RESEARCH ARTICLE

Climate-induced reduction in metabolically suitable habitat for U.S. northeast shelf marine species

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Abstract

The U.S. northeast shelf (USNES) has been experiencing rapid ocean warming, which is changing the thermal environment that marine species inhabit. To determine the effect of current and future ocean warming on the distribution of five important USNES fish species (Atlantic cod [*Gadus morhua*], black sea bass [*Centropristis striata*], cunner [*Tautogolabrus adspersus*], spiny dogfish [*Squalus acanthias*], summer flounder [*Paralichthys dentatus*]), we applied species-specific physiological parameters from laboratory studies to calculate the Metabolic Index (MI). The MI for each species was calculated across a historical (1972–2019) and contemporary (2010–2019) climatology for each season. Broadly, the oceanic conditions in the winter and spring seasons did not limit metabolically suitable habitat for all five species, while portions of the USNES in the summer and fall seasons were metabolically unsuitable for the cold water species (Atlantic cod, cunner, spiny dogfish). The warmer water species (black sea bass, summer flounder) experienced little metabolically suitable habitat loss, which was restricted to the most southern portion of the distribution. Under a doubling of atmospheric CO_2, metabolically suitable habitat is projected to decrease substantially for Atlantic cod, restricting them to the Gulf of Maine. Cunner are projected to experience similar habitat loss as Atlantic cod, with some refugia in the New York Bight, and spiny dogfish may experience habitat loss in the Southern Shelf and portions of Georges Bank. In contrast, black sea bass and summer flounder are projected to experience minimal habitat loss restricted to the southern inshore portion of the USNES. The utility of using MI for co-occurring fish species in the USNES differed, likely driven by species-specific physiology and whether the southern edge of a population occurred within the USNES.

Introduction

Anthropogenic climate change is reshaping our world, and within the marine environment, ocean warming has become a pervasive issue. Fish are ectotherms, and as such, rising ocean temperature will subsequently increase metabolism and energy demands [1]. Warmer temperatures outside of the thermal niche of a fish can lead to a variety of effects that range in severity level. At the extremes, fish in temperatures too warm may experience higher mortality [2] or cease feeding [3]. At temperatures eliciting a less severe response, fish may experience higher metabolism, which is manageable if energy demands are met through feeding [4, 5]. If energy demands are not met, fish must partition energy stores towards metabolic maintenance, reducing available energy for growth and reproduction [6]. For fish that are sufficiently mobile, another common response to ocean warming is migration out of unsuitable regions, leading to species distribution shifts [7]. Distribution shifts can be poleward [8, 9] or towards deeper water [10]. Investigating the cause and extent of species distribution shifts based on ocean warming is important for both understanding changes in ecosystems and species assemblages [11] and for avoiding future conflicts in fisheries management as fish transverse state or national boundaries [12].

Species-specific physiological metrics can relate animal performance (*i.e.*, growth, reproduction, survival) to environmental temperature, and therefore provide a mechanistic link between temperature and effects on an organism and their population. The Metabolic Index (MI) is a ratio of environmental oxygen supply to animal oxygen demand, the latter of which is affected by temperature through species-specific thermal sensitivities of laboratory-derived metabolic traits [13]. In particular, the critical oxygen partial pressure, P_{crit}, measures the efficacy of a species physiological oxygen supply system and, when measured at the resting (standard, SMR) metabolic rate, indicates the minimum oxygen level required for maintenance metabolism. The species-specific parameters are defined through the relationship of the natural log of P_{crit} and inverse temperature, which necessitates measuring P_{crit} at two or more temperatures. Once the species-specific parameters are defined, MI can be calculated throughout a species range by obtaining *in situ* measured or modeled temperature and oxygen data. MI values typically range from 1–10, and the lowest MI where species are present is defined as the MI_{crit}, which is presumed to represent an oxygen-limitation on habitability [13]. Thus, projected MI values are used to assess metabolically suitable habitat where the temperature and oxygen levels result in MI values that are at or above the MI_{crit}. The MI_{crit} typically averages ~3 for a variety of marine species [14], which means environmental oxygen partial pressure is ~3 times what is required for SMR ($MI_{crit} = \sim 3 * P_{crit}$). In other words, temperature and oxygen conditions that lead to MI values above the MI_{crit} provide organisms with enough available oxygen for baseline maintenance metabolism *and* activities that promote individual and population fitness including feeding, swimming, evading predators, and reproduction.

Although there is no current consensus on whether oxygen-limitation is the exact mechanism setting thermal limits [15–18], MI does often correlate with the edges of species habitats, and has tracked spatial changes in habitat due to ocean warming and/or deoxygenation for some marine species [13, 14]. For example, Duncan et al. [19] demonstrated that MI was better at predicting the edges of suitable habitat for red roman reef fish (*Chrysoblephus laticeps*) than other commonly used physiological metrics including absolute aerobic scope (difference between maximum and standard metabolic rate). The better performance of MI was driven in part by incorporating a bidirectional change in hypoxia tolerance from cold to warm temperatures that was not captured in absolute aerobic scope. MI has also been used to identify interspecific differences in species physiological performance and subsequent changes in habitat loss under future climate change scenarios as seen in two brittle stars, *Ophioderma cinereum*

and *Ophiomastix wendtii* [20]. However, there are species where the MI framework does not work well, such as for the diel migrating Humboldt squid (*Dosidicus gigas*; [21]), which highlights that species-specific physiology and ecology are important to consider when developing the MI framework. Altogether, these species-specific MI models can provide powerful insight into current and future changes in metabolically suitable habitat and provide another predictive tool for addressing how and when the availability of habitat will change within a specific study region.

The US northeast shelf (USNES), which extends from Cape Hatteras to the Gulf of Maine, provides habitat to many ecologically and economically important living marine resources. This region has been experiencing rapid ocean warming [22, 23], primarily through changes in regional circulation associated with a weakening Atlantic meridional overturning circulation [24, 25]. Ocean warming along the USNES is a driver of species distribution shifts, and has been reported previously (*e.g.*, [26–32]). These studies focused on defining species suitable habitat through the statistical relationship of temperature (and in some cases, additional abiotic factors such as salinity or rugosity) to abundance, biomass or presence/absence data from fisheries-independent surveys. In theory, these statistical correlations provide ranges of suitable and limiting temperatures that can be tracked over time to show recent distribution shifts and project future impacts [33, 34]. Complementing these studies with a separate metric, such as MI, would allow for a new perspective on the effects of warming on fish species within the USNES that provides estimates of current and future suitable habitat based on physiological principles. Additionally, the MI allows for the integration of oxygen availability as another important metric that could lead to changes in suitable habitat.

The purpose of this study was to use species-specific trends in MI to investigate MI critical values, changes in MI over time, and future projections of metabolically suitable habitat for five USNES fish species: Atlantic cod (*Gadus morhua*), black sea bass (*Centropristis striata*), cunner (*Tautogolabrus adspersus*), spiny dogfish (*Squalus acanthias*), and summer flounder (*Paralichthys dentatus*). Fish species were selected based on those that had distribution data from fishery-independent trawl surveys as well as parameters from laboratory physiology studies that determined P_{crit} at two or more temperatures. The study domain was restricted to the USNES because we also wanted to investigate how MI performs in the context of fisheries management, where this study domain also represents the spatial stock unit for species and/or populations north of Cape Hatteras, North Carolina. While the broad latitudinal ranges of these species overlap, cunner and Atlantic cod tend toward colder waters, spiny dogfish are intermediate, and black sea bass and summer flounder extend into warmer waters leading to potential different physiological adaptations.

Methods

Defining spatial units for analysis

Temperature (˚C), oxygen (kPa, expressed as PO_2), and fish distribution (presence-absence) data were spatially organized into strata to provide a common scale of measurement. Strata selection was first based on those designated in the Northeast Fisheries Science Center (NEFSC) fishery trawl survey and were obtained from the NOAA github server (https://github.com/NOAA-EDAB/FisheryConditionLinks/tree/master/NES_BOTTOM_TRAWL_STRATA). Some smaller strata were combined to create larger sampling units to increase sample sizes of temperature and dissolved oxygen data within a stratum based on modifications from Walsh et al. [35] and Chen et al. [36]. Specifically, smaller offshore and inshore strata were combined within the same latitudinal bands. To designate strata, letter codes were provided based on across-shelf location (inshore (I), midshelf (M) and offshore (O) locations),

and number codes were provided to designate along-shelf positions with 01–19 from south to north (Fig 1). Two NEFSC strata units spanned across (south to north) the Hudson Canyon. Due to observed differences in physical dynamics between the northern and southern flanks of the Hudson Canyon [37], these strata were divided accordingly, whereby the split north and south flanks were combined with their respective northern and southern counterparts (M05, O05, M04, and O04 in this paper; in Fig 1). In total, 43 distinct strata were defined.

The shelf was also divided into regions with similar hydrographic characteristics based on Walsh et al. [35] and Mountain [38]. Regions included the Southern Shelf, New York Bight, Southern New England, Georges Bank, and Gulf of Maine (Fig 1). Strata were classified within these regions based on their locations.

Temperature and oxygen data

Temperature and dissolved oxygen data, the two environmental parameter inputs for MI calculations, were compiled across the USNES. Bottom values (at depth) for temperature and oxygen were chosen because they represented the spatial habitat where fish were collected in bottom trawl surveys, and can also be a better predictor of species distributions from bottom trawl surveys when compared to sea surface temperature (*i.e.*, [39]). Bottom temperature data were obtained from du Pontavice et al. [40]. This long term, high-resolution bottom temperature time-series is derived from bias-corrected simulations of the Northwest Atlantic Ocean Regional Ocean Modelling System (ROMS-NWA; [41]) for the period 1972–1992 and from raw output from the Global Ocean Physics Reanalysis (Glorys12v1 reanalysis; [42]) for the period 1993–2019. Bottom temperature data were available in a regular 1/12˚ horizontal grid over the USNES. Temperature data were assigned to specific strata and classified by season and year. Seasons were defined as winter (Dec-Feb), spring (Mar-May), summer (Jun-Aug) and fall (Sept-Nov). For each specific grouping of individual years from 1972–2019 and season, a mean temperature was calculated. The highest resolution calculation was at the stratum, year, and season level to make direct comparisons with the fishery data that were collected during spring and fall seasons.

Bottom dissolved oxygen data from 1972 to 2019 across the spatial domain of the USNES were retrieved from CTD casts fitted with oxygen optodes and accessed through the NCEI database, MARMAP survey, and BCO-DMO database (accessed through https://www.ncei.noaa.gov). There are currently no consistent surveys that measure oxygen at a regular basis within the USNES. Dissolved oxygen units from these data sources were converted into PO_2 if they were not already reported in units of partial pressure. Bottom PO_2 was defined as the deepest measurement from a CTD cast if it was within the bottom 20% of the total water column.

The final number of PO_2 data measurements was 7,752 and highlighted the sparsity of PO_2 data across time and space on the USNES, and provided insufficient coverage needed to calculate mean PO_2 at the resolution of stratum/season/year. With a goal of at least 5 measurements per strata/season/year and a total of 43 strata x 4 seasons x 48 years, ~41,000 measurements would be needed. As such, we used shelf-wide seasonal mean PO_2 values calculated from the available data for the inputs to calculate MI to provide seasonal temporal variation (Table 1). These seasonally averaged oxygen values were used across all years and strata. PO_2 averages over region or interannual time scales was not considered due to uneven distribution of raw data within regions and decades (Fig A in S1 Text).

Incorporation of fishery data

Fishery-independent data were used to provide information on species distribution over space and time to define the species-specific MI_{crit} (see below). Five fish species were selected for this
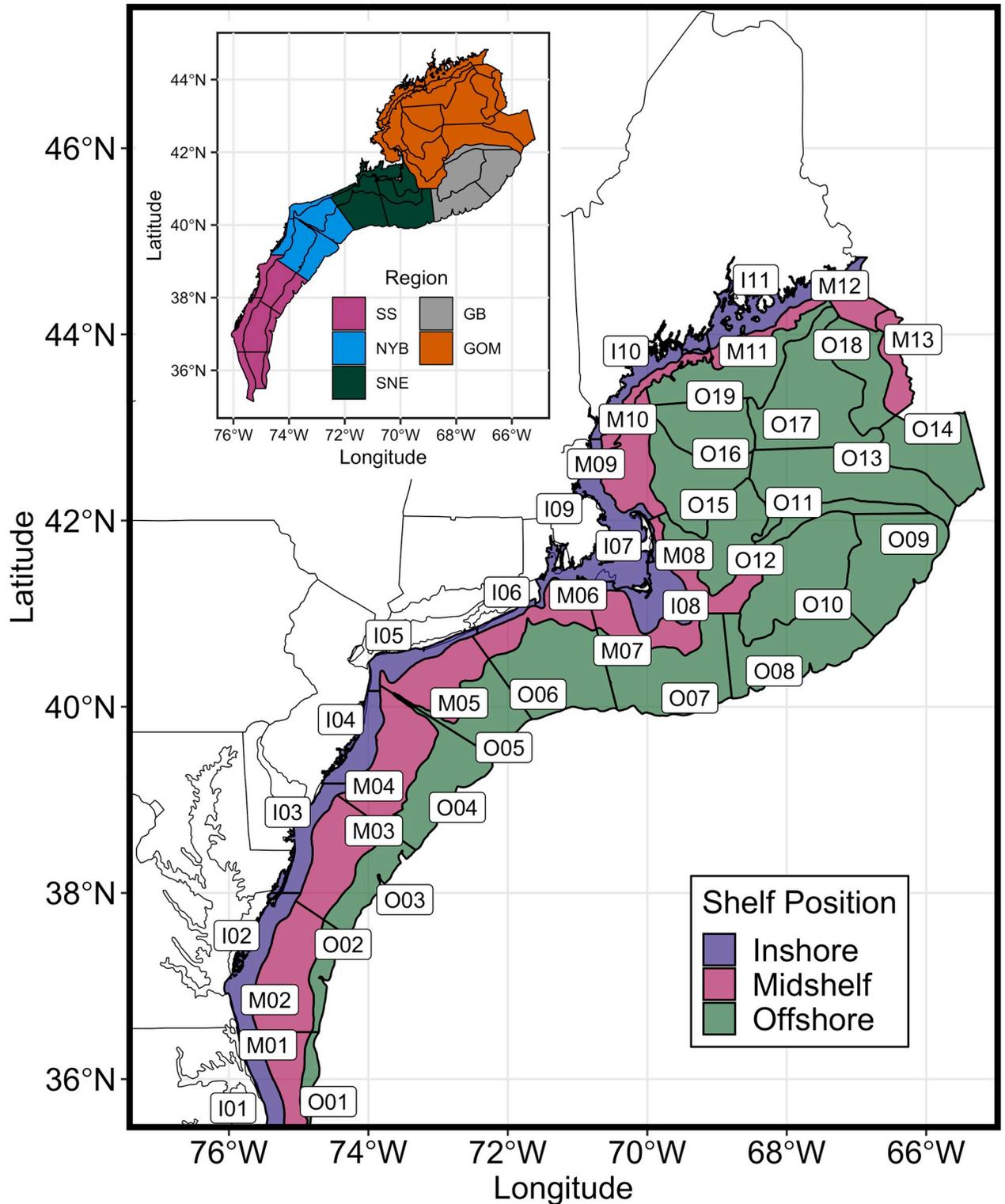
Fig 1. Spatial units (strata) defined for this study. Letter codes indicate across-shelf position (I = Inshore, M = Midshelf, O = Offshore) and number codes indicate along-shelf position from lower numbers in the south and higher in the north The colors indicate offshore (green), midshelf (magenta), and inshore (purple). The map inset shows the designation of regions across the shelf where SS = Southern Shelf, NYB = New York Bight, SNE = Southern New England, GB = George's Bank, and GOM = Gulf of Maine. United States state outline data was obtained from the R package 'maps' (cran.r-project.org/package = maps).

Table 1. Levels of oxygen (kPa) used in MI calculations for present and future climatologies.

Time period	Winter	Spring	Summer	Fall
Present	18.29	19.49	17.67	17.21
(1972–2019)				
Future	17.78	18.99	17.13	16.64
(+ 80yrs)				

Oxygen was averaged across the entire spatial and temporal domain during the present climatology, and the oxygen projection was calculated by defining a shelf-wide average change in oxygen and applying that value to each season (the model does not provide seasonal oxygen projections).

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analysis: Atlantic cod, black sea bass, cunner, spiny dogfish, and summer flounder. These species were chosen because they have the required physiological parameters determined from laboratory studies and are collected in the spring and fall NEFSC trawl surveys. Additionally, these species represent an array of cold and warm water species. Data from the NEFSC bottom trawl survey was accessed to include data from 1972–2019 and across the strata domain. After 2008, the NEFSC bottom trawl survey no longer sampled the furthest inshore strata within our "inshore" designations, and complementary trawl surveys were employed including the trawl surveys from the NorthEast Monitoring and Assessment Program (NEAMAP) and Massachusetts Divisions of Marine Fisheries (MADMF). For each fish species and season (spring, fall), data were aggregated into the strata. For each stratum, season and year, a presence or absence was assigned for each fish. Presence/absence data were chosen instead of biomass because the derived species-specific MI_{crit} represents a threshold of where fish are or are not found. This contrasts to other uses of species distribution data that defines optimal habitat based on conditions that lead to higher biomass or abundance.

Identification of thermal habitat through species distribution models has been assessed before using data from all of these trawl surveys (*i.e.*, [39, 43]), and presence/absence data tends to be more robust to potential error in survey differences. These fishery-independent data sources were chosen because they provide standardized fishery distribution data, have been used in prior studies that develop species distribution models for USNES fishes (*i.e.*, [29]), and are used regularly in stock assessments. Additionally, while some of the focal species in our study can inhabit different portions of the water column, the NEFSC bottom trawl survey has been shown to resolve sufficient data coverage for the stock assessments of pelagic species that are caught in the trawl [44]. Also, for species that are associated with structure (*i.e.*, black sea bass), recent stock assessments showed no bias in estimation of biomass from bottom trawl surveys vs. incorporating fishing gear better suited for rocky, structured bottom [45].

Calculation of species-specific MI parameters

MI (ϕ, Eq 1) was calculated for the five species by first obtaining the species-specific metabolic parameters, A_o and E_o. The natural log of the critical PO_2, or P_{crit}, from laboratory studies (S1 Table) was regressed against the inverse measurement of temperature (Fig 2). A_o and E_o are species-specific terms derived from the y-intercept and the slope, respectively, of that regression [13]. A_o is a measure of the physiological oxygen supply (*i.e.*, capacity of organism to supply tissues with oxygen, *not* environmental oxygen supply) and E_o is the temperature sensitivity parameter where a steeper slope (higher E_o) indicates increased temperature
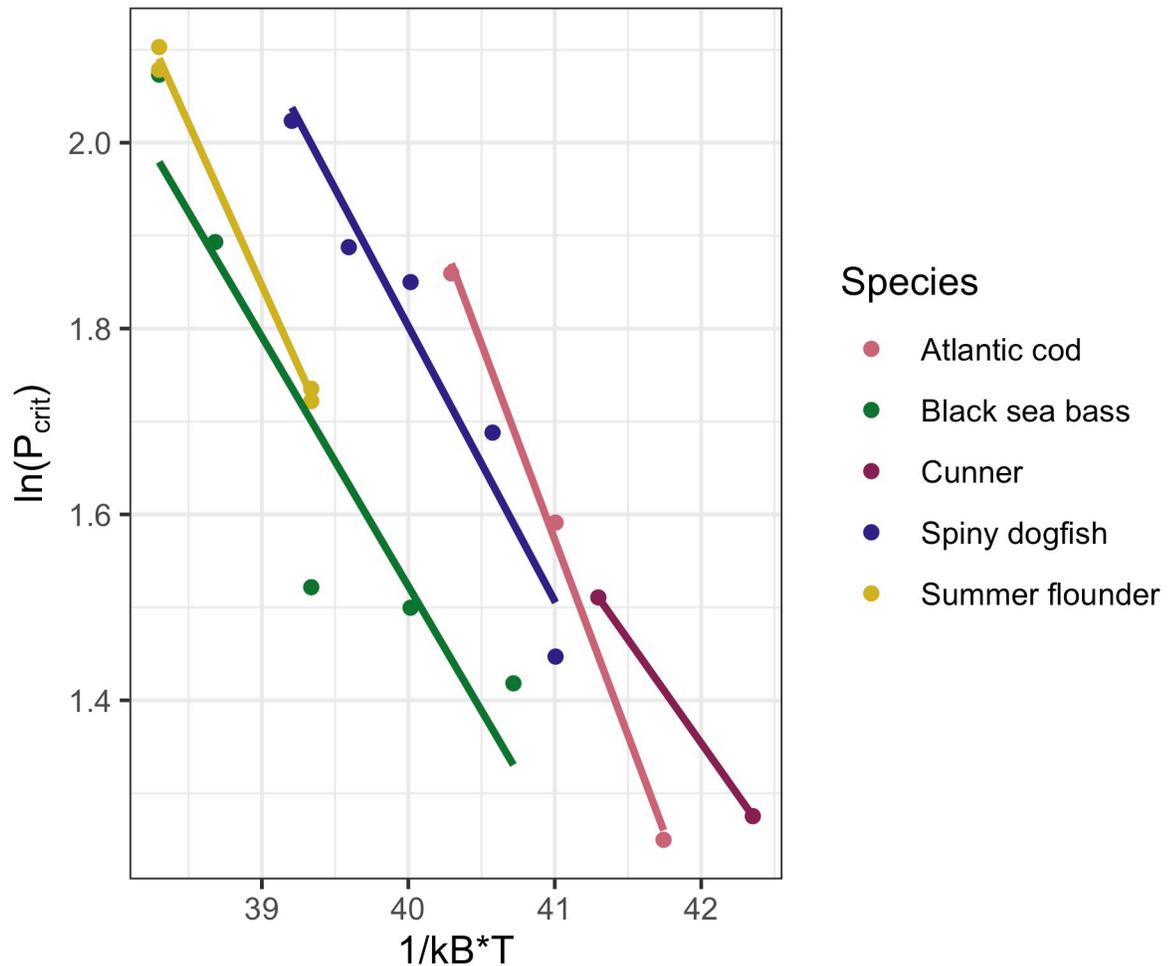
Fig 2. The temperature sensitivity of five USNES species. The y-intercept (A_o) represents the hypoxia tolerance of the species, while the slope of the line (E_o) indicates the thermal sensitivity of the fish, whereby a steeper (more negative due to inverse temperature) slope indicates higher temperature sensitivity. The cold water species (Atlantic cod, cunner, spiny dogfish) are found to the right of the warm water species (summer flounder, black sea bass), which reflects the range of experimental temperatures tested based on species thermal tolerances.

sensitivity. MI was then calculated according to Eq 1,

$$\phi = A_o B^n \frac{PO_2}{e^{(-E_o/K_BT)}} \tag{1}$$

where K_B is the Boltzmann constant ($K_B = 8.6173324^{-05}$ eV; relates kinetic energy with temperature), T is temperature (K), PO_2 is environmental oxygen pressure (kPa), and B is body mass raised to a scaling coefficient, n. The P_{crit} is largely insensitive to body mass [46, 47] meaning that the scaling coefficient, n, is typically near 0 (*i.e.*, no effect of body mass on the MI), because physiological oxygen supply evolves to meet demand regardless of size [16]. In this study, comparisons of MI within a single season (*e.g.*, fall) were made with constant averaged seasonal environmental PO_2 (oxygen availability) and varying MI was primarily due to temperature.

   After species-specific parameters were obtained, MI for each species was calculated across all strata, years, and seasons using Eq 1. The stratum-based mean was used for temperature for

each year, and for PO_2, a seasonal-based mean across the entire spatial domain and years was used. Additionally, we identified the presumptive limiting MI value (MI_{crit}) [14] for each species using presence-only subset of fishery data in the fall season (the warmest season) throughout the entire timeseries. Data from fall was used because 1) fall in the USNES is typically the warmest season with concomitantly slightly lower PO_2; and 2) spring tends to be one of the coldest seasons, and without summer fishery data, the combination of the two seasons (*i.e.*, the warmest and coldest seasons) leads to a bimodal distribution of MI that slightly skews the data. Preliminary analyses assessed the potential bias of eliminated spring fishery presence data and found 1–6% change in MI_{crit} estimate. MI_{crit} was defined as the 2.5[th] percentile of the cumulative distribution function of the subset data (S1 Fig). The MI_{crit} can also be visualized in an oxygen-temperature state space to show combinations of temperature and oxygen values that lead to MI_{crit}, where minimal species presences are expected on the right-hand side of the MI_{crit} line. A full example from the derivation of species-specific parameters to visualizing MI_{crit} in the oxygen-temperature state space is shown in Fig 3.

The performance of the presumed MI_{crit}, which was identified using mean temperature and PO_2 in each stratum, can be assessed based on whether or not the derived line delineates oxygen and temperature conditions where species are likely present (left hand side; see Fig 3e). MI_{crit} was tested against the raw PO_2 and temperature values from the CTD data that was used to generate the averaged seasonal oxygen calculations. These data were binned to the nearest 0.5kPa and 0.5˚C, and merged with the stratum-based fishery data based on the season and CTD cast latitude and longitude. Across the entire time series (1972–2019), fishery data were used to provide the proportion of times fish were present within the 0.5kPa and 0.5˚C bins. These proportion of presences were compared to the individual species MI_{crit} and whether or not presences were more common on the left-hand side of the curve. While using the CTD data provided coarse data coverage, it allowed us to assess the performance of MI_{crit} on a different environmental data set than what was used to derive MI_{crit}.

Trends in MI

The change in metabolically suitable habitat across space and time was assessed for both the historical (1972–2019) and contemporary (2010–2019) climatologies (S2 Fig). A historical climatology was used to represent the average of a long-term trend in oceanic conditions within the USNES and provide the largest range of MI values (also to calculate MI_{crit} from). The contemporary climatology was used to explore the recent effect of warming on suitable habitat and compare to the longer time series; for this reason, we chose overlapping year ranges. For each season, strata were given a "risk" level based on the number of years the stratum MI reached MI_{crit} or lower across the entire time series. On this scale, a stratum was given a value of 0 if it never reached MI_{crit} and a 1 if it reached MI_{crit} in every year of the time series. These "risk" levels were calculated across all years of the time series for both climatologies, historical and contemporary, and for each species. While the contemporary climatology had fewer years to assess (10 vs 48), calculating the "risk" for this time period allowed us to assess the frequency of a stratum reaching MI_{crit} over the last 10 years in concert with recent warming.

Projection of future MI and habitat loss

Future MI was projected under a doubling of atmospheric CO_2 in the CM2.6 high-resolution global climate model (1/10˚ ocean component) developed by the NOAA Geophysical Fluid Dynamics Lab (GFDL) [24]. The CM2.6 model simulation is an idealized climate scenario where atmospheric CO_2 increases 1% per year until it doubles by model year 70 and remains stable until model year 80. We used the projected change in ocean bottom temperature and
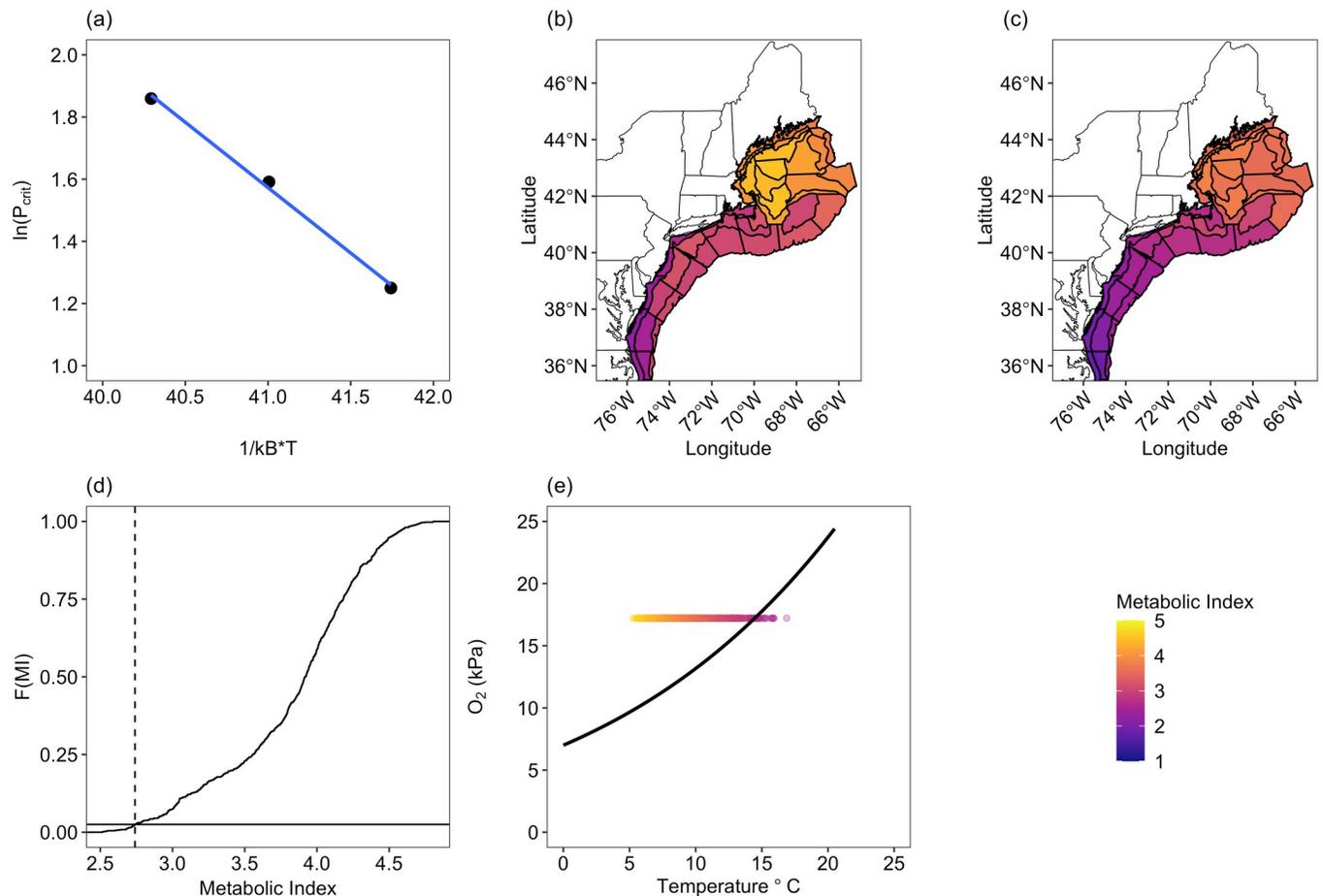
Fig 3. Derivation of Metabolic Index parameters for Atlantic cod. The regression of the $ln(P_{crit})$ to inverse temperature (same as Fig 1) (a) is used to define the species-specific parameters, which can be used to calculate MI from temperature and oxygen values for each year of the time series, for example 1972 (b) and 2019 (c). Across the time series, MI values from strata where Atlantic cod were present during fall are used to build the cumulative distribution function of MI for presence-only scenarios (d). The MI_{crit} (vertical dashed line) is defined as the 2.5[th] percentile (horizontal solid line) of the cumulative distribution function. The presumed MI_{crit} can also be visualized in an oxygen-temperature state-space (e) with the same presence-only fishery data and the corresponding MI values for a given temperature and seasonally averaged oxygen value; species presences are expected to be on the left-hand side of the curve where the oxygen level is sufficient at the given temperature and the corresponding MI values are higher than MI_{crit}. Because the absolute lowest MI value was not used to define MI_{crit}, there are some species presences on the right-hand side of the curve. United States state outline data was obtained from the R package 'maps' (cran.r-project.org/package = maps).

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dissolved oxygen from model years 60 to 80, averaging these two decades of projections, to provide a delta value under a doubling of atmospheric CO_2. The temperature projections were available on a monthly time-scale allowing for the calculation of seasonally averaged deltas for each stratum (S3 Fig). The stratum- and season-based deltas were then added to the respective strata and seasonal means from the historical climatology (1972–2019). The CM2.6 model provides projected annual dissolved oxygen (moles/kg) on the same 1/10° spatial scale. To remain consistent with the spatial resolution of PO_2 in the historical climatology, we calculated an average oxygen delta for the entire shelf, which provided one oxygen projection value that was converted to kPa and then added to the oxygen averages for each season (Table 1). Converting oxygen units (moles/kg to kPa) is temperature-dependent, so for each season an average seasonal projected temperature was used, which led to minor seasonal deviations in the PO_2 projection (PO_2 projection delta range 0.50–0.57). Altogether, similar to the analyses on past MI

trends, the future projections provided higher resolution temperature estimates and less spatially explicit oxygen estimates.

The projected change in MI was calculated for each species using model projections under a doubling of atmospheric CO_2. The MI values for both the historical and future climatologies were compared with the MI_{crit} values for each species to determine if a certain stratum was historically metabolically unsuitable or if a stratum will become metabolically unsuitable into the future, respectively. We identified the increase in metabolically unsuitable habitat as synonymous to habitat loss. To assess the potential sensitivity of the average projected oxygen values used, an oxygen level was calculated for each species and season where 50% and 100% habitat loss would occur. These oxygen levels were back-calculated using the species-specific MI_{crit} and projected stratum-based temperature to provide the limiting PO_2 level for each stratum, and the PO_2 level that resulted in an accumulation of 50 and 100% habitat loss was identified. These projected limiting oxygen levels were used to compared with the oxygen projections used in our analyses to assess the degree of additional decrements in oxygen that would lead to further metabolically suitable habitat loss.

Results

Species-specific MI_{crit}

For the five USNES species, the three colder water species (Atlantic cod, cunner and spiny dogfish) had slightly lower MI_{crit} values than the warmer water species, black sea bass and summer flounder (~2.8–2.9 vs ~3.2; Table 2), which was still relatively similar compared to MI_{crit} values derived across many marine species [14]. MI_{crit} performance was assessed based on the ability of MI_{crit} to delineate where species occur in an oxygen and temperature state space based on raw CTD data that was not used to define MI_{crit}. Under this metric, MI_{crit} performed well for Atlantic cod and cunner (Fig 4). For spiny dogfish, MI_{crit} was less able to delineate species presence/absences at colder temperatures, which suggests oxygen may not be a limiting mechanism below ~17°C. For the warm water species, black sea bass and summer flounder, MI_{crit} did not perform as well. First, there were a number of presences on the right-hand side of MI_{crit}, which suggests fish were caught in ocean conditions that should be metabolically limiting using this framework. Second, the proportion of presences increased in temperature and oxygen conditions near MI_{crit} and species absences were more prevalent further away from MI_{crit}. This suggests that for the warm water species MI_{crit} either does not define conditions that lead to limiting habitat *or* the warm water species are living near their habitat limits within the USNES.

Table 2. The species-specific parameters defined for MI calculations.

Species	E_o	A_o	MI_{crit}
Atlantic cod	0.42	$6.68e^{-07}$	2.74
Black sea bass	0.27	$4.77e^{-04}$	3.26
Cunner	0.22	$2.20e^{-03}$	2.95
Spiny dogfish	0.30	$1.20e^{-04}$	2.87
Summer flounder	0.35	$1.96e^{-05}$	3.23

Values are defined from the linear regressions where E_o = slope and A_o = intercept. The species-specific MI_{crit} is also provided.
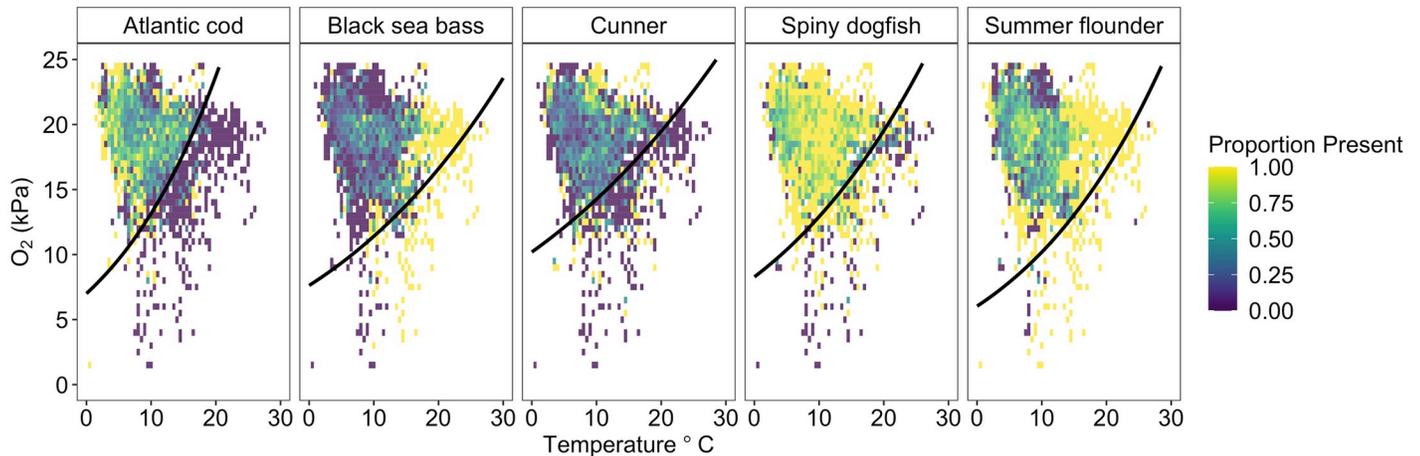
Fig 4. Performance of species-specific MI$_{crit}$. The species-specific MI$_{crit}$ (black line) indicate the oxygen and temperature conditions that lead to MI$_{crit}$. The heat map of proportion present (yellow = present to purple = absent) for each 0.5˚C and 0.5kPa grid is also plotted in the temperature and oxygen state space for each species. If MI$_{crit}$ successfully delineates species presence/absence based on environmental conditions, then species presences would be expected on the left-hand side of the line and absences on the right-hand side of the line.

MI trends: 1972–2019

Within the framework of assessing the number of times MI reached or fell below MI$_{crit}$, winter and spring never reached MI$_{crit}$ for any of the species, which suggests no limitations on metabolic habitat suitability in these seasons. In the summer and fall, portions of the shelf reached MI$_{crit}$ or below throughout the time series, but the degree to which MI$_{crit}$ was repeatedly reached differed by location and species. During summer, metabolically limiting habitat was primarily constricted to the inshore and southern portions of the shelf (Fig 5), and the proportion of times a stratum was at or below MI$_{crit}$ increased in those locations during the recent warming period (2010–2019; Fig 5). During fall, the proportion of observations of sub-critical MI increased in strata northward and eastward across the shelf compared to summer (Fig 6), and this pattern intensified during the recent warming period (Fig 6). Across the different USNES species, the cold water fishes (*i.e.*, Atlantic cod, cunner and spiny dogfish) experienced a higher instance and amount of habitat at or below their MI$_{crit}$, while the warm water species rarely experienced metabolically limiting habitat except for the most southern and inshore portions of the shelf.

The amount of warming during the recent climatology from 2010 to 2019 led to an increase in the amount of habitat at or below critical limits for Atlantic cod, cunner and spiny dogfish when compared to the historical climatology. For example, during the fall for Atlantic cod, the number of strata that reached MI$_{crit}$ at least 75% of the time increased from 7 to 10 strata out of 43 total (16.28 to 23.26%). Cunner and spiny dogfish also experienced an increase in number of strata reaching MI$_{crit}$ at least 75% of the time but to a lesser degree than Atlantic cod. For black sea bass and summer flounder, there were no strata that reached MI$_{crit}$ at least 75% of the time during 1972–2019, yet during the 2010–2019 climatology, 1 stratum (I01; summer and fall) reached MI$_{crit}$ 80% of the time for summer flounder. This indicates that recent warming is increasing the frequency that certain portions of the shelf become metabolically unsuitable.
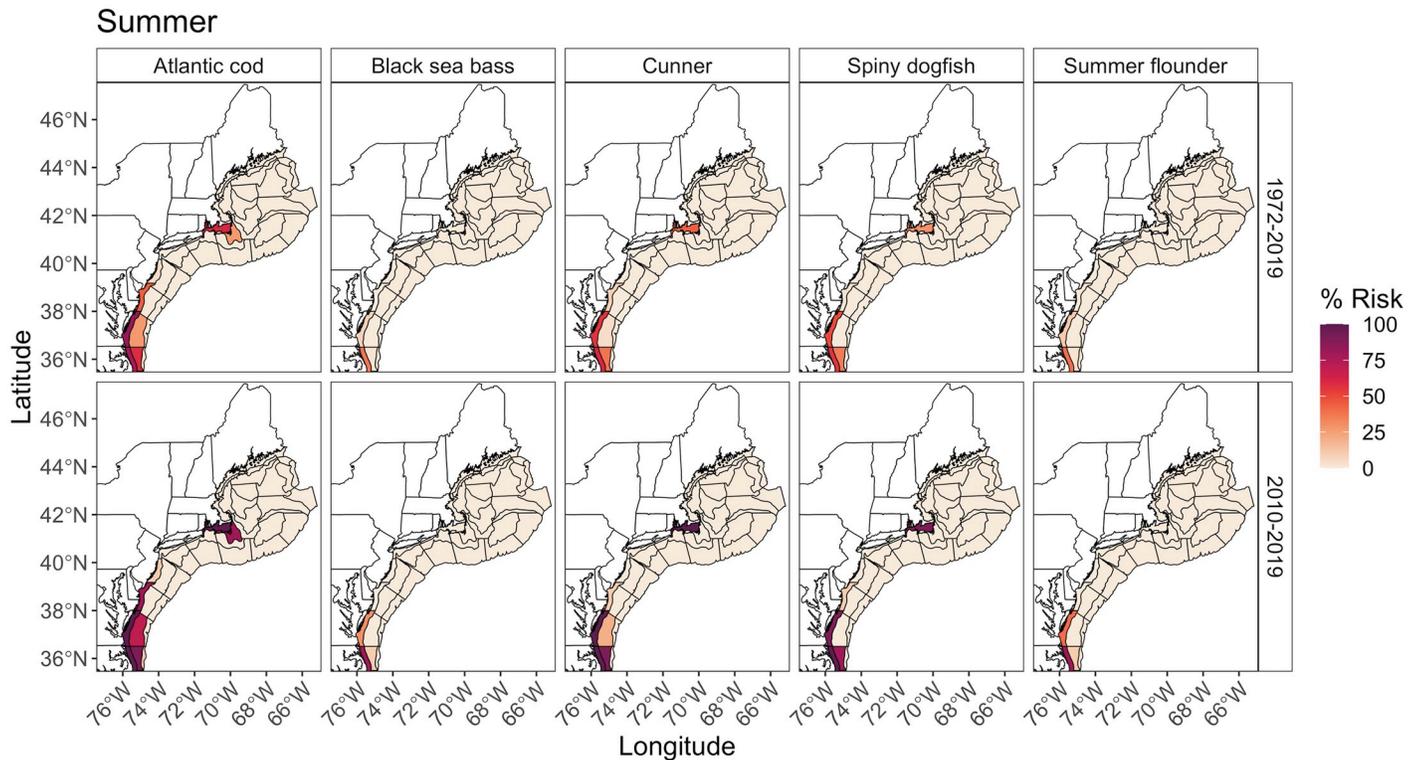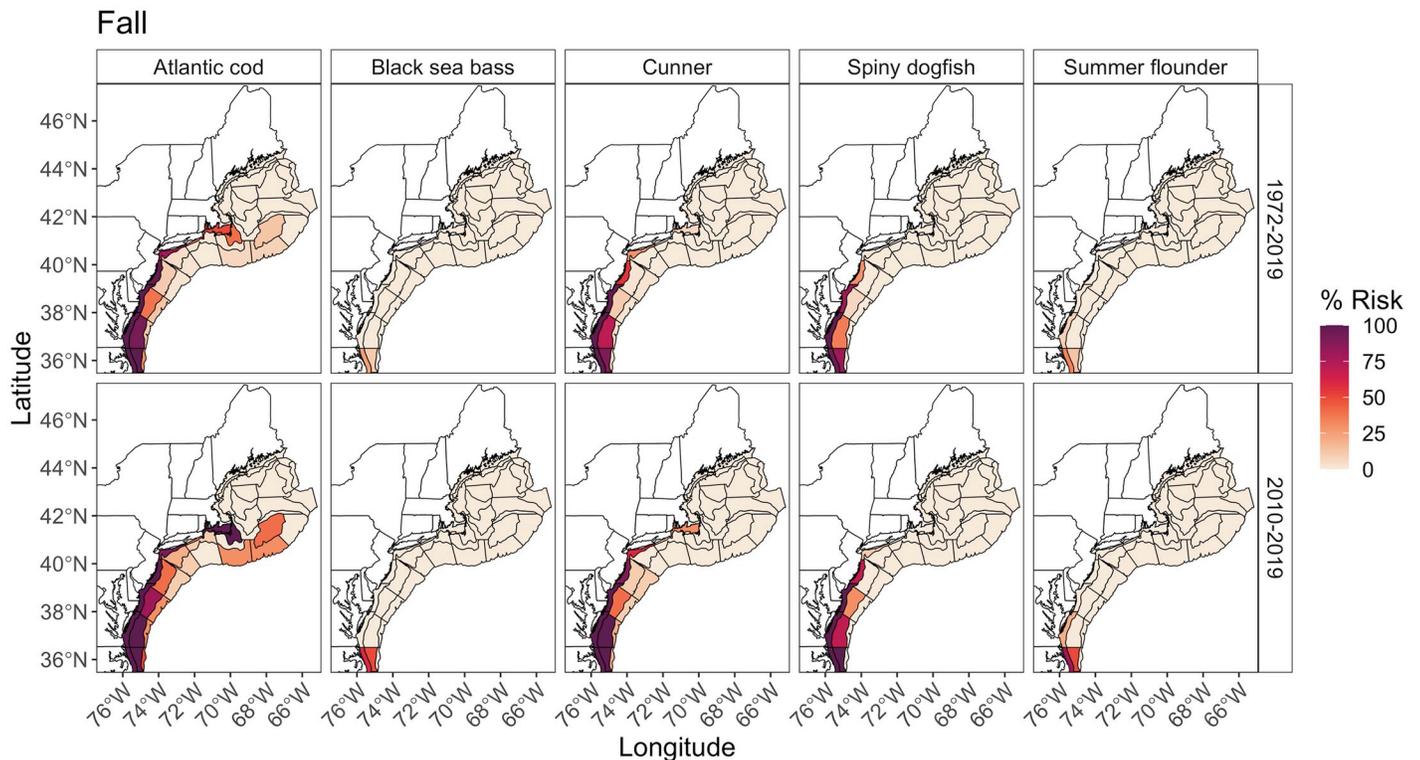
Fig 5. Strata "at-risk" during summer. The strata "at-risk" based on proportion of years a stratum was at or below a species-specific MI_{crit} across the historical climatology (top panel) and contemporary climatology (bottom panel) during the summer. If a stratum is tan (0% risk), then it never reached MI_{crit} during any year across the respective timeseries while if a stratum is dark purple (100% risk), then that stratum reached or surpassed MI_{crit} for 100% of the years. United States state outline data was obtained from the R package 'maps' (cran.r-project.org/package = maps).

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Projection of future MI and habitat loss under a doubling of atmospheric CO_2

Presumed habitat loss, defined by locations where MI is less than MI_{crit}, is substantial under a doubling of atmospheric CO_2 (Fig 7) for Atlantic cod, cunner, and spiny dogfish, particularly in summer and fall. The warm water species, black sea bass and summer flounder, are projected to experience minimal habitat loss. Winter and spring show minimal to no habitat loss (S4 Fig), respectively, for all species. Although warming is occurring in winter and spring, the absolute temperatures are not warm enough to reach MI_{crit} for any examined species. During summer, the cold water species are projected to experience some metabolically suitable habitat loss in the southern inshore and midshelf portions of the USNES as well as inshore portions of Southern New England; fall is projected to see the largest amount of metabolically suitable habitat loss with some species (*i.e.*, Atlantic cod) habitat restricted to the Gulf of Maine.

There were substantial differences in loss of metabolically suitable habitat across the five species. For Atlantic cod and cunner, most of the USNES south of the Gulf of Maine is projected to reach MI_{crit} in the fall, with slight refugia in the midshelf portion of the New York Bight. During summer, these two species are projected to experience less metabolically suitable habitat loss than in fall with inshore southern strata as well as inshore strata in Southern New England reaching MI_{crit}. Spiny dogfish are projected to experience a loss of metabolically habitat in the Southern Shelf and inshore portions of the New York Bight and Southern New England. Black sea bass and summer flounder may experience minimal loss in habitat under a

Fig 6. Strata "at-risk" during fall. The strata "at-risk" based on proportion of years a stratum was at or below a species-specific MI_{crit} across the historical climatology (top panel) and contemporary climatology (bottom panel) during the fall. If a stratum is tan (0% risk), then it never reached MI_{crit} during any year across the respective timeseries while if a stratum is dark purple (100% risk), then that stratum reached or surpassed MI_{crit} for 100% of the years. United States state outline data was obtained from the R package 'maps' (cran.r-project.org/package = maps).

doubling of CO_2, reaching MI_{crit} only in the southern inshore and midshelf portions of the Southern Shelf. This result may reflect the fact that the presumed MI_{crit} for each of the warm water species did not perform well within the study domain of the USNES.

The limiting oxygen levels to reach 50 and 100% habitat loss under projected warming differed by species and season (Table 3), and follows the progression of losing ~5% of MI per kPa loss below air-saturation, regardless of temperature [16]. During fall, the oxygen value used in the above projections (Fig 7) led to 50% habitat loss or more for Atlantic cod, and would have to drop an additional ~1kPa to reach 50% habitat loss for cunner and spiny dogfish. For black sea bass and summer flounder, oxygen would have to decrease to ~13kPa for a 50% loss of habitat, a greater than 3kPa decrease from the value used in the projections, and far greater than any drop expected from large-scale ocean deoxygenation [48]. Across all seasons, the cold and warm water species each had similar oxygen levels that would lead to 100% habitat loss at ~13kPa vs ~10kPa, respectively. These oxygen levels may represent an oxygen threshold for those species where regardless of a wide range of temperatures across the seasons (~5-25°C), habitat would become metabolically unsuitable throughout the USNES.

Discussion

Throughout the USNES, MI for five important fish species has been decreasing in step with continued ocean warming in the region, yet the decrement and consequence varied by species. When assessing the past trends in MI calculated with seasonal PO_2 means, and subsequently
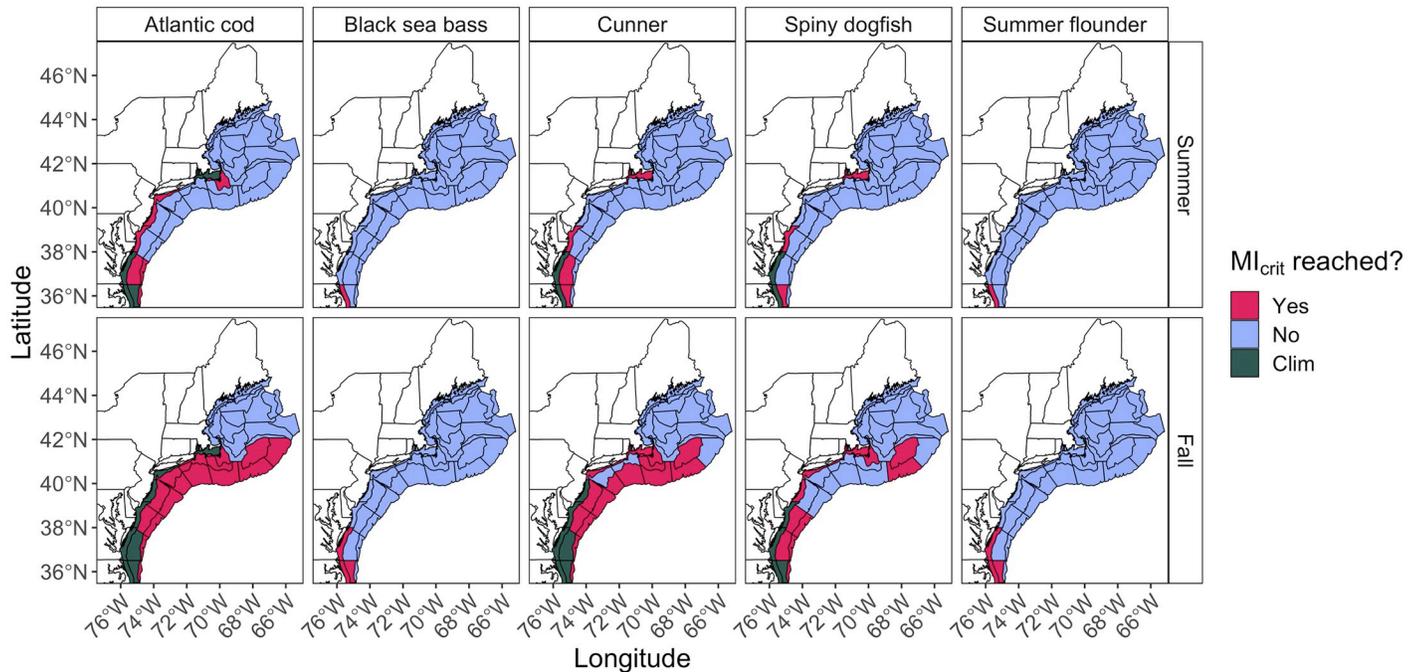
Fig 7. Future projections of metabolically suitable habitat loss. Projections are shown under a doubling of atmospheric CO_2, 60–80 years into the future for each species for both summer (top) and fall (bottom). Individual species are shown in columns. Green strata indicate MI_{crit} was reached in the current climatology (1972–2019), pink indicates MI_{crit} will be reached under a doubling of CO_2 and blue shows that the stratum does not reach limiting MI_{crit} values into the future. United States state outline data was obtained from the R package 'maps' (cran.r-project.org/package = maps).

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constant environmental oxygen availability, the differences in thermal sensitives of metabolic traits led to species-specific variation in MI across time and space within a season. For the cold water species (Atlantic cod, cunner, spiny dogfish), the calculated MI frequently fell below MI_{crit} across the USNES, and showed an increase in the frequency habitat was unsuitable during recent warming (2010–2019). In line with these trends, these species are projected to

Table 3. The oxygen level (kPa) for 50 and 100% habitat loss for each species and season under a doubling of atmospheric CO_2.

Species	% Habitat loss	Winter	Spring	Summer	Fall
Atlantic cod	50	13.78	12.99	15.13	16.64[a,b]
	100	11.78	10.99	12.13	13.64
Black sea bass	50	11.78	10.99	12.13	13.64
	100	9.78	9.99	10.13	10.64
Cunner	50	13.78	13.99	15.13	15.64
	100	12.78	11.99	13.13	13.64
Spiny dogfish	50	12.78	11.99	14.13	15.64
	100	10.78	10.99	11.13	12.64
Summer flounder	50	9.78	9.99	11.13	12.64
	100	8.78	7.99	9.13	9.64[b]

Oxygen levels to reach a specific % habitat loss are based on back-calculating oxygen for the respective future temperature of a stratum and MI_{crit} for a species.

[a]Note, this value is the same as the future oxygen value for the fall climatology, which means 50% of habitat was already limiting in the future climatology.

[b]To provide a reference for the oxygen values presented in kPa, at 15°C and 33psu, the highest value in fall (16.64kPa) is 79% air saturation and 4.79 mL/L, and the lowest value in fall (9.64kPa) is 46% air saturation and 2.77 mL/L.

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experience substantial metabolically suitable habitat loss under a doubling of atmospheric CO_2, especially during fall. However, for the warm water species (black sea bass, summer flounder), habitat at or below MI_{crit} was frequently occupied, suggesting the calculated MI_{crit} in this study did not perform as well. As such, these species also did not experience metabolically suitable habitat loss across the historical (1972–2019), contemporary (2010–2019), and future climatologies, except for in the most southern and inshore regions of the shelf. Interestingly, black sea bass and summer flounder populations extend into the US Southeast shelf, which may suggest that species-specific MI_{crit} is an evolutionary trait representative of the whole geographic population. As such, MI_{crit} may not be able to delineate metabolically suitable habitat in sub-populations found at higher latitudes than the latitudinal lower limit of the species, which would suggest these species will not experience a loss of metabolically suitable habitat in the USNES. This distinction may be important to consider when assessing the use of various physiological tools to project suitable habitat, broadly for global change biology and regionally for fisheries management when management jurisdictions have already been set.

For the most part, our results agreed with other studies focused on USNES fish habitat shifts [29, 39, 49, 50]. For Atlantic cod, all four studies confirmed loss of habitat into the future due to warming, although we found less evidence that spring warming limits adult Atlantic cod and surpasses critical MI values (but see differences in life stages: [51]). A decrease in black sea bass fall thermal habitat in southern inshore locations agreed with Kleisner et al. [49]. Cunner loss in thermal habitat was also reported in Morley et al. [29], and summer flounder minimal habitat loss was also found in Kleisner et al. [49] and Morley et al. [29]. Spiny dogfish showed contrasting results from recent stock assessments showing no change in spiny dogfish abundance over time and other studies on the USNES [29, 39, 49, 50] that showed increasing suitable habitat with warming. In contrast, we showed the loss of metabolically suitable habitat based on increasing frequency of locations within the USNES reaching or dropping below MI_{crit}. These discrepancies could be due to a myriad of reasons including but not limited to differing physiology of *Squalus* sharks compared to teleosts, development of physiological parameters based on sub-populations, and interpretations of suitable thermal habitat either based on the change in amount of *limiting* vs *optimal* habitat.

Species-specific differences in MI_{crit}

For the five USNES fish species, MI_{crit} values fell within the 2–5 MI range proposed by Deutsch et al. [13, 14], but differed between species based on native thermal ranges. MI_{crit} values were lowest in the colder water species while the warmer water species had higher MI_{crit} values. For the cold water species, Atlantic cod and cunner, the MI_{crit} (defined by mean conditions for a stratum) agreed well with temperature and oxygen conditions delineating the boundary of individual fish occurrences across strata and seasons (Fig 4). However, for the warm water species, black sea bass and summer flounder, MI_{crit} did not appear to discriminate habitat where fish are absent and fish presences were higher closer to and below the MI_{crit} (Fig 4). These fish also have southern conspecifics inhabiting the US Southeast shelf, but the degree of genetic similarity between the northern and southern stocks differs for the two species. For black sea bass, the southern and northern stocks are identified as genetically distinct [52], yet for summer flounder there is no major genetic dissimilarity between the two stocks [53]. Moreover, Deutsch et al. [14] identified MI_{crit} values for 72 marine species, including some in this study. Our MI_{crit} values for black sea bass and summer flounder were almost identical to Deutsch et al. [14] (S2 Table), which is intriguing because both studies used different data sources both for the physical parameters and for species distributions. Because Deutsch et al. [14] also used species distribution data from the southern stocks of black sea bass and summer flounder, we

suggest that MI_{crit} may be an evolutionary trait that can delineate metabolically suitable habitat at the lower latitudinal limits of an entire population, but may not represent physiological limits of higher latitude conspecifics with localized adaptations.

For Atlantic cod and cunner, our MI_{crit} values differed from Deutsch et al. [14]. In addition, species-specific E_o values between the two studies were similar for cunner but differed for Atlantic cod (S2 Table). For Atlantic cod, physiological values used to define E_o and A_o were from a different study than in Deutsch et al. [14] because we purposely only used data from studies that measured P_{crit} via the onset of anaerobic metabolism and not mortality (*i.e.*, L50). MI_{crit} disagreement for the cold water species may also be due to our study using a more spatially explicit domain (*i.e.*, USNES) than in Deutsch et al. [14]. The spatial domain and resolution of our environmental and fishery data were at the strata level covering the extent of the USNES while for Deutsch et al. [14] data were analyzed beyond the USNES and in a 1˚ x 1˚ grid. Our temperature and oxygen measurements also differed in that Deutsch et al. [14] used modeled data from the World Ocean Atlas in the same 1˚ x 1˚ grid. This resolution is insufficient to use for analyses assessing local dynamics along the USNES due to the size, complex bathymetry, and oceanography of the shelf, which require finer-resolution models to resolve the biogeochemistry [24]. While we simplified oxygen, temperature dynamics were more representative of the USNES dynamics than would have been resolved at a 1˚ x 1˚ grid.

Historical and contemporary MI trends

Across all seasons, MI decreased between the historical (1972–2019) and contemporary (2010–2019) climatologies, but MI fell below MI_{crit} for the cold water species (and rarely for the warm water species) only in the summer and fall seasons. The USNES experiences cold bottom temperature during winter and spring seasons, and starts to warm during late summer and fall when storms pass through mixing the warm surface layer to depth [54]. As such, late summer and fall are the warmest seasons for bottom temperature [55]. Therefore, most demersal species on the USNES are more likely to experience limiting MI values in the late summer and fall when the temperature is highest. Summer and fall coincide with fish spawning seasons and juvenile settlement, both life stages that can have narrower thermal windows [56]. This suggests that, at the warm limits of a species distribution, habitat may be constrained by the changes in summer and fall bottom temperature. However, within the domain of the USNES, this trend was only evident for the cold water species and there was minimal metabolically suitable habitat loss for the warm water species, which only experienced loss in the most inshore and southern strata.

While warming across the 1972–2019 time period has been occurring in winter and spring, no fish in this study experienced a sub-critical MI value during winter and spring throughout the study period. Warming winters may be problematic for some species, such as Atlantic cod in Southern New England [51], yet this was not apparent in our data. However, for some USNES species, winter warming may be beneficial, especially to warmer water species living at their northern range edges (*i.e.*, black sea bass, [52]). Warmer winters can facilitate increased young-of-the-year survival [57] and can benefit species by increasing recruitment [58]. MI values well above MI_{crit} are of unknown significance, and as such, the consequences of warming in winter and spring may be better explored using another physiological metric that can distinguish suitable habitat based on cold-intolerances.

Our MI trend results provide a broad account of how the extent of metabolically suitable habitat has changed over time, but may mask finer-scale and/or new emerging oceanographic phenomena that lead to abrupt, intense and abnormal periods of warming within a season. For example, marine heatwaves are becoming more persistent in the USNES [30, 31],

increasing water temperature for periods of time throughout a given year. Specific to the USNES, the summer season may also experience rapid warming driven by an increase in warm core ring activity. These warm core rings are eddies shed off of the Gulf Stream that can distribute warm and salty water onto the mid- to outer-shelf during summer months [59, 60]. Altogether, the increase in frequency and magnitude of abrupt and intense warming events could lead to rapid decreases in MI on shorter temporal scales not demonstrated in our data. The cumulative effect of these events is unknown, but how species respond to these changes may differ based on their propensity and/or time-course to return to previously thermally inhabitable water [61].

Future metabolically-suitable habitat loss

Under a doubling of atmospheric CO_2, future metabolically suitable habitat loss, as defined as strata where MI is at or below MI_{crit}, will be substantial for the cold water species, yet the warm water species will experience minimal habitat loss. Fall may see the highest extent of habitat loss, with many species restricted to the Gulf of Maine and small mid-shelf portions in the New York Bight. Habitat loss may also occur in summer, mainly for inshore/mid-shelf and southern portions of the USNES, but increased model resolution including higher frequency of warm core ring intrusions would project warmer temperatures on the mid- and outer-shelf than used in our model [60]. We project no spring- and only minimal winter loss of metabolically suitable habitat loss in the Southern Shelf. Despite a decrease in MI, winter warming could also lead to the opening of new habitat in mid-shelf and inshore regions that were historically too cold. Finally, while our projections provide individual assessments on season-specific habitat loss, an unexplored but important component to consider will also be the connectivity between populations who undergo seasonal migrations, and how shifts in distribution during one season may alter habitat use in other seasons.

Atlantic cod may experience the most amount of habitat loss under a doubling of atmospheric CO_2, leading to metabolically suitable habitat restricted to the Gulf of Maine, as has been shown in other studies focused on Atlantic cod (*i.e.*, [39]). Importantly, MI_{crit} was defined for Atlantic cod across all fish presences within the NOAA NEFSC bottom trawl survey, yet within the USNES, Atlantic cod is managed as two stocks (Gulf of Maine and Georges Bank), and Southern New England fish are managed with the Georges Bank stock, although they may be genetically different [62]. Therefore, within this dataset, the different cod stocks were not differentiated when defining MI_{crit} (and were also not distinguished in the laboratory physiology studies). The general shift in Atlantic cod distribution has been poleward and deeper, especially as Atlantic cod are at their southern population limits in Southern New England and Georges Bank [26]. Our assessment between the historical and contemporary time periods would also support this observation.

Black sea bass may experience minimal habitat loss into the future, and only in a few areas in the most southern inshore and midshelf portions of the USNES. Black sea bass are a warm water species, and the Northern stock (the focus of this study) are the most northern within the full range of black sea bass [52], which may influence MI_{crit} (see above). Winter and spring warming have been linked to black sea bass distribution shifts in the spring [27] and increased recruitment from larval overwintering survival [58], which suggests warming in these seasons may be beneficial for black sea bass. Walsh et al. [35] showed that adult black sea bass center of biomass rate of movement was nonsignificant during fall, and perhaps extirpation of black sea bass out of warming regions has not occurred yet. As such, black sea bass will likely experience lower amounts of habitat loss in the summer and fall seasons compared to the other USNES species. Black sea bass maximum tolerable temperature was around 24°C [63]. The only

stratum in this data set whose mean temperature reached 24˚C or higher was stratum I01 (inshore Southern Shelf; Fig 1), which started to reach this temperature in the early 2000s.

Cunner were similar to Atlantic cod in that they may experience a substantial amount of habitat loss into the future. Out of the five species studied, cunner are the only non-targeted species by recreational and commercial fisheries, and previous attempts at discerning thermal habitat have been unsuccessful [64]. Cunner abundance has decreased in inshore portions of Southern New England [65] and has increased in parts of the Gulf of Maine [66]. We project that cunner will experience suitable habitat loss within the Southern Shelf, New York Bight, Southern New England, and Georges Bank. This result corroborates with Morley et al. [29] who showed a shift in distribution poleward with accompanying southern habitat loss.

Spiny dogfish projected summer and fall habitat loss was less extensive than Atlantic cod or cunner, but showed significant loss in the Southern Shelf and inshore regions throughout the USNES. This result contrasts with other studies that demonstrate a benefit to spiny dogfish with recent warming [28, 39, 49, 67], and a potential southward distribution shift [26]. Importantly, some of these studies (*e.g.*, [39]) analyzed change in thermal habitat during the spring (March, April, May), where we also show no habitat below MI_{crit} (*i.e.*, no habitat loss in spring; S4 Fig). Physiology-based studies on spiny dogfish have shown 21˚C to be a physiological thermal limit under normoxia [68, 69], and under a doubling of atmospheric CO_2, spiny dogfish thermal limit would be around 16˚C (at PO_2 = 16.64kPa). A challenge for identifying current and future changes to spiny dogfish is also driven by their highly migratory behavior and division into two distinct subpopulations, which can differ in their thermal tolerances [70]. The animals used in the laboratory study that provided species-specific parameters likely captured individuals from the northern subpopulation of spiny dogfish [69], which are shown to have lower thermal tolerances than their southern counterparts [70].

Summer flounder minimal projected habitat loss is similar to black sea bass for both summer and fall. Interestingly, summer flounder distribution has been shifting northward and eastward over time in both spring and fall [27]. Suggested drivers of this shift include bottom temperature trends [7], climate variability with the Gulf Stream Index [71], and fishing pressure [27]. However, other studies suggest the drivers remain unresolved as temperature and fishing pressure explain some but not most of the variation in the data [72]. Our MI_{crit} analyses suggest that temperature is a driver in limiting habitat at the most inshore and southern portions of the shelf, and other temperature dynamics along the USNES may affect the population through other mechanisms (*i.e.*, [73]).

Considerations when building the MI framework

Species-specific physiological parameters are valuable tools that can be used to investigate how changing environments may affect species distributions. Most papers focused on species distribution and temperature use statistical relationships between where fish are found and the temperatures they reside in to develop species distribution models (*e.g.*, [28]). These studies are instrumental for investigating how ocean warming will affect the USNES ecosystem as they can provide estimates of optimal habitat across a range of temperatures as well as incorporate more physical features such as salinity and rugosity into their models. Only focusing on temperature can sometimes mask true vulnerability to environmental change [50], especially for some benthic organisms with a high affinity towards structure [74]. The use of MI differs in that oxygen is also incorporated and the assessment of suitable habitat is based on current physiological understanding, using data that are defined independently of the collection of fishery data. Also, the framework of assessing MI with respect to MI_{crit} primarily focuses on defining habitat *limits* instead of *optimal* habitat. For species distribution models that do focus

on habitat limits, developing an MI-based habitat model can be a complementary method that, along with oxygen data, provides an additional step of interpretation between statistical correlations of temperature to presence/absence and physiological limits that were derived in the laboratory. When the two methods are in alignment (*i.e.*, Atlantic cod), it can be theorized that the trends seen in the species distribution models are likely driven by oxygen-limited thermal tolerance. However, when the two methods do not agree (*i.e.*, spiny dogfish), additional data gaps are exposed that can guide subsequent research areas to improve our projections.

By defining limiting habitat, MI is more useful in identifying and tracking the shift in species ranges at the warm edge, which necessitates a clear shift in the edge that is synchronized with changes in temperature [75] and occurs within the spatial domain of the study. Furthermore, the MI approach is predicated on the assumption that temperature-dependent hypoxia tolerance determines the warm-water range edges, which may not be true for some species. If the range edges are set by some other factor, then MI_{crit} may be misleading or irrelevant [18]. Understanding the context of MI_{crit} is also relevant for black sea bass and summer flounder where MI_{crit} did not seem to distinguish limiting habitat within the USNES, which may have been a consequence of defining habitat limits in the northern portion of an entire range. However, our study domain was purposefully constrained to the USNES which is defined by specific spatial management zones used by NOAA's Northeast Fisheries Science Center as well as regional management councils that include the Mid-Atlantic and New England Fishery Management Councils. Our results demonstrate the use of one physiological metric, MI, may be better suited for species whose range edge occurs within the USNES, which is an important distinction when identifying appropriate physiological metrics that could be integrated into management frameworks.

How the species-specific metrics are defined is important to consider when making comparisons across species and applying them towards describing and projecting species responses to environmental change. The calculation of the laboratory-based species-specific parameters used in the MI equation come from studies that measure P_{crit} at multiple temperatures and the methodologies used to calculate P_{crit} can differ between studies (*e.g.*, [76, 77]). Many laboratory experiments subject animals to acute exposures of different temperatures and oxygen, obfuscating the potential to understand acclimation potential, but the duration of exposure can affect performance of particular physiological measurement end points [63]. As such, while we may have shown differing sensitivities between the cold and warm water species, it is still unknown whether the species would respond similarly to a slow, climate-induced temperature change. Finally, for species with subpopulations or spatially explicit stocks, the collection locations of experimental animals may also skew the derived species-specific parameters should P_{crit} (*i.e.*, hypoxia tolerance) differ between these subpopulations or stocks. Altogether, these caveats highlight the need for continued assessment of species physiological performance in the laboratory so that potential influence in study design can be disentangled from actual responses in the natural environment.

In this study, we did not use modeled bottom ocean PO_2 because the sparsity of PO_2 observations in the USNES precluded model validation, which led to a coarser investigation on MI in the USNES. High-resolution ocean models are required for the USNES due to its high complexity in regional ocean circulation and bathymetry [24], and biogeochemical models that can resolve PO_2 at these resolutions are not common or have yet to be validated. We did test a modeled oxygen product for potential use, but found poor agreement with the raw data (methods described in S1 Text). However, the modeled oxygen product provided a range of spatial anomalies in oxygen data that could potentially represent variation in oxygen from the seasonal averages we used. To investigate the potential source in error when calculating MI, the oxygen spatial variability defined in the modeled oxygen was tested using a Monte Carlo

simulation. Overall, we found our seasonal oxygen means did not significantly affect our interpretation of changes in metabolically suitable habitat (full explanation in S1 Text). In addition, the relationship between environmental PO_2 and MI is documented (*i.e.*, [16]), and can be used to identify threshold PO_2 values that lead to substantial habitat loss (Table 3). While it is very unlikely these oxygen levels would represent future oceanic conditions in the USNES, they are useful when gauging the potential effect of hypoxic events. As methods and technology for ocean observing advance, future incorporation of PO_2 values could be used with critical threshold PO_2 values to identify regions of concern along the USNES.

Conclusions

Ocean warming along the USNES has already affected important fish species [49]. As warming continues into the future [24], Atlantic cod and cunner may experience a substantial loss in presumed metabolically suitable habitat, spiny dogfish may experience some loss in habitat, and black sea bass and summer flounder may be less vulnerable to climate change-induced warming. Recognizing these impacts on species allows for adaption and/or mitigation of negative consequences in the fishing community [78] and on ecosystems [79]. By using a physiologically-based approach, we demonstrated the utility of MI in estimating metabolically suitable habitat for some species as a complementary methodological tool for understanding the effects of ocean warming on species distributions. We also revealed that MI may not be sensitive enough at the regional scale for animals whose distributions extend beyond the study (or management) region and suggest future uses of MI consider the scale and species of interest.

Supporting information

S1 Table. Species critical oxygen values and associated temperatures used in this study.
[a]Data for summer flounder included two studies, which reported similar values. [b]Summer flounder and cunner were the only fish with two temperature bins.
(DOCX)

S2 Table. Comparison of species E_o and MI_{crit} between studies. Values of E_o and MI_{crit} are compared between this study (top value for each species) and Deutsch et al. [14] (bottom value for each species). Same study indicates if the species-specific parameters used in this study and in Deutsch et al. [14] were calculated from the same laboratory study. [a]We used two studies and a calculated mean, one of which was the same as in Deutsch et al. [14].
(DOCX)

S1 Fig. Determination of MI_{crit} for each species. MI_{crit} (vertical dashed line) was defined as the 2.5[th] quantile (horizontal solid line) of the cumulative distribution function of fish presences in the fall. The resulting MI_{crit} value is shown at the top of the graph for each species.
(TIF)

S2 Fig. Stratum-averaged temperature for each climatology. Average temperature is provided for both the historical (1972–2019) and contemporary (2010–2019) climatologies for each season. United States state outline data was obtained from the R package 'maps' (cran.r-project.org/package = maps).
(TIF)

S3 Fig. Temperature trends for the historical climatology and projected deltas. The historical climatology (top) is from 1972 to 2019 and the temperature deltas (bottom) are calculated under a doubling of atmospheric CO_2. The future temperature values for each stratum used in

calculating projected MI were obtained by adding the temperature deltas to the stratum mean. Under a doubling of atmospheric CO_2, note the faster warming in the offshore strata as well as into the Gulf of Maine. United States state outline data was obtained from the R package 'maps' (cran.r-project.org/package = maps).
(TIF)

S4 Fig. Future projections of metabolically suitable habitat loss for winter and spring. Projections are shown under a doubling of atmospheric CO_2, 60–80 years into the future for each species for both winter (top) and spring (bottom). Individual species are shown in columns. Green strata indicate MI_{crit} was reached in the current climatology (1972–2019), pink indicates MI_{crit} will be reached under a doubling of CO_2 and blue shows that the stratum does not reach limiting MI_{crit} values into the future. Note: no habitat is metabolically unsuitable under the current climatology and only Atlantic cod may experience habitat loss in the winter. United States state outline data was obtained from the R package 'maps' (cran.r-project.org/package = maps).
(TIF)

S1 Data. Spreadsheet with supporting data for historical and future climatologies.
(XLSX)

S1 Text. Methods to determine sensitivity of MI to oxygen variability. Additional preliminary tests were conducted to determine if modelled oxygen would be appropriate for analysis and, if not, the potential effect varying oxygen levels may have on our interpretation of limiting metabolically suitable habitat. Fig A in S1 Text: raw oxygen values for each region and season. Fig B in S1 Text: analysis of observed vs. modeled oxygen data. Fig C in S1 Text: spatial oxygen anomalies. Fig D in S1 Text: sensitivity analysis of varying oxygen from 1972–2019 climatology. Fig E in S1 Text: sensitivity analysis of varying oxygen from 2010–2019 climatology.
(DOCX)

Acknowledgments

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Visualization: Emily Slesinger.

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References

1. Bennett AF. Activity metabolism of the lower vertebrates. Annu Rev Physiol. 1978; 400: 447–469. https://doi.org/10.1146/annurev.ph.40.030178.002311 PMID: 345952

2. Rodgers GG, Donelson JM, McCormick MI, Munday PL. In hot water: sustained ocean warming reduces survival of a low-latitude coral reef fish. Mar. Biol. 2018; 165: 1–10.

3. Chabot D, Koenker R, Farrell AP. The measurement of specific dynamic action in fishes. J Fish Biol. 2016; 88: 152–172. https://doi.org/10.1111/jfb.12836 PMID: 26768974

4. Biro PA, Post JR, Booth DJ. Mechanisms for climate-induced mortality of fish populations in whole-lake experiments. Proc Natl Acad Sci U S A. 2007; 104: 9715–9719. https://doi.org/10.1073/pnas.0701638104 PMID: 17535908

5. Pörtner HO, Peck MA. Climate change effects on fishes and fisheries: Towards a cause-and-effect understanding. J Fish Biol. 2010; 77: 1745–1779. https://doi.org/10.1111/j.1095-8649.2010.02783.x PMID: 21078088

6. Rijnsdorp AD, Peck MA, Engelhard GH, Möllmann C, Pinnegar JK. Resolving the effect of climate change on fish populations. ICES J Mar Sci. 2009; 66: 1570–1583.

7. Pinsky ML, Worm B, Fogarty MJ, Sarmiento JL, Levin SA. Marine taxa track local climate velocities. Science. 2013; 341: 1239–1242. https://doi.org/10.1126/science.1239352 PMID: 24031017

8. Monllor-Hurtado A, Pennino MG, Sanchez-Lizaso JL. Shift in tuna catches due to ocean warming. PLoS One. 2017; 12: 1–10. https://doi.org/10.1371/journal.pone.0178196 PMID: 28591205

9. Smith KA, Dowling CE, Brown J. Simmered then boiled: Multi-decadal poleward shift in distribution by a temperate fish accelerates during marine heatwave. Front Mar Sci. 2019; 6: 1–16.

10. Dulvy NK, Rogers SI, Jennings S, Stelzenmüller V, Dye SR, Skjoldal HR. Climate change and deepening of the North Sea fish assemblage: A biotic indicator of warming seas. J Appl Ecol. 2008; 45: 1029–1039.

11. Perretti CT, Fogarty MJ, Friedland KD, Hare JA, Lucey SM, McBride RS, et al. Regime shifts in fish recruitment on the Northeast US Continental Shelf. Mar Ecol Prog Ser. 2017; 574: 1–11.

12. Pinsky ML, Reygondeau G, Caddell R, Palacios-Abrantes J, Spijkers J, Cheung WWL. Preparing ocean governance for species on the move. Science. 2018; 360: 1189–1192. https://doi.org/10.1126/science.aat2360 PMID: 29903965

13. Deutsch C, Ferrel A, Seibel B, Pörtner HO, Huey RB. Climate change tightens a metabolic constraint on marine habitats. Science. 2015; 348: 1132–1136.

14. Deutsch C, Penn JL, Seibel B. Metabolic trait diversity shapes marine biogeography. Nature. 2020; 585: 557–562. https://doi.org/10.1038/s41586-020-2721-y PMID: 32939093

15. Lefevre S, Bayley M, McKenzie DJ. Measuring oxygen uptake in fishes with bimodal respiration. J Fish Biol. 2016; 88: 206–231. https://doi.org/10.1111/jfb.12698 PMID: 26358224

16. Seibel BA, Deutsch C. Oxygen supply capacity in animals evolves to meet maximum demand at the current oxygen partial pressure regardless of size or temperature. J Exp Biol. 2020; 223: jeb210492. https://doi.org/10.1242/jeb.210492 PMID: 32376709

17. Seibel BA. Ch. 27: Animal response to hypoxia in estuaries and effects of climate change *in Climate Change and Estuaries*. 2023. Kennish M. J., Paerl H. W. and Crosswell J. R., Eds. CRC Press.

18. Seibel BA. On the validity of using the Metabolic Index to predict the responses of marine fishes to climate change. *Reference Module in Life Sciences*. 2024. Elsevier.

19. Duncan MI, James NC, Potts WM, Bates AE. Different drivers, common mechanism; the distribution of a reef fish is restricted by local-scale oxygen and temperature constraints on aerobic metabolism. Conserv Physiol. 2020; 8: 1–16.

20. Lucey NM, Deutsch CA, Carignan M-H, Vermandele F, Collins M, Johnson MD, et al. Climate warming erodes tropical reef habitat through frequency and intensity of episodic hypoxia. PLOS Clim. 2023; 2(3): e0000095.

21. Seibel BA, Birk MA. Unique thermal sensitivity imposes a cold-water energetic barrier for vertical migrators. Nat Cliam Chang. 2022; 12: 1052–1058.

22. Pershing AJ, Alexander MA, Hernandez CM, Kerr LA, Le Bris A, Mills KE, et al. Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. Science. 2015; 350: 809–812. https://doi.org/10.1126/science.aac9819 PMID: 26516197

23. Chen Z, Kwon YO, Chen K, Fratantoni P, Gawarkiewicz G, Joyce TM. Long-term SST variability on the Northwest Atlantic continental shelf and slope. Geophys Res Lett. 2020; 47: 1–11.

24. Saba VS, Griffies SM, Anderson WG, Winton M, Alexander MA, Delworth TL, et al. Enhanced warming of the Northwest Atlantic Ocean under climate change. J Geophys Res Oceans. 2016; 120: 1–15.

25. Caesar L, Rahmstorf S, Robinson A, Feulner G, Saba V. Observed fingerprint of a weakening Atlantic Ocean overturning circulation. Nature. 2018; 556: 191–196. https://doi.org/10.1038/s41586-018-0006-5 PMID: 29643485

26. Nye JA, Link JS, Hare JA, Overholtz WJ. Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. Mar Ecol Prog Ser. 2009; 393: 111–129.

27. Bell RJ, Richardson DE, Hare JA, Lynch PD, Fratantoni PS. Disentangling the effects of climate, abundance, and size on the distriubtion of marine fish: an example based on four stocks from the Northeast US shelf. ICES J Mar Sci. 2015; 72: 1311–1322.

28. Kleisner KM, Fogarty MJ, McGee S, Barnett A, Fratantoni P, Greene J, et al. The effects of sub-regional climate velocity on the distribution and spatial extent of marine species assemblages. PLoS One. 2016; 11: 1–21. https://doi.org/10.1371/journal.pone.0149220 PMID: 26901435

29. Morley JW, Selden RL, Latour RJ, Frölicher TL, Seagraves RJ, Pinsky ML. Projecting shifts in thermal habitat for 686 species on the North American continental shelf. PLoS One. 2018; 13: 1–28. https://doi.org/10.1371/journal.pone.0196127 PMID: 29768423

30. Northeast Fisheries Science Center (NEFSC). 2022a. State of the Ecosystem 2022: Mid-Atlantic. Northeast Fisheries Science Center,

31. Northeast Fisheries Science Center (NEFSC). 2022b. State of the Ecosystem 2022: New England. Northeast Fisheries Science Center,

32. Roberts SM, Halpin PN, Clark JS. Jointly modeling marine species to inform the effects of environmental change on an ecological community in the Northwest Atlantic. Sci Rep. 2022; 12: 1–12.

33. Manderson J, Palamara L, Kohut J, Oliver MJ. Ocean observatory data is useful for regional habitat modeling of species with different vertical habitat preferences. Mar Ecol Prog Ser. 2011; 438: 1–17.

34. Kohut J, Palamara L, Curchitser E, Manderson J, DiDomenico G. Cooperative development of dynamic habitat models informed by the Integrated Ocean Observing System (IOOS) informs fisheries management decision making in the coastal ocean. OCEANS. 2016;2015—MTS/IEEE Washington: 1–8. MTS.

35. Walsh HJ, Richardson DE, Marancik KE, Hare JA. Long-term changes in the distributions of larval and adult fish in the northeast U.S. shelf ecosystem. PLoS One. 2015; 10: 1–31. https://doi.org/10.1371/journal.pone.0137382 PMID: 26398900

36. Chen Z, Kwon YO, Chen K, Fratantoni P, Gawarkiewicz G, Joyce TM, et al. Seasonal prediction of bottom temperature on the Northeast U.S. continental shelf. J Geophys Res Oceans. 2021; 126: 1–27.

37. Chant RJ, Wilkin J, Zhang W, Choi B, Hunter E, Castelao R, et al. Dispersal of the Hudson River Plume in the New York Bight. Oceanogr. 2008; 21: 148–161.

38. Mountain DG. Variability in the properties of shelf water in the Middle Atlantic Bight, 1977–1999. J Geophys Res Oceans. 2003; 108: 1–11.

39. Selden RL, Batt RD, Saba VS, Pinsky ML. Diversity in thermal affinity among key piscivores buffers impacts of ocean warming on predator-prey interactions. Glob Change Biol. 2018; 24: 117–131. https://doi.org/10.1111/gcb.13838 PMID: 28731569

40. duPontavice H, Chen Z, Saba VS. A high-resolution ocean bottom temperature product for the northeast U.S. continental shelf marine ecosystem. Prog Oceanogr. 2023; 210: 102948.

41. Shchepetkin AF, McWilliams JC. The regional oceanic modeling system (ROMS): A split-explicit, free-surface, topography-following-coordinate oceanic model. Ocean Model. 2005; 9: 347–404.

42. Fernandez E, Lellouche JM. Product user manual for the global ocean physical reanalysis product GLORYS12V1. Copernicus Product User Manual. 2018; 4: 1–15.

43. Nazzaro L, Slesinger E, Kohut J, Saba GK, Saba VS. Sensitivity of marine fish thermal habitat models to fishery data sources. Ecol Evol. 2021; 11: 13001–13013. https://doi.org/10.1002/ece3.7817 PMID: 34646448

44. Turner SM, Manderson JP, Richardson DE, Hoey JJ, Hare JA. Using habitat association models to predict Alewife and Blueback Herring marine distriubtions and overlap with Atlantic Herring and Atlantic Mackerel: can incidental catches be redcued? ICES J Mar Sci. 2016; 73: 1912–1924.

45. Northeast Fisheries Science Center (NEFSC). 2017. 62nd northeast regional stock assessment workshop (62nd SAW) assessment summary report. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northeast Fisheries Science Center, Reference Document 17–03 Woods Hole, Massachusetts.

46. Nilsson GE, Östlund-Nilsson S. Does size matter for hypoxia tolerance in fish? Biol Rev. 2008; 83: 173–189. https://doi.org/10.1111/j.1469-185X.2008.00038.x PMID: 18397180

47. Pan YK, Ern R, Esbaugh AJ. Hypoxia tolerance decreases with body size in red drum *Sciaenops ocellatus*. J Fish Biol. 2016; 89: 1488–1493.

48. Schmidtko S, Stramma L, Visbeck M. Decline in global oceanic oxygen content during the past five decades. Nature. 2017; 542: 335–339. https://doi.org/10.1038/nature21399 PMID: 28202958

49. Kleisner KM, Fogarty MJ, McGee S, Hare JA, Moret S, Perretti CT, et al. Marine species distribution shifts on the U.S. Northeast Continental Shelf under continued ocean warming. Prog Oceanogr. 2017; 153: 24–36.

50. McHenry J, Welch H, Lester SE, Saba V. Projecting marine species range shifts from only temperature can mask climate vulnerability. Glob Change Biol. 2019; 25: 4208–4221. https://doi.org/10.1111/gcb.14828 PMID: 31487434

51. Langan JA, McManus MC, Zemeckis DR, Collie JS. Abundance and distribution of Atlantic cod (*Gadus morhua*) in a warming southern New England. Fish Bull. 2020; 118: 145–156.

52. McCartney MA, Burton ML, Lima TG. Mitochondrial DNA differentiation between populations of black sea bass (*Centropristis striata*) across Cape Hatteras, North Carolina (USA). J Biogeogr. 2013; 40: 1386–1398.

53. Hoey JA, Pinsky ML. Genomic signatures of environmental selection despite near-panmixia in summer flounder. Evol Appl. 2018; 11: 1732–1747. https://doi.org/10.1111/eva.12676 PMID: 30344639

54. Rasmussen LL, Gawarkiewicz G, Owens WB, Lozier MS. Slope water, gulf stream, and seasonal influences on southern Mid-Atlantic Bight circulation during the fall-winter transition. J Geophys Res Oceans. 2005; 110: 1–16.

55. Richaud B, Kwon YO, Joyce TM, Fratantoni PS, Lentz SJ. Surface and bottom temperature and salinity climatology along the continental shelf off the Canadian and U.S. East Coasts. Cont Shelf Res. 2016; 124: 165–181.

56. Dahlke F, Wohlrab S, Butzin M, Pörtner H. Thermal bottlenecks in the lifecycle define climate vulnerability of fish. Science. 2020; 369: 65–70. https://doi.org/10.1126/science.aaz3658 PMID: 32631888

57. Hurst TP. Causes and consequences of winter mortality in fishes. J Fish Biol. 2007; 71: 315–345.

58. Miller AS, Shepherd GR, Fratantoni PS. Offshore habitat preference of overwintering juvenile and adult black sea bass, *Centropristis striata*, and the relationship to year-class success. PLoS One. 2016; 11: e0147627.

59. Gawarkiewicz G, Todd RE, Zhang W, Partida J, Gangopadhyay A, Monim M, et al. The changing nature of shelf-break exchange revealed by the OOI pioneer array. Oceanogr. 2018; 31: 60–70.

60. Gangopadhyay A, Gawarkiezicz G, Nishchitha E, Silva S, Monim M, Clark J. An observed regime shift in the formation of warm core rings from the Gulf Stream. Sci Rep. 2019; 9: 12319. https://doi.org/10.1038/s41598-019-48661-9 PMID: 31444372

61. Suryan RM, Arimitsu ML, Coletti HA, Hopcroft RR, Lindeberg MR, Barbeaux SJ, et al. Ecosystem response persists after a prolonged marine heatwave. Sci Rep. 2021; 11:6235 https://doi.org/10.1038/s41598-021-83818-5 PMID: 33737519

62. Zemeckis DR, Martins D, Kerr LA, Cadrin SX. Stock identification of Atlantic cod (*Gadus morhua*) in US waters: an interdisciplinary approach. ICES J Mar Sci. 2014; 71: 1490–1506.

63. Slesinger E, Andres A, Young R, Seibel B, Saba V, Phelan B, et al. The effect of ocean warming on black sea bass (*Centropristis striata*) aerobic scope and hypoxia tolerance. PLoS One. 2019; 14: 1–22.

64. Shackell NL, Ricard D, Stortini C. Thermal habitat index of many Northwest Atlantic temperate species stays neutral under warming projected for 2030 but changes radically by 2060. PLoS One. 2014; 9: e90662. https://doi.org/10.1371/journal.pone.0090662 PMID: 24599187

65. Collie JS, Wood AD, Jeffries HP. Long-term shifts in the species composition of a coastal fish community. Can J Fish Aquat Sci. 2008; 65: 1352–1365.

66. Witman JD, Lamb RW. Persistent differences between coastal and offshore kelp forest communities in a warming Gulf of Maine. PLoS One. 2018; 13: 1–32.

67. Sagarese SR, Frisk MG, Cerrato RM, Sosebee KA, Musick JA, Rago PJ. Application of generalized additive models to examine ontogenetic and seasonal distributions of spiny dogfish (*Squalus acanthias*) in the Northeast (US) shelf large marine ecosystem. Can J Fish Aquat Sci. 2014; 71: 847–877.

68. Bockus AB, LaBreck CJ, Camberg JL, Collie JS, Seibel BA. Thermal range and physiological tolerance mechanisms in two shark species from the Northwest Atlantic. Biol Bull. 2020; 38: 131–144. https://doi.org/10.1086/708718 PMID: 32412839

69. Andres AM, Slesinger E, Young RE, Saba GK, Saba VS, Phelan BA, et al. Thermal sensitivity of metabolic performance in *Squalus acanthias*: the efficacy of aerobic scope as a predictor of viable thermal habitat. Mar Ecol Prog Ser. 2024; forthcoming.

70. Carlson AE, Hoffmayer ER, Tribuzio CA, Sulikowski JA. The use of satellite tags to redefine movement patterns of spiny dogfish (*Squalus acanthias*) along the U.S. east coast: Implications for fisheries management. PLoS One. 2014; 9: e103384.

71. O'Leary CA, Miller TJ, Thorson JT, Nye JA. Understanding historical summer flounder (*Paralichthys dentatus*) abundance patterns through the incorporation of oceanography-dependent vital rates in Bayesian hierarchical models Cecilia. Can J Fish Aquat Sci. 2019; 76: 1275–1294.

72. Perretti CT, Thorson JT. Spatio-temporal dynamics of summer flounder (*Paralichthys dentatus*) on the Northeast US shelf. Fish Res. 2019; 215: 62–68.

73. Henderson EM, Mills KE, Thomas AC, Pershing PJ, Nye JA. Effects of spring onset and summer duration on fish species distribution and biomass along the Northeast United States continental shelf. Rev Fish Biol Fish. 2017; 27: 411–424.

74. Roberts SM, Boustany AM, Halpin PN. Substrate-dependent fish have shifted less in distribution under climate change. Comm Biol. 2020; 3: 1–7. https://doi.org/10.1038/s42003-020-01325-1 PMID: 33067547

75. Fredston A, Pinsky M, Selden RL, Szuwalski C, Thorson JT, Gaines SD., et al. Range edges of North American marine species are tracking temperature over decades. Glob Change Biol. 2021; 27: 3145–3156. https://doi.org/10.1111/gcb.15614 PMID: 33759274

76. Claireaux G, Chabot D. Responses by fishes to environmental hypoxia: Integration through Fry's concept of aerobic metabolic scope. J Fish Biol. 2016; 88: 232–251. https://doi.org/10.1111/jfb.12833 PMID: 26768976

77. Seibel BA, Andres A, Birk MA, Burns AL, Shaw CT, Timpe AW, et al. Oxygen supply capacity breathes new life into critical oxygen partial pressure (Pcrit). J Exp Biol. 2021; 224: 1–12. https://doi.org/10.1242/jeb.242210 PMID: 33692079

78. Rogers LA, Griffin R, Young T, Fuller E, St. Martin K, Pinsky ML. Shifting habitats expose fishing communities to risk under climate change. Nat Clim Change. 2019; 9: 512–516.

79. McMahan MD, Grabowski JH. Nonconsumptive effects of a range-expanding predator on juvenile lobster (*Homarus americanus*) population dynamics. Ecosphere. 2019; 10: e02867