



Climate vulnerability and resilience in the most valuable North American fishery

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Managing natural resources in an era of increasing climate impacts requires accounting for the synergistic effects of climate, ecosystem changes, and harvesting on resource productivity. Coincident with recent exceptional warming of the northwest Atlantic Ocean and removal of large predatory fish, the American lobster has become the most valuable fishery resource in North America. Using a model that links ocean temperature, predator density, and fishing to population productivity, we show that harvester-driven conservation efforts to protect large lobsters prepared the Gulf of Maine lobster fishery to capitalize on favorable ecosystem conditions, resulting in the record-breaking landings recently observed in the region. In contrast, in the warmer southern New England region, the absence of similar conservation efforts precipitated warming-induced recruitment failure that led to the collapse of the fishery. Population projections under expected warming suggest that the American lobster fishery is vulnerable to future temperature increases, but continued efforts to preserve the stock's reproductive potential can dampen the negative impacts of warming. This study demonstrates that, even though global climate change is severely impacting marine ecosystems, widely adopted, proactive conservation measures can increase the resilience of commercial fisheries to climate change.

climate impacts | resilience | harvest strategies | population dynamics | American lobster

Ensuring that fisheries are sustainable and resilient to increasing climate impacts is one of the extraordinary challenges facing marine ecosystems and coastal communities worldwide. Current climatic trends reflecting accumulation of greenhouse gas emissions over the past decades are already impacting global fisheries and societies that depend on them (1–3), and efforts to reduce emissions may not be effective before another several decades (4). It is thus necessary to identify immediate solutions to build resilience and adapt to expected changes. Such proactive management requires a detailed understanding of how environmental change and management policies interact, and quantitative projections based on this understanding (5). The complexity of the biophysical and socioeconomical mechanisms at play (6) and potential synergistic effects of environmental change and management policies (7, 8) pose a challenge for developing these projections. In this study, we use a model that links ocean temperature, predator density, and fishing to population dynamics to evaluate the role of warming and harvest strategies in the simultaneous collapse of the American lobster (*Homarus americanus*) fishery in southern New England (SNE) and record-breaking landings in the Gulf of Maine (GoM). Mechanisms that explained recent population trajectories are then used in projections to identify harvest strategies that promote resilience of climate-vulnerable fisheries.

The fishery for American lobster is the most valuable fishery in both the United States and Canada, with a combined landed value of more than \$US 1.5 billion in 2015 (9, 10). The overall increase in lobster abundance belies different trajectories within the range of the species. The fishery in the GoM, near the center

of the species' range, has increased dramatically, while the fishery at the warmer southern edge in SNE has effectively collapsed (11). The exceptional warming rate in the northwest Atlantic, well above the global average (12), may have contributed to these divergent trajectories (13) (Fig. 1). Warming waters have been associated with decreased juvenile habitat (14, 15) and increased prevalence of epizootic shell disease (16) in the southern region, and with expanded juvenile habitat in the north (17, 18). These environmental changes have been accompanied by the decline of large-bodied predators in the GoM, which may have added to the regional differences in population trajectories (17, 19).

The two regions also differ in their approach to fisheries management. Coastal communities in Maine, where 83% of US lobster landings occurred in 2015, have a high economic reliance on lobster that has grown in concert with lobster abundance and with declines in other fisheries (20). While the high reliance on this one fishery creates socioeconomic risk in a changing climate, it has encouraged a strong conservation ethos among the 3,500+ active owner–operators in the fishery. The fishery is divided into local lobster zones (~1,000 km²) with comanagement authority, and, within these zones, harvesters have informal individual and community fishing territories (21). Instead of quota management, an approach that is often considered the state of the art in fishery

Significance

Climate change is impacting global fisheries and societies that depend on them. Identifying climate adaptation measures requires understanding how environmental changes and management policies interact in driving fishery productivity. Coincident with the recent exceptional warming of the northwest Atlantic Ocean, the American lobster has become the most valuable fishery resource in North America. Here we show that interactions between warming waters, ecosystem changes, and differences in conservation efforts led to the simultaneous collapse of lobster fishery in southern New England and record-breaking landings in the Gulf of Maine. Our results demonstrate that sound, widely adopted fishery conservation measures based on fundamental biological principles can help capitalize on gains and mitigate losses caused by global climate change.

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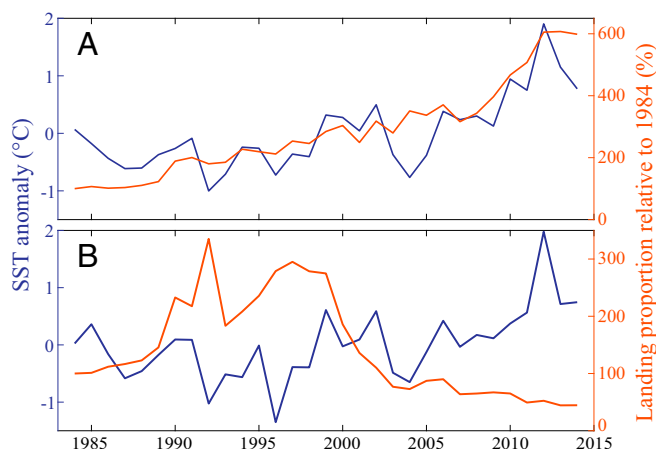


Fig. 1. Trends in SST anomalies (blue lines) from 1984 to 2014 and landings (orange lines) of American lobster. (A) GoM. (B) SNE.

management, the lobster fishery is managed through a series of fishing effort controls and size limitations. These include minimum landing sizes and harvester-driven initiatives to discard lobsters above a certain size and to protect reproductive females using a process called “v-notching” (harvesters clip a V-shaped mark into the tails of egg-bearing females, offering protection from harvest as landing V-notched lobsters is prohibited). Although minimum legal sizes have been imposed in the south, preservation of large reproductive lobsters was not championed, creating a natural experiment to understand the relative impact of environmental change and harvest strategies on an important commercial species.

We developed a model that integrates multiple effects of ocean temperature, predator density, and fishing on lobster population dynamics. A key goal of our approach was to develop a single model that can explain lobster population dynamics across a range of habitats. The components of the model were developed sequentially using life history, macroecology, and population dynamics theories. We first quantified the life history trade-offs between accelerated growth, earlier maturation, and reduced fecundity of smaller-bodied adults that typically occur when ectotherms are exposed to warmer conditions or under strong size-selective harvesting. Second, we developed a function that synthesizes the impact of temperature and fishing on the size spectrum of lobster predators. Under warm conditions, the abundance of smaller-bodied lobster predators increases, while increased fishing pressure selectively removes larger individuals from the assemblage of predatory fishes. Finally, we linked the recruitment of age-1 lobsters to the estimated egg production based on the abundance and size of adults. The function incorporates a quadratic temperature term to allow for an optimal summer temperature for lobster recruitment (17). The complete lobster population model was validated by comparing hindcasted abundance with abundance estimates from the most recent stock assessment (11).

Results and Discussion

When forced with observed monthly landings and water temperatures, the model captures the past dynamics of both the GoM ($r^2 = 0.75$) and SNE lobster stocks ($r^2 = 0.81$, Fig. 2). Model-estimated mean abundance increased by 515% from 1985 to 2014 for the GoM stock, and decreased by 78% from 1997 to 2014 for the SNE stock. However, when temperatures were fixed at the 1984–1999 average, variations in abundances were much smaller for both stocks (Fig. 2A and B). This suggests that recent rapid warming in the northwest Atlantic has played an integral role in driving the boom in the American lobster fishery in the GoM and its collapse in the warmer SNE region.

Temperature effects on recruitment (number of 1-y-old lobsters) was the primary factor driving population abundance. Increased

individual growth rate and reduced size at maturity (22) led to an increase in egg production in the GoM stock, but to a modest increase in recruitment (Fig. 2C). However, the production of 1-y-old lobsters per egg was greatly enhanced by the northeastward shift of the estimated 16.4 °C optimal summer temperature (Fig. 3), boosting GoM stock abundance in recent years, and explaining the northeast shift in lobster distribution (23) and the current record high landings in Atlantic Canada (10). In contrast, summer inshore temperatures in the south increasingly exceeded the thermal optimum for lobster recruitment (Fig. 3), resulting in recruitment failure in the SNE stock (15).

Differences in predation pressure and prevalence of shell disease also contributed to the disparate population trajectories. Fishing of large predators, including Atlantic cod, reduced predation mortality on lobsters, precipitating the rise of lobster abundance in the GoM (Fig. 2C). We estimated that, without the removal of large predators, lobster abundance in the GoM would have increased by 434% instead of 515% since 1985. In SNE, the more diverse communities of small predators maintained an elevated predation mortality on smaller lobsters, canceling out the reduction of predation mortality caused by the removal of larger predators (Fig. 2D). In contrast, the outbreak of shell disease in 1998 increased the natural mortality in SNE, contributing to the stock collapse in the region (Fig. 2D).

Preserving larger, more fecund females is an ongoing issue in fisheries management, and differences in the level of protection afforded to large lobsters in the two regions amplified the effects of ecosystem changes. In 1917, lobster harvesters in Maine began a V-notching program to preserve reproductive females, and V-notching of all egg-bearing females has since been mandatory. In the 1930s, harvesters and legislators in Maine collectively decided to impose a maximum size limit of 128 mm carapace length (CL). In contrast, in SNE, a maximum size limit varying from 133 mm to 171 mm CL among areas was imposed only in 2008, and the practice of V-notching is voluntary and less common. We evaluated the role of these conservation measures on past stock dynamics by applying the management measures from one stock to the other. Model simulations revealed that, without conservation measures to protect large lobsters and reproductive females, lobster abundance in the GoM would have increased by 242% instead of 515% (Fig. 2A). On the other hand, if more restrictive conservation measures had been implemented earlier in SNE, the stock abundance would have decreased by only 57% instead of 78% (Fig. 2B). Our results suggest that, because of their higher fecundity, preserving large females can dampen the negative effects and amplify the benefits of warming.

We used the model to project trends in American lobster fisheries out to 2050 using temperature conditions from the ensemble of climate projections of the Climate Model Intercomparison Project Phase 5 (CMIP5) under representative concentration pathway (RCP) 8.5. Using constant exploitation rates equal to the average of the last 5 y, model projections indicate that the GoM lobster fishery is vulnerable to future temperature increases (Fig. 4A). The warmest temperature scenario that we explored (~ 0.05 °C \cdot y $^{-1}$) gives the largest and steepest decline in abundance (–62% relative to 2014; Fig. 4A), while the coolest scenario (~ 0.03 °C \cdot y $^{-1}$) shows a more gradual decline (–40% relative to 2014; Fig. 4A). The projected decline in abundance is caused by temperature-induced decreases in recruitment and increases in predation mortality on small lobsters. Model projections also showed that maintaining measures to preserve large reproductive females can mitigate negative impacts of warming on the GoM lobster fishery in future decades (Fig. 4B). However, an outbreak of shell disease would amplify the temperature-induced decreases in abundance. Model projections for the southern stock showed that no recovery to the abundance levels observed in the mid-1990s can be expected. A slight recovery to the mid-1980s levels is possible if temperature follows the coolest scenario (Fig. 4C) or if shell disease were to disappear (Fig. 4D).

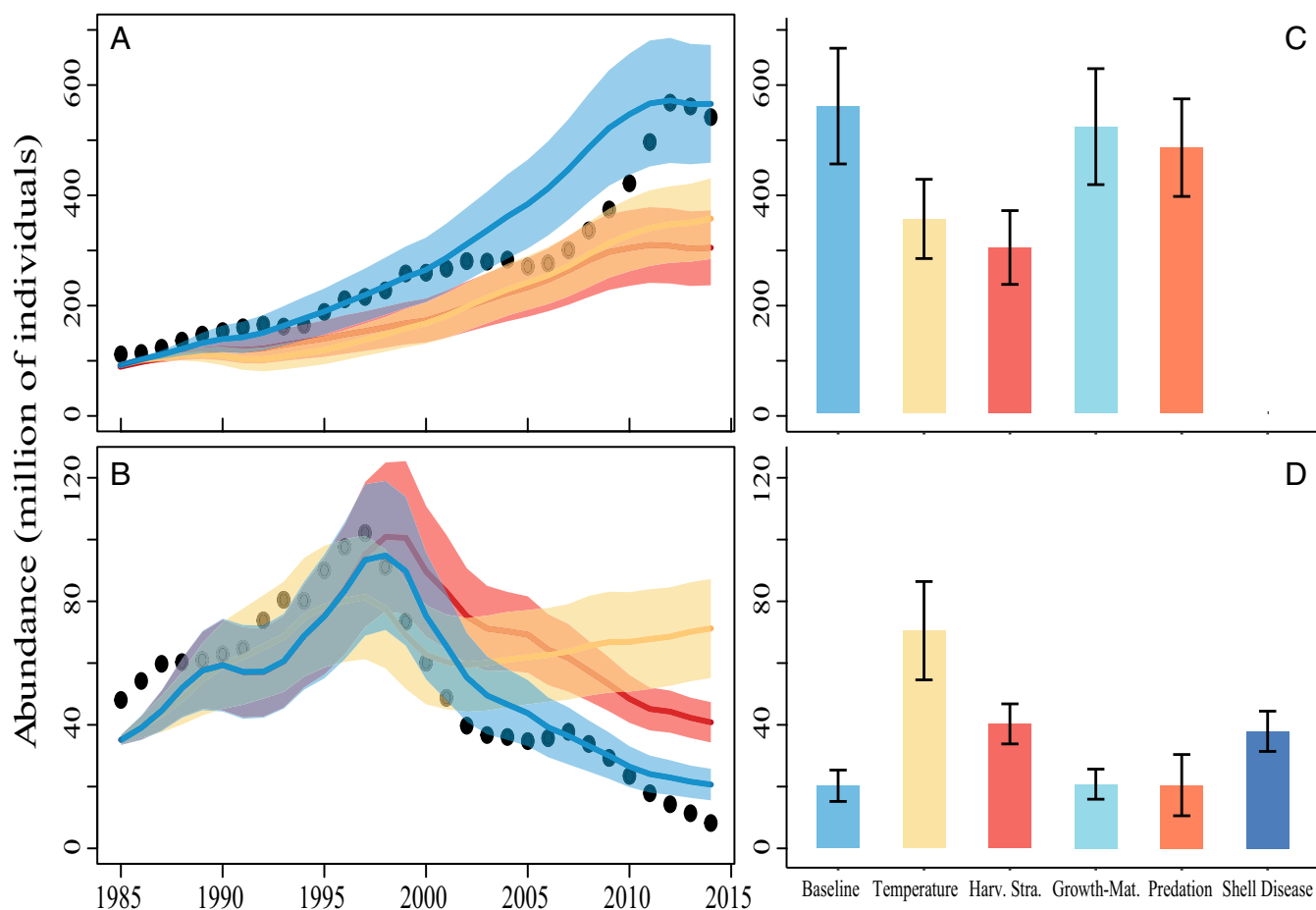


Fig. 2. Hindcast of abundance of American lobster across multiple scenarios. (A and B) Estimated abundance from 1985 to 2014 for the (A) GoM and (B) SNE stocks. Dots indicate abundance estimates from the last stock assessment (15). The blue lines show model hindcast with observed temperatures and actual harvest strategies. Yellow lines show model hindcast with constant temperature set at the average of the 1984–1999 time period. Red lines show model hindcast with switched harvest strategies (maximum size limits and V-notching) between the two stocks. Colored areas show 95% confidence intervals. (C and D) Estimated abundance in 2014 for (C) GoM and (D) SNE stocks. Baseline, Temperature, and Harv. Stra. (harvest strategies) correspond to the blue, yellow, and red lines, respectively, on A and B. Growth-Mat. corresponds to a scenario in which we assumed that growth and maturity were kept constant. Predation corresponds to a scenario in which we assumed no removal of predators by fishing. Shell Disease corresponds to a scenario that assumed no shell disease in SNE. Error bars show 95% confidence intervals.

Model assumptions and limitations in climate forecasts call for caution when interpreting projections of absolute abundances. First, the relatively coarse resolution of climate models limits the ability to predict the frequency and strength of processes affecting recruitment, such as marine heat waves, storms, and variation in coastal currents (24). Recent high-resolution climate projections show that the northwest Atlantic should warm at 3 times the global average rate (25). This result suggests that the warmest scenario used in this study may be more realistic. Second, we assumed that current stock boundaries reflect actual population units with independent demography. This assumption was necessary given the limited understanding of American lobster population structure. While previous studies have suggested connectivity between management units, including the potential for upstream regions on the Canadian shelf to contribute larvae to the GoM region (26), recruitment mostly originates from local sources within the stock area (27). Third, our model does not consider the potential for rapid evolutionary adaptation (28), which could help the species counter stressful temperature conditions. Finally, our model assumes that temperature is the sole climatic driver of population changes. Other stressors of climate change, such as acidification and deoxygenation, are affecting marine ecosystems (29) and may impact lobster productivity in the future.

There is a growing appreciation for how protecting large individuals can increase population resilience to elevated exploitation rates (30) and reduce fluctuations caused by climate variability (31). The northern cod population in Atlantic Canada experienced truncation of its age structure by selective fishing (32), which impeded its resilience to several years of combined high exploitation rates and poor environmental conditions and precipitated its collapse. Similarly, the disproportionate removal of larger individuals of five fish species in the Barents Sea increased populations' sensitivity to environmental fluctuations, because population growth rates became more dependent on recruitment than on adult survival (33, 34). Consistent with these results, the lack of conservation measures to preserve large lobsters in SNE, combined with higher mortality rates caused by an outbreak of epizootic shell disease, precipitated the recruitment failure caused by rapid warming. In contrast, the maintenance of a high egg production in the GoM prepared the fishery to capitalize on favorable ecosystem conditions (i.e., lower predation mortality and optimal temperature). These results demonstrate that sound harvest strategies based on fundamental biological principles can dampen negative and reinforce positive effects of ecosystem changes.

The development of current harvest strategies in Maine was facilitated by the flexibility of Maine's Lobster Management

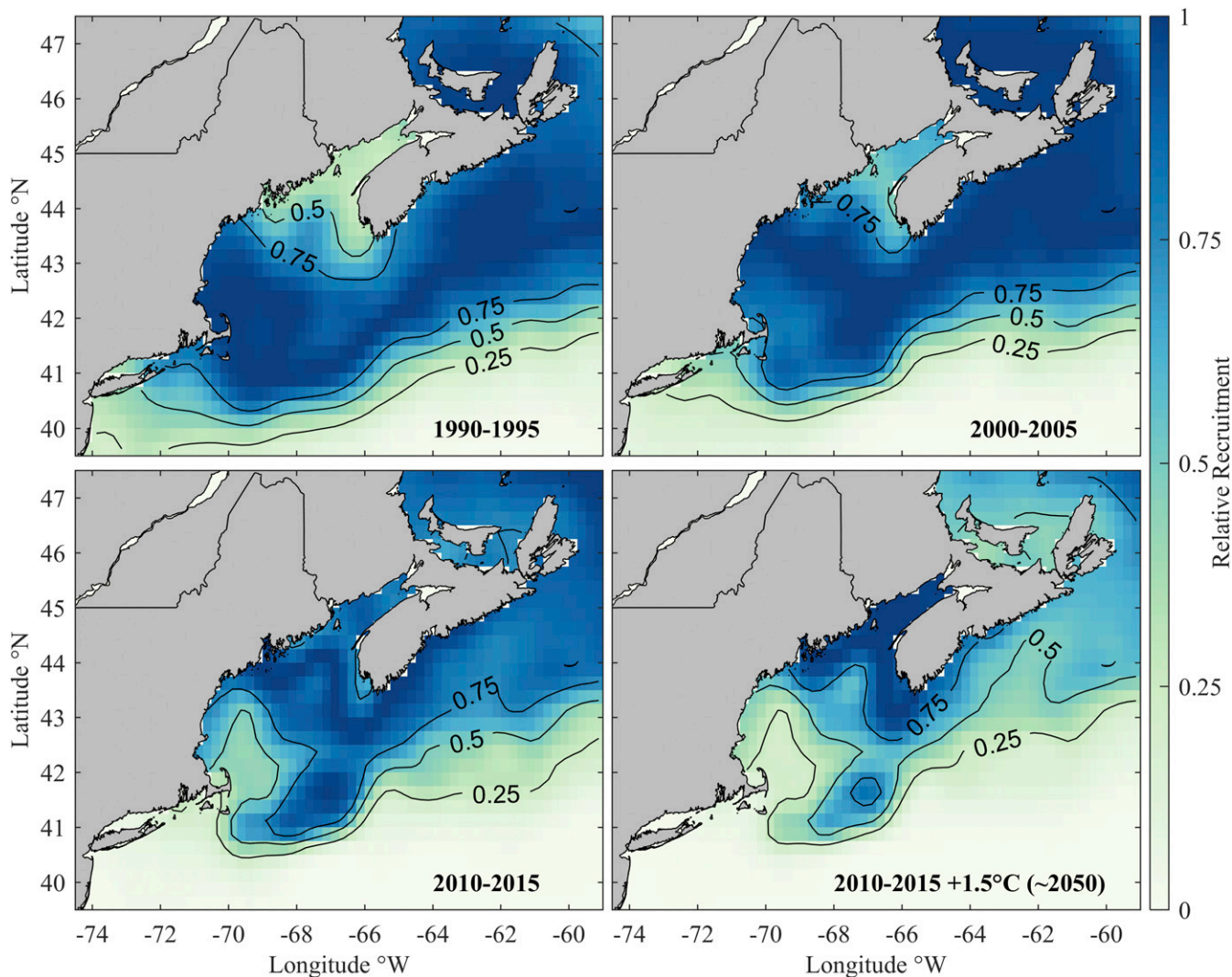


Fig. 3. Spatial recruitment index. Recruitment was estimated using a Ricker model based on TEP and a quadratic SST term. On this figure, recruitment was normalized across years and across the spatial domain.

Zone Law, and by the ability of industry leaders to influence legislation (35). The informal establishment of territorial use rights promoted a strong conservation ethos in the industry, encouraging the adoption of sustainable harvest strategies to the detriment of immediate economic returns. The case study of the American lobster confirms that a strong sense of resource stewardship and flexible governance facilitate the adoption of effective conservation measures and confer resilience in fisheries. However, at the fishing community level, continued reliance on one successful fishery may present a risk (20), especially given that rates of ecosystem changes can outpace reactive management decision processes (12). Coastal communities should adopt anticipatory adaptation measures, such as diversifying their portfolios of economic opportunities (36), to build resilience against the multiple impacts of climate change.

Materials and Methods

Population Dynamics Model. The dynamics of lobster populations from the GoM and SNE were reconstructed using a temperature-dependent size-based model (Fig. S1). The number of lobsters at size was simulated using a cohort equation,

$$N_{s,x,y,t+1} = N_{s,x,y,t} e^{-M_{s,x,y}/12} + R_{s,x,y,t} - C_{s,x,y,t}, \quad [1]$$

where $N_{s,x,y,t}$ is the number of lobsters of stock s in size bin x (43 size bins from 13 mm to 223 mm CL) in year y and month t , $C_{s,x,y,t}$ is the number of

lobsters landed, $M_{s,x,y}$ is the instantaneous rate of natural mortality, and $R_{s,x,y,t}$ is the number of recruits. Individual growth was modeled using a temperature-dependent von Bertalanffy growth function (see *SI Materials and Methods*).

The instantaneous rate of natural mortality was modeled with three components: a predation mortality (M_p), a background mortality (M_o), and a disease mortality (M_d). The disease mortality was imposed only for SNE starting in 1998 following the outbreak of the epizootic shell disease that occurred in the region (11, 16). Because of the limited information of the effect of shell disease, we set $M_d = 0.1$ for all size classes (11). The background mortality ensured that nonpredated large lobsters experienced mortality and was assumed to be a function of asymptotic mass (37), $M_{o,s,y} = \tau m_{\infty}^{-\lambda_{s,y}}$. The predation mortality built upon previous work on community size spectrum (38, 39). Predation mortality for a lobster of mass m was assumed to be proportional to the density of predators $N_p(m_p, s, y)$ in mass bin m_p , for stock s and year y , to the probability of being ingested during an encounter with a predator $\varphi(m_p, m)$, and to the volume search by an individual predator $V(m_p)$,

$$M_p(m, s, y) = \int_{m_p \min}^{m_p \max} N_p(m_p, s, y) \varphi(m_p, m) V(m_p) dm_p. \quad [2]$$

The volume search by a predator was assumed to be an allometric function of mass (40) $V(m_p) = \theta m_p^{\alpha}$. The probability of ingestion was modeled using a function similar to a log-normal density function (41),

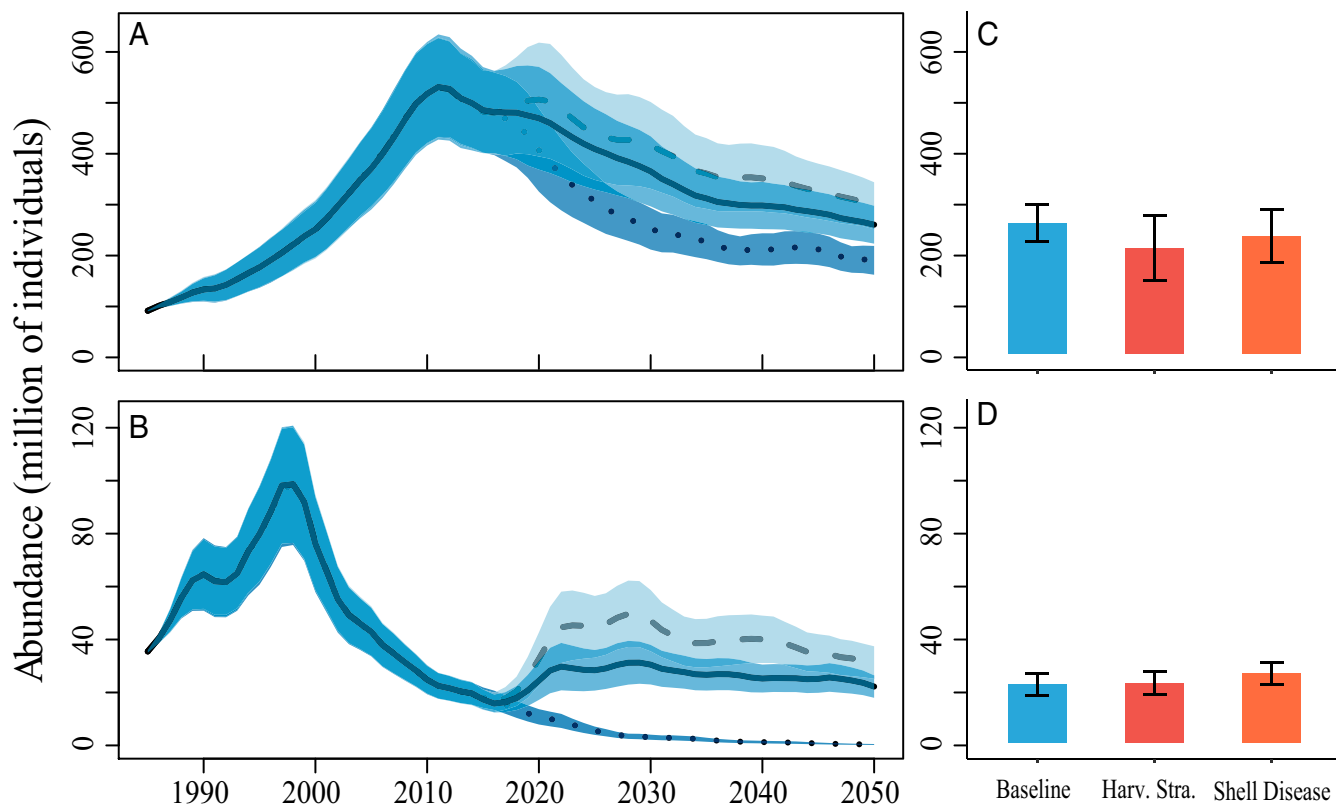


Fig. 4. Projections of American lobster abundance. (A and B) Estimated abundance from 1985 to 2050 for the (A) GoM and (B) SNE stocks. Projections use the mean (solid lines), the 5th percentile (dashed lines), and the 95th percentile (dotted lines) of temperature projections from the CMIP5 ensemble of climate projections using RCP 8.5. Colored areas show 95% confidence intervals. (C and D) Estimated abundance in 2050 for (C) GoM and (D) SNE stocks using mean temperature projections but alternative harvest strategies and shell disease. Baseline corresponds to solid lines on A and B. Harv. Stra. tests the effects of inverting maximum size limits and participation in V-notching between the stocks. Shell Disease tests the effects of inverting shell disease prevalence between the stocks. Error bars show 95% confidence intervals.

$$\varphi(m_p, m) = \exp\left(-\ln\left(\frac{m/\rho}{m_p}\right)^2\right), \quad [3]$$

where ρ is the preferred predator–prey size ratio, and σ is the width of the function (Table S1); $\varphi(m_p, m)$ takes a value of 1 at ρ . Finally, the density of predators was modeled with a linear size spectrum,

$$\log(Np(m_p, r, y)) = \mu(r, y) + \log(m_p) * \vartheta(r, y). \quad [4]$$

The size spectrum of lobster predators was compiled based on abundance data from scientific bottom-trawl surveys. Parameters μ and ϑ were region-specific and varied annually due to the effects of temperature and fishing on the size spectrum (see *SI Materials and Methods*).

Following evidence of cannibalism in the species (42), we used a Ricker model to estimate recruit numbers from total egg production (TEP) (see *SI Materials and Methods*). We extended the Ricker model with a quadratic temperature term to consider thermal optimum for lobster settlement (43). The model was fitted to both the GoM and SNE stock combined using a mixed-effects model, allowing for stock specific productivities but a common temperature effect,

$$R_{s,y} = \alpha_s \text{TEP}_{s,y-1}^{\beta_s} e^{\gamma \text{SST}_y} e^{\delta \text{SST}_y^2} \varepsilon_{s,y}, \quad [5]$$

where $R_{s,y}$ is the number of recruits for stock s at year y , SST_y is the summer inshore sea surface temperature (SST) from the year of settlement, α_s and β_s are random effect coefficients specific to each stock, γ and δ are fixed effect coefficients common to both stocks, and $\varepsilon_{s,y}$ is a log-normal error. Recruitment occurred in July (66%) and October (34%), and recruits were distributed to the first three size classes with the following proportions: 0.658, 0.334, and 0.008 (44). This stock recruitment (SR) function assumed that the two stocks correspond to closed populations: No dispersal of eggs or exchange of recruits occurs between the two populations and with other lobster populations.

Model Simulations. We evaluated the model's capacity to reconstruct past dynamics for the GoM and SNE lobster stocks by comparing our abundance estimates with abundance estimates from the last stock assessment report (11). Model uncertainty was quantified by a bootstrap of the residuals of the predator size spectrum, maturity, and SR functions (1,000 iterations). We also considered the uncertainty arising from averaging temperature data and projections across the spatial domains by sampling temperature from a normal distribution of mean and SD estimated using all of the temperature cells that composed each spatial domain (see *SI Materials and Methods*).

Using different hindcast simulation scenarios, we evaluated the role of five factors that may have contributed to the simultaneous collapse of the lobster fishery in SNE and record landings in the GoM. The “baseline” simulation used observed temperatures and actual harvest strategies. The “temperature” simulation used constant temperatures equal to the mean of the first half of the time series (1984–1999) to evaluate the role of the recent rapid warming in the northeast United States. The “harvest strategies” simulation evaluated the role of the difference in harvest strategies by swapping management strategies between the two regions. V-notching and a maximum size limit of 128 mm CL were imposed in SNE starting in 1996, while no V-notching and a maximum size limit of 140 mm CL were imposed in the GoM throughout the time series. In the “growth and maturity” simulation, growth rate and size at maturity were set constant and equal to values observed in 1984. In the “predation” simulation, we removed temporal trends in the lobster predator size spectrum to evaluate the role of the fishing of predators in lobster abundance. Finally, in the “shell disease” simulation, we removed the natural mortality effects caused by shell disease in SNE.

Lastly, we performed five model projections out to 2050 to evaluate future impacts of warming, changes in harvest strategies, and shell disease prevalence on population abundance. The first three projections used the mean, 5th percentile, and 95th percentile of the ensemble of climate projections of CMIP5 (see *SI Materials and Methods*). Projections from only RCP 8.5 were used to limit the number of simulations, and because projections of the radiative forcing are similar across the RCPs out to ~2050 (45). Exploitation

rates were set constant and equal to the average of the last 5 y (2010–2014). The harvest strategies observed in 2014 were used. In the fourth simulation, we switched harvest strategies between the two stocks, similar to the hindcast “harvest strategies” simulation. V-notching was applied to SNE instead of GoM, and maximum fishing sizes of 140 mm CL and of 128 mm CL were applied to the GoM and SNE stocks, respectively. In the fifth simulation, we removed the shell disease mortality from the SNE stock and applied it to the GoM stock. The fourth and fifth simulations used the mean of the ensemble of climate projections and the 2010–2014 average exploitation

rates. In the five model projections, predator density was modeled as a function of projected temperature and fishing pressure using the same linear size spectrum function as in the model hindcast (Eq. 2).

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