NRC Research Press

ARTICLE

Evaluating benthic impact of the Gulf of Maine lobster fishery using the Swept Area Seabed Impact (SASI) model

Andrew G. Goode, Jonathan H. Grabowski, and Damian C. Brady

Abstract: The Magnuson–Stevens Fishery Conservation and Management Act mandates US fisheries minimize adverse effects of fishing on essential fish habitat (EFH). The Gulf of Maine (GoM) American lobster (*Homarus americanus*) fishery is the most valuable US fishery and can deploy more than three million traps annually. To date, the impact of this fishery on benthic EFH has not been addressed quantitatively. To evaluate the impact of the GoM lobster fishery on EFH, we incorporated lobster fishing effort into a model linking habitat susceptibility and recovery to area impacted by fishing gear: the Swept Area Seabed Impact model. Impact to EFH was localized along the coast and highest along midcoast Maine. Upwards of 13% of the benthos is in the process of recovery, but between 99.92% and 99.96% of initially affected habitat fully recovers. These estimates suggest that lobster fishing negligibly contributes to accumulation of EFH damage in the GoM due to the expansive area fished and the small footprint of each trap. Identifying areas of persistent impact is crucial in developing effective fisheries management for critical marine habitats.

Résumé : La Magnuson–Stevens Fishery Conservation and Management Act impose aux pêches états-uniennes de minimiser les effets néfastes de la pêche sur les habitats essentiels du poisson (HEP). De toutes les pêches aux États-Unis, la pêche au homard (*Homarus americanus*) dans le golfe du Maine (GdM) est celle qui revêt la plus grande valeur, plus de trois millions de pièges pouvant être déployés annuellement dans le cadre de ces activités. À ce jour, l'incidence de cette pêche sur les HEP benthiques n'a pas été examinée de manière quantitative. Afin d'évaluer l'incidence de la pêche au homard dans le GdM sur les HEP, l'effort de pêche au homard a été intégré dans un modèle qui relie la susceptibilité et le rétablissement des habitats à la superficie ayant subi des impacts des engins de pêche : le modèle d'impact sur la superficie balayée du fond marin. L'impact sur les HEP est concentré le long de la côte et est le plus grand le long du littoral central du Maine. Plus de 13 % du benthos est en cours de rétablissement, mais de 99,92 % à 99,96 % des habitats initialement touchés se rétablissent complètement. Ces estimations donnent à penser que la pêche au homard a un effet négligeable sur l'accumulation de dommages aux HEP dans le GdM en raison de l'ampleur de la région exploitée et de la faible empreinte de chaque piège. La détermination des zones d'impact persistant est d'importance clé pour la mise en place d'une gestion efficace de la pêche dans le but de protéger les habitats marins essentiels.

Introduction

The Gulf of Maine (GoM) lobster (*Homarus americanus*) fishery is the most valuable fishery in the United States (MDMR 2019*a*; NMFS 2019). Over the past three decades, the annual lobster landings in the GoM have rapidly increased, effectively multiplying historical landings fivefold (NMFS 2015). Lobster population expansion has been attributed to relaxed top-down pressure (Jackson et al. 2001; McMahan et al. 2013; Wahle et al. 2013), herring bait subsidization (Saila et al. 2002; Grabowski et al. 2010), increased algal habitat for juveniles due to reductions in urchin populations (Bologna and Steneck 1993; Steneck et al. 2004), and ocean warming shifting this species' range northward (Pinsky et al. 2013) and offshore (Tanaka and Chen 2016; Mazur et al. 2020) due to increased habitat thermal suitability (LeBris et al. 2018; Goode et al. 2019). Alongside population increase, advancements in fishing technology (i.e., vessels and traps; ASMFC 1996) has increased fishing effort and gear abundance in the GoM (Steneck et al. 2017). However, increases in fishing activity may come with unintended consequences. Every type of fishing gear that interacts with the benthos, to some extent, can damage essential fish habitat (EFH) crucial to the reproduction, development, and protection of fish species (Grieve et al. 2014; Grieve et al. 2015). Impacts to EFH by fishing gear include changes to sediment habitats as well as the damage and (or) loss of emergent epiflora (Bridger 1972; Peterson et al. 1983; Currie and Parry 1996; Watling and Norse 1998; Watling et al. 2001). Such impacts by fishing gear can also greatly reduce benthic structural diversity and alter population productivity (Dayton et al. 1995; Watling and Norse 1998). Therefore, the increase in fishing effort by the GoM lobster fishery may be inadvertently increasing degradation of EFH.

The Magnuson–Stevens Fishery Conservation and Management Act 1996 (USA) mandates that EFH be protected, to the extent practicable, from fishing-related impacts. The large spatial footprint and potential impact of the GoM lobster fishery necessitates a more comprehensive understanding of how the frequency and intensity of lobster fishing effort affects EFH in the GoM. To assess this impact, a quantitative framework examining habitat–gear interactions is necessary.

The Swept Area Seabed Impact (SASI) model is a method by which we can estimate the potential impact of fishing gear on

Received 7 August 2020. Accepted 19 December 2020.

A.G. Goode and D.C. Brady. School of Marine Sciences, University of Maine, Orono, ME 04469, USA.
J.H. Grabowski. Marine Science Center, Northeastern University, Nahant, MA 01908, USA.

Corresponding author: A. Goode (email: andrew.goode@maine.edu).

the EFH of the benthos (NEFMC 2011; Grabowski et al. 2014). The SASI model was developed to assess the benthic impacts of the most common bottom fishing gears in New England (e.g., otter trawls, scallop dredges, hydraulic clam dredges, gillnets, longlines, and lobster traps). Briefly, the SASI model determines what percentage of the fishing gear's footprint functionally reduces the biological and (or) geological EFH features of the benthos based on gear abundance, fishing frequency, and substrate classification. This modeling approach can help identify regions of high impact by fishing gear and, importantly, the degree to which these habitats are able to recover.

Here, we estimate the potential functional reduction of biological and geological EFH features by the GoM lobster fishery using the SASI model. Specifically, we simulate two different effort scenarios that represent the maximum and minimum potential impacts of the GoM lobster fishery on EFH. We also estimate the recovery potential of functionally reduced EFH and the accumulation of functionally reduced EFH over time. This application of the SASI model aims to quantify temporal dynamics and spatial variability in the functional reduction of EFH within the GoM and identify regions where persistent impacts occur. Delineating such locations will help fisheries management target their attention and (or) develop actions that better protect regions that are more prone to damage.

Methods

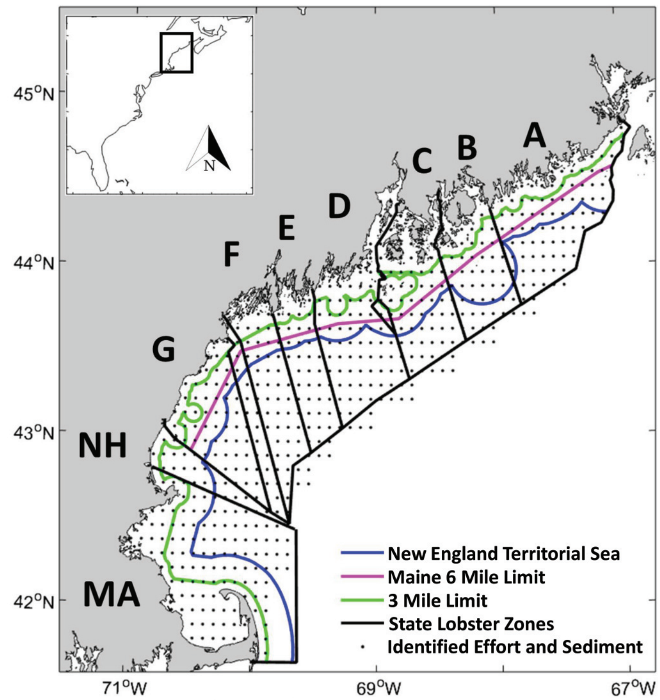
The Gulf of Maine (GoM) lobster fishery

The American lobster in the United States is regulated by both state and federal lobster management areas. Lobster fishing grounds are subdivided into seven federally regulated management areas that range from Cape Hatteras, North Carolina, to the Maine–Canada border. The coastal GoM is federal nearshore Management Area 1 and is the domain over which we are conducting our study. This management region is further subdivided into state-level fishing management areas: Maine zones A–G, New Hampshire, and northern Massachusetts (Fig. 1). Across these zones and depending on distance from shore, lobster fishing regulations and practices vary substantially (McCarron and Tetreault 2012; NMFS 2015).

The Swept Area Seabed Impact (SASI) model

Developed by the New England Fishery Management Council's Habitat Plan Development Team, the SASI model is a quantitative framework designed to assess the vulnerability of EFH to six of the most commonly fished bottom-tending gears in New England: trawls, scallop dredges, gillnets, longlines, traps, and hydraulic clam dredges (NEFMC 2011; Grabowski et al. 2014). This SASI team convened an expert panel of scientists, conducted an extensive literature review, and developed a framework to combine peer-reviewed, habitat-specific susceptibility and recovery rates into a single quantitative assessment of fishing gear impacts to benthic EFH. Marine substrates were subdivided into five categories based upon substrate data availability and usefulness in regional resource and fisheries management: mud, sand, granule–pebble, cobble, and boulder (Table 1). Predominant biological and geological EFH features were identified and assigned to each substrate type (refer to online Supplementary material, Table S1[1]). Biological EFH features necessitated a greater depth of analysis. Commonly found marine species were assigned to various biological feature functional groups, and the relative importance of these species to each functional group was determined. A vulnerability assessment was developed to organize and generate quantitative estimates of susceptibility and recovery values for each biological and geological EFH feature group (Supplemental Tables S2, S3[1]). Results from this assessment were combined to estimate substrate-specific susceptibility and recovery scores to then be utilized in estimating fishing gear-specific impacts to benthic EFH. Further information on the literature review and evidence considered can be found in NEFMC (2011) and Grabowski et al. (2014).

Fig. 1. Geographic boundaries of the Gulf of Maine used in our application of the Swept Area Seabed Impact (SASI) model. Letters denote lobster management zones. Map was created in Matlab using M_Map base layers. Boundary data were sourced from the NOAA Data Discovery Portal (NOAA 2019). The geographic limits represent distance from shore in nautical miles; 1 n.mi. = 1.852 km.



Applying SASI to the lobster fishery

Four parameters are required to evaluate potential habitat impact using the SASI model: (*i*) fishing gear abundance (number of traps), (*ii*) fishing frequency (deployments per day), (*iii*) seabed substrate composition and distribution, and (*iv*) susceptibility of each substrate type to damage by fishing gear (percent area functionally reduced).

Fishing gear abundance

The GoM American lobster fishery is not subject to mandatory vessel trip reports or vessel monitoring systems, which are typical methods of gathering fishing effort data. In lieu of this, determination of high-resolution fishing effort data has been the topic of research from a multitude of organizations. Fishing effort has been estimated by the Island Institute Mapping Working Waters project (The Island Institute 2012, 2016), the State of Maine Department of Marine Resources (MDMR) Lobster Sea Sampling Program (MDMR 2016), the Maine Lobsterman's Association dasymetric mapping effort (Brehme et al. 2015), and the National Marine Fisheries Service (NMFS) Vertical Line Model (NMFS 2014). We chose to use the NMFS Vertical Line Model in our analysis based on the utilization of federal- and state-level fishing activity data, monthly varying endline estimates, and consistent spatial resolution of gridded endline estimates.

Fishing effort was characterized by the number of vertical lines per 10 $\times$ 10 arcmin area from the Vertical Line Model. The number of vertical lines was assumed to be homogeneously distributed

[1]Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2020-0305.

Table 1. Sediment class identification and corresponding susceptibility and recovery values using the Swept Area Seabed Impact (SASI) model.

		Biological features		Geological features	
USGS sediment classification	SASI sediment classification	Susceptibility (% reduced)	Recovery time (years)	Susceptibility (% reduced)	Recovery time (years)
Bedrock	Boulder	16.8±0.6	2.0±0.4	5.3±0.6	2.7±2.3
Boulders	Boulder				
Gravel	Cobble	16.1±1.5	1.9±0.3	10.2±4.7	2.4±2.0
Gravelly sediment	Granule–pebble	16.1±1.3	2.0±0.3	5.3±0.6	0.5±0.1
Sand	Sand	13.0±2.5	1.6±0.4	13.7±2.8	0.5±0.1
Silty sand	Sand				
Clayey sand	Sand				
Sand–silt–clay	Sand				
Sandy silt	Mud	13.3±2.8	1.4±0.6	17.5±0.6	0.5±0.1
Silt	Mud				
Clayey silt	Mud				
Sandy clay	Mud				
Silty clay	Mud				
Clay	Mud				

Note: Values are mean and standard error.

Table 2. Model assumption of zones in the Gulf of Maine.

				Min. traps per line scenario				Max. traps per line scenario			
Zone	Season	Days between hauls (in-season)	Days between hauls (off-season)	0–3 n.mi.	3–6 n.mi.	6–12 n.mi.	>12 n.mi.	0–3 n.mi.	3–6 n.mi.	6–12 n.mi.	>12 n.mi.
A	Apr.–Dec.	3	7	1	3	(5)	(7.5)	3	(5)	(10)	(20)
B	May–Oct.	3	10.5	1	3	(5)	(7.5)	3	(5)	(10)	(20)
C	Mar.–Dec.	4	10.5	1	3	(5)	(7.5)	3	(5)	(10)	(20)
D	Mar.–Dec.	4	12	1	3	(5)	(7.5)	3	(5)	(10)	(20)
E	Apr.–Dec.	3	9.5	1	3	(5)	(7.5)	3	(5)	(10)	(20)
F	Apr.–Dec.	2.5	7	1	3	(5)	(7.5)	3	(5)	(10)	(20)
G	Apr.–Nov.	4.5	8.5	1	3	(5)	(7.5)	3	(5)	(10)	(20)
C–D overlap	Mar.–Dec.	4	11.25	NA	3	(5)	NA	NA	(5)	(10)	NA
F–G overlap	Apr.–Dec.	3.5	7.75	1	3	(5)	(7.5)	3	(5)	(10)	(20)
NH	Apr.–Jan.	3.4	9	1	(5)	(5)	(7.5)	3	(10)	(10)	(20)
MA	Apr.–Dec.	3	7	1	(5)	(5)	(7.5)	3	(10)	(10)	(20)
Outside	Apr.–Nov.	3.4	9	NA	NA	NA	(7.5)	NA	NA	NA	(20)

Note: Values in parentheses assume two endlines per trawl. 1 n.mi. = 1.852 km.

within each 10 × 10 arcmin area. Each 10 × 10 arcmin area was subdivided into four 5 × 5 arcmin areas to better characterize distance from shore and management zone. We used the lobster gear report summary from McCarron and Tetreault (2012) to allocate the number of traps fished per endline and to vary the number of traps per endline as a function of lobster management zone and distance from shore.

We estimated two effort scenarios to capture the potential bounds in lobster fishing effort. The Atlantic Large Whale Take Reduction Plan management area requirements (NMFS 2015) were used to assign maximum and minimum trap per trawl limits based on distance from shore. Applying these trap per trawl limits to the Vertical Line Model, variations in lobster gear configuration and fishing practices, and fishery regulations (Table 2), we estimated the maximum and minimum number of traps fished within the GoM.

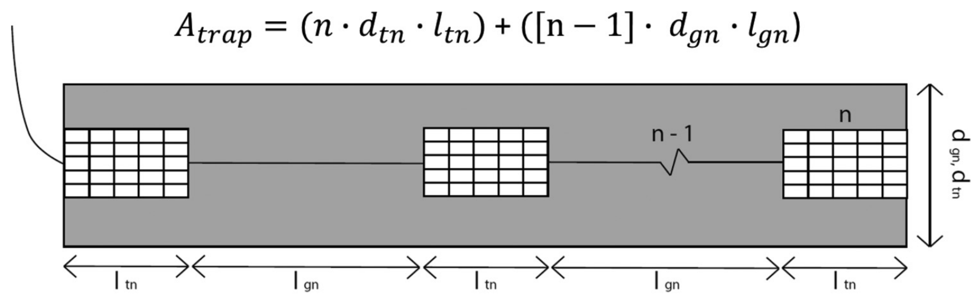
Fishing frequency

The Maine Lobstermen's Association conducted a survey from northern Maine to Massachusetts to identify how lobster fishing practices vary along the coast, distance from shore, and throughout the year (McCarron and Tetreault 2012). Although fishing practices vary at the individual level, the survey aimed to determine the most common gear configurations adopted by lobster fishers and the timeframes over which most fishing occurs. The survey identified how frequently fishers haul their traps, how this frequency changes during the year, and differences in these patterns among fishing zones. We used the values and timeframes identified from this survey to calculate the number of gear hauls by the GoM lobster fishery.

Seabed substrate composition and distribution

We gathered seabed sediment classification data from the United States Geological Survey (USGS) East Coast Sediment Texture Database (McMullen et al. 2014). This database characterizes sediments as one of 14 potential classifications (Table 1) and has been used to investigating lobster habitat suitability (Tanaka and Chen 2016) and macrobenthos variability (McHenry et al. 2017). However, the SASI model simplifies marine substrates into five categories: mud, sand, granule–pebble, cobble, and boulder (NEFMC 2011; Grabowski et al. 2014). To convert the substrate classification scheme from the USGS to that used by the SASI model, we consolidated substrate class based on similarity in Shepard classification and Wentworth scale (e.g., sand dominated sand–silt–clay mixtures were categorized as sand according to the SASI model; Supplemental Fig. S1[1]; Wentworth 1922; Shepard 1954; Schlee and Webster 1967; Poppe et al. 2004). Sediment classification was linearly interpolated over a 0.5-arcmin resolution grid. The relative percentage of each substrate type per 5 × 5 arcmin area was determined using the interpolated sediment classification grid. One-way ANOVA and Tukey–Kramer post hoc tests were performed to identify significant

Fig. 2. Visual representation of variables used to determine the area swept clear by lobster trap trawls. The grey area is the total area swept clear.



Model Variable	Description
A_{trap}	Area Swept Clear
n	Number of Traps
n - 1	Number of Groundlines
d_{tn}	Lateral Drag Distance of a Trap (m)
d_{gn}	Lateral Drag Distance of a Groundline (m)
l_{tn}	Trap Length (m)
l_{gn}	Groundline Length (m)

differences in rocky substrate cover by lobster management zone. The variance of substrate percent cover was determined and standardized by the maximum possible variance using the USGS and SASI sediment classifications. Standardized variance values closer to one represent a more homogeneous substrate distribution, while values closer to zero represent a more heterogeneous substrate distribution per 5 × 5 arcmin area. We used a Wilcoxon signed rank nonparametric test to identify whether the downscaling of sediment classification significantly changed the spatial complexity of substrate classification.

Substrate susceptibility to damage

The SASI model vulnerability assessment estimated the susceptibility of EFH to damage by fishing gear interactions (NEFMC 2011; Grabowski et al. 2014). Susceptibility was defined as the percent reduction in functional value that any feature provides to a fish species (e.g., an EFH feature with an S score of 100% would have no functional value after being disturbed by fishing gear). Susceptibility scores are estimates of the reduction in functional value of substrate-associated EFH features after a single-pass fishing event. The size, fragility, and relative abundance of geological features and species present were considered when assigning susceptibility scores per substrate. Susceptibility scores were typically highest for more invasive, mobile gears compared with fixed gears (NEFMC 2011; Grabowski et al. 2014). Traps have susceptibility scores ranging from 5.3% to 17.5% depending on substrate and type of EFH feature (Table 1; NEFMC 2011; Grabowski et al. 2014).

Evaluating area of impact

Using fishing gear abundance and fishing frequency, we estimated the area of the seabed that is swept by lobster fishing gear. The area of the seabed swept by lobster fishing gear is influenced by the number of traps, trap size, length of groundline between traps, and how far the gear is dragged along the seabed (Fig. 2). Since dragging can substantially increase the area of the seabed interacted by lobster fishing gear, we assumed that the entire area of the seabed between the first and last trap on a lobster trawl is impacted during a hauling event (Fig. 2; Schweitzer et al. 2018; Stevens 2020). This approach produces comparable estimates of interacted benthos to other studies (Schweitzer et al. 2018; Stevens 2020). We calculated the area of the seabed swept by lobster fishing gear (ASC; m^2) at each location (i) and month (m) as follows:

$$\mathrm{ASC}_{\mathrm{trap},i,m} = \left[\sum_{1}^{n_{i,m}} (d_{tn} \cdot l_{tn}) + \sum_{1}^{n_{i,m}-1} (d_{gn} \cdot l_{gn})\right] \cdot f_{i,m}$$

where $n_{i,m}$ is the number of traps, $n_{i,m} - 1$ is the number of groundlines between traps, d_{tn} is the lateral distance the nth trap moves over the seabed, l_{tn} is the length of the nth trap, d_{gn} is the lateral distance of the nth groundline that moves over the seabed, l_{gn} is the length of the nth groundline, and $f_{i,m}$ is the haul frequency of the fishing gear (NEFMC 2011). Consistent with NEFMC report (2011), we assumed that lobster trap length and the side-to-side dragging of traps were both 1 m. Given the low probability that fishing gear falls on, and functionally damages, the same exact area of the benthos multiple times, we assumed that every fishing event interacts with a new area of the benthos. Since the SASI model considers repeated interactions on an EFH feature to not increase the area or degree of impact, this assumption likely produced an overestimate of the area functionally damaged by fishing gear.

We then applied the seabed substrate composition and corresponding susceptibility scores to determine the area of the seabed functionally damaged. We calculated the area of the seabed functionally damaged by actively fished gear (A; m^2) at each 5 × 5 arcmin location (i) per month (m) as follows:

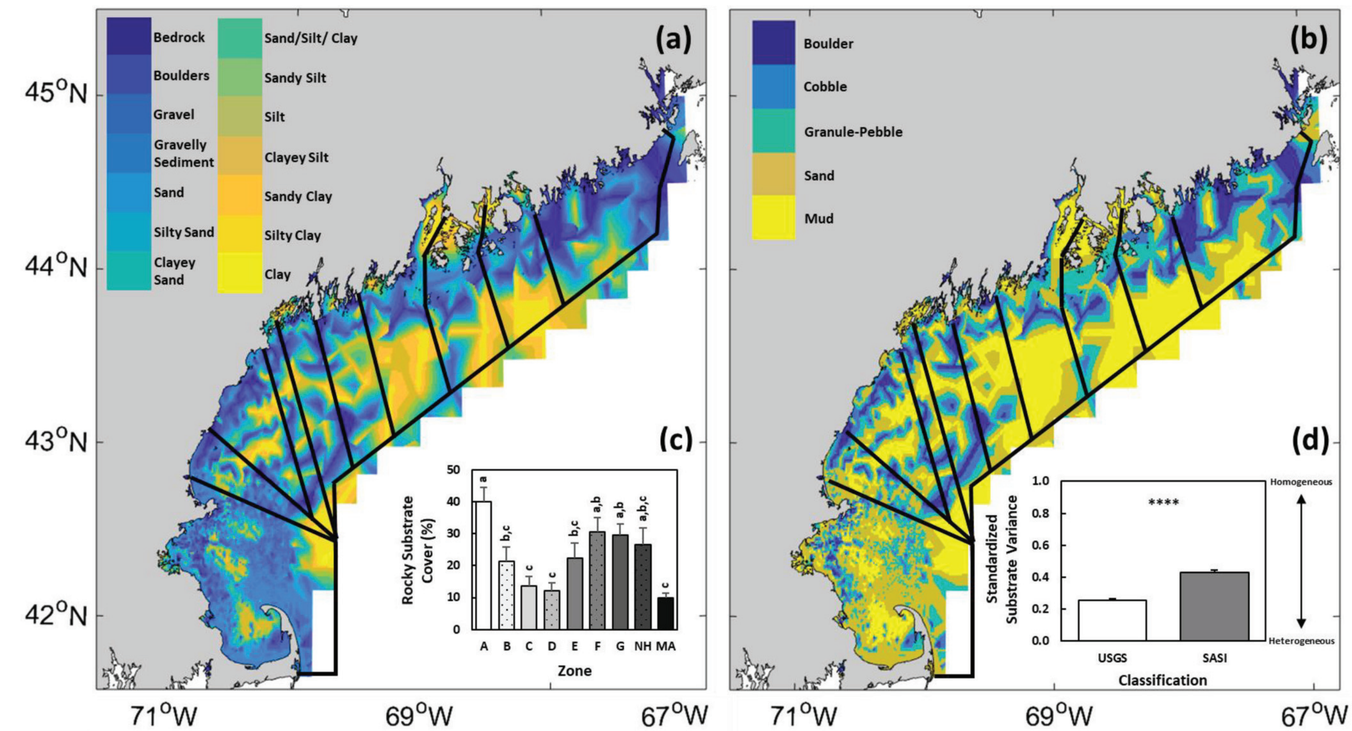
$$A_{i,m} = \sum_{1}^{h=5} (\mathrm{ASC}_{i,m} \cdot P_{h,i} \cdot S_{h,i})$$

where h is the habitat substrate type, $P_{h,i}$ is the proportion of the 5 × 5 arcmin area of each substrate type, and $S_{h,i}$ is the susceptibility of the benthos to functional reduction.

Recovery assessments

We conducted two recovery potential assessments of functionally damaged EFH. The first assessment determined how much

Fig. 3. Sediment classification of the Gulf of Maine. (*a*) Sediment classification using the USGS East Coast Sediment Texture Database. (*b*) Sediment classification using the SASI model. (*c*) Zonal distribution of rocky substrate cover. Values are mean and standard error. Letters denote statistical similarity. (*d*) Normalized substrate variance per 5 × 5 arcmin area between substrate classification schemes. Values are mean and standard error. 1 = homogeneous, 0 = heterogeneous. Asterisks (****) denotes a significant difference at the $p < 0.0001$ level. Map was created in Matlab using M_Map base layers. Sediment data were sourced from USGS (McMullen et al. 2014).



of the area functionally damaged in a year can fully recover. Full recovery occurs when the initially damaged area of the seafloor remains undisturbed by fishing activity long enough to recover its functional contribution as EFH (Table 1). To calculate this, we simulated the random overlap of continued fishing gear on already damaged habitats. The proportion of fishing overlap at each location ($P_{\text{overlap},i}$) was the amount of initially damaged EFH that remains damaged via repeated interactions with fishing gear and was calculated as follows:

$$P_{\text{overlap},i} = \sum_{1}^{h=5} \left(\frac{A_{\text{annual},i,h} \cdot A_{\text{month},i,h} \cdot T_h}{B_i^2} \right)$$

where h is the habitat substrate type, $A_{\text{annual},i,h}$ is the annual area of EFH functionally reduced, $A_{\text{month},i,h}$ is the monthly average area of EFH functionally reduced, T_h is the time of recovery in months, and B_i is the available bottom area.

The second recovery assessment estimated the accumulation of EFH damage over time. Benthic community status following impact by fishing gear exists at an equilibrium state between depletion rate and recovery (Jennings et al. 2012; Pitcher et al. 2017). This theoretical framework can be extrapolated to fishing gear impacts over large spatial scales. Like benthic communities, the status of EFH is a balance between additional impact and rate of recovery (NEFMC 2011). Equilibrium occurs where added fishing impact balances the rate of habitat recovery and the area of impacted benthos at which this occurs can be estimated. The accumulated area (A) of the seabed functionally damaged at each location (i) over time was calculated as follows:

$$A_{t+1,i} = A_{t,i} + A_{\text{month},i} - A_{t,i} \cdot \frac{1}{T_i}$$

where t is time in months, $A_{\text{month},i}$ is the monthly average area of EFH functionally reduced, and T_i is the time of recovery in months. If we ignore the first two terms and set monthly added damage equal to the rate of recovery:

$$A_{\text{month},i} = A_{t,i} \cdot \frac{1}{T_i}$$

We can then solve for the area at which this balance occurs. We estimated the cumulative area of the seabed that is functionally reduced as follows:

$$A_{t,i} = A_{\text{month},i} \cdot T_i$$

This procedure was conducted for each location (i) accounting for variability in substrate (h) recovery times:

$$A_{\text{cumulative},i} = \sum_{1}^{h=5} (A_{i,\text{month},h} \cdot T_h)$$

For both recovery assessments, we increased the time required for EFH to recover as depth increased. Baseline recovery rates were assigned to each EFH and substrate type (Table 1), and we increased the time of recovery by one standard error with each additional 50 m of depth, as suggested in Grabowski et al. (2014; Supplemental Fig. S2[1]).

Data analysis and visualization

The areas of EFH functional reduction were collated by distance from shore. Then we used a three-way ANOVA and Tukey–Kramer post hoc test to determine differences in EFH damage as a function of distance from shore, between annual and cumulative damage, and between geological and biological EFH features. The annual area of EFH functional reduction was averaged over each lobster management zone and one-way ANOVAs and Tukey–Kramer post hoc tests determined which zones experienced higher or lower areas of EFH damage. We then conducted *t* tests assuming unequal variances to determine whether there were differences in the annual area of biological or geological EFH functional reduction and whether there were differences in the remaining area of biological or geological EFH functionally reduced after recovery. All maps were generated using Matlab version R2020a and the M_Map mapping software (Pawlowicz 2020).

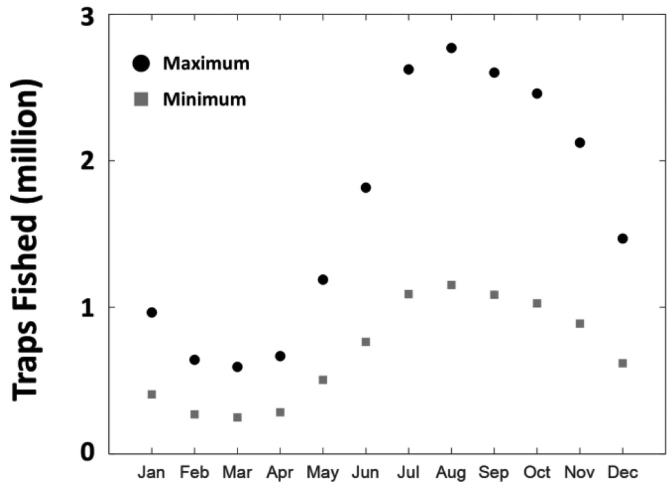
Results

Benthic habitat characterizations were consolidated before being used in the SASI model within the GoM. Of the areas in which fishing effort data were available, we associated 613 5×5 arcmin areas with a SASI sediment type (Fig. 1). Downscaling sediment classification from the USGS to SASI classification scheme retained large-scale patterns of substrate distribution (Figs. 3*a* and 3*b*). For example, both classifications show that the percent cover of rocky substrate differed significantly by zone ($F_{[8,533]} = 10.6$, $p < 0.001$; Fig. 3*c*). Zones A, F, G, and NH had the highest percent cover of rocky substrate, while zones B, C, D, and MA had the lowest. Despite retaining large-scale patterns of substrate distribution, the consolidation of sediment classification significantly changed the substrate complexity per 5×5 arcmin area. Standardized SASI substrate variance (mean $\pm$ SE = 0.43 $\pm$ 0.01) was significantly higher than the USGS classification scheme (0.26 $\pm$ 0.01; $n = 1120$, $Z = -20.3$, $p < 0.0001$; Fig. 3*d*). Thus, converting USGS sediment classifications to the SASI model shifts sediment complexity to be more homogeneous, a necessary simplification by the SASI model to relate substrate type to benthic community structure.

The Vertical Line Model estimate of lobster fishing effort is consistent with previous approaches (McCarron and Tetreault 2012) and produced total trap estimates comparable to the number of traps legally allowed to fish (MDMR 2019*b*). Highest fishing effort occurred along midcoast and northern Maine (Supplemental Fig. S3[1]). Fishing activity gradually increased from January to the beginning of May–June and gradually decreased beginning in September and ending around December–January (Supplemental Fig. S3, S4[1]), consistent with Boenish and Chen (2018). This seasonality was also present in our estimates of total traps fished in the GoM, where the maximum number of traps fished occurred in August, and the minimum number of traps fished occurred in March (Fig. 4). Using the two fishing effort scenarios, we estimated the seasonal minimum and maximum number of traps fished. We estimated the lowest number of traps fished during the year as 0.24 and 0.59 million traps, and the highest amount fished as 1.15 and 2.77 million traps for the minimum and maximum trap per endline scenario, respectively (Fig. 4). The maximum trap per endline scenario of 2.77 million traps is comparable to the estimates of lobster traps fished reported by Auster and Langdon (1999) and the average annual number of trap tags sold by the MDMR from 1998 to 2018 (2.94 million tags; MDMR 2019*b*). Therefore, we present the results of our analysis using the maximum trap per endline scenario.

Annual EFH functional reduction was unevenly distributed between lobster management zones and largely reflected the distribution of fishing gear. Specifically, annual EFH functional reduction ranged from 0.01% to 5.74% per 5×5 arcmin area and was significantly higher for biological features (mean $\pm$ SE = 1.17% $\pm$ 0.03%) than geological features (= 0.94% $\pm$ 0.03%; t_{1038} = 5.63, $p < 0.0001$; Fig. 5). This significant difference was driven by higher susceptibility scores for biological compared with geological habitat features (Table 1). The majority of biological EFH impacts occurred between 0 and 3 n.mi. (1 n.mi. = 1.852 km) from shore (Supplemental Fig. S5[1]; $F_{[11,2336]} = 111.8$, $p < 0.0001$) and in lobster management zones NH, F, E, D, A, and C, highest to

Fig. 4. Estimated traps fished in the Gulf of Maine. Black circles are the maximum trap per endline scenario. Grey squares are the minimum trap per endline scenario.



lowest impact, respectively (Fig. 5; $F_{[8,557]} = 7.63$, $p < 0.0001$). Similarly, impacts to geological EFH features were greatest between 0 and 3 n.mi. (Supplemental Fig. S5[1]; $F_{[11,2336]} = 111.8$, $p < 0.0001$) and in lobster management zones D, E, F, NH, C, and MA, highest to lowest impact, respectively (Fig. 5; $F_{[8,557]} = 8.19$, $p < 0.0001$).

The recovery potential of functionally reduced EFH varied significantly by type of EFH feature. After the necessary time to recover, we estimated the area that remained functionally reduced via continued gear interaction. These areas ranged between 0 and 15 670 m^2 or 0% to 0.025% of each 5×5 arcmin area. Significantly more biological EFH features (mean $\pm$ SE = 559 $\pm$ 47 m^2, 0.00096% $\pm$ 0.00001%) remained functionally reduced compared with geological features (222 $\pm$ 19 m^2, 0.00036% $\pm$ 0.00003%; $t_{808} = 7.43$, $p < 0.0001$; Fig. 6). These areas of continued impact correspond to ~0.08% and 0.04% of the initial area functionally reduced for biological and geological EFH features, respectively. Thus, ~99.92% and 99.96% of the functionally reduced biological and geological EFH, respectively, fully recover within their assigned period of recovery.

While patterns in accumulated functional reduction of EFH over time was similar to annual functional reduction across zones, we did observe a significant shift in accumulated functional reduction offshore. Offshore habitats were more susceptible to accumulating functionally reduced EFH because the model attributes longer recovery times to deeper, offshore habitats. Recovery times of less than a year allow recovery to outpace additional impact and result in a cumulative area of EFH functional reduction that is less than the area reduced annually (Fig. 7). Conversely, recovery times greater than a year allow additional disturbances to outpace recovery such that the cumulative area of EFH functional reduction becomes greater than the area reduced annually (Fig. 7). Longer recovery times correspond to larger areas of cumulative EFH functional reduction and longer periods until added damage balances recovery. Thus, cumulative functional reduction to EFH was higher offshore compared with annual values (Supplemental Fig. S5[1]; $F_{[11,2336]} = 118.8$, $p < 0.0001$). However, the geological and biological habitat features are differentially affected. There was a larger percent increase in the area of functional reduction for biological (mean $\pm$ S.E. = 1.51% $\pm$ 0.03%) than geological features (0.38% $\pm$ 0.06%; $t_{824} = 17.2$, $p < 0.0001$; Supplemental Fig. S5[1]). Cumulative EFH functional reduction ranged from 0% to 12.8% per 5×5 arcmin area and was significantly higher for biological (2.73% $\pm$ 0.07%) than geological features (1.07% $\pm$ 0.04%; $t_{995} = 21.0$, $p < 0.0001$; Fig. 8). Biological features were functionally reduced the greatest in lobster management

Fig. 5. Annual area (%) of functionally reduced essential fish habitat (EFH) in the Gulf of Maine. Inset: Zonal distribution of annual EFH functional reduction. Values are mean and standard error. Letters denote statistical similarity. Map was created in Matlab using M_Map base layers.

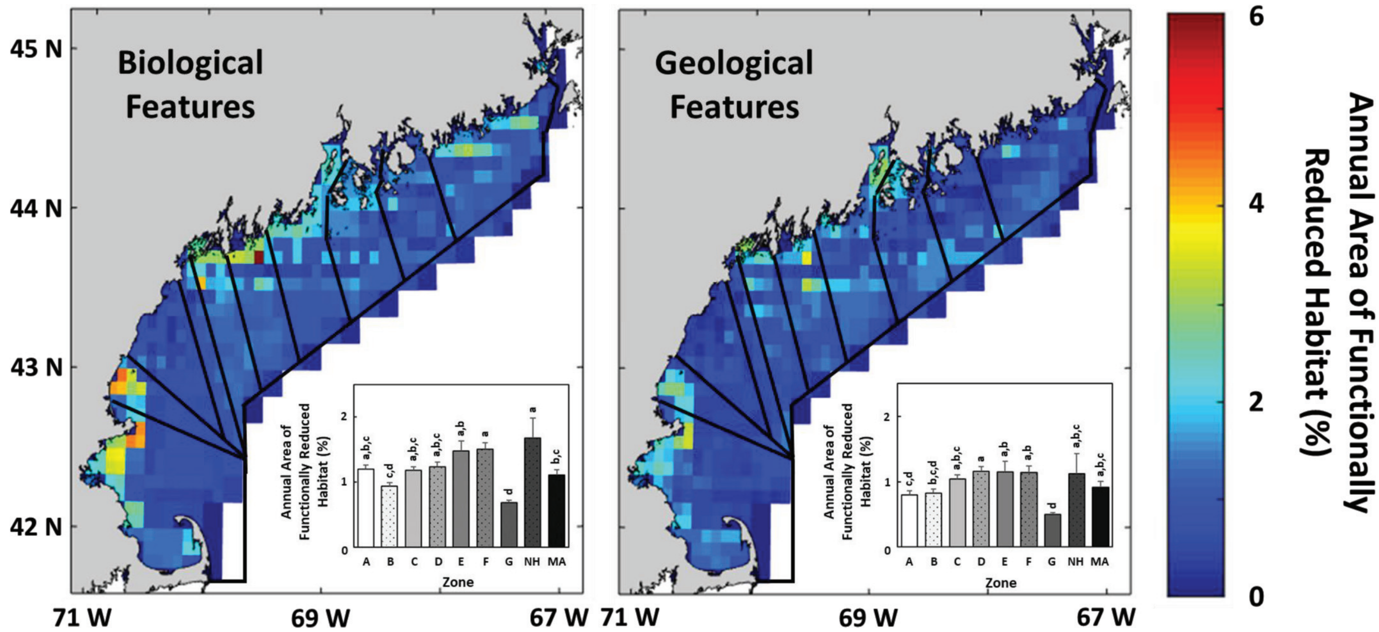


Fig. 6. Recovery potential of initially functionally reduced EFH, indicating the area (m^2 and %) that remains functionally reduced per 5 × 5 arcmin area via continued gear interaction. Values are mean and standard error. Asterisks (****) denotes a significant difference at the $p < 0.0001$ level.

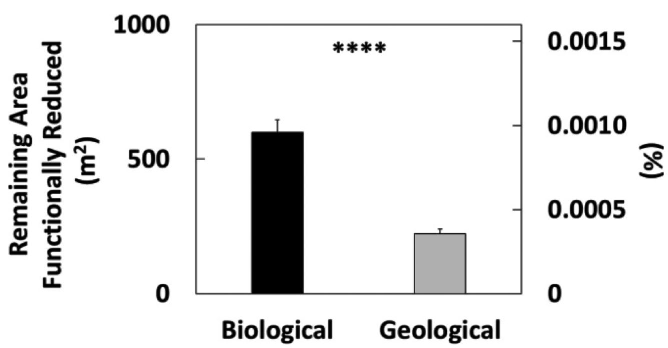
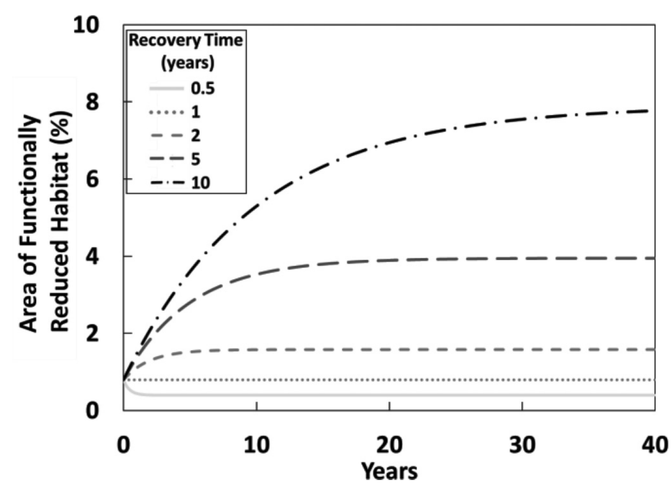


Fig. 7. Example of accumulation of EFH area (%) functionally reduced on substrates with varying recovery times.



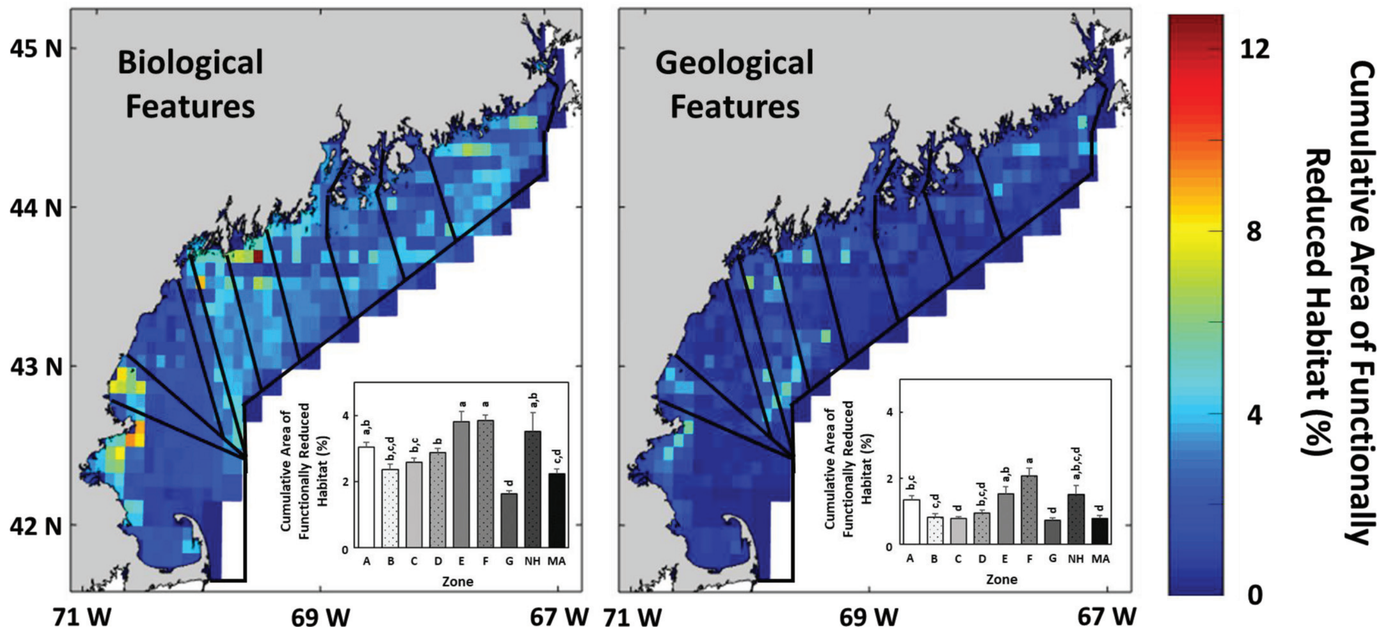
zones F, E, NH, and A, highest to lowest, respectively (Fig. 8; $F_{[8,557]} = 14.7$, $p < 0.0001$). Similarly, geological features were functionally reduced the greatest in lobster management zones F, E, and NH (Fig. 8; $F_{[8,557]} = 12.7$, $p < 0.0001$).

Discussion

The Magnuson–Stevens Fishery Conservation and Management Act established that EFHs be protected, to the extent practicable, from fishing-related impacts. The GoM has supported some of the most iconic and valuable fisheries in North America. One such example is the American lobster fishery, which is currently the most valuable single-species fishery in the United States (MDMR 2019*a*; NMFS 2019) with nearly three million traps fished annually (MDMR 2019*b*). To evaluate the impact of the GoM lobster fishery on benthic EFH, we used a quantitative framework that relates habitat-specific impacts from fishing gear on EFH: the SASI model (NEFMC 2011; Grabowski et al. 2014).

All fishing gear can impact habitat; however, our results demonstrate that EFH features impacted by the GoM lobster fishery are capable of near full recovery. The capacity of EFH to recover is linked to variation in substrate-specific susceptibility and recovery scores in the SASI model. Biological EFH features are impacted to a greater extent due to their higher susceptibility and longer recovery times for the more abundant substrate types within the GoM (Table 1; Fig. 3; NEFMC 2011; Grabowski et al. 2014). Longer recovery times in deeper habitats (Supplemental Fig. S2[1]) increase the areas offshore in the process of recovery (Fig. 8, Supplemental Fig. S5[1]). However, the relatively large area fished dilutes the functional reduction of EFH annually and reduces the probability of multiple gear deployments on the same EFH features. The low probability of repeated gear interactions and low susceptibility of EFH to damage by lobster traps (NEFMC 2011; Grabowski et al. 2014;

Fig. 8. Cumulative area (%) of functionally reduced EFH. Inset: Zonal distribution of cumulative EFH functional reduction. Values are mean and standard error. Letters denote statistical similarity. Map was created in Matlab using M_Map base layers.



Grieve et al. 2014) result in >99.9% functional recovery of EFH features (Fig. 6).

Our estimates of fishing effort by the GoM lobster fishery conform well to other gear abundance metrics. Our maximum traps per endline scenario yielded an estimated 2.77 million traps fished, a value comparable to the estimates of traps fished by Auster and Langdon (1999) and the average number of trap tags sold by the MDMR from 1998 to 2018 (2.94 million tags; MDMR 2019*b*). Since it is difficult to determine what percentage of trap tags sold are fished, we cannot reliably determine the accuracy of our estimates to the actual number of traps fished. Nevertheless, our maximum trap per endline scenario produced estimates comparable to the only verifiable metric of lobster traps in the GoM, which also presents an upper limit to the possible number of traps fished.

Ongoing changes in the distribution of fishing effort may cause varying degrees of benthic disturbance that shift over time and affect the total amount of EFH that is damaged. For example, lobster fishing effort has tracked abundance shifts northeastward (Steneck and Wilson 2001; Kleisner et al. 2017), attributable to rapid warming (Pershing et al. 2015; Friedland et al. 2020) and increased habitat suitability (Tanaka and Chen 2016; LeBris et al. 2018; Goode et al. 2019; Mazur et al. 2020). Additionally, limited entry to the GoM lobster fishery has shifted the age of license holders to 50–65 years old (Stoll et al. 2016; Stoll 2017), few younger potential lobster fishers are replacing those that exit the fishery (Supplemental Fig. S6[1]), and state requirements for number of licenses sold per existing licenses retired (MDMR 2020) are reducing the number of fishers and total fishing effort (MDMR 2019*b*). Declines in young-of-year lobster suggest uncertainty in future landings (LeBris et al. 2018; Oppenheim et al. 2019), potentially affecting the size and distribution of the GoM lobster fishery. As this fishery continues to adapt to management regulation of the North Atlantic right whale (*Eubalaena glacialis*) (e.g., Record et al. 2019), a likely result will be an increase in the minimum required number of traps per endline. Such a change would increase the amount of groundline that interacts with benthic EFH in part because of the greater distance over which longer trap trawls are dragged (Schweitzer et al. 2018; Stevens 2020) and would change the areas in which these gear configurations can be fished. As this fishery continues to change, so too will the areas impacted by fishing gear and their potential to recover. Moreover, our application of the SASI model is flexible and could be used to evaluate how various management alternatives affect fishing effort, behavior, and potential impact to EFH over longer time scales.

The limited availability of high spatial and temporal resolution endline estimates of GoM lobster fishing effort is perhaps the largest information bottleneck for more accurate future projections of habitat impact (Boenish and Chen 2018). For example, the relatively coarse spatial resolution (10× 10 arcmin) of the NMFS Vertical Line Model limits the extent to which we can identify localized areas of persistent fishing disturbance. Although we can effectively compare effort across the GoM, smaller bedforms targeted by fishing cannot be distinguished. Inability to characterize targeted fishing effort may underestimate impact and overestimate recovery potential on heavily impacted bedforms that are predicted to have lower biodiversity (Sousa 1979; Sousa 1984) and lower resilience to community shifts (Holling 1973). Less-targeted bedforms, however, may have reduced impacts and have a higher probability of fully recovering, possibly balancing out total estimates of impact. Implementation of common monitoring practices (e.g., 100% vessel trip reporting or vessel monitoring systems) would provide comprehensive, real-time estimates of fishing effort needed to address these issues.

Recovery time strongly influences the accumulation of damage and the recovery potential of EFH, highlighting the importance of accurate evaluation of regional-, substrate-, and fishing gear-specific rates of recovery. Commensurate with other studies, the SASI model revealed that EFH features are more susceptible to, and take longer to recover from, mobile fishing gears (e.g., Auster and Langdon 1999; Kaiser et al. 2000). We demonstrated that substrates with even moderate recovery times (∼5 years) can take over 10 years to reach a balance between new impacts and recovery (Fig. 7). Thus, even slight increases in recovery time can dramatically increase the area of recovering EFH. For example, sensitive deep-sea corals and sponges can take an estimated 20 and 30 years, respectively, to recover population biomass following damage by trawling (Rooper et al. 2011). The SASI model's ability to incorporate EFH features with multidecade recovery rates may potentially be limited by the availability of long-term recovery studies (Grabowski et al. 2014). However, we contend that the recovery rates used by the SASI model are well-informed based on the relative species composition within our study domain. Sensitive, long-recovering deep-sea corals occur well outside Federal Lobster Management Area 1, and the relative abundance of other sensitive fauna (e.g., corals and sponges) is relatively low (Supplemental Fig. S7[1]; McHenry et al. 2017). The lower abundance and comparatively faster recovery (e.g., Henry et al. 2003) of these faunae dampen their impact on overall recovery rates and the sensitivity of our results to varying recovery times.

While SASI is a useful starting point to start quantitatively characterizing the complex interactions between habitat and fishing gear, there are assumptions and generalizations that can introduce limitations. The SASI model treats repeated gear encounters on EFH as independent events that do not increase the magnitude of impact on EFH (NEFMC 2011; Grabowski et al. 2014). This assumption does not account for how initial disturbances could be more or less impactful than subsequent impacts (e.g., Hall-Spencer and Moore 2000), how added damage to EFH may further decrease biodiversity (e.g., Sousa 1984), or how persistent disturbances may shift benthic assemblages to new stable states that provide less functional benefit to fish (Lewontin 1969). The SASI model's simplification of substrate complexity and biotic assemblages underestimates the variability of the benthos and the distribution of EFH. Simplification of substrate classification (Fig. 3) results from the fact that in situ studies rarely investigate fishing gear – habitat interactions at the granularity of the USGS classification system. Additionally, substrate characteristics alone can only partially explain benthic biodiversity of the GoM (McHenry et al. 2017), despite the lower biodiversity compared with similar large marine ecosystems (Witman et al. 2004). While incorporation of other potential abiotic drivers (e.g., temperature, salinity, and current structure; McHenry et al. 2017) could increase the realism and accuracy of the SASI model, the current assumptions are key to parameterizing the SASI model in a complex marine environment.

Indirect anthropogenic factors also alter the benthos, and determining their relative impact is important when assessing the health of EFH. The macrobenthos community has changed multiple times due to fishing impacts on keystone species and will continue to shift as the ocean experiences climate change (Harris and Tyrrell 2001). For example, overfishing of demersal groundfish relaxed top-down pressures on urchin populations, which contributed to a benthic regime shift from macroalgal communities to urchin barrens (Steneck et al. 2002). Not long thereafter, targeted fishing on urchins resulted in a shift back towards macroalgal communities composed of more invasive algae and devoid of large-bodied fish predators (Steneck et al. 2002). Each of these trophic cascades altered benthic communities without direct physical manipulation and made a lasting impact thought to have helped bolster the GoM lobster fishery (Steneck and Wahle 2013). Additionally, climate change continues to impact the health and distribution of native and nonnative species. Thermally mediated range expansion of invasive and novel species (e.g., European green crab (*Carcinus maenas*), Tepolt and Somero 2014; Asian shore crab (*Hemigrapsus sanguineus*), Stephenson et al. 2009; black seabass (*Centropristis striata*), McMahan et al. 2020) is facilitating displacement of native fauna via competition or direct predation (e.g., Race 1982; Brenchley and Carlton 1983; Eastwood et al. 2007). Ocean acidification exacerbates thermal stress and acts to decrease native fauna resilience to change and disease (Lesser 2016; Harrington et al. 2020). So, while evaluating direct impact by fisheries on EFH is important, we contend that fishery impact must be contextualized in the scope of many processes affecting the environment.

While we have done our best to simulate lobster fishing effects on benthic habitats, additional work needs to be conducted to evaluate impacts on EFH more holistically over the coastal New England Shelf. We have, to the best of our ability, estimated the impact of lobster fishing on benthic EFH in Federal Lobster Management Area 1. This area, despite being the primary source of US lobster landings (NMFS 2019), is only a fraction of the American lobster fishery, and separate analyses would be necessary for other management areas. While our study agrees with previous efforts that fixed gears have relatively low impacts, EFH is also impacted by several other, more invasive, fisheries (NEFMC 2011; Grabowski et al. 2014). Thus, a cumulative model including all fisheries is an important next step. Fishery co-occurrence would almost certainly change the area of impact and recovery potential of EFH (e.g., NEFMC 2011). However, the presence of fixed gears may act to preclude more damaging fishing activities (e.g., trawling) and protect regions with sensitive EFH (Kaiser et al. 2000). Conversely, fishers typically avoid trawling in highly structured, more vulnerable habitats like cobble and boulder bottom due to the risk of gear hang-ups that result in damage and loss of gear, whereas fixed gears can be deployed across a wider range of bottom types. Understanding these multifishery dynamics and relative impacts would provide a valuable tool to assess the vulnerability and status of EFH. Lastly, while models play an important role in fisheries science, perhaps one of their most important functions is to identify information gaps. Application of the SASI model to the GoM lobster fishery has highlighted several needs to better characterize fishing gear impacts. Our specific recommendations for improved model estimations include (*i*) higher resolution fishing effort data, (*ii*) ability to evaluate targeted bedforms, (*iii*) the impact of multiple gear disturbances on the same patch of bottom, (*iv*) better characterization of benthic assemblages and their association with abiotic factors (e.g., depth, substrate, salinity), and (*v*) the sensitivity of our results to highly susceptible, long-recovering species such as deep sea corals and emergent sponges.

A relatively unknown aspect of North America's largest fishery, the GoM lobster fishery, is to what extent does fishing effort impact the EFH of the GoM (see NEFMC 2011). We employed a quantitative framework that relates habitat-specific impacts from fishing gear on EFH, the SASI model, to estimate the area of EFH functionally reduced by the GoM lobster fishery. Trap estimates were generated using current management regulations and the most comprehensive estimates of lobster fishing effort in the GoM. Annual estimates of functionally reduced EFH average less than 2% of the total available area, while the accumulation of functionally reduced EFH over time averages less than 3%. We found that between 99.92 and 99.96% of annually functionally reduced EFH features can fully recover despite 13% of some areas being in the process of recovery. Our results suggest that the GoM lobster fishery has minimal impacts to EFH features of the GoM. Our analysis was ultimately limited by the granularity of the input data with respect to benthic geological and biological habitat type and the spatial and temporal variability in effort. Nevertheless, we present a baseline impact analysis and a flexible approach that will undoubtedly be improved as new information becomes available. Our model also provides a valuable resource for management strategy evaluation. The flexibility of our application of the SASI model has the potential to compare the impacts of various lobster fishery management scenarios and evaluate the lasting impacts to EFH.

Acknowledgements

This activity is supported by National Science Foundation award No. IIA-1355457 to Maine EPSCoR at the University of Maine, National Sea Grant award No. NA19OAR4170395 to Damian Brady at the University of Maine, and by the Fund for the Advancement of Sustainable Maine Lobster.

References

ASMFC. 1996. A review of the population dynamics of the American lobster in the Northeast. ASMFC Special Report 61. Atlantic States Marine Fisheries Commission. Available from http://www.asmfc.org/publications/special-reports.

Auster, P.J., and Langdon, R.W. 1999. The effects of fishing on fish habitat. Am. Fish. Symp. **22**: 150–187.

Boenish, R., and Chen, Y. 2018. Spatiotemporal dynamics of effective fishing effort in the American lobster (*Homarus americanus*) fishery along the coast of Maine, U.S.A. Fish. Res. **199**: 231–241. doi:10.1016/j.fishres.2017.11.001.

Bologna, P.A.X., and Steneck, R.S. 1993. Kelp beds as habitat for American lobster *Homarus americanus*. Mar. Ecol. Prog. Ser. **100**: 127–134. doi:10.3354/meps100127.

Brehme, C.E., McCarron, P., and Tetreault, H. 2015. A dasymetric map of Maine lobster trap distribution using local knowledge. Prof. Geogr. **67**(1): 98–109. doi:10.1080/00330124.2014.883956.

Brenchley, G., and Carlton, J. 1983. Competitive displacement of native mud snails by introduced periwinkles in the New England intertidal zone. Biol. Bull. **165**(3): 543–558. doi:10.2307/1541464. PMID:29324006.

Bridger, J.P. 1972. Some observations of penetration into the sea bed of tickler chains on a beam trawl. ICES CM. 1972/B.

Currie, D.R., and Parry, G.D. 1996. Effects of scallop dredging on a soft sediment community: A large-scale experimental study. Mar. Ecol. Prog. Ser. **134**: 131–150. doi:10.3354/meps134131.

Dayton, P.K., Thrush, S.F., Agardy, M.T., and Hofman, R.J. 1995. Environmental effects of marine fishing. Aquatic Conserv: Mar. Freshw. Ecosyst. **5**: 205–232. doi:10.1002/aqc.3270050305.

Eastwood, M.M., Donahue, M.J., and Fowler, A.E. 2007. Reconstructing past biological invasions: niche shifts in response to invasive predators and competitors. Biol. Invasions, **9**: 397–407. doi:10.1007/s10530-006-9041-5.

Friedland, K.D., Morse, R.E., Manning, J.P., Melrose, D.C., Miles, T., Goode, A.G., et al. 2020. Trends and change points in surface and bottom thermal environments of the US Northeast Continental Shelf Ecosystem. Fish. Oceanogr. **29**(5): 396–414. doi:10.1111/fog.12485.

Goode, A.G., Brady, D.C., Steneck, R.S., and Wahle, R.A. 2019. The brighter side of climate change: How local oceanography amplified a lobster boom in the Gulf of Maine. Global Change Biol, **25**(11): 3906–3917. doi:10.1111/gcb.14778.

Grabowski, J.H., Bachman, M., Demarest, C., Eayrs, S., Harris, B.P., Malkoski, V., et al. 2014. Assessing the Vulnerability of Marine Benthos to Fishing Gear Impacts. Rev. Fish. Sci. **22**(2): 142–155. doi:10.1080/10641262.2013.846292.

Grabowski, J.H., Clesceri, E.J., Baukus, A.J., Gaudette, J., Weber, M., and Yund, P.O. 2010. Use of herring bait to farm lobsters in the Gulf of Maine. PLoS ONE, **5**(4): e10188. doi:10.1371/journal.pone.0010188. PMID:20419167.

Grieve, C., Brady, D.C., and Polet, H. 2014. Best practices for managing, measuring, and mitigating the benthic impact of fishing — Part 1. Mar. Stewardship Counc. Sci. Ser. **2**: 18–88.

Grieve, C., Brady, D.C., and Polet, H. 2015. Best practices for managing, measuring and mitigating the benthic impacts of fishing — Part 2. Mar. Stewardship Counc. Sci. Ser. **3**: 81–120.

Hall-Spencer, J.M., and Moore, P.G. 2000. Scallop dredging has profound, long-term impacts on maerl habitats. ICES J. Mar. Sci. **57**(5): 1407–1415. doi:10.1006/jmsc.2000.0918.

Harrington, A.M., Harrington, R.J., Bouchard, D.A., and Hamiln, H.J. 2020. The synergistic effects of elevated temperature and CO_2-induced ocean acidification reduced cardiac performance and increase disease susceptibility in subadult, female American lobsters *Homarus americanus* H. Milne Edwards, 1837 (Decapoda: Astacidea: Nephropidae) from the Gulf of Maine. J. Crust. Biol. **40**(5): 634–646. doi:10.1093/jcbiol/ruaa041.

Harris, L.G., and Tyrrell, M.C. 2001. Changing community states in the Gulf of Maine: synergism between invaders, overfishing and climate change. Biol. Invasions, **3**: 9–21. doi:10.1023/A:1011487219735.

Henry, L., Kenchington, E.L., and Silvaggio, A. 2003. Effects of mechanical experimental disturbance on aspects of colony responses, reproduction and regeneration in the cold water octocoral *Gersemia rubiformis*. Can. J. Zool. **81**(10): 1691–1701. doi:10.1139/z03-161.

Holling, C.S. 1973. Resilience and stability of ecological systems. Annu. Rev. Ecol. Syst. **4**: 1–23. doi:10.1146/annurev.es.04.110173.000245.

Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science, **293**(5530): 629–638. doi:10.1126/science.1059199. PMID:11474098.

Jennings, S., Lee, J., and Hiddink, J.G. 2012. Assessing fishery footprints and the trade-offs between landings value, habitat sensitivity, and fishing impacts to inform marine spatial planning and an ecosystem approach. ICES J. Mar. Sci. **69**(6): 1053–1063. doi:10.1093/icesjms/fss050.

Kaiser, M.J., Spence, F.E., and Hart, P.J.B. 2000. Fishing-gear restrictions and conservation of benthic habitat complexity. Conserv. Biol. **14**(5): 1512–1525. doi:10.1046/j.1523-1739.2000.99264.x.

Kleisner, K.M., Fogarty, M.J., McGee, S., Hare, J.A., Moret, S., Perretti, C.T., and Saba, V.S. 2017. Marine species distribution shifts on the U.S. Northeast Continental Shelf under continued ocean warming. Prog. Oceanogr. **153**: 24–36. doi:10.1016/j.pocean.2017.04.001.

LeBris, A., Mills, K.E., Wahle, R.A., Chen, Y., Alexander, M.A., Allyn, A.J., et al. 2018. Climate vulnerability and resilience in the most valuable North American fishery. Proc. Natl. Acad. Sci. U.S.A. **115**(8): 1831–1836. doi:10.1073/pnas.1711122115. PMID:29358389.

Lesser, M.P. 2016. Climate change stressors cause metabolic depression in the blue mussel, *Mytilus edulis*, from the Gulf of Maine. Limnol. Oceanogr. **61**: 1705–1717. doi:10.1002/lno.10326.

Lewontin, R.C. 1969. The meaning of stability. Brookhaven Symposia in Biology, **22**: 313–23.

Mazur, M.D., Friedland, K.D., McManus, M.C., and Goode, A.G. 2020. Dynamic changes in American lobster suitable habitat distribution on the Northeast U.S. Shelf linked to oceanographic conditions. Fish. Oceanogr. **29**(4): 349–365. doi:10.1111/fog.12476.

McCarron, P., and Tetreault, H., 2012. Lobster Pot Gear Configurations in the Gulf of Maine [online]. Available from http://www.bycatch.org/sites/default/files/Lobster_Gear_Report_0.pdf [accessed 13 June 2017].

McHenry, J., Steneck, R.S., and Brady, D.C. 2017. Abiotic proxies for predictive mapping of nearshore benthic assemblages: implications for marine spatial planning. Ecol. Appl. **27**(2): 603–618. doi:10.1002/eap.1469. PMID:27862606.

McMahan, M.D., Brady, D.C., Cowan, D.F., Grabowski, J.H., and Sherwood, G.D. 2013. Using acoustic telemetry to observe the effects of a groundfish predator (Atlantic cod, *Gadus morhua*) on movement of the American lobster (*Homarus americanus*). Can. J. Fish. Aquat. Sci. **70**: 1625–1634. doi:10.1139/cjfas-2013-0065.

McMahan, M.D., Sherwood, G.D., and Grabowski, J.H. 2020. Geographic variation in life-history traits of black sea bass (*Centropristis striata*) during a rapid range expansion. Front. Mar. Sci. **7**: 567758. doi:10.3389/fmars.2020.567758.

McMullen, K.Y., Paskevich, V.F., and Poppe, L.J. 2014. GIS data catalog (ver. 3.0). *Edited by* L.J. Poppe, K.Y. McMullen, S.J. Williams, and V.F. Paskevich. *In* USGS east-coast sediment analysis: Procedures, database, and GIS data. US Geological Survey Open-File Report 2005-1001. Available from http://pubs.usgs.gov/of/2005/1001/.

MDMR. 2016. DMR Lobster Sea Sampling Program. State of Maine – Department of Marine Resources [online]. Maine Department of Marine Resources. Available from http://www.maine.gov/dmr/science-research/species/lobster/seasampling.html [accessed 13 June 2017].

MDMR. 2019*a*. Historical Maine Fisheries Landings Data. State of Maine – Department of Marine Resources [online]. Available from http://www.maine.gov/dmr/commercial-fishing/landings/historical-data.html [accessed 13 June 2019].

MDMR. 2019*b*. Maine Lobster Fishing License and Trap Tag Counts – Department of Marine Resources [online]. Available from https://www.maine.gov/dmr/science-research/species/lobster/licenses-tags.html [accessed 1 September 2019].

MDMR. 2020. Maine Lobster Limited Entry and Apprentice Program [online]. Available from https://www.maine.gov/dmr/science-research/species/lobster/limitedentry.html [accessed 15 July 2020].

NEFMC. 2011. Appendix D — The Swept Area Seabed Impact (SASI) approach: a tool for analyzing the effects of fishing on Essential Fish Habitat [online]. New England Fishery Management Council. Available from www.nefmc.org/library/omnibus-habitat-amendment-2 [accessed 13 June 2017].

NMFS. 2014. Final Environmental Impact Statement for Amending the Atlantic Large Whale Take Reduction Plan: Vertical Line Rule Volume 1 and 2 [online]. Available from https://www.greateratlantic.fisheries.noaa.gov/protected/whaletrp/eis2013/ [accessed 13 June 2017].

NMFS. 2015. Atlantic Large Whale Take Reduction Plan: Northeast Trap/Pot Fisheries Requirements and Management Areas [online]. Available from http://www.greateratlantic.fisheries.noaa.gov/protected/whaletrp/index.html [accessed 13 June 2017].

NMFS. 2019. Commercial Fisheries Statistics – Annual Commercial Landings by Group [online]. Available from https://www.st.nmfs.noaa.gov/commercial-fisheries/commercial-landings/annual-landings-with-group-subtotals/index [accessed 13 June 2019].

NOAA. 2019. NOAA Data Discovery Portal [online]. National Oceanic and Atmospheric Administration. Available from https://www.data.noaa.gov. [accessed 13 June 2019].

NOAA. 2020. NOAA Deep-Sea Coral Data Portal [online]. Available from https://www.deepseacoraldata.noaa.gov. [accessed 1 October 2020].

Oppenheim, N.G., Wahle, R.A., Brady, D.C., Goode, A.G., and Pershing, A.J. 2019. The cresting wave: larval settlement and ocean temperatures predict change in the American lobster harvest. Ecol. Appl. **29**(8): e02006. doi:10.1002/eap.2006. PMID:31541510.

Pawlowicz, R. 2020. M_Map: A mappingpackage for MATLAB, version 1.4m. [Computer software]. Available from www.eoas.ubc.ca/~rich/map.html.

Pershing, A.J., Alexander, M.A., Hernandez, C.M., Kerr, L.A., Le Bris, A., Mills, K.E., et al. 2015. Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. Science, **350**(6262): 809–812. doi:10.1126/science.aac9819. PMID:26516197.

Peterson, C.H., Summerson, H.C., and Fegley, S.R. 1983. Relative efficiency of two clam rakes and their contrasting impacts on seagrass biomass. Fish. Bull. **81**: 429–434.

Pinsky, M.L., Worm, B., Fogarty, M.J., Sarmiento, J.L., and Levin, S.A. 2013. Marine taxa track local climate velocities. Science, **341**(6151): 1239–1242. doi:10.1126/science.1239352.

Pitcher, R.C., Ellis, N., Jennings, S., Hiddink, J.G., Mazor, T., Kaiser, M.J., et al. 2017. Estimating the sustainability of towed fishing-gear impacts on seabed habitats: a simple quantitative risk assessment method applicable to data-limited fisheries. Methods Ecol. Evol. **8**: 472–480. doi:10.1111/2041-210X.12705.

Poppe, L.J., Eliason, A.H., and Hastings, M.E. 2004. A visual basic program to generate sediment grain-size statistics and to extrapolate particle distributions. Comput. Geosci. **30**: 791–795. doi:10.1016/j.cageo.2004.05.005.

Race, M. 1982. Competitive displacement and predation between native and introduced mud snails. Oceologia, **54**: 337–347. doi:10.1007/BF00380002.

Record, N.R., Runge, J.A., Pendleton, D.E., Balch, W.M., Davies, K.T.A., Pershing, A.J., et al. 2019. Rapid climate-driven circulation changes threaten conservation of endangered North Atlantic right whales. Oceanography, **32**(2): 162–169. doi:10.5670/oceanog.2019.201.

Rooper, C.N., Wilkins, M.E., Rose, C.S., and Coon, C. 2011. Modeling the impacts of bottom trawling and the subsequent recovery rates of sponges and corals in the Aleutian Islands, Alaska. Cont. Shelf Res. **31**(17): 1827–1834. doi:10.1016/j.csr.2011.08.003.

Saila, S.B., Nixon, S.W., and Oviatt, C.A. 2002. Does lobster trap bait influence the Maine inshore trap fishery? N. Am. J. Fish. Manage. **22**: 602–605. doi:10.1577/1548-8675(2002)022<0602:DLTBIT>2.0CO;2.

Schlee, J., and Webster, J. 1967. A computer program for grain-size data. Sedimentology, **8**(1): 45–53. doi:10.1111/j.1365-3091.1967.tb01305.x.

Schweitzer, C.C., Lipcius, R.N., and Stevens, B.G. 2018. Impacts of a multi-trap line on benthic habitat containing emergent epifauna within the Mid-Atlantic Bight. ICES J. Mar. Sci. **75**(6): 2202–2212. doi:10.1093/icesjms/fsy109.

Shepard, F.P. 1954. Nomenclature based on sand–silt–clay ratios. J. Sediment. Res. **24**(3): 151–158. doi:10.1306/D4269774-2B26-11D7-8648000102C1865D.

Sousa, W.P. 1979. Disturbance in marine intertidal boulder fields: The nonequilibrium maintenance of species diversity. Ecology, **60**: 1225–1239. doi:10.2307/1936969.

Sousa, W.P. 1984. The role of disturbance in natural communities. Annu. Rev. Ecol. Syst. **15**: 353–391. doi:10.1146/annurev.es.15.110184.002033.

Steneck, R.S., Graham, M.H., Bourque, B.J., Corbett, D., Erlandson, J.M., Estes, J.A., and Tegner, M.J. 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. Environ. Conserv. **29**(4): 436–459. doi:10.1017/S0376892902000322.

Steneck, R., Parma, A.M., Ernst, B., and Wilson, J.A. 2017. Two lobster tales: lessons from the convergent evolution of TURFs in Maine (U.S.A.) and the Juan Fernández Islands (Chile). Bull. Mar. Sci. **93**(1): 13–33. doi:10.5343/bms.2016.1006.

Steneck, R.S., Vavrinec, J., and Leland, A.V. 2004. Accelerating trophic-level dysfunction in kelp forest ecosystems of the Western North Atlantic. Ecosystems, **7**: 323–332. doi:10.1007/s10021-004-0240-6.

Steneck, R.S., and Wahle, R.A. 2013. American lobster dynamics in a brave new ocean. Can. J. Fish. Aquat. Sci. **70**: 1612–1624. doi:10.1139/cjfas-2013-0094.

Steneck, R.S., and Wilson, C.J. 2001. Large-scale and long-term, spatial and temporal patterns in demography and landings of the American lobster, *Homarus americanus*, in Maine. Mar. Freshw. Res. **52**(8): 1303–1319. doi:10.1071/MF01173.

Stephenson, E.H., Steneck, R.S., and Seeley, R.H. 2009. Possible temperature limits to range expansion of non-native Asian shore crabs in Maine. J. Exp. Mar. Biol. Ecol. **375**: 21–31. doi:10.1016/j.jembe.2009.04.020.

Stevens, B.G. 2020. The ups and downs of traps: environmental impacts, entanglement, mitigation, and the future of trap fishing for crustaceans and fish. ICES J. Mar. Sci. fsaa135. doi:10.1093/icesjms/fsaa135.

Stoll, J.S. 2017. Fishing for leadership: The role diversification plays in facilitating change agents. J. Environ. Manage. **199**: 74–82. doi:10.1016/j.jenvman.2017.05.011. PMID:28527377.

Stoll, J.S., Beitl, C.M., and Wilson, J.A. 2016. How access to Maine's fisheries has changed over a quarter century: The cumulative effects of licensing on resilience. Global Environ. Chang. **37**: 79–91. doi:10.1016/j.gloenvcha.2016.01.005.

Tanaka, K., and Chen, Y. 2016. Modeling spatiotemporal variability of the bioclimate envelope of *Homarus americanus* in the coastal waters of Maine and New Hampshire. Fish. Res. **177**: 137–152. doi:10.1016/j.fishres.2016.01.010.

Tepolt, C.K., and Somero, G.N. 2014. Master of all trades: thermal acclimation and adaptation of cardiac function in a broadly distributed marine invasive species, the European green crab, *Carcinus maenas*. J. Exp. Biol. **217**: 1129–1138. doi:10.1242/jeb.093849. PMID:24671964.

The Island Institute. 2012. Mapping Working Waters: Maine's Commercial Fisheries [online]. Available from http://www.islandinstitute.org/resource/mapping-working-waters-offshore-fisheries [accessed 13 June 2017].

The Island Institute. 2016. Lobster and Ocean Planning; Lobster and Ocean Planning Report [online]. Available from http://www.islandinstitute.org/resource/lobster-and-ocean-planning [accessed 13 June 2017].

Wahle, R.A., Brown, C., and Hovel, K. 2013. The geography and body-size dependence of top-down forcing in New England's lobster–groundfish interaction. Bull. Mar. Sci. **89**(1): 189–212. doi:10.5343/bms.2011.1131.

Watling, L., Findlay, R.H., Mayer, L.M., and Schick, D.F. 2001. Impact of a scallop drag on the sediment chemistry, microbiota, and faunal assemblages of a shallow subtidal marine benthic community. J. Sea Res. **46**: 309–324. doi:10.1016/S1385-1101(01)00083-1.

Watling, L., and Norse, E.A. 1998. Disturbance of the Seabed by Mobile Fishing Gear: A Comparison to Forest Clearcutting. Concerv. Biol. **12**(6): 1180–1197. doi:10.1046/j.1523-1739.1998.0120061180.x.

Wentworth, C.K. 1922. A scale of grade and class terms for clastic sediments. J. Geol. **30**: 377–392. doi:10.1086/622910.

Witman, J., Etter, J., and Smith, F. 2004. The relationship between regional and local species diversity in marine benthic communities: a global perspective. Proc. Natl. Acad. Sci. U.S.A. **101**: 15664–15669. doi:10.1073/pnas.0404300101. PMID:15501917.