

Collapse, recovery and collapse of an important fishery

Alexander C. Hansell¹, Melanie Barrett², Steven X. Cadrin³, Cole Carrano³,
Jessie Kittel³, Christopher M. Legault¹

¹Northeast Fisheries Science Center, Woods Hole, MA, USA

²Fisheries and Oceans Canada, St. Andrews, NB, Canada

³University of Massachusetts Dartmouth, School for Marine Science and Technology,
New Bedford MA, USA

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Abstract

Georges Bank is a shallow plateau off the coast of New England that has supported productive fisheries for centuries. One of these fisheries targeted yellowtail flounder (*Limanda ferruginea*), which at its peak caught over 21 000 mt a year. However, the stock has fluctuated, with periods of high abundance (1970s and 2000s) and low stock size (1990s and 2020s). A review published twenty years ago documented the collapse of the stock in the 1990s and subsequent recovery in the 2000s, hypothesizing the major reason for recovery was bilateral science and successfully coordinated management intervention. Unfortunately, by the time that review was published, the stock had started to decrease again and collapsed in the 2010s. We provide an updated historical review of the fishery and past stock assessments. We conduct new analyses of empirical indicators of spatial distribution and growth for Georges Bank yellowtail flounder and project the stock into the future using the most recent stock assessment. Results suggest that fishing was the likely cause of initial stock depletion while environmental changes, particularly bottom temperature, has limited recovery in recent years. Projections suggest that the population can increase in the future but its ability to increase is related to bottom temperature on Georges Bank. These results give insight into the dynamics an iconic New England fishery and stock, as well as, provide a unique opportunity to study the fluctuations of a stock through multiple periods of recovery and collapse.

Key words: Environment, Overfishing, Stock Assessment, Yellowtail flounder

Introduction

A fishery collapse occurs when a fish population declines so substantially that it can no longer sustain a fishery. Fishery collapses can negatively affect marine habitat, the economy and cause cultural disruption. Historically, the most common hypothesis for a collapse was overfishing, where excessive removals reduced the stock causing reproductive impairment (Roughgarden and Smith, 1996; Pauly *et al.*, 2005). Technological advances in the 20th century allowed commercial fisheries to harvest many marine resources at unsustainable rates. For example, the Northwest Atlantic cod fishery off of Newfoundland was one of the world's most productive fisheries. However, the introduction of large factory trawlers at the conclusion of World War II led to unsustainable removals and the collapse of the fishery in the 1990s (Hutchings and Myers, 1994). Similarly, New England's groundfish industry collapsed on Georges Bank with the introduction of factory trawlers in the 1960s and 1970s (Fogarty and Murawski, 1998).

Overfishing is often attributed as the primary cause of stock depletion, but changes in the environment can

also lead to reductions in fish productivity. For example, the collapse of the Pacific sardine fishery in the 1940s (Jacobson and MacCall, 1995) and the Peruvian anchoveta fishery in the 1970s (Pauly and Tsukayama, 1987) were hypothesized to be the result of a combination of fishing and changes in sea surface temperatures. The collapse of the Southern New England lobster fishery has been attributed to warming water temperatures linked to shell disease (Glenn and Pugh, 2006). Fisheries collapses have also been attributed to other factors including political interventions, inaccurate science, distant water fishing fleets, changes in natural predator abundance, and the environment (Mullon *et al.*, 2005).

Georges Bank is a shallow plateau (40 000 km²) located off the coast of New England, separated to the north and south by deep channels (Fig. 1). The Bank has been subject to many environmental fluctuations that are predicted to continue into the future (Fogarty and Murawski, 1998; Wainwright *et al.*, 1993; Mountain and Kane, 2010). This region is characterized by high productivity that has supported fisheries for centuries (Fogarty and Murawski, 1998). The yellowtail flounder fishery on Georges Bank

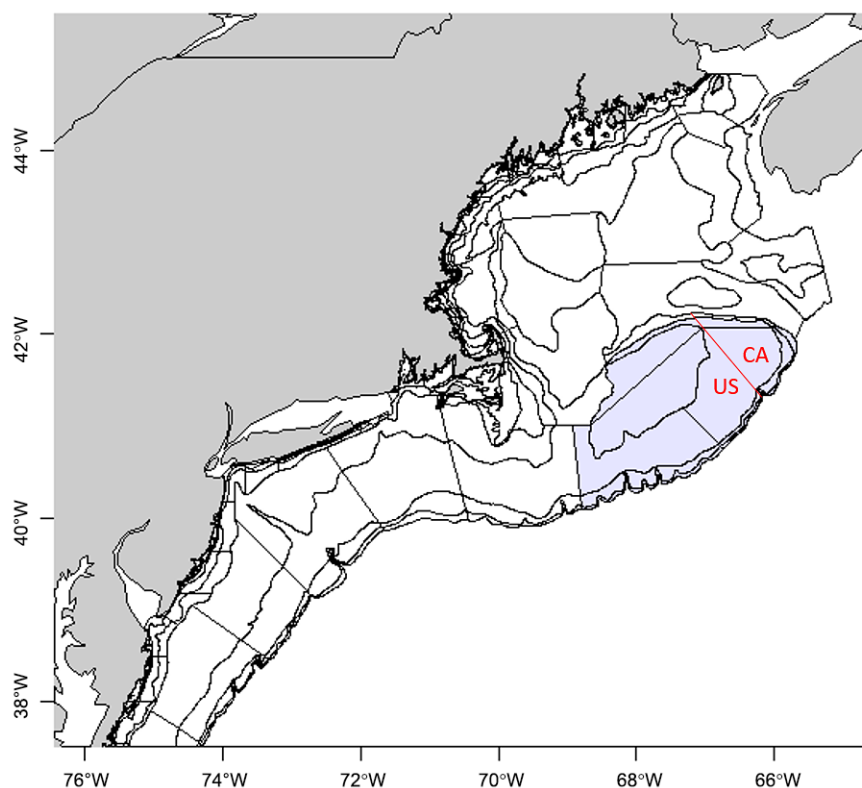


Fig. 1. Georges Bank, the Hague line (marked in red) separates the bank between US and Canadian territorial waters. The blue shaded area is Georges Bank and the bathymetric lines represent different survey strata used by the Northeast Fisheries Science Center bottom trawl survey.

started in the 1930s and was considered one of the principal groundfish stocks. Fisheries targeted primarily cod, haddock and yellowtail flounder on the Bank and the area was open to international fishing until 1977. However, by the 1990s overfishing had led to the collapse of the industry (Fogarty and Murawski, 1998; Stone *et al.*, 2004).

Stone *et al.* (2004) documented the collapse of the Georges Bank yellowtail flounder fishery and its subsequent recovery. Their work examined empirical indicators of distribution shifts, age-structure, and trends of exploitation and biomass, demonstrating that the stock was capable of rapid recovery in response to international collaboration and fisheries regulations. However, by the time the paper was published, the stock was already starting to decline again despite continued international collaboration (Stone and Legault, 2005; NEFSC, 2024). In more recent years, stock biomass has been at an all-time low despite these continued regulations and international collaborations. Therefore, reinvestigation of the potential drivers of the Georges Bank yellowtail flounder fishery collapses is needed to understand why bi-lateral science and management did not prevent the second collapse. Understanding drivers of the different collapses can be used to inform management for improved rebuilding plans.

We review available information as well as conduct updated analyses to assess the primary drivers of the initial fishery collapse, subsequent recovery and following collapse of the Georges Bank yellowtail flounder fishery. A historical review of the Georges Bank fishery and stock assessments are provided to understand potential anthropogenic drivers that could cause the different collapses. We also review the most recent stock assessment (NEFSC, 2024) that incorporates process error and environmental covariates, which allows for the direct comparison of fishery and environmental impacts on the population. We conduct new analyses of empirical trends of spatial distribution and growth to determine if these have changed over time. We also use the most recent stock assessment to estimate new projections to see how the stock might change in the future. Results provide valuable information on yellowtail flounder and provide information on the primary drivers of the two different collapses of the yellowtail flounder fishery.

The fishery

A New England fishery for yellowtail flounder developed in the 1930s, coincident with a decline in winter flounder abundance (Royce *et al.*, 1959; Lux, 1964). Yellowtail

were caught in otter trawls targeting other groundfish species and scallops. The fishery for yellowtail flounder was historically divided into Southern New England, Georges Bank, and Cape Cod (Lux, 1964). Fishing effort shifted from Southern New England to Georges Bank in the 1940s leading to landings increasing by over 700% by the end of the decade (Royce *et al.*, 1959; Fig. 2). By 1940, New Bedford, Massachusetts had become the principal port for landing flatfishes because of industry infrastructure and proximity to fishing grounds. From 1940–1961 over one-half of all US yellowtail were landed in New Bedford, Massachusetts (Lux, 1964). Landings decreased in the 1950s, possibly from a warming environment (Royce *et al.*, 1959; Lux, 1964; Lux and Nichy, 1969; Sissenwine, 1974).

In the 1960s and early 1970s, distant water fleets targeted Georges Bank groundfish and herring (Fig. 2). During this time fishery removals increased, reaching an all-time high of roughly 21 000 mt in the late 1960s and early 1970s (Fig. 2). Despite regulations developed by the International Commission for the Northwest Atlantic Fisheries (*e.g.*, minimum mesh sizes, minimum fish sizes, spawning closures, annual quotas) decreases in catch were being associated with too much fishing (Kulka, 2012; Brown and Hennemuth, 1971; Sissenwine, 1977).

The US Magnuson-Stevens Act established an exclusive economic zone, excluded distant-water fisheries, and formed regional fishery management councils in 1976. An initial management plan was adopted in 1977 that relied on total allowable catches (TACs), but there was limited enforcement of quotas. Fishing removals decreased somewhat in the early 1980s (Brown *et al.*, 1980; Clark *et al.*, 1981) although misreporting among the stock areas was considered a problem. Increases in mesh size in 1982 and 1983 also contributed to an increase in biomass (McBride and Clark, 1983), but effort was still considered to be too high (Overholtz and Murawski, 1985). In 1984, a maritime boundary was established splitting Georges Bank between the US and Canada. Canada did not have a directed fishery for yellowtail until 1993 (Stone *et al.*, 2004).

Multiple management changes occurred in the 1990s for US and Canada that included limitations on fishing effort (*i.e.*, limited days at sea), increased minimum mesh size regulations, and year-round area closures. A Canadian fishery developed to target yellowtail flounder on eastern Georges Bank in the 1990s, and the US fleet was temporarily allowed access to a closed area to target yellowtail flounder in 2004 (Stone and Legault, 2005). Access to this closed area is a primary reason why fishery

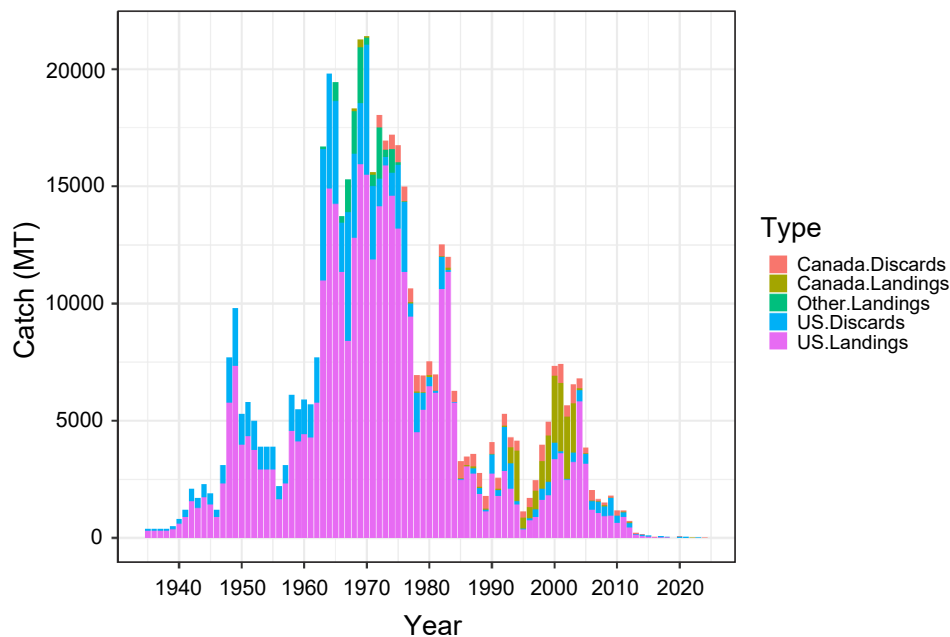


Fig. 2. Catch of yellowtail flounder by disposition on Georges Bank.

catches increased in the early 2000s. However, by 2010 fishery catch started to decline (Fig. 2). Since this decrease, yellowtail has had a limited market and is primarily caught as bycatch in the scallop fishery (NEFSC, 2024). The scallop fishery is the second most lucrative fishery in the region and high catches of yellowtail flounder can lead to accountability measures that closed scallop fisheries in some years (O’Keefe and DeCelles, 2013).

Population assessments

Early stock assessments of Georges Bank yellowtail flounder relied on catch curves, tagging experiments, and a detailed understanding of the fishing fleets operating at the time (Brown *et al.*, 1980). These assessments consistently estimated high fishing mortality rates, relative to natural mortality ($M = 0.2$), but suggested that fishing had a limited impact on the stock. Early analyses of population dynamics also suggested that temperature could play an important role in stock abundance (Royce *et al.*, 1959; Lux, 1964; Lux and Nichy, 1969). The first analytical stock assessment for Georges Bank yellowtail flounder found high fishing mortality and low stock abundance in the 1980s (NEFSC, 1989). Subsequent assessments found similar results (NEFSC, 1991; NEFSC, 1994), and concluded the stock had collapsed by the mid 1990s (NEFSC, 1994). Canadian catch was first incorporated in the assessment in 1996, but did not change the perception of the stock (Gavaris *et al.*, 1996). The effect of strong management measures (*e.g.*, reduced days-at-sea, increased minimum mesh size, year-round closed areas) were detected by the end of the 1990s by virtual population analysis and surplus production models that both estimated an increase in stock biomass (Cadrin *et al.*, 1999; Stone *et al.*, 2004).

The Transboundary Resources Assessment Committee (TRAC), a joint US-Canadian scientific body, conducted its first joint assessment of Georges Bank yellowtail flounder in 1998 using a virtual population analysis (Neilson and Cadrin, 1998). Retrospective patterns that revised previous stock estimates downward and increased fishing mortality estimates appeared in 2000 (NDWG, 2000) and continued in subsequent assessments (NEFSC, 2002; Stone and Legault, 2003; Legault and Stone, 2004). There were diagnostic problems with the stock assessment in the early 2000s and 2010s with these issues becoming severe in the 2010s. In 2014, the analytical assessment was rejected in favor of an empirical approach that relied on survey trends (O’Brien and Clark, 2014). Catch advice was initially derived from area-swept survey biomass and a target exploitation rate but was revised to a constant quota, conditional on survey biomass remaining within predefined bounds (O’Brien and Clark, 2014). In 2024, a peer review panel supported the recommendation to use a state-space model, the Woods Hole Assessment Model (WHAM, Stock and Miller, 2021), to assess the stock at the conclusion of a multiyear research track assessment (aka benchmark assessment, NEFSC, 2024).

Spatial distribution

A common theory in ecology is that population abundance is positively correlated with spatial range (MacCall, 1990; Holt *et al.*, 1997). As a population decreases, it can contract to preferred habitat (Shackell *et al.*, 2005). Spatial contractions can make it easier for fisheries to target a resource and can violate a common assumption that catch rates are proportional to abundance. Catch rates can stay high or stable in the concentrated areas while population abundance declines (Erisman *et al.*, 2011). Fish can also shift their distribution in response to changing ocean conditions (Nye *et al.*, 2009; Pinsky *et al.*, 2013). We conducted new analyses of the spatial distribution of yellowtail flounder using fisheries independent surveys to examine if spatial distribution changed.

Fisheries surveys are a common tool to explore spatial distributions of marine fishes because they have consistent spatio-temporal sampling. Three fisheries independent surveys cover the entire Georges Bank stock area: Fisheries and Oceans Canada winter survey (DFO, since 1987), and the Northeast Fisheries Science Center (NEFSC) spring and fall surveys (since 1968 and 1963, respectively). All three surveys are based on a stratified random design. The same stratified-mean indices of relative abundance that are derived for stock assessment were used to explore trends in relative abundance. Maps were created to explore visual changes in spatial use. A Gini index (Wuillez *et al.*, 2007) was used to measure the spatial distribution for the three different surveys. The Gini index provides a measure of spatial aggregation, with lower values indicate wider distribution and higher values indicate higher concentrations. A Gini index does not provide fine scale measurements of changes in center of gravity or effective area occupied. A loess smoother was fit to the Gini coefficients from each survey to inform long-term trends. The analyses conducted here use a terminal year of 2022, which is the last year in the most recent stock assessment.

High catch rates in the fall and spring NEFSC surveys occurred in the 1960s and early 1970s, catch rates were low in all three surveys in the 1980s and early 1990s, catch rates increased from the late 1990s to early 2010s, with high abundance in the southeast portion of Georges Bank. Two high values for the DFO survey in 2008 and 2009 resulted from large catches in single tows creating high uncertainty for these estimates (Figs. 3–4). Catch rates decreased again after 2010 (Figs. 3–4). The loess smoothers of the Gini coefficients shows an increasing trend for all three surveys, indicating the yellowtail flounder are becoming more concentrated in specific habitat on Georges Bank. The loess trend shows an increase in coefficient values for all three surveys until the early 2000s, with the highest Gini coefficients for the NEFSC spring and DFO survey occurring during that time period. However, since the early 2000s the Gini coefficients continue to increase for the NEFSC fall survey

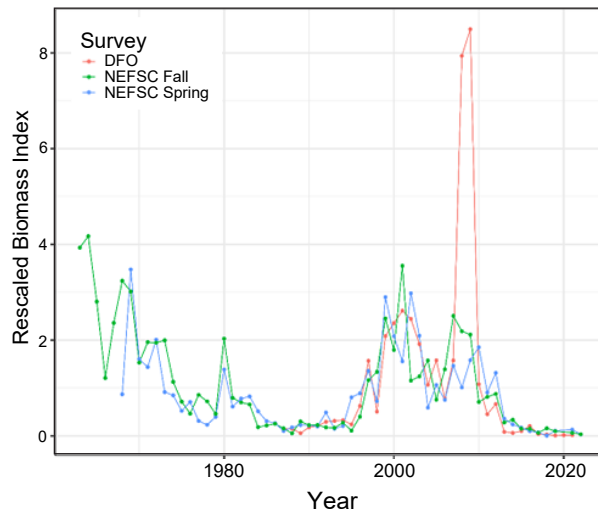


Fig. 3. Annual relative biomass estimates from the three surveys that cover Georges Bank. Results were scaled to the mean for comparison.

and decline for the other two surveys, suggesting seasonal differences in distribution (Fig. 5).

Size and growth

Size and growth information are important for understanding the population dynamics of a stock and can be used as empirical indicators to inform fisheries management. For example, a lack of smaller fish can indicate reduced recruitment. In contrast, fewer larger fish may indicate slower growth, or higher natural or fishing mortality (Miranda *et al.*, 2024). Empirical length and age data are available for the entire time series for both the NEFSC spring and fall surveys. However, individual weights were not collected on the NEFSC surveys until 1995. Empirical age data is available from the DFO survey since 2004. We produced new analyses of trends in size and growth. These analyses focus on ages one through six, because few fish older than age six were caught in the fisheries and surveys. The stock assessment aggregates these ages into an age-6+ group (NEFSC, 2024). Analyses focused on trends in mean length and mean weight to understand temporal trends in growth. These inputs are commonly used in stock assessment and provide indications about changes in growth.

Mean length at age trends from the NEFSC spring survey suggest older fish were smaller towards the end of the time series (Fig. 6). In the fall survey, mean size at age decreased for most ages in the 1990s followed by an increase. In both seasons, age classes had more overlapping mean size towards the end of the time series compared to the beginning (Figs. 6–7). The DFO time series shows a contraction in mean length with similarities between ages two and age-6+ (Fig. 6). Additionally, no

age-one fish were caught since 2019. Trends in mean weight at age show a decreasing trend in weight at age for older fish in the NEFSC spring and DFO surveys. At the end of the time series there is less variability in weight at age between ages from all three surveys (Fig. 7). The number of biological samples are lower in recent years due to reduced catch rates in all three surveys (Fig. 4).

Temporal trends in the environment, recruitment, biomass, and fishing mortality

We reviewed the most recent stock assessment for Georges Bank yellowtail flounder and used the results to explore temporal trends. The most recent stock assessment applied the Woods Hole Assessment Model (WHAM), which is an age-structured model that allows for the inclusion of environmental variables and process error on different population dynamic processes (Stock and Miller, 2021). The stock assessment time series starts in 1973 with a terminal year of 2022. The assessment performed well with no major diagnostic issues. The model includes time varying selectivity to account for management and targeting changes. The assessment model estimates random effects for abundance at age transitions to account for annual changes in survival. A Beverton-Holt stock recruit relationship was used to model recruitment with changes in the stock recruit parameters informed by a stock specific bottom water temperature time series. This relationship assumes that recruitment is impacted by both stock size and bottom temperature (Supplemental material; NEFSC, 2024).

Environmental trends were thoroughly reviewed during the research track stock assessment using a multi-faceted approach that involved a literature review, exploratory analyses, and exploration within the stock assessment (Kittel *et al.*, 2024; NEFSC, 2024). For Georges Bank yellowtail flounder, this approach hypothesized that water temperature was likely influencing natural mortality or recruitment (Kittel *et al.*, 2024; NEFSC, 2024). An annual time series for Georges Bank was derived from a data product that interpolates monthly bottom temperature at relatively high spatial resolution (Du Pontavice *et al.*, 2023). Stock assessment model diagnostics (*e.g.*, convergence, residuals, Mohn's rho predictive performance) supported using the bottom temperature covariate to estimate changes in the parameters of the Beverton-Holt stock recruit relationship (NEFSC, 2024). Conversely, model diagnostics did not support including a covariate to estimate time varying natural mortality (Supplemental material; NEFSC, 2024).

The stock assessment model fit to the bottom water temperature time series shows that the coldest water temperatures were in the 1970s and early 2000s (Fig. 8). During this same time, recruitment was estimated to be higher (Figs. 8–9). In contrast, bottom water temperature

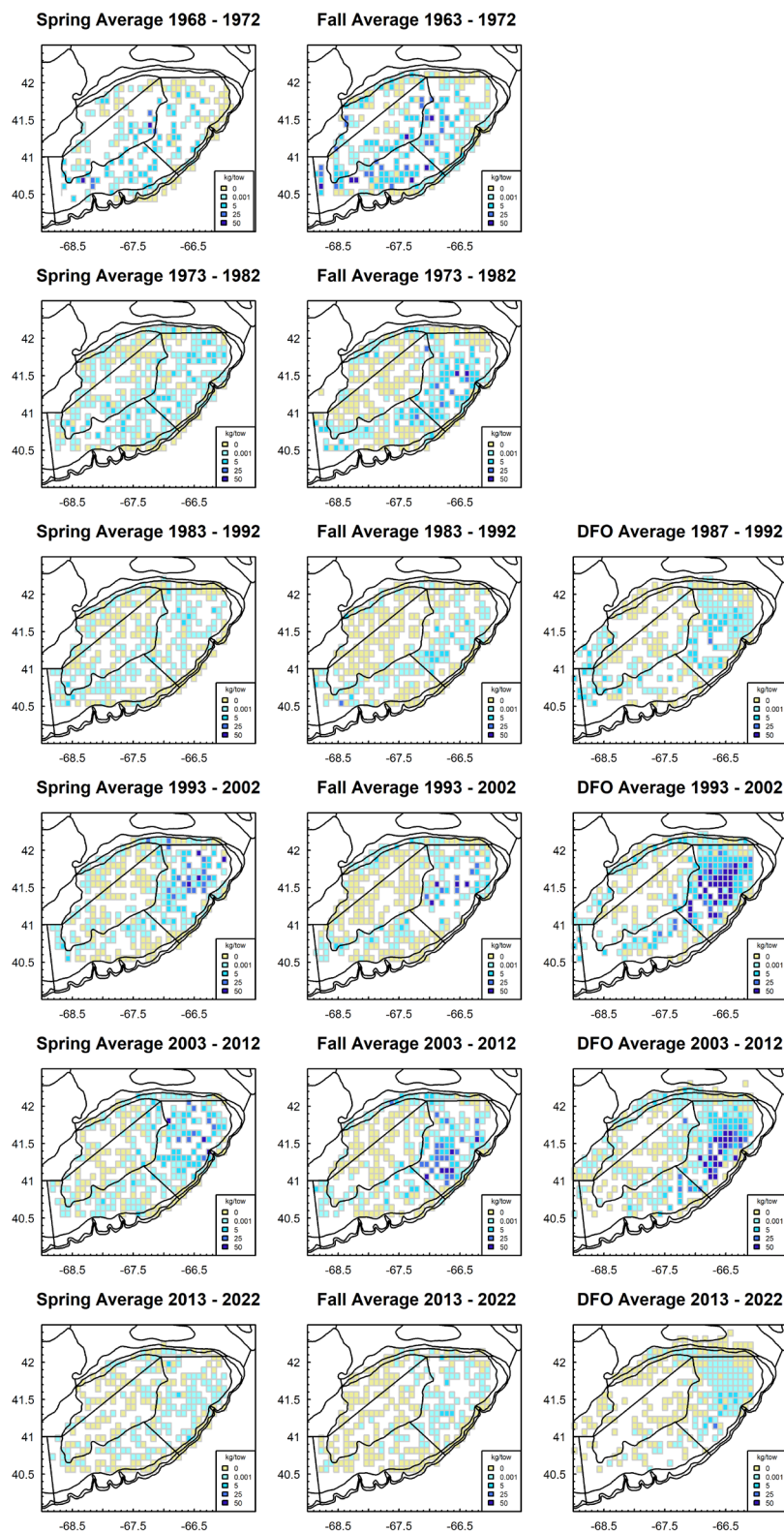


Fig. 4. The spatial distribution of survey catches on Georges Bank. Blue squares represent areas of high yellowtail flounder biomass per tow while yellow squares represent low biomass per tow.

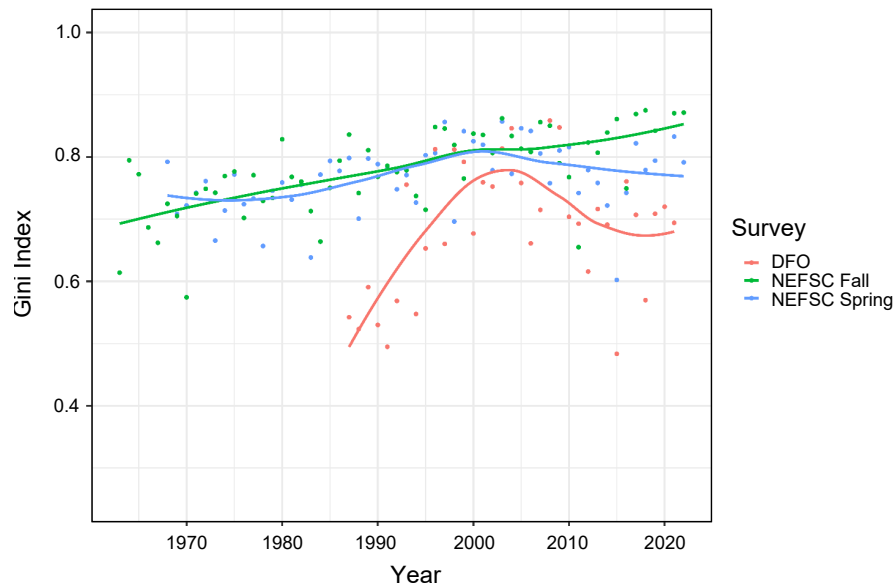


Fig. 5. Gini coefficient for Georges Bank yellowtail flounder surveys. The coloured lines are loess smoothers for the corresponding surveys.

started to warm around 2010 and has been warmest since 2015 (Fig. 8). During this time period, recruitment was estimated to be low (Figs. 8–9).

Annual maximum sustainable yield reference points (SSB_{msy} , F_{msy} , and R_{msy}) derived from equilibrium expectations for annual conditions and their relationship to temporal trends in spawning stock biomass, fishing mortality and recruitment show distinct periods of productivity and overexploitation. Spawning stock biomass is estimated to be high and above the reference point at the beginning of the time series followed by decreases in the 1980s and continued low values until the mid 1990s (Fig. 9). In the 1980s and 1990s spawning stock biomass was below the reference point, indicating that the stock was overfished (Fig. 9). Recruitment was high in the 1970s, followed by lower levels of recruitment in the 1980s–1990s, with some productive years (Fig. 9). Fishing mortality was high until the mid 1990s, suggesting that overfishing was occurring during this time. Following this reduction, spawning stock biomass and recruitment increased in the early 2000s when overfishing was no longer occurring. Fishing mortality has remained low since the end of the 1990s, except for a brief increase in the mid 2000s, which is associated with increases in US and Canadian fishing effort. Overfishing has not occurred since the 2004 closed-area access program. By the 2010s, spawning stock biomass and recruitment started to decrease despite reduced fishing effort and catch. Spawning stock biomass, recruitment and fishing effort have remained low since 2010 (Fig. 9).

Future projections

The stock assessment model can be used to project the stock into the future. Short-term projections (3-year) were used to inform future fishing quotas. In this study, we used the stock assessment model to conduct long term projections to explore if the stock could recover in the future. Projection trends were compared to maximum sustainable yield reference points that were calculated based on current environmental conditions. Current conditions of the stock were used in the projection period: weight at age (2-year average), natural mortality (constant), fleet selectivity (with 1st order autoregressive process error), maturity (constant), recruitment and bottom temperature (NEFSC, 2024). Future bottom temperatures were not available but they are needed to inform recruitment in the projection period. Two methods of estimating bottom temperature in the projection period were explored, a 1st order autoregressive process and recent mean. The recent recruitment period was determined using a changepoint analysis and was assumed to be from 2009–2022 (NEFSC, 2024). Under both scenarios the stock was projected 100 years into the future assuming the fishing mortality rate from the last year of the assessment.

For the autoregressive process on bottom temperature, bottom temperature slowly cools from the terminal year estimate (2022) to the time series mean. The average bottom temperature from the recent recruitment period estimated warmer bottom water in the projection period. Assuming colder bottom temperatures in the projection

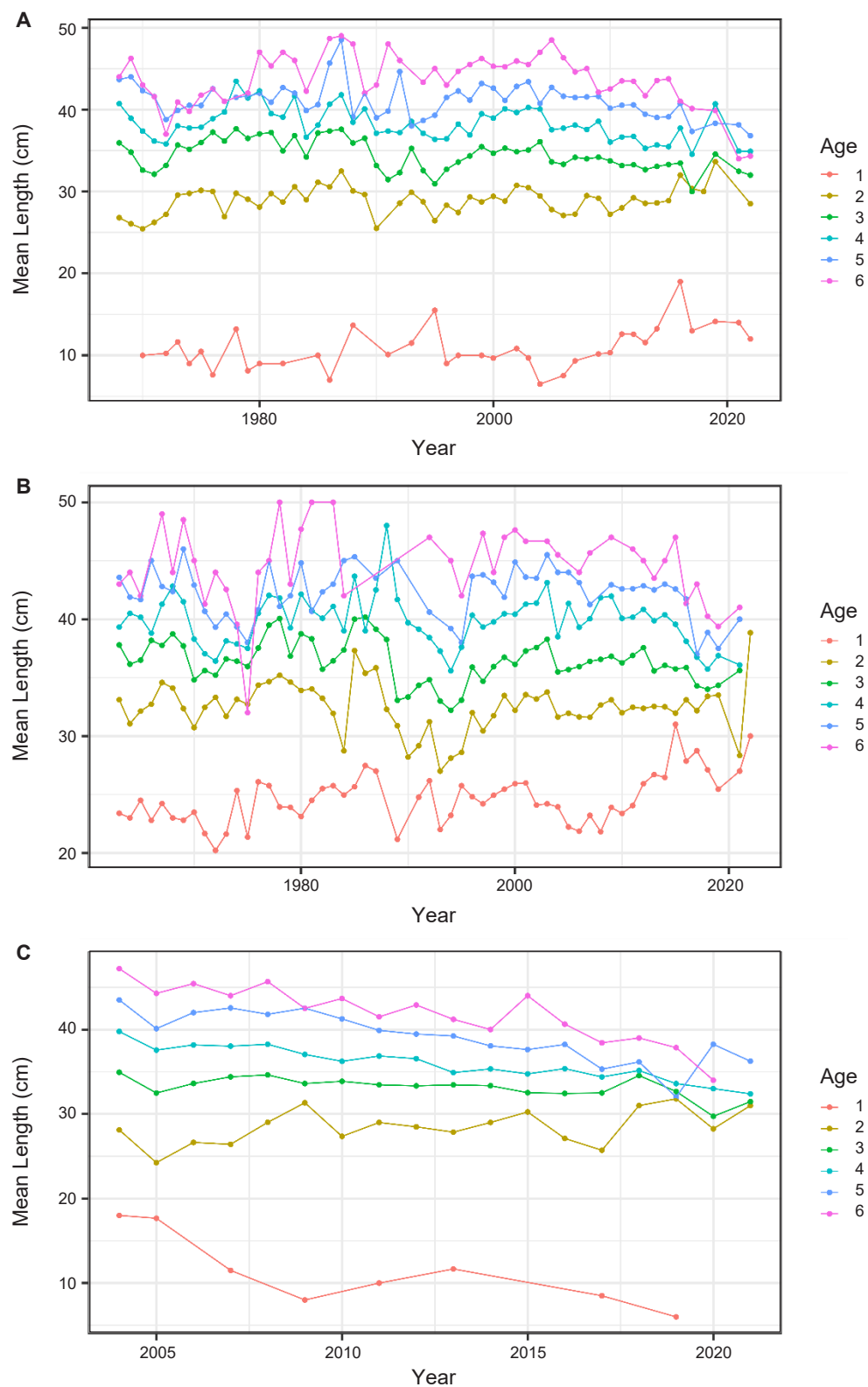


Fig. 6. Georges Bank yellowtail flounder trends in mean length at age for each survey and season: NEFSC spring (A), NEFSC fall (B), DFO (C).

period allowed recruitment and biomass to be higher in the projection period (Fig. 10). Under both scenarios, the stock size was able to increase above SSB_{msy} in the future, suggesting that despite current low population size the stock has the ability to recover under different environmental conditions. However, this recovery is still below historical high estimates from the 1970s and 2000s (Fig. 10). Thus, it is unlikely that Georges Bank yellowtail will support a level of fishery removals that have historically been taken from this stock.

Discussion

A review of biomass trends from the most recent stock assessment suggests biomass was high in the 1970s, followed by decreases in the 1980–90s, with the stock declared collapsed in 1994. Biomass increased in the 2000s with biomass above SSB_{msy} for large periods of the early 2000s followed by subsequent decreases to all-time lows in the 2020s, indicating the stock had collapsed again. Fishing mortality was high through the mid 1990s followed by a subsequent decrease with some fluctuations through the 2020s.

Stone *et al.* (2004) hypothesized that the primary driver of stock collapse in the 1990s was overfishing, and subsequent recovery in the early 2000s was due to effective bi-lateral science and coordinated management. The results presented here support those hypotheses with the most recent assessment estimating a sharp decline in fishing mortality in the mid 1990s. These reductions are likely due to the implementation of TACs, closed areas, decreased days-at-sea, and increases in mesh size (Stone *et al.*, 2004). The implementation of bi-lateral science and precautionary management during this time also likely benefited the stock and fishery. Subsequent decreases since 2010 are likely due to different factors because similar management measures remain. Thus, it is unlikely that fishing is the primary driver of stock dynamics in recent years (Fig. 9).

Over the last several decades, variability in ocean conditions have been well documented on Georges Bank, with observed changes in salinity, temperature, and predator/prey abundance (Wallace *et al.*, 2018; Tsou and Collie, 2001; Mountain and Kane, 2010). Changing environmental conditions were suggested to have possibly led to reduced recruitment of Georges Bank yellowtail flounder in the 1980s and early 1990s (Stone *et al.*, 2004). A review of the stock assessment model suggests that bottom water temperature impacts recruitment (Fig. 8). Estimated water temperatures from the stock assessment suggest slightly colder water temperatures in the 1970s, warmer temperatures in the 1980/1990s followed by colder temperatures in the 2000s. These fluctuations in cold water temperature coincide with periods of improved recruitment and subsequent larger stock size (Figs. 8–9).

Additionally, warmer temperatures since 2010 are the primary reason stock size remains low despite low fishing mortality (Figs. 8–9).

Temperature can impact multiple aspects of recruitment including timing, egg viability, food availability, larval growth and mortality (Takade-Heumacher *et al.*, 2014). It is unclear what the specific mechanism is for Georges Bank yellowtail flounder. However, it has long been hypothesized that warm temperatures could lead to reduced recruitment (Royce *et al.*, 1959; Lux, 1964; Lux and Nichy, 1969). Previous research, has linked recruitment deviations to water temperature for yellowtail flounder on Georges Bank (Brodziak and O'Brien, 2005; Takade-Heumacher *et al.*, 2014) and the adjacent stock in southern New England (Sissenwine, 1974, 1977; Sullivan *et al.*, 2005).

For yellowtail flounder, the majority of research exploring changing ocean conditions have focused on the Southern New England stock. This population is thought to be most susceptible because it is at the Southern extent of the species range (Hare *et al.*, 2016). Unlike the Georges Bank stock, abundance of the Southern New England stock has been decreasing since the 1980s with no signs of recovery (NEFSC, 2024). Previous research applications of the stock assessment have used a cold pool index to improve recruitment estimation, which measures the spatial extent and persistence of cold bottom water across the mid-Atlantic bight (Miller *et al.*, 2016; Xu *et al.*, 2017). The most recent stock assessment currently uses the Gulf Stream index to estimate deviations in recruitment, which measures the latitude above average of the Gulf Stream position (NEFSC, 2024). The Gulf of Maine/Cape Cod stock is the northernmost yellowtail flounder stock in the US and no environmental indicators are currently included in the stock assessment. However, it is hypothesized that fish might be shifting deeper in this region to account for changes in water temperature (Nye *et al.*, 2009).

On Georges Bank, new analyses of spatial distribution suggest that yellowtail flounder were most widely distributed in the 1970s, which corresponds to a period of high stock size (Figs. 4,5,9). However, since then there has been a steady contraction in spatial range (Fig. 4). During the periods of highest stock size in the 2000s, the DFO and to a lesser extent the spring NEFSC survey suggest that there was a restriction in spatial use, with fish occupying less habitat (Figs. 4, 5). Large spatial contractions like this can make the population especially vulnerable to fishing, but fishing mortality rates were not high at these times (Erisman *et al.*, 2011, Fig. 9). The “Basin Hypothesis” has been suggested for yellowtail flounder on the Grand Bank and Georges Bank (Pereria *et al.*, 2012; Adams *et al.*, 2018), which theorizes that when population abundance is high yellowtail occupy a wide range of habitats (MacCall, 1990). The Gini coefficients provide

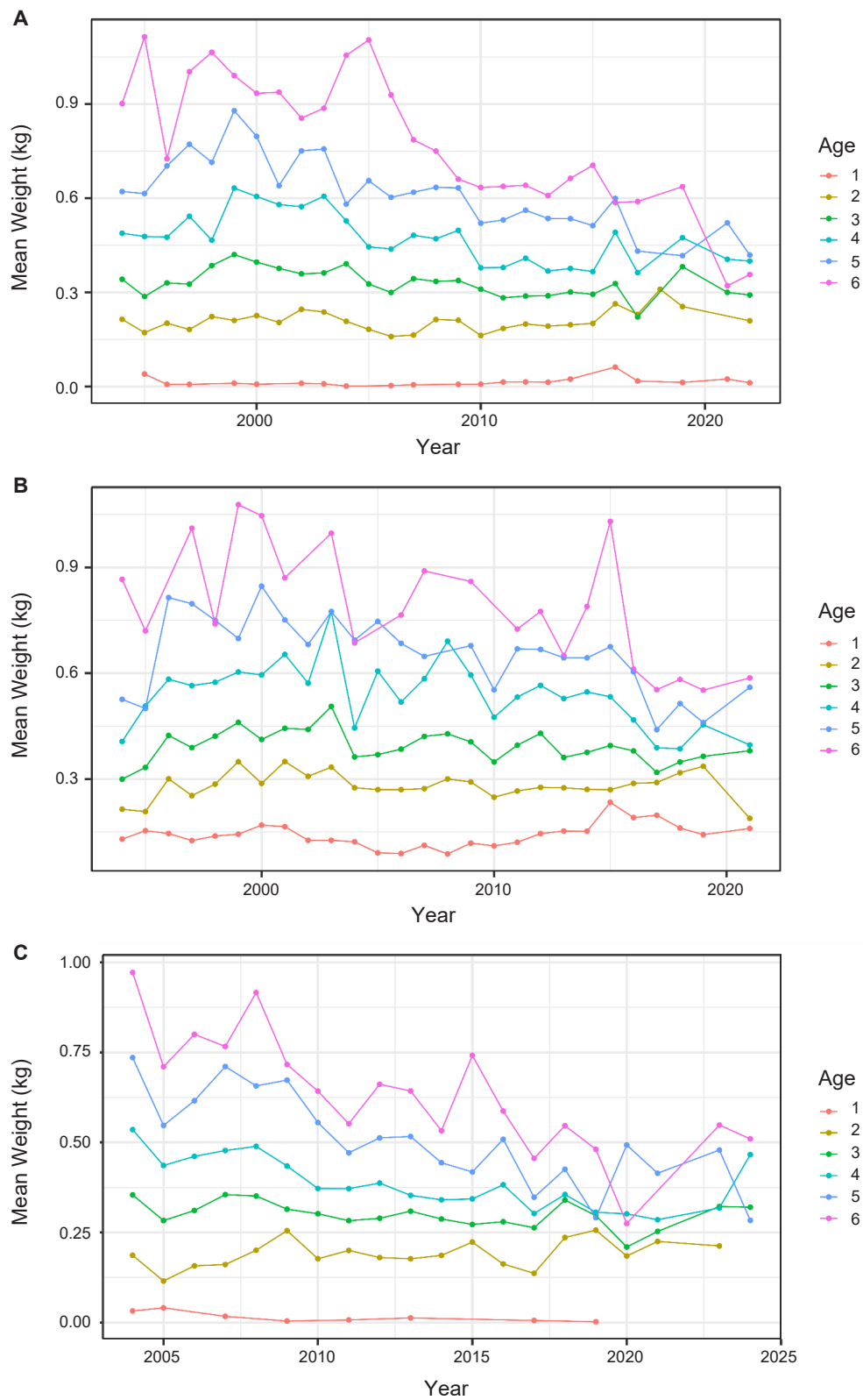


Fig. 7. Georges Bank yellowtail flounder trends in mean weight at age for each survey and season: NEFSC spring (A), NEFSC fall (B), DFO (C).

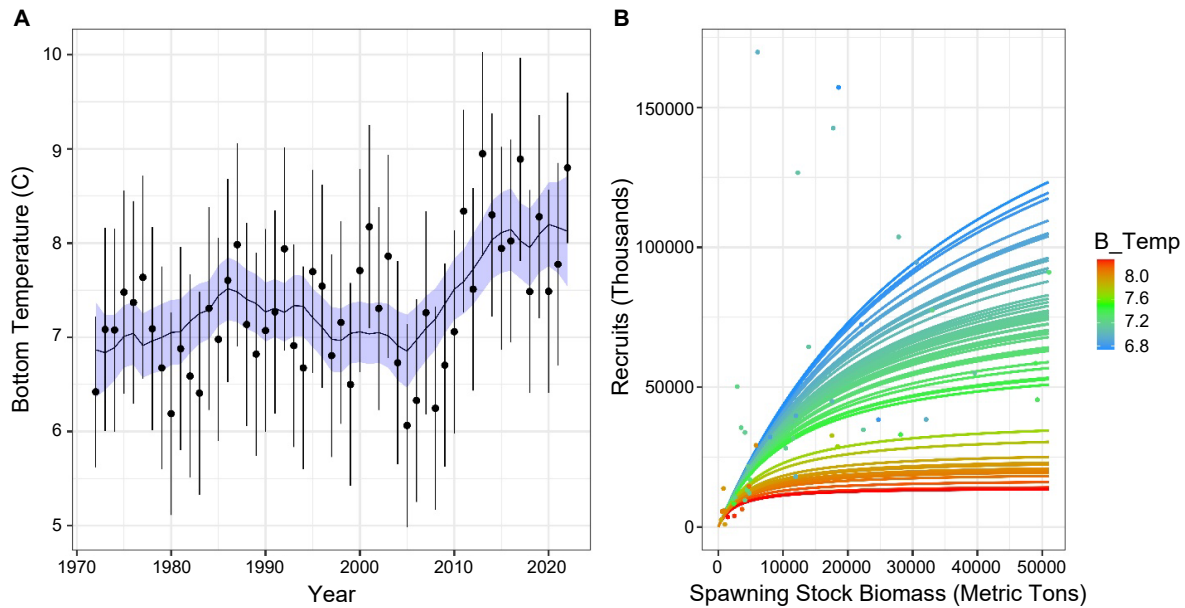


Fig. 8. Bottom water temperature (A) used in the stock assessment model to predict recruitment. The horizontal black line is the stock assessment model fit to bottom temperature while the blue is the 90% confidence intervals. Black dots are the observed bottom temperature and confidence limits are the associated standard deviations. The Beverton-Holt stock recruit relationship (B) influenced by water temperature and used to estimate recruitment.

a measure of spatial dispersion; however, the results vary among the seasonal surveys. The Gini coefficients suggest that in the fall NEFSC survey yellowtail flounder are occupying less habitat at lower population sizes. The opposite trend occurs in the spring with the NEFSC and DFO surveys estimating fish are occupying less habitat at larger population sizes in the early 2000s (Fig. 5). It is possible that these differences could be due to seasonal environmental conditions, especially because the Spring NEFSC and DFO sample at a similar time of year. Additionally, differences could be due to changes in size structure between the different surveys. The conflict in results, and the use of a single spatial metric, prevent confirmation of the “Basin Hypothesis”. Future research should consider additional spatial metrics (*e.g.*, center of gravity, Moran, 1950) and could look to link environmental covariates to dispersion metrics.

Thermal preferences could be altering the spatial use of yellowtail flounder on Georges Bank. The optimal temperature for yellowtail flounder on Georges Bank is hypothesized to be roughly 7°C (Hyun *et al.*, 2014). Since 2009, the average bottom water temperature on Georges Bank has been warmer than 7°C (Fig. 8). This suggests future work should consider exploring time varying availability and spatial distribution shifts of yellowtail flounder. Spatial shifts could be incorporated into future stock assessments with time varying catchability and/or selectivity parameters or the use of spatio-temporal models to standardize survey data (Wilberg *et al.*, 2009; Cao *et al.*, 2017).

Length data from the NEFSC spring and fall survey cover the periods of high stock size (1970s and 2000s) and low stock size (1990s and 2010s). Mean length tended to be larger when the stock was larger and smaller when the stock was lower. Additionally at lower stock biomass, mean length at age one is more similar to mean length at age two (Fig. 6). All length and weight information indicates that fish have been shorter and lighter than they were historically and there is more overlap in size among adjacent ages, indicating reduced growth (Figs. 6–7). Observed changes in size at age could be the result of environmental factors, such as changes in water temperature or prey composition. Future work should explore potential drivers of observed changes in size.

Growth is an important component of stock productivity because natural mortality and reproductive potential usually scale with size. Fish that are larger are less likely to be eaten and produce more offspring (Miranda, *et al.*, 2024). Typically, fishing gear releases small fish and retains larger fish, which can influence the size structure of the population (Enberg *et al.*, 2012). The environment can also influence growth, with restrictions in thermal range possibly negatively affecting growth (Boltaña *et al.*, 2017). Reduced growth, low stock size and reduced fishing at the end of the time series suggest that density dependent factors are not influencing growth for Georges Bank yellowtail.

New long-term projections from this study suggest that the Georges Bank yellowtail flounder stock can increase again

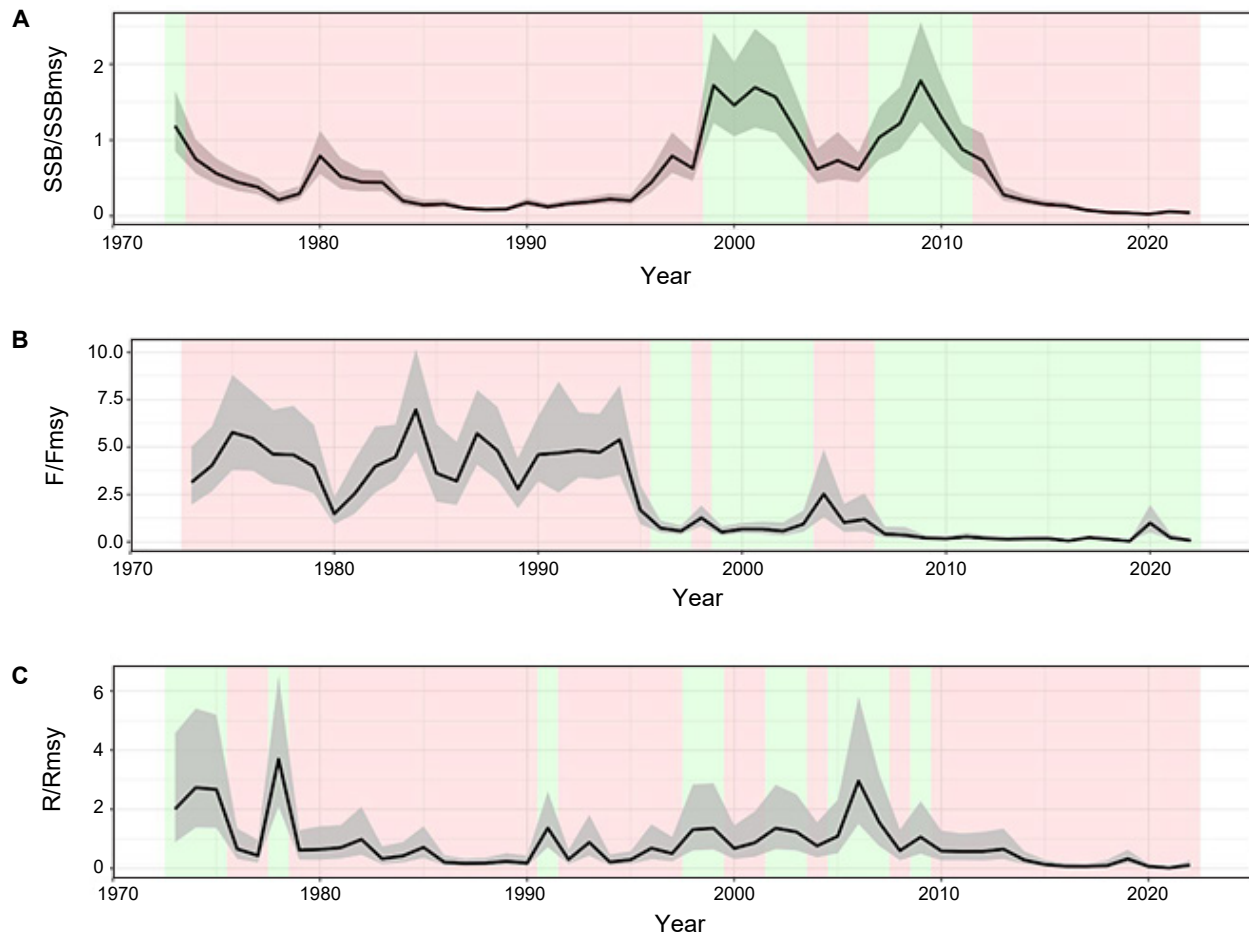


Fig. 9. Spawning stock biomass, recruitment and fishing mortality trends relative to reference points for Georges Bank yellowtail flounder. Shaded grey areas are the 90% confidence intervals. Red areas highlight times where R and SSB are below the reference point and F is above the reference point, while green highlight the opposite. Annual maximum sustainable yield reference points are used to determine status.

in the future. The rate and extent of increase will be based on biology, fishing mortality and bottom temperature. Based on the current assessment, colder bottom temperatures will allow the stock to increase faster and support larger stock sizes. More work is needed on how to treat bottom water temperature in the projection period. Especially since short term projections are often used to inform fisheries management. For example, it is probably not appropriate to assume the most recent conditions (2009–2022) will hold in the future. Additionally, the autocorrelated temperature projection allows the first several years in the projection period to be correlated with terminal year estimates of bottom temperature. This might be appropriate for short-term projections, but over the long-term bottom temperature reverts back to the mean of the entire time series. For long term predictions, neither approach is realistic given the dynamic nature of Georges Bank and predictions of future ocean conditions (Wallace *et al.*, 2018; Cheng *et al.*, 2022). WHAM can fit to future estimates of a covariate in the projection period, but this information is not available for the bottom temperature time series used in the assessment (Du Pontavice *et al.*,

2023). Thus, future work should explore using climate projections in the stock assessment projection period.

Several take home lessons can be learned from the collapses of the Georges Bank yellowtail fishery. Lesson 1: Overfishing can drive a fishery collapse but international collaboration and strong management can drive a recovery. This is observed by the fishery collapse in 1994 being driven by overfishing and the subsequent international collaborations on stock assessment (*e.g.*, TRAC) and strong fishery management measures (*e.g.*, days at sea, changes in mesh size) rebuilding the stock in the early 2000s. Lesson 2: Changing environment conditions can override effective management. Despite continued international collaboration and effective management still being in place the stock collapsed again in 2010. A review of the most recent stock assessment suggests that the second collapse was due to warming water temperatures. Lesson 3: The importance of exploring environmental data in stock assessment. Advances in stock assessment modeling (*e.g.*, WHAM) allowed for the direct incorporation of environmental

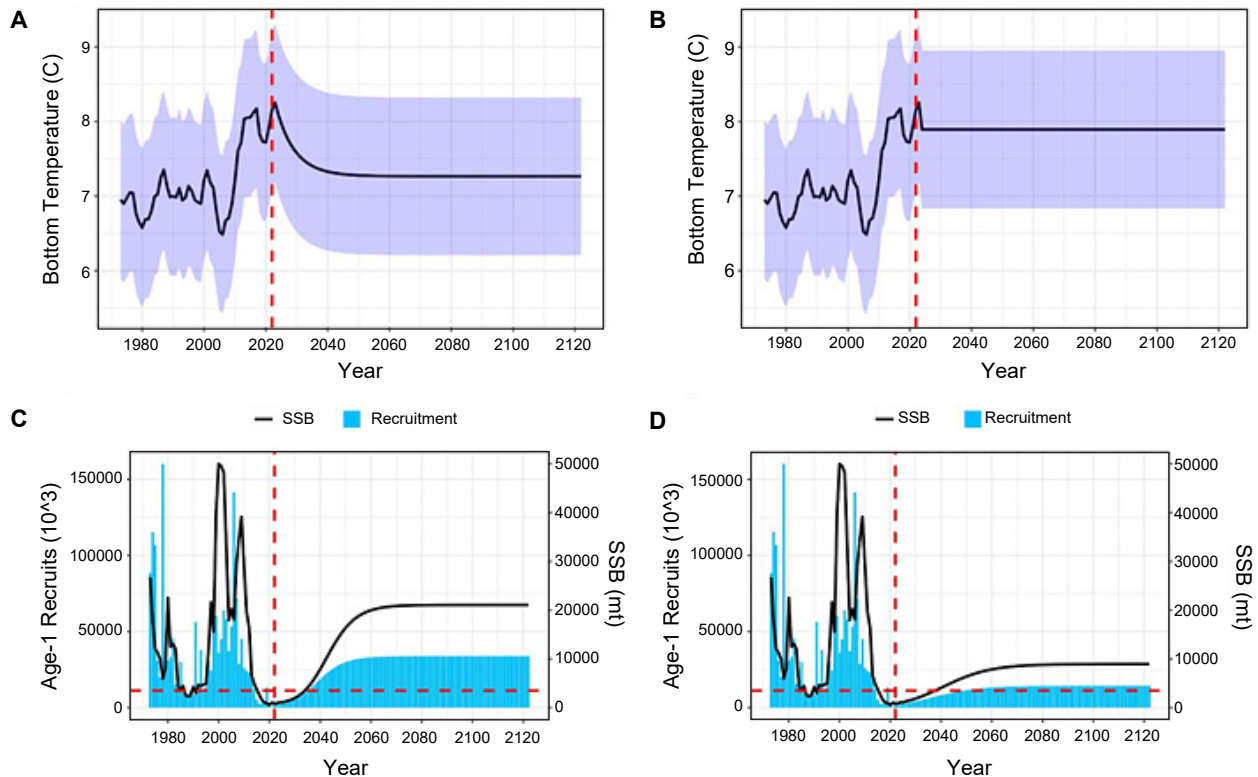


Fig. 10. Long-term projections (100 year) of the Georges Bank stock assuming an AR1 process on bottom temperature (A, C) and current conditions (B, D; mean: 2009:2022). The vertical dashed red line is the final year of the assessment, while the horizontal dashed red line is the current SSB_{msy} reference point.

variables to determine mechanistic links of the different collapses. Being able to include environmental variables directly into the stock assessment makes it easier to communicate results to stakeholders and managers. Thus, we recommend other stock assessments explore environmental drivers on population dynamic processes. Lesson 4: Stock recovery can still occur under current environmental conditions but the stock will not be able to support historic levels of fishing. Scientists and managers need to adapt expectations (*e.g.*, biological reference points) to account for these changes. Ultimately, the collapses of Georges Bank yellowtail flounder serve as a valuable case study, highlighting that fishery collapses can be caused by different factors and the importance of understanding the impact of fishing as well as a changing environment.

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