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Contributions of a conservation measure that protects the spawning stock to drastic increases in the Gulf of Maine American lobster fishery

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ABSTRACT: V-notching, a conservation measure intended for the protection of mature female lobsters, has been hypothesized to have contributed to the dramatic increase in American lobster *Homarus americanus* landings and stock biomass in the Gulf of Maine. To evaluate the impact of this conservation measure, scenarios examining different v-notching compliance rates and v-notch definitions were simulated using an individual-based lobster simulator with different recruitment dynamics scenarios. In the model, v-notching with a high compliance rate and a strict definition of the 'notch' increased spawning stock biomass by 33–632%. Without a stock–recruitment relationship, v-notching with high compliance and a strict definition decreased landings by 2%. With a weak or strong stock–recruitment relationship, v-notching with high compliance and a strict definition increased landings by 33–85%. Without a high v-notching compliance rate (i.e. 90 or 100% compliance) or a strict definition of the notch, the lobster stock and fishery would not have experienced such large positive increases in biomass and landings. These results suggest that input controls, such as protecting the spawning stock, can provide significant benefits to both the fish population and fishery. The framework proposed in this study can be extended to evaluate the protection of spawning females in other fisheries.

KEY WORDS: Fisheries management · Conservation · Simulation · Population dynamics · Fish recruitment · Crustacea

1. INTRODUCTION

Various types of regulations have been used in fisheries management, such as input controls (i.e. fishing effort controls, maximum and minimum legal sizes, and protection of specific life history stages) and output controls (i.e. quotas). Output controls, which directly constrain the catch, are often considered to be more efficient than input controls (Kompas et al. 2004). Although input controls do not directly control catch, they can still help sustain fisheries. Understanding how regulations have contributed to fish population status and fishery output is important for the success of a fishery.

The Maine American lobster *Homarus americanus* fishery has not experienced overfishing or been overfished since 2001 (ASMFC 2015). The fishery experienced a dramatic increase in landings over the past 3 decades with the landings and biomass at record highs (ASMFC 2015) (see Fig. 1). In 2017, over 50 000 metric tonnes (mt) were landed in the Maine lobster fishery (Maine DMR 2018), making up 76% of the revenue from Maine's fish and seafood landings (over $433 million USD; Maine DMR 2018). The state of Maine is dependent on the lobster fishery, and a collapse could disrupt the state's economy and fishing communities (Steneck et al. 2011). Henry & Johnson (2015)

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found that lobster fishers may not be resilient to future threats to this fishery.

Fishermen and scientists believe that both conservation measures and environmental factors have led to the drastic increases in the Maine lobster landings and biomass (Acheson & Steneck 1997, Acheson & Gardner 2010, Le Bris et al. 2018). Various hypotheses have been developed to explain the increase in the Gulf of Maine (GOM) lobster population and fishery landings, such as reduced biomass of major predators leading to increased juvenile lobster survival rates (e.g. Atlantic cod; Crooks & Soule 1999, Hanson & Lanteigne 2000), warming water temperature resulting in higher growth rates (Spees et al. 2002), increased herring bait use in the lobster fishery (Grabowski et al. 2010), improved lobster-suitable habitat (Tanaka & Chen 2016), increased spatial variability of lobster larvae (Steneck & Wilson 2001), and the industry-initiated v-notching conservation measure, which became a formal management measure in 1947 (Acheson 1997). The Canadian and Irish lobster fisheries (Collins & Lien 2002, Tully 2001) also practice v-notching, although it was implemented decades later.

The idea behind the v-notching conservation measure is that when an egg-bearing lobster is caught in a trap, the lobster fisher can choose to cut a 'V'-shaped notch in her tail and release her back to sea to reproduce and grow larger, increasing her reproductive potential for the future. Other lobster fishers that catch these v-notched lobsters must release them as well, because it is illegal to land v-notched lobsters. A v-notch typically grows out after around 2 molts, but this depends on the definition of a v-notch. For example, with a strict definition, a lobster with any size of a notch is considered v-notched and is illegal to land. With less strict definitions, lobsters with notches that are less than 1/8th to 1/4th of an inch (3–6 mm) are not considered v-notched and are legal to land (NOAA 2014). With this less strict definition, a v-notch may only last for 1 molt. V-notching is thought to be particularly effective in protecting large female lobsters, which extrude the most eggs (Acheson & Knight 2000). Large female lobsters can produce around 100 000 eggs, whereas smaller lobsters may have tens of thousands of eggs (Fogarty 1995). Eggs from large lobsters also have more calories per egg, which may positively affect larval growth and survival (Attard & Hudon 1987). V-notching has been found to have positive impacts on lobster fisheries and populations. Daniel et al. (1989) and Tully (2001) found that the v-notch conservation measure increased the reproductive potential of lobster populations. In the Maine lobster fishery, v-notched lobsters were found to have 9 times more eggs than unnotched lobsters (Daniel et al. 1989). In the Wexford lobster fishery in Ireland, v-notched lobsters contributed to 59% of the population's reproductive potential, which was determined by a mark–recapture study in which reproductive potential was based on the size and number of released v-notched lobsters, and incorporated growth and mortality (Tully 2001).

The v-notching conservation measure was initially established from the support of the fishing industry and not scientific evidence (Acheson 1997). Maine lobster fishers are known for their conservation ethics because of their support for the v-notch procedure as well as other conservation measures (Acheson & Gardner 2010). They usually comply with and self-enforce (Acheson & Steneck 1997) this measure, because they believe it is essential to the sustainability of the fishery (Acheson & Gardner 2010), the most important conservation measure in the fishery (Acheson & Steneck 1997, Acheson & Knight 2000, Acheson & Gardner 2010), and one of the reasons for the high landings (Acheson & Steneck 1997).

The limited understanding of the effectiveness of v-notching has raised some concerns from stakeholders regarding the necessity of this measure. A few decades ago, federal and state scientists argued that the v-notching conservation measure should be eliminated, because they thought that v-notching was ineffective at conserving the population (Acheson & Steneck 1997) and that v-notched lobsters could get infected (Acheson & Knight 2000). Maine lobster fishers continued to believe fully in the conservation measure even when v-notching was considered ineffective by others. In 2009, approximately 91% of Maine lobster fishers believed that v-notching was effective in conserving the lobster stock (Acheson & Gardner 2010); some wanted even more strict enforcement of the conservation measures (Acheson & Gardner 2010), and for lobster fishers in other regions (such as Canada) to v-notch as well (Acheson & Steneck 1997). However, in recent years, some lobster fishers have chosen not to follow the v-notching procedure (Hall 2014). The lack of a good understanding of the effect of v-notching on the lobster population and fishery may be the cause of such unwillingness. This calls for a careful evaluation of this conservation measure and the dissemination of results to the industry as to whether or not v-notching is critical to the sustainability of the fishery.

When conducting such a study, variability in fishing behavior, v-notch definitions, and lobster recruitment dynamics should be considered. Because the v-notch conservation measure is voluntary, it is important to consider variability in compliance rates (i.e. the percent of lobsters caught with eggs that will be v-notched by a lobster fisher). Also, different American lobster management areas have different v-notch definitions; some areas have less strict definitions while others have very strict definitions. Additionally, stock–recruitment dynamics are often difficult to define in a changing environment, which adds to the uncertainty in our effort to evaluate the effectiveness of v-notching (ASMFC 2015). Given the changing environmental conditions in the GOM, which may greatly influence lobster recruitment and growth dynamics (ASMFC 2015, McMahan et al. 2016, Tanaka & Chen 2016), an improved understanding of the effectiveness of v-notching in regulating lobster population dynamics is urgent and necessary. However, no systematic and comprehensive study has been done to evaluate and quantify the measure's contribution to the improved lobster stock and landings with consideration of multiple stock–recruitment relationships, variability among individual lobsters, variation in management compliance, and variation in v-notch definitions.

Many factors can influence lobster landings and abundance, so it is difficult to separate the effects of a single regulatory measure from that of other potential influences; however, computer simulations designed to mimic the dynamics of a fishery can allow us to evaluate the impacts of a regulation of interest while controlling for other potentially confounding factors. The goal of this study was to identify the role of the v-notch conservation measure in the GOM lobster fishery taking into account different conservation compliance rates, v-notch definitions, and recruitment dynamics scenarios. As many lobster fisheries have invested in or considered using the v-notch measure, the impacts of this study can be extended outside the GOM lobster fishery, and can provide insights on the impacts of protecting spawning females in a fishery. Here, we evaluated v-notching by simulating this management measure over a range of scenarios within a previously developed and parameterized individual-based lobster simulator (IBLS) (Chen et al. 2005, Chang 2015, Mazur et al. 2019). Our results will further our understanding of the effects and trade-offs of the v-notching measure on the lobster population and fishery.

2. MATERIALS AND METHODS

2.1. Individual-based lobster simulator

In this study, the IBLS was used to simulate the Maine American lobster *Homarus americanus* fishery. The simulator uses a probabilistic approach which is flexible in mimicking biological and fishery processes. The IBLS was first developed by Chen et al. (2005) and Chang (2015) and most recently modified, reconditioned, and tuned with recent fishery and biological data by Mazur et al. (2019). Probabilities of the different life history and fishery processes in the IBLS depend on the size and sex of the lobster and the timestep considered. In the IBLS, each individual lobster 'experiences' fishery and life history processes, such as being caught in the fishery, being protected from the fishery due to minimum/maximum legal sizes, dying of natural mortality, maturing, molting, becoming egg-bearing, being v-notched, and/or losing notches due to molting. Each individual lobster is characterized by the state variables size (carapace length [CL], in mm), sex, maturity status, egg status, survival status (if the lobster is alive or dead due to either fishing or natural mortality), and v-notch presence. Recruitment occurs in the summer and fall, when molting occurs. Three steps were conducted in R v.3.5.2 (R Core Team 2019) to complete the simulations: (1) input data and relationships were selected and aggregated; (2) input data were used in an executable file to run the simulations; and (3) output data were aggregated and analyzed.

2.2. Input data and spatial-temporal resolution

The spatial domain of the model was the GOM lobster stock area, whose boundary is defined by the National Marine Fisheries Service statistical reporting area lines (ASMFC 2015). The model considers this area as one area. The temporal range considered in this study was from 1982–2013, because this was the period considered in the most recent American lobster stock assessment model output (ASMFC 2015).

Most of the probabilities and other input data were taken from the most recent GOM American lobster stock assessment (ASMFC 2015), but fishing effort data were compiled from the Maine Department of Marine Resources (DMR) harvester data, and the historical v-notching compliance rates and v-notch definitions were obtained from personal communications with scientists and managers (Mazur et al. 2019). Even though the GOM lobster stock area includes federal as well as Maine, New Hampshire, and Massachusetts state waters, fishing effort data only from the state of Maine were used, because most landings are from inshore Maine waters (ASMFC 2015).

2.3. Recruitment dynamics

In this study, 4 different recruitment scenarios were considered, including scenarios with no relationship between recruitment and spawning stock biomass (SSB) because the American lobster stock–recruitment relationship is not clear (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m631p127_supp.pdf). In the first scenario, recruitment was drawn from estimated historical recruitment of the corresponding year from the stock assessment (ASMFC 2015), assuming no stock–recruitment relationship. Under the assumption that estimated historical recruitment from the stock assessment has some uncertainty, recruitment was drawn from a normal distribution with the estimated historical recruitment value of the corresponding year from the stock assessment as the mean with a coefficient of variation (CV) of 10%.

Recruitment is estimated annually in the stock assessment and divided into summer and fall portions (ASMFC 2015); therefore, in all the recruitment simulation scenarios, annual estimated recruitment values were used and the resulting recruitment values were divided into summer and fall portions. Around 66% of recruitment occurs in the summer; 33% occurs in the fall (ASMFC 2015).

In the second recruitment simulation scenario, recruitment values were randomly assigned from normal distributions, with means and standard deviations estimated from the stock assessment output corresponding to 5 levels of SSBs (ASMFC 2015; Fig. 1, Table 1), with higher recruitment values corresponding to more recent years (Fig. 1). This approach partially considers the possible relationships between SSB and annual recruitment. SSB was the SSB in the summer, because this is when lobster eggs

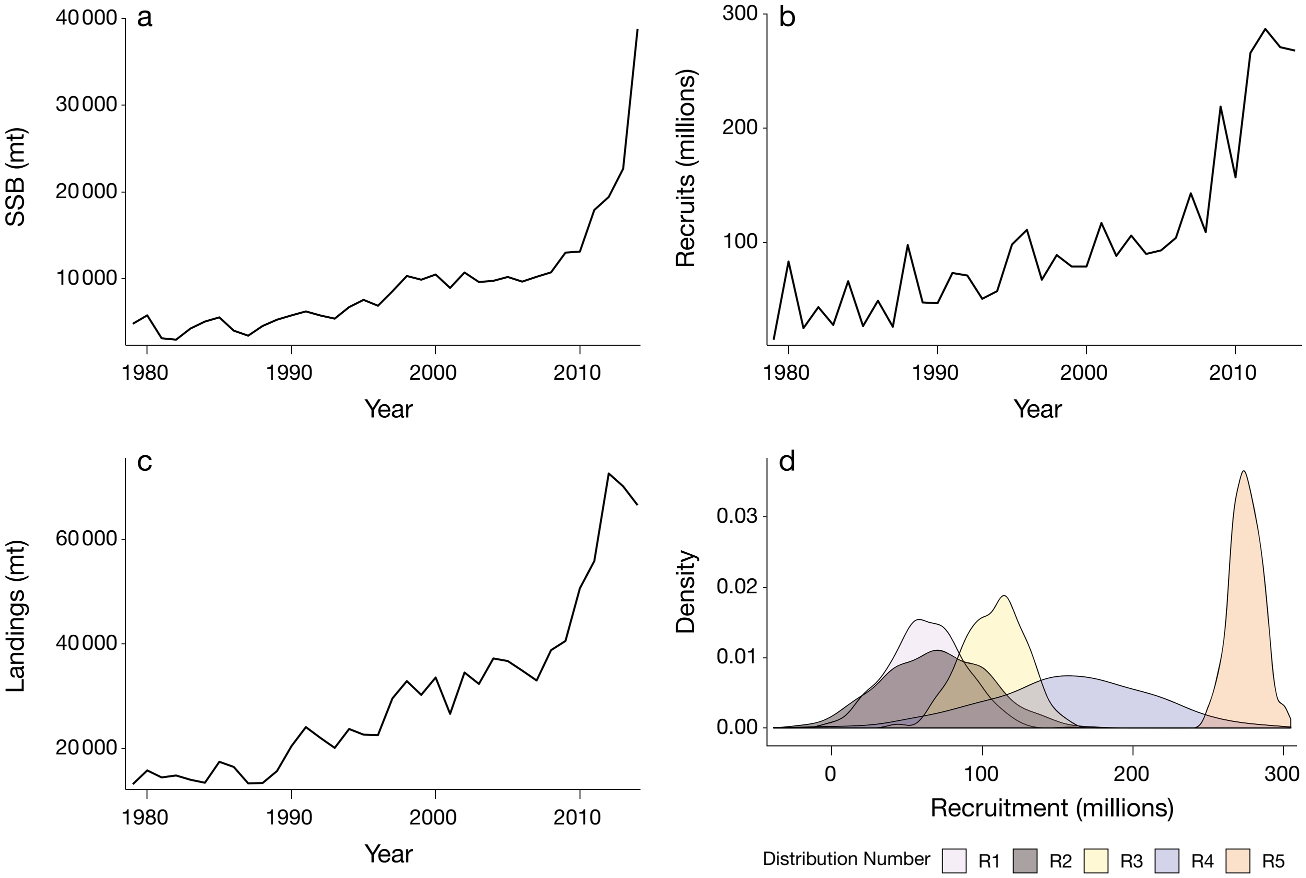

Fig. 1. Estimated American lobster (a) spawning stock biomass (SSB), (b) recruitment, and (c) landings from the ASMFC (2015) stock assessment over time. (d) Normal distributions of recruitment from the stock assessment that correspond to 5 different SSB levels: R1: SSB < 10 000 mt; R2: SSB ≥10 000 but <12 500 mt; R3: SSB ≥12 500 but <16 000 mt; R4: ≥16 000 but <19 000 mt; R5: SSB ≥ 19 000 mt

Table 1. American lobster recruitment and spawning stock biomass (SSB) means and SDs of the normal distributions of recruitment values corresponding to 5 levels of SSB

SSB level (mt)	Recruitment mean (millions)	Recruitment SD (millions)	SSB mean (mt)	SSB SD (mt)
<10 000	62.05	25.84	7232.45	1968.92
≥10 000 but <12 500	69.32	32.57	11050.11	1025.5
≥12 500 but <16 000	107.18	21.18	14061.74	1308.39
≥16 000 but <19 000	161.67	55.15	17831.86	436.64
≥19 000	274.67	10.97	20035.9	394.27

hatch (Ennis 1995). SSB was lagged by 6 yr, which is considered the average time a young-of-the-year lobster takes to reach size at recruitment (Campbell & Robinson 1983, Fogarty & Idoine 1986). To simulate the recruitment of a given year, a random number was drawn from the normal distribution of recruitment values that corresponded to the SSB from 6 yr before. For the first 6 yr (1982–1988), the first recruitment simulation scenario was used, in which recruitment values are drawn from a normal distribution with a mean of the estimated historical recruitment of the corresponding year from the stock assessment. Historical recruitment was assumed for the first 6 yr, because a change in v-notching would not affect recruitment until 6 yr later; therefore, these scenarios simulate a change in v-notching in 1982. As this approach incorporates a relationship between recruitment and SSB, but not a theoretical stock–recruitment relationship, from here on, these scenarios are referred to as weak stock–recruitment relationship scenarios.

The third recruitment simulation scenario used a stock–recruitment model, as these models are commonly used to predict recruitment. To define the stock–recruitment model, the SSB lagged by 6 yr and recruitment data from the stock assessment were fit to a variety of Ricker and Beverton-Holt models (see Chang et al. 2016). With a stock–recruitment model, recruitment gradually increases with SSB. This differs from the weak stock–recruitment relationship scenarios, which suddenly switch recruitment distributions with increasing SSB. To find the best model, 4 different stock–recruitment models were developed: Ricker and Beverton-Holt models with no temperature and with average bottom water temperature in the summer and fall. The model with the lowest Akaike's information criterion (AIC) value was chosen for this recruitment simulation scenario. The temperature value was the annual average GOM bottom water temperature in the summer and fall months (July–December) from 1982–2013, obtained from Finite-Volume Community Ocean Model (FVCOM) stations (Chen et al. 2006). Bottom water temperature was chosen, as it has a large role in driving lobster distribution (Chang et al. 2010); summer and fall were chosen, because recruitment occurs in these seasons (ASMFC 2015).

The Ricker model with no temperature was $R = \alpha S e^{-\beta S} e^{\varepsilon}$ (Ricker 1954, 1958); the Ricker model with temperature was $R = \alpha S e^{-\beta S} e^{\gamma T} e^{\varepsilon}$ (Penn & Caputi 1986). The Beverton-Holt model with no temperature was $R = \frac{S}{\alpha + \beta S} e^{\varepsilon}$ (Beverton & Holt 1957); the Beverton-Holt model with temperature was $R = \frac{S}{\alpha + \beta S} e^{\gamma T} e^{\varepsilon}$ (Quinn & Deriso 1999). In these models, R is the number of recruits, S is the SSB, T is the average bottom water temperature of the GOM in the summer and fall months, α is the density-independent parameter proportional to fecundity, β is the density-dependent parameter, γ is a coefficient expressing the magnitude of the effect of temperature, and ε is the multiplicative error term. The parameters α, β, and γ had a range of values, based on 90% CIs determined by bootstrapping, which were randomly selected from in the simulations. As in the second recruitment simulation scenario, for the first 6 yr (1982–1988), the first recruitment simulation scenario was used, in which recruitment values are drawn from a normal distribution with a mean of the estimated historical recruitment of the corresponding year from the stock assessment.

The fourth recruitment simulation scenario was a stock–recruitment model with an increased density-dependence effect. The purpose of this recruitment simulation scenario was to determine how sensitive the results were to density-dependence effects. This recruitment scenario followed the same methods as the third recruitment scenario, except the β distribution was modified. For this scenario, we drew β from a normal distribution with a mean of 3×10^{-9} and a standard deviation of 1×10^{-9}.

2.4. V-notching scenarios

Within the IBLS, we addressed the following question: What is the effect of v-notching on lobster landings and biomass? To answer this question, different v-notching conservation compliance levels (0, 50, and 100%) and different numbers of molts until a v-notch grows out (1 or 2 molts) were simulated with the 4 different recruitment simulation scenarios from 1982–2013 (Table 2). These simulations focused on the long-term effects of different notch definitions and compliance regimes.

Tully (2004) pointed out that determining the contributions of v-notching and other conservation measures would be impossible if the measures were concurrent. However, with the IBLS, it is possible to identify the contribution of concurrent conservation measures, because each conservation measure is simulated as a separate process. Indeed, many conservation measures can be applied concurrently to the fishery. This approach may lend itself to handling more complex management problems in situations involving varying compliance rates and enforcement criteria.

Conservation measures can be evaluated with different enforcement criteria with the IBLS. This is realistic for measures that are not based on size or presence of eggs, which are clearly measured. In this case, the size of a notch that is considered a v-notch can differ, so considering different criteria or v-notch definitions is necessary for understanding the measure's impact on the fishery and population.

The number of molts until a v-notch grows out depends on how strict the v-notch management definitions are; from here on, 2 molts will be referred to as a strict definition and 1 molt will be referred to as a less strict definition. With a strict definition, more molts are needed for the v-notch to grow out because any size notch is considered a v-notch. Lobster fishers can keep the lobsters after approximately 2 yr with a less strict definition and 4 yr with a strict definition, since mature female lobsters tend to molt every other year. The state of Maine currently has a zero tolerance v-notch definition, meaning that a lobster with any notch depth is illegal to land; however, in other lobster management areas a lobster with a notch of less than 1/4th to 1/8th of an inch (3–6 mm) can be landed.

Table 2. Different American lobster v-notching scenarios

Scenario	Compliance rate (%)	Definition	Time until a v-notch grows out (yr)
Reference	90	Strict	4
0	0	NA	NA
50-S	50	Strict	4
100-S	100	Strict	4
50-L	50	Less strict	2
100-L	100	Less strict	2

When evaluating conservation measures, a benefit of using the IBLS is that different compliance rates can be applied in the simulation. Instead of only considering scenarios of implementing a conservation measure or not, conservation measures can be implemented with varying degrees of compliance, which is more realistic. Compliance may differ based on fishermen's reactions to management measures, so consideration of the response of fishermen is necessary when evaluating the impact of management. Maintaining varying degrees of compliance is especially realistic in cases where the conservation measure is difficult to enforce.

In these simulations, the probability of a legal-sized lobster being v-notched by a lobster fisher if it is caught with eggs represents the v-notching compliance rate, meaning that 0, 50, or 100% of legal-sized lobsters caught with eggs are v-notched. If the lobster is v-notched, it is released back to the population and protected from harvest for 1 or 2 molts. If the lobster is not v-notched, it is released back to the population and can be harvested in the next timestep. Simulations were performed 50 times for each scenario from 1982–2013 due to computational demands.

The results from these simulations were compared with those for the reference scenario, or the historical scenario. The reference scenario simulates what occurred in the fishery using the first recruitment scenario, or historical recruitment. Historically, there was a 90% v-notching compliance rate and a strict v-notching definition (Mazur et al. 2019), and these were implemented in the reference scenario as well.

We used independent samples *t*-tests to determine if the final SSBs and cumulative landings were significantly different ($\alpha < 0.05$) between scenarios.

3. RESULTS

In general, v-notching positively affected American lobster *Homarus americanus* SSB, but more so with a stock–recruitment relationship (Fig. 2). V-notching positively affected cumulative landings with a stock–recruitment relationship but negatively affected cumulative landings without a stock–recruitment relationship (Fig. 2). Both high compliance and a strict definition increased the positive effect of v-notching (Fig. 2). Because the Ricker models did not predict recruitment well (Fig. S1), determining the effect of v-notching from these scenarios was difficult.

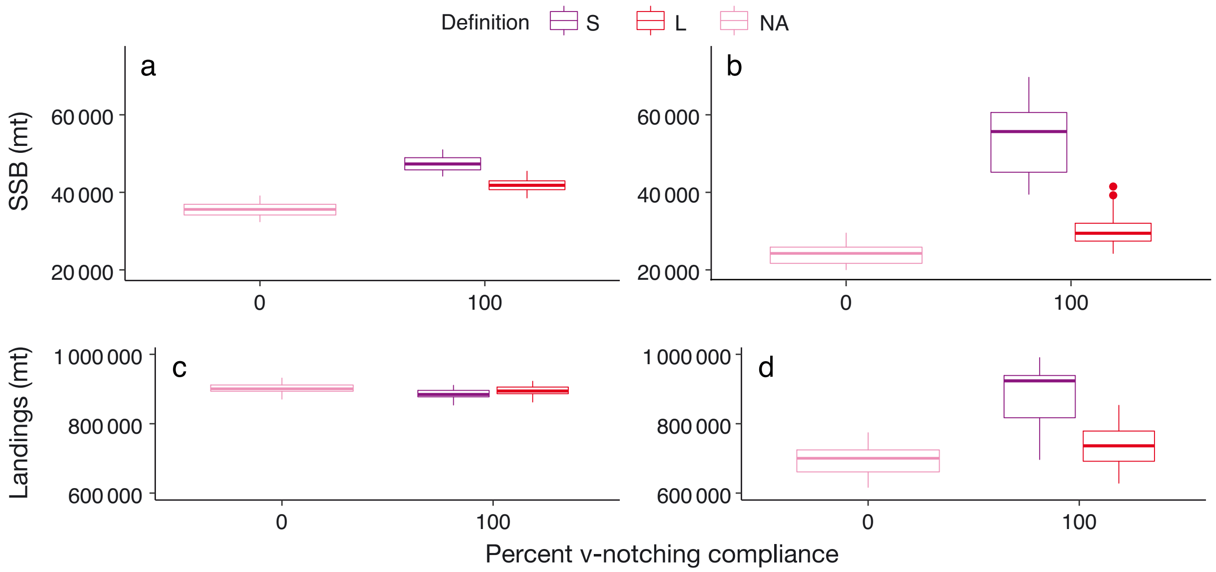

Fig. 2. American lobster v-notching scenario results. (a,b) Spawning stock biomass (SSB) in the last year of simulations (2013) of 0 % and 100 % v-notching compliance rates with different definitions and with (a) historical recruitment and (b) recruitment from the weak stock–recruitment relationship. (c,d) Cumulative landings of scenarios with 0 % and 100 % v-notching compliance rates with different definitions and with (c) historical recruitment and (d) recruitment from a weak stock–recruitment relationship. S: strict; L: less strict; NA: no v-notch definition because there was 0 % compliance. Box midline = median; upper box limit = 75 % quartile, upper hinge; lower box limit = 25 % quartile, lower hinge; lower whisker: smallest observation greater than or equal to lower hinge – 1.5 × interquartile range (IQR); upper whisker = largest observation less than or equal to upper hinge + 1.5 × IQR. These are the same for all boxplots in the figure

With the historical recruitment scenario, higher v-notching compliance and a stricter v-notch definition significantly (p-values $< 1.60 \times 10^{-5}$) positively affected SSB (33 % higher with 100 % compliance and a strict definition than with 0 % compliance) (Fig. 3, Table 3, Table S1 in the Supplement). However, the difference in SSB between the 100 % compliance with a strict definition scenario and the reference scenario (i.e. what occurred in the fishery) was not significant ($p = 0.79$) (Fig. 3, Table S1). The SSBs with 100 % v-notching compliance with a less strict definition were slightly less than the SSBs with 50 % v-notching compliance with a strict definition (Fig. 3, Table 3).

The landings of the different scenarios did not notably differ from each other over time in the historical recruitment scenarios (Fig. 3). However, v-notching had a negative effect on cumulative landings (1.9 % higher with 0 % compliance than with 100 % compliance and a strict definition). Most of the cumulative landings of the various scenarios differed significantly (p-values < 0.04), except for the cumulative landings of the strict definition scenarios and reference scenario (p-values > 0.05), the 50 % compliance with a strict definition and the 100 % compliance with a less strict definition scenarios ($p = 0.228$), and the less strict definition scenarios ($p = 0.348$) (Table S5). The scenario with no v-notching had the highest cumulative landings, followed by the scenarios with less strict definitions, then the scenario with 50 % compliance with a strict definition, and then the 100 % compliance with a strict definition and reference scenarios (Fig. 3, Table 4).

For the weak stock–recruitment relationship scenarios, v-notching positively affected SSBs (285 % higher with 100 % compliance and a strict definition than with 0 % compliance) (Fig. 4, Table 3). The SSBs from the reference scenario (i.e. what occurred in the fishery) were slightly below the SSBs from the 100 % compliance with a strict definition scenario (Fig. 4, Table 3). The final SSBs were highest with the 100 % v-notching compliance with a strict definition (Fig. 4, Table 3). Scenarios with strict definitions resulted in an increase in SSB that was not observed in the less strict definition scenarios (Fig. 4). Also, the final SSBs in each of the scenarios differed significantly (p-values $< 4.17 \times 10^{-5}$), except for the difference between the 100 % compliance with a strict definition and reference scenarios ($p = 0.79$) (Table S2).

For the weak stock–recruitment relationship scenarios, v-notching had a positive effect on cumulative landings (33 % higher with 100 % compliance and a strict definition than with 0 % compliance) (Fig. 4, Table 4). The landings of the 100 % compli-

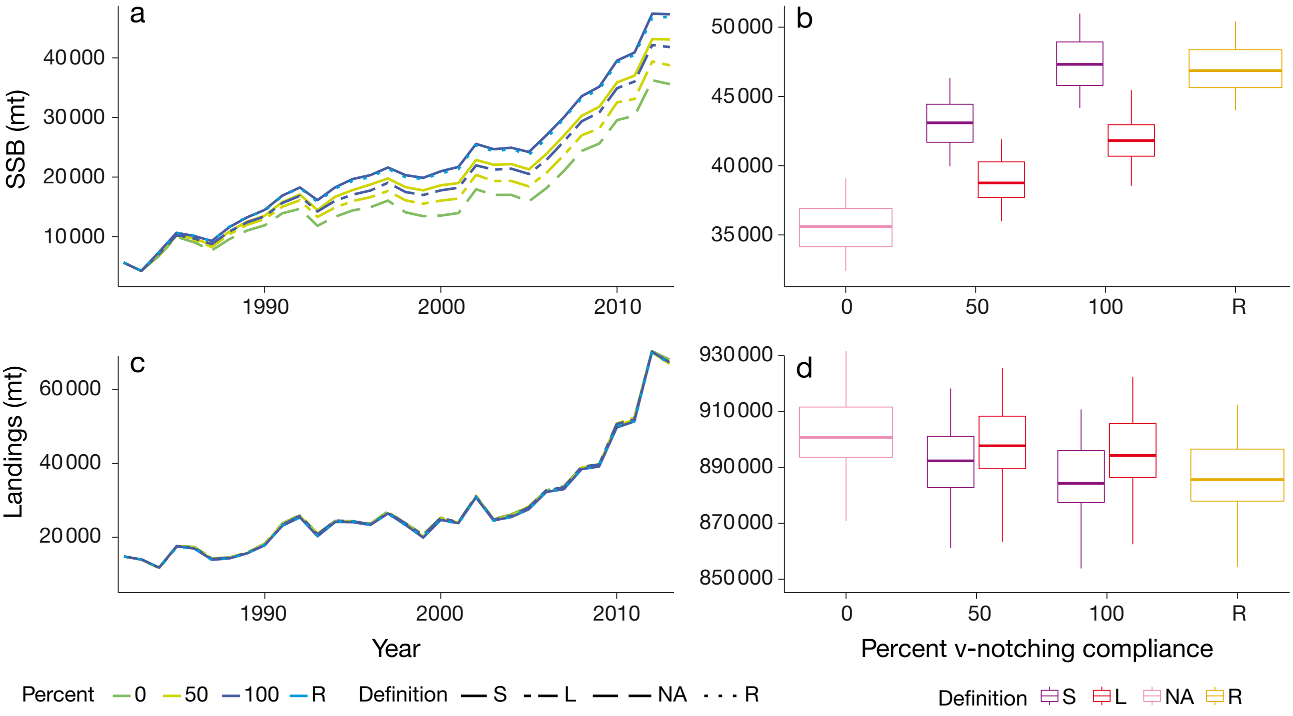

Fig. 3. Median American lobster (a) spawning stock biomass (SSB) and (c) landings from 1982–2013 with 0, 50, and 100 % v-notching probabilities, with strict (S) and less strict (L) definitions, and with historical recruitment. (b) SSB and (d) cumulative landings in the last year of the simulations (2013) of 0, 50, and 100 % v-notching compliance rates with different definitions and with historical recruitment. Results from the reference or historical scenarios are also included. NA: no v-notch definition because there was 0 % compliance; R: reference scenario with 90 % compliance and a strict definition

ance and strict definition and reference scenarios increased dramatically after 2005, unlike the landings from the other scenarios (Fig. 4). Like the SSBs, the landings were highest with 100 % compliance and a strict definition, followed by the reference scenario landings, landings with 50 % compliance and a strict definition, landings with 100 % compliance and a less strict definition, landings with 50 % compliance and a less strict definition, and then landings with 0 % compliance (Fig. 4, Table 4). The landings from the reference and the 100 % compliance and strict definition scenarios were similar throughout the time series (Fig. 4). In the scenarios with 100 % compliance and a less strict definition and 50 % compliance and a strict definition, the landings were similar (Fig. 4, Table 4). Most of the cumulative landings differed significantly (p-values < 0.04), except for the cumulative landings from the 100 % compliance with a strict definition and reference scenarios ($p = 0.74$), from the 50 % compliance with a strict definition and 100 % compliance with a less strict definition scenarios ($p = 0.33$), and from the 50 % compliance with a less strict definition and 0 % compliance scenarios ($p = 0.08$) (Table S6).

When theoretical stock–recruitment models estimated recruitment, the best model was the Ricker model without temperature. The AIC value for the Ricker model without temperature was the lowest (57.6), followed by the AIC value for the Beverton-Holt model with temperature (58.9394), and the Ricker model with temperature (58.9396). The Beverton-Holt model without temperature did not converge. The predicted recruits from the best model overall followed the same trend as the historical recruits; however, the model tended to overestimate recruits at intermediate levels of SSB and underestimate recruits at high and low levels of SSB (Fig. S1).

Because the Ricker model could not accurately estimate lobster recruitment at low and high SSBs, the SSBs in all scenarios with recruitment estimated from the Ricker model and the Ricker model with an increased density-dependence effect were lower than the reference SSB (Figs. 5 & 6, Table 3). With the Ricker models, v-notching had a positive effect on SSB (468–632 % higher with 100 % compliance and a strict definition than with 0 % compliance) (Figs. 5 & 6, Table 3); 100 % compliance with a strict definition most positively affected SSB, and the SSBs with no v-

Table 3. Median, lower CI (80 %), and upper CI (80 %) of the American lobster spawning stock biomass (SSB; in metric tonnes, mt) from the last year of each of the recruitment, v-notching compliance, and v-notch definition scenarios

Scenario	Median (mt)	Lower CI (mt)	Upper CI (mt)
Reference scenario (90 % compliance with a strict definition)	46 868	44 863	48 991
Historical recruitment			
0 %	35 600	33 273	37 698
50 % with a strict definition	43 096	40 924	45 715
100 % with a strict definition	47 316	44 920	49 262
50 % with a less strict definition	38 755	36 592	40 905
100 % with a less strict definition	41 817	39 653	44 202
Weak stock–recruitment relationship			
0 %	13 674	11 455	15 555
50 % with a strict definition	24 321	21 621	29 264
100 % with a strict definition	52 616	33 188	59 172
50 % with a less strict definition	18 026	14 865	21 115
100 % with a less strict definition	22 192	20 016	25 773
Ricker model recruitment			
0 %	4049	4671	5314
50 % with a strict definition	19 141	16 787	21522
100 % with a strict definition	29 631	27 161	32844
50 % with a less strict definition	10 769	9202	12 269
100 % with a less strict definition	15 733	14 633	18 212
Ricker model recruitment with increased density-dependence			
0 %	4266	3794	5103
50 % with a strict definition	16 250	14 861	17 873
100 % with a strict definition	24 224	22 534	26 945
50 % with a less strict definition	9578	8755	11 104
100 % with a less strict definition	14 085	12 681	15 469

notching decreased over time (Figs. 5 & 6). The SSBs in the other scenarios did not increase drastically over time (Figs. 5 & 6). With an increased density-dependence effect, the results were similar to that of the regular Ricker model, but the differences between the compliance and definition scenarios were smaller (Fig. 6, Fig. 8, Table 3). All the final SSBs significantly differed from each other (p-values $< 2.71 \times 10^{-13}$) (Tables S3 & S4).

Like the SSBs, cumulative landings were positively affected by v-notching with recruitment from the Ricker models (80–85 % higher with 100 % compliance and a strict definition than with 0 % compliance) (Figs. 5 & 6, Table 4). Cumulative landings from the reference scenario were higher than that of all the different v-notching scenarios with recruitment estimated from the Ricker models (Figs. 5 & 6 , Table 4). Regardless, the landings increased with 100 % compliance (Figs. 5 & 6). Similar to the SSBs with recruitment from the Ricker model, the landings also decreased with no compliance (Figs. 5 & 6). V-notching significantly positively affected landings (p-values $< 4.10 \times 10^{-8}$) (Tables S7 & S8). There were no large differences between the cumulative landings of the regular Ricker model and the Ricker model with an increased density-dependence effect, but there were larger differences between the compliance and defi-

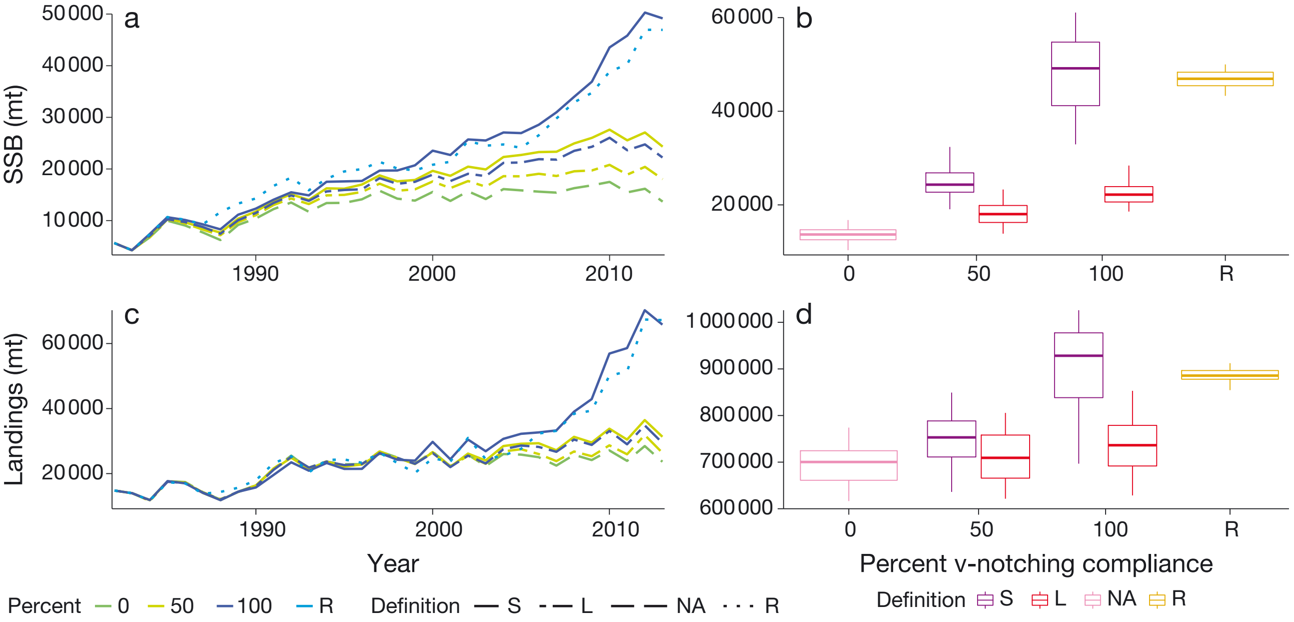

Fig. 4. Same as Fig. 3, but showing the results of the simulations with the weak-stock recruitment relationship

nition scenarios with the regular Ricker model than with the Ricker model with an increased density-dependence effect (Figs. 5 & 6, Table 4).

Table 4. Median, lower CI (80 %), and upper CI (80 %) of the cumulative landings of American lobster (in metric tonnes, mt) of each of the recruitment, v-notching compliance, and v-notch definition scenarios

Scenario	Median (mt)	Lower CI (mt)	Upper CI (mt)
Reference scenario (90 % with a strict definition)	885 641	866 906	902 586
Historical recruitment			
0 %	900 705	881 989	920 561
50 % with a strict definition	892 349	872 429	1 176 305
100 % with a strict definition	884 293	867 689	903 623
50 % with a less strict definition	897 743	877 295	913 353
100 % with a less strict definition	894253	877 563	913 492
Weak stock–recruitment relationship			
0 %	700 318	645 521	741 212
50 % with a strict definition	753 058	674 208	812 215
100 % with a strict definition	928 331	742 080	995 844
50 % with a less strict definition	709 219	644 956	782 125
100 % with a less strict definition	736 278	667 777	801 478
Ricker model recruitment			
0 %	347 086	332 866	366 472
50 % with a strict definition	525 284	502 732	563 015
100 % with a strict definition	624 020	605 157	675 085
50 % with a less strict definition	440 004	416 481	468 897
100 % with a less strict definition	494 312	468 181	529 320
Ricker model recruitment with density-dependence			
0 %	279 149	264 276	290 662
50 % with a strict definition	431 833	408 764	458 245
100 % with a strict definition	515 884	488 519	548 969
50 % with a less strict definition	362 657	341 657	379 928
100 % with a less strict definition	403 271	385 252	435 226

4. DISCUSSION

The results of this study support the consensus among lobster fishers that the protection of spawning female American lobsters *Homarus americanus*, in this case by v-notching, has had a positive impact on the GOM lobster population and fishery. The magnitude of the positive impact of v-notching depended on the assumptions of the stock–recruitment relationship, compliance rate, and v-notch definition. V-notching always had a positive impact on SSB, and the impact on cumulative landings depended on the stock–recruitment relationship.

In all scenarios, v-notching preserved SSB, which can act as a buffer if there were a downturn in the fishery or population. With historical recruitment, even if only half of the egg-bearing lobsters that were caught were v-notched, there would still be a significant positive impact on the population (21 % larger with 50 % compliance and a strict definition than with 0 % compliance). With the assumption of a weak

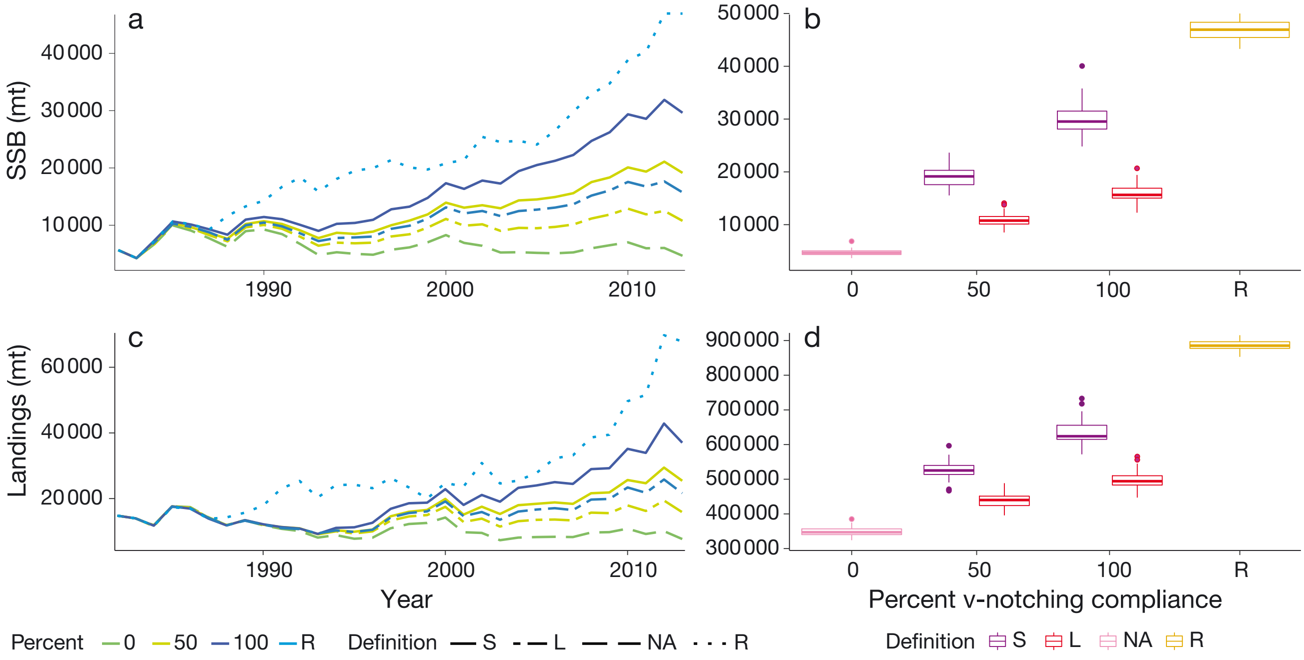

Fig. 5. Same as Fig. 3, but showing the results of the simulations with the Ricker stock–recruitment model

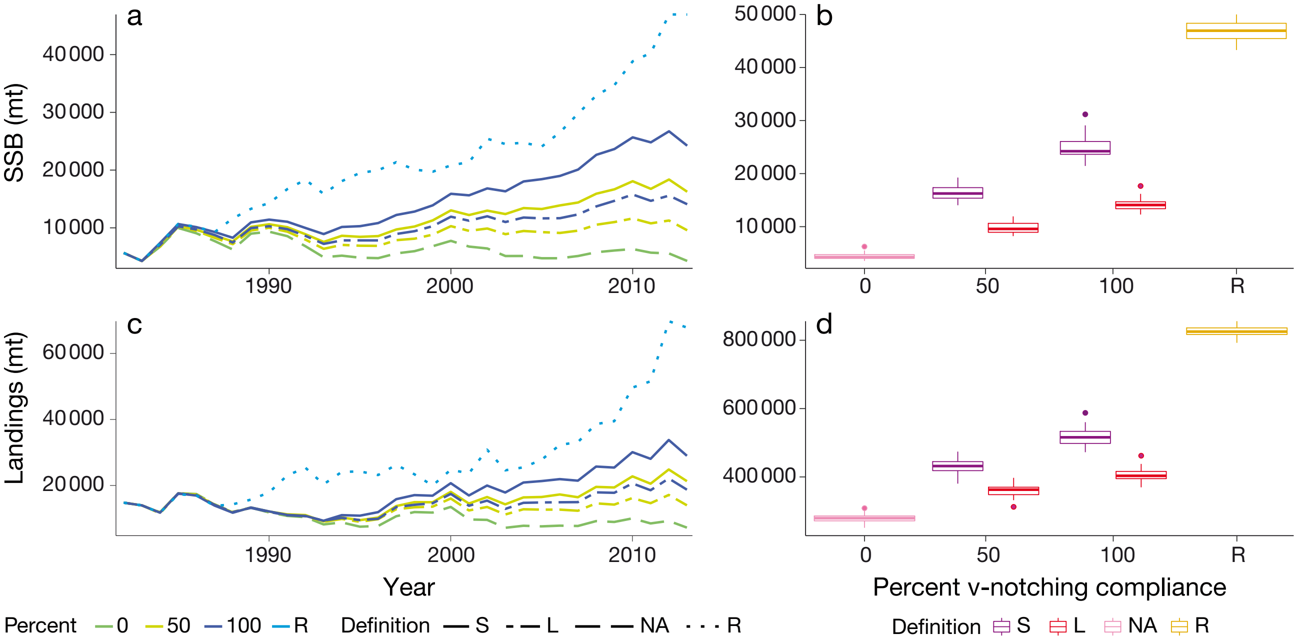

Fig. 6. Same as Fig. 3, but showing the results of the simulations with the Ricker stock–recruitment model with an increased density-dependence effect

stock–recruitment relationship, v-notching had even greater impacts on the population, as the protected spawning stock contributed recruits into the fishery (285 % larger with 100 % compliance and a strict definition than with 0 % compliance). Under this weak stock–recruitment relationship recruitment scenario, there were even more advantages to a higher v-notch compliance rate and strict v-notch definition. SSB did not experience such a dramatic increase without high compliance rates and a strict definition. With the assumption of a stock–recruitment model, a higher v-notch compliance and a strict v-notch definition had a significant large positive impact as well (468–632 % higher with 100 % compliance and a strict definition than with 0 % compliance). Preserving SSB becomes increasingly important in the face of climate change, since warming waters may have deleterious effects on the lobster population. Le Bris et al. (2018) projected the American lobster fishery with warming water temperatures and found that management measures for conserving the reproductive potential can help mitigate the negative effects of climate change.

The impact of v-notching on landings depended on the compliance, definition, and recruitment scenario. In historical recruitment scenarios, no v-notching produced the highest cumulative landings (1.9 % higher with 0 % compliance than with 100 % compliance and a strict definition). With the assumption of a stock–recruitment relationship, v-notching had a positive impact on landings (33–85 % higher with 100 % compliance and a strict definition than with 0 % compliance).

The results from these simulations also suggest that the v-notch definition had an important role. In all recruitment simulation scenarios, even 100 % compliance with a less strict definition did not produce more SSB than 50 % compliance with a strict definition. In the weak stock–recruitment relationship scenarios, even with 100 % compliance rate but with a less strict definition, the SSB and landings would not have experienced a dramatic increase.

A strict definition of a v-notch only benefits SSB and does not reduce landings with a stock–recruitment relationship, suggesting that all areas should use a strict definition of a v-notch (i.e. takes at least 2 molts to grow out). Without high compliance and a strict definition, there is a risk of a negative impact on the fishery. The state of Maine has the strictest definition of a v-notch, but other US states and Canada currently have a less strict definition of a v-notch.

The v-notching conservation measure sustained viable levels of fishery activity and is appropriate assuming that one objective of management is to maximize yield, under sustainability restraints. With conservation of biomass and an increase in landings, v-notching can be considered a tool for community-based conservation, in which both conservation and development are achieved (Berkes 2004). These results suggest that input controls, such as v-notching, can significantly benefit fish populations and fisheries.

However, v-notching compliance has decreased in recent years in the Maine lobster fishery. In this study, we simulated constant compliances to determine the effect of v-notching; currently, the magnitude of the change in compliance and when this change began to occur is unknown. Future studies should focus on lobster fishers' behavior regarding v-notching — more specifically, when the v-notching compliance began to decrease and how v-notching compliance changes with the status of the lobster population.

Future studies should also focus on understanding lobster recruitment, as the model results are dependent upon recruitment assumptions. This is especially important in understanding the effects of a conservation measure that protects the spawning stock with the long-term objective of increased recruitment. It was difficult to compare the results from the Ricker model recruitment scenarios to the reference scenario, because the Ricker model did not accurately capture historical recruitment. In general, the Ricker models were unable to represent the observed data, especially at high and recent SSBs. As a result, the results from the Ricker model scenarios could not be easily used to determine the effect of v-notching. However, if there were no stock–recruitment relationship, regulations that protect the spawning stock would not be important for the future of the fishery. In reality there is a stock–recruitment relationship that the data cannot show because of possibly large measurement errors, spatial differences in stock–recruitment relationships, and influences from environmental factors aside from temperature (Hilborn & Walters 1992). Chang et al. (2016) found that different stock–recruitment relationships existed at different spatial scales for the American lobster, possibly resulting from retention of pelagic larvae by oceanic circulations in the GOM (Xue et al. 2008), and the best model was at a medium spatial scale. Additionally, the productivity of American lobsters in the GOM may be changing due to increasing water temperatures which has caused an increase in suitable habitat (Tanaka and Chen 2016). This partially explains why a stock–recruitment relationship was difficult to find at a large spatial and temporal scale, such as the whole GOM from 1982–2013.

5. CONCLUSIONS

The IBLS model results showed that v-notching has a significant positive impact on the GOM lobster SSB (33–632 % higher with 100 % compliance and a strict definition than with 0 % compliance) regardless of the stock–recruitment assumption and a significant positive impact on landings (33–85 % times higher with 100 % compliance and a strict definition than with 0 % compliance) with a stock–recruitment relationship. The higher the compliance rate and the stricter the v-notch definition, the greater the positive impact on the fishery and population. The stock–recruitment relationship assumed in the model can influence the magnitude of the positive effect of v-notching. The framework proposed in this study can be extended to evaluate conservation and management measures in other fisheries.

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