TOR 1: ECOSYSTEM AND CLIMATE INFLUENCES

Identify relevant ecosystem and climate influences on the stock. Characterize the uncertainty in the relevant sources of data and their link to stock dynamics. Consider findings, as appropriate, in addressing other TORs. Report how the findings were considered under impacted TORs.

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Data and Code Availability: Code and data related to TOR 1 material can be found here: https://github.com/Northeast-Climate-Integrated-Modeling/Cod-Research-Track-Stock-Assessment/tree/main/ToR1_Ecosystem_and_Climate

Profile of Ecosystem and Climate Influences on Atlantic Cod

Overview

A review of the scientific literature was undertaken to characterize existing research that has identified ecosystem and climate influences on the Atlantic cod stock dynamics. The aim of this review was to characterize the state of knowledge on this topic such that these relationships could be considered, as appropriate, in addressing other Terms of Reference (TORs) in the Atlantic cod research track process. The WG's consensus on the most appropriate spatial assessment units includes four spatial units for assessment: 1) eastern Gulf of Maine, 2) western Gulf of Maine (winter and spring spawners combined), 3) Georges Bank, and 4) Southern New England (including the Mid Atlantic Bight; see TOR 9 for more information). However, the following literature review section refers to the current two stock structure unit system when referencing cod stocks as those were the stock structure units at the time the cited literature was published.

Background

The range of Atlantic cod along the northwestern Atlantic extends from Greenland to Cape Hatteras, North Carolina, with the majority of biomass in US waters in the western Gulf of Maine and Georges Bank regions. Historically, productivity of the cod fisheries has been high. However, cod in these regions have experienced substantial population declines since the 1990s and according to the most recent Gulf of Maine (NOAA*a* 2021) and Georges Bank (NOAA*b* 2021) assessments, both stocks are overfished. These population declines have been attributed to various influencing factors including fishing pressure (Shelton et al. 2006; Brander 2007; Lily et al. 2008; Hilborn and Kitzinger 2009), an allee effect (i.e., depensation; Walters and Kitchell 2001; Rowe et al. 2004; Keith and Hutchings 2012), and environmental conditions such as changes in water temperature (Nye et al. 2009; Friedland et al. 2013; Pershing et al. 2015; Nian et al. 2021), predator and prey composition (Rothschild 2007; Lily et al. 2008; Neuenhoff et al. 2019), and atmospheric circulation patterns (Meng et al. 2016).

There have been large-scale changes in the ecosystem conditions of the Gulf of Maine and Georges Bank regions in the past few decades. In the Gulf of Maine, the average annual temperature has increased approximately 1.6 °C since 1895 at the surface (Fernandez et al. 2020) and 0.68 °C since 1982 at the bottom (Kavanaugh et al. 2017, Figure 1.1). This warming trend has been linked to shifting proportions of water coming from the southward flowing Labrador Current and northward flowing Gulf Stream (Nye et al. 2010; Saba et al. 2016; Alexander et al. 2019). The year 2019 marked the second lowest proportion of Labrador Slope Water that entered the Gulf of Maine since 1978 (National Marine Fisheries Service and Northeast Fisheries Science Center 2021). This region has also experience increased periodicity of marine heat waves (ocean temperatures above the 90th percentile for more than five consecutive days) with the top four strongest marine heatwave events in Georges Bank on record all occurring within the past 5 years (2015, 2016, 2020, 2021; NEFSC 2022). Changes in water temperature affect ocean stratification timing and intensity. Warmer temperatures are associated with longer stratification periods and could subsequently affect nutrient profiles and mixing in the Gulf of Maine (Balch et al 2012; Fernandez et al. 2020), productivity (Balch et al. 2016), and food webs in this region (Record et al. 2019; Pershing et al. 2021). Other observed changes in this region include changes in patterns of ocean circulation (Brickman et al. 2018; Caesar et al. 2018), ocean and coastal acidification (Gledhill et al. 2015), changes in seasonal length and timing (Thomas et al. 2017; Staudinger et al. 2019), changes in precipitation or storm frequency and intensity (Balch et al. 2012; Klein et al. 2017), and sea level rise (Dangendorf et al. 2019, IPCC 2019).

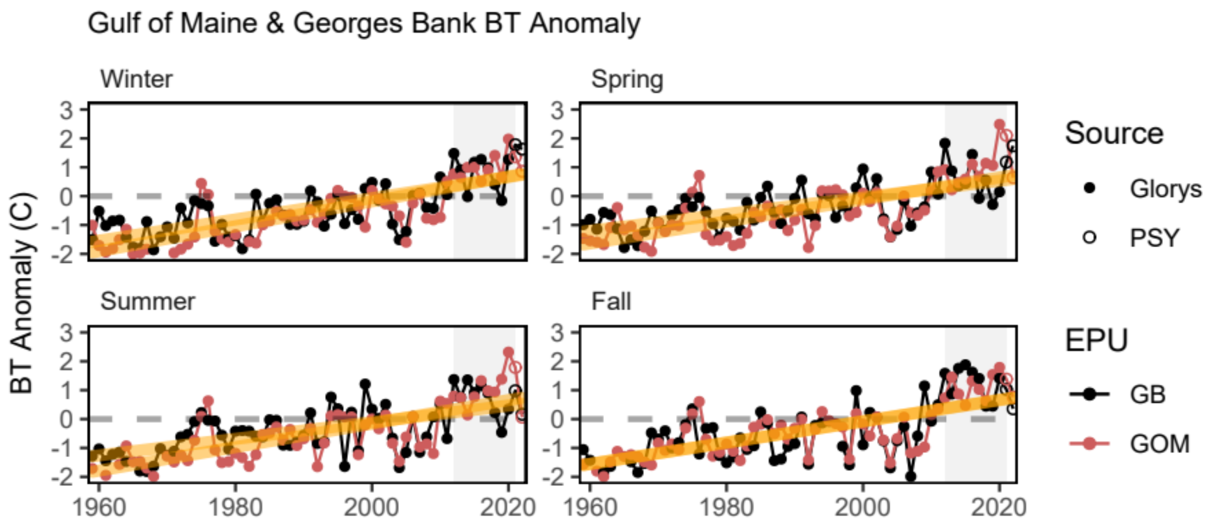

Figure 1.1. Annual Gulf of Maine and Georges Bank seasonal bottom temperature anomalies. Data are obtained from GLORYS, a global ocean reanalysis product that provides high resolution data on ocean physics and incorporates real time observations. Data from the last two years (open circles) are from a near-real-time model (PSY) and are considered preliminary. Sourced from 2023 State of the Ecosystem Report: New England (NEFSC; Lucey et al. 2023).

Ecosystem Influences on Recruitment

Temperature

Temperature can affect Atlantic cod spawning ground location and the timing of spawning events. Drinkwater (2005) suggested that cod spawning grounds will likely move northward and spawning events will likely occur earlier in the season with warming ocean temperatures. When adults are exposed to warmer water temperatures prior to spawning, they experience faster gonad development and as a result, are ready to spawn earlier in the season (Drinkwater 2005). Neuheimer and MacKenzie (2014) estimated spawning timing under future climate regimes and suggested that warmer areas, such as Georges Bank, would exhibit a smaller advancement in spawning time than cod stocks in colder areas. A shift in the location or timing of spawning events could lead to temporal or spatial mismatches in optimal growth, feeding, dispersal, or survival conditions for cod larvae (Rijnsdrop et al. 2009; Klein et al. 2017).

Cod stocks inhabiting relatively cold (< 6 °C) bottom water temperatures exhibited a positive relationship between recruitment and warming whereas cod stocks inhabiting relatively warm bottom water temperatures (> 6.5 °C) exhibited a negative relationship between recruitment with increasing temperatures (Drinkwater 2005; Mantzouni and MacKenzie 2010). Dean et al. (2019) found a significant negative correlation between increasing bottom temperature and recruitment of spring-spawned Gulf of Maine cod, but this relationship did not hold for winter-spawned cod. Similarly, another study found temperature was not consistently significantly related to variations in recruitment success of Atlantic cod (Rindorf 2020). Out of 21 cod stocks by Rinford (2020, only 3 stocks had significant correlations between recruitment and temperature (Rindorf 2020). Under a climate warming scenario of sustained temperature increases between 1-3 °C, both the Gulf of Maine and Georges Bank Atlantic cod stocks would likely demonstrate declines in stock numbers due to decreased recruitment (Drinkwater 2005).

Downwelling Winds and Ocean Currents

Downwelling favorable winds have also been correlated with strong recruitment of cod, which is thought to be due to increased retention of spring-spawned larvae (Churchill et al. 2011; Siceloff and Howell 2013; Hare et al. 2015). More recent data, however, was found to lessened the correlation between wind and recruitment (Hare et al. 2015). Thus, wind stress may be less influential on recruitment and stock abundance for cod than previously thought (Langan et al 2020). Recruitment success has also been associated with the position of the north wall of the Gulf Stream, as a more northward wall is associated with a strengthening of the Georges Bank gyre, resulting in higher egg and larval retention (Canada-US EMFM Workshop Report 2018). The warming of the Gulf of Maine associated with this northward shift in the Gulf Stream, as well as alterations in the Atlantic Multidecadal Oscillation (AMO) and Pacific Decadal Oscillation, has been associated with reductions in recruitment of Atlantic cod (Groeger and Fogarty 2011; Pershing et al. 2015). In the Gulf of Maine, the Maine Coastal Current has also been associated with larval retention, where the degree of connectivity between the Eastern Maine Coastal Current (EMCC) and the Western Maine Coastal Current (WMCC) influences the amount of settlement of cod in the western Gulf of Maine (Churchill et al. 2017).

North Atlantic Oscillation

In addition, the North Atlantic Oscillation (NAO) has demonstrated significant effects on recruitment (Groeger and Fogarty 2011). In an analysis of 22 North Atlantic cod stocks, Stige et al. (2006) found a positive NAO to have a general negative effect on cod recruitment for the southernmost stocks, but a general positive effect for the northernmost cost stocks. However, Stige et al. (2006) did not find significant density-dependent effects between the NAO effect and spawning stock biomass.

Ecosystem and Climate Influences on Natural mortality

Temperature and Prey Availability

Water temperature affects the natural mortality of cod at multiple life stages. Changes in water temperature can impact the timing of egg hatching which can impact survival rates and subsequently recruitment potential (Buckley et al. 2010). Exposure to increased temperatures has been associated with faster growth rates in early development stages, reducing the amount of time spent in the egg and larval phase, when predation and mortality rates are highest (Drinkwater 2005, Klein et al. 2017). Cod eggs and larvae also have a thermal lethal limit of 12°C, so increases in water temperature near or past this threshold may also increase natural mortality during these stages (Drinkwater 2005).

Increasing water temperature may also have a negative effect on food availability for cod. Increases in temperature over time are expected to lead to increased stratification and decreased phytoplankton productivity (Kristiansen et al. 2013). Declines in important zooplankton species to Atlantic cod have already been observed across the Northeast U.S. continental shelf due to changing temperatures (Friedland et al. 2013). Decreases in prey availability, in conjunction with expected elevated metabolic costs will likely increase the risk of cod larval mortality via starvation (Kristiansen et al. 2013).

Climate change may cause increased natural mortality in adult cod due to changes in fish condition related to changing energy content of prey and changes in growth such that a higher proportion of fish are susceptible to predation (i.e. smaller size; Bundy and Gamble 2018). Cod production has a positive relationship with mean bottom temperature for stocks in regions where the average bottom temperature does not surpass 12 °C (Dutil and Brander 2003). However, Drinkwater (2005) projected that if average North Atlantic bottom temperatures warm beyond 12 °C, cod will “disappear”, either by seeking colder waters or through natural mortality. However, the relationship between cod presence-absence and temperature may be indirect, with cod responding to changes in prey availability rather than changes in temperature (Drinkwater 2005).

Reduced fitness in adults from persistent climate changes could also initiate a negative feedback loop in which adults with reduced fitness develop lower quality eggs, disadvantaging future offspring as they continue to face future environmental stressors (Klein et al. 2017). However, cod may have the capacity to adapt to warming temperatures if the rate of warming is not too fast (Langan et al 2020).

Predation

Predation is a source of cod mortality and as seal populations in the Northeast U.S. recover, predation by these marine mammals has been seen as a concern for cod. Overall, the number of pupping sites in the U.S. has increased (1 in 1988 to 9 in 2019) and population increases in the U.S. are hypothesized to be supplemented by the large breeding populations observed in Canada (NMFS and NEFSC 2021). Although this concern is growing as gray seal populations recover, stomach content analyses showed that minimal impacts on cod were expected in 2000 due to comparatively small and localized population sizes of gray seals in the GOM (Baraff and Loughlin 2000). Across studies in New England waters, cod was never shown to represent more than 26% of observed seal diets and that the cod consumed were typically smaller than those targeted by fisheries (Baraff and Loughlin 2000). Harbor and gray seals on average consumed 28% and 12% (respectively) the amount of large gadids harvested by the commercial fishery, and cod was expected to represent a low portion of this consumption due to low stock size in U.S. waters (Smith et al. 2015). Nonetheless, quantifying consumption by harbor and gray seals is difficult due to diet differences based on factors such as ontogeny, sex (Beck et al. 2005, 2007), location (Breed et al. 2006), and season, as well as the legal restrictions that confound the ability to get representative samples (e.g., samples are generally restricted to bycatch, young-of-year and pups, and scat). Novel techniques like fatty-acid analyses and DNA PCR techniques will continue to improve understanding of seal diets (Flanders et al. 2020).

It is important to note that the effects of seal predation may be location specific, depending on local abundance, and vary by season. For example, a recent study found varied results for trends in gray seal recovery in the Gulf of Maine (Wood et al. 2020). Between 1994-2019, there was an 11.5% increase in seal pups born around Seal Island, but only a 0.2% decrease in pups born around Green Island, Maine (Figure 1.2, Wood et al. 2020). Ampela (2009) found that cod made a considerable proportion of gray seal diet in winter months (47% by biomass from

December-March) but comprised a much lower proportion of the diet in the spring, summer, and fall (17%, 25%, and <0.01% by biomass respectively). One potential bias in these estimates is that cod are considered to have more "robust otoliths" compared to other species, increasing the probability of otolith recovery and overestimation of cod in this method of diet analysis (Ampela 2009). On the other hand, gray seals have also been observed avoiding the heads of cod and "belly biting" by fishermen (Ampela 2009; Benoît et al. 2011), which could lead to underestimation of cod in otolith recovery analyses if otoliths are not ingested. If gray seals consume 25-50% of cod by utilizing this "optimal-foraging" technique and targeting the most energy-rich parts of prey, the percentage of natural mortality (M) attributed to gray seals increases by 50% (Benoît et al. 2011). Based on the information we have gathered from literature, we currently cannot accurately measure the extent to which gray seals are reducing the population of cod. There are opportunities for further research to address the existing uncertainties and limitations regarding the connection between gray seal populations, their diets, and the natural mortality of cod.

Dogfish (*Squalus acanthias*) are another predator of cod, however the current state of knowledge on the predation impact of dogfish is unclear due to conflicting findings and existing caveats across multiple studies. One diet study using fishery independent data found cod in 0.02% of dogfish stomachs (Smith and Link 2010), whereas a study using fishery-dependent data found cod DNA in 10.5% of dogfish stomachs (Pitchford et al. 2020). Regardless of the magnitude of predation impact, dogfish and cod do have high prey overlap, increasing competition for available resources (Morgan and Sulikowski 2015). Dogfish are also a source of prey for gray seals and have been thought to contribute to their recovery (Bryon and Morgan 2016). Despite the possible low predation rates of gray seals and dogfish on cod, according to Bryon and Morgan (2016), there is a concern that the existing cod population might be unable to withstand the cumulative mortality resulting from predation by these two predators. This source of cod natural mortality is dependent upon other other factors such as availability of other prey species to seals and dogfish.

The impact of cannibalism (the predation on small cod by larger cod) is thought to be density-dependent, and impacts from cannibalism are less likely to be detected for stocks at lower levels (Link et al. 2009). Thus, natural mortality via cannibalism is likely minimal for

Atlantic cod in the Gulf of Maine and Georges Bank regions. A stomach content analysis study of 19,645 cod stomachs revealed <2% composition from Gadiformes, suggesting weak evidence for cannibalism (Smith and Link 2010). In addition to density-dependence, cannibalism in cod is also likely impacted by prey availability (i.e. when prey abundance is low, cannibalism in cod is thought to increase; Lily et al. 2008). Cannibalism has also been found to increase with ontogeny, with instances occurring most frequently in individuals >100 cm (Link and Garrison 2002).

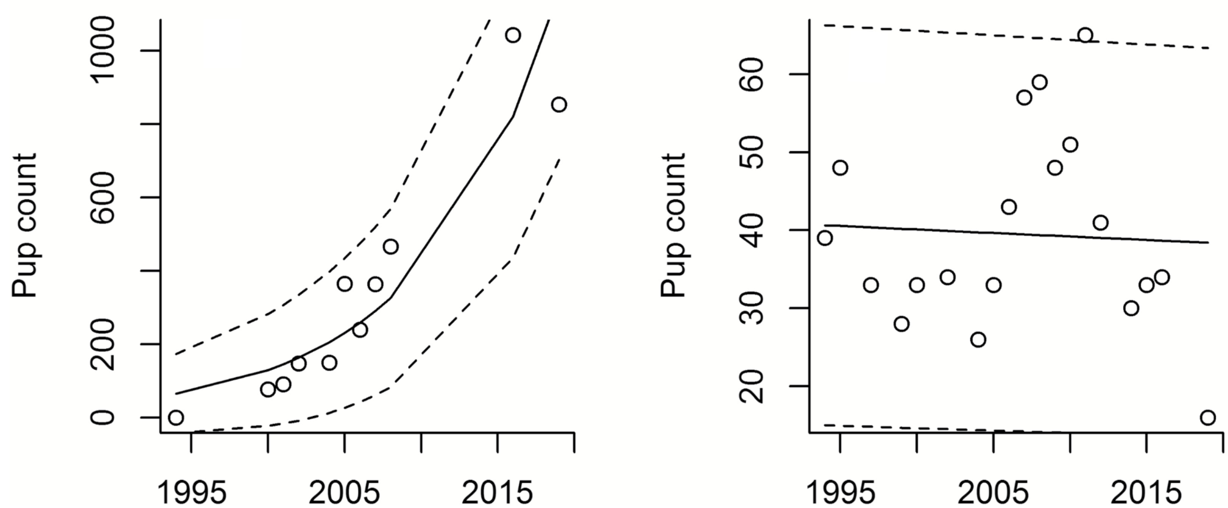

Figure 1.2. Estimated mean rates of increase (solid line) and 95% CIs (dashed lines) in number of gray seal (*Halichoerus grypus atlantica*) pups born at Seal Island, ME (left) and Green Island, ME (right) pupping colonies from 1994 to 2019. Figure from Wood et al. (2020).

Ecosystem Influences on Growth and Maturity

Temperature

Temperature has a significant effect on both growth and maturity of cod in the North Atlantic. For every 2 °C increase in bottom temperature, the age of maturity is estimated to decrease by one year (Drinkwater 2005). Cod on Georges Bank were found to grow faster and reach maturity one year earlier than those in the Gulf of Maine, with stock biomass and environmental conditions experienced by juveniles impacting maturity timing (O'Brien 1999; Northeast Fisheries Science Center 2013). Regional differences in growth have been attributed to temperature, with Gulf of Maine cod exhibiting higher condition factors, growth, and food conversion efficiencies under warmer temperatures than neighboring Canadian stocks (Purchase and Brown 2001). However, a recent analysis revealed a discernible growth increase in age 2 Gulf of Maine cod from 1970s to 2010s, while a significant decline in growth was observed for age 2 cod within the Georges Bank management unit over the same period (McBride and Smedbol 2022).

Growth rate is expected to increase in Gulf of Maine cod as temperatures continue to warm (Fogarty et al. 2008; McBride and Smedbol 2022), but early life survival is expected to decline under the same conditions (Fogarty et al. 2008). Increases in temperature and subsequent decreases in age at maturity and increased growth rates may result in increased productivity if a higher proportion of the population is mature (Drinkwater 2005). Overall, the relationship between temperature and growth/maturation in Atlantic cod seems to be consistent with the Metabolic Theory of Ecology (Brown et al. 2004), where increases in temperature have been associated with faster growth, earlier maturation, and increased natural mortality rates (Wang et al. 2014). However, it is important to recognize that high fishing pressure, which is also associated with driving early maturation, can confound the relationship between temperature and early maturation.

Food Availability

Along Georges Bank, increased growth rates in Atlantic cod larvae were observed following an increase in large and lipid-rich copepods such as *Pseudocalanus* spp. (Buckley and Durbin 2006) and *Calanus finmarchicus* (Green et al. 2004) during the late 1990s. In 2004, Mateo (2007) found lower growth performance of cod on Georges Bank compared to the Gulf of Maine region. In addition to differences in prey availability and quality between these regions, upper thermal limits were approached for the Georges Bank cod, whereas temperatures were lower and more consistent in the Gulf of Maine, which may have also influenced the lower growth performance. Tallack (2009) observed faster growth but smaller asymptotic sizes in the Georges Bank stock compared to the Gulf of Maine cod stock.

Ecosystem Influences on Distribution and Habitat Use

Temperature and Depth

Cod exhibit seasonal migrations that are influenced by changes in environmental conditions. Spring spawners in the western Gulf of Maine migrate inshore to spawn in the spring, offshore to feed in the summer and fall, and are known to overwinter in offshore basins with depths greater than 150m (Zemeckis et al. 2017). However, ocean warming may result in earlier spring migrations and delayed fall returns for cod across the northwest Atlantic (Drinkwater 2005).

Despite the evidence that the ocean climate and ecosystem have changed and are continuing to change in the Gulf of Maine and Georges Bank regions, the observed thermal habitats that many species inhabit have not changed significantly over time (Nye et al. 2010). This suggests that these species are shifting distributions in pursuit of optimal habitat conditions. Between 1968 and 2007, Georges Bank cod demonstrated a decrease in area occupied and a 1.48 km/year northward shift in center of biomass, and Gulf of Maine cod shifted deeper and further south which was associated with a continual warming trend and changes in circulation (Atlantic Multidecadal Oscillation) across the Northeast US continental shelf (Nye et al. 2009). Probability of occurrence is lower in regions where annual mean bottom temperature is greater than 12 C as metabolic costs are too high (Dutil and Brander 2003). Under climate change, temperatures in all areas currently occupied by cod are expected to exceed cod's thermal optimum by 2050 (Rogers et al. 2019), resulting in decreased habitat suitability (Rogers et al. 2019; Fogarty et al. 2008; Kleisner et al. 2017). At least one study attributed the southwestern shift in the center of gravity for Gulf of Maine cod and lower area occupied to localized depletion rather than warming bottom temperatures (Guan et al. 2017). Similarly, one study along the Scotian shelf also found fishing pressure in inshore waters to explain 72% of the positive correlation between age and depth distribution of cod (Frank et al. 2018). However, a later study challenged Frank et al.'s (2018) findings as they were only performed on a single stock.

Bottom Type

Young-of-year cod have a preference for cobble bottom substrates or other complex habitats after settlement (Grabowski et al. 2018) and adult cod have known associations with hard-bottom and coarse grain sediments (Siceloff and Howell 2013). Conroy et al. (2018) observed adult cod also preferring complex, but shallow habitats, such as in kelp forests. Residency in these forests declined however, with increasing temperatures during the late summer, indicating potential thermal constraints associated with habitat use (Conroy et al. 2018).

Prey Availability

Prey availability and distribution can also influence cod habitat use. Increased cod abundance was observed in response to increased sand lance abundance on Stellwagen Bank, and cod were generally more concentrated when feeding on sand lance than when feeding on other prey species like herring (Richardson et al. 2014). In the 1920s cod were known to aggregate in Muscongus Bay in the fall to feed on young of year alewives, but have disappeared from this area following the collapse of alewife populations (Ames and Lichter 2013).

Stakeholder's Perspectives on Ecosystem and Climate Influences on Atlantic Cod

The WG held a meeting on February 9, 2022 to engage with fishery stakeholders. The meeting focused on soliciting feedback to identify key ecosystem and climate influences on cod stock dynamics and impacts on fleet response to changing conditions. Roughly 70 participants including fishermen, industry representatives, managers, and scientists participated and their feedback is summarized below. Because this group of participants represents a small portion of Atlantic cod stakeholders, the following feedback is not expected to be fully representative of all possible viewpoints held by stakeholders in this fishery. See **WP 1** for additional detail.

Surveys

Potential mismatches between the timing and location of sampling conducted by the Northeast Fisheries Science Center (NEFSC) bottom trawl survey sampling and cod presence were raised as a concern. One attendee expressed concern about surveys that operate solely during the day as the majority of cod are harvested at night in certain areas. A WG member clarified that the NEFSC survey samples during both the day and night, but the industry-based survey only operated during the day. Another attendee raised concerns that they had observed earlier arrival and later departure of cod but the consistent timing of the NEFSC bottom trawl surveys meant that these changes would not be reflected in the survey. One attendee raised the concern that changes in the lobster fishery footprint had made the fishery-independent trawl survey data collection more sporadic in areas with increased lobster gear. Information on the inshore distribution of cod was also viewed as lacking in the assessment process and it was suggested that additional use of inshore surveys that capture more data on cod may provide valuable insights.

Environmental Change

Many stakeholders agreed that temperature can be an ecosystem stressor for cod. Attendees also discussed the correlation between temperature and biomass of cod, and some of the resulting effects such as observed distribution shifts. One recounted 2010 as a turning-point year in terms of noticeable temperature increases. An individual noted that 2011-2013 winters were warm and memorable due to the noticeable decrease in fish abundance and noted that abundance increased again during the cold winter of 2014. Though biomass seems to be correlated with water temperatures, one attendee claimed that cod don't emigrate from an area unless the winter is "very warm". Increases in temperature have also led fish to arrive sooner, leave later, and an overall change in their distribution over time, according to one attendee. These shifts in distribution could alter the availability to the survey.

One attendee observed stronger tides in the Gulf of Maine over the most recent 20 years and changing tidal strength was associated with changing behavioral response of cod (distribution) and other species in the region, although no change in the overall species composition was noted. Another attendee mentioned that haddock's large population size was likely to influence cod stocks, and noted that inshore surveys observed high haddock abundance and little co-occurrence with cod. Changing temperature and stock biomass were also expected to impact cod's response to other ecosystem stressors.

Increased worms in cod, haddock, gray sole, and many other species were observed. Several stakeholders attributed this increase to the increased gray seal population. A WG member noted that cod and haddock worms have an intermediate snail host, but could not comment further on why worm presence has increased.

Several at the meeting reported recent observations of a slime in the water where cod were targeted and had decreased catch rates when the slime was present. The slime was orange and stringy, observed in 25 fathoms depth, and was reported between June and the end of October. Attendees questioned whether similar observations and catch rates were observed in the NEFSC survey operating during this time period. High salp abundance was also reported during this time period.

Predation/ Prey

There was an extensive discussion of predation of cod at the meeting and most of the discussion was focused on gray seals. Some attendees were curious about gray seal abundance, distribution, and what data would be needed to better understand the impacts these predators have on cod. Many indicated an increase in gray seals over the past several decades. In the Nantucket shoals region, one individual commented on the observed seasonal shifts in gray seal's diets and noted that gray seals prey upon cod at a higher rate in the fall than they do in the spring.

Other predator species of concern were spiny dogfish and black sea bass (*Centropristis striata*). One individual brought up the larger biomass of these other predators in comparison to gray seals, how they are moving northward, and how they "eat everything". It was suggested to look into the overlap in spatial distributions between cod, black sea bass, and spiny dogfish. Cormorants, white sharks, and bluefin were also mentioned as additional predators of cod. Cormorants have been observed by some fishermen to eat juvenile cod, which may potentially affect recruitment. However, based on the amount of discussion surrounding these additional predators, they do not seem to be as impactful as seals, dogfish, and black seabass. Overall, many noted an observed increase in predator population numbers and attributed this to increased water temperatures in some cases.

Only two comments were made regarding the prey of cod. One individual noted an "ecosystem shift" due to notable decreases in sand lance (*Ammodytes dubius*), a prey species for cod, since the 1990's. Another attendee noted that reduced sand lance in recent years could be attributed to shifting mackerel distribution into the region as mackerel prey on sand lance.

Regulatory Impacts

Several stakeholders noted caution in WG interpretation of shifts in fishing location as these may not be in response to environmental changes but rather in response to changing allocations (e.g. shift to deeper waters may be a sign of switching to target species like hake and dogfish). Changes in the sector system were also highlighted as drivers of shifts in operation of the fishery.

It was noted that cod catches had declined on Georges Bank in response to harvest plans and fishing strategies that shifted harvest to redfish, pollock, and haddock. Fishermen emphasized the need to consider regulatory changes when interpreting trends in fishery data to avoid drawing erroneous conclusions that trends were due to environmental changes alone. Several fishermen noted that increases in the lobster fishery footprint had reduced access to certain areas by the cod fishery and the NEFSC bottom trawl survey.

Indicator Identification

Ecosystem influences on Atlantic cod were identified in the Ecosystem Profile (section above). The Term of Reference 1 (TOR 1) subgroup discussed these ecosystem linkages and identified several potential indicators that could be developed to monitor relevant ecosystem information. The TOR 1 subgroup then narrowed down the list of indicators on the basis of theoretical merit (the ability of the indicator to inform knowledge of a key process) and operational merit (the ability of the indicator to be created and analyzed in a timely manner). These discussions helped the TOR 1 subgroup reduce the number of indicators under consideration by eliminating redundant indicators (indicators that addressed the same linkage or process) as well as indicators that would not be feasible to create and/or analyze under the constraints of the WG's timeline. The TOR 1 subgroup presented this reduced group of indicators to the full working group and discussed the reasoning behind each indicator. Following this presentation, the full working group and interested collaborators provided comments and suggestions on the proposed indicators. Based on the feedback from the group, final indicator groups were identified. Each of these indicator groups consists of data from a single source, but in several cases, the data was aggregated over multiple geographic and monthly and/or seasonal periods. The selected indicators are described below; see WP 2 for information about indicators that were considered but not selected for further analysis.

Selected indicators

1. **Sea surface temperature** (proxy for spawning, egg development, recruitment)
    a. **Linkage to cod:** Cod spawning and early life history are associated with optimal temperatures. Warmer temperatures will likely decrease cod spawning and egg survival (Klein et al. 2017) and therefore would ultimately decrease recruitment.

    b. **Relevance to management:** Decreased recruitment potential associated with changes to sea surface temperature could be incorporated into the assessment model and would improve the determination of stock status and projections.

2. **Bottom temperature** (proxy for growth)
    a. **Linkage to cod:** Cod growth peaks between temperatures of 10-15C (Drinkwater 2005). Temperatures within this range would optimize cod growth, while temperatures outside this range would be detrimental for cod growth.
    b. **Relevance to management:** Changes with growth associated with changes in bottom temperature could be used to inform expectations for weights at age.
3. **Gulf Stream Index**
    a. **Linkage to cod:** The north wall of the Gulf Stream impacts the gyres on Georges Bank and the retention of larvae; therefore the position of the north wall may affect cod recruitment success. Larval retention is expected to be higher in years with a more northward north wall of the Gulf Stream (CAUSES 2018).
    b. **Relevance to management:** Changes to recruitment potential associated with the position of the Gulf Stream could be incorporated into the assessment model and would improve the determination of stock status and projections.
4. **Marine heatwaves**
    a. **Linkage to cod:** Temperatures above optimal could increase mortality of cod.
    b. **Relevance to management:** Changes to natural mortality associated with more frequent marine heatwave events could be incorporated into the assessment model and would improve the determination of stock status and projections.
5. **Zooplankton**
    a. **Linkage to cod:** Zooplankton are an important prey item for larval and juvenile cod. Higher zooplankton density would improve the fitness and survival of the early life stages of cod.
    b. **Relevance to management:** Changes to recruitment potential associated with the density of important zooplankton prey could be incorporated into the assessment model and would improve the determination of stock status and projections.

Exploratory Analysis of Relationships between Stock Dynamics and Ocean Climate

We used generalized additive models (GAMs) to examine relationships between key aspects of Atlantic cod stock dynamics (i.e., recruitment, distribution, and growth) and ocean climate variables. Time series of relevant environmental variables included sea surface (SST) and bottom temperature anomalies, the Gulf Stream Index (GSI), zooplankton abundance anomalies for *Calanus finmarchicus* and *Pseudocalanus spp.*, and mean cumulative heatwave index. Spawning stock biomass (SSB) was also included to explore density dependent effects. These environmental and climatic variables were related to time series of stock variables (across 4 stock areas: WGOM, EGOM, GB, and SNE) which included age 1 abundance and recruits per spawning stock biomass (R/SSB) as proxies for recruitment success, mean population depth and latitude of occurrence as proxies of distribution, and mean relative condition and weight at age (WAA) anomaly as proxies of growth. These variables were calculated from the Northeast Fisheries Science Center (NEFSC) fall and spring bottom trawl surveys. Although there is evidence for two biological stocks within the WGOM stock area (McBride and Smedbol 2022), the geographic overlap between these populations makes it difficult to partition the available data to each population. Thus, this analysis uses the available data for the WGOM stock area and does not explicitly account for the mix of two biological populations in this area.

One of the primary purposes for these exploratory analyses is to identify relevant ecosystem and climate influences on the stocks and to provide recommendations of prominent drivers for use in other TORs. While environmental effects on recruitment, distribution, and growth were examined, only the findings from the recruitment analysis were used to inform the environmental covariates considered in stock assessment models of Atlantic cod (see ToR 4 section of WG report). Therefore, this brief overview will highlight the recruitment analysis and its subsequent results. For more information about the all analyses performed (recruitment, distribution, and growth) and for details on the methodology, see the technical report regarding this exploratory analysis (WP 3).

Recruitment

Temperature-related independent variables were recurring significant drivers in both recruitment (log of age 1 abundance) and recruitment rate (R/SSB) models. Amongst all (8) recruitment models where at least 1 significant environmental driver was identified, 7 of the models included a significant temperature-related indicator (Table 1.1). Although the specific temperature-related indicators varied (bottom temperature anomaly, SST anomaly, or heatwave), all temperature variables displayed a general negative relationship between recruitment and increasing temperatures (Figure 1.3). These results suggest that cod recruitment decreases under warming temperatures. One exception to the general negative trend in recruitment-temperature relationships was in the spring EGOM recruitment rate model, where SST anomaly was significant and displayed a curvilinear relationship (Figure 1.3F). This suggests the presence of thermal thresholds at both colder ($<0.0\ \Delta°C$) and warmer than average ($>1.5\ \Delta°C$) spring sea surface temperatures in EGOM, where recruitment success of cod is either positively or negatively impacted, respectively. We speculate this relationship may also be different as a result of the limited data availability on EGOM cod compared to stock areas such as the WGOM, which consistently demonstrated a negative relationship pattern.

Table 1.1. Significant environmental drivers revealed in recruitment GAM analysis by season and stock area. If a season or stock area model combination is not listed, that indicates that model either did not have any significant environmental drivers identified or that there was not enough data to run the analysis. Each row of table represents a different season x stock area model run. Relationship trends listed are generalized and represent trends over where the majority of the observations occur. In models where multiple significant independent variables were returned as significant, relationship trend patterns are listed respective to the variable order in the "Independent Variable" column.

Season	Stock Area	Dependent Variable	Independent Variable	Deviance Explained	Relationship Trend
Spring	EGOM	R/SSB	SST Anomaly	68.8%	Varies
Spring	EGOM	Log Age 1	SST Anomaly + Calanus abundance anomaly	45.8%	Negative, Constant
Spring	WGOM	R/SSB	Bottom temperature Anomaly	18.6%	Negative
Spring	WGOM	Log Age 1	Heatwave	50.9%	Negative
Fall	EGOM	Log Age 1	SST Anomaly	22.4%	Negative
Fall	WGOM	R/SSB	SST Anomaly	10.7%	Negative
Fall	WGOM	Log Age 1	Bottom temperature Anomaly	38.6%	Negative
Fall	GBK	Log Age 1	SSB	23.1%	Positive

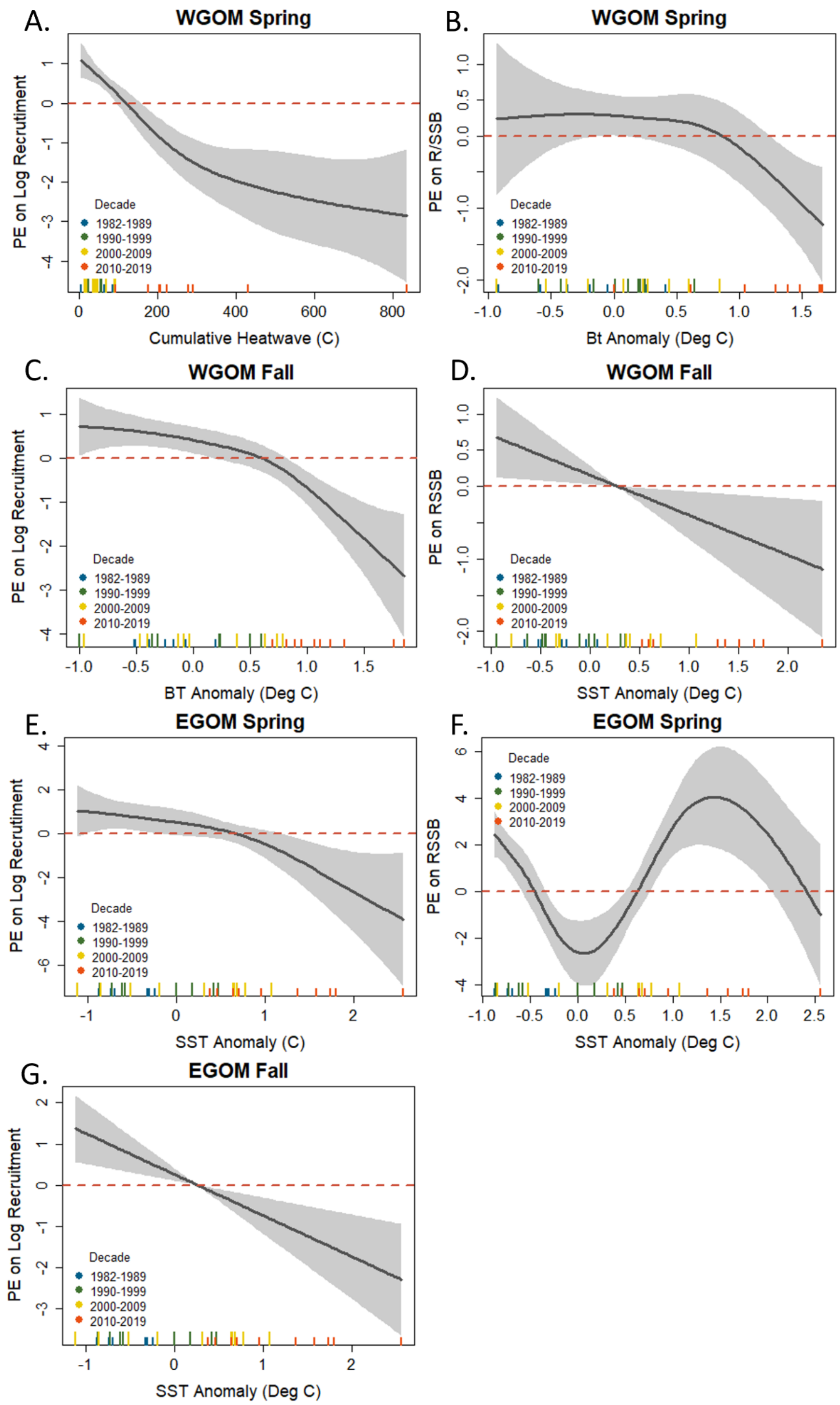

Figure 1.3. GAM response curves for models with significant temperature-related indicators. Recruitment models are in the left column and recruitment rate models are in the right column. “PE” denotes the partial effect the independent variable has on the dependent variable, either recruitment (log of age 1 abundance indices) or recruitment rate (R/SSB). Rug plot lines along the x-axis of each plot indicate distribution of the independent data, colored by decade as denoted in the legend. Shaded regions indicate the standard error confidence intervals.

TOR 1 Chapter Summary

Distribution

Based on the results from both the literature review and the exploratory GAM analyses (see WP 3 for exploratory modeling results related to distribution), the WG recommends that *Calanus* abundance and heatwave indices be considered for analyses relating to cod distribution for all stock areas. There is also evidence for density-dependent effects relating to distribution, which the WG recommends that further exploration is needed.

Recruitment

Recruitment analyses revealed bottom temperature anomaly, SST anomaly, and the heatwave index as significant drivers for the WGOM stock, and SST anomaly and calanus abundance anomaly significant for the EGOM stock. No significant drivers were identified for the GB or SNE stocks.

Growth

For growth analyses, the heatwave index, GSI, and *Pseudocalanus* abundance anomalies were significant for the WGOM stock and bottom temperature anomaly was the only significant driver identified for the EGOM stock. For Georges Bank, the WG recommends calanus abundance anomaly, the heatwave index, and SST anomaly be considered, and no significant drivers were identified for SNE cod. See WP 3 for exploratory modeling results related to growth.

Natural Mortality

Temperature and predation surfaced as important drivers of natural mortality in the ecosystem profile for cod, however no GAM analyses were performed for natural mortality. The WG recommends referencing Working Paper 14 for insights regarding natural mortality of cod across stocks.

Table 1.2. Provides a summary of indicators identified from literature review and GAM analyses. This table notes the aspects of cod stock dynamics examined (column 1), the most frequently recurring indicators identified from the literature review (column 2), indicators identified from the GAM analysis by stock dynamic and stock area (column 3), and notes on how the outcomes of the TOR 1 process could relate to management (column 4).

Population Dynamic	**Most frequent indicators identified from literature and their linkage to cod**	**Final indicators recommended from GAM analyses (most recurring significant indicators)**	**Relevance to Management**
Distribution and Habitat Use	Temperature • Changes in spawning location and time (bottom temp) • Northward shift observed in GB and southward shift observed in GOM (AMO) Depth • Juveniles inhabit deeper waters • Overwinter in depths >150m Bottom Type • Associated with hard-bottom and coarse grain sediments, boulder reefs	*GAM distribution analysis was not separated by stock area* All Stocks: • *Calanus* Abundance Anomalies • Heatwave Index	Could inform catchability as distributions change
Recruitment	Temperature (bottom temp) • Changes in spawning location and timing • Correlation between colder waters and higher recruitment Downwelling winds/ Gulf Stream Index • Related to increased retention of larvae	WGOM: • Bottom Temperature Anomaly • SST Anomaly • Heatwave Index EGOM: • SST Anomaly • Calanus Abundance Anomaly GB: • No significant drivers identified SNE: • No significant drivers identified	Could improve recruitment estimates
Growth and Maturity	Temperature • Affects growth rates directly and indirectly (food availability) ○ Greatest growth rates observed between 10-15 C • Age at maturity decreases with increasing temperatures (bottom	WGOM: • Heatwave Index • Gulf Stream Index • Pseudocalanus Abundance Anomaly EGOM: • Bottom Temperature	Could improve growth and maturity assumptions

	temp)	Anomaly GB: • Calanus Abundance Anomaly • Heatwave Index • SST anomaly SNE: • No significant drivers identified	
Natural Mortality	Temperature • Cold temperatures prolong time in developmental stages, increasing predation (SST) • Eggs/larvae have a limit of 12 C (SST) • Decreases in prey availability & increased metabolic costs under warmer temps leads to starvation (bottom temp) • Warmer temps could lead to smaller sizes at maturity, which could increase susceptibility to predation (bottom temp) Predation • Direct effect from seals & other fish	GAM analyses were not explored for natural mortality	Could improve natural mortality estimates

Spurious vs. Causal Relationships

The WG recommends future research to further explore the likelihood of spurious relationships identified. The WG ran a brief causal analysis (following the methods from Sugihara et al. 2012) on WGOM data to get an idea of causal vs. likely spurious relationships between the environmental and stock data that was examined, however this approach could be expanded across all stocks and could be more formally considered in the indicator recommendation process. These causal analyses should also be expanded to include structural equation models and confirmatory analyses. In addition, there was evidence of density dependent effects throughout the GAM analyses and the WG recommends future research efforts to further explore these effects in how they may affect or confound relationships between environmental variables and stock data.

Data availability

The WG was not able to identify any significant drivers for the SNE stock due to limited data availability and lack of positive occurrence data. The WG recommends more attention for the TOR1 process should be given to the SNE stock, either through use of alternate or additional data (if available), or exploring different approaches that are better suited for zero-inflated data.

The GAM analyses utilized data with 2019 as the final year. This was due in part because the NEFSC bottom trawl survey was shortened to a fraction of its normal spatial and temporal extent in the spring of 2020 and did not take place in the fall of 2020 due to covid restrictions, and because the final year of the various environmental data sources also varied. 2019 was the most recent year where data was consistently available for all stock areas and all data sources. Therefore, the WG recommends future research to re-explore these relationships as more data become available and the analysis can be explored over a longer time series of data.

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