawl survey (1984–2013) Fall NEFSC bottom-trawl survey (1984–2013)
Survey selectivity at size	Double logistic
Fishing mortality rate	Instantaneous
Natural mortality rate	0.15 year ⁻¹

scenario 6 were used did not differ from the status from the UMM base case but the statuses from the UMM in which IBLs scenario 7 outputs were used did differ from the status from the UMM base case, the breaking point of sensitivity would lie somewhere between the shifts represented in the 2 IBLs scenarios.

The next step was to produce growth matrices and estimate a size at maturity for a shift representative of half-way between these 2 shifts. For molting probability, the shift in this step was the average probability of both G1 and G2 for each season since the last molt. For molt increment probability, this shift was the average probability of both G1 and G2 for each size increase in millimeters. For size at maturity, it was simply the average of 85.21 and 79.61 mm CL. Historical fishery statuses and BRPs were then calculated for these new UMM scenarios. Retrospective patterns were also evaluated, and results from these tests can be found in [Supplementary Figures 2–12](#). To further determine the breaking point of sensitivity, we used these new UMM scenarios in the methods described in the previous paragraph in place of either the UMM scenario in which IBLs scenario 6 was used or the UMM scenario in which IBLs scenario 7 was used (depending on whether the results of these new scenarios were significantly different from the UMM base case). This process of determining a breaking point of sensitivity was repeated and continued until a breaking point within one-sixteenth of a shift was found. The results of the sensitivity analyses described in this section can help determine the sensitivity of the UMM to growth and size at maturity and can help to focus future research efforts toward direct linkages of climate change to these life history parameters for use in stock assessment of American lobster.

Results

Target and threshold BRPs for the 7 UMM scenarios can be found in Table 3, and all accompanying reference abundance plots showcasing historical fishery statuses as compared to those of the UMM base case can be found

in Figure 2. Terminal-year stock statuses did not change across any of the 7 UMM runs in this study (Table 4). Most alterations in historical reference abundance from the UMM base case appeared to be related to magnitude: consistent overestimations of abundance per year (except in the UMM scenario in which outputs from IBLs scenario 2 were used, where abundance was underestimated) but similar temporal trends, with slight alterations causing some discrepancies in historical fishery statuses. There was no clear pattern in how each instance of discrepancy across the runs either improved or worsened stock status estimates. Instances of consecutive years differing from the UMM base case are much more relevant because these instances are indicative of larger trend-based differences and not simply 1-year lags that seem to be the reason behind solitary instances of differing years. These instances of differences across consecutive years appeared in only one UMM scenario: scenario 7. In this scenario, a growth shift of G2 and a size at maturity of 79.61 mm CL were used (the large climate effect scenario).

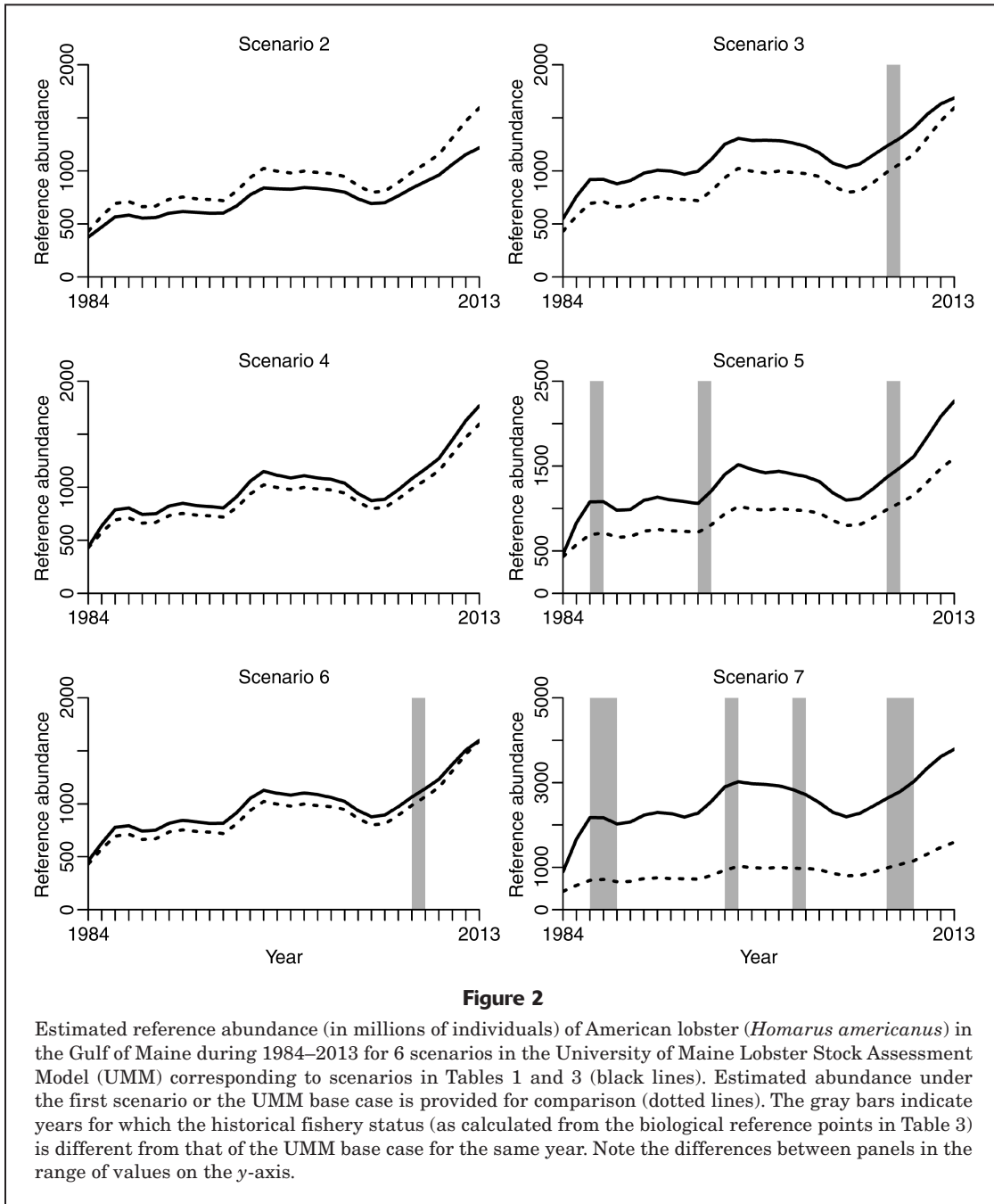
Given that a change in size at maturity of over 10 mm CL did not appear to cause differences between consecutive years in reference abundance independent of a change in growth, a sensitivity analysis was not conducted for this variable. Likewise, changes in growth independent of size at maturity did not appear to cause consecutive-year differences. Therefore, a sensitivity analysis was not conducted for growth independent of size at maturity.

In the biologically realistic scenarios (UMM scenarios in which data from IBLs scenarios 6 and 7 were used), the combination of G1 and the size at maturity of 85.21 mm CL resulted in no consecutive-year differences in historical fishery status when compared to use of the UMM base case. However, the combination of G2 and the size at maturity of 79.61 mm CL resulted in consecutive-year differences compared to use of the UMM base case. Therefore, the breaking points of sensitivity existed somewhere between a small climate effect scenario (G1 and the size at maturity of 85.21 mm CL) and a large climate effect scenario (G2 and the size at maturity of 79.61 mm CL). Results from this sensitivity analysis for these biologically

Table 3

Target and threshold biological reference points (BRPs) for abundance (in millions of individuals) for all University of Maine Lobster Stock Assessment Model (UMM) scenarios for American lobster (*Homarus americanus*) in the Gulf of Maine. In each UMM scenario, the growth transition matrices and size at maturity produced with the corresponding scenario of the individual-based lobster simulator model were used (Table 1). The time series used in the UMM is from the period from 1984 through 2013.

BRP	UMM scenario						
	1	2	3	4	5	6	7
Target	976.0	823.1	1256.3	1078.1	1403.6	1067.0	2857.5
Threshold	707.8	579.6	919.6	801.2	1074.9	788.9	2170.5



realistic scenarios can be found in Figure 3. The final breaking point was between the growth shifts of 1.4375 and 1.5000 and the size at maturity values of 82.41 and 82.76 mm CL.

Discussion

Traditional sensitivity analyses are bottom-up: they are designed to determine how model output changes when specific parameters are altered (Booshehrian et al., 2012; Salciccioli et al., 2016). This practice is commonly used in

stock assessment procedures to determine model stability and quantify uncertainty (Rosenberg and Restrepo, 1994; Hilborn, 2003; Salciccioli et al., 2016). The UMM scenarios in this study that involved IBL scenarios 1–5 are an example of this classic type of analysis. The UMM scenarios in this study that involved IBL scenarios 6–7, however, represent a top-down approach to sensitivity analysis. In this top-down approach, a large model-free mechanism controlled how multiple variables changed together and would affect model results. In this type of approach, the aim is to answer the question of how sensitive the model is to this large mechanism, which was climate change in this study.

Table 4

Terminal-year stock abundance (in millions of individuals) and stock status from each University of Maine Lobster Stock Assessment Model (UMM) scenario for American lobster (*Homarus americanus*) in the Gulf of Maine. Also presented are proportions of each estimate of terminal-year abundance in relation to the target reference point. Stock status is presented in comparison to the biological reference points in Table 3. In each UMM scenario, the growth transition matrices and size at maturity produced with the corresponding individual-based lobster simulator model were used (Table 1). The time series used in the UMM is from the period from 1984 through 2013.

Terminal-year parameter	UMM scenario						
	1	2	3	4	5	6	7
Abundance estimate	1594.5	1217.9	1687.7	1769.5	2265.5	1599.5	3792.7
Stock status	>target	>target	>target	>target	>target	>target	>target
Abundance proportion	1.63	1.48	1.34	1.64	1.61	1.50	1.33

Climate change affects molting probability, molt increment probability, and size at maturity of American lobster together. Therefore, this type of analysis is important to determine these cumulative effects on model outputs, succeeding where traditional sensitivity analyses fail. This type of analysis is sometimes referred to as a global sensitivity analysis and is very rarely used in fishery stock assessments (Lehuta et al., 2010; Saltelli et al., 2019; García, 2020). We agree with the notion of Saltelli et al. (2019) that a lack of the use of this method throughout the fields of environmental science and biology is concerning. We further postulate that both a bottom-up approach and a top-down approach may be beneficial and increasingly imperative in a changing world to ensure that a stock assessment model is stable under ensemble changes brought by large mechanisms.

The sensitivity of the UMM to growth and size at maturity is relatively and biologically low. Size-at-maturity values associated with breaking points in the biologically realistic scenarios are not expected to reach such low levels for at least 50 years (Le Bris et al., 2017; IPCC, 2019; Brickman et al., 2021). The relationship of growth of American lobster to temperature and climate change are well-known (Aiken, 1977; Le Bris et al., 2017), but strict predictions cannot be easily extrapolated and may be less appropriate (Punt et al., 2014). This information, coupled with the fact that most information on these parameters found in laboratory settings may not be directly applicable to scenarios designed to represent conditions in the wild (Jury and Watson, 2013), means that forecasting growth and size at maturity of American lobster is incredibly challenging. An advantage of our modeling framework is that strict relationships of tested parameters to the large mechanism (e.g., climate change or temperature change) are not necessary. The framework is not meant to be used to determine future changes to modeling efforts, but rather results from using it can highlight the limitations of a stock assessment under climate change.

It is important to consider that our study was focused on abundance as an output of interest because it is used to set

management targets and thresholds. However, climate-driven changes to maturity and growth likely affect other aspects of a population and fishery dynamics, such as spawning stock biomass, recruitment, and fishing mortality. The aim of our study was not to analyze the effects of climate change on the full suite of outputs for population and fishery dynamics but rather was to understand whether determinations of fishery stock status would have been different under the climate effects we simulated.

Estimates of terminal-year stock status, most relevant to management of American lobster, did not change over all UMM scenarios in this study, indicating the robustness of the UMM to changes in life history parameters. However, results from using the combination of shifts in growth and size at maturity indicate differences in hind-casted fishery statuses. Consequently, scenarios tested in this study may not alter input data enough to produce different results for current management, but given that historical deviations were present, caution should be given to the assumptions of low sensitivity. Deviations of historical stock statuses were mostly related to magnitude, representing overestimations of abundance of American lobster throughout the time series but having very similar temporal trends. This result is due to the use of relative BRPs calculated for each scenario as opposed to the use of static values over all scenarios. Lobster management, like much of fisheries management in general, is more concerned with trends (ASMFC, 2015) than absolute values. Therefore, large shifts in growth and size at maturity can alter model results but would not have severely affected historical management decisions based on stock status.

As expected, these UMM scenarios all had worse model fits (higher objective function values) than the UMM base case (see [Supplementary Table](#)). These worse fits are most likely due to the approximation of biologically unrealistic, freely estimated parameters in an attempt to fit to the input data while also using the growth and size-at-maturity data provided (Slezak et al., 2010). These differences in fit are not relatively high, even for the largest shifts in this study, but in work on other models,

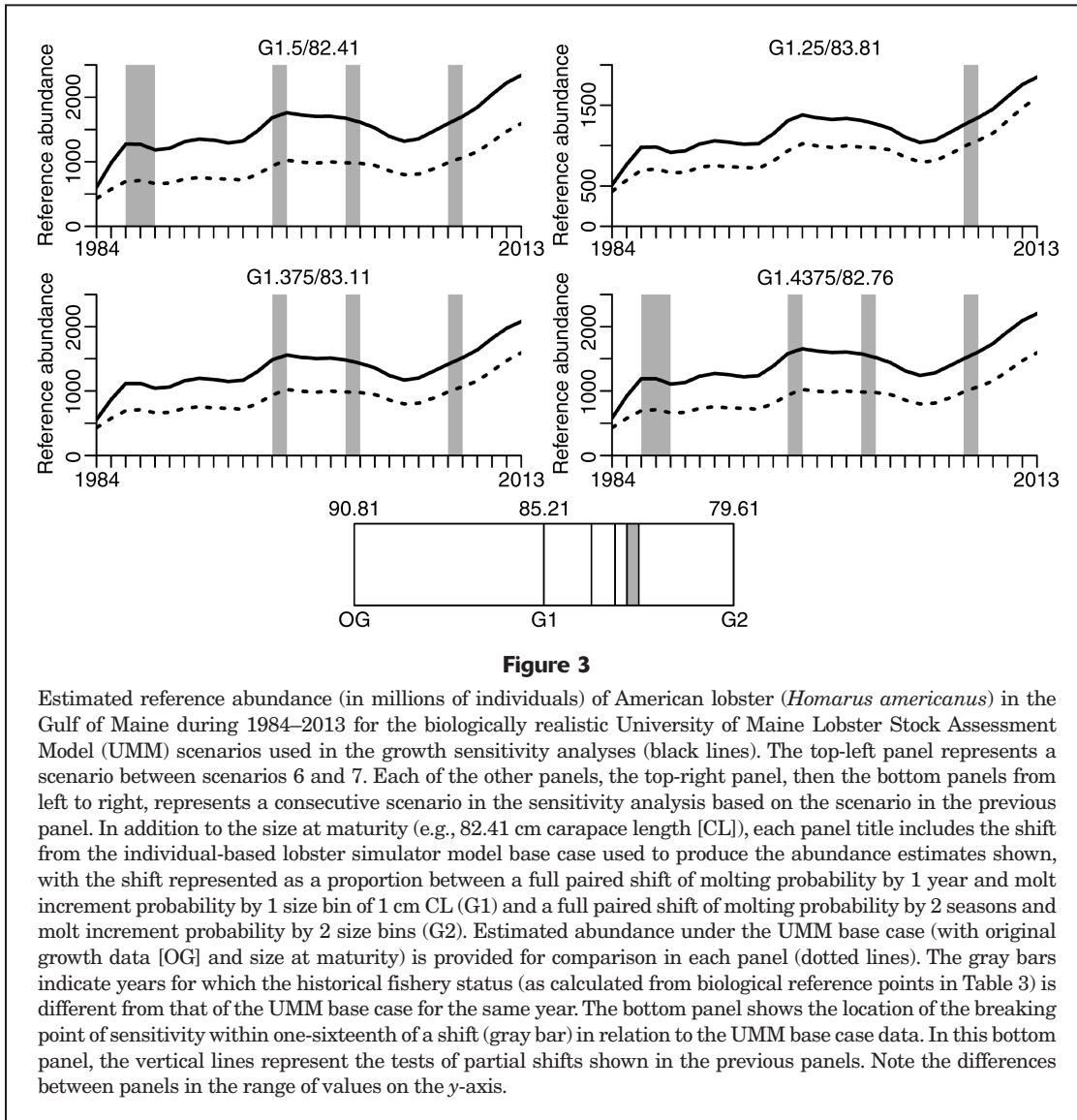


Figure 3

Estimated reference abundance (in millions of individuals) of American lobster (*Homarus americanus*) in the Gulf of Maine during 1984–2013 for the biologically realistic University of Maine Lobster Stock Assessment Model (UMM) scenarios used in the growth sensitivity analyses (black lines). The top-left panel represents a scenario between scenarios 6 and 7. Each of the other panels, the top-right panel, then the bottom panels from left to right, represents a consecutive scenario in the sensitivity analysis based on the scenario in the previous panel. In addition to the size at maturity (e.g., 82.41 cm carapace length [CL]), each panel title includes the shift from the individual-based lobster simulator model base case used to produce the abundance estimates shown, with the shift represented as a proportion between a full paired shift of molting probability by 1 year and molt increment probability by 1 size bin of 1 cm CL (G1) and a full paired shift of molting probability by 2 seasons and molt increment probability by 2 size bins (G2). Estimated abundance under the UMM base case (with original growth data [OG] and size at maturity) is provided for comparison in each panel (dotted lines). The gray bars indicate years for which the historical fishery status (as calculated from biological reference points in Table 3) is different from that of the UMM base case for the same year. The bottom panel shows the location of the breaking point of sensitivity within one-sixteenth of a shift (gray bar) in relation to the UMM base case data. In this bottom panel, the vertical lines represent the tests of partial shifts shown in the previous panels. Note the differences between panels in the range of values on the y-axis.

this phenomenon should be considered. Caution should be used when using this approach, and careful attention should be paid to the freely estimated parameters of the model.

It is important to note the combined effects of shifts in growth and size at maturity. The largest alteration in comparison to the UMM base case occurred when the largest effects from growth and size at maturity were combined. In contrast, results from use of shifts that were smaller than that alteration indicate that combined effects may not be strictly additive, and future work should be focused on the complex relationships of growth, size at maturity, and temperature, especially as they pertain to the American lobster stock assessment model. Quantifying the relationships between these parameters and thermal habitat is a research priority (ASMFC, 2015), but another priority is to develop modeling capacity to handle temporally dynamic life history parameters. If climate change affects

key life history characteristics, traditional stock assessments in which static values for variables, such as growth, size at maturity, and others, are used may be inaccurate (Correa et al., 2021).

A problem, however, highlights a key limitation of the analysis used in the current stock assessment model: climate change affects many other aspects of the life history of American lobster besides growth and size at maturity. Key life history information, such as natural mortality (Mills et al., 2013) and recruitment (Goode et al., 2019; Tanaka et al., 2019), as well as important stock assessment model parameters, such as fishery-dependent and fishery-independent catchability or exploitation (Maunder et al., 2006; Conn, 2010; Shelton et al., 2014), are likely affected by changes in thermal habitat. Complex relationships with all of these factors exist, and a fully comprehensive top-down sensitivity analysis would see climate effects on all of them together.

The top-down approach used in the framework of our study can be used to examine a specific category of life history traits, but in future analyses, this work should be expanded to include effects from other life history and fishery components. Such a fully comprehensive analysis, however, would be possible only after individual studies, such as the one we describe herein or was done by Hodgdon et al. (2020), in which the UMM was tested in the presence of thermal effects on survey catchability, are completed. Temporally dynamic life histories in stock assessment may require quantification of relationships with environmental conditions, but use of them would ultimately increase accuracy in model results and precision of forecasts. Another avenue for future research would be the application of a management strategy evaluation within the current framework. In this work, the IBLs would be used as an operating model so that results from the UMM could have a “true” population to use in comparisons.

Ultimately, knowing the breaking points does not aid management if there is a lack of knowledge on the life history parameters tested a priori, specifically a lack of information concerning the relationship with each of them to thermal habitat and hypotheses as to the predicted scale of future change. Foremost, the need to quantify the relationship that parameters related to life history traits of American lobster have with a changing climate is critical and is a concern that management shares (ASMFC, 2015). Such work is considered essential because comparison of predicted changes to the stock assessment model’s breaking points aids in determining research necessity. If the breaking points are higher than the predicted changes, changes under climate change may not significantly affect stock assessments if data for the life history parameters (e.g., growth and size at maturity) are not updated. If the breaking points are lower than the predicted changes, modeling efforts with parameter data that have not been updated may no longer yield accurate results, and the aim of future research should be to improve understanding of those parameters for which information is old.

Conclusions

In this study, we used a novel top-down sensitivity analysis for American lobster in the Gulf of Maine. This framework has great potential to better the management of the fishery for this species, but it should be expanded in future work. Lobster and, by extension, crustacean physiology and life history are directly linked to the environment and most often are consequences of thermal habitat (Madeira et al., 2012). As climate change alters the thermal habitats of crustaceans, the data used in stock assessment methods that rely on life history characteristics can become out of date. This issue can be mitigated with persistent monitoring efforts and scientific research. However, many crustacean fisheries, even in well-funded jurisdictions such as the United States, have

limited resources for such cost-intensive research efforts. The framework proposed in this paper can be used to possibly lessen research loads by prioritizing the input parameters to which a specific stock assessment model is most sensitive under the top-down mechanism of climate change. A complete analysis of dependent and independent effects from all variables together under this framework has the potential to aid management practices, to advance crustacean stock assessment, and to steer future research projects.

Resumen

Las especies de crustáceos son socioeconómica y ecológicamente cruciales en todo el mundo. Para los crustáceos, como ectotermos, el cambio climático antropogénico amenaza con alterar significativamente las características clave de su historia de vida, como la talla de madurez y la tasa de crecimiento. Dado que es difícil determinar la edad de los crustáceos, los datos de longitud se utilizan en las evaluaciones de sus poblaciones; sin embargo, los cambios en la maduración y el crecimiento, por efecto del clima pueden influir en gran medida en el desempeño de los modelos estructurados por talla en la evaluación de las poblaciones. Acoplamos modelos individuales y estructurados por talla para la langosta americana (*Homarus americanus*) frente al noreste de Norteamérica, en el golfo de Maine, para realizar un novedoso análisis de sensibilidad del efecto de los parámetros de entrada de madurez y crecimiento en los resultados del modelo. Para este análisis, utilizamos un enfoque ascendente (con parámetros modificados de forma independiente) y un enfoque descendente (con parámetros modificados de forma conjunta a medida que se preveía su influencia por el cambio climático). Encontramos que nuestro modelo de evaluación de la población de langosta americana es resiliente a los cambios relativamente extremos de los parámetros biológicos de entrada. Para la evaluación de poblaciones de crustáceos con modelos estructurados por talla, recomendamos ampliar los análisis de sensibilidad para incluir la evaluación de la influencia de los cambios provocados por el clima sobre los parámetros de entrada basados en los rasgos del ciclo de vida que varían con el tiempo.

Acknowledgments

We thank all members of the Chen Lab at the University of Maine and Stony Brook University for their help and feedback throughout this process. We would also like to thank B. Shank of the NOAA Northeast Fisheries Science Center for providing much supportive feedback and to J. Kipp of the Atlantic States Marine Fisheries Commission for supplying the necessary trawl survey data. This study was financially supported by the National Marine Fisheries Service Sea Grant Joint Fellowship Program in Population and Ecosystem Dynamics and Marine Resource Economics (award no. NA20OAR4170464).

Literature cited

- Aiken, D. E.
1977. Molting and growth in decapod crustaceans, with particular reference to the lobster *Homarus americanus*. In Workshop on lobster and rock lobster ecology and physiology. CSIRO Circ. 7 (B. F. Phillips and J. S. Cobb, eds.), p. 41–73. CSIRO, Melbourne, Australia.
- Aiken, D. E., and S. L. Waddy.
1976. Controlling growth and reproduction in the American lobster. Proc. Annu. Meet. World Maric. Soc. 7:415–430. [Crossref](#)
- ASMFC (Atlantic States Marine Fisheries Commission).
2015. American lobster benchmark stock assessment and peer review report, 417 p. ASMFC, Arlington, VA. [Available from [website](#).]
2020. 2020 American lobster benchmark stock assessment and peer review report, 447 p. ASMFC, Arlington, VA. [Available from [website](#).]
- Audzijonyte, A., E. Fulton, M. Haddon, F. Helidoniotis, A. J. Hobday, A. Kuparinen, J. Morrongiello, A. D. M. Smith, J. Upston, and R. S. Waples.
2016. Trends and management implications of human-influenced life-history changes in marine ectotherms. Fish Fish. 17:1005–1028. [Crossref](#)
- Booshehrian, M., T. Möller, R. M. Peterman, and T. Munzner.
2012. Vismon: facilitating analysis of trade-offs, uncertainty, and sensitivity in fisheries management decision making. Comput. Graph. Forum 31:1235–1244. [Crossref](#)
- Brander, K.
2010. Impacts of climate change on fisheries. J. Mar. Syst. 79:389–402. [Crossref](#)
- Brickman, D., M. A. Alexander, A. Pershing, J. D. Scott, and Z. Wang.
2021. Projections of physical conditions in the Gulf of Maine in 2050. Elem. Sci. Anthropol. 9(1):00055. [Crossref](#)
- Chang, J.-H.
2015. Population dynamics of American lobster: environmental, ecological, and economic perspectives. Ph.D. diss., 160 p. Univ. Maine, Orono, ME. [Available from [website](#).]
- Chen, Y., M. Kanaiwa, and C. Wilson.
2005. Developing and evaluating a size-structured stock assessment model for the American lobster, *Homarus americanus*, fishery. N.Z. J. Mar. Freshw. Res. 39:645–660. [Crossref](#)
- Comeau, M., and F. Savoie.
2001. Growth increment and molt frequency of the American lobster (*Homarus americanus*) in the southwestern Gulf of St. Lawrence. J. Crustac. Biol. 21:923–936. [Crossref](#)
- Conn, P. B.
2010. Hierarchical analysis of multiple noisy abundance indices. Can. J. Fish. Aquat. Sci. 67:108–120. [Crossref](#)
- Correa, G. M., C. R. McGilliard, L. Ciannelli, and C. Fuentes.
2021. Spatial and temporal variability in somatic growth in fisheries stock assessment models: evaluating the consequences of misspecification. ICES J. Mar. Sci. 78:1900–1908. [Crossref](#)
- Doney, S. C., M. Ruckelshaus, J. E. Duffy, J. P. Barry, F. Chan, C. A. English, H. M. Galindo, J. M. Grebmeier, A. B. Hollowed, N. Knowlton, et al.
2012. Climate change impacts on marine ecosystems. Annu. Rev. Mar. Sci. 4:11–37. [Crossref](#)
- Doney, S. C., D. S. Busch, S. R. Cooley, and K. J. Kroeker.
2020. The impacts of ocean acidification on marine ecosystems and reliant human communities. Annu. Rev. Environ. Resour. 45:83–112. [Crossref](#)
- García, D.
2020. FLBEIA fisheries management simulation model. Definition of new criteria and guidelines for efficient validation of the model using global sensitivity analysis. Ph.D. diss., 229 p. Univ. Basque Ctry., Leioa, Spain. [Available from Univ. País Vasco, Barrio Sarriena s/n, 48940 Leioa, Spain.]
- Gattuso, J.-P., A. K. Magnan, L. Bopp, W. W. L. Cheung, C. M. Duarte, J. Hinkel, E. Mcleod, F. Micheli, A. Oschlies, P. Williamson, et al.
2018. Ocean solutions to address climate change and its effects on marine ecosystems. Front. Mar. Sci. 5:337. [Crossref](#)
- Goode, A. G., D. C. Brady, R. S. Steneck, and R. A. Wahle.
2019. The brighter side of climate change: how local oceanography amplified a lobster boom in the Gulf of Maine. Glob. Chang. Biol. 25:3906–3917. [Crossref](#)
- Herrick, F. H.
1911. Natural history of the American lobster. Fish. Bull. 29:149–408.
- Hilborn, R.
2003. The state of the art in stock assessment: where we are and where we are going. Sci. Mar. 67(suppl. 1):15–20. [Crossref](#)
- Hodgdon, C. T., K. R. Tanaka, J. Runnebaum, J. Cao, and Y. Chen.
2020. A framework to incorporate environmental effects into stock assessments informed by fishery-independent surveys: a case study with American lobster (*Homarus americanus*). Can. J. Fish. Aquat. Sci. 77:1700–1710. [Crossref](#)
- Huey, R. B., and J. G. Kingsolver.
1993. Evolution of resistance to high temperature in ectotherms. Am. Nat. 142:S21–S46.
- IPCC (Intergovernmental Panel on Climate Change).
2019. Technical summary In IPCC special report on the ocean and cryosphere in a changing climate (H.-O. Pörtner, D. C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, K. Mintenbeck, A. Alegria, M. Nicolai, A. Okem, et al., eds.), p. 39–69. Camb. Univ. Press, Cambridge, UK. [Available from [website](#).]
- Jury, S. H., and W. H. Watson III.
2013. Seasonal and sexual differences in the thermal preferences and movements of American lobsters. Can. J. Fish. Aquat. Sci. 70:1650–1657. [Crossref](#)
- Le Bris, A., A. J. Pershing, J. Gaudette, T. L. Pugh, and K. M. Reardon.
2017. Multi-scale quantification of the effects of temperature on size at maturity in the American lobster (*Homarus americanus*). Fish. Res. 186:397–406. [Crossref](#)
- Le Bris, A., K. E. Mills, R. A. Wahle, Y. Chen, M. A. Alexander, A. J. Allyn, J. G. Schuetz, J. D. Scott, and A. J. Pershing.
2018. Climate vulnerability and resilience in the most valuable North American fishery. Proc. Natl. Acad. Sci. 115:1831–1836. [Crossref](#)
- Lehuta, S., S. Mahévas, P. Petitgas, and D. Pelletier.
2010. Combining sensitivity and uncertainty analysis to evaluate the impact of management measures with ISIS-fish: marine protected areas for the Bay of Biscay anchovy (*Engraulis encrasicolus*) fishery. ICES J. Mar. Sci. 67:1063–1075. [Crossref](#)
- Little, S. A., and W. H. Watson III.
2003. Size at maturity of female American lobsters from an estuarine and coastal population. J. Shellfish Res. 22:857–863.
2005. Differences in the size at maturity of female American lobsters, *Homarus americanus*, captured throughout the range of the offshore fishery. J. Crustac. Biol. 25:585–592. [Crossref](#)
- Lorenzen, K.
2016. Toward a new paradigm for growth modeling in fisheries stock assessments: embracing plasticity and its consequences. Fish. Res. 180:4–22. [Crossref](#)

- Madeira, D., L. Narciso, H. N. Cabral, and C. Vinagre.
2012. Thermal tolerance and potential impacts of climate change on coastal and estuarine organisms. *J. Sea Res.* 70:32–41. [Crossref](#)
- Maunder, M. N., and A. E. Punt.
2013. A review of integrated analysis in fisheries stock assessment. *Fish. Res.* 142:61–74. [Crossref](#)
- Maunder, M. N., and K. R. Piner.
2015. Contemporary fisheries stock assessment: many issues still remain. *ICES J. Mar. Sci.* 72:7–18. [Crossref](#)
- Maunder, M. N., J. R. Sibert, A. Fonteneau, J. Hampton, P. Kleiber, and S. J. Harley.
2006. Interpreting catch per unit effort data to assess the status of individual stocks and communities. *ICES J. Mar. Sci.* 63:1373–1385. [Crossref](#)
- Mazur, M., B. Li, J.-H. Chang, and Y. Chen.
2018. Using an individual-based model to simulate the Gulf of Maine American lobster (*Homarus americanus*) fishery and evaluate the robustness of current management regulations. *Can. J. Fish. Aquat. Sci.* 76:1709–1718. [Crossref](#)
- Mills, K. E., A. J. Pershing, C. J. Brown, Y. Chen, F.-S. Chiang, D. S. Holland, S. Lehuta, J. A. Nye, J. C. Sun, A. C. Thomas, et al.
2013. Fisheries management in a changing climate: lessons from the 2012 ocean heat wave in the Northwest Atlantic. *Oceanography* 26(2):191–195. [Crossref](#)
- NEFSC (Northeast Fisheries Science Center).
1996. Report of the 22nd northeast regional stock assessment workshop (22nd SAW): stock assessment review committee (SARC) consensus summary of assessments. Northeast Fish. Sci. Cent. Ref. Doc. 96-13, 242 p. [Available from [website](#).]
- Punt, A. E.
2003. The performance of a size-structured stock assessment method in the face of spatial heterogeneity in growth. *Fish. Res.* 65:391–409. [Crossref](#)
- Punt, A. E., T. Huang, and M. N. Maunder.
2013. Review of integrated size-structured models for stock assessment of hard-to-age crustacean and mollusc species. *ICES J. Mar. Sci.* 70:16–33. [Crossref](#)
- Punt, A. E., T. A'amar, N. A. Bond, D. S. Butterworth, C. L. de Moor, J. A. A. De Oliveira, M. A. Haltuch, A. B. Hollowed, and C. Szuwalski.
2014. Fisheries management under climate and environmental uncertainty: control rules and performance simulation. *ICES J. Mar. Sci.* 71:2208–2220. [Crossref](#)
- Rosenberg, A. A., and V. R. Restrepo.
1994. Uncertainty and risk evaluation in stock assessment advice for U.S. marine fisheries. *Can. J. Fish. Aquat. Sci.* 51:2715–2720. [Crossref](#)
- Salciccioli, J. D., Y. Crutain, M. Komorowski, and D. C. Marshall.
2016. Sensitivity analysis and model validation. *In* Secondary analysis of electronic health records, p. 263–271. Springer, Cham, Switzerland.
- Saltelli, A., K. Aleksankina, W. Becker, P. Fennell, F. Ferretti, N. Holst, S. Li, and Q. Wu.
2019. Why so many published sensitivity analyses are false: a systematic review of sensitivity analysis practices. *Environ. Model. Softw.* 114:29–39. [Crossref](#)
- Shelton, A. O., J. T. Thorson, E. J. Ward, and B. Feist.
2014. Spatial semiparametric models improve estimates of species abundance and distribution. *Can. J. Fish. Aquat. Sci.* 71:1655–1666. [Crossref](#)
- Slezak, D. F., C. Suárez, G. A. Cecchi, G. Marshall, and G. Stolovitzky.
2010. When the optimal is not the best: parameter estimation in complex biological models. *PLoS ONE* 5(10):e13283. [Crossref](#)
- Tanaka, K. R., J. Cao, B. V. Shank, S. B. Truesdell, M. D. Mazur, L. Xu, and Y. Chen.
2019. A model-based approach to incorporate environmental variability into assessment of a commercial fishery: a case study with the American lobster fishery in the Gulf of Maine and Georges Bank. *ICES J. Mar. Sci.* 76:884–896. [Crossref](#)
- Waller, J. D., K. M. Reardon, S. E. Caron, B. P. Jenner, E. L. Summers, and C. J. Wilson.
2021. A comparison of the size at maturity of female American lobsters (*Homarus americanus*) over three decades and across coastal areas of the Gulf of Maine using ovarian staging. *ICES J. Mar. Sci.* 78:1267–1277. [Crossref](#)
- Zhang, Y., Y. Chen, and Y.-J. Chang.
2011. Estimating biological reference points using individual-based per-recruit models for the Gulf of Maine American lobster, *Homarus americanus*, fishery. *Fish. Res.* 108:385–392. [Crossref](#)