

Measuring and Modeling Changes in Fish Condition in the Northeast U.S. Shelf Marine Ecosystem

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Abstract

The relationship between fish length and weight, also known as condition, is important to fisheries as the associated parameters are used to track fish health and estimate fish landings. The temperature-size rule indicates that warming waters lead to faster growth at young ages but a smaller size at maturity and into later ages, but it does not specify if size parameters are equally affected. There is a lack of research on whether increased sea temperature affects the relationship between length and weight. The Northeast U. S. Shelf has been warming substantially for more than a decade, yet most studies of size parameters, particularly length-weight relationships, were conducted prior to this warming period. In this study, these parameters were recalculated from more recent data to investigate changes over time that span the recent warm years. This re-analysis showed that 14 out of 62 species experienced significant decreases in the β coefficient of the length-weight relationship $W = \alpha * L^\beta$. Four fish (Atlantic cod, American plaice, Atlantic herring, and spiny dogfish) were selected for in-depth analyses of these changes over distinct spatial regions of the Northeast U.S. Shelf. An interaction was found between the length-weight relationship and the ecological production unit (EPU) where the individuals were caught. For these four fish species, the question of whether there has been a decrease in the number of individuals in the 90th percentile by length caught over time was explored. Our results indicate a significant decline in large individuals as a proportion of the total number of individuals caught in each decade. As it is known that fish condition also impacts reproductive capabilities and thus population dynamics, a theoretical model was constructed to understand how sensitive population dynamics are to hypothetical changes in condition.

Introduction

The temperature-size rule is a hypothesized and widely documented biological phenomenon that associates increased temperatures with a smaller size at maturity in ectotherms (Atkinson 1994). More extreme effects can be observed on aquatic ectotherms at higher latitudes, as they have a lower tolerance to extreme temperatures and a narrower thermal tolerance than fish at mid and low latitudes (Porter and Peck 2010). As the Northeast U. S. Shelf has been warming at a rate 2.5 times faster than the rest of the world's oceans, a more pronounced effect on fish size is possible in this region (Mills et al. 2024). Size can influence an individual's fecundity, growth rate, and lifespan, all of which are important biological parameters that affect population dynamics. Thus, broad ecological impacts of changes in size and condition are expected as water temperatures rise (Atkinson 1994, Daufresne et al. 2009, Barneche 2018).

The temperature-size rule attempts to explain how fish size can decrease as waters warm, but there is a lack of research on whether this change will affect size parameters equally. The relationship between individual length and weight, also known as condition, has been used to approximate fishery removals, estimate stock biomass and audit survey catch data (Wigley et al. 2003). It is certainly possible that length and weight would decrease proportionally as fish size decreases, and thus increased sea temperatures would have no effect on the relationship between these variables. Although a direct link between the temperature-size rule and changes in biological condition may not exist, warming waters affect physiological mechanisms (such as growth and metabolic rates), interspecific and intraspecific competition (decreased size could lead to increased abundance as populations readjust to carrying capacity), and habitat availability – all of which could hypothetically lead to decreases in body condition. While there is already a well-supported hypothesis that biological size at maturity decreases as waters warm, we seek to discover if a similar phenomenon is occurring with fish condition. An in-depth study of length-weight parameters based on data from 1992-1999 was conducted by Wigley et al. (2003), but calculating these parameters based on more recent data may yield insight into how rising sea temperatures may affect this relationship.

Changes in this relationship may differ for fish with different life history strategies. Winemiller and Rose proposed that fish can be categorized based on their juvenile survivorship, fecundity, and generation time into three groups: periodic, opportunistic, and equilibrium (1994). These strategies dictate how fish respond and adapt to environmental changes, and thus the magnitude of the change in their size parameters as a result of rising sea temperatures may vary across these groups.

In this report, we attempt to determine if length-weight relationships have changed over time, whether these changes vary for fish aligning with different life history strategies, and if these changes differ spatially over the Northeast U.S. Shelf. We further analyze changes in fish size over time by determining whether there has been a decrease in observations of large (90th percentile by length) fish in more recent decades. Lastly, we constructed a population simulation model and conducted a sensitivity analysis to determine how sensitive population dynamics are to changes in condition.

Methods

1.1: Data source

We used data from the NEFSC bottom trawl survey to conduct these analyses. The seasonal survey has been conducted since 1970 and spans the Northeast U.S. Shelf from Cape Hatteras, North Carolina to the Gulf of Maine (Grosslein 1969, Azarovitz 1981, Politis 2014). It has been conducted in all seasons of the year, but spring and fall surveys have been more consistent than winter and summer, and we used only spring and fall data for our analyses. The survey follows a stratified random sampling design, with strata defined based on depth, bottom habitat type, and latitude. Stations are randomly selected within each stratum proportional to the stratum area. At each station, a bottom trawl net is towed for a standardized time and speed to sample the fish community. The catch is sorted to species, counted and weighed. Abundance and biomass measures at the species-tow level are adjusted using standard calibration factors that account for changes in vessels, gear, and doors over the duration of the survey (Sissenwine and Bowman 1978, Byrne and Forrester 1991, Miller et al. 2010). For all fish or a sub-sample (depending on the number caught), individual lengths are measured to the nearest 1 cm. Over the range of lengths observed for a species, individual weights have been measured for a representative subsample of the catch since 1992.

1.2: Length-weight relationships

We selected data on individual lengths and weights for fish from two time periods: the earliest seven years in the dataset, 1992-1999 (which were used in Wigley et al. (2003)) and the most recent seven years, 2016-2023. These periods will be referred to as the “Wigley” time period (1992-1999) and the “recent” time period (2016-2023) throughout this report.

A log-log transformation was applied to the length-weight relationship $W = \alpha * L^\beta$ (where W = individual weight (in kg), L = individual length (in cm), and α and β are the length-weight relationship parameters). The resulting relationship used is $\log(W) = \log(\alpha) + \beta * \log(L)$.

For these 62 species, the model predicting $\log(W)$ from the interaction between $\log(L)$ and time period was used to estimate the β coefficient of the length-weight relationship. The significance of the interaction term $\log(L) * TimePeriod$ was used to determine whether or not there was a significant increase or decrease in the β coefficient between the Wigley and recent time periods.

Length-weight coefficients of the log-log transformed relationship were calculated for all species in the trawl survey dataset with at least five observations in each time period. For several species, individuals with weights above a certain threshold were uncommon and their

recorded weight values appeared to be questionable. These observations were excluded from this analysis, and they included American plaice with recorded weights above 4 kg, Atlantic herring with recorded weights above 2 kg, bluntnose stingray with recorded weights above 100 kg and bluntnose stingray that were smaller than 15 cm long but had a recorded weight over 10 kg, little skate with recorded weights above 4 kg, and longfin squid and northern shortfin squid with recorded weights above 1 kg. One northern kingfish whose recorded weight was above 1 kg with a length under 20 cm was also excluded from the analysis.

1.3: Spatial analysis of length-weight relationships

Atlantic cod, American plaice, Atlantic herring, and spiny dogfish were selected for a more in-depth, spatial analysis of changes in the β coefficient of the length-weight relationship over time. These fish were chosen as representatives of different life history strategies, with Atlantic herring representing an opportunistic species, spiny dogfish as an equilibrium species, and Atlantic cod and American plaice as periodic species. Two species were included as representatives of the periodic group because of the heavy overfishing of Atlantic cod during the time period of data collection, which likely impacted the size of and number of individuals in the dataset. Including American plaice in addition to Atlantic cod in the analysis of periodic species allowed us to examine changes in the length-weight relationship for two species with similar life history strategies, but differing degrees of fishery-related impacts on their populations.

A spatial interaction was explored by including ecological production units (EPUs) in the model. There are four EPUs spanning the Northeast U.S. Shelf: the Mid-Atlantic Bight, Georges Bank, Gulf of Maine, and Scotian Shelf (Figure 1). For these four species, the three-way interaction between EPU, time period, and $\log(L)$ in predicting $\log(W)$ was analyzed, and spatial differences in the β coefficient were used to construct a model.

For this more in-depth analysis, a different selection of time periods was chosen to incorporate all 31 years of trawl surveys during which individual length and weight measurements were recorded. For these species, the data were broken up into three time periods of approximately ten years each: “early” (1992-2002), “middle” (2003-2013), and “late” (2014-2023). These periods were only used for the spatial analysis of these four fish species.

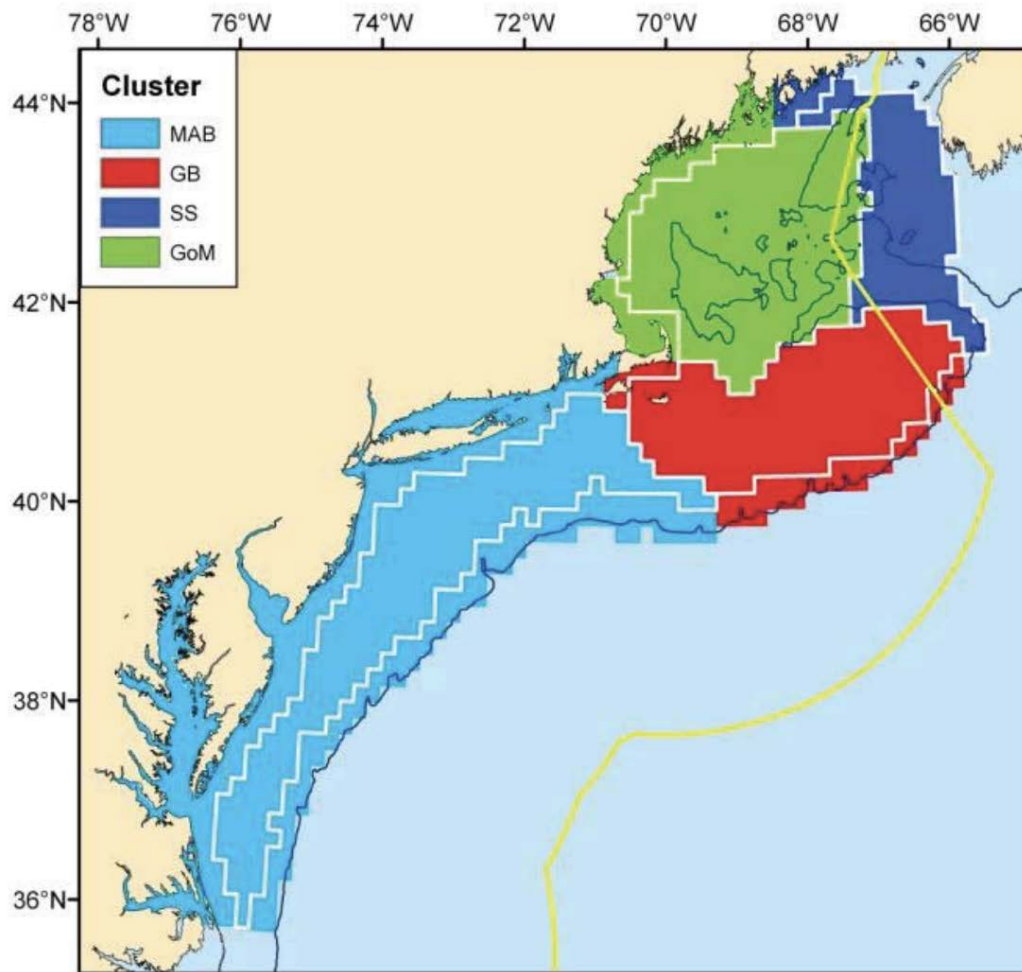


Figure 1: Map of the Northeast U. S. Shelf EPU's (Gamble et al. 2016). The Mid-Atlantic Bight (MAB) is pictured in light blue, the Scotian Shelf (SS) is in dark blue, Georges Bank (GB) is in red, and the Gulf of Maine (GoM) is in green.

As in the non-spatial analysis, Atlantic herring recorded with individual weights over 2 kg and American plaice with individual weights over 4 kg were excluded from the analysis. As there were only two American plaice caught in the Mid-Atlantic Bight EPU, these observations were also excluded, and this EPU was removed from the American plaice analysis. All fish whose individual weight was recorded as < 0.001 kg were also excluded from the analysis.

1.4: Analyses of the proportion of large fish

For the four species selected for spatial analyses (Atlantic cod, American plaice, spiny dogfish, and Atlantic herring), a further analysis was conducted to determine if there was a decrease in the number of individual fish in the 90th percentile by length over time. Data from the NEFSC trawl survey dataset on the number of fish at length caught per tow between 1970 and 2023 was used to determine the 90th percentile threshold for each species. The individuals in the 90th percentile by length in the whole dataset were then separated by the decade in which they were caught: the 1970s, 1980s, 1990s, 2000s, and 2010s and 2020s combined. The number of 90th percentile individuals caught in each decade was then divided by the total number of individuals of the species caught in each decade to account for differences in total catch across time. Thus the final values give information about the proportion of individuals in each decade that belong to the 90th percentile by length in the whole dataset.

1.5: Population modeling

A theoretical population model for a general fish species was created to analyze the sensitivity of spawning stock abundance to various parameters. The model includes four age classes: age-1, age-2, age-3, and age-4+. Age classes 3 and 4+ are reproductive in the model. Four theoretical functions underlie the population model. These functions are based on general biological understandings of how different parameters influence each other. There are functions to model density-dependent survival (Figure 2), condition-dependent fecundity (Figure 3), recruitment (Figure 4), and the effect of condition on survival (Figure 5). The fixed model parameters used for each function are included in Table 1. The model and its functions are designed to simulate a general fish species that represents an intermediate strategy between opportunistic and periodic life histories.

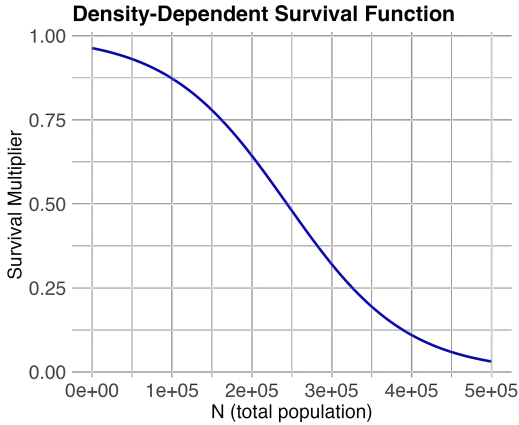


Figure 2: The logistic density-dependent survival function $Survival\ Rate = \frac{1}{e^{(c*N)+b}}$, where c is the coefficient controlling the sensitivity of survival, b ensures a higher survival rate at a low population size, and N is the total female population at the given time-step.

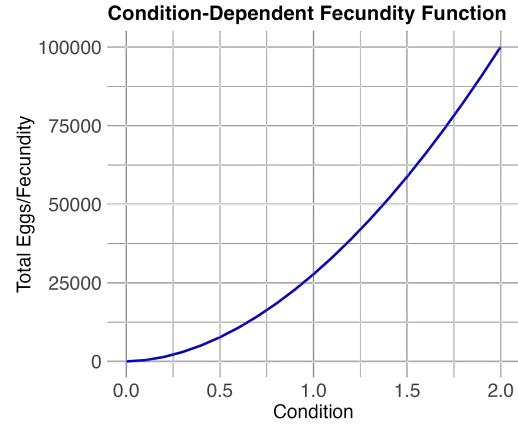


Figure 3: A non-linear condition function determines how many eggs a female can produce: $E = \alpha_1 * C^{\beta_1}$, where C is the condition of the fish (a condition of 1 means a fish weighs exactly what one would expect for a fish of that length), E is the total number of eggs the fish produces, and α_1 and β_1 are the parameters of the equation.

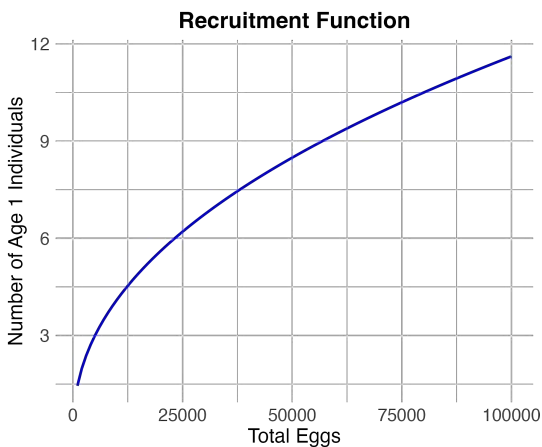


Figure 4: A non-linear recruitment function determines how many eggs survive to age 1: $N_1 = \alpha_2 * E^{\beta_2}$, where N_1 is the number of age-1 individuals in the population, E is the total number of eggs produced by a mature female, and α_2 and β_2 are the parameters of the equation. It is based on the Beverton-Holt recruitment function, but models recruitment for each individual instead of the entire population.

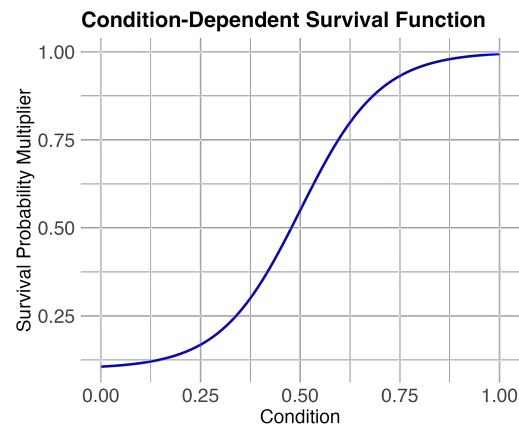


Figure 5: The logistic condition-dependent survival function is used to model the effect of condition on survival in sensitivity analyses: $Survival\ Rate = \frac{k}{1+e^{-r*(C-x_0)}} + off$. In this equation, k is the asymptotic survival rate, r is the steepness of the logistic curve, x_0 is the midpoint of the logistic curve, and off is a baseline survival rate.

Table 1: The fixed parameter values of the four functions implemented in the model. These values ensure that the population being modeled can be described as an intermediate between an opportunistic and periodic species.

Function	Parameter Values
Density-Dependent Survival	$c = 0.000013399$ $b = -3.27$
Condition and Total Eggs	$\alpha_1 = 27741.45$ $\beta_1 = 1.85$
Recruitment and Age-1 Individuals	$\alpha_2 = 0.064$ $\beta_2 = 0.45$
Condition-Dependent Survival	$k = 0.9$ $r = 10$ $x_0 = 0.5$ offset = 0.1

The simulation was run for 100 years and the total spawning stock abundance (sum of age-3 and age-4+ individuals) was calculated and stored at the final timestep. A sensitivity analysis was conducted on the parameters of fecundity (varying the total number of eggs produced by each female, not dependent on condition), recruitment, condition-dependent fecundity, condition-dependent survival, and a condition-dependent fecundity and condition-dependent survival two-way analysis (where condition affects both egg production and survival). Each parameter was varied between 0.1 and 1 in increments of 0.1. We calculated the number of timesteps required to reach the maximum population growth rate (the inflection point) and examined how this value changed with parameter adjustments.

Results

2.1: Changes in length-weight parameters

There were 62 fish species with at least 5 observations in both the Wigley time period (1992-1999) and the recent time period (2016-2023). For these 62 species, the model predicting $\log(W)$ from the interaction between $\log(L)$ and time period was used to estimate the β coefficient of the length-weight relationship. Of these 62 species, 14 showed a significant decrease in the β coefficient from the Wigley time period to the recent time period, meaning they were thinner at a given length in recent years. Another 15 species showed a significant increase, meaning they were heavier at length in recent years. For 33 species, no significant change was detected (Figure 6).

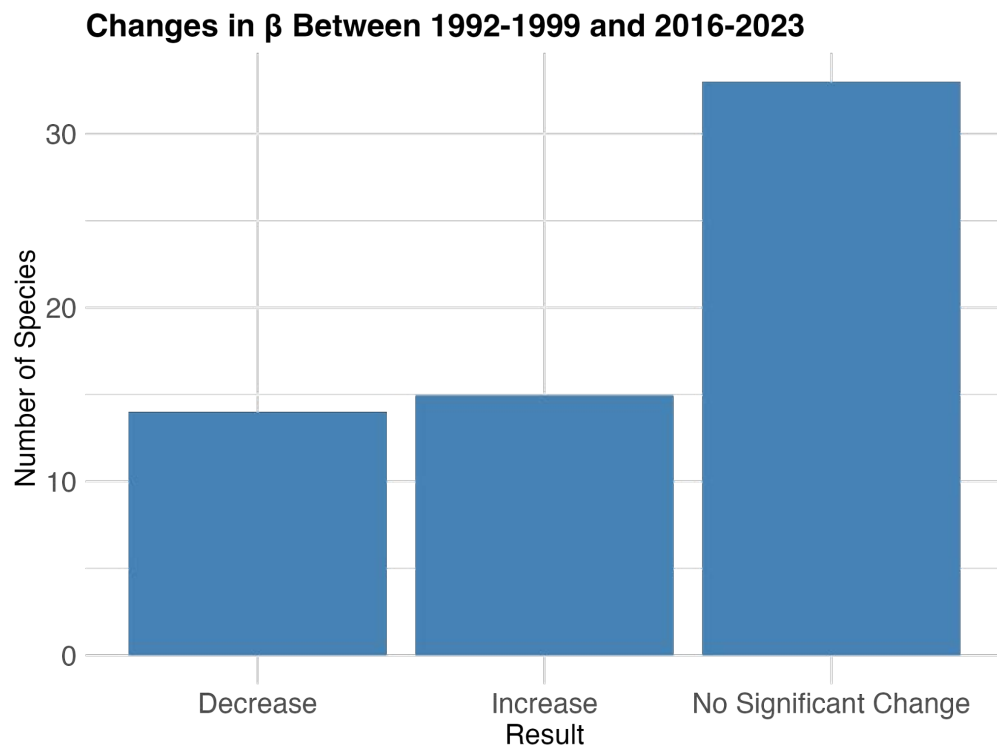


Figure 6: Number of species with a significant decrease, significant increase, or no significant change in the β coefficient of the length-weight relationship $W = \alpha * L^\beta$ between 1992-1999 and 2016-2023.

2.2: Spatial differences in length-weight relationships for selected species

Analyses focused on Atlantic cod, American plaice, Atlantic herring and spiny dogfish evaluated how $\log(\text{weight})$ was influenced by the interaction between $\log(\text{length})$ and time period plus the interaction between $\log(\text{length})$ and EPU.

2.2.1: Atlantic Cod

There were 27,062 Atlantic cod in the dataset for which weight, length, and EPU data were available. In Georges Bank, there was a significant decrease in the β coefficient between the early and middle periods (decrease of 0.0167: $p = 0.0315$) and a significant increase between the middle and late periods (increase of 0.0332: $p < 0.0001$) (Figure 7a). The β coefficient increased between the early and late period, but it was not statistically significant (increase of 0.0164: $p = 0.093$). In the Gulf of Maine, there was a decrease of 0.0138 in the β coefficient between the early and late periods, which was not statistically significant ($p = 0.0845$). There was no significant difference in β across any two time periods in the Mid-Atlantic Bight or the Scotian Shelf.

2.2.2: American Plaice

A total of 38,355 American plaice were sampled between 1992 and 2023 that had length, weight, and EPU data available. On Georges Bank, there was a very significant increase in the β coefficient between the early and middle periods (increase of 0.0658: $p = 0.0003$), followed by an equally significant decrease between the middle and late periods (decrease of 0.0663: $p = 0.0003$) (Figure 7b). The net change from the early to late period was thus negligible (decrease of 0.00058; $p = 0.9995$). On the Scotian Shelf, there was also no significant change in the β coefficient between the early and late periods (increase of 0.00397: $p = 0.9725$). In this EPU, there was a significant decrease from the early to middle periods (decrease of 0.0433: $p = 0.0145$) and a nearly equivalent increase from the middle to late period (increase of 0.0473: $p = 0.0131$). The changes thus offset each other in this EPU as well. In the Gulf of Maine, there was no significant change from the early to middle period (increase of 0.006: $p = 0.4792$), but a very significant decrease from the early to late period (decrease of 0.0298: $p < 0.0001$) and middle to late period (decrease of 0.0359: $p < 0.0001$).

2.2.3: Atlantic Herring

Length, weight, and EPU data were available for 49,230 Atlantic herring. Between the early and late periods, there was a significant decrease in the β coefficient in Georges Bank (decrease of 0.0674: $p = 0.0310$) and the Gulf of Maine (decrease of 0.101: $p < 0.0001$), a significant increase in the Mid-Atlantic Bight (increase of 0.114: $p < 0.0001$), and no significant change in the Scotian Shelf (decrease of 0.0145: $p = 0.7941$) (Figure 7c).

2.2.4: Spiny Dogfish

There were 41,381 spiny dogfish for which length, weight, and EPU data were available.

A very significant decrease in the β coefficient between the early and late periods was observed for Georges Bank (decrease of 0.126: $p < 0.0001$), the Mid-Atlantic Bight (decrease of 0.0653: $p < 0.0001$), and the Scotian Shelf (decrease of 0.125: $p = 0.0003$) (Figure 7d). In the Gulf of Maine, however, there was very little change in the β coefficient between the early and late period (decrease of 0.0016; $p = 0.996$).

Figure 7a

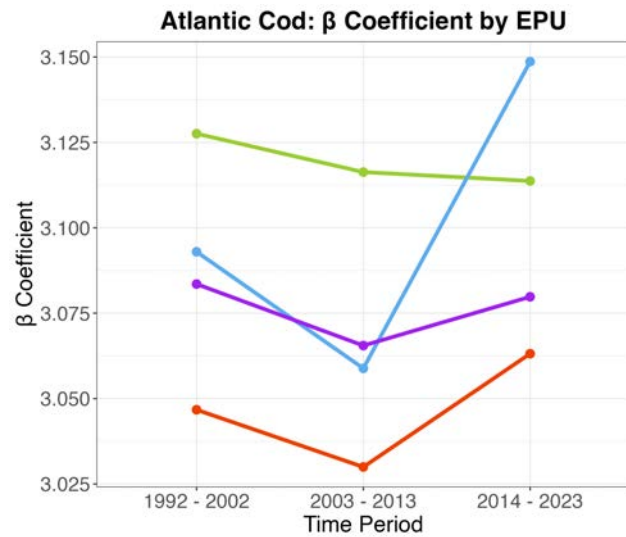


Figure 7b

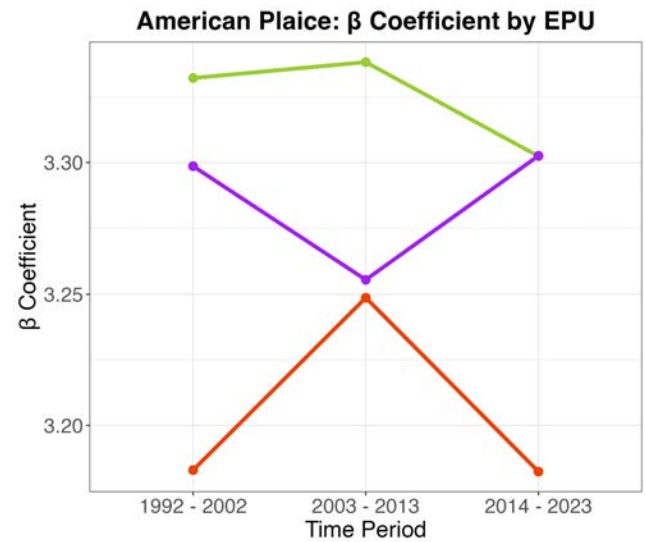


Figure 7c

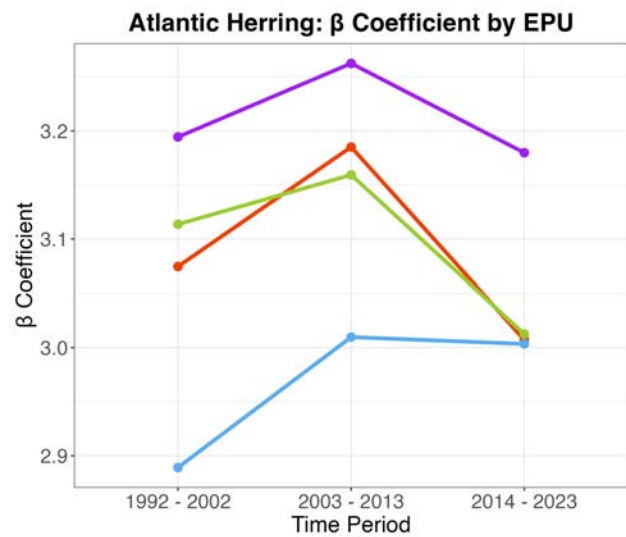
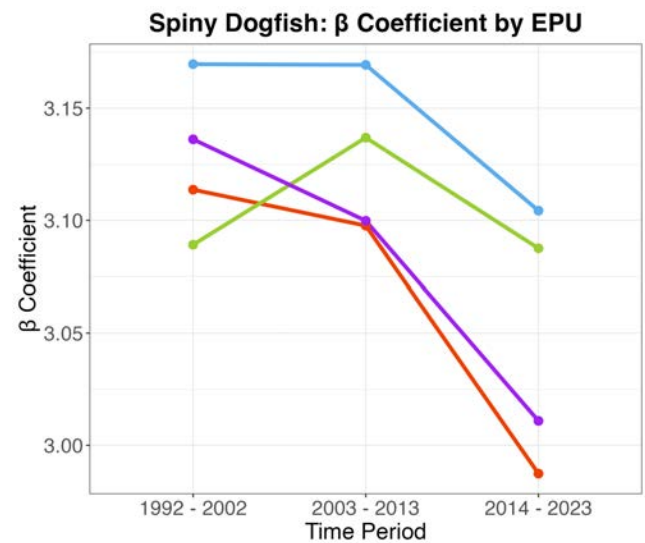


Figure 7d



EPU GB GOM MAB SS

Figure 7(a-d): Spatial changes by EPU in the β coefficient of the length-weight relationship over time for Atlantic cod (a), American plaice (b), Atlantic herring (c), and spiny dogfish (d).

2.3: Changes in the number of large fish

For all species analyzed (Atlantic cod, American plaice, Atlantic herring, and spiny dogfish), there was a large decrease in the number of individual fish at or above the 90th percentile of length in each decade as a proportion of the total number of fish caught in that decade. For Atlantic cod, 12.1% of all individuals caught in the 1970s belonged to the 90th percentile of length, compared to 11.4% in the 1980s, 9% in the 1990s, 7.02% in the 2000s, and only 2.88% in the 2010s and early 2020s (Figure 8a). A similar pattern can be seen with American plaice: 14.92% of American plaice caught in the 1970s were in the 90th percentile by length, while only 3.73% of American plaice caught in the 2010s and 2020s belonged to this subset (Figure 8b).

Nearly 17% of Atlantic herring caught in the 1970s were in the 90th percentile of herring by length, and 18.5% of all individuals caught in the 1980s belonged to this group of large fish. A decrease in the portion of large herring is seen in all subsequent decades: 6.5% in the 1990s, 4.49% in the 2000s, and 1.84% in the 2010s and 2020s (Figure 8c).

For spiny dogfish, a decrease in the percent of individuals in the 90th percentile by length can also be seen over time: this value stands at 17.8% in the 1970s, 15.1% in the 1980s, 10.2% in the 1990s, 9.19% in the 2000s, and decreases to only 5.12% in the 2010s and early 2020s (Figure 8d).

Figure 8a

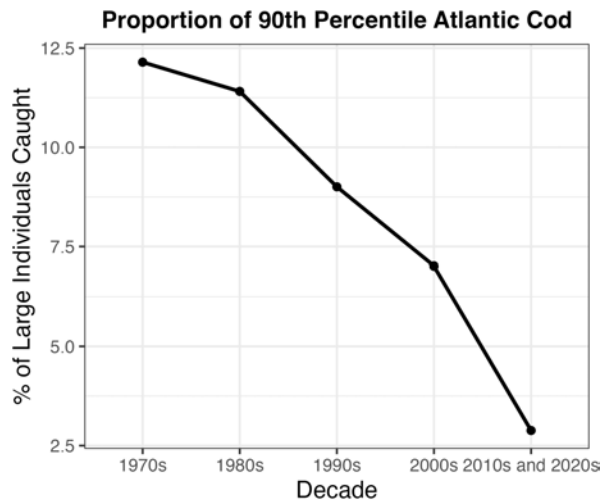


Figure 8b

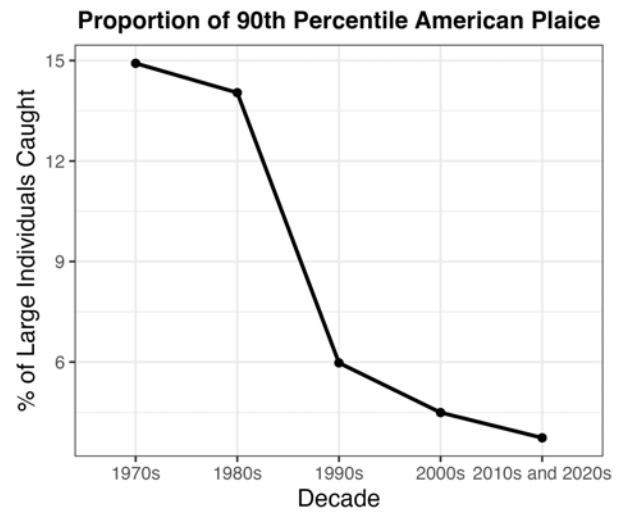


Figure 8c

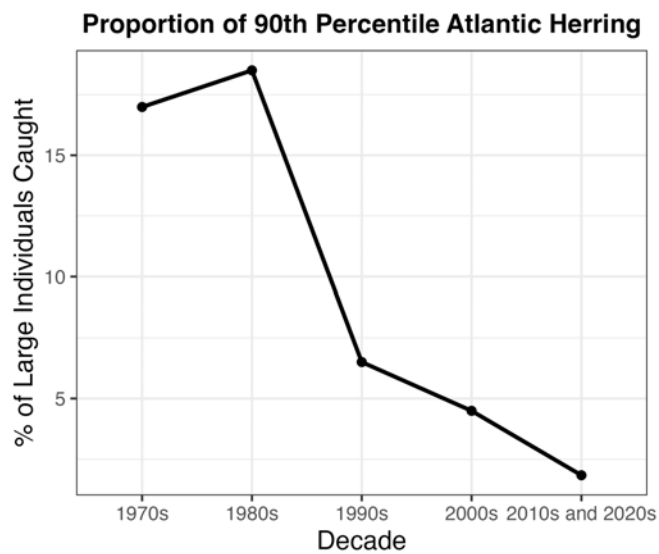


Figure 8d

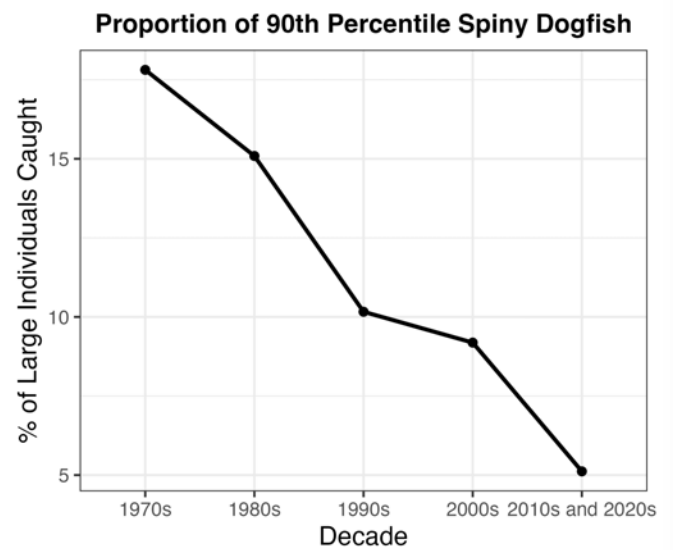


Figure 8(a-d): Percent of catch in each decade that represented 90th-percentile by length individuals of Atlantic cod (a), American plaice (b), Atlantic herring (c), and spiny dogfish (d).

2.4: Population model sensitivity analysis

The results of the initial sensitivity analyses show that mostly all simulations eventually produce the maximum spawning population abundance (~40,000). This result can be attributed to the population density function constraining the spawning population at maximum carrying capacity. There were exceptions where parameters were set at the highest values, and the momentum of population growth unintentionally exceeded the density function and grew exponentially. An example of this is shown in Figure 9 with the condition parameter. These scenarios should be considered unintentional model artifacts and not be included in the sensitivity analyses. Ideally, the density function would be strengthened to control for runaway growth and the sensitivity analyses be rerun. To gain better insights into the sensitivity of different population dynamics parameters, we calculated the timestep of maximum population growth instead of the maximum and minimum spawning stock abundances. This metric allowed us to compare the growth rates of the population as we varied each parameter.

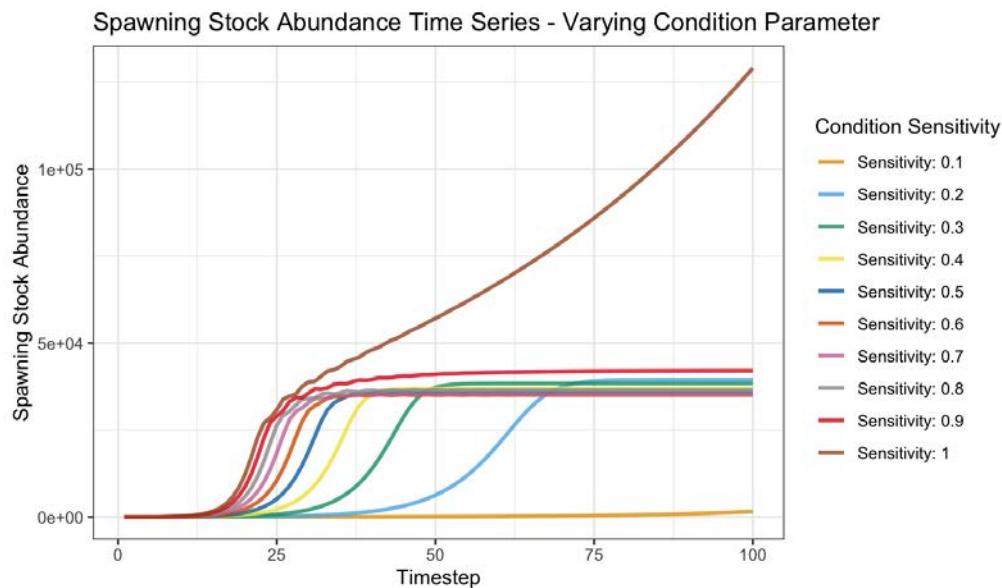


Figure 9: Time series plot displaying the projected spawning stock abundance as the sensitivity of the condition-dependent fecundity parameter varies between 0.1 and 1.

The timestep of the inflection point by the sensitivity adjustment to each parameter is shown in Figure 10. At a sensitivity level of 100%, all models behaved identically, requiring 23 timesteps to reach their maximum population growth rate. When parameter values were reduced, the rate of population growth declined, but the degree of decline varied across parameters. Fecundity (total eggs) was the least sensitive parameter: the model still reached its maximum growth rate even when fecundity was reduced to 10% of its original value. The condition-

dependent fecundity parameter was the second least sensitive, showing a slower decline compared to other parameters. The population growth rate was most sensitive to variability in the recruitment parameter, with time to the maximum growth rate increasingly being extended as recruitment was reduced to lower percentages of its original value.

Both models in which survival depended on condition exhibited much higher sensitivity to parameter reductions. When the survival-related parameters were reduced to less than 50% of their original values, the population failed to reach its maximum growth rate (as measured by the inflection point) within the first 100 timesteps. This indicates that calculating the inflection point of these runs in the same way as for the other parameters does not provide a reliable measure of the effects of condition-dependent survival, and therefore cannot be directly compared to the condition-dependent fecundity, total eggs, and recruitment parameters shown in Figure 10. Between these two survival-based models, the condition two-way model (with both fecundity and survival dependent on condition) was slightly more sensitive than the survival-only model, although both followed similar overall trends.

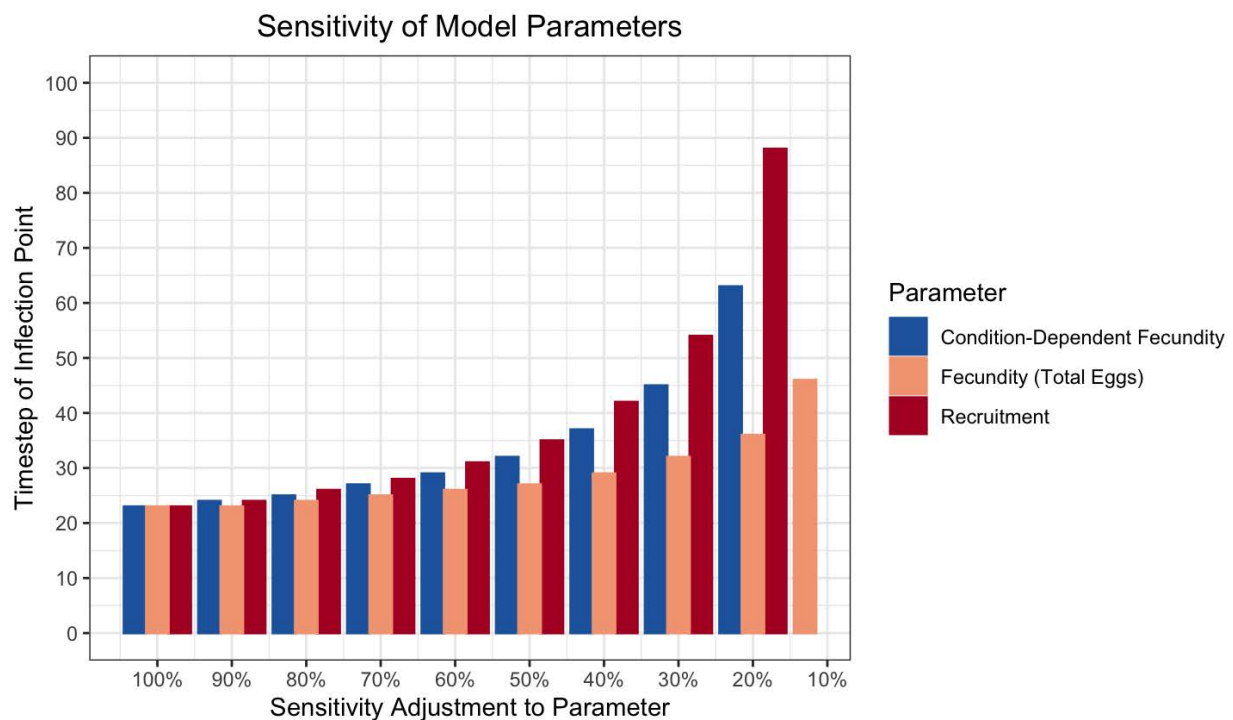


Figure 10: Bar plot displaying a sensitivity analysis of the model parameters in terms of the timestep to reach the maximum population growth rate (inflection point) as parameter sensitivity varies between 100% and 10%.

Discussion

Results from this study found that many fish species on the Northeast U.S. Shelf have experienced changes in condition between study periods spanning 1992-1999 and 2016-2023. For 14 out of 62 (22.58%) fish species, significant decreases in the β coefficient were detected, indicating that these fish were lower in weight relative to their length during the later period than in the earlier period. There were 15 (24.19%) fish species included in this analysis that saw an increase in the β coefficient over time, and the remaining 33 species showed no significant change. It thus appears that more fish saw an increase in condition between the Wigley time period and the recent time period for many fish in the dataset, which was inconsistent with our hypothesis. Determining the distinguishing factors for species that experienced a decrease in body condition over time versus those that experienced an increase is important to understand how warming waters and changing environmental conditions may impact species differently. Moreover, the direction and magnitude of these changes should be considered when modeling future projections of these species, as changes in fish condition may continue to occur as physical and ecological conditions of the region continue to change. Over half of the fish included in this analysis showed no significant change in the β coefficient. However, this apparent stability may mask underlying variability among species across space, seasons, or life stages that our analysis was unable to capture.

Of the four species selected for a deeper spatial analysis, each species showed spatial changes in both the direction and magnitude of changes the β coefficient. In the Gulf of Maine, Atlantic cod, American plaice, and Atlantic herring all experienced significant decreases in the β coefficient between the early and late periods, yet the changes in β were different for these species in the other EPU. These species were most prevalent in the Gulf of Maine EPU and thus more data existed for this region, which could have led to more accurate results. For spiny dogfish, however, no change in β was detected from the early to late period in the Gulf of Maine, but a substantial decrease was observed in every other EPU. The exact reasons for the differing results are unclear, but it indicates that spiny dogfish condition is decreasing significantly in waters that are farther south in Georges Bank and the Mid-Atlantic Bight. While the Gulf of Maine is warming at a faster rate than most of the world's waters (Pershing et al. 2015, Mills et al. 2024), it still remains a cooler environment for individuals compared to waters at lower latitudes. Thus it is possible that some of the spiny dogfish population moved to the Gulf of Maine to preserve their internal temperature and thus maintain a constant condition. Alternatively, it may be that higher population levels of spiny dogfish in the Georges Bank and Mid-Atlantic Bight have created resource limitations that have impacted the condition of spiny dogfish in these areas.

Observing these changes from a spatial perspective is important to understand how fish in different regions are adapting to changing environmental conditions. Spiny dogfish and American plaice were among the 17 species in the non-spatial analysis that showed increases in the β coefficient between 1992-1999 and 2016-2023, but their length-weight relationships are much more complicated after the spatial interaction is considered. For example, spiny dogfish condition actually decreased significantly in three of the four EPU's analyzed. Conducting a spatial analysis for more species may yield more informative results than a combined-EPU analysis, and region-specific data could inform more localized sustainability efforts.

The changes observed in this study appear to vary more by species than by functional group. While both Atlantic cod and American plaice can be classified as having periodic life history strategies, changes in β differ for each species, particularly when evaluated at the EPU scale. As many species caught in this dataset hold an intermediate role among the functional groups discussed by Winemiller and Rose (1992), a deeper analysis of these species based on their framework may not be conclusive as to which types of fish species have been most affected by declines in condition. Analyzing these changes based on a different grouping of species may yield more informative results: for example, grouping species based on their body shape (such as fusiform, flat, or elongated body types) or on their tendency to occupy benthic or pelagic positions in the water column are two other groupings to consider. Focusing on the common traits between species that have seen significant declines in condition could possibly provide greater insight into how certain characteristics affect growth-related adaptability in the face of environmental triggers, including warming waters. A more in-depth analysis on which species (or groups of species) are experiencing the largest declines in β over time could help us understand where sustainability efforts should be focused and how the population dynamics of affected species will change over time as condition, and thus fecundity, decreases.

It is well known that sea surface temperatures in the study region have increased over this time period (Mills et al. 2024), and this analysis revealed that the proportion of large fish caught in each decade has declined as well. This observation is consistent with the temperature size rule, as it is possible that temperature changes are driving this decline. The substantial decline in prevalence of large individuals could have major effects on population dynamics, as these large fish contribute disproportionately to reproductive output (Barneche 2018). For some species – especially Atlantic cod, as the heavy overfishing of the species led to a significant decrease in the size of the stock and major reduction of the fishery – fishing pressure may have contributed to this decline (Pershing et al. 2015). Fishing pressure differs for the four species analyzed in this study, however; yet for each population, the lowest percentage of large fish caught was in the most recent time period. Therefore even if these changes can partially be attributed to

fisheries, other factors must be at play as well. Regardless of the reasons behind this decline, the consequences of losing these 90th-percentile fish by length could be contributing to population declines and may further exacerbate them if sustainability efforts are not implemented.

Estimates from the population simulation model were very sensitive to fish condition. While recruitment is widely recognized as a key source of uncertainty in population dynamics models (Myers and Barrowman 1996, Vert-pre et al. 2013), our sensitivity analyses indicated that population estimates were only slightly less sensitive to condition as they were to recruitment. As this model is designed to simulate population dynamics for a species holding an intermediate position between an opportunistic and periodic fish, these results cannot be generalized for all species included in this analysis. Deeper work into simulating population impacts of changing condition for periodic, opportunistic, and equilibrium groups separately—or for individual species to reflect nuances within functional groups—would likely be more informative and more useful in applied fisheries science and management processes. Regardless, this result shows high sensitivity of population outcomes to condition, which points to the imperative of detecting changes in condition and incorporating these changes in population modeling efforts.

As significant changes in the β coefficients of the length-weight relationship were observed for the majority of species observed in this study, updating these parameters for estimation purposes for landings and stock assessments is necessary to ensure accuracy of results. Population dynamics may change drastically for species that experience changes in condition, which will be necessary to consider in modeling and projections for the future. Rising sea temperatures may continue to affect these species, and therefore monitoring changes in the length-weight relationship into the future is necessary to better understand the impacts of ocean warming on the condition of aquatic ectotherms.

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Supplementary Results:

Table S1: Results on the change in β from the Wigley period (1992-1999) to the Recent (2016-2023) period for all 62 species included in this analysis. s_{β} is the standard error of the slope estimate. Either a significant increase, significant decrease, or no significant change was observed.

	β in Wigley Period	s_{β} (Wigley)	β in Recent Period	s_{β} (Recent)	P-value	Result
Acadian Redfish	3.176	0.00352	3.203	0.00544	<0.001	Increase
Alewife	2.868	1.42273	3.672	1.4322	0.58	No Significant Change
American Plaice	3.271	0.00387	3.31	0.00575	<0.001	Increase
American Shad	3.153	0.02172	3.225	0.04042	0.076	No Significant Change
Atlantic Angel Shark	2.956	0.01119	3.159	0.03609	<0.001	Increase
Atlantic Cod	3.079	0.0039	3.08	0.00515	0.82	No Significant Change
Atlantic Croaker	3.088	0.01843	3.091	0.02336	0.894	No Significant Change
Atlantic Halibut	3.184	0.01779	3.254	0.0446	0.118	No Significant Change
Atlantic Herring	3.055	0.01162	3.022	0.01328	0.014	Decrease
Atlantic Mackerel	3.319	0.00883	3.262	0.01214	<0.001	Decrease
Atlantic Sharpnose Shark	3.079	0.05858	3.01	0.10586	0.519	No Significant Change
Atlantic Sturgeon	3.245	0.15517	3.455	0.32231	0.521	No Significant Change
Atlantic Torpedo	2.996	0.02932	3.78	0.48288	0.109	No Significant Change
Atlantic Wolffish	3.044	0.04343	2.798	0.06916	<0.001	Decrease
Barndoor Skate	3.273	0.00506	3.342	0.05551	0.209	No Significant Change
Black Sea Bass	2.929	0.00462	3.021	0.00841	<0.001	Increase
Blackbelly Rosefish	3.051	0.01438	3.051	0.03772	0.995	No Significant Change

Blueback Herring	3.404	0.02548	3.246	0.05325	0.003	Decrease
Bluefish	3.048	0.01089	3.044	0.012	0.737	No Significant Change
Bluntnose Stingray	3.269	0.0194	3.193	0.03336	0.023	Decrease
Buckler Dory	2.907	0.01517	3.039	0.06849	0.055	No Significant Change
Bullnose Ray	3.055	0.02582	3.293	0.06294	<0.001	Increase
Butterfish	3.234	0.00657	2.927	0.00906	<0.001	Decrease
Cleannose Skate	3.214	0.01263	3.481	0.09107	0.003	Increase
Cownose Ray	3.097	0.02226	3.257	0.06735	0.018	Increase
Cusk	3.15	0.02767	3.177	0.0322	0.411	No Significant Change
Fourspot Flounder	3.262	0.00852	3.148	0.01118	<0.001	Decrease
Goosefish	2.926	0.00329	2.909	0.00896	0.068	No Significant Change
Haddock	3.052	0.00248	3.077	0.00393	<0.001	Increase
Little Skate	3.121	0.00729	3.125	0.0089	0.604	No Significant Change
Longhorn Sculpin	3.09	0.0164	3.068	0.01788	0.212	No Significant Change
Northern Kingfish	3.125	0.03216	3.278	0.74041	0.836	No Significant Change
Northern Seabobin	3.228	0.01183	3.471	0.22139	0.272	No Significant Change
Ocean Pout	3.22	0.00927	3.311	0.01306	<0.001	Increase
Offshore Hake	3.093	0.00944	3.146	0.06987	0.449	No Significant Change
Pollock	3.045	0.00863	3.111	0.01017	<0.001	Increase
Red Hake	3.149	0.0032	3.047	0.00432	<0.001	Decrease
Rosette Skate	3.142	0.01387	2.989	0.09129	0.093	No Significant Change
Roughtail Stingray	2.903	0.04509	3.029	0.07657	0.103	No Significant Change
Sand Tiger	3.192	0.15933	3.293	0.28263	0.725	No Significant Change
Sandbar Shark	2.856	0.14032	3.171	0.17357	0.075	No Significant Change
Scup	3.121	0.00445	3.134	0.00935	0.177	No Significant Change

Sea Raven	3.116	0.01888	3.17	0.02269	0.018	Increase
Silver Hake	3.199	0.00286	3.096	0.00375	<0.001	Decrease
Smooth Butterfly Ray	2.893	0.05682	3.074	0.1111	0.132	No Significant Change
Smooth Dogfish	3.1	0.01444	2.993	0.01772	<0.001	Decrease
Smooth Skate	3.085	0.00827	3.134	0.03353	0.146	No Significant Change
Southern Stingray	2.967	0.17337	3.143	0.64287	0.785	No Significant Change
Spiny Butterfly Ray	3.132	0.02052	3.199	0.03821	0.082	No Significant Change
Spiny Dogfish	3.076	0.00577	3.14	0.00699	<0.001	Increase
Spot	3.287	0.03563	3.208	0.07913	0.323	No Significant Change
Spotted Hake	3.097	0.01018	3.107	0.01113	0.384	No Significant Change
Striped Bass	3.047	0.01898	3.048	0.02554	0.948	No Significant Change
Summer Flounder	3.237	0.00373	3.21	0.00712	<0.001	Decrease
Thorny Skate	3.133	0.0138	3.118	0.01657	0.383	No Significant Change
Weakfish	3.047	0.01351	2.964	0.01432	<0.001	Decrease
White Hake	3.176	0.00357	3.194	0.00552	<0.001	Increase
Windowpane	3.071	0.00514	2.936	0.00754	<0.001	Decrease
Winter Flounder	3.093	0.00382	3.081	0.00647	0.063	No Significant Change
Winter Skate	3.21	0.00663	3.299	0.00879	<0.001	Increase
Witch Flounder	3.307	0.00459	3.225	0.00712	<0.001	Decrease
Yellowtail Flounder	3.087	0.00483	3.119	0.00864	<0.001	Increase