ECOSYSTEM AND CLIMATE INFLUENCES ON YELLOWTAIL FLOUNDER

Jessie Kittel, Steve Cadrin, Conor McManus, Hubert duPontavice, Alex Hansell, Tara Dolan, Chris Legault, Chuck Adams, Lisa Kerr, Jamie Behan, Scott Large, Abby Tyrell, and Larry Alade

Yellowtail Flounder Research Track Working Paper. November 4 2024

Summary – Yellowtail flounder inhabit the continental shelf of the northwest Atlantic and historically supported target fisheries off New England. However, the Georges Bank and Southern New England-Mid Atlantic stocks have declined in recent decades and have not recovered despite severely restricted fisheries, suggesting that productivity may be negatively affected by climate change. Ocean waters off New England are warming faster than the global average, and decreased yellowtail flounder productivity has been associated with ocean warming in the region. US stock assessments of yellowtail flounder have exhibited retrospective patterns, in which contemporary estimates of abundance decrease when a new year of data is added, presenting a major source of uncertainty for determining stock status and informing rebuilding plans.

A literature review identified stock specific differences and indicated that yellowtail flounder are indeed vulnerable to climate variability, affecting their distribution, recruitment, and potentially other components of production such as natural mortality and growth. The environmental covariates identified as having the most support for further exploration include the Atlantic Multidecadal Oscillation (AMO), North Atlantic Oscillation (NAO), bottom temperature, Gulf Stream Index (GSI), and the cold pool index. Generalized Additive Models (GAMs) were applied to explore relationships between the identified environmental variables and stock dynamics to determine what data should be explored in yellowtail flounder stock assessment models. Several potential climate impacts were identified.

Recruitment of yellowtail flounder off southern New England was correlated to the Gulf Stream Index and the Mid-Atlantic Bight Cold Pool. Recruitment of yellowtail flounder on Georges Bank was correlated with bottom temperature, and the Atlantic Multidecadal Oscillation. Recruitment indices of CCGOM yellowtail flounder were correlated with bottom temperature and AMO. Results suggest weight-at-length was larger when ocean waters were warmer.

Background

Yellowtail flounder, *Limanda ferruginea* (a.k.a, *Myzopsetta ferruginea*), is a small-mouthed flatfish that inhabits continental shelf waters between the Gulf of St. Lawrence and the Mid-Atlantic Bight. The US fishery for yellowtail flounder is managed by the New England Fisheries Management Council (NEFMC) for three distinct stocks: Cape Cod Gulf of Maine (CCGOM), Southern New England Mid-Atlantic (SNEMA), and Georges Bank (GB). Tagging studies have revealed limited movement and interaction among these three stocks (Cadrin 2010; Wood & Cadrin 2013). Spatial distribution of the Georges Bank stock extends beyond the Exclusive Economic Zone (EEZ) and is co-managed with Canada.

As a cold-water obligate species, yellowtail flounder is susceptible to changes in temperature and other oceanic conditions (Lucey & Nye 2010). At present, stocks of yellowtail flounder on Georges Bank and off Southern New England-Mid Atlantic are historically low with limited signs of recovery, despite efforts to reduce fishing activity and relative fishing mortality (NEFSC 2022, TRAC 2023). Lux (1964) was the first to observe that the lowest levels of apparent abundance (for all stocks) coincided with the highest temperatures. The yellowtail flounder fishery grew in the 1940s as an alternative to the declining winter flounder market (Royce et al. 1959). Nye et al. (2009) proposed a hypothesis attributing the yellowtail flounder's failure to fully recover from overfishing, particularly at the southern edge of its habitat range, to the elevated shelf temperatures.

Like many other groundfish stocks in the Northeast U.S., retrospective patterns pose a significant source of uncertainty in recent yellowtail flounder stock assessments. Kerr et al. (2022) explored the potential mechanisms underlying the retrospective patterns across multiple Northeast groundfish stocks. Consistent patterns among various stocks suggested that common drivers have not been adequately accounted for in previous stock assessments. Kerr et al. (2022) identified that lagged trends in oceanic thermal conditions and associated aspects of shelf warming accounted for a substantial portion of the variance in Mohn's rho values. Recent stock assessments (including subsequent updates) have emphasized the importance of considering the potential impacts of environmental variables on recruitment (SNEMA), condition (GB), mortality (GB), and other relevant parameters (SAW54 NEFSC 2012; TRAC 2014; GARM3 NEFSC 2008).

There are distinct oceanic characteristics of the Northeast continental shelf the U.S. and Canada. Water temperatures in this area typically range 5-30°C (Johnsen et al. 1999). Environmental conditions in this region are influenced by the North Atlantic Oscillation (NAO), which is the atmospheric pressure difference between the Subtropical (Azores) High and the Subpolar Low and has decadal patterns. The NAO exhibits cyclical patterns, with positive indices indicating warmer and wetter conditions, and negative values indicating colder and drier years (Marshall et al. 2001). Another driver of environmental conditions in the region is the Atlantic Multidecadal Oscillation (AMO), which varies on longer time scales of 30 to 40 years. The AMO is a measure of sea surface temperature anomalies and is associated with warmer conditions and increased storm activity during positive years, in contrast, cooler conditions prevail during negative years (Nye et al. 2014). These cyclical environmental conditions can have substantial impacts on marine habitats, particularly for near-shore and shallow-water species. Atmospheric and oceanic conditions vary seasonally, annually, and have lagged effects on the marine ecosystem. For example, there is a two-year lag between NAO changes and subsequent alterations in the Gulf Stream (Taylor & Stephens 1998). Klein et al. (2016) reviewed numerous studies investigating the nonlinear interactions between environmental factors and their biological impacts. These studies suggest that the effects may be cumulative, resulting in more pronounced outcomes when combined, rather than when examined in isolation.

The Labrador Current and Gulf Stream play pivotal roles in transporting cold and warm water, and anomalies in these currents can impact temperature and other environmental conditions. The Labrador current brings cold arctic and subarctic water from the North, and the Gulf Stream brings warm water from the Gulf of Mexico (Richardson 2001). The Mid-Atlantic Bight cold pool, a seasonally formed body of cold water, is established annually through the interaction of the Gulf Stream and Labrador Current. This phenomenon brings colder waters onto the Continental Shelf, typically occurring from late spring through early fall, coinciding with yellowtail flounder spawning. Several studies have linked the cold pool to recruitment in the SNEMA stock (Sullivan et al. 2000, 2005; Miller et al. 2016; du Pontavice et al. 2022). The position of the Gulf Stream partially determines the characteristics of Atlantic Temperate

Slope Water (which is relatively warm and saline) and Scotian Shelf Water (which is relatively cold and fresh), which mix in the Gulf of Maine (GOM). The proportions of Atlantic Temperate Slope Water and Scotian Shelf Water entering the GOM influence the mass water properties and shelf water volume along the Northeast shelf (Seidov et al. 2021).

Climate change is impacting the New England marine ecosystem. The GOM region was warmest on record from 2015–2020, and seasonal water temperatures have been near record high since 2012, with more frequent and intense heat waves (e.g., 2021 GB heat wave intensity was record high; Pershing et al. 2021; NEFSC 2023). The Mid-Atlantic cold pool has been warming and shrinking and there has been a northward shift in the Gulf Stream, with warm slope water and little cold water from the Labrador current (NEFSC 2023). Warming, changes to circulation patterns, and phenological changes have impacted many components of the marine ecosystem. Climate change and impacts are expected to continue, including warmer surface and bottom temperatures, decreased surface and bottom salinity and increased stratification (Pershing et al. 2021).

Hare et al. (2016) used methodology developed by Morrison et al. (2015) to estimate the vulnerability of various species on the Northeast US continental shelf to climate change impacts. Yellowtail flounder was given an overall vulnerability rank of low. Biological sensitivity was also ranked as low, although climate exposure was considered high. The high climate exposure ranking was based on marine habitats for all life stages, and the values for ocean surface temperature and ocean acidification exposure factors were high. For biological sensitivity, stock status was the only attribute to receive a “high” score out of the 12 metrics measured. However, despite scoring low on biological sensitivity, Hare et al. (2016) noted that climate change is expected to negatively impact yellowtail flounder, partly because poor recruitment was linked to warming water temperatures (Sissenwine 1974) and the Mid-Atlantic cold pool (Sullivan et al. 2005). They also noted that the spatial distribution of yellowtail flounder was linked to water temperature and that their habitat range has been shifting Northward as the water temperatures have increased (Murawski 1993; Nye et al. 2009). Yellowtail flounder’s depth and substrate preferences might also justify a higher score for habitat specialization (Johnson et al. 1999).

The impact of climate change is expected to vary both in nature and magnitude for the three New England stocks of yellowtail flounder. The SNEMA stock is likely to be more susceptible to temperature changes compared to the CCGOM or GB stocks. This vulnerability stems from the SNEMA stock being situated at the southernmost extent of the species' range, near its upper thermal limits and are therefore likely to migrate poleward (Hare et al. 2016).

In contrast, the CCGOM stock is anticipated to respond to rising temperatures by moving towards deeper waters instead of shifting poleward. This is because northward movement would expose the stock to shallower waters in the Bay of Fundy and Scotian Shelf (Nye et al. 2009). Additionally, temperatures within the GOM exhibit greater stability when compared to the SNEMA region. However, despite this stability, the GOM has experienced changes such as decreased salinity and increased stratification (Friedland & Hare 2007), which could adversely affect its suitability as yellowtail flounder habitat (Laurence & Howell 1981; Sullivan et al. 2005).

In summary, climate change has been reshaping oceanic conditions in the region. Extensive research indicates that environmental factors, such as sea surface temperature (influenced by NAO), bottom temperature (affected by the AMO), salinity (altered by NAO and AMO through changes in precipitation or temperature-driven evaporation), Gulf Stream Index (GSI, an indicator of the strength or intensity of the Gulf Stream current), and the cold pool (influenced by the availability of water transported to the cold pool) significantly impact the population dynamics of yellowtail flounder.

The objective of this review is to identify relevant ecosystem and climate influences on yellowtail flounder stocks off New England. The scientific literature on yellowtail flounder was reviewed to identify environmental effects on several aspects of population dynamics. Several potential relationships between environmental indices and yellowtail flounder populations were explored to identify which indices should be considered in stock assessment.

Literature Review of Environmental Effects on Yellowtail Flounder

Scientific literature on yellowtail flounder was reviewed to identify environmental effects on spatial distribution, recruitment, growth, maturity, and natural mortality. Case studies were reviewed from throughout the geographic range of yellowtail flounder but focused on New England stocks.

<u>Environmental Effects on Spatial Distribution</u>

Oceanic conditions are undergoing changes that are influencing the distribution of preferred habitat for yellowtail flounder. They are frequently found in waters shallower than 100 m but have been caught between 10 and 1250 m. Walsh (1992) found that the distribution for adults and juveniles was based more on depth than temperature. Truesdell (2013) found that juvenile yellowtail flounder increase in abundance with depth up to 85 m. Yellowtail flounder are typically associated with flat bottom, and adults prefer sand, sand-shell, and rock-sand sediments (Bowering and Brodie 1991; Scott 1982; DeLong & Collie 2004). Conversely, they are seldom found in muddy areas (Simpson & Walsh 2004).
Spawning, egg, and larval stages are impacted by water temperature. Spawning occurs when the water temperature is between 5°C and 12°C. Eggs are found in waters ranging from 2° to 15° C. However, the temperature range with the highest densities of yellowtail flounder varies depending on the time of year. Eggs typically hatch between 10° C and 11° C, but studies have found that hatching time is much shorter at higher temperatures (14.5 days at 4° C versus 4.5 days at 14°C; Johnson et al. 1999). During the pelagic larval stage, larvae typically stay in the upper water column in water temperatures ranging between 5° and 17°C. Depending on the season and location, larvae can be subject to large changes in water temperatures (Laurence and Howell 1981). Walsh (2015) identified a northward shift in larval yellowtail flounder, resulting in a decrease in the proportion of larvae in the Northern Mid-Atlantic Bight (MAB and Southern New England (SNE) areas, while showing an increase in the northeast GB region. Before the recent trends in climate, the preferred depth range of yellowtail flounder was 37 to 73 m (Johnson et al. 1999). The preferred depth identified by Delong and Collie (2004) was 55 m. However, Bell et al. (2022) demonstrated that temperature fluctuations directly affect the location of yellowtail flounder's favored habitat. As a result of these habitat changes, catchability of yellowtail flounder in trawl surveys may also be changing. Unaccounted for changes in catchability can result in perceived changes in abundance when no changes have occurred. Yellowtail flounder now occupies areas where it was previously absent or not found in high concentrations, potentially affecting the survey's ability to capture a representative proportion of the population. Moreover, the changing climate is altering

oceanic conditions both temporally and spatially, further exacerbating these habitat changes. As temperatures rise, there is expected to be a shift in the thermal habitat of yellowtail flounder towards higher latitudes or deeper waters (Morley et al. 2018). This change in habitat could also lead to alterations in the timing of species migrating onshore or offshore. Consequently, the overlap between the spring and fall surveys conducted by NEFSC may undergo modifications due to shifts in the timing and locations of fish movements.

The change in depth preferences of yellowtail flounder has been substantiated by the research conducted by Hyun et al. (2014). They examined fishing locations from electronic monitoring and confirmed that GB yellowtail flounder migrated to deeper waters during the periods of 2000-2004 and 2006-2010. According to their findings, bottom temperature played a more significant role in driving the movement to deeper waters than the distribution of predatory species. They estimated that the optimal water temperature for yellowtail flounder ranges from 6.8°C to 7.1°C. This emphasizes the influence of bottom temperature on the species' behavior and habitat selection.

The availability of suitable habitat for yellowtail flounder showed a decline during the spring and an increase during the fall. Helser and Brodziak (1996) found a significant association between distribution patterns and both depth and bottom temperature from spring NEFSC surveys. However, in the fall surveys, fewer years demonstrated such associations. On average, this study found that yellowtail flounder were typically found at depths of 55 m across both surveys and on an interannual basis. During the spring surveys, yellowtail flounder exhibited a consistent preference for specific depths. However, their preferences for bottom temperature fluctuated, often mirroring changes in the surrounding environment. In most years, yellowtail flounder were concentrated in waters with temperatures of 4.8°C during the spring and 10.5°C during the fall. Tagging studies revealed a temperature range of 2° to 15°C, while the depth range varied from 11-120 m, with an average depth of 26 m (Cadrin and Moser 2006). Adams et al. (2018) observed an eastward shift of the GB yellowtail flounder stock and a northeastward shift of the SNEMA stock in the spring. Furthermore, a contraction in area occupancy was detected around the center of gravity for both stocks, indicating a decrease in their respective ranges. Notably, the SNEMA stock exhibited the most substantial range contraction. Regarding factors influencing area occupancy, Adams et al. (2018) identified biomass as the most important predictor, while bottom temperature had the least influence. These findings highlight the potential divergent responses of yellowtail flounder stocks to climate change and emphasize the complex interplay between environmental factors and population dynamics.

Studies indicate that distributional shifts in yellowtail flounder are likely to occur in response to changes on either end of the temperature spectrum. A recent investigation focused on the Grand Bank stock revealed a southward shift during periods of exceptionally cold temperatures. Subsequently, when the water temperature returned to pre-cold levels, the stock reverted to its previous distributional range (Robertson et al. 2021).

Although temperature is related to yellowtail flounder distribution (Murawski 1993; Helser and Brodziak 1996), longer-term and larger-scale predictors such as AMO (Nye et al. 2018) or NAO (Sullivan et al. 2005) are more effective predictors. Murawski (1993) suggested that sedentary fish species inhabiting shallower waters, like yellowtail flounder, exhibit smaller-scale distributional shifts compared to warm-water migratory species. In contrast, Nye et al. (2018) found that the SNEMA yellowtail stock displayed a large range change and proposed that sedentary species do not readily adapt to interannual temperature fluctuations, so their best response to long-term temperature increases would be a change in distribution.

Lowman et al. (2021) identified several factors that influenced yellowtail flounder bycatch in the scallop fishery, including latitude, longitude, management area, temperature, zenith angle, season, month, and year. Unlike previous studies, depth and sediment type were not identified as significant factors, although depth exhibited a significant interaction with temperature and management area.
Adams et al. (2018), Pereira et al. (2012), and Simpson and Walsh (2004) provided support for the basin hypothesis in their studies. The basin hypothesis proposes that there is a density-dependent influence on habitat distribution (MacCall 1990). Specifically, when yellowtail flounder populations are high, they occupy a wider range of habitats. However, during periods of low population levels and reduced competition, individuals tend to concentrate in the most optimal and preferred habitat types. Brodie et al. (1998) discovered a positive correlation between the range of yellowtail flounder and stock abundance on the Grand Banks, but no significant correlation with bottom temperature was found. Pereira et al. (2012) found that the area occupied by flounder increased by a factor of two when abundance was high, and local density increased predominantly in higher quality habitat that had been closed to commercial fishing.

Changes in the distribution of important prey species, such as euphausiids, which form a significant part of the yellowtail flounder's diet, have also been observed. These prey species have shifted their distribution poleward, as documented by Lasley-Rasher et al. (2015). Nocturnal off-bottom movements were found to be common among yellowtail flounder (Cadrin and Westwood 2004). These movements can persist for several hours. Walsh and Morgan (2004) also reported similar findings for yellowtail flounder on the Grand Banks and suggested that these off-bottom movements were associated with shifts to different habitats. Truesdell (2013) found that there were higher catches of yellowtail flounder at night. Similarly, the NEFSC survey catches more yellowtail at night than during the day.

These findings contribute to our understanding of the factors influencing the habitat distribution and behavior of yellowtail flounder. Density-dependent effects, changes in prey distribution, and population abundance play important roles in shaping the species' spatial dynamics and movement patterns. The combined preferences for fixed-location substrate and spatially dynamic temperature may be decreasing the intersection of preferred bottom types and temperatures (Hare et al. 2012) that are available to yellowtail flounder (e.g., sandy habitat with 5°C to 10°C bottom temperatures), thereby decreasing the available habitat and carrying capacity of the environment.

Environmental Effects on Recruitment

Recruitment of yellowtail flounder appears to be influenced by several aspects of the environment, from local physical conditions (e.g., temperature, salinity) to regional oceanographic patterns (GSI, Cold Pool Index), to larger-scale oceanographic and atmospheric conditions (AMO, NAO). Environmental conditions have been shown to impact the condition of the yolk sac, further emphasizing the connection between temperature and recruitment success (Howell 1980). Temperature exerts a significant influence on various aspects of fish recruitment, including spawning timing, egg viability, larval growth and mortality, food availability, and adult growth (Takade-Heumacher et al. in 2014). Perretti et al. (2017) found three different recruitment regimes occurred for multiple species of groundfish in the Northeastern continental shelf region: 1980s had low success, 1990s had high success, the 2000s had low success. These recruitment regimes coincided with copepod abundance and size structure regimes (Perretti et al. 2017).

Temperature has been identified as a significant factor in explaining variations in yellowtail recruitment (Sissenwine 1974, 1977). Other investigations, such as the work of Sullivan et al. (2000), found associations between recruitment and ocean bottom temperature conditions. Temperature plays a crucial role in shaping ocean stratification and vertical thermal structure. Changes in these thermal characteristics can have important implications for recruitment dynamics. Sullivan et al. (2005) hypothesized that prolonged warm conditions would likely lead to a decrease in settlers within the Mid-Atlantic Bight (MAB).

Laurence and Howell (1981) observed that when salinity levels were low, at both low and high temperatures, only 10-30% of the embryos of yellowtail flounder survived to hatch. At intermediate temperatures and high salinity, embryo survival significantly increased to 70-90%. Furthermore, the size of the larvae upon hatching was influenced by both salinity and temperature, with larger larvae observed at moderate salinity levels and mid to upper temperature ranges. In a more recent study conducted by Walsh et al. (2004), a negative correlation between recruitment and salinity was found. The 2012 benchmark stock assessment of SNEMA yellowtail flounder included a term of reference to "Investigate causes of annual recruitment variability, particularly the effect of temperature" (NEFSC 2012). Recruitment was lower when the cold pool was warmer and smaller. Because of a trend in the Cold Pool Index over the time series (cold pool shrinking and warming), stock productivity was decreasing because of changing environmental conditions. An environmentally explicit stock-recruitment model provided a better fit than those based on spawning stock biomass alone. Based on the change in climate and exploratory stock-recruitment modeling, reference points were based on recruitment estimates from the recent period, 1990-2010 (NEFSC 2012).

In a comprehensive study by Xu et al. (2017), the effects of various factors including the NAO index, Cold Pool Index (CPI), Gulf Stream North Wall (GSNW), and GSI were examined to understand their influence on recruitment deviations of yellowtail flounder. The study revealed that the GSI, which influences a range of physical and biological conditions on the continental shelf, may provide a better explanation for recruitment deviations compared to the CPI. By considering the broader context of physical and biological shelf conditions, the GSI offers valuable insights into the complex interactions that impact the recruitment dynamics of this species.

The AMO represents a long-term, large-scale shift in oceanic conditions encompassing factors such as temperature and circulation. This phenomenon holds implications for various regions and can influence the dynamics of marine ecosystems. During the positive phase of the AMO, the GOM experiences elevated land and ocean temperatures, accompanied by increased rainfall and river flow. Conversely, in the Southern New England (SNE) and Mid-Atlantic Bight (MAB) regions, a positive AMO phase is associated with reduced rainfall and river flow (Enfield et al. 2001; Sutton and Hodson 2007). Considering these changes, Nye et al. (2009) suggested that the rise in temperature and alterations in circulation patterns resulting from a positive AMO phase could potentially amplify the mortality rates of fish during their early life stages, particularly in the southern reaches of their distribution. Furthermore, shifts in circulation may lead to the transportation of eggs and larvae to less suitable nursery habitats. Additionally, changes in stratification, attributable to the AMO phases, may introduce further challenges.

Stocks in the northern part of a species' range may experience more favorable conditions for recruitment unlike those in the southern regions. These inconsistencies highlight the varying impacts of the AMO on different geographic areas and underscore the importance of considering these dynamics in understanding the recruitment patterns of individual stocks.

Brodziak and O'Brien (2005) examined various environmental factors and their influence on recruit per spawner anomalies. Among these factors, they found that the NAO, with a lag of two years, exerted the most substantial impact. However, the observed trends differed among stocks. For the Georges Bank stock, positive anomalies in recruit per spawner were associated with positive NAO values. In contrast, the CCGOM stock exhibited negative recruit per spawner anomalies when NAO was positive. Interestingly, the SNEMA stock did not have any significant predictor variables in relation to NAO. However, they did determine that the geostrophic current plays a relatively insignificant role in predicting abnormalities in yellowtail flounder recruits per spawner.

Sullivan et al. (2005) identified a correlation between NAO and air temperature with SNEMA recruitment. Similarly, Pershing et al. (2005) established a link between zooplankton abundance and the NAO. Johnson (2000) examined the match-mismatch hypothesis relating prey of larval Yellowtail Flounder with subsequent recruitment in the Southern New England and Georges Bank stocks during 1977-1987. There was no clear demonstration of a match or mismatch for strong or weak year classes. The association between the Mid-Atlantic Bight (MAB) cold pool and recruitment success in the SNEMA stock has been consistently observed in multiple studies (Sullivan et al. 2000, 2005; Du Pontavice et al. 2022; Miller et al. 2016). The MAB cold pool is a seasonal accumulation of cold water formed through oceanic processes. However, over the past 45 years, the cold pool has weakened, diminished in size, and exhibited shorter duration (Du Pontavice et al. 2022). Given that the SNEMA stock resides at the southern extent of its range, it likely relies on the presence of the cold pool for optimal recruitment conditions.

Du Pontavice et al. (2022) demonstrated that incorporating the Cold Pool Index (CPI) in stock assessment models reduced retrospective patterns and improved their predictive power for recruitment and spawning stock biomass (SSB). They also emphasized that recruitment is among the most sensitive biological parameters to environmental influences. The cold pool and its relationship to recruitment may serve as a critical bottleneck in the yellowtail flounder's life history (Haltuch et al. 2019). Sullivan et al. (2005) found that years with colder and longer-lasting cold pool conditions were associated with stronger recruitment. Moreover, Sullivan et al. (2015) highlighted the connection between recruitment and the NAO, which influences winter air temperatures and likely affects the formation of the cold pool through atmospheric forcing and cooling (Mann and Lazier, 1996). Additionally, Miller et al. (2016) identified the MAB cold pool as an important predictor of recruitment, and its inclusion in models enhanced model performance and reduced residual variability.

Environmental Effects on Growth and Maturity

Growth and maturity patterns exhibit variations among yellowtail flounder stocks and between sexes. Sexual dimorphism is observed in growth, with females exhibiting a faster growth rate compared to males (Lux and Nichy 1969; Cadrin 2003). Yellowtail flounder display early maturation compared to most other fish species, with nearly all females reaching maturity by the age of three (Wood and Cadrin 2013). Wood and Cadrin (2013) also reported a lower tag recovery rate for males compared to females, indicating the presence of sex-specific growth rates.

Ross and Nelson (1992) examined the influences of stock abundance and bottom-water temperature on growth dynamics of GB Yellowtail Flounder. Growth rates were highly correlated with stock abundance but not with temperature. Annual temperature fluctuations of the magnitude studied appeared to exert only modest influence on growth rates. However, this study is based on yellowtail flounder growth before the warming of the last three decades. Perez (2022) found that the condition factor for yellowtail flounder on Georges Bank is not constant over time.

Regarding regional differences, yellowtail flounder found in the northern part of the continental shelf (CCGOM stock) grow slower compared to those inhabiting the southern portion of their range (GB and SNEMA; Cadrin et al. 1998; Cadrin 2010). This aligns with the findings of Scott (1954), who observed that yellowtail flounder located further north, specifically in the middle ground and western bank areas of the Scotian Shelf, grew slower compared to those in the vicinity of Cape Cod. Scott (1954) further noted that the northern fishing areas harbored older, slower-growing fish, whereas the Cape Cod area contained smaller, younger individuals.

Based on data obtained from the commercial fishery, most of the somatic growth for SNEMA yellowtail occurs between April and December. However, there has been a gradual decline in fish condition (measured by weight-at-age and length-at-age) for this stock since the 1990s, with some signs of improvement in the 2010s (Cadrin et al. 1998; Takade-Heumacher et al. 2014). Recent trends in age and length composition indicate a skew towards younger and smaller fish (Takade-Heumacher et al. 2014). In relation to these observations, Takade-Heumacher et al. (2014) proposed that changes in the NAO could be influencing fish abundance, catch, and condition, potentially through alterations in metabolic rate. They suggested that growth dynamics, as reflected in the von Bertalanffy growth parameter, may have undergone changes in response to temperature or other environmental conditions, leading to reduced weight gain in the fish.

DeCelles and Vidal (2020) estimated maturity ogives for the CCGOM yellowtail stock that demonstrate a decline in both length and age at 50% maturity from 1976 to 2014. Their study also revealed a shift towards earlier maturation at smaller sizes, indicating potential influences from factors such as temperature changes or fisheries-induced evolution.

Environmental Effects on Natural Mortality

The natural mortality for yellowtail flounder is believed to exceed an exponential rate of 0.2 (Legault et al. 2014; Alade 2014). Sullivan et al. (2005) concluded that elevated water temperatures had a detrimental effect on the survival rates of yellowtail flounder eggs and planktonic larvae in the Mid-Atlantic Bight (MAB) region, resulting in decreased settlement. They postulated that this negative impact could be attributed to indirect factors such as increased activity of benthic predators or food scarcity. Nye et al. (2009) further highlighted that large-scale temperature and circulation changes associated with the AMO had the potential to escalate mortality rates, particularly in the southern range. Additionally, early life stages were identified as being particularly susceptible to adverse effects when exposed to lethal temperatures during hatching.

Pershing et al. (2021) found greater prevalence of diseases affecting fish species in the Gulf of Maine. Specifically, the parasitic protozoan *Ichthyophonus*, which impacts yellowtail flounder, has exhibited an increasing prevalence in recent years (Pershing et al. 2021). According to the 2012-2014 seasonal bycatch survey (Legault et al. 2014), approximately 3% of yellowtail flounder were found to be infected with this pathogen. Rago and Huntsberger (2014) explored the potential consequences of varying levels of *Ichthyophonus* prevalence and infection rates on natural mortality, considering the influence of fishing pressure. They determined that certain levels of prevalence and infection rates could lead to elevated natural mortality rates. However, it is currently unknown if current rates of prevalence are higher than in the past even though lethality has increased. Huntsberger et al. (2017) sampled infected fish in the Georges Bank region and observed that the infected individuals were primarily concentrated in the eastern part of Georges Bank. Furthermore, a substantial proportion (81%) of the infected fish exhibited severe infections.

Pershing et al. (2021) emphasized the anticipated consequences of warming temperatures on distributional shifts, which are likely to result in alterations in the spatial overlap between predator and prey species. In the case of yellowtail flounder, this could potentially lead to an elevated risk of encountering predators and a diminished probability of locating prey. Moreover, the expanding range of species better adapted to the changing temperatures may introduce heightened competition for shared resources, presenting an additional challenge for yellowtail flounder. As a consequence of these increasing risks, the sustainable level of fishing pressure that can be maintained is expected to decline. However, Tsou and Collie (2001) did not find yellowtail flounder to be a significant prey species in their study. The reduced availability of prey species is a factor that can contribute to increased natural mortality rates in yellowtail flounder populations. Several studies have observed a decline in important prey species that play a crucial role in various life stages of yellowtail flounder. Pershing et al. (2021) documented a decrease in the abundance of Calanus finmarchichus, a vital zooplankton species that serves as a crucial food source for yellowtail flounder larvae. This species is also an essential prey item for forage fish, which in turn become prey for older groundfish species. Furthermore, Legault (2013) identified a recent decline in the condition factor of yellowtail flounder, which may be a contributing factor to low recruitment and increased natural mortality.

In efforts to improve assessment models and better understand population dynamics, Stock et al. (2021) demonstrated that incorporating a two-dimensional autocorrelation smoother for the survival or natural mortality parameter in a state-space age-structured assessment model enhanced the model's fit. This approach also reduced retrospective patterns in key indicators such as spawning stock biomass (SSB), fishing mortality (F), and recruitment.

Exploratory Data Analyses

Data sources

We explored relationships between environmental variables (Table 1) and recruitment or growth using age-1 abundance indices from the Northeast Fisheries Science Center (NEFSC) bottom trawl surveys, conducted during both the fall and spring seasons. These datasets present standardized, stratified mean counts of yellowtail flounder per trawl, classified by age. The dataset encompasses a broad temporal span, spanning from 1963 to 2023, encompassing three distinct stocks and two distinct survey periods. The mean abundance-at-age 1 and weight-at-age 1 data encompassed the years from 1963 to 2021 for all stocks, with certain years missing. The exclusion of the most recent years' survey data from the analyses was due to its unavailability for all environmental variables.

North Atlantic Oscillation (NAO) data were obtained from the NOAA National Centers for Environmental Information (https://www.ncdc.noaa.gov/teleconnections/nao/). These data are monthly anomalies of the surface sea level pressure difference (hPa) calculated as deviations from the 1950-2000 climatological daily mean and standard deviation base period. The NAO index is based on the surface sea-level pressure difference between the Subtropical High and the Subpolar Low. The phases vary monthly and are associated with basin-wide changes in the intensity and location of the North Atlantic jet stream and storm track. Strong positive phases are associated with higher-than-normal temperatures in the eastern US. These data span from January 1950 to the present and are calculated over 0-90 °N latitude. The NAO index is updated monthly.

Atlantic Multidecadal Oscillation (AMO) index data were available from the NOAA Physical Sciences Laboratory (Enfield et al. 2001; https://psl.noaa.gov/data/timeseries/AMO/). The AMO is a series of long-term (20 to 40-year phases) changes of sea surface temperature with warm and cold phases that vary by 1 degree F from one extreme to the other. This time series spans from 1948-present and is calculated from the Kaplan SST dataset, which represent gridded global SST anomalies. The AMO index is recorded at a monthly time interval, the unsmoothed dataset was used in this study. The AMO index is updated annually.

The Cold Pool Index, Persistence index, and Extent index (CPI, PI, and EI) are alternative measures of the Mid Atlantic Bight cold pool, a seasonal cold-water mass found on the continental shelf that occurs in late spring and continues through early fall that has been tied to the recruitment of yellowtail flounder in multiple studies (Sullivan et al. 2005; Miller et al. 2016; du Pontavice et al. 2022). The cold pool index is a way to account for the intensity, persistence, and spatial extent of the cold pool by using bottom temperature data (du Pontavice et al. 2022). The data used here was sourced from du Pontavice et al. (2022) and has an index value for each year. Cold pool indices are updated annually (NEFSC 2024).

The Gulf Stream Index (GSI) is the degrees latitude above the average Gulf Stream position based on ocean temperature at 200 m (15 C) depth between 55°W to 75°W. Ocean temperature data used for this analysis are available at https://resources.marine.copernicus.eu/?option=com_csw&view=details&product_id=SEALEVEL_GLO_PHY_L4_REP_OBSERVATIONS_008_047.

Bottom temperature (BT)- The high-resolution bottom temperature data was sourced from du Pontavice et al. (2023). Bottom temperature observations for the Northeast U.S. continental shelf were interpolated using a high-resolution ocean model. The interpolation process involved integrating in situ observations from various sources, such as research surveys and buoys, with model outputs to create a comprehensive and continuous temperature dataset. This method allowed for the generation of a robust representation of bottom temperatures across the region. For the yellowtail working group, the modeled temperature data were spatially and temporally aggregated to match the specific needs of stock assessment (i.e., stock-specific bottom temperatures). Spatial aggregation was achieved by averaging temperatures within defined geographic regions corresponding to yellowtail flounder stocks. The data were aggregated into monthly or seasonal averages. To update the temperature series, new observations can be continuously incorporated into the model, ensuring that the dataset remains current.

When environmental time series data were available monthly, we computed 12-month and 6-month means leading up to each survey. This process produced four indices for these environmental variables, resulting in a single 6-month mean variable and a 12-month mean variable for each of the two NEFSC surveys. This approach was adopted to ensure that the data accurately represented the environmental conditions at the time when the cohort of new recruits would have entered the ecosystem.

Subsequently, the aggregated and lagged environmental variables were paired with the corresponding recruitment index from the surveys. All environmental data were utilized throughout the entire time series for yellowtail flounder.

<u>Statistical Analyses</u>

Prior to model fitting, correlation was tested between environmental variables to assess their independence. When a high correlation was identified between variables, the selection of variables for the final (reduced) model was based on Akaike information criterion (AIC) values (Zuur et al. 2009). In cases where both the six and 12-month versions of an environmental variable remained in a model, the version with the highest % deviance explained was chosen. To establish the most suitable distribution family for each response variable, histograms were inspected, and residual patterns were examined. For the recruitment models, a Tweedie distribution was assumed for the high frequency of zero values.

Three versions of the GAM models were explored as alternative approaches to accounting for yellowtail flounder stocks and multiple environmental variables.

'Each index-all stocks': The first approach ('each index-all stocks') tested the effect of each environmental variable on all stocks. These GAMs described the relationship between the recruitment index (response variable) and an individual environmental variable (predictor variable) while taking into account the different stocks. This was done for each environmental variable (one for each survey).
Example formula:
(All.Stocks_NEFSC_Fall) ~ s(bottom temperature 6 month lag, by = stock)

'*All indices-each stock*': The second approach ('all indices-each stock') tested the effect of multiple environmental indices on each stock individually. These GAMs described the relationship between the

recruitment index for an individual stock (response variable) and multiple environmental variables (predictor variables).
Example formula:
(SNEMA_NEFSC_ Fall) ~ s(cold pool index) + s(persistence index) + s(extent index) + s(AMO 6 month lagged mean) + s(AMO 12 month lagged mean) + s(NAO 6 month lagged mean) + s(NAO 12 month lagged mean) + s(GSI 6 month lagged mean) + s(GSI 12 month lagged mean) + s(bottom temperature 6 month lagged mean) + s(bottom temperature 12 month lagged mean)
This model was fitted with all the environmental covariates, and then the model was reduced by removing insignificant environmental variables based on AIC values, this was done for each of the recruitment indices (numbers-at-age 1 and weight-at-age 1).

'*Each index-each stock*': The third approach ('each index-each stock') tested the effect of each index on each individual stock. These 'each index-each stock' GAMs described the relationship between the recruitment index for an individual stock (response variable) and a single environmental variable (predictor variable). This was done for each survey separately.
Example formula:
(SNEMA_NEFSC_ Fall) ~ s(bottom temperature 6 month lag)
The Mid-Atlantic Bight cold pool-related indices (CPI, PI, and EI) were only evaluated for the SNEMA stock. The geographic location of the cold pool only overlaps with the SNEMA stock and therefore was not considered for the CCGOM or GB stocks.
Model fitting and the creation of several plots were accomplished using the mgcv package in Rstudio (R Core Team, 2023). Additionally, we employed the MuMIn package (Barton, 2024) and gratia package (Simpson, 2023) at various stages of this process, either for plotting the models or assisting in model selection. Model validation was based on analysis of residuals, Akaike information criterion (AIC), significance, and percent deviance explained (%DE).

The SNEMA stock had the strongest relationships with GSI, bottom temperature, and cold pool indices for the fall survey data and with AMO and bottom temperature for the spring survey data. The CCGOM stock had the strongest relationships with AMO and bottom temperature for the spring survey data and had no strong relationships for the fall survey data. The GB stock had the strongest relationships with AMO and bottom temperature for the fall survey data and with bottom temperature for the spring survey data.

Models generally fit the data well (Figure 1). The SNEMA and GB stocks tended to exhibit stronger associations with environmental variables than the CCGOM stock (Table 2.2, Figures 2-10). The SNEMA stock had significant relationships in most models. The GB stock also has significant relationships with several environmental variables. However, the relationships observed in the SNEMA stock were generally stronger.

In the 'each index-each stock' models, all cold pool-related indices were statistically significant (Table 2, Figure 10). However, only the fall extent index was retained in the final 'all indices-each stock' models. In the models of spring surveys, the extent index and persistence index were linear, and the cold pool index displayed a pronounced non-linear relationship.

GAM results suggest environmental indices had generally less significant effects on growth, but bottom temperature and GSI had the strongest relationships with weight at age. Similarly to the recruitment GAMs, the SNEMA and GB stocks tended to exhibit stronger associations with environmental variables than the CCGOM stock (Table 3, Figures 11-19). However, this was mostly in the Spring survey GAMs. The SNEMA stock had more linear relationships in most models compared to the other two stocks. The GB stock had the most significant relationships with several environmental variables.

Discussion

Based on these results, the Yellowtail Flounder Research Track Working Group (WG) made several data and model decisions. The WG decided to apply time-varying size at age from annual samples or multi-annual samples for all three stocks. The WG also decided to explore environmental covariates to recruitment deviations, with SNEMA recruitment informed by lagged GSI or Cold Pool Index, GB recruitment informed by lagged bottom temperature or AMO, and CCGOM recruitment informed by lagged bottom temperature. The same environmental covariates were also recommended for exploration on time varying natural mortality.

References

Adams CF, Alade LA, Legault CM, O'Brien L, Palmer MC, Sosebee KA, Traver ML. 2018. Relative importance of population size, fishing pressure and temperature on the spatial distribution of nine Northwest Atlantic groundfish stocks. PLoS One. 13(4):e0196583.

Bartoń K. 2024. MuMIn: Multi-Model Inference. R package version 1.48.4, https://CRAN.R-project.org/package=MuMIn.

Brodie WB, Walsh SJ, Atkinson DB. 1998. The effect of stock abundance on range contraction of yellowtail flounder (*Pleuronectes ferruginea*) on the Grand Bank of Newfoundland in the Northwest Atlantic from 1975 to 1995. Journal of Sea Research 39: 139-152.

Brodziak J, O'Brien L. 2005. Do environmental factors affect recruits per spawner anomalies of New England groundfish? ICES Journal of Marine Science 62: 1394–1407.

Bowering WR, Brodie WB. 1991. Distribution of commercial flatfishes in the Newfoundland-Labrador region of the Canadian northwest Atlantic and changes in certain biological parameters since exploitation. Neth. J. Sea Res. 27: 407-422.

Cadrin SX. 2010. Interdisciplinary analysis of yellowtail flounder stock structure off New England. Reviews in Fisheries Science 18: 281–299.

Cadrin SX, Moser J. 2006. Partitioning on-bottom and off-bottom Behavior: a case study with yellowtail flounder off New England. ICES C.M. 2006/Q:14.

Cadrin SX, Overholtz WJ, Neilson JD, Gavaris S, Wigley SE. 1998. Stock assessment of Georges Bank yellowtail flounder for 1997. Northeast Fish. Sci. Cent. Ref Doc. 98-06.

DeCelles, GR, Vidal T. 2020. Long-term changes in the maturation and growth of Cape Cod/Gulf of Maine yellowtail flounder *Limanda ferruginea*. Marine Ecology Progress Series, 633, 169-180.

du Pontavice H, Chen Z, Saba VS. 2023. A high-resolution ocean bottom temperature product for the northeast U.S. continental shelf marine ecosystem. Progress in Oceanography, 102948.

du Pontavice H, Miller TJ, Stock BC, Chen Z, Saba VS, Hidalgo M. 2022. Ocean model-based covariates improve a marine fish stock assessment when observations are limited. ICES Journal of Marine Science 79: 1259–1273.

Enfield DB, Mestas-Nuñez AM, Trimble PJ. 2001. The Atlantic multidecadal oscillation and its relation to rainfall and river flows in the continental US. Geophysical Research Letters 28: 2077-2080.

Hare JA, Manderson JP, Nye JA, Alexander MA, Auster PJ, Borggaard DL, Capotondi AM, Damon-Randall KB, Heupel E, Mateo I, O'Brien L, Richardson DE, Stock CA, Biegel ST. 2012. Cusk (*Brosme brosme*) and climate change: assessing the threat to a candidate marine fish species under the US Endangered Species Act. ICES Journal of Marine Science 69: 1753-1768.

Hare JA, Morrison WE, Nelson MW, Stachura MM, Teeters EJ, Griffis RB, Alexander MA, Scott JD, Alade L, Bell RJ, Chute AS. 2016. A vulnerability assessment of fish and invertebrates to climate change on the northeast US continental shelf. PLoS ONE 11(2): e0146756.

Helser TE, Brodziak JKT. 1996. Influence of temperature and depth on distribution and catches of yellowtail flounder, Atlantic cod, and haddock in NEFSC bottom trawl surveys. Northeast Fisheries Science Center Reference Document 96-05e. 24 p.

Howell WH. 1980. Temperature effects on growth and yolk utilization in yellowtail flounder, *Limanda ferruginea*, yolk-sac larvae. Fishery Bulletin 78: 731-739.

Huntsberger, C. J., Hamlin, J. R., Smolowitz, R. J., & Smolowitz, R. M. (2017). Prevalence and description of *Ichthyophonus* sp. in yellowtail flounder (*Limanda ferruginea*) from a seasonal survey on Georges Bank. Fisheries Research 194: 60-67.

Johnson DL, Morse WW, Berrien PL, Vitaliano JJ. 1999. Essential fish habitat source document. Yellowtail flounder, *Limanda ferruginea*, life history and habitat characteristics. NOAA Technical Memorandum NMFS-NE-140.

Johnson DL. 2000. Preliminary examination of the match-mismatch hypothesis and recruitment variability of yellowtail flounder, *Limanda ferruginea*. Fishery Bulletin 98: 854-863.

Kerr, L., Barajas, M., & Wiedenmann, J. 2022. Coherence and potential drivers of stock assessment uncertainty in Northeast US groundfish stocks. ICES Journal of Marine Science 79: 2217-2230.

Klein, E. S., Smith, S. L., & Kritzer, J. P. 2017. Effects of climate change on four New England groundfish species. Reviews in Fish Biology and Fisheries 27: 317-338.

Lasley-Rasher, R. S., Brady, D. C., Smith, B. E., & Jumars, P. A. 2015. It takes guts to locate elusive crustacean prey. Marine Ecology Progress Series 538: 1-12.

Laurence GC, Howell WH. 1981. Embryology and influence of temperature and salinity on early development and survival of yellowtail flounder *Limanda ferruginea*. Mar. Ecol. Prog. Ser. 6: 11-18.

Legault CM. 2013. Synthesis of Information Presented for Georges Bank Yellowtail Flounder Diagnostic Benchmark: Putting the Pieces Together. TRAC Working Paper 2014/46.

Legault CM, Cadrin SX. 2014. A Guided Tour through the Yellowtail Flounder Literature for the 2014 Georges Bank Yellowtail Flounder Diagnostic and Empirical Approach Benchmark. TRAC Working Paper 2014/28.

Lowman BA, O'Keefe CE, Cadrin SX. 2021. Predictive Models of Yellowtail Flounder Bycatch in the US Sea Scallop Fishery on Georges Bank. Journal of Northwest Atlantic Fishery Science 52: 1–18.

Lucey SM, Nye JA. 2010. Shifting species assemblages in the Northeast US Continental Shelf Large Marine Ecosystem. Mar Ecol Prog Ser 415: 23–33.

Lux FE. 1964. Landings, fishing effort, and apparent abundance in the yellowtail flounder fishery. ICNAF Res. Bull 1: 5-21.

Lux FE, Nichy FE. 1969. Growth of yellowtail flounder, *Limanda ferruginea* (Storer), on three New England fishing grounds. ICNAF Res. Bull. 6: 5-25.

MacCall AD. 1990. Dynamic Geography of Marine Fish Populations. University of Washington Press.

Marshall J, Johnson H, Goodman J. 2001. A study of the interaction of the North Atlantic Oscillation with ocean circulation. Journal of Climate 14: 1399-1421.

Mann KH, Lazier JR. 2005. Dynamics of marine ecosystems: biological-physical interactions in the oceans. John Wiley & Sons.

Miller TJ, Hare JA, Alade LA. 2016. A state-space approach to incorporating environmental effects on recruitment in an age-structured assessment model with an application to southern New England yellowtail flounder. Can. J. Fish. Aquat. Sci. 73: 1261–1270.

Morley, J.W., Selden, R.L., Latour, R.J., Frölicher, T.L., Seagraves, R.J. and Pinsky, M.L., 2018. Projecting shifts in thermal habitat for 686 species on the North American continental shelf. PloS one, 13(5):e0196127.

Murawski SA. 1993. Climate change and marine fish distributions: forecasting from historical analogy. Transactions of the American Fisheries Society 122: 647-658.

NEFSC (Northeast Fisheries Science Center). 2012. 54th Northeast Regional Stock Assessment Workshop (54th SAW) Assessment Report. NEFSC Ref. Doc. 12-18.

NEFSC (Northeast Fisheries Science Center). 2022. Management Track Assessments Fall 2022. NEFSC Tech. Memo. 305; 167p.

NEFSC (Northeast Fisheries Science Center). 2023. 2022 State of the Ecosystem, New England. https://doi.org/10.25923/ypv2-mw79.

NEFSC (Northeast Fisheries Science Center). 2024 Technical Documentation, State of the Ecosystem Report. https://noaa-edab.github.io/tech-doc/National Oceanic and Atmospheric Administration (NOAA). (n.d.). Oceanography. NOAA Fisheries - Northeast Fisheries Science Center. Retrieved from https://apps-nefsc.fisheries.noaa.gov/nefsc/ecosystem-ecology/oceanography.html

Nye JA, Link JS, Hare JA, Overholtz WJ. 2009. Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. Marine Ecology Progress Series 393: 111–129.

Nye, J.A., Baker, M.R., Bell, R., Kenny, A., Kilbourne, K.H., Friedland, K.D., Martino, E., Stachura, M.M., Van Houtan, K.S. and Wood, R., 2014. Ecosystem effects of the Atlantic multidecadal oscillation. Journal of Marine Systems 133: 103-116.

Pereira JJ, Schultz ET, Auster PJ. 2012. Geospatial analysis of habitat use in yellowtail flounder *Limanda ferruginea* on Georges Bank. Marine Ecology Progress Series 468: 279-290.

Perretti, C. T., Fogarty, M. J., Friedland, K. D., Hare, J. A., Lucey, S. M., McBride, R. S., ... & Wuenschel, M. J. 2017. Regime shifts in fish recruitment on the Northeast US Continental Shelf. Marine Ecology Progress Series, 574, 1-11.

Pershing AJ, Alexander MA, Brady DC, Brickman D, Curchitser EN, Diamond AW, McClenachan L, Mills KE, Nichols OC, Pendleton DE, Record NR, Scott JD, Staudinger MD, Wang Y. 2021. Climate impacts on the Gulf of Maine ecosystem: A review of observed and expected changes in 2050 from rising temperatures. Elem Sci Anth, 9: 1. DOI: https://doi.org/10.1525/elementa.2020.00076.

Perez, PJ. 2022. Ecological factors influencing the yellowtail flounder population in Closed Area II Access Area on Georges Bank. [Unpublished master's dissertation]. University of Massachusetts Dartmouth.

R Core Team. 2023. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rago P, Huntsberger C. 2014. Are Current Prevalence Rates of *Ichthyophonus* Consistent with High Natural Mortality? TRAC Working Paper 2014/11.

Richardson PL. 2019. Florida Current, Gulf Stream, and Labrador Current. Pp. 351-361 In JK Cochran, HJ Bokuniewicz & PL Yager (eds.) Encyclopedia of Ocean Sciences, Third Edition. Elsevier.

Robertson MD, Gao J, Regular PM, Morgan MJ, Zhang F. 2021. Lagged recovery of fish spatial distributions following a cold-water perturbation. Scientific reports. 11: 9513.

Ross MR, Nelson GA. 1992. Influences of stock abundance and bottom-water temperature on growth dynamics of haddock and yellowtail flounder on Georges Bank. Transactions of the American Fisheries Society 121: 578-587.

Royce WF, Buller RJ, Premetz ED. 1959. Decline of the yellowtail flounder (*Limanda ferruginea*) off New England. Fishery Bulletin 146: 169-267.

Scott JS. 1982. Selection of bottom type by groundfishes of the Scotian Shelf. Can. J. Fish. Aquat. Sci. 39: 943-947.

Seidov D, Mishonov A, Parsons R. 2021. Recent warming and decadal variability of Gulf of Maine and Slope Water. Limnology and Oceanography 66: 3472-3488.

Simpson G. 2023. gratia: Graceful ggplot-Based Graphics and Other Functions for GAMs Fitted using mgcv. R package version 0.9.2.9011, https://gavinsimpson.github.io/gratia/.

Sissenwine MP. 1974. Variability in recruitment and equilibrium catch of the Southern New England yellowtail flounder fishery. J. Cons. Int. Explor. Mer. 36: 15–26.

Sissenwine MP. 1977. A compartmentalized simulation model of the Southern New England yellowtail flounder, *Limanda ferruginea*, fishery. Fishery Bulletin. 75: 465-482.

Stock, B. C., Xu, H., Miller, T. J., Thorson, J. T., & Nye, J. A. 2021. Implementing two-dimensional autocorrelation in either survival or natural mortality improves a state-space assessment model for Southern New England-Mid Atlantic yellowtail flounder. Fisheries Research, 237, 105873.

Sullivan MC, Cowen RK, Steves BP. 2005. Evidence for atmosphere–ocean forcing of yellowtail flounder (*Limanda ferruginea*) recruitment in the Middle Atlantic Bight. Fisheries Oceanography 14: 386-399.

Sutton, R. T., & Hodson, D. L. 2007. Climate response to basin-scale warming and cooling of the North Atlantic Ocean. Journal of Climate 20: 891-907.

Takade-Heumacher H, Liu O, Smith SL, Kritzer J, Fujita R, Fund ED. Exploring hypotheses for reduced growth and truncated size structure of Georges Bank yellowtail flounder. TRAC Working Paper 2014/44.

Taylor AH, Stephens JA. 1998. The North Atlantic oscillation and the latitude of the Gulf Stream. Tellus A: Dynamic Meteorology and Oceanography 50: 134-142.

TRAC (Transboundary Resources Assessment Committee). 2023. Georges Bank Yellowtail Flounder. TRAC Status Report 2023/02.

Truesdell S. 2013. Modeling Juvenile Atlantic cod and yellowtail flounder abundance on Georges Bank and in the Gulf of Maine using 2-stage generalized additive models. A final report to the Closed Area Technical Team of the New England Fisheries Management Council. Orono, ME.

Walsh SJ. 1992. Factors influencing distribution of juvenile yellowtail flounder (*Limanda ferruginea*) on the Grand Bank of Newfoundland. Neth. J. Sea Res. 29: 193-203.

Walsh SJ, Morgan MJ. 2004 Observations of natural behaviour of yellowtail flounder derived from data storage tags. ICES Journal of Marine science 61: 1151-1156.

Walsh HJ, Richardson DE, Marancik KE, Hare JA. 2015. Long-term changes in the distributions of larval and adult fish in the northeast US shelf ecosystem. PLoS One 10(9): e0137382.

Xu H, Miller TJ, Hameed S, Alade LA, Nye JA. 2018. Evaluating the utility of the Gulf Stream Index for predicting recruitment of Southern New England-Mid Atlantic yellowtail flounder. Fish. Oceanogr. 27: 85–95.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. 2009. Mixed effects models and extensions in ecology with R. New York: Springer.

Table 1. Response variables (recruitment indices, recruitment) and explanatory variables (environmental covariates) included in the GAMs. All the following environmental variables in the table (except the cold pool-related variables, see "SNEMA only") were calculated for each of the NEFSC surveys (fall and spring). The total number of individual environmental covariates explored for each stock was 20 (with six additional cold pool related variables for the SNEMA stock). The acronyms beside each variable will be used throughout the remainder of this report.

Dependent variables (recruitment indices)	**Independent variables (environmental covariates)**
Survey index Number-at-Age 1	Mean AMO for the 6 months preceding survey (AMO 6)
Weight-at-age 1 (weight-at-age)	Mean AMO for the 12 months preceding survey (AMO 12)
	Mean NAO for the 6 months preceding survey (NAO 6)
	Mean NAO for the 12 months preceding survey (NAO 12)
	Mean GSI for the 6 months preceding survey (GSI 6)
	Mean GSI for the 12 months preceding survey (GSI 12)
	Mean bottom temperature for the 6 months preceding survey (BT 6)
	Mean bottom temperature for the 12 months preceding survey (BT 12)
	Annual mean Cold Pool index (CPI)- SNEMA only
	Annual mean Persistence index (PI)- SNEMA only
	Annual mean Extent index (EI)- SNEMA only

Table 2. Environmental effects on recruitment indices for each stock and survey (yellow highlight: significant relationship; dark green: all three model types significant; blue box >40% Deviance Explained, % DE; '·' and dark grey row: not significant; '6 or 12': 6-month or 12-month lagged index).

Index	Stock	Survey	Env Var	Each index-all stocks	All indices-each stock	Each index-each stock	Each index-each stock DE (%)	6 or 12
NAA	SNEMA	Fall	CPI	NA	.	<2e-16	44.9	
			PI	NA	.	1.27E-06	32.8	
			EI	NA	0.01088	2.66E-06	31.9	
			NAO 6	.	.	.	.	
			AMO 6	4.11E-07	.	5.90E-05	33.9	
			GSI 6	< 2e-16	.	< 2e-16	54	N
			BT 6	< 2e-16	.	< 2e-16	47.7	N
			NAO 12	6.87E-05	.	0.0108	18.2	
			AMO 12	9.36E-07	.	8.73E-05	28.5	
			GSI 12	< 2e-16	0.00485	< 2e-16	61.7	Y
			BT 12	< 2e-16	0.05177	< 2e-16	47.3	Y
		Spring	CPI	NA	.	< 2e-16	53.8	
			PI	NA	.	1.36E-06	27.8	
			EI	NA	.	< 2e-16	31	
			NAO 6	2.74E-05	.	0.000159	29.3	
			AMO 6	2.58E-05	0.0811	0.000949	31.5	Y
			GSI 6	5.11E-07	.	2.47E-05	27.8	
			BT 6	6.95E-07	.	8.36E-06	50.5	
			NAO 12	0.00358	.	0.00776	15.9	
			AMO 12	0.000102	0.0265	0.00137	28.1	N
			GSI 12	8.33E-07	.	1.75E-05	27.4	
			BT 12	4.02E-07	.	9.57E-06	41	
	CCGOM	Fall	NAO 6	.	.	.	.	
			AMO 6	.	.	.	.	
			GSI 6	.	.	0.0886	9.22	
			BT 6	.	.	.	.	
			NAO 12	.	.	.	.	
			AMO 12	.	.	.	.	
			GSI 12	0.0757	.	0.0583	9.15	
			BT 12	.	.	.	.	
		Spring	NAO 6	.	.	0.0893	5.96	
			AMO 6	0.017744	0.01455	0.00941	13.7	N
			GSI 6	.	.	.	. 13.4	
			BT 6	0.0772	.	0.00227	50.2	?
			NAO 12	.	.	0.0015	53.1	
			AMO 12	0.014884	0.03135	0.0074	15.5	Y
			GSI 12	.	.	.	. 18.6	
			BT 12	0.02702	0.00692	0.00194	49.1	?
	GB	Fall	NAO 6	.	.	.	.	
			AMO 6	0.00809	0.0192	0.0137	7.31	
			GSI 6	6.14E-06	.	5.63E-05	23.9	
			BT 6	6.28E-07	0.00841	4.28E-05	19.9	N
			NAO 12	0.001	.	0.0014	12	
			AMO 12	0.0875	0.02078	.	.	
			GSI 12	1.24E-06	.	2.28E-05	25.3	
			BT 12	< 2e-16	0.00043	< 2e-16	41.7	Y
		Spring	NAO 6	.	.	.	.	
			AMO 6	0.000139	.	0.000368	23.1	
			GSI 6	0.00209	.	0.00321	24.3	
			BT 6	2.71E-05	0.0452	0.000265	24	Y
			NAO 12	.	.	.	.	
			AMO 12	0.000201	.	0.000466	24.7	
			GSI 12	0.00838	.	0.0139	16.6	
			BT 12	0.00035	0.0602	0.00252	19.5	N

Index	Stock	Survey	Env Var	Each index-all stocks	All indices-each stock	Each index-each stock	Each index-each stock DE (%)	6 or 12
NAA	SNEMA	Fall	CPI	NA	.	<2e-16	44.9	
			PI	NA	.	1.27E-06	32.8	
			EI	NA	0.01088	2.66E-06	31.9	
			NAO 6	.	.	.	.	
			AMO 6	4.11E-07	.	5.90E-05	33.9	
			GSI 6	< 2e-16	.	< 2e-16	54	N
			BT 6	< 2e-16	.	< 2e-16	47.7	N
			NAO 12	6.87E-05	.	0.0108	18.2	
			AMO 12	9.36E-07	.	8.73E-05	28.5	
			GSI 12	< 2e-16	0.00485	< 2e-16	61.7	Y
			BT 12	< 2e-16	0.05177	< 2e-16	47.3	Y
		Spring	CPI	NA	.	< 2e-16	53.8	
			PI	NA	.	1.36E-06	27.8	
			EI	NA	.	< 2e-16	31	
			NAO 6	2.74E-05	.	0.000159	29.3	
			AMO 6	2.58E-05	0.0811	0.000949	31.5	Y
			GSI 6	5.11E-07	.	2.47E-05	27.8	
			BT 6	6.95E-07	.	8.36E-06	50.5	
			NAO 12	0.00358	.	0.00776	15.9	
			AMO 12	0.000102	0.0265	0.00137	28.1	N
			GSI 12	8.33E-07	.	1.75E-05	27.4	
			BT 12	4.02E-07	.	9.57E-06	41	
	CCGOM	Fall	NAO 6	.	.	.	.	
			AMO 6	.	.	.	.	
			GSI 6	.	.	0.0886	9.22	
			BT 6	.	.	.	.	
			NAO 12	.	.	.	.	
			AMO 12	.	.	.	.	
			GSI 12	0.0757	.	0.0583	9.15	
			BT 12	.	.	.	.	
		Spring	NAO 6	.	.	0.0893	5.96	
			AMO 6	0.017744	0.01455	0.00941	13.7	N
			GSI 6	.	.	.	. 13.4	
			BT 6	0.0772	.	0.00227	50.2	?
			NAO 12	.	.	0.0015	53.1	
			AMO 12	0.014884	0.03135	0.0074	15.5	Y
			GSI 12	.	.	.	. 18.6	
			BT 12	0.02702	0.00692	0.00194	49.1	?
	GB	Fall	NAO 6	.	.	.	.	
			AMO 6	0.00809	0.0192	0.0137	7.31	
			GSI 6	6.14E-06	.	5.63E-05	23.9	
			BT 6	6.28E-07	0.00841	4.28E-05	19.9	N
			NAO 12	0.001	.	0.0014	12	
			AMO 12	0.0875	0.02078	.	.	
			GSI 12	1.24E-06	.	2.28E-05	25.3	
			BT 12	< 2e-16	0.00043	< 2e-16	41.7	Y
		Spring	NAO 6	.	.	.	.	
			AMO 6	0.000139	.	0.000368	23.1	
			GSI 6	0.00209	.	0.00321	24.3	
			BT 6	2.71E-05	0.0452	0.000265	24	Y
			NAO 12	.	.	.	.	
			AMO 12	0.000201	.	0.000466	24.7	
			GSI 12	0.00838	.	0.0139	16.6	
			BT 12	0.00035	0.0602	0.00252	19.5	N

Table 3. Environmental effects on weight-at-age for each stock and survey (‘·’ and dark grey row: not significant; Deviance Explained, % DE; ‘6 or 12’: 6-month or 12-month lagged index).

				Each index-all stocks		Each index-each stock		
Index	Survey	Env Var	Stock	p-value	%DE	p-value	%DE	
WAA	Fall	AMO 6	CCGOM	.		0.0113	10.2	
		AMO 12	SNEMA	.		0.0717	19.5	*
			CCGOM	.		0.00329	14.1	
		GSI 6	SNEMA	0.0679	5.49	0.00452	19.8	
			CCGOM			0.00105	25	
			GB	0.0223		0.000174	28.8	*
		GSI 12	SNEMA	0.0503	6.34	0.00197	25.7	
			CCGOM	.		0.000245	23.3	
			GB	0.0126		4.49E-05	36.5	*
		BT 6	SNEMA	< 2e-16	78.8	0.000109	23.6	
			CCGOM	< 2e-16		0.000552	19.6	
			GB	7.32E-05		9.37E-05	33	*
		BT 12	SNEMA	< 2e-16	77.7	0.000561	24.8	
			CCGOM	< 2e-16		0.000469	20.2	
			GB	2.39E-06		2.34E-06	42	*
		CPI	SNEMA	NA		0.000249	34	
		PI	SNEMA	NA		0.000426	18.8	
		EI	SNEMA	NA		0.000478	30.5	
	Spring	NAO 6	SNEMA	0.05977	25.9	0.0139	15.1	
			CCGOM	0.07286		.	4.96	
			GB	0.00765		0.0203	30.6	*
		NAO 12	SNEMA	.		0.0205	12.8	
		AMO 6	SNEMA	.		0.0672	25.6	
		AMO 12	SNEMA	.		0.132	26.6	
		GSI 6	SNEMA	0.02735	39.3	0.0135	15.5	
			CCGOM	0.00336		0.00562	46.7	
			GB	0.00102		0.00206	51.7	*
		GSI 12	SNEMA	0.0659	22.5	0.0475	10.3	
			CCGOM	0.0238		0.0533	22.4	
			GB	0.0111		0.0161	32.1	*
		BT 6	SNEMA	0.011846	42.5	0.000229	30.5	
			CCGOM	4.82E-07		0.0426	25.3	
			GB	0.000899		0.00926	32.9	*
		BT 12	SNEMA	.	39	0.00293	20.7	
			CCGOM	3.48E-07		0.0221	27.8	
			GB	0.000114		0.00538	30.8	*
		CPI	SNEMA	NA		0.00747	17.5	
		PI	SNEMA	NA		0.0202	13.5	
		EI	SNEMA	NA		0.0194	13.9	

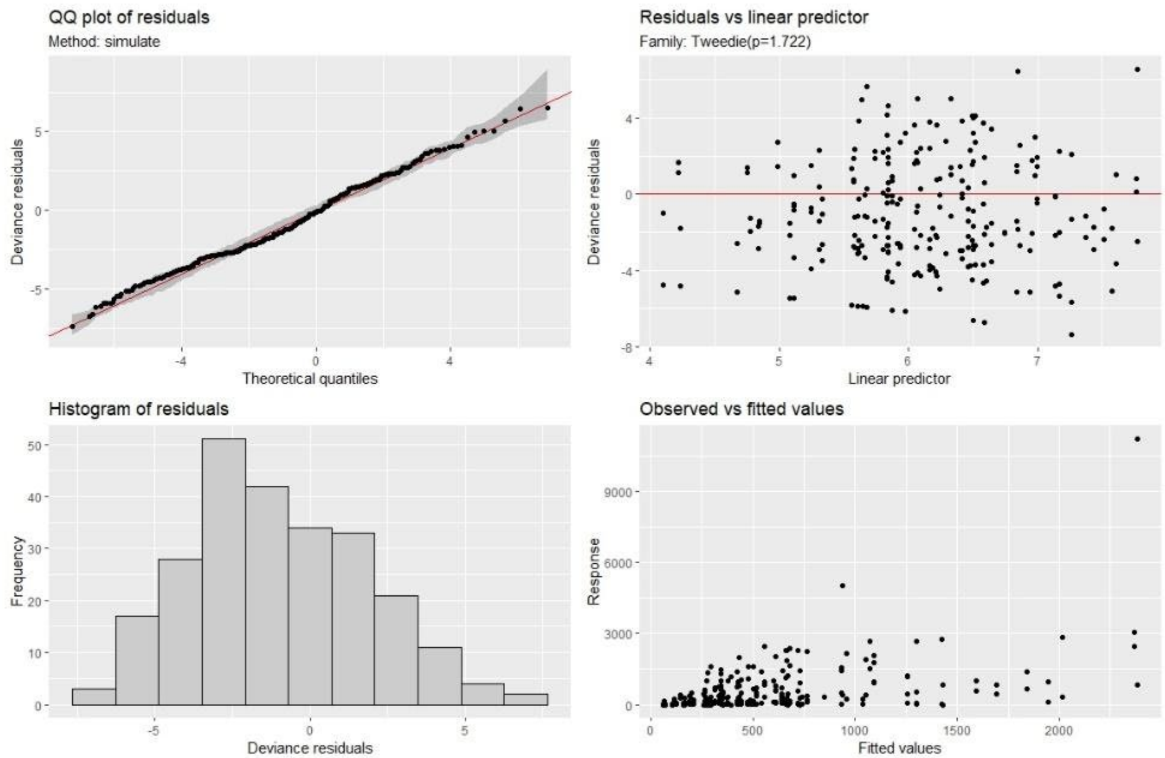

Figure 1. Example diagnostic plots used to determine the model fit of the models.

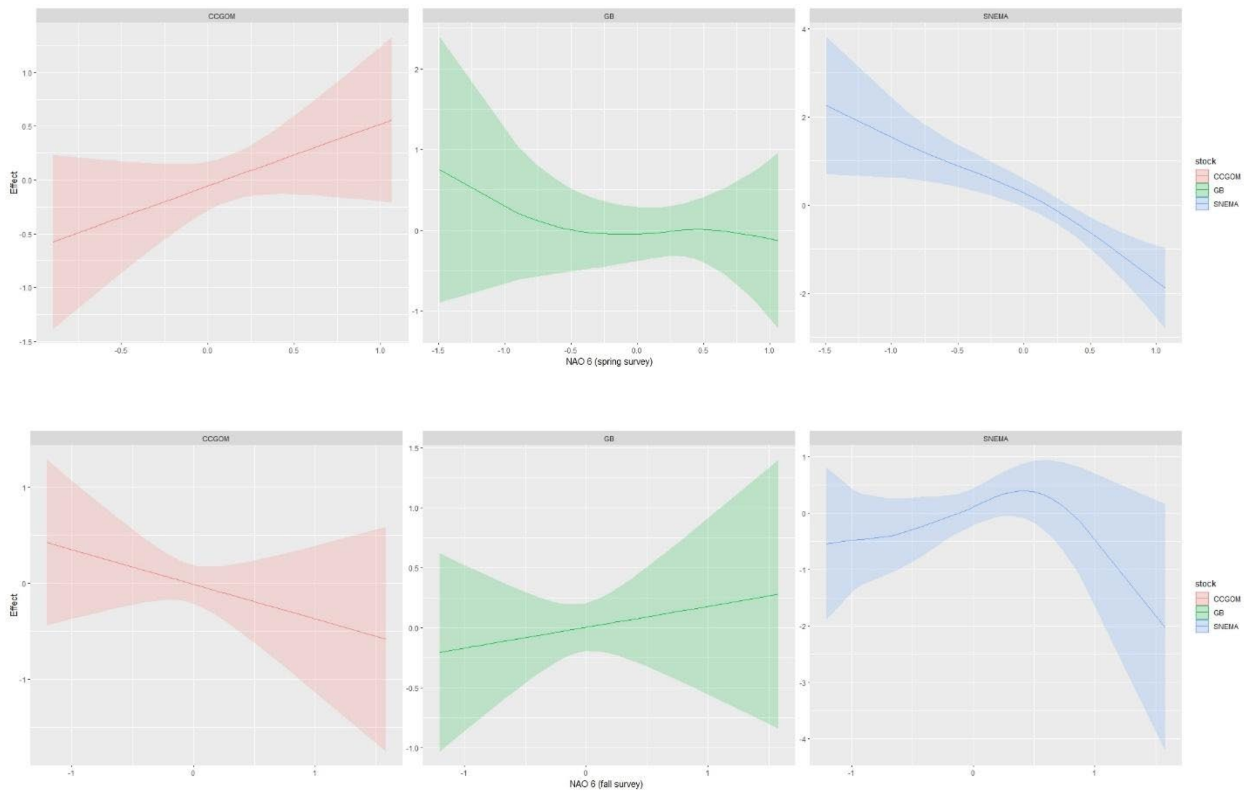

Figure 2. Partial effects of the NAO 6-month on fall and spring surveys of recruitment from 'each index-all stocks' GAMs for all three stocks. The top three plots are for the spring survey and the bottom three plots are for the spring survey. The CCGOM stock is in red, the GB stock in green, and the SNEMA stock in blue.

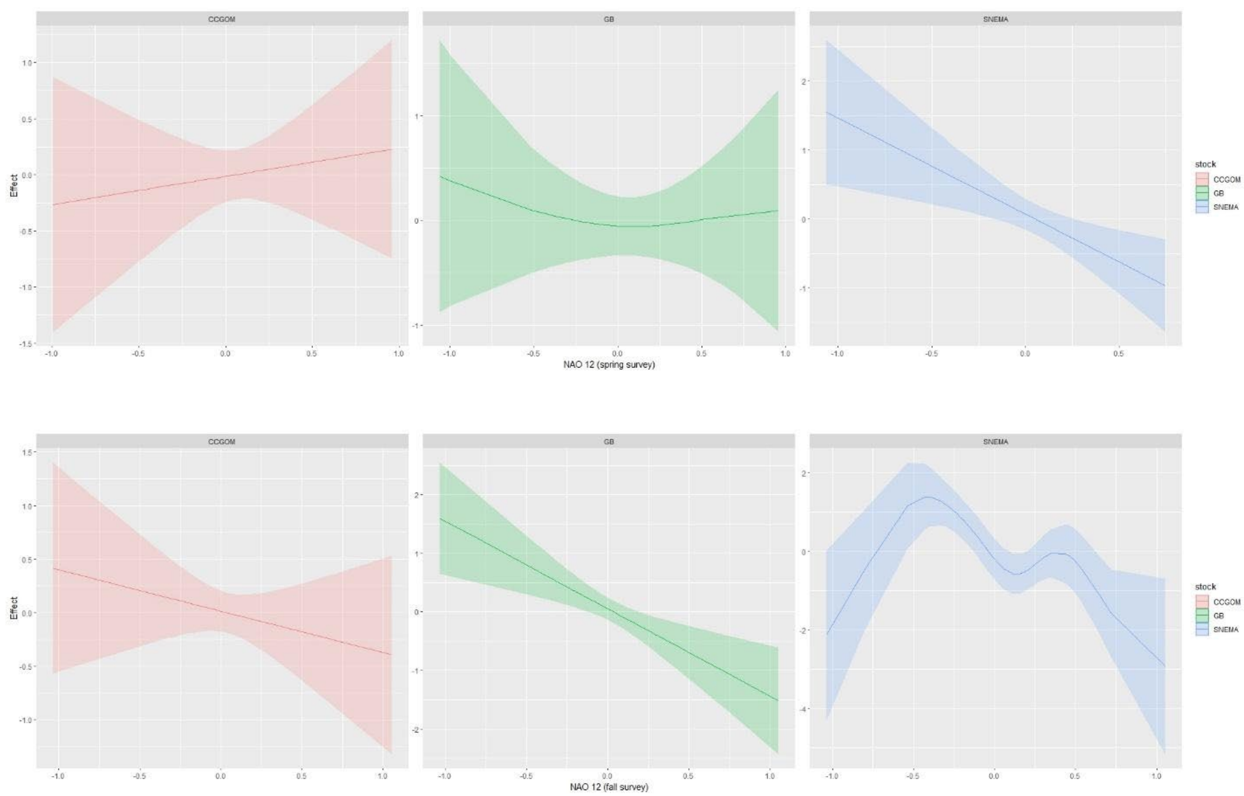

Figure.3. Partial effects of the NAO 12-month on fall and spring surveys of recruitment from ‘each index-all stocks’ GAMs for all three stocks. The top three plots are for the spring survey and the bottom three plots are for the spring survey. The CCGOM stock is in red, the GB stock in green, and the SNEMA stock in blue.

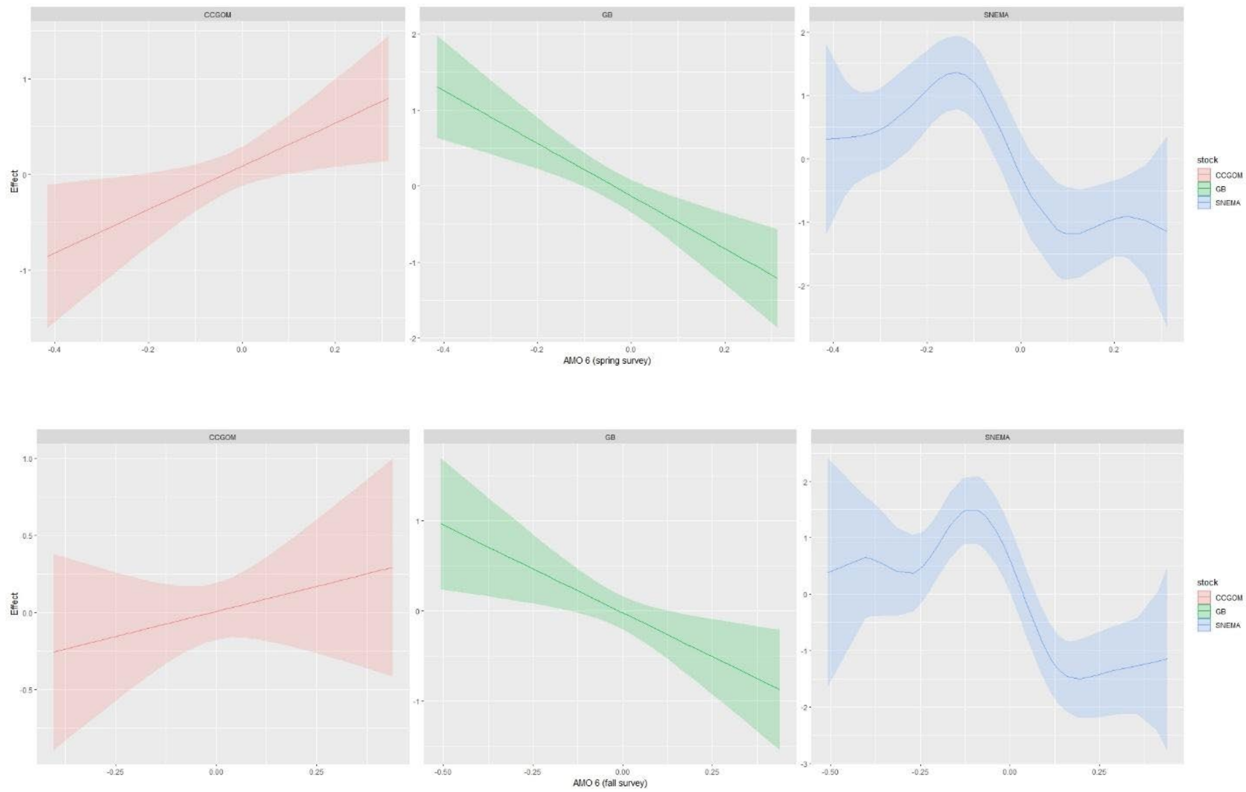

Figure 4. Partial effects of the AMO 6-month on fall and spring surveys of recruitment from 'each index-all stocks' GAMs for all three stocks. The top three plots are for the spring survey and the bottom three plots are for the spring survey. The CCGOM stock is in red, the GB stock in green, and the SNEMA stock in blue.

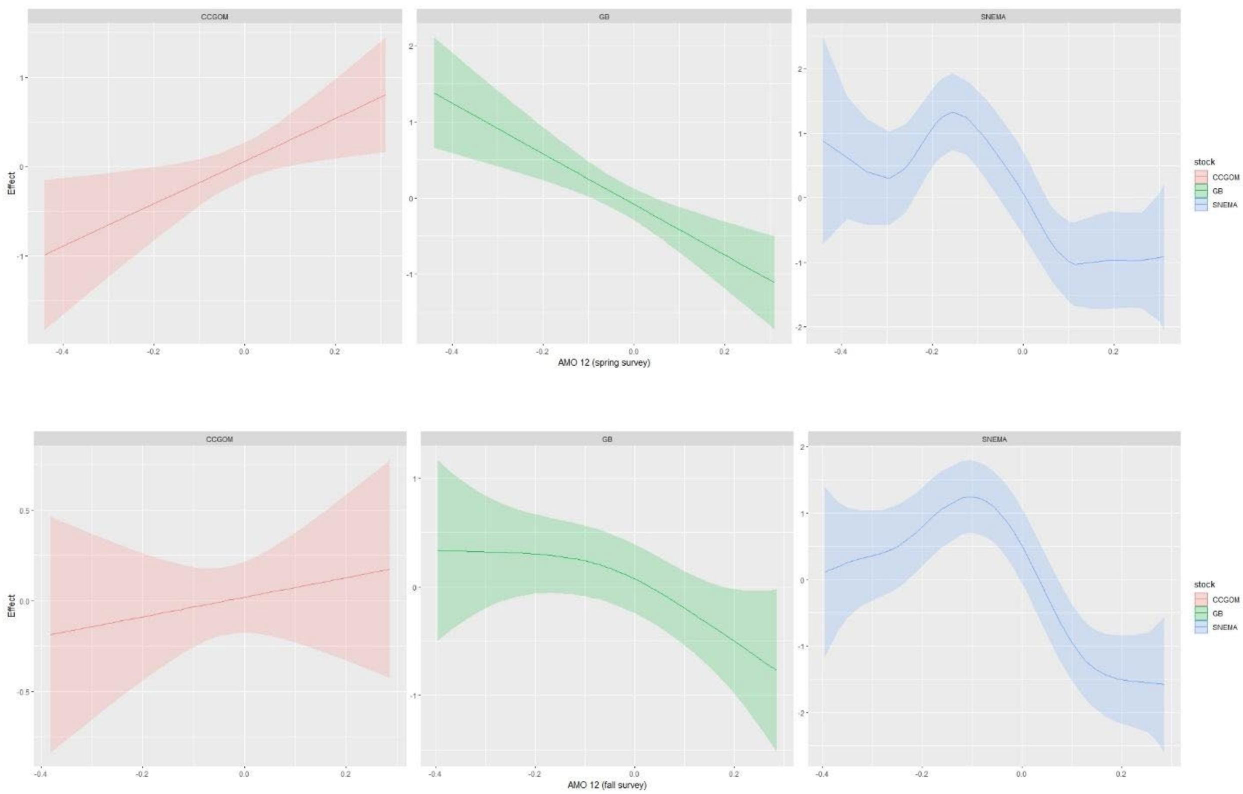

Figure.5. Partial effects of AMO 12 month on fall and spring surveys of recruitment from ‘each index-all stocks’ recruitment GAMs for all three stocks. The top three plots are for the spring survey and the bottom three plots are for the spring survey. The CCGOM stock is in red, the GB stock in green, and the SNEMA stock in blue.

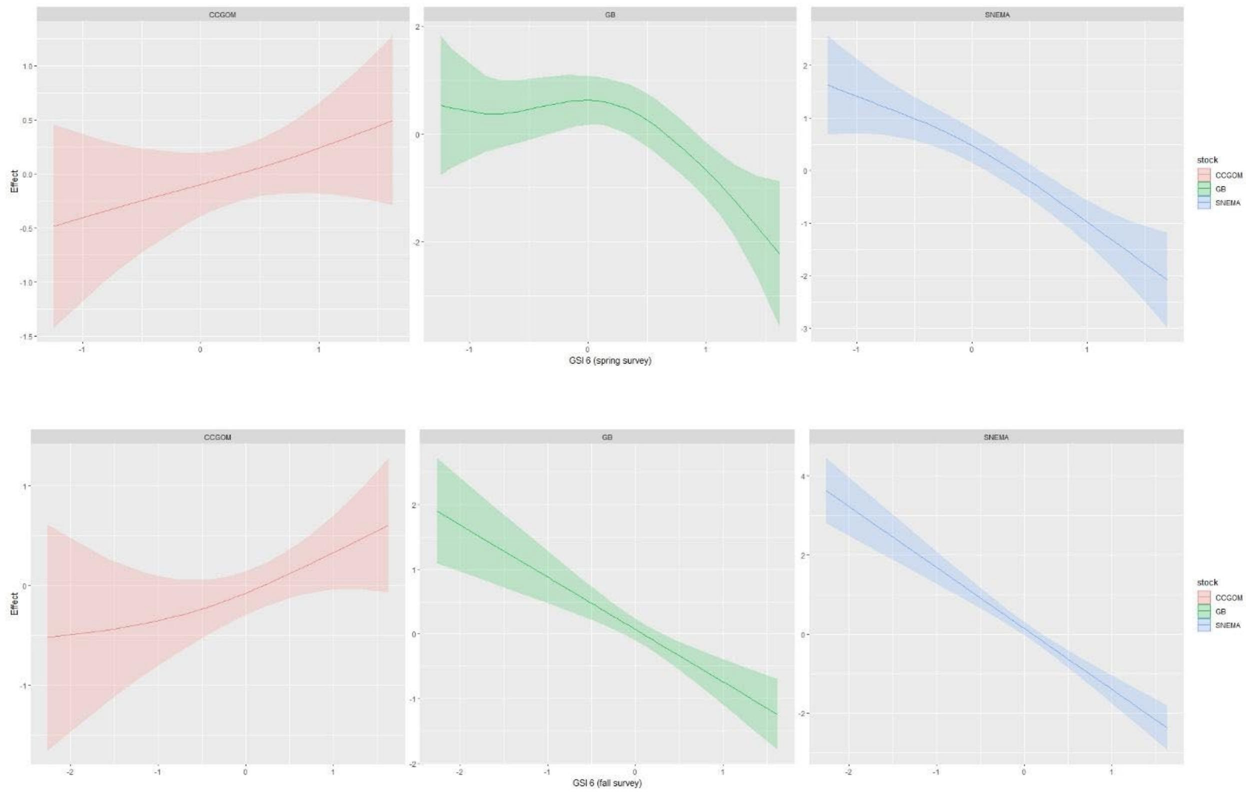

Figure6. Partial effects of GSI 6-month on fall and spring surveys of recruitment from ‘each index-all stocks’ GAMs for all three stocks. The top three plots are for the spring survey and the bottom three plots are for the spring survey. The CCGOM stock is in red, the GB stock in green, and the SNEMA stock in blue.

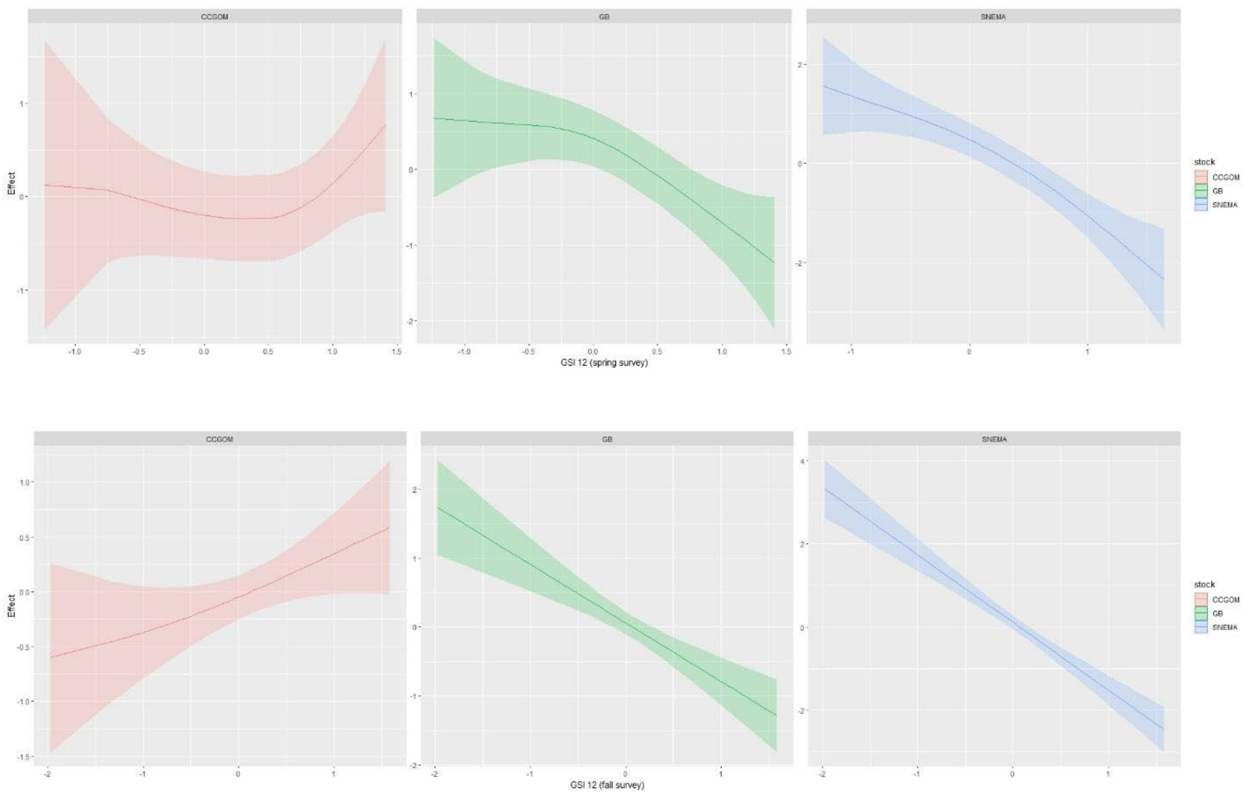

Figure 7. Partial effects of GSI 12-month on fall and spring surveys of recruitment from 'each index-all stocks' GAMs for all three stocks. The top three plots are for the spring survey and the bottom three plots are for the spring survey. The CCGOM stock is in red, the GB stock in green, and the SNEMA stock in blue.

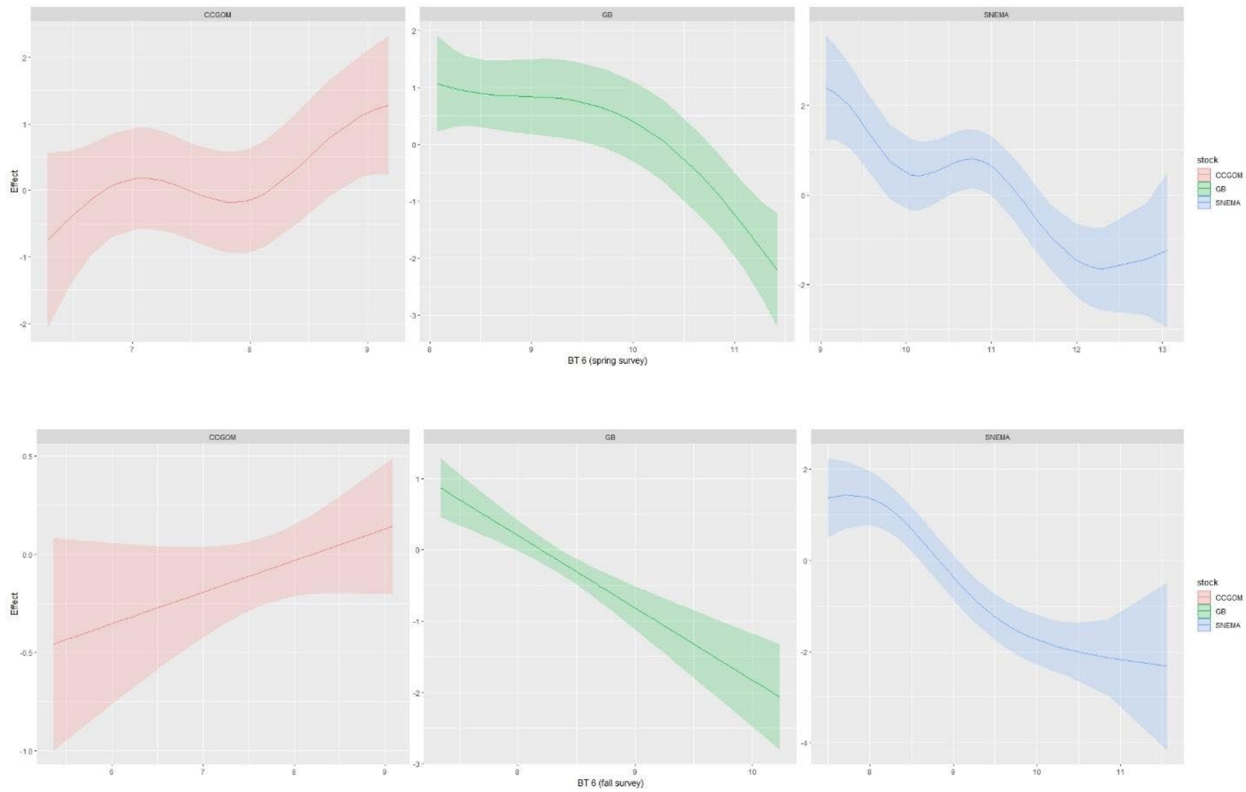

Figure 8. Partial effects of BT 6-month on fall and spring surveys of recruitment from 'each index-all stocks' GAMs for all three stocks. The top three plots are for the spring survey and the bottom three plots are for the spring survey. The CCGOM stock is in red, the GB stock in green, and the SNEMA stock in blue.

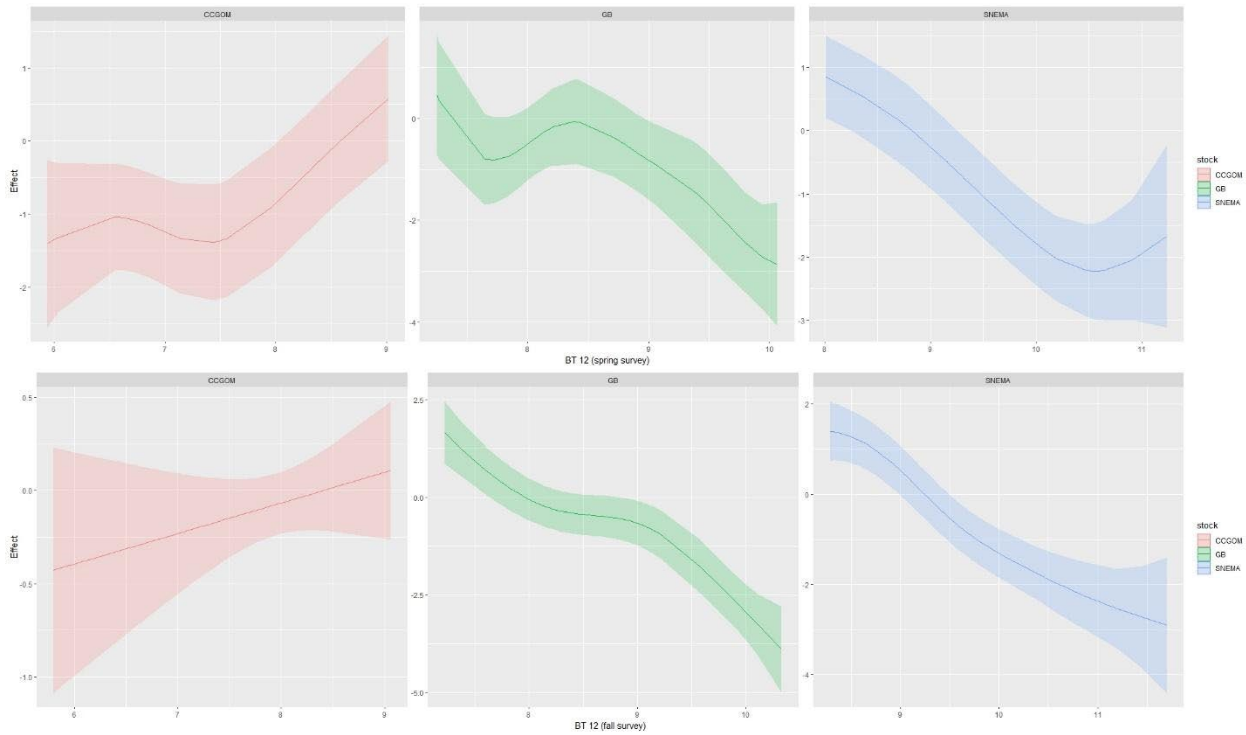

Figure.9. Partial effects of BT 12-month on fall and spring surveys of recruitment from ‘each index-all stocks’ GAMs for all three stocks. The top three plots are for the spring survey and the bottom three plots are for the spring survey. The CCGOM stock is in red, the GB stock in green, and the SNEMA stock in blue.

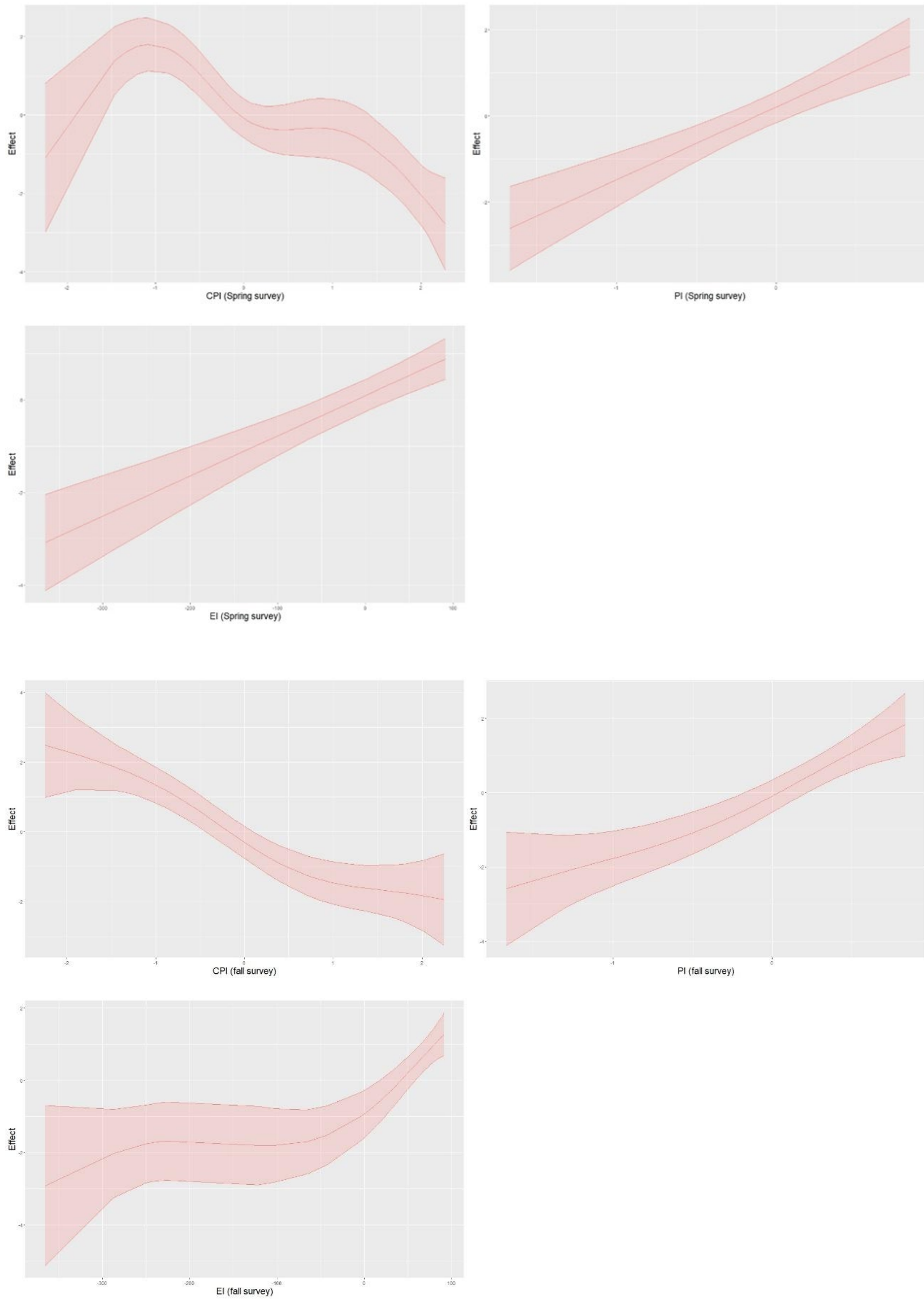

Figure10. Partial effects of cold pool indices (CPI, PI, and EI) on fall and spring surveys of recruitment from ‘each index-each stock’ GAMs and are only for the SNEMA stock. The top three plots are for the spring survey and the last three plots are for the spring survey.

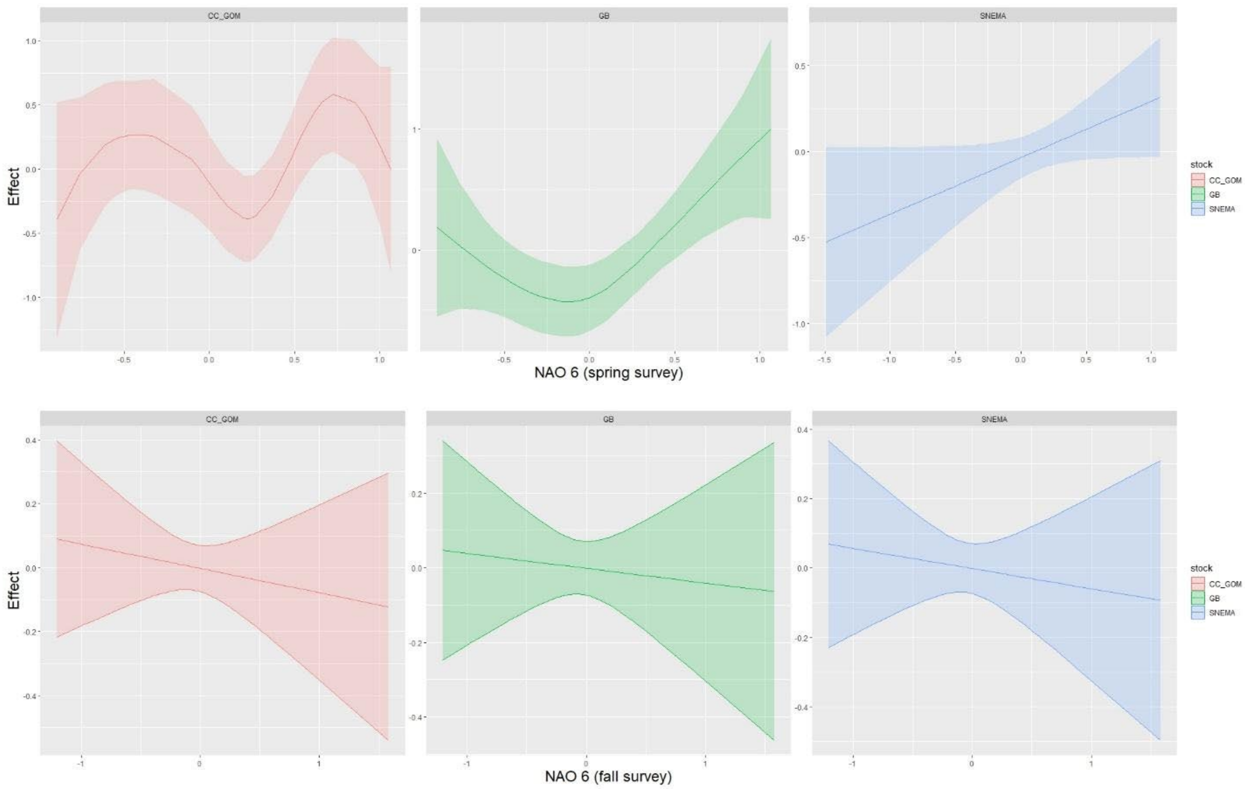

Figure 11. Partial effects of NAO 6-month on fall and spring surveys of weight-at age from 'each index-all stocks' GAMs for all three stocks. The top three plots are for the spring survey and the bottom three plots are for the spring survey. The CCGOM stock is in red, the GB stock in green, and the SNEMA stock in blue.

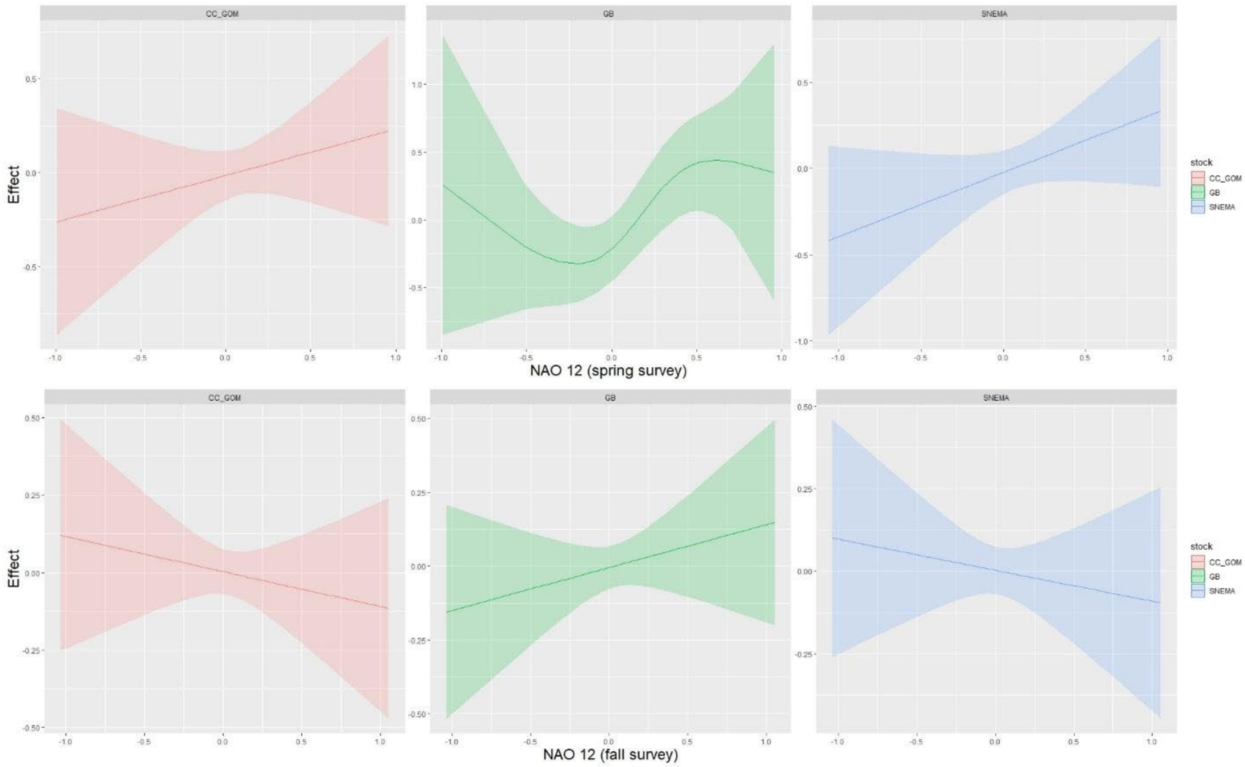

Figure 12. Partial effects of NAO 12-month on fall and spring surveys of weight-at age from 'each index-all stocks' GAMs for all three stocks. The top three plots are for the spring survey and the bottom three plots are for the spring survey. The CCGOM stock is in red, the GB stock in green, and the SNEMA stock in blue.

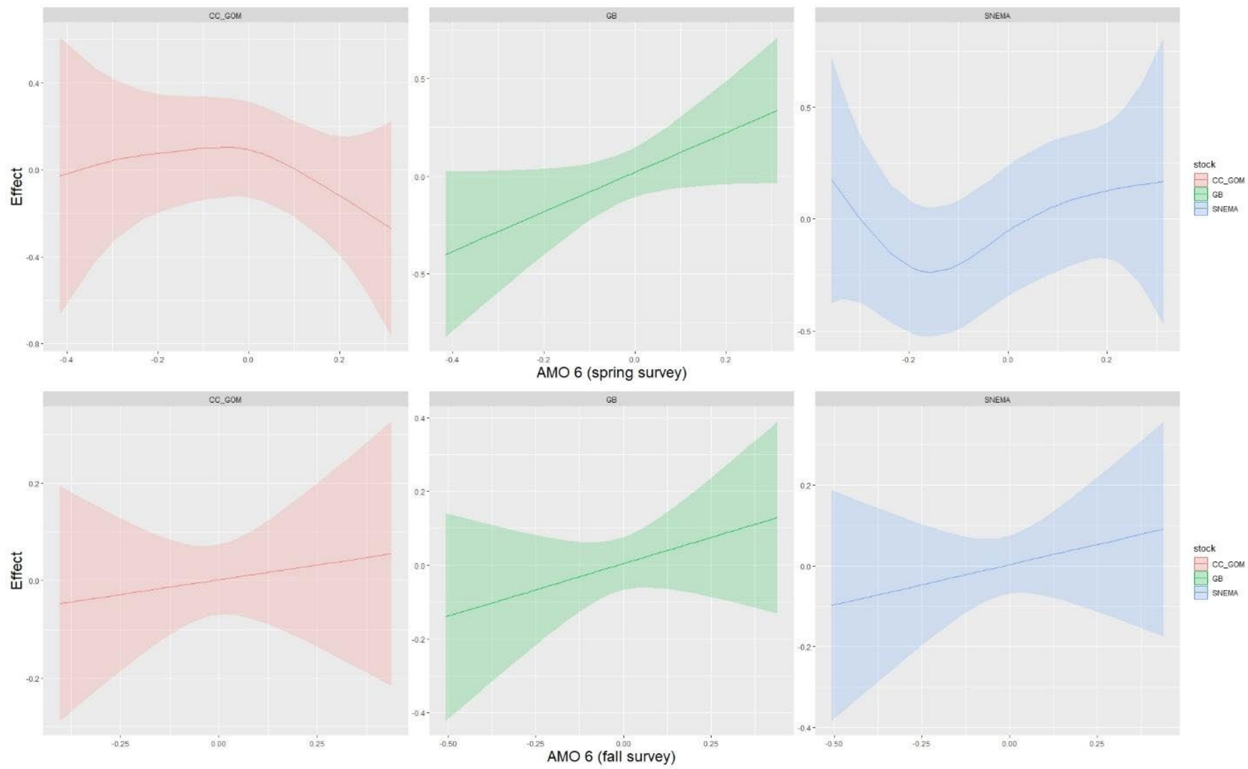

Figure 13. Partial effects of AMO 6-month on fall and spring surveys of weight-at age from ‘each index-all stocks’ GAMs for all three stocks. The top three plots are for the spring survey and the bottom three plots are for the spring survey. The CCGOM stock is in red, the GB stock in green, and the SNEMA stock in blue.

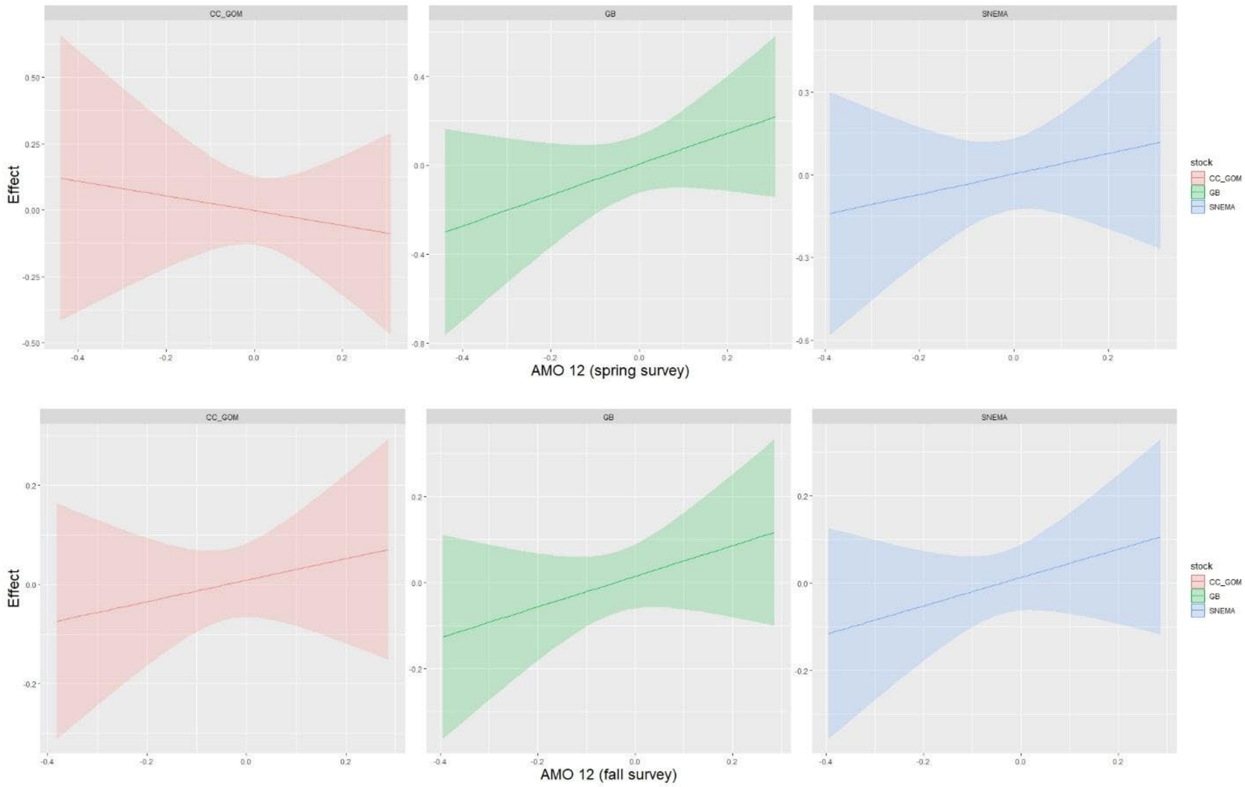

Figure 14. Partial effects of AMO 12-month on fall and spring surveys of weight-at age from 'each index-all stocks' GAMs for all three stocks. The top three plots are for the spring survey and the bottom three plots are for the spring survey. The CCGOM stock is in red, the GB stock in green, and the SNEMA stock in blue

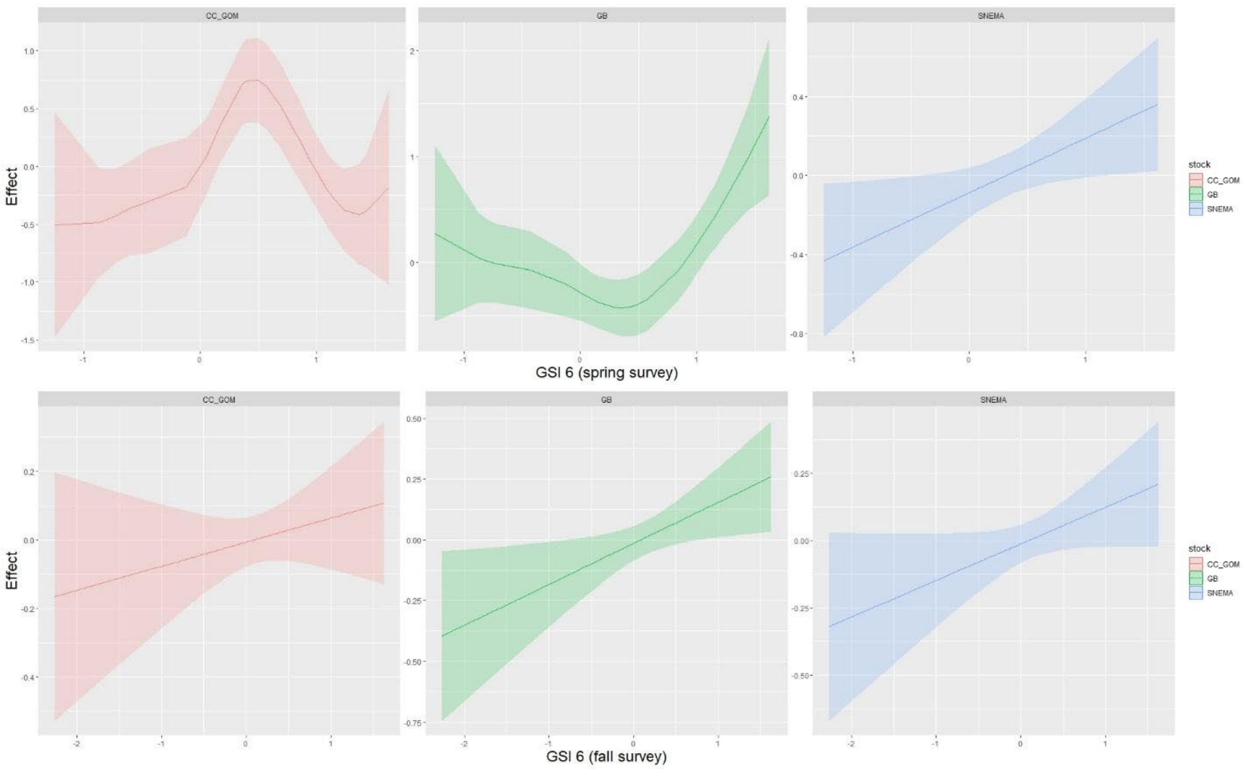

Figure 15. Partial effects of GSI 6-month on fall and spring surveys of weight-at age from ‘each index-all stocks’ GAMs for all three stocks. The top three plots are for the spring survey and the bottom three plots are for the spring survey. The CCGOM stock is in red, the GB stock in green, and the SNEMA stock in blue

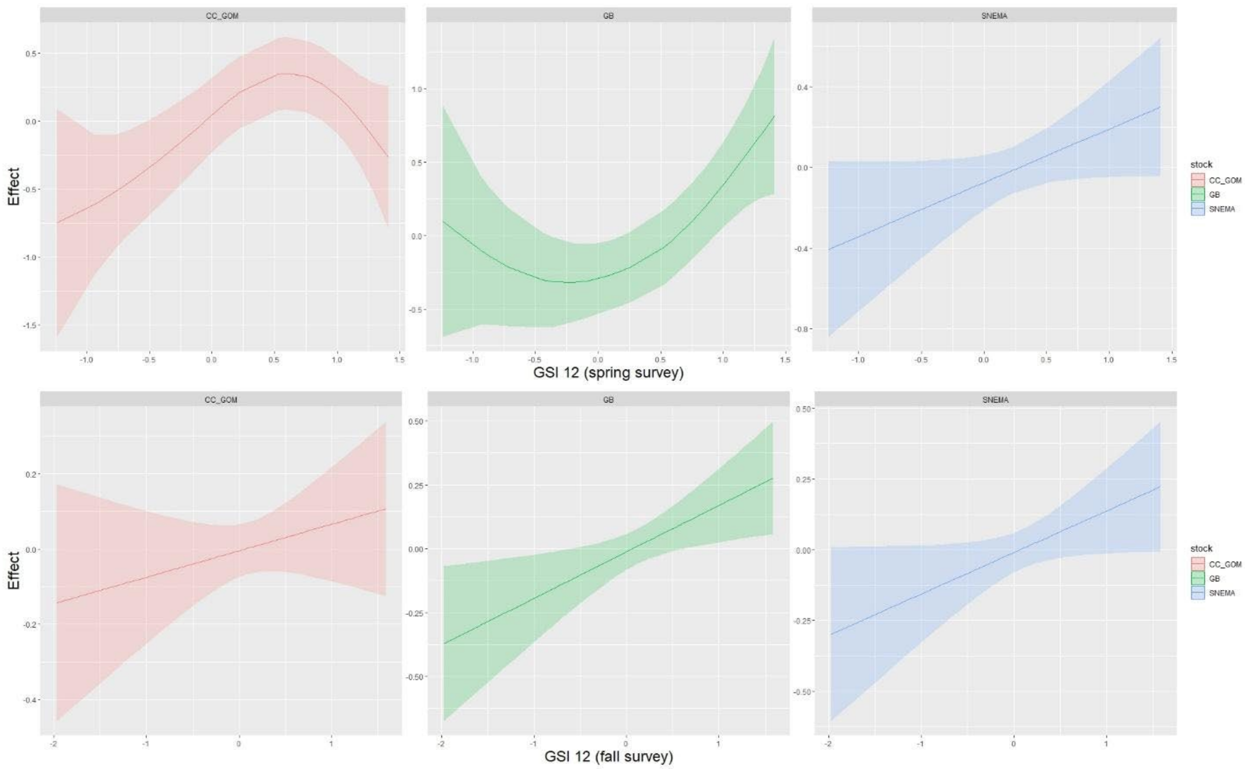

Figure 16. Partial effects of GSI 12-month on fall and spring surveys of weight-at age from 'each index-all stocks' GAMs for all three stocks. The top three plots are for the spring survey and the bottom three plots are for the spring survey. The CCGOM stock is in red, the GB stock in green, and the SNEMA stock in blue.

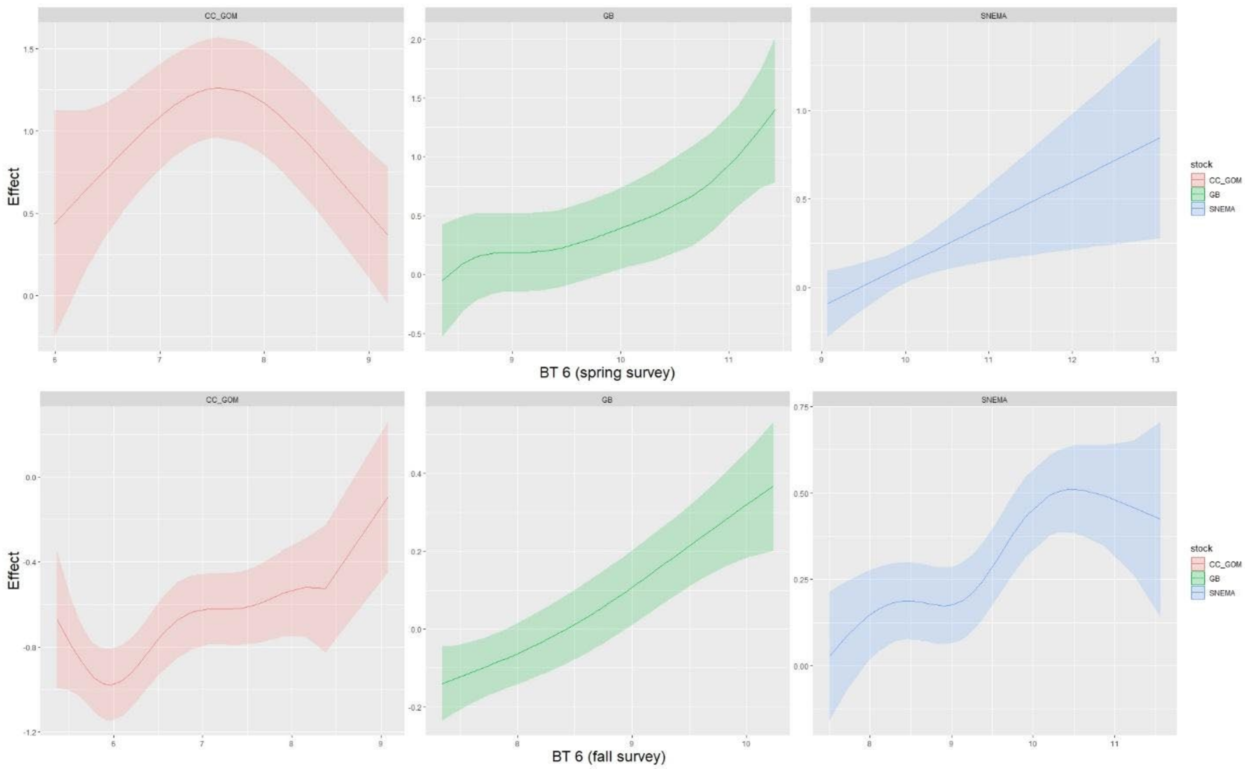

Figure 17. Partial effects of BT 6-month on fall and spring surveys of weight-at age from ‘each index-all stocks’ GAMs for all three stocks. The top three plots are for the spring survey and the bottom three plots are for the spring survey. The CCGOM stock is in red, the GB stock in green, and the SNEMA stock in blue.

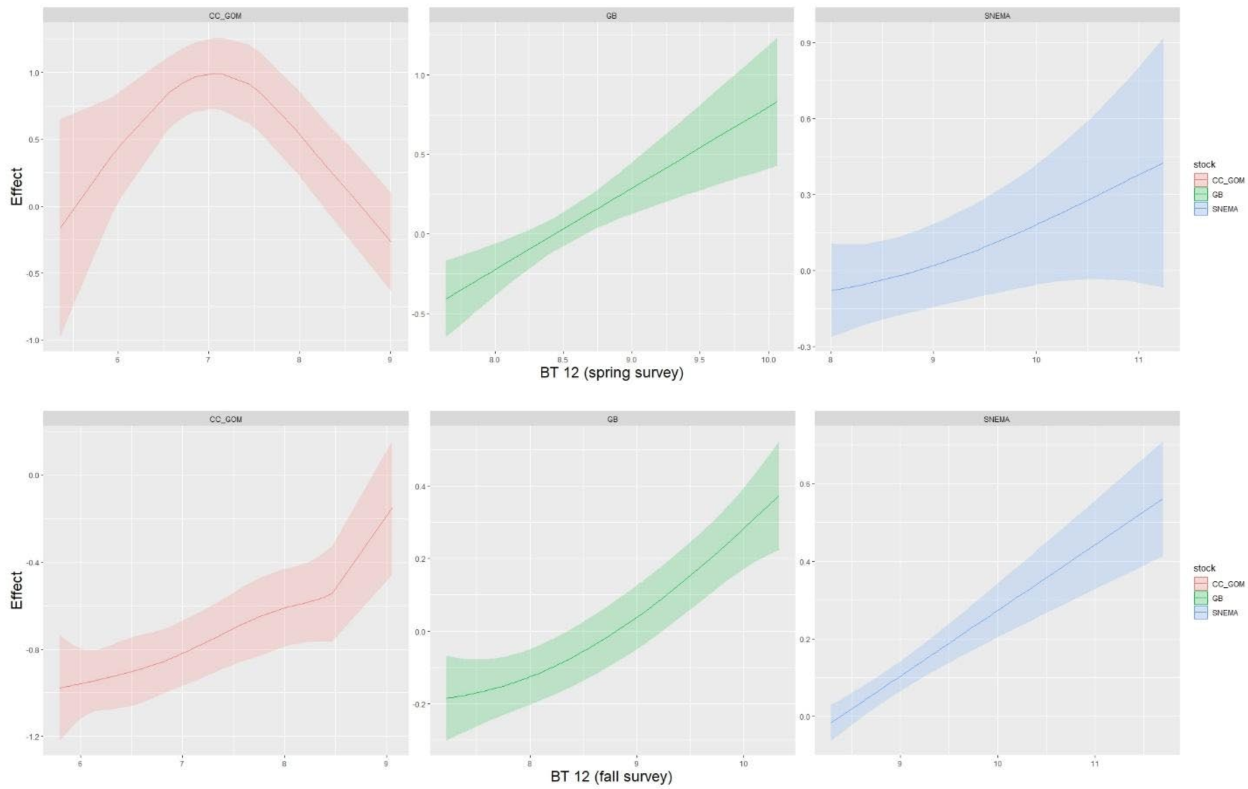

Figure 18. Partial effects of BT 12-month on fall and spring surveys of weight-at age from ‘each index-all stocks’ GAMs for all three stocks. The top three plots are for the spring survey and the bottom three plots are for the spring survey. The CCGOM stock is in red, the GB stock in green, and the SNEMA stock in blue.

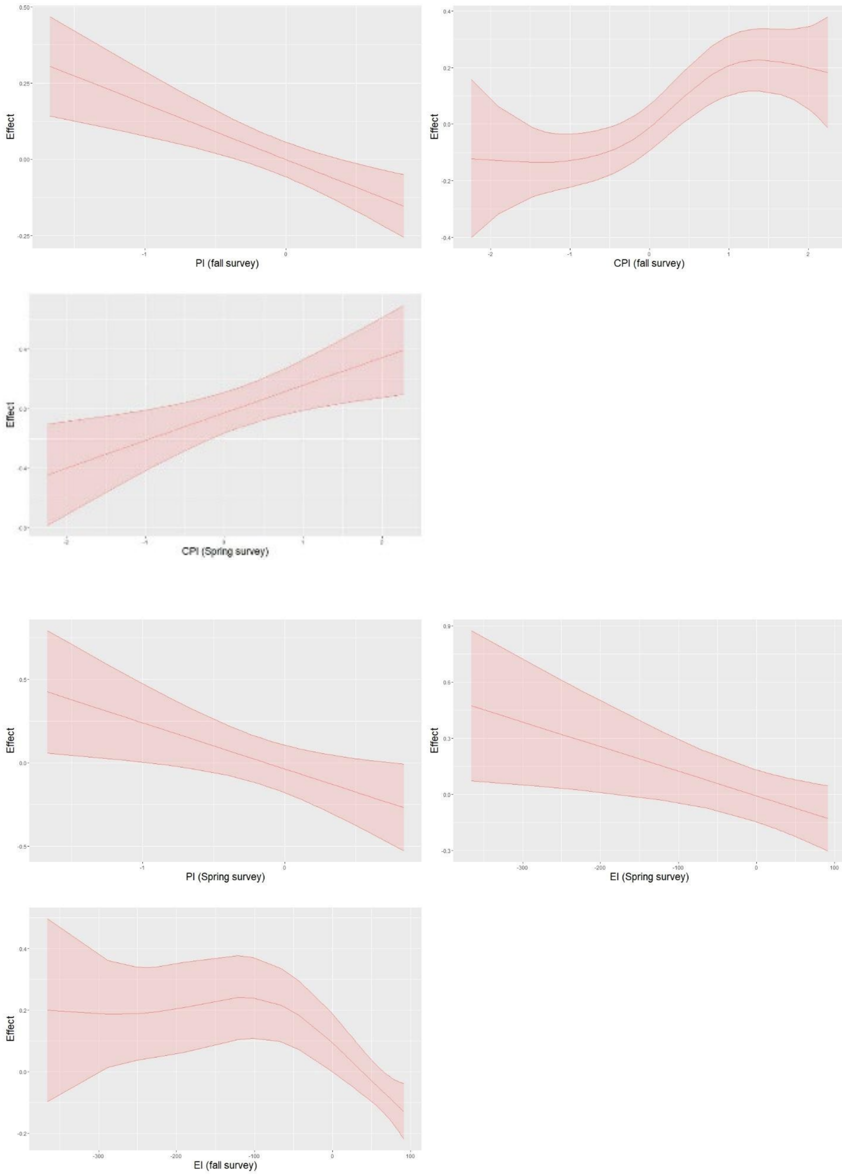

Figure 19. Partial effects of cold pool indices (CPI, PI, and EI) on fall and spring surveys of weight-at age from 'each index-each stock' GAMs and are only for the SNEMA stock. The top three plots are for the spring survey and the last three plots are for the spring survey.