Golden Tilefish Ecosystem and Socioeconomic Profile

TOR 1: Identify relevant ecosystem and climate influences on the stock.

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Background

Ecosystem and Socioeconomic Profile

Ecosystem and socioeconomic profiles (ESP) are a standardized framework for compiling and evaluating relevant stock-specific ecosystem and socioeconomic indicators in order to explore potential drivers within the stock assessment process (Shotwell et al., 2023). The ESP initiates the development of stock-specific informed indicators, serving as an on-ramp for ecosystem-linked stock assessments (Shotwell et al., 2022). For Northeast Fisheries Science Center (NEFSC) managed stocks, species with upcoming research track assessments are prioritized for ESP development.

Once a stock has been identified as a candidate for an ESP, the first step is a systematic literature review to identify relevant ecosystem and socioeconomic processes by life history stage, where possible. In this step, the goal is to create an ecological synthesis that facilitates a mechanistic understanding of drivers for the stock. The available data are then reviewed to collate a standard set of metrics and combined with the literature search to develop a conceptual model, which is a visual aid to outline drivers and their proposed impact on the stock. A life history table can be used to evaluate the processes that affect the stock in order to identify possible vulnerabilities or bottlenecks relative to current stock indices. Next, a suite of indicators relevant to stock performance are proposed, developed and analyzed. The scientific advice provided by an ESP can inform the stock assessment in multiple ways, ranging from providing additional context and research recommendations to suggesting new covariates that can inform dynamic processes within the assessment modeling framework.

Stock Assessment

Golden tilefish (*Lopholatilus chamaeleonticeps*), are primarily caught by a relatively small number of commercial longline vessels as well as a recreational fishery (to a much lesser extent). The stock assessment has relied heavily on fishery-dependent commercial catch per unit effort (CPUE) as indices of abundance because the fishery independent surveys use gear that does not reliably catch golden tilefish (Nitschke 2021) due to their burrowing nature and habitat preferences. The primary abundance index is derived from vessel trip reports collected from 1994-2022. The last management track assessment for golden tilefish occurred in 2021, but did not include ecosystem information. We hope to address knowledge gaps in the relationship between golden tilefish and environmental and socioeconomic drivers in this assessment and begin to supplement inclusion of ecosystem indicators in the stock assessment process. To do so, we will use both the recruitment index from the 2021 stock assessment as well as a haul-level CPUE estimate from a combination of high-resolution fishery-dependent trawl data sets of incidental catch.

The northern stock ranks high in climate vulnerability, exposure, and biological sensitivity to environmental fluctuations (Hare et al., 2016; Nesslage et al., 2021). Holistic risk assessments suggest that this fishery ranks low in most risk element categories aside from low to moderate in biomass status and moderate to high in climate risk (Gaichas et al., 2018). Although the fishery and its management have been fairly stable, there are no indices of current reproductive success and our understanding of the drivers of strong year class pulses that appear to occur every 6-7 years is incomplete (Nitschke 2023).

We use an ESP framework to address TOR1 because it is iterable, applicable to data limited stocks, and flexible (Shotwell et al., 2023). By initiating this framework now, future working groups can update the existing indicators or create and assess new ones. For golden tilefish, where limited early life history information exists and only commercial indices of abundance are used in the assessment model, we conducted only the beginning stage of indicator analysis (Shotwell et al., 2023). The purpose is to create a final indicator suite to provide context for generating hypotheses and future research directions on the pressures influencing the stock.

Life History

Literature Review and Conceptual Model

A review of the scientific literature on golden tilefish habitat and distribution, size and growth, and ecological linkages was conducted to identify existing research that explores ecosystem and climate influences on golden tilefish stock dynamics. The aim of this review was to compile the current understanding of the various life history characteristics of golden tilefish as they relate to underlying processes around habitat preference, physical oceanography, and food availability (Table 1, Table 2). This information, detailed below, was encapsulated in a conceptual model (Figure 2) to identify which environmental indicators may be linked to these underlying processes across relevant spatial and temporal scales. These linkages were then developed into a list of ecosystem indicators.

Habitat and Distribution

Golden Tilefish inhabit the outer continental shelf and upper continental slope of the entire U.S. East Coast and in the Gulf of Mexico (Dooley 1978). There are two genetically distinct stocks: a northern stock residing in the Mid-Atlantic Bight region, ranging from Veatch Canyon to just south of Hudson Canyon (Grimes and Turner 1999, Figure 1), and a genetically-distinct southern stock ranging from south of Cape Hatteras to the Gulf of Mexico (Katz et al., 1983). The range of golden tilefish is restricted by substrate type and temperature regime (Guida 2005) and very little migration is thought to occur. They are considered stenothermic, with a narrowly defined thermal habitat (9-14 °C) (Able et al., 1993; Grimes et al., 1986; Grimes and Turner 1999) and while they inhabit a wide range of depths (80-305 m), they are most often found between 100-200 m (Dooley 1978). Vertical burrows are the preferred habitat, but they are also known to occupy other habitat types consisting of rocks, boulders, and pueblo habitats, occurring on the side of submarine canyon walls (Grimes et al., 1986). Smaller burrows at shallow and more northern sites are less stable due to seasonal variations in bottom temperature, such that some seasonal habitats are only occupied in summer and fall when water temperatures are between 9-14°C (Grimes et al., 1986).

Golden tilefish spawn from March through November with a peak in June (Grimes et al., 1988). Tilefish reach maturity at 2-4 years of age at sizes between 60-65 cm for females and 65-70 cm for males. They are serial spawners, releasing anywhere between 195,000 to 10 million eggs in total throughout the spawning season, averaging 2.28 million eggs per female or 500,000 for first time spawners (Grimes et al., 1988). Spawning females have only been found in a narrow temperature band (10.16-14.9 °C). The width and extent of this band varies seasonally; extending beyond Nantucket Shoals and along southern Georges Bank in the summer and fall, and then retreating to Long Island in the winter and spring (Steimle et al., 1999).

Size and Growth

Habitat use in relation to age and growth remains relatively unstudied (Dawson 2021; Lombardi-Carlson and Andrews 2015), and therefore substantial knowledge gaps exist, inhibiting insight into golden tilefish life history. Much of the information regarding early life history development of golden tilefish is documented in the Essential Fish Habitat Source Document (Steimle et al., 1999) and is summarized below. Golden tilefish eggs are non adhesive and buoyant in the water column. Eggs have been found around the continental shelf break from Georges Bank to Cape Hatteras at water column depths ranging from 80-800 m between March to November, owing to their serial spawning activity across a broad latitudinal range (Steimle et al., 1999). Golden tilefish eggs are 1.16-1.25 mm in size and are typically found in saline waters (34-36 psu) across a moderately broad temperature range (8-19°C). Eggs hatch after ~40 hours, with a peak in observations in July, about a month later than peak egg abundance, according to MARMAP surveys. Larvae are similarly broadly distributed along the outer continental shelf, but are found slightly higher in the water column at shallower depths (50-150 m). Larvae are 2.6-9.0 mm in size and settle once they reach anywhere from 9-15 mm (Fahay 2007). They are observed at similar salinities as eggs but are less tolerant of low temperatures with a narrower thermal range of 13-18 °C. Juveniles are as widely distributed as eggs and larvae, but are found in small burrows or on rocky and clay bottom types along the shelf break as well as in submarine canyon walls and flanks. Early juveniles (15-500 mm) around 1 years of age are observed from April through July. At this stage the thermal band widens again (8-18 °C), suggesting juveniles may have a wider thermal tolerance than adults.

Golden tilefish have a long life span, with the oldest tilefish on record living up to 46 (females) and 39 (males) years of age, however new studies on radiometric dating techniques suggest that tilefish may live as long as 50 years (NOAA Fisheries Species Directory). Golden tilefish grow slowly, reaching a maximum size of 110 cm focal length (Turner et al., 1983);

however, the average size and age of harvested fish is 61 cm around 4-5 years of age (NOAA Fisheries Species Directory). Until age 4, both males and females grow roughly 10 cm/yr (Turner et al., 1983), but more recent studies estimate an even slower growth rate closer to 6 cm/yr (Dawson 2021). After age 4, males grow faster, reaching sizes 50-120 cm long, while females are a bit smaller (50-100 cm) (Grimes et al., 1988; Lombardi-Carlson 2012).

Ecological Linkages

Golden tilefish larvae likely prey on larger zooplankton, such as calanus copepods that serve as an important food source for many commercially important species (Steimle et al., 1999). *Calanus spp*. are lipid rich, herbivorous species that eat phytoplankton, in particular larger diatoms (Hobbs et al., 2020). Juveniles prey on decapods, other crustaceans, small fish, and benthic epifauna. Juvenile predators include goosefish, sharks, dogfish, and conger eels. Adult golden tilefish are opportunistic benthic foragers, feeding during the day on shrimp, crabs, clams, snails, worms, anemones, and sea cucumbers. They also consume fishes, squid, bivalves, and holothurians (Dooley 1978) and display cannibalism on smaller tilefish. They are largely non-migratory, although they can move to remain within their preferred temperature band, and can be considered a demersal secondary consumer. Monkfish, goosefish, spiny dogfish, conger eels, large bottom-dwelling sharks (such as dusky and sandbar sharks), and lampreys are the main predators of adult golden tilefish (NOAA Fisheries Species Directory), although by far the most important predator of tilefish are conspecifics (Freeman and Turner 1977). Golden tilefish influence food web dynamics as top-level predators and marine ecosystem engineers, creating available habitat for other species via their burrowing activity (Coleman and Williams 2002).

Hare et al., (2016) characterized golden tilefish as having a high overall vulnerability rank along with high biological sensitivity and climate exposure. Environmental variables driving this high risk of exposure are sea surface temperature and ocean acidification. Golden tilefish inhabit a very narrow temperature range and increased ocean acidification can negatively impact survival, growth, and abundance. Nesslage et al., (2021) identified low frequency climate variables that likely influence recruitment class pulses every 6-7 years: a negative Atlantic Multidecadal Oscillation (AMO) index coupled with a positive North Atlantic Oscillation (NAO) work together to drive fluctuations in recruitment and landings in lags of 3-7 years. Strong, negative NAO phases are associated with below-average temperatures in the northwest Atlantic while positive phases of the NAO tend to correspond with above-average temperatures (Hurrell 1995). A massive die off of golden tilefish occurred in 1882 as a result of an extreme negative phase of the NAO one year prior causing intrusion of cold sub-Arctic water from the Labrador Current onto the Northeast Shelf (Freeman and Turner, 1977, personal communications with industry members, 2024). Fisher et al., (2014) found that warmer water temperatures from positive NAO phases correlated with faster adult growth rates and higher fecundity in lags of 1-2 years for positive NAO-induced warm water to reach golden tilefish habitat and 3-4 years to impact golden tilefish growth and recruitment to the fishery. The significant positive lagged correlation between landings and NAO broke down with the rise of the modern longline fishery in the 1970s.

A more northerly position of the Gulf Stream and recession of the Labrador current were also linked to increases in golden tilefish CPUE when minimal cold water is present in their range (Nessalge et al., 2021). Large, abrupt temperature changes (possibly due to Gulf Stream movement or other oceanographic processes) may cause tilefish to cease feeding (Able et al., 1993). Seasonal cooling may also force golden tilefish to concentrate as the narrow band in temperature along the continental shelf they inhabit is reduced in the winter-spring (Grimes et al., 1980; Grimes et al., 1986; Nesslage et al., 2021). In addition to oceanographic and habitat considerations, ecological connections to food sources may also be important. For instance, recruitment regimes (low in 1980s, high in 1990s, low in 2000s) for large Northeast Shelf (NES) species coincided with regimes in copepod abundance. Increased zooplankton abundance could lead to increased larval growth, or higher parental condition through increased benthic flux (Peretti et al., 2017).

Industry Perspective - Socioeconomic Input

A significant component of an ESP is the evaluation of socioeconomic information and indicators to improve understanding of stock dynamics and evaluate potential ecosystem linkages. In an effort to begin to develop a suite of socioeconomic indicators, we gathered details from recent Golden Tilefish Fishery Performance Reports as well as through personal conversations with golden tilefish captains, commercial vessel owners, fishers and dealers. The northeast fishing fleet is small, however we were able to speak with 5 individuals representing 4 fishing vessels, with an average of 38 years of experience fishing for and specifically targeting golden tilefish.

The 2023 Golden Tilefish Fishery Performance Report (MAFMC 2023) indicates no changes in golden tilefish aggregation in 2019-2020 as the water temperature remained stable (9-14°C), but notes that large tilefish are centered in and around canyons in the Mid-Atlantic Bight. Three industry members reported recent changes in distribution or abundance of golden tilefish, with one reporting that distributions have not changed but densities have shifted. There were multiple reports that in recent years, tilefish are less available in the east around Atlantis and Veatch Canyons and more concentrated further west near Hudson Canyon. Industry members had mixed responses as to whether or not golden tilefish congregate in a particular season - some recount high concentrations of tilefish in the early spring during the 1980s with a shift to late winter months in recent years. This is consistent with reports in the literature that state that the catch rate was highest in the winter and spring when available 9-14°C habitat was at a minimum (Grimes and Turner 1999). Finally, vessel owners and captains state that sediment preferences of golden tilefish (muddy, soft bottom and rocky canyon walls) have not changed over time.

Industry members call attention to the increased presence of dogfish, a main predator of golden tilefish and competitor for fishing hooks, as an important variable of concern. Competition for hooks between dogfish and skates in the winter and spring has increased dramatically, a common agreement amongst our conversations. The presence of dogfish, historically 2-3 months in the winter, is now more common throughout much of the year and can last 8 months into the late spring and early summer (MAFMC 2023).

The impacts of weather and climate variability on fishing ability and availability came up in multiple conversations. Consensus was that very cold bottom temperatures have the ability to potentially push golden tilefish off of the shelf edge and that severe weather conditions in recent winters (specifically 2013-2019) significantly affected tilefish operations. While stormy conditions have existed for many years, recent changes to storm patterns have made fishability difficult to predict in winter months (MAFMC 2023; personal communications with industry members, 2024).

There was not a consensus amongst industry members over the best time to fish for golden tilefish. Some respondents consider winter and spring as the most ideal seasons, while others place importance over less interaction and competition between tilefish and other species in the summer months. Catch rates of golden tilefish have historically reached a peak in the spring when their preferred 9-14°C temperature band is at its lowest spatial extent and declined in the summer when surrounding waters warm and the fish disperse (Grimes and Turner 1999). In recent years, however, a slight downward trend in landings in the winter and increase in landings from May to June has been observed (Nitschke 2021). Hook size amongst fishermen was selective for size but not sex. Fishers typically steer clear of very small hooks to avoid catching under market-size fish and to preserve spawners.

A key detail in our conversations with respondents is the consensus of interannual variability of golden tilefish landings is driven largely by factors outside environmental variables, including the implementation of the Individual Fishing Quota (IFQ) quota system, participation in profitable fisheries, increased fuel costs, and economics (market prices). The cooperative nature of the fishery allows fishers to have some degree of control over the supply, but quotas have reduced the amount of fishing each vessel can do, limiting some vessels to part-time versus year-round fishing. There was consensus that any potential commercial fishing regulations on a proposed marine sanctuary at Hudson Canyon would have major impacts on the fishery.

Environmental, distribution, age and length analyses

Larval analysis

The long-term shelf-wide ichthyoplankton and hydrographic survey data collected by the NEFSC in the Northwest Atlantic from 1973-2023 was analyzed to better understand golden tilefish larval geographical distribution and environmental preferences.

Methods

Golden tilefish larvae have been collected by the NEFSC Marine Resources Monitoring, Assessment and Prediction Program (MARMAP) between 1977-1987 and the NEFSC Ecosystem Monitoring Program (EcoMon) from 1992-present. Relative proportions of larval size classes in relation to bottom temperature were calculated when data was available. Larval samples for this species are sparsely collected (in space and time) during these surveys, so presence/absence was calculated and used for the majority of analyses. For surveys in which coincident bottom temperature and bottom salinity data were available, the mean surface and bottom temperatures and salinity were calculated across season and tow for each group (present/absent). T-tests were performed to assess differences in average temperature and salinity between the tows where larvae were present versus where they were absent. All analyses were restricted to larval events within the proposed golden tilefish habitat (Figure 1), defined as locations between (36.50°N, -75.00°W) and (41.16°N, -64.00°W) and bottom depths greater than 50 meters.

Results

Larval distribution is shown in Figure 3 and summarized in Appendix D; Table D.1. Golden tilefish larvae are rarely collected in these surveys, appearing in only 11% of cruises in 33 out of 53 years (see Appendix D; Table D.1., Figure D.1). The number of larvae caught is not different between the MARMAP and EcoMon surveys ($t(21) = 1.44$, $p = 0.92$) and has not significantly increased over time ($F(1,28) = 3.056$, $p = 0.09$). Most of the larvae were collected in the summer months of July, August and September and prefer a narrow band of temperatures (10-16 °C) regardless of the season (Figure 4). There were no larvae collected during the winter months of January and March across all years, and only two larval events occurred in February, one in 1985 (35.7167°N, -74.9167°W) and one in 2001 (36.3500°N,-74.8147°W). There was no coincident temperature or salinity measurement available for those tows. A total of 134 larval lengths were available in this dataset, 90 of which had corresponding in-situ bottom temperatures. Golden tilefish hatch at a size of around 2.6 mmNL and remain pelagic until they grow to about 9.0-15.5 mmSL at which point they descend to the bottom (Fahay 2007). Based on this information, larval lengths were sorted into three categories: “hatchling” (≤2.8 mmNL), “pelagic” (≥ 2.8 mmNl and ≤ 9 mmSL) and “settler” (> 9 mmSL) to examine differences among larval stages. The relative proportion of each larval stage was plotted as a function of bottom temperature across seasons (Figure 5). In general, the pelagic larval stage accounted for 73% of the sample (n = 66), was associated with the widest range of temperatures (7-23°C) and accounted for the greatest proportion of larvae collected in both the spring and fall (Figure 5). The hatchling larval stage represented 25% of the sample (n = 22), collected only in the summer and fall, and occupied a warmer, narrower band of the temperature range (~11-18°C). The settlers, or larger larvae expected to settle to the bottom, were only 3% of the sample (n = 2) and found only in the spring and fall (Figure 5).

Overall, tows with larval events were associated with significantly warmer mean bottom temperatures and a smaller range of temperatures than tows without larval events, in the seasons in which golden tilefish larvae were caught ($p < 0.05$, Figure 6). Interestingly, instances where the majority of larvae were collected in the documented preferred temperature band happened only in the fall months (October, November, December). Tows with positive larval events were characterized by significantly higher bottom salinities on average than tows where no larvae were caught ($p<0.05$, Figure 7). Tows where tilefish larvae were absent showed greater variability in salinity, whereas positive tows were associated with a smaller range of salinity, often higher than what has been described previously in the literature (Table 1, Figure 7). While the connection between golden tilefish larvae and surface temperature and salinity is less clearly described in the literature, the patterns are consistent with what was observed at depth. The surface waters were significantly warmer in tows where tilefish larvae were caught as compared to not (Appendix D; Figure D.2). Tows with larvae also had higher median surface salinity than those without, with significantly higher means in the fall and spring (Appendix D; Figure D.3).

Discussion

While golden tilefish larvae are not readily or often caught in the ‘bongo’ plankton samplers (61 cm diameter with 0.333 and 0.555 mesh nets) used on the MARMAP and EcoMon surveys (Reid et al., 1999), enough data exists to get a picture of the distribution and habitat preferences of this early life history stage. The number of larvae caught has been fairly consistent over time and are associated with warmer and saliter waters. The results suggest that larvae are most abundant in the summer months (July, August, September) which aligns with the timing of peak spawning months of June and July for this species (Grimes et al., 1988). The larvae in this study were associated with a narrow band of bottom temperatures (~7-16°C) and bottom salinities (~31.471 - 36.301 psu) which is fairly consistent with what has been observed and documented in other studies (Table 1).

Indicator Analysis

Indicator selection

An in-depth literature review informed the development of a conceptual model (Figure 2) to isolate ecosystem indicators with potential influences on the population dynamics and life history of golden tilefish. Specifically, we focused on indicators that may impact the underlying processes of distribution, habitat use, and recruitment success. For each indicator, we used ecologically-informed temporal lags to explore effects on different life history stages. Here we briefly explain the data sources for the full list of possible indicators and then in each section will specify which were selected and why.Indicators were selected for each of the following categories, habitat condition, physical oceanography, and food availability.

Proposed indicators and working group comments

The TOR1 group discussed potential indicators with the working group at various meetings. The working group was supportive of the proposed indicators. The indicators that working group members suggested as important were bottom temperature, bottom salinity and sediment.

Ecosystem indicators

Environmental conditions can influence the health and distribution of a stock, thus it is important to identify and track changes in relevant environmental variables (i.e. ecosystem indicators) that influence population processes. Climate related ecosystem changes can lead to shifts in habitats and important ecological interactions, which can alter the distribution and productivity of a given stock. With large enough ecosystem changes, management measures for a given stock may be less effective, and management objectives may not be met (NEFSC, 2024). Below we outline important ecosystem indicators, their link to golden tilefish, and documented observations of the indicator. This information is provided to highlight potential management considerations for changing environmental conditions relevant to golden tilefish.

1. Indicators of habitat condition

- a. Cold pool index/extent/persistence: An area of cold water (sub 10°C) along the northeast shelf in the Mid-Atlantic Bight up to the southern flank of Georges Bank.
    - i. Linkage to golden tilefish: The lower bound of temperature preference for eggs and larvae and juveniles is between 8-13 °C. If the cold pool has a larger extent or persists for a longer time, environmental conditions are not optimal for early life history stages and recruitment success. Area-days with sub-surface temperature between 13-18 °C promote increased larval success, leading to more recruitment.
    - ii. Evidence for linkage: Pierdominico et al., 2015
    - iii. Observations: The yearly cold pool index as well as the spatial extent and duration of the cold pool has been, on average, declining since 1960 (Figure 9d-f).
- b. Bottom temperature:
    - i. Linkage to golden tilefish: Optimal bottom temperature for golden tilefish is between 9-14 °C. Temperatures outside this range may impact spawning location/success and recruitment success.
    - ii. Evidence for linkage: Grimes and Turner 1999; Nesslage et al., 2021; Steimle et al., 1999
    - iii. Observations: Bottom water temperature, while fluctuating over time, has risen 1°C since 2010 (Figure 8b).
- c. Bottom salinity

        i. Linkage to golden tilefish: Optimal bottom salinity for adult golden tilefish is 33-36 psu for juveniles and adults. Salinities outside this range may affect spawning and recruitment success.
        ii. Evidence for linkage: Steimle et al., 1999; Hare et al., 2016
        iii. Observations: Bottom salinity at 78m is steadily increasing from 2000-2020, rising 0.5 psu over the past two decades (Figure 8c).
    d. Sediment
        i. Linkage to golden tilefish: Golden tilefish prefer habitat with high malleability (clay, sand).
        ii. Evidence for linkage: Wenner and Barans 2001; Grimes and Turner 1999
        iii. Observations: Sediment type may control the geographic distribution and abundance of golden tilefish. The fishery for the Hudson Canyon area is restricted to locations with Pleistocene clay substrate (MAFMC 2019).
    e. Rugosity measurement of terrain complexity
        i. Linkage to golden tilefish: Burrows observed on canyon edges
        ii. Evidence for linkage: Grimes and Turner 1999; Grimes et al., 1986
        iii. Observations: Hard bottom habitats support high levels of biodiversity (Dunn and Halpin 2009).
    f. Marine heat wave duration/intensity:
        i. Linkage to golden tilefish: Temperature extremes may cause mortality events for juveniles/larvae, leading to low recruitment
        ii. Evidence for linkage: Fisher et al., 2014
        iii. Observations: Short-term extreme temperature events, which occur periodically in both surface and bottom waters, can produce acute stress on marine organisms, especially when the baseline temperature is increasing.

2. Indicators of physical oceanography

    a. Sea surface temperature
        i. Linkage to golden tilefish: Sea surface temperatures can be used as a proxy for water mass movement, which may cause displacement or mortality of eggs and larvae
        ii. Evidence to linkage: Nesslage et al., 2021; Fisher et al., 2014; Hare et al., 2016
        iii. Observations: Sea surface temperatures within the golden tilefish strata have hovered around 15°C since 2000 (Figure 8a).
    b. Shelf water volume anomalies
        i. Linkage to golden tilefish: The position of the shelf-slope front and an increase of shelf water volume brings cold shelf water onto the shelf slope, which may result in mortality.
        ii. Evidence for linkage: Freeman and Turner 1977

        iii. Observations: Mean shelf water volume within the golden tilefish strata is trending downward post-2000 (Figure 8d).
    c. Number of days of persistent front
        i. Linkage to golden tilefish: The shelf break front in the MAB is a boundary between the cool, less saline water of the continental shelf and warm, highly saline continental slope water. Golden tilefish maintain high site fidelity and prefer stable, warm temperatures.
        ii. Evidence for linkage: Freeman and Turner 1977
        iii. Observations: The movement and strength of the shelf break front is seasonal with high interannual variability and is influenced by the Gulf Stream position and location of warm core rings.
    d. Shelf break jet location/velocity
        i. Linkage to golden tilefish: The shelf break jet separates relatively cold, fresh shelf water from warmer, saltier water over the continental slope, maintaining a pocket of warm, suitable habitat for golden tilefish.
        ii. Evidence for linkage: Freeman and Turner 1977
        iii. Observations: The strength and position of the shelf break jet is highly variable and dependent on a complex combination of dynamic oceanographic processes.
    e. Salinity maximum frequency and location
        i. Linkage to golden tilefish: Influx of water mass may impact retention, displace eggs and larvae from optimal spawned locations
        ii. Evidence for linkage: Frisk et al., 2018; Hare et al., 2016
        iii. Observations: Salinity maximum intrusions have increased in frequency in the past two decades and may be linked to formation rates of Warm Core Rings by the Gulf Stream (Gawarkiewicz et al., 2022).
    f. Gulf Stream Index
        i. Linkage to golden tilefish: A more northerly position of the Gulf Stream (positive Gulf Stream Index) pushing warm water onto the shelf.
        ii. Evidence for linkage: Nesslage et al., 2021; Able et al., 1993
        iii. Observations: The mean Gulf Stream Index has shifted from a more southerly average position of the Gulf Stream in the 1970-1990s to a more northerly average position post-2000 (Figure 9a).

3. Indicators of food availability
    a. Primary productivity
        i. Linkage to golden tilefish: Years of high primary productivity support strong recruitment year classes
        ii. Evidence for linkage: Peretti et al., 2017; Nitschke 2023
        iii. Observations: Primary production varies largely between regions of the Northeast U.S. Continental Shelf Large Marine Ecosystem (NES LME). In particular, primary production declines moving offshore from the coast to

the shelf break (NOAA Fisheries).

    b. Chlorophyll
        i. Linkage to golden tilefish: Chlorophyll-*a* concentrations are an indication of the level of primary production occurring in pelagic waters inhabited by early life stage golden tilefish
        ii. Evidence for linkage: Steimle et al., 1999
        iii. Observations: The spatial average of the monthly median chlorophyll-*a* concentration in the golden tilefish strata shows high interannual variability but no clear trend from 2000-2020 (Figure 9b).
    c. Calanus abundance
        i. Linkage to golden tilefish: Food source for early life stages of golden tilefish.
        ii. Evidence for linkage: Peretti et al., 2017
        iii. Observations: Within the NEUS LME, Morse et al., (2017) documented both changes in overall zooplankton abundance and in the relative abundance of dominant species, including Calanus.
    d. Phytoplankton size class/Microplankton
        i. Linkage to golden tilefish: Microplankton are prey for zooplankton and may act as proxy for abundance of zooplankton, which are consumed by larval tilefish.
        ii. Evidence for linkage: Steimle et al., 1999
        iii. Observations: The monthly median of microplankton abundance averaged across golden tilefish strata shows a great deal of interannual variability but displays no clear trend from 2000-2020 (Figure 9c).

Socioeconomic indicators

1. Fuel price
2. Storminess index
3. Dogfish/skate interactions

Indicators selected for development

Based on working group feedback on the indicators described above, combined with necessary modifications due to data or analysis constraints, the following were further developed. Aside from sediment and rugosity index, a time series of each indicator was plotted with associated confidence intervals and analyzed for trend when applicable (Figures 8,9).

Ecosystem indicators

1. Habitat condition
    a. Cold pool index/extent/persistence
    b. Bottom temperature
    c. Salinity

        - d. Sediment/rugosity
2. Physical Oceanography
    - a. Sea surface temperature
    - b. Gulf Stream Index
    - c. Shelf water volume, shelf water temperature, shelf water salinity
3. Food availability
    - a. Microplankton abundance
    - b. Chlorophyll *a*

Socioeconomic indicators

No socioeconomic indicators were developed for this iteration of ToR1.

Indicators needing further research before development

Based on working group feedback on the indicators described above, combined with necessary modifications to indicators due to data or analysis constraints, the following indicators were not selected for development at this point in time.

Ecosystem indicators

1. Marine heat waves
2. Primary productivity
3. Salinity maximum intrusions

Socioeconomic indicators

4. Dogfish interactions
5. Fuel price
6. Storminess index

Methods

Data sources

Tilefish data

Model Recruitment Estimate

Recruitment for golden tilefish is estimated within the Age Structured Assessment Program (ASAP) model (Legault and Restrepo 1998). The 2017 ASAP model was developed at the SARC 58 benchmark assessment and uses a pooled age-length-key (due to the lack of age data) along with year specific keys for more recent data (Nitschke, 2021). The model output contains an age-1 recruitment index from 1970-2020 (Figure 10). The estimated age of recruitment is one year but recruitment age to the fishery is roughly 4-5 years. For this analysis, we used age-1 model recruitment estimates from the 2021 Golden Tilefish Management Track Assessment. Model-derived recruitment estimates for golden tilefish averaged 1.48 million age-1 fish per year from 1971-2020 (Nitschke 2021).

Golden tilefish populations in the Northwest Atlantic experience strong recruitment year class "pulses" on average every 6-7 years. Recent strong year classes occurred in 1993, 1998, 1999, 2005, and 2013. The 2017 year class is estimated to be above average (2.1 million), as these fish are just beginning to enter the fishery (Nitschke 2021). There is evidence to suggest that increases in fishery CPUE and model biomass are due to the influence of strong recruitment year classes (McBride et al., 2013; Nitschke 2023). Declines in CPUE have been observed when there are no recent recruitment pulses; for example, CPUE has decreased in recent years as the 2013 recruitment class ages out of the fishery (Nitschke 2023).

Recruitment is dependent on larval settlement and subsequent survival, but timing and habitat criteria for settlement is unknown (Dawson 2021). Furthermore, recruitment represents the endpoint or combined outcome of disparate processes influencing various life stages over a wide range of spatial and temporal scales. However, it is possible to identify key biotic or abiotic drivers that can inform recruitment estimates and predictions (Sharma et al., 2019). We acknowledge the drawbacks and uncertainty in using model derived estimates as a dependent variable but still elected to explore relationships between the timeseries of annual recruitment and environmental indicators because it is often done in studies that evaluate the impacts of environmental drivers on fished stocks (Haltuch et al., 2019; Marshall et al., 2019) and because other information on juveniles and pre-recruits is lacking.

Study Fleet/Observer Incidental CPUE

Two high-resolution fishery-dependent data sets containing catch and effort data from the NEFSC's Study Fleet and Observer Programs, were combined to generate haul-level CPUE values, using a guild approach (NEFSC 2016; Drew 2022; Cheng et al., 2023; Hoyle et al., 2024). The NEFSC Study Fleet generates a large dataset from fishers log books including high resolution catch, effort, and environmental data (Palmer et al., 2009; Bell et al., 2017; Jones et al., 2022). The Northeast Fisheries Observer Program (Brooke 2015) generates catch data collected onboard commercial fishing vessels by trained biological scientists who collect data on catch, fishing effort, biological characteristics, and socioeconomic information. This combined data set captures both incidental golden tilefish catch as well as catch data for a suite of other commonly occurring species from trawl fisheries (Jones and Salois, 2024). Golden tilefish CPUE was generated from these undirected golden tilefish trips and expanded using species associations, in order to introduce plausible zeros and reduce bias (NEFSC 2016; Dettloff 2021; Drew 2022, Jones and Salois, 2024). This data set ranges from 2000 to 2022 and yielded ~4,600 total catches of golden tilefish and ~2,900 catches when reduced to only small mesh sizes (< 5.5 in) (Figure11). Golden tilefish catch from undirected trawl trips ranges from off Georges Bank to just below Norfolk Canyon, with highest catch rates in and north of Hudson Canyon (Figure 12). Work by Jones and Salois (2024) suggests that the Study Fleet/Observer trawl CPUE is indexing golden tilefish around 4 years of age, which provided an excellent index to explore potential environmental drivers of recruitment. More information on the construction of this dataset can be found under ToR3: “Exploring a CPUE index from trawl gear using high-resolution catch data”.

Golden tilefish is a data-poor species, where Vessel Trip Report (VTR) based CPUE is currently the only index of abundance (Nitschke 2021). Assessing golden tilefish CPUE from incidental and undirected catch is a new approach that may not fully represent the entire Mid-Atlantic and New England golden tilefish population because relationships with ecosystem drivers may vary slightly depending on location. The addition of data from the Study Fleet and Observer programs is a new resource that may prove beneficial to the assessment process.

Ecosystem indicator data

Habitat Condition

Habitat condition indicators include bottom temperature, salinity at depth and sediment size. GLORYS12 (E.U. Copernicus Marine Service Information, 2023), a global eddy-resolving physical ocean and sea ice model (1993-2023) with high resolution (1/12°), data was used for temperature and salinity at four depths: bottom temperature and salinity for overall habitat conditions, salinity at 78 m for larvae and recruits, salinity at 92 m for recruits and juveniles, and salinity at 110 meters for juveniles and adults. All hydrographic data were spatially cropped to the tilefish strata, which was identified as the collection of 14 individual NEFSC bottom trawl survey strata that pertain to tilefish habitat and fishery locations (Figure 1). In addition, *in situ* bottom temperature data coincident with catch locations from the Study Fleet was available for a subset of tows. This data was filtered for depths > 50 m and averaged for each month. Sediment data was used to quantify the benthic habitat at fishing locations. The sediment data classifies soft-sediments based on their grain size, describing sediments ranging from mud and silt to medium and coarse sand (Anderson et al., 2010; The Nature Conservancy 2016).

Three variables were used to represent the timing and strength of the seasonal cold pool in the Mid-Atlantic Bight (duPontavice et al., 2022; Chen et al., 2018). The cold pool index quantifies the interannual strength of the cold pool, where positive values indicate years with a stronger cold pool (Chen and Curchitser 2020). The cold pool spatial extent index is based on the total area where bottom temperatures remain below 10 °C for at least 2 months between June and September. Positive values represent a larger cold pool area and negative values indicate a smaller spatial extent. The persistence index represents the duration of the cold pool, which ends when bottom temperature rises above 10 °C after it is formed each year. Positive persistence index values indicate a longer persistence of cold pool conditions whereas negative values indicate a shorter persistence of the cold pool.

Physical Oceanography

Sea surface temperatures were obtained from GLORYS12 (E.U. Copernicus Marine Service Information 2023), averaged for each month, and spatially cropped to the golden tilefish strata (Figure 1). Most of the other physical oceanography indices are derived from data submitted for the State of the Ecosystem (SOE) reports and maintained in ecodata (Bastille and Hardison, 2018); more detail than this brief description can be found in the SOE technical documentation (NEFSC, 2023).

Shelf water volume is a measure of the volume of water inshore of the shelf-slope front, a narrow transition region between masses of cool, low salinity shelf water and warm, high salinity slope water (Linder and Gawarkiewicz 1998). This was derived from CTD data from NEFSC surveys (Fratantoni et al. 2015). In this analysis, shelf water is defined as all water having salinity < 34 psu (Mountain 1991). The position of the shelf-slope front varies interannually with higher shelf water values associated with the front being closer to the shelf break (Forsyth et al., 2015; Gawarkiewicz et al., 2018). For this indicator, smaller values indicate that the front is pushed inshore such that there is more Slope Sea water on the shelf. Lastly, the Gulf Stream Index (GSI), a measure of the Gulf Stream position relative to the mean position, was used as an offshore indicator. The GSI is based on ocean temperature at 200m (15 °C) depth between 55W to 75W (Pérez-Hernández and Joyce 2014). Positive values indicate that the Gulf Stream is in a more northerly position, whereas negative values indicate a more southerly position.

Food Availability

Microplankton, the largest phytoplankton size class (> 20 μm), and total chlorophyll a are indicators explored as proxies for food availability for golden tilefish. Microplankton represents the chlorophyll concentration of just the larger phytoplankton, predominantly diatoms, whereas total chlorophyll includes nanoplankton (2-20 μm) and picoplankton (< 2 μm) in addition to microplankton (Turner et al., 2021). Both of these data products are derived from the European Space Agency's Ocean Colour Climate Change Initiative (OC-CCI) satellite ocean color data (version 6.0) (Sathyendranath et al., 2019). The daily level 3 (L3) mapped (4 km resolution, sinusoidally projected) OC-CCI dataset is comprised of merged SeaWIFS, MERIS, MODIS-Aqua, VIIRS and Sentinel3A-OLCI global data. The L3 OC-CCI products include chlorophyll a (CHL-CCI), remote sensing reflectance (Rrs(λ)), and several inherent optical property products (IOPs). The CHL-CCI blended algorithm attempts to weight the outputs of the best-performing chlorophyll algorithms based on the water types present, which improves performance in nearshore water compared to open-ocean algorithms. Phytoplankton size classes (PSC), including microplankton, are calculated according to Turner et al., (2021). The regionally tuned abundance-based model is based on the three-component model of Brewin et al., (2010) that varies as a function of sea surface temperature (SST) (Brewin et al., 2017; Moore and Brown 2020). Sea Surface Temperature (SST) data include the 4 km nighttime NOAA Advanced Very High Resolution Radiometer (AVHRR) Pathfinder (Casey et al., 2010;

Saha et al., 2018) and the Group for High Resolution Sea Surface Temperature (GHRSST) Multiscale Ultrahigh Resolution (MUR, version 4.1) Level 4 data (Chin et al., 2017; JPL MUR MEaSUREs Project 2015). AVHRR Pathfinder data are used as the SST source until 2002 and MUR SST in subsequent years.

Indicator Time Series

Analysis

Regression Analyses

To determine the predictiveness of the selected environmental indicators, we computed correlations and linear regressions between each environmental indicator and a subset of the recruitment index time series (1998 - 2020). The recruitment index was truncated to account for the increased uncertainty in the recruitment estimates prior to 2000 (pers. communications with the lead assessment scientist), as well as to preserve years that were associated with strong year classes and possible environmental effects from the powerful 1997-1998 El Niño event (McPhaden 1999). For these models, golden tilefish were assumed to reach 1 year of age during summer of the given recruitment year, having hatched the prior summer (indicated by a 1 year lag, age 0), as this timeline coincided with tilefish peak spawning season (Grimes et al., 1988). The winter and spring seasons lagged by 1 year, thus, provide context about the environment prior to hatching of eggs and may be investigated for parental effects.

Mean monthly values for each of the ecosystem indicators were computed for two time points, (1) the time of recruitment, when fish were 1 year of age, and (2) at a 1 year lag in order to explore potential environmental signals at time of birth (age 0). Each environmental indicator was then grouped across seasons, where, winter = January-March, spring = April-June, summer = July-September, fall = October-December. This allowed us to test the direction and strength of seasonal environmental relationships across different time periods of the estimated early life history stages.

Linear regressions and Pearson's correlation analysis were also used to examine relationships between the ecosystem indicators and Study Fleet/Observer incidental CPUE index. Environmental indicators were either extracted at the time and location of each haul (bottom temperature, bottom salinity, microplankton abundance, sea surface temperature, chlorophyll *a*) or from monthly data averaged across the golden tilefish strata, corresponding to the month of each haul (shelf water indicators, cold pool indicators, gulf stream index). Regressions and correlations were then conducted on the monthly averages of indicators and CPUE. As the incidental CPUE index was estimated to represent fish that are 3-4 years old (Jones and Salois 2024), all environmental indicators were lagged by 3 and 4 years to explore associations between environmental conditions and tilefish recruits (age 1) and larvae (age 0). Regressions and correlations between each indicator and the incidental CPUE index were also computed by season as above.

Generalized Additive Models

In an effort to explore the relationships between catch-per-unit effort for the trawl fishery and a suite of environmental covariates, we fit generalized additive models (GAM) to the Study Fleet/Observer CPUE index. For the GAMs, the response variable, CPUE, was compared to ecosystem predictor variables across two time points, time of catch (age 4) and CPUE with a lag of 3 years (age 1). Predictor variables consisted of 24 candidate oceanographic metrics selected from the conceptual model (see Appendix C, Table C.1.). The results of the CPUE regression analyses, which identified significant trends between CPUE and 9 of the candidate variables (Table 3), served as the initial variable selection step for our GAM. The second variable selection step included examining correlations and multicollinearity among the predictor variables (Appendix C; Tables C.2., C.3.) using variance inflation factors (VIF). Variance inflation factors measure how much the variance of a regression coefficient is inflated if more than one independent variable (in this case, the indicators) are correlated (Shrestha 2020). Values of VIF > 5 specify highly correlated variables. All indicators with VIF scores greater than 5 (cold pool extent and persistence, microplankton (at time of catch), sea surface temperature, shelf water salinity, and shelf water temperature with 3 year lag) were removed from the final model. To further reduce multicollinearity, we made choices informed by the indicator selection processes, to select the most ecologically relevant indicators to early life history stages of golden tilefish. For instance, microplankton was chosen over chlorophyll-*a*, as the strength and significance of the relationship between microplankton and CPUE was greater. Additionally, our literature review and indicator selection process identified microplankton as a potential food source for *Calanus* species (an abundant copepod in the Mid-Atlantic Bight region), which likely make up a large portion of the zooplankton diet of larval tilefish (Steimle et al., 1999), suggesting a more direct relationship to food availability compared to chlorophyll-*a*. Sediment grain size, latitude, longitude, year, and month for each trawl are included as smooths. Models were trained on a subset of the full data using a simple training/testing data splitting algorithm, selecting 70% of the data to be used for training with the remaining 30% retained for analysis. Model residuals and concurvity were examined (Appendix C; Figures C.1,C.2.). The final GAM model adjusted for multicollinearity was fit assuming a tweedie distribution with a log link function to account for positive skew and over dispersion:

$$\mathit{cpue}_i \sim \mathit{te}(\mathit{lat}_i, \mathit{lon}_i) + \mathit{ti}(\mathit{year}_i, \mathit{month}) + s(\mathit{bottom\_temp}_i) + s(\mathit{bottom\_salinity}_i) + s(\mathit{shelfwater\_volume\_lag3}_i) + s(\mathit{microplankton\_lag3}_i) + s(\mathit{sediment\_grain\_size}_i) + \mathit{gulf\_stream\_position} + \mathit{gulf\_stream\_position\_lag3}$$

Root-mean-square error was calculated to compare the training and testing datasets and estimate the prediction accuracy of the model. Model predictions using the testing dataset moderately followed the model data (Figure 14). While the residuals indicate bias due to the zero-inflated nature of the data, the final model had fairly good predictive ability (RMSE: 2.848789).

Results

Regressions

Recruitment

Regression analysis of ecosystem indicators and model recruitment estimates yielded mixed results in uncovering potential drivers of golden tilefish recruitment (Table 3, Appendix A). There was no linear trend or significant correlation between recruitment and sea surface temperature (Appendix A., Figure A.1). Recruitment decreased with increasing bottom temperature in winter of year 0, prior to spawning and birth (Appendix A., Figure A.2). Similarly, there was a significant negative correlation between recruitment and salinity (at both 78m and 92m depth) in winter of year 0 (Appendix A., Figure A.3).

Physical oceanography indicators showed considerable linkages to recruitment. Both the cold pool persistence index and spatial extent index were negatively correlated with recruitment at age 1; however, the trend does not exist during year 0 (Appendix A., Figure A.4a,b). A positive cold pool index was moderately correlated with higher recruitment at age 1, contrasting with indices of spatial extent and persistence, but the trend was not significant (Appendix A., Figure A.4c). High recruitment was negatively correlated with shelf water volume in the spring of recruitment year but positively correlated in the spring of year 0. There were no discernible trends in shelf water temperature or salinity at age 1 or 0 (Appendix A., Figure A.5). Further, there were no significant trends between the Gulf Stream Index and recruitment index (Appendix A., Figure A.6).

Golden tilefish recruitment relationships with indicators of food availability showed mixed results. There was no explicit relationship between chlorophyll-a and recruitment in either the year of recruitment or birth year (Appendix A. Figure A.8). Conversely, recruitment showed a significant positive relationship with microplankton abundance in the fall of year 0 (Appendix A. Figure A.7).

Study Fleet/Observer Incidental CPUE

Regression analysis revealed significant linear trends between the incidental golden tilefish CPUE index (derived from Study Fleet/Observer trawl fisheries) and indicators of habitat condition, physical oceanography, and food availability (Table 3). At time of catch (age ~4), CPUE declined as sea surface temperature increased with significant trends in the winter, spring, and summer (Appendix A. Figure B.1). At a recruitment age of 1 (CPUE 3 year lag), CPUE declined in the spring but rose in the winter in response to increasing sea surface temperatures. A weak, positive linear relationship also exists between sea surface temperature and CPUE in the winter before birth (age 0). Indicators of bottom temperature and salinity revealed no significant linear trends with CPUE, however catches are clustered in a narrow band of temperatures between 10-14℃ and salinities between 34-36 psu (Appendix A. Figures B.2,B.3).

There were no significant linear trends between the CPUE at time of catch (age ~4) and shelf water volume or shelf water salinity (Appendix A. Figure B.4). However, CPUE decreased as shelf water temperature increased, particularly in the summer and winter months. CPUE exhibited a strong negative correlation with shelf water volume in lags of 3 (recruitment) and 4 (birth) years. The trend and significance of the recruit year matches that of the age-1 recruitment index currently used in the stock assessment. Moderate positive linear trends occur between CPUE and shelf water temperature and salinity at lags of 3 years. CPUE was significantly related to Gulf Stream Index, with decreased catch in the winter, spring, and summer when the Gulf Stream is in a more northerly position (Appendix A. Figure B.5). Catch is negatively correlated with a lagged (northerly) Gulf Stream in the summer but positively correlated in the winter. A moderate negative relationship exists between cold pool persistence and extent and CPUE at lags of 3 and 4 years (Appendix A. Figure B.6), indicating increased golden tilefish catch when the cold pool is spatially limited and breaks down earlier in the years of birth and recruitment. No linear trends were observed between CPUE and the cold pool index at time of catch, recruitment year, or birth year.

Indicators of food availability (microplankton and chlorophyll-*a*) both exhibit a positive relationship with CPUE in the spring and summer of the year of catch. Catch was lowest in the summer, and highest in the spring and fall which was also associated with increased phytoplankton biomass. At age-1 (3 year lag), a significant (weak) positive linear trend between microplankton and CPUE in fall matches that of model recruitment estimate (Appendix A. Figure B.7). The same trend is seen in the spring of golden tilefish birth year (4 year lag), possibly at the time of spawning.

Generalized Additive Models

The final GAM identified 10 covariates that were important predictors of golden tilefish catch-per-unit-effort, including spatial (latitude and longitude), temporal (year and month), and environmental (bottom temperature, bottom salinity, shelf water volume (3 year lag), shelf water temperature, microplankton (3 year lag), and Gulf Stream position (time of catch and 3 year lag) variables (Appendix C, Table C.2.; Figure 13). The indicators in this model accounted for 28% of the total deviance. Space accounted for much of the variation in the model, and the spatial smoother accounted for the interacting effects of latitude and longitude, highlighting a hotspot of catch around 39° N x 72° W, corresponding to the area of continental shelf surrounding Hudson Canyon (Figure 13; see also Figure 1). This area is consistent with areas of high golden tilefish availability in the literature, as well as from expert observations from industry members. Temporally, CPUE was substantial in the summer months prior to 2015. In recent years (> 2018), catch has shifted towards the fall and winter months with the lowest CPUE now in the summer. Golden tilefish fishermen state that they have been targeting winter months as there is less competition with other fishers during this time.

Catch increased when bottom temperatures were between 10-14°C and salinity between 34-36 psu, mirroring the regression analysis results. CPUE values increased with lower shelf water volume at time of recruitment (lag 3 years). Catch is variable across the range of shelf water temperatures (10-15°C), with a peak between 11-12°C. There is a unimodal relationship between catch and increased microplankton abundance at time of recruitment. CPUE declined with increased sediment grain size, indicating higher golden tilefish catch in habitats with finer sediment (e.g.: mud, very fine sand). The relationship between golden tilefish CPUE and the position of the Gulf Stream differs between time of catch and recruitment (3 year lag). Tilefish are more likely to be caught when the Gulf Stream is in a more northerly position at the time of catch. Conversely, when lagged three years (concurrent with the time of recruitment), a southerly position of the Gulf Stream is associated with higher catch.

Discussion

Literature comparison and agreement with industry perspective

The results presented in this analysis identify potential ecosystem drivers of golden tilefish dynamics and corroborate published literature and past examinations of the relationships between golden tilefish and environmental drivers. Bottom temperature (10-14℃) and salinity (34-36 psu) ranges from both regression and generalized additive model (GAM) analyses of incidental tilefish catch from trawl fisheries match the habitat descriptions of golden tilefish documented in the literature (Grimes et al., 1986; Grimes and Turner 1999; Steimle et al., 1999). Recruitment index values were associated with bottom temperatures between 9-12°C and salinities between 34-36 psu, further solidifying previously documented golden tilefish habitat preferences. Temperature and salinity ranges also validate the models produced by Frisk et al., (2018).

Our GAM results indicated changes in the timing of golden tilefish catch in recent years. The model quantified reports by golden tilefish industry members who noted a shift in prime fishing seasons from summer to winter and spring. While this model was only fed incidental catch data, the fact that it was able to pick up that signal highlights the value of this trawl-based catch index for the tilefish fishery. GAM results indicate that habitats where golden tilefish were caught were characterized by small sediment grain sizes, with the majority of the distribution centered around the Hudson Canyon area of the Northeast Shelf. This is consistent with well-documented habitat characterizations in the literature (Grimes et al.1986; Grimes and Turner 1999; Guida 2005) and quantifies the fishers ecological knowledge that was documented in our conversations with industry.

The position of the shelf-break front varies inter-annually, with years of higher shelf water volume indicating that the front is pushed further towards the shelf break and years with lower volume indicating the front is pushed inshore, resulting in more slope water on the shelf (Linder and Gawarkiewicz 1998, Fratantoni and Pickart 2007). The observed declines in CPUE with increased shelf water volume (indicating shelf break front is closer to the shelf edge) and lower shelf water temperature on the continental shelf edge coincide with hypotheses made after a mass mortality event of golden tilefish in the late 1800s. It is believed that this large-scale die-off of golden tilefish was due to an offshore movement of cold shelf water, trapping golden tilefish within a band of cold shelf water alongside deeper Slope Sea cold water on the offshore edge of its habitat (Freeman and Turner 1977). Our results indicate that increased shelf water volume may also have considerable effects on recruitment. We found recruitment estimates decline in the spring for age 1 recruits when the shelf break front is pushed closer to the shelf edge and there is less Slope Sea water on the shelf, which is consistent with the idea that increases in shelf water may provide unfavorable conditions for tilefish. Conversely, we found increased recruitment was correlated with increases in shelf water volume in the spring of year 0, which corresponds to the start of the spawning season for golden tilefish. This may suggest that the movement of water masses along the slope edge (more than the thermal/saline habitat itself) may be playing a role in recruitment success. Specifically, we suspect the position and variability of the shelf-break front in the spring and summer months (when spawning is occuring) may influence the retention (or displacement) of larvae in spawning grounds.

Nesslage et al., (2021) found an association between a positive Gulf Stream Index (increased warm water) and increased CPUE with lags up to 3 years. Our CPUE lags of 1 and 2 years as well as winter at a lag of 3 years also showed a significant positive correlation with a more northerly position of the Gulf Stream (Figure 15). Able et al., (1993) documented a reduction or cessation of feeding in golden tilefish resulting from large, abrupt temperature changes after a shift in the Gulf Stream. An important caveat in this relationship is the large spatial extent of the Gulf Stream. The Gulf Stream Index is relative to the Gulf Stream as a whole and can neutralize itself if the average position is highly positive in one area and negative or neutral in another. These results are likely due to a combination of water mass movement from the Gulf Stream and continental shelf water and food availability. A more western Gulf Stream Index, now included in the State of the Ecosystem reports, may be a better indicator in future assessments.

New information

Declines in age 1 recruitment with increases in salinity during the winter prior to birth (at depths of 78m and 92m) may be related to processes driving the influx of water masses transporting warm, salty water to upper ocean layers inhabited by early life-stage golden tilefish, which have increased in frequency in recent years (Gawarkiewicz et al. 2022). The positive correlation between microplankton abundance and recruitment estimates in the fall (following birth) also places great importance of considering environmental indicators throughout the water column when exploring early life-stages, since larval golden tilefish are suspended higher in the water column (relative to juveniles and adults) and are more likely to be affected by the dynamics of their physical environment and ability to forage during this time.

Our GAM results support the findings of Nessalge et al. (2021) where a northerly shift in the Gulf Stream was associated with greater CPUE. Interestingly, when we compared a lagged

Gulf Stream Index to approximate the time at which fish would be recruiting (age-1), an opposite trend appeared, where a southerly shift of the Gulf Stream was correlated to higher CPUE values. This result warrants further investigation, as early life stages of golden tilefish are able to withstand wider ranges in temperature (8-19°C, Steimle et al., 1999) and may not receive as much benefit from warmer Gulf Stream waters as adult tilefish.

While the suite of environmental indicators chosen for this study explained only a moderate amount of variation in catch, the data used in this analysis was derived from undirected golden tilefish catch and yet was still able to pick up important environmental signals previously defined for this species. Since golden tilefish remain a relatively data-poor stock, this work highlights the value of this new CPUE index (derived from trawl fisheries) in begining to make some inferences on drivers of tilefish recruitment, as this data is likely indexing younger fish (3-4 years old) than the LPUE index of abundance used in the assessment (Nitschke 2021, Jones and Salois 2024). The addition of data from the Study Fleet and Observer programs is a new resource that may prove beneficial to the assessment process.

Indicator Agreement

Multiple environmental indicators showed consistent trends across datasets and life history stages. The incidental CPUE index (derived from Study Fleet and Observer data sets) declined with increases in sea surface temperature at both time of catch (around age 4) and with a 3 year lag (near age-1 recruitment), however this trend did not match trends between SST and the recruitment index. Bottom temperature and bottom salinity indicators, while exhibiting no clear linear trends, coincided with habitat descriptions across life history with both the incidental CPUE index (derived from Study Fleet and Observer data sets) and recruitment index. Age-1 fish from both the new CPUE index and recruitment index were negatively correlated with shelf water volume, cold pool spatial extent, and cold pool persistence. Golden tilefish were positively correlated with microplankton abundance across three different developmental stages: ages 3-4 (CPUE index: no lag), ages 0-1 (CPUE index: 3 year lag), and as larvae (recruitment index: 1 year lag). Furthermore, the correlation between microplankton abundance in the fall and fish of larval ages across both data sets increases our confidence that this may be a useful indicator of food availability, with potential implications for understanding drivers of growth and development for tilefish early life stages.

Research Recommendations

Nesslage et al., (2021) was a key study in identifying long-term, low-frequency climate drivers on golden tilefish in an attempt to explain observed 6-7 year pulses in recruitment. This study attempts to further explain these recruitment pulses by placing emphasis on high frequency, seasonal environmental indicators on a dataset that indexed fish aged 3-4 years old. Our work provides context for potential environmental indicators that may influence golden tilefish recruitment, including salinity at depth, shelf water volume, and microplankton abundance, yet more research is needed to understand ecological drivers of recruitment and better understand the recruitment pulses observed in this data-poor fishery. Our recommendation is that future research should focus on the following primary areas concerning golden tilefish size distribution, availability, recruitment, and early life history:

> **(i)** Environmental indicators identified here may have potential as a modifier to the recruitment parameter but should be further developed before incorporation into the WHAM framework. In the indicator refining process, we recommend using methods to track and quantify the propagation of uncertainty as environmental data used to develop the indicators are averaged in space or time (Punt 2024).
>
> **(ii)** Exploring environmental indicators at different spatial scales to see how scale impacts results. For this work, indicators were cropped to the entire golden tilefish strata, but we recommend future work partitions that strata into two spatial domains (1) North and (2) South of Hudson Canyon as environmental conditions and oceanographic dynamics are quite variable in the region and can differ greatly between the northern and southern edges of the shelfbreak.
>
> **(iii)** Increased exploration of alternative data streams to better capture the size distribution of the fish caught in this fishery, such as electronic monitoring onboard vessels (to collect length data) or electronic size monitoring programs (to collect paired length and weight) at processing facilities, as has been done for other species.
>
> **(iv)** High resolution catch and effort data show promise in developing our understanding of the ecological associations of tilefish. Therefore, increasing volumes of data from these programs could be highly beneficial moving forward. Additionally, increased information on the size distributions of tilefish encountered in directed and non-directed fishing activities would be very useful.
>
> **(v)** Continued and increased use of novel survey data (tilefish longline survey, Gulf of Maine Bottom Longline survey) to document geographic and size distribution of tilefish.
>
> **(vi)** Identification of golden tilefish spawning locations. Cooperative research aboard commercial fishing vessels to collect coincident oceanographic and biological (egg and larvae) data.
>
> **(vii)** Socioeconomic indicators were not developed for examination in TOR1. Future research should include socioeconomic indicators in the data analysis. Conversations with golden tilefish fishers and vessel owners identified interannual variability from other, non-environmental drivers, such as quotas, weather, fuel costs, economics, and more profitable fisheries. Datasets for fuel prices and storminess index, in particular, are available and may provide a jumping off point for socioeconomic indicator development.

Conclusions

Ecosystem Considerations

- Regression analysis revealed 9 ecosystem indicators that are significantly correlated with golden tilefish CPUE at time of catch and with a 3 year lag (age 1). Golden tilefish CPUE declines with increases in sea surface temperature (at time of catch and at age 1), shelf water volume (at age 1), shelf water temperature (at time of catch), Gulf Stream Index (at time of catch and summer at age 1), and cold pool extent and persistence (at age 1). CPUE increased with increasing shelf water temperature and salinity (at age 1), Gulf Stream Index (winter at age 1), microplankton abundance (at time of catch and fall at age 1), and chlorophyll *a* concentration (at time of catch).
- Regression analysis revealed 5 ecosystem indicators that are significantly correlated with an age-1 recruitment index and with a 1 year lag (time of birth). Golden tilefish model recruitment declines with increasing salinity (time of birth), shelf water volume (age 1), and cold pool extent and persistence (age 1). Recruitment increases with microplankton abundance in fall of their birth year.
- Generalized additive model (GAM) results highlighted temporal changes in golden tilefish catch from summer to winter/spring, supporting comments by industry members. Golden tilefish prefer small sediment sizes and their distribution is concentrated near Hudson Canyon.
- Bottom temperature (10-14℃) and salinity (34-36 psu) ranges from both regression and generalized additive model (GAM) analysis of study fleet and observer golden tilefish catch are consistent with the habitat descriptions documented in literature (Grimes et al., 1986; Grimes and Turner 1999; Steimle et al., 1999).
- Golden tilefish larval data collected from MARMAP and EcoMon surveys revealed significantly warmer mean bottom temperatures and higher bottom salinities in tows with positive larval events versus tows with no larvae. Surface water temperatures and salinities were also higher in tows with tilefish larvae compared to those without.

Tables

Table1. Information collected from literature review on golden tilefish habitat and distribution, phenology, age, length, and growth parameters, energetics, predators, and prey for each life history stage.

Stage	Habitat & Distribution	Phenology	Age, Length, Growth	Energetics	Diet	Predators/ Competitors
Recruit	Shelf break, submarine canyon walls, and flanks; Georges Bank to Cape Hatteras Large vertical burrows in clay or sand 80-540m (but usually 100-200 m)	Seasonal cooling in Spring may force tilefish to concentrate within preferred temperature Pulses of recruitment every 6-7 years	Females: 50-100 cm; 46 years Males: 50-120 cm; 39 years	Narrow band of temperatures 9-14C; 33-36 psu	Bottom feeders: Juvenile tilefish, other fish, decapods, benthic epifauna	Sharks, lampreys
Spawning		Serial spawning; March-Nov, peaking in June	2-4 years, 60-65 cm (female) 65-70 cm (male) at maturity	2.28 mil eggs per female; 500k for first time spawner 10.16-14.9C		
Egg	Non-adhesive and buoyant in water column on shelf break; Georges Bank to Cape Hatteras 80-800 m	March-Nov	1.16-1.25 mm	8-19C; 34-36 psu		
Larvae	Water column on outer continental shelf; Georges Bank to Cape Hatteras 50-150 m	Feb-Oct, peaks Jul-Oct	2.6-9.0 mm	13-18C; 33-35 psu	Probably prey on zooplankton	
Juvenile	Shelf break, submarine canyon walls, and flanks; Georges Bank to Cape Hatteras Small burrows or rocks/clay 80-540 m (but usually 100-200 m)	Early juveniles Apr-July	15-500 mm	8-18C; 33-36 psu	Decapod crustaceans, small fish, benthic epifauna	Adult tilefish, goosefish, sharks, dogfish, conger eels
Pre-Recruit			Until age 4, both males and females grow 10 cm/yr. After age 4, males grow faster.			

Table 2. Environmental impacts on golden tilefish life history and fishery performance detailed in previous literature.

Environmental Impacts on	**Notes**	**References**
Recruitment	1. 6-7 year class pulse likely due to negative AMO 2. Large, abrupt temperature changes (possibly due to Gulf Stream positionIndex?) may cause tilefish to cease feeding 3. Local positive temperature anomalies correlated with recruitment and growth (1-2 year lag for +NAO-induced slope temperature to reach tilefish habitat + 3-4 year lag for tilefish growth and recruitment to fishery)* 4. Recruitment regimes (low in 80s, high in 90s, low in 00s) for large NES species coincided with regimes in copepod abundance. Increased zooplankton abundance could lead to increased larval growth, or higher parental condition through increased benthic flux	1. Nesslage et al. 2021 2. Able et al. 1993 3. Fisher et al. 2014 4. Perretti et al. 2017
Natural mortality	1. 1882 die off as a result of extreme negative NAO (one year prior) causing intrusion of cold sub-Arctic water	1. Fisher et al. 2014
Distribution/Habitat Use	1. Seasonal cooling thought to concentrate populations 2. Inhabit narrow band of warm bottom temperatures (9-14℃) along the continental shelf, burrowing into the sediment 3. Correlation between soft sediment (clay/sand) with high malleability and tilefish occurrence 4. Tilefish burrow substrate must be cohesive, ability to maintain a firm shape without collapse when excavated (e.g. Pleistocene clays of Hudson Canyon) 5. Tilefish concentrate in shallow depths inshore of Veatch Canyon in the late winter and spring in conjunction with decreasing bottom water temperatures both inshore and further east on Georges Bank	1. Nesslage et al. 2021 2. Grimes and Turner 1999 3. Grimes and Turner 1999 4. Wenner and Barans 2001 5. Grimes et al. 1980
Growth/Maturity	1. Spawning females found in narrow temperature range (10.16-14.99℃) 2. Reduced subarctic slope water from +NAO correlated with faster adult growth rates and higher fecundity	1. Sedberry et al. 2006 2. Fisher et al. 2014
Fishery/Landings	1. AMO (-) and NAO (+) likely work together to increase landings (lags of 3-7 years) 2. Labrador current (decrease) and Gulf Stream index (increase) raise CPUE (minimal influx of cold water) 3. Catch rates high in spring when 9-14℃ habitat at its lowest spatial extent, lowest in summer when 9-14℃ habitat expanded and fish dispersed 4. In recent years, there was a slight downward trend in landings in the winter (Nov-Feb) and a slight upward trend in landings from May-June	1. Nesslage et al. 2021 2. Nessalge et al. 2021 3. Grimes and Turner 1999 4. Nitschke 2023

Table 3. Environmental indicator trends with study fleet and observer CPUE and model recruitment estimates with lags. Arrows represent direction of trend with negative trends indicated by a downward facing arrow and positive trends indicated by an upwards facing arrow. If the trend was significant, the arrows are red (negative) or blue (positive). Gray arrows represent trends that were non-significant. Dashed lines indicate no trend.

	CPUE No Lag (Age 4)	CPUE 3y Lag (Age 1)	Rec. Estimate (Age 1)	Rec. 1y Lag (Age 0)
SST	↓	↓	–	–
BT	–	–	–	–
Salinity	–	–	–	↓
SW Volume	–	↓	↓	↑ spring
SW Temp.	↓	↑	–	–
SW Salinity	–	↑	–	–
GSI	↓	↑ winter ↓ summer	–	–
CP Extent	–	↓	↓	↓
CP Persistence	–	↓	↓	↓
CP Index	–	–	↑	–
Microplankton	↑	↑ fall	–	↑ fall
CHL-a	↑	–	–	–

🟨	No trend, but matches literature	⬆	Positive significant trend	–	No trend
⬛	Not tested	⬇	Negative significant trend	⬆ ⬇	Non-significant trend (+ or -)

Figures

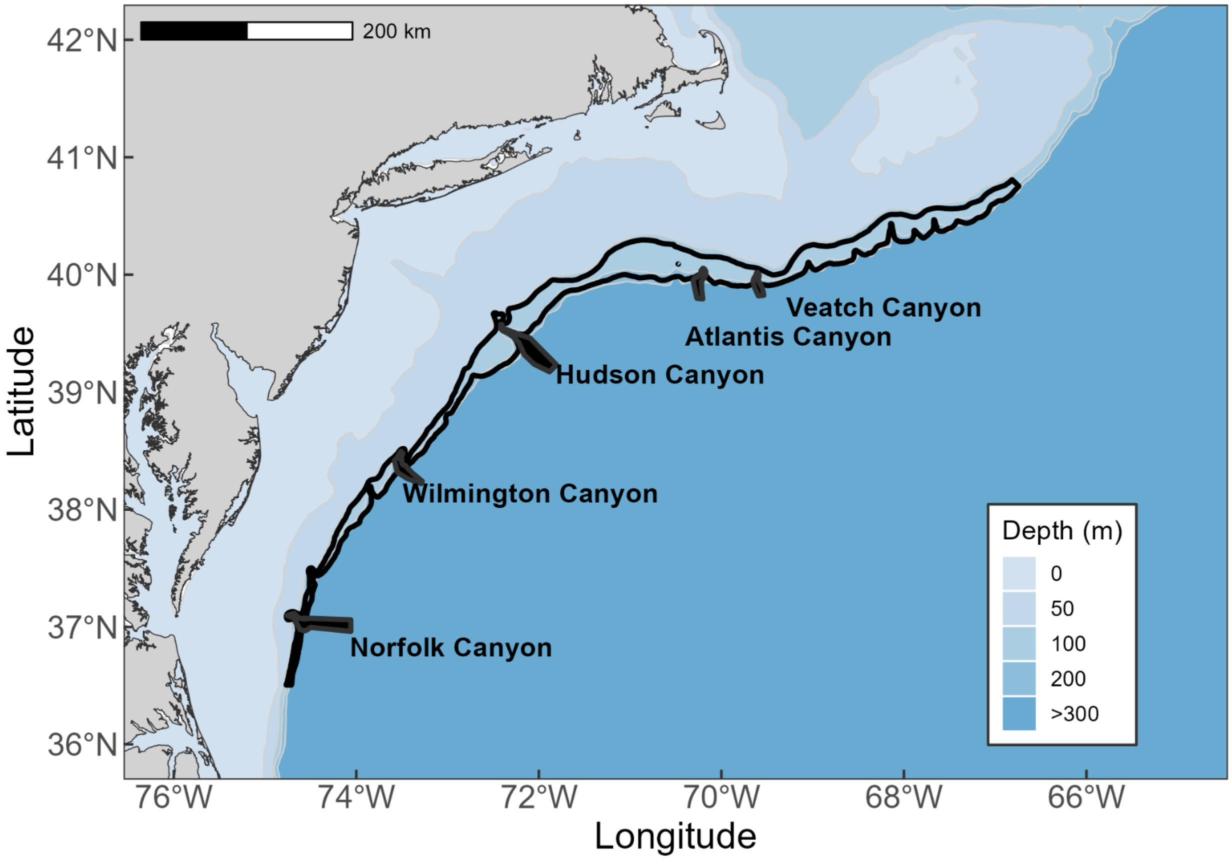


Figure 1. Map of golden tilefish habitat and distribution. The golden tilefish strata used to explore indicators was identified as the collection of 14 individual strata from the NES bottom trawl strata (Azarovitz 1981) that were relevant to tilefish habitat and fishery locations.

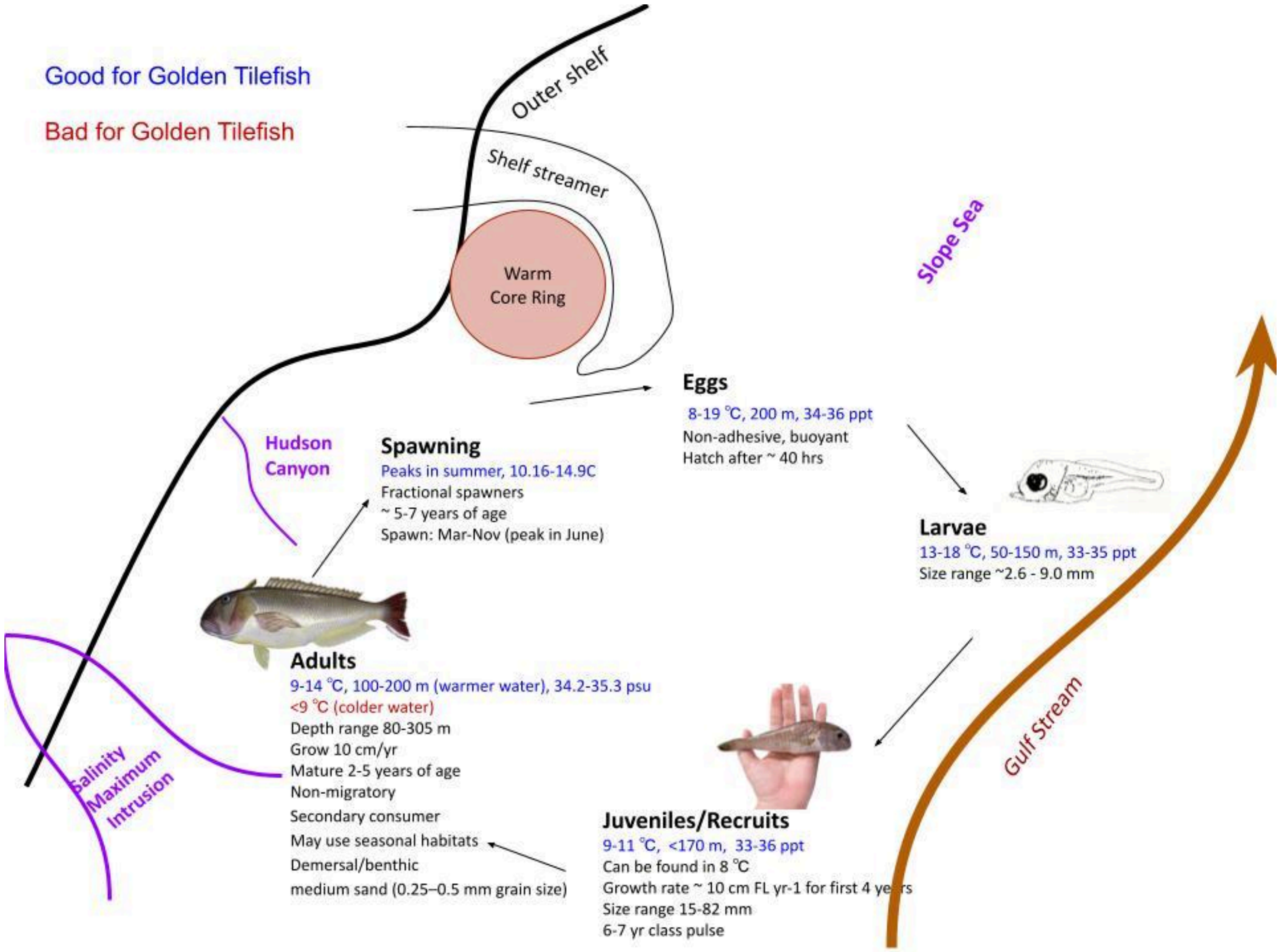


Figure 2. Conceptual model of golden tilefish life history stages and potential ecosystem impacts. Blue text represents conditions that are favorable for tilefish. Red text indicates unfavorable conditions.

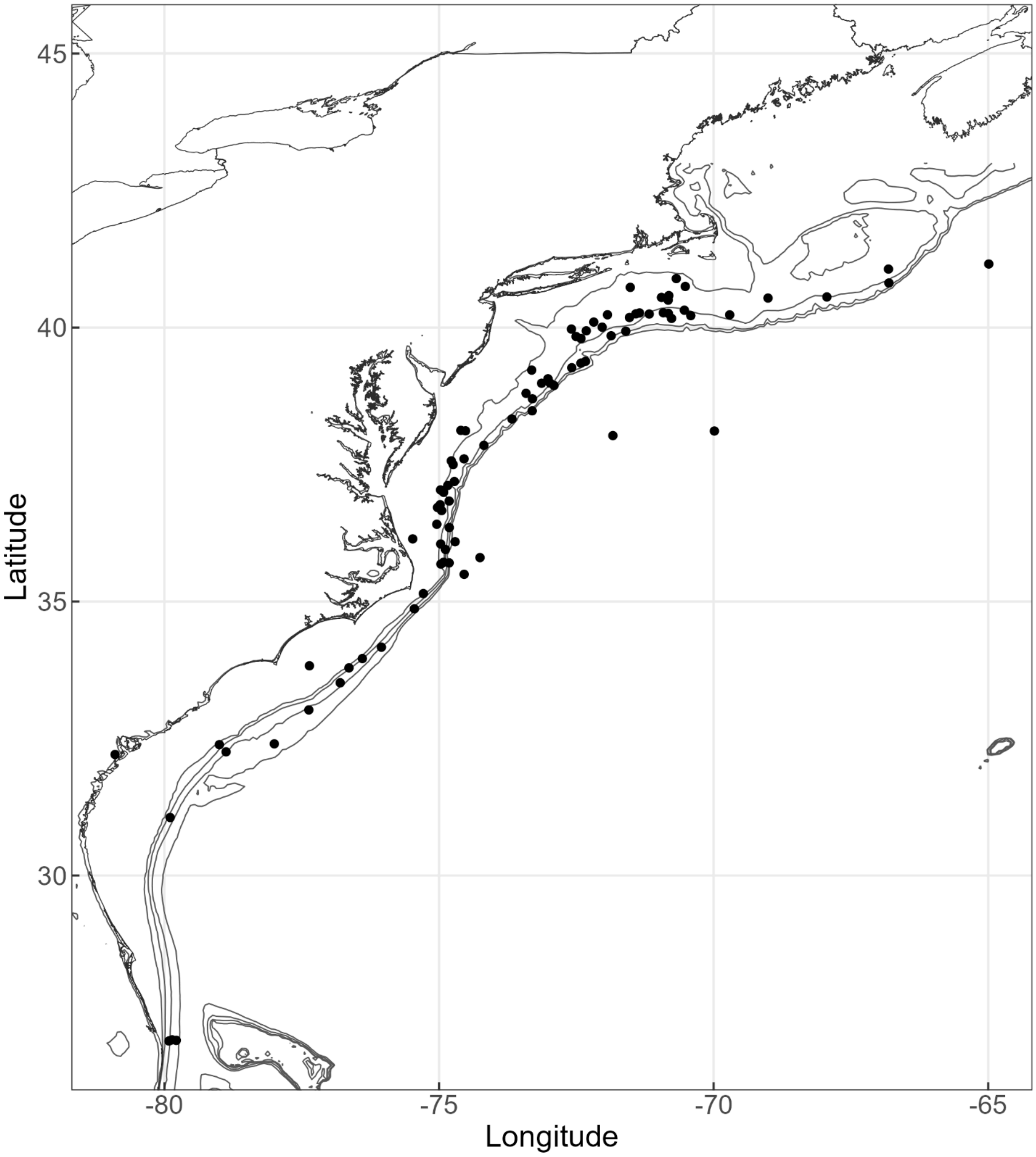


Figure 3. Map of golden tilefish larval distribution in the Northwest Atlantic. Points represent the locations where larvae were caught from both MARMAP + EcoMon Ichthyoplankton Surveys from 1977-2023. The total number of tows recorded in this data set is 41058, and the number of tows containing tilefish larvae is 85.

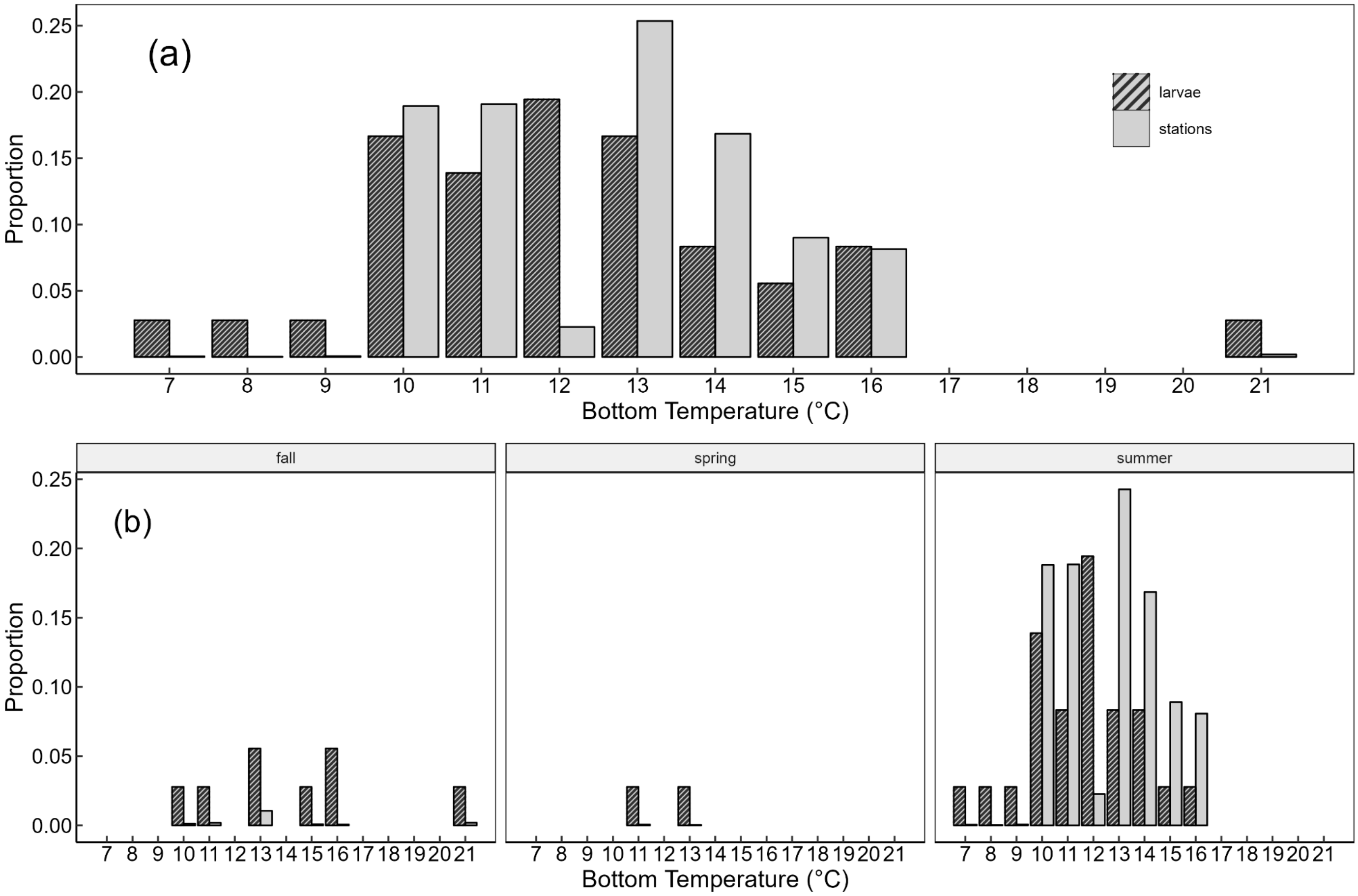


Figure 4. Proportion of tows with larvae present relative to in-situ bottom temperature measurements from NEFSC MARMAP and EcoMon surveys, all years combined (1977-2023). Solid gray bars represent the proportion of all stations surveyed, striped bars represent the proportion of all tows with positive larval catches (present). Panel (a) represents all larval events across time and (b) shows larval events by season. The seasons were categorized as follows, Fall: October, November,December; Spring: April, May, June; Summer: July, August, September.

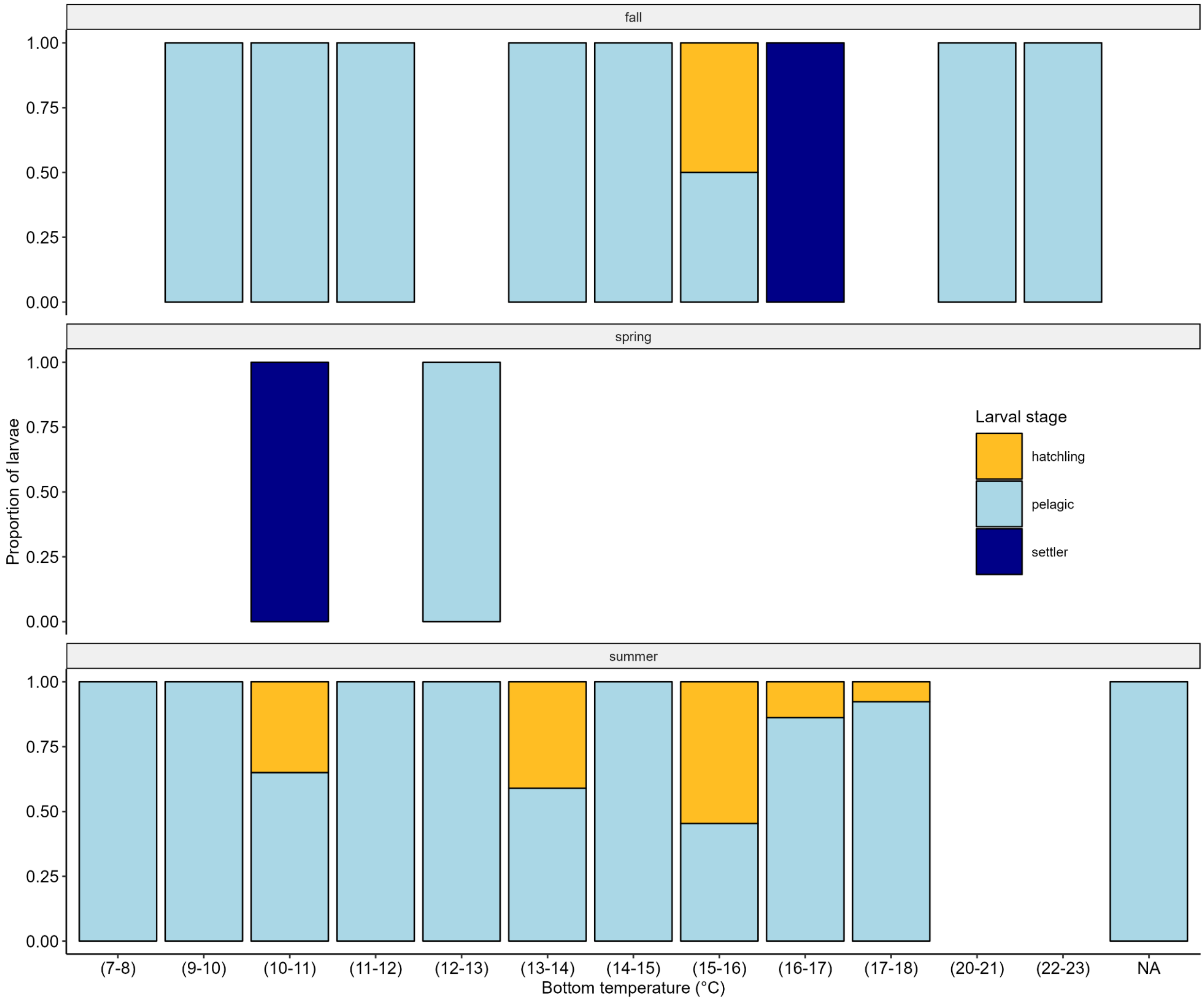


Figure 5. Proportion of larval lengths relative to bottom temperature. The three larval stages were categorized by size, where"hatchling" refers to larvae measuring ≤2.8mmNL, "pelagic" larvae refers to those measuring between 2.8 mmNL and 9 mmNL, and "settler" describes larvae measuring greater than 9.0 mmSL. The seasons were categorized as follows, Fall: October, November,December; Spring: April, May, June; Summer: July, August, September.

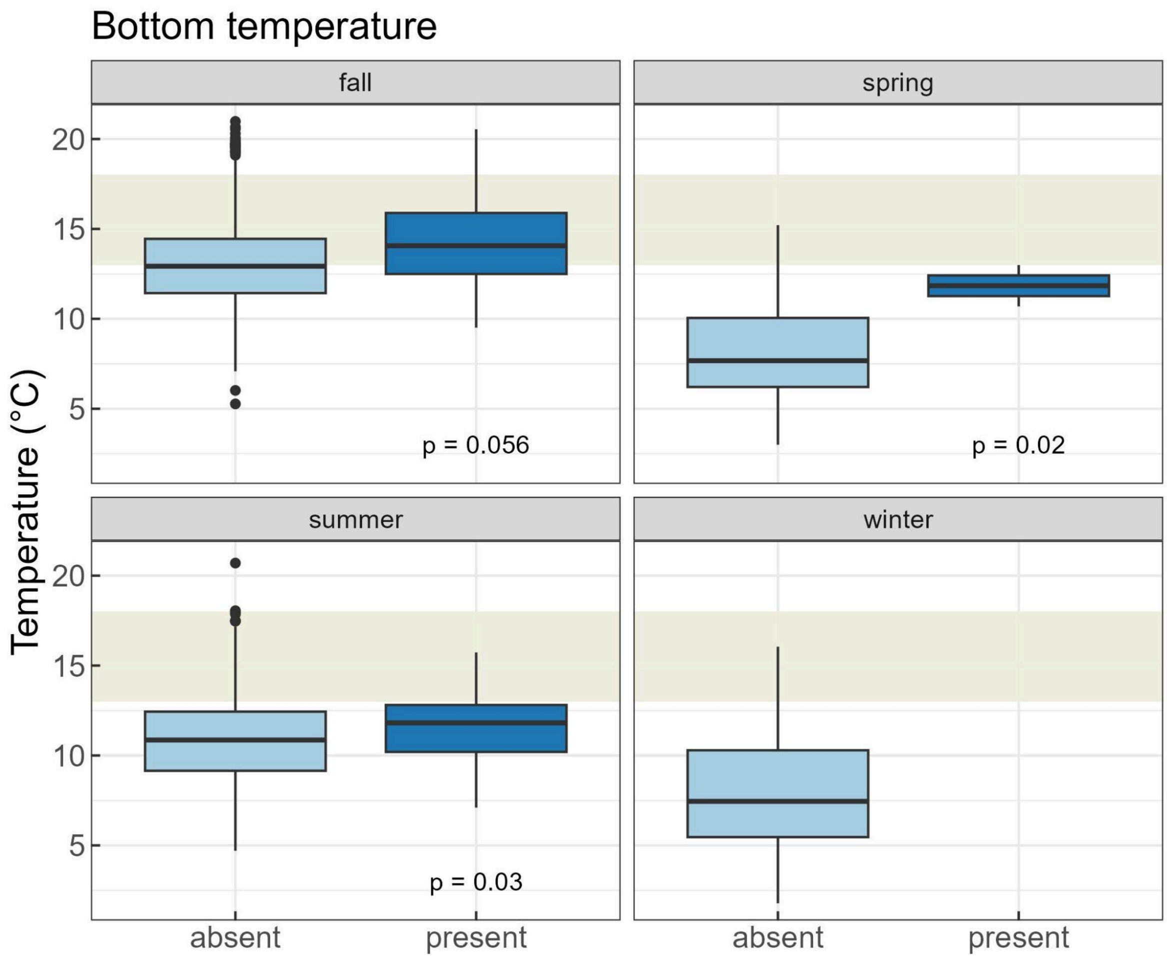


Figure 6. The presence and absence of larvae collected across a range of bottom temperatures. Light blue boxes represent the tows where golden tilefish larvae were absent and dark blue boxes represent the tows where golden tilefish larvae were present. The horizontal shaded region (tan) represents the range of temperature preferences (13-18°C) described in the literature (see Table 1). The seasons were categorized as follows, Fall: October, November,December; Spring: April, May, June; Summer: July, August, September.

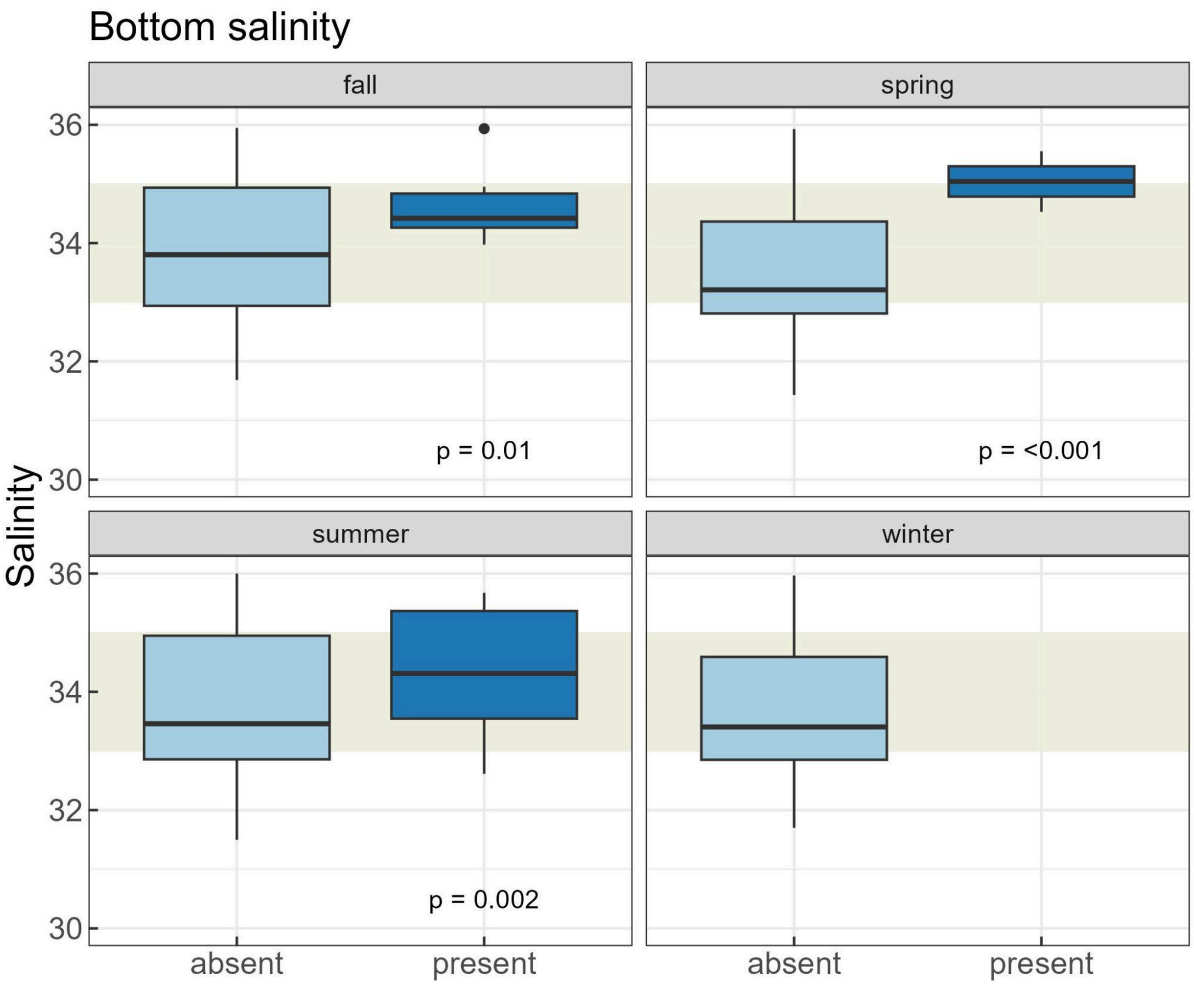


Figure 7. The presence and absence of larvae collected across a range of bottom salinity. Light blue boxes represent the tows where golden tilefish larvae were absent and dark blue boxes represent the tows where golden tilefish larvae were present. The horizontal shaded region (tan) represents the range of salinity preferences (33-15 psu) described in the literature (see Table 1). The seasons were categorized as follows, Fall: October, November,December; Spring: April, May, June; Summer: July, August, September.

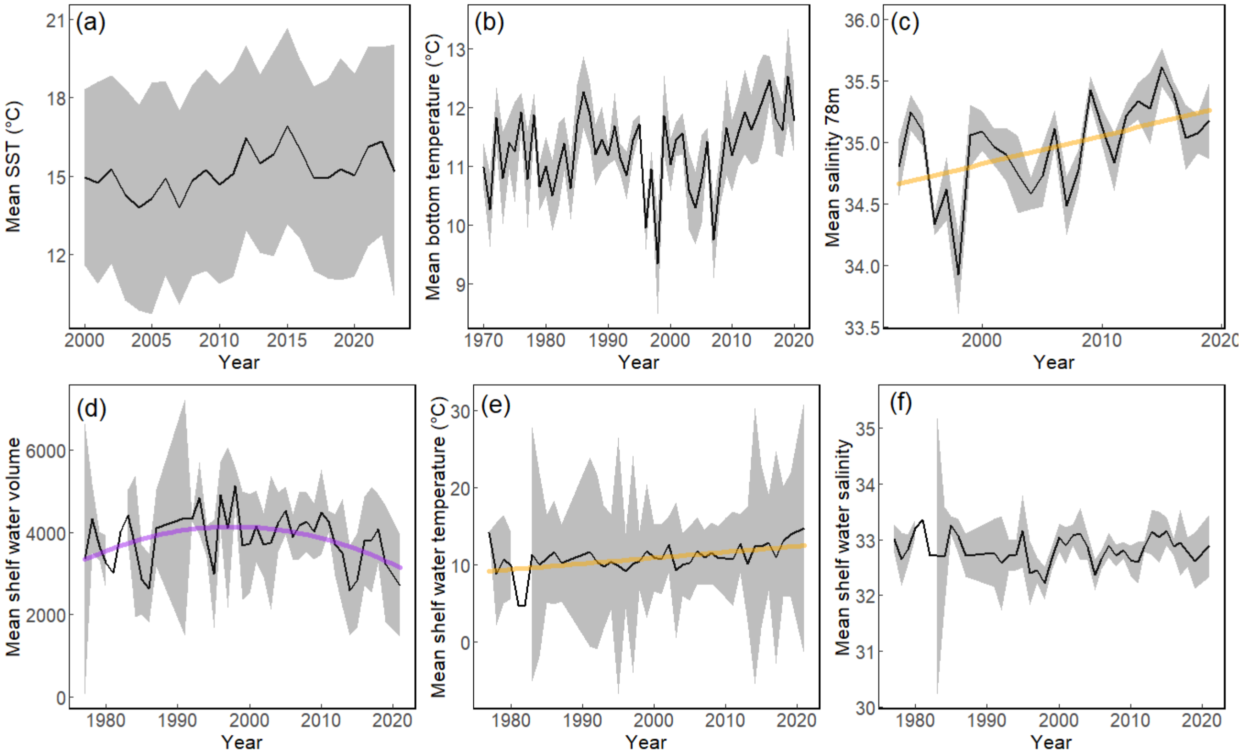


Figure 8. Time series of environmental indicators. The annual regional average (weighted by pixel area) is shown in black, with 95% confidence intervals indicated by the gray shaded area. When applicable, significant trends are shown in yellow (positive) or purple (negative). Panel descriptions: (a) satellite sea surface temperature, (b) GLORYS12V1 bottom temperature product, (c) GLORYS12V1 salinity product extracted at 78 meters subsurface, and (d,e,f) are metrics related to the water masses on the continental shelf, specifically, shelf water volume, shelf water temperature and shelf water salinity, respectively.

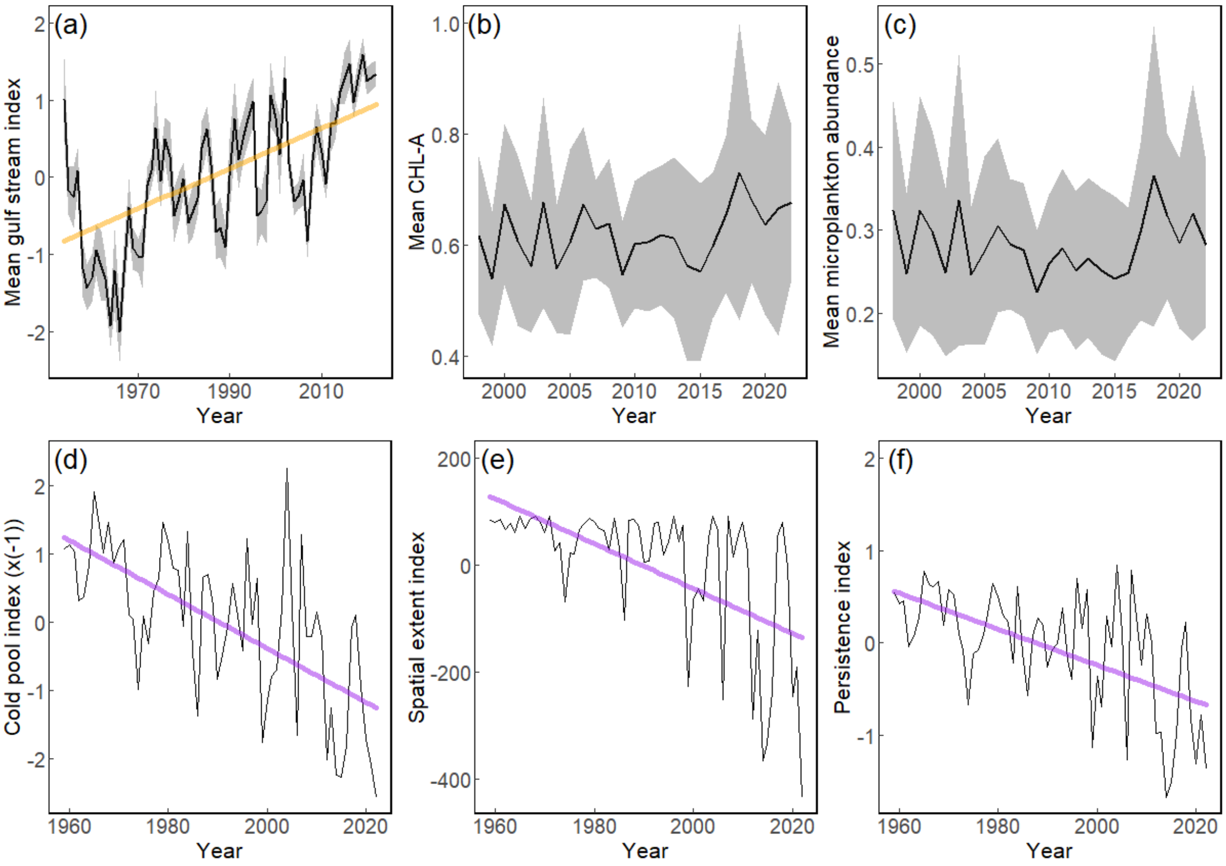


Figure 9. Time series of environmental indicators. The annual regional average (weighted by pixel area) is shown in black, with 95% confidence intervals indicated by the gray shaded area. When applicable, significant trends are shown in yellow (positive) or purple (negative). Panel (a) is the mean Gulf Stream Index, (b) satellite chlorophyll, (c) mean microplankton abundance for the Mid-Atlantic Bight region, (d,e,f) are indices of the cold pool, specifically, cold pool index, spatial extent index and persistence index, respectively.

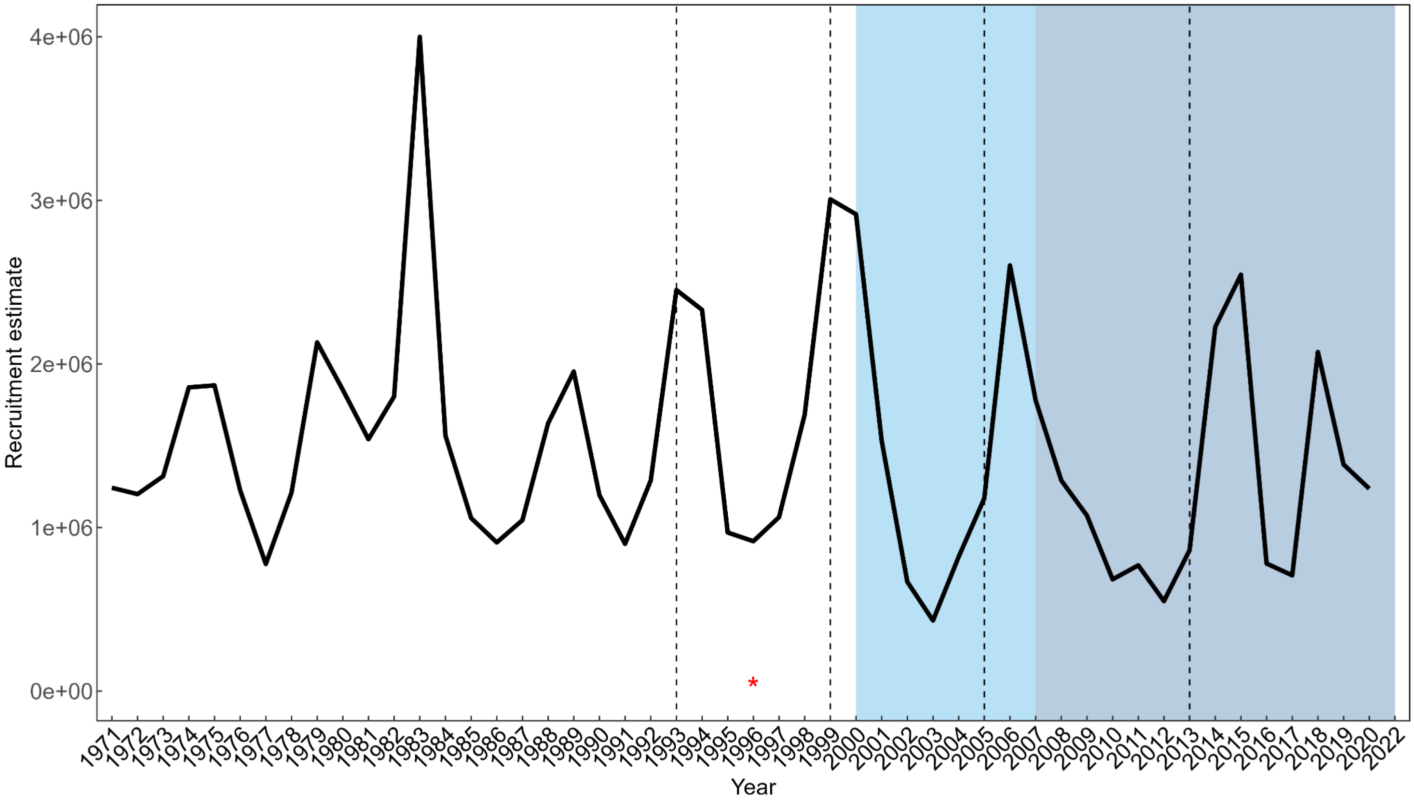


Figure 10. Age-1 recruitment estimate from the 2021 tilefish assessment. Light blue shaded region represents the temporal range of observer records and red shaded region represents temporal range of study fleet records. The 'purple' region is where they overlap. The vertical dashed lines represent strong year classes for this species (Nesslage et al., 2021). Red asterisk marks the year that the stock was deemed 're-built'.

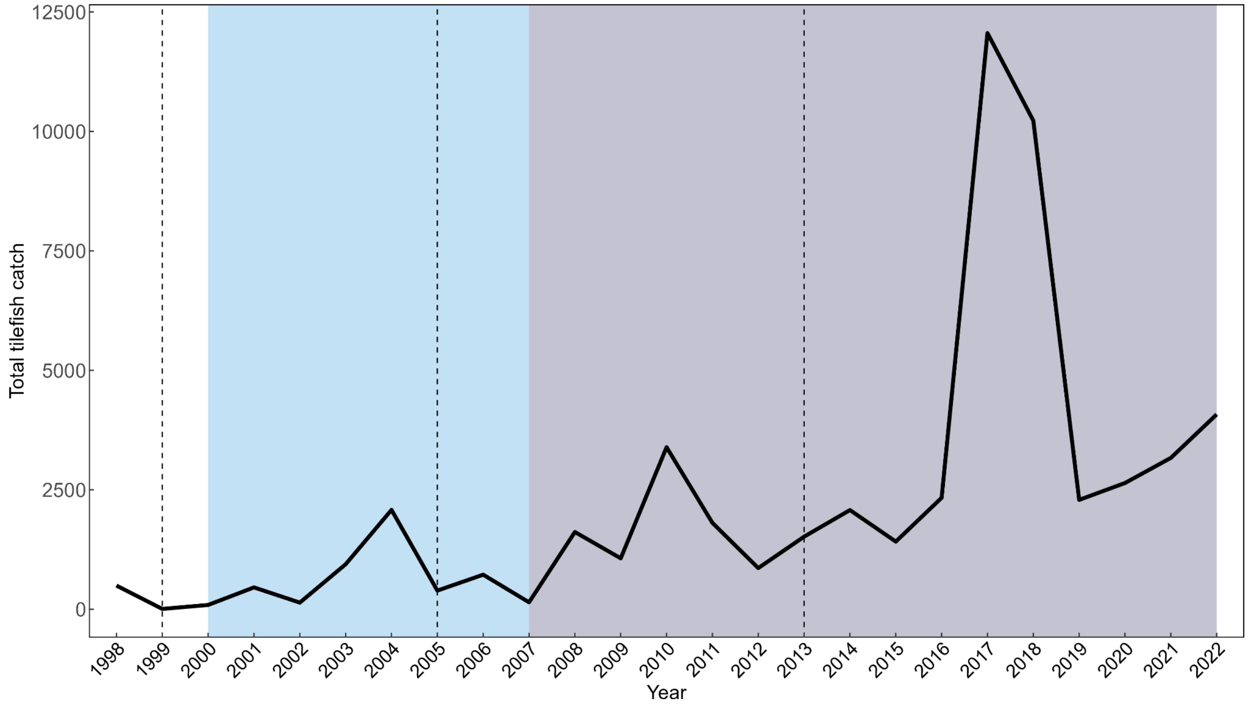


Figure 11. Sum of catch (not accounting for effort), across years. Light blue shaded region represents the temporal range of observer records and red shaded region represents temporal range of study fleet records. The 'purple' region is where they overlap. Note that 2000-2005 for observer records had low sample size/number of vessels for tilefish, making the shaded region likely the best region to use for analysis. The vertical dashed lines represent strong year classes for this species (Nesslage et al., 2021).

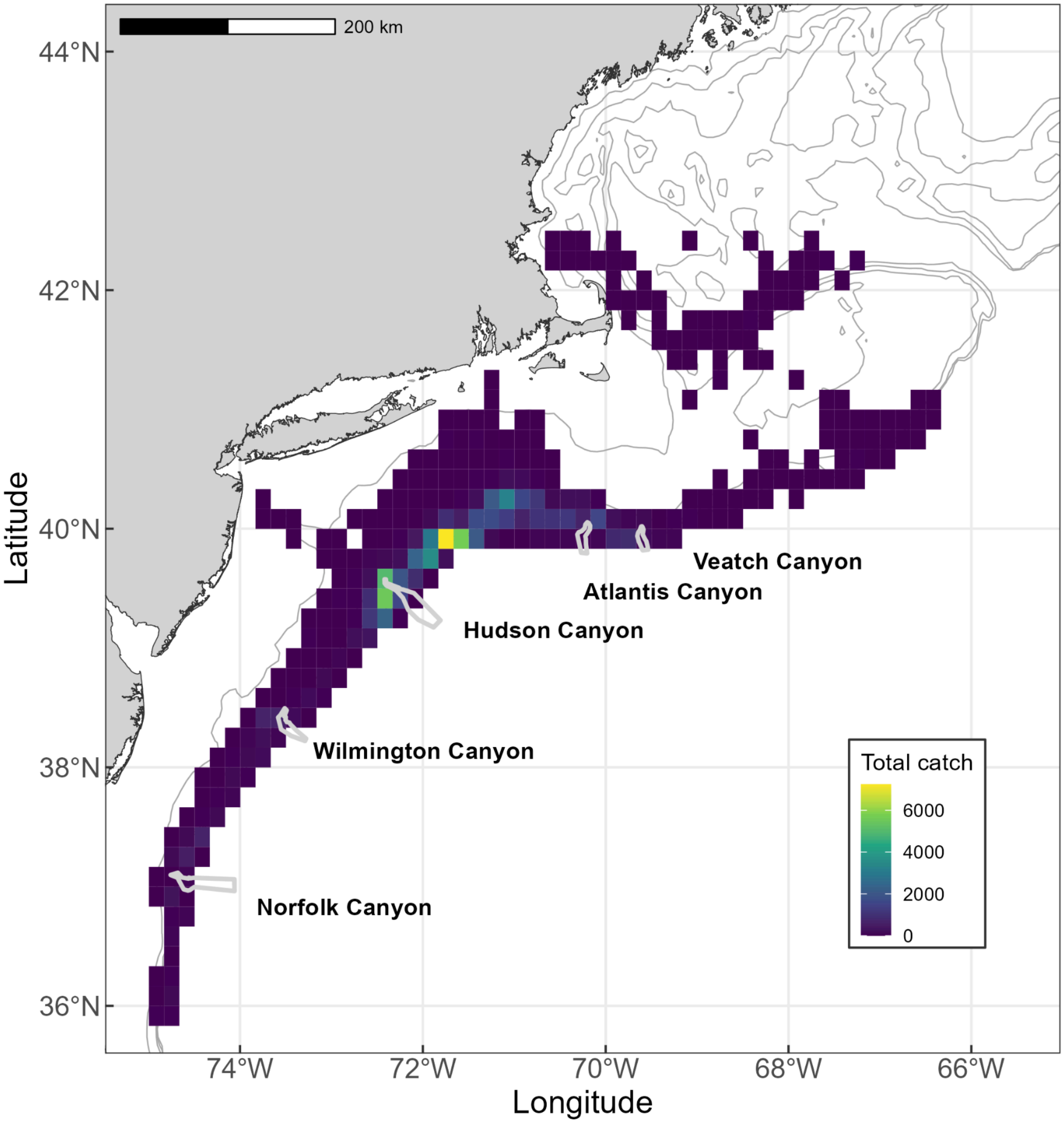


Figure 12. Map of total summed catch for undirected trawl trips from the NEFSC's Study Fleet and Observer programs. Zeros have been added using species association methodology (via jaccard similarity index, see Jones and Salois working paper for more details).

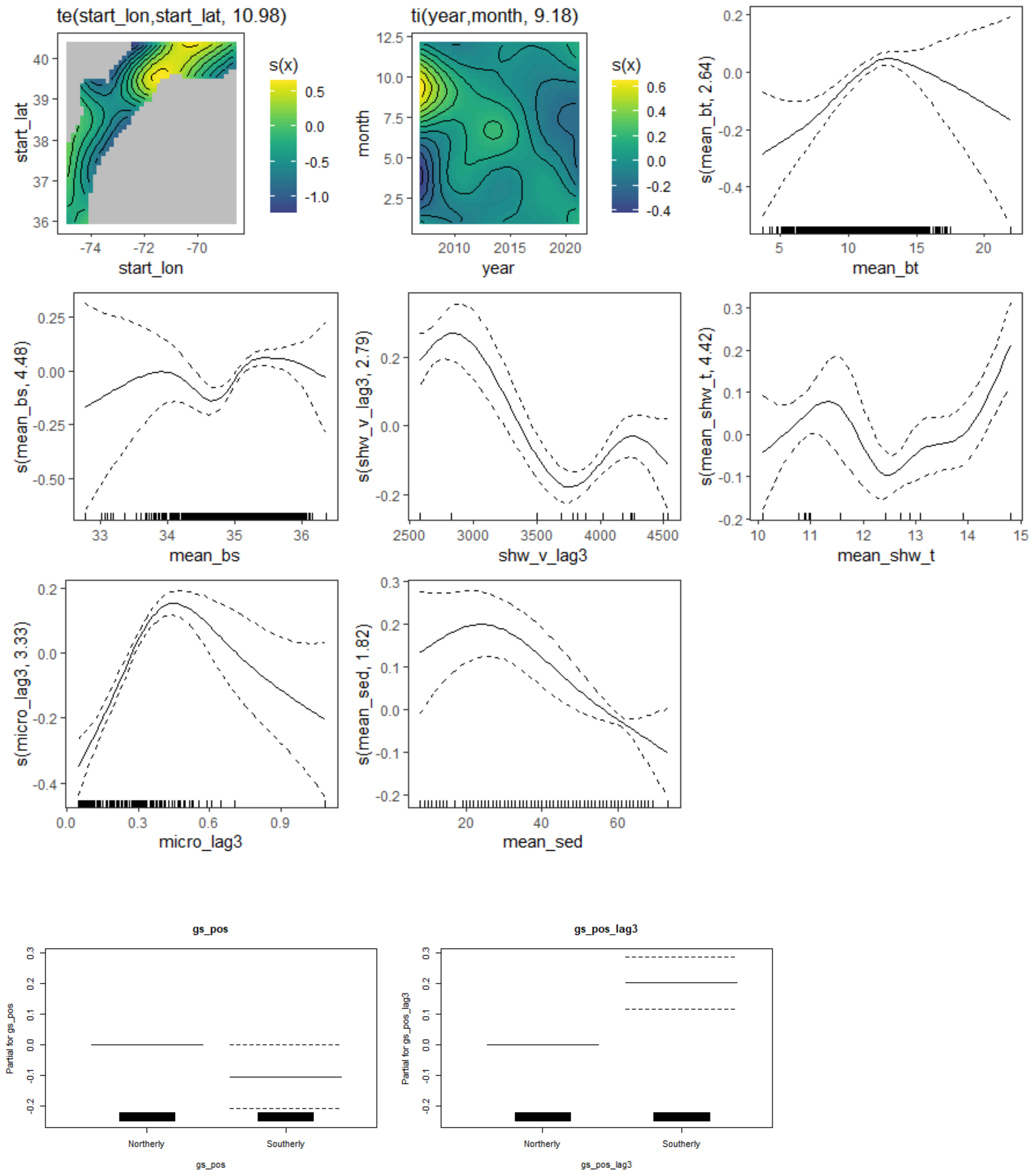


Figure 13. Generalized additive model partial residual plots for variables with significant relationships to catch per unit effort (CPUE). Covariates are plotted against their splines (held constant); thus, the *y* axis represents changes in CPUE (the response variable) relative to its mean. The black tick marks inset along the *x* axis of each plot are the actual values of each variable. The

gray shaded region flanking each smooth is the 95% confidence interval for the mean shape of the effect. Smooths are presented in order of the strength of their relationship to CPUE.

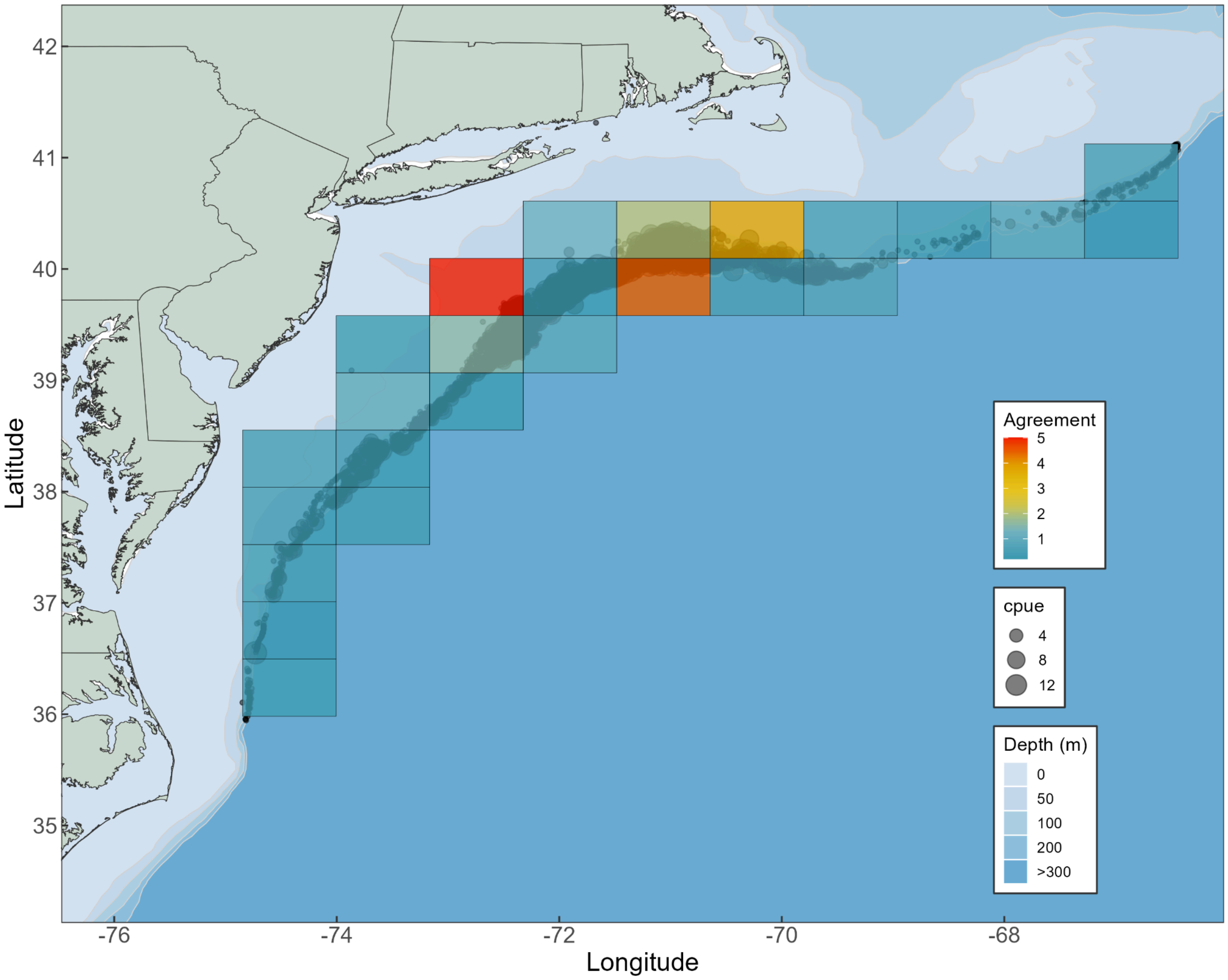
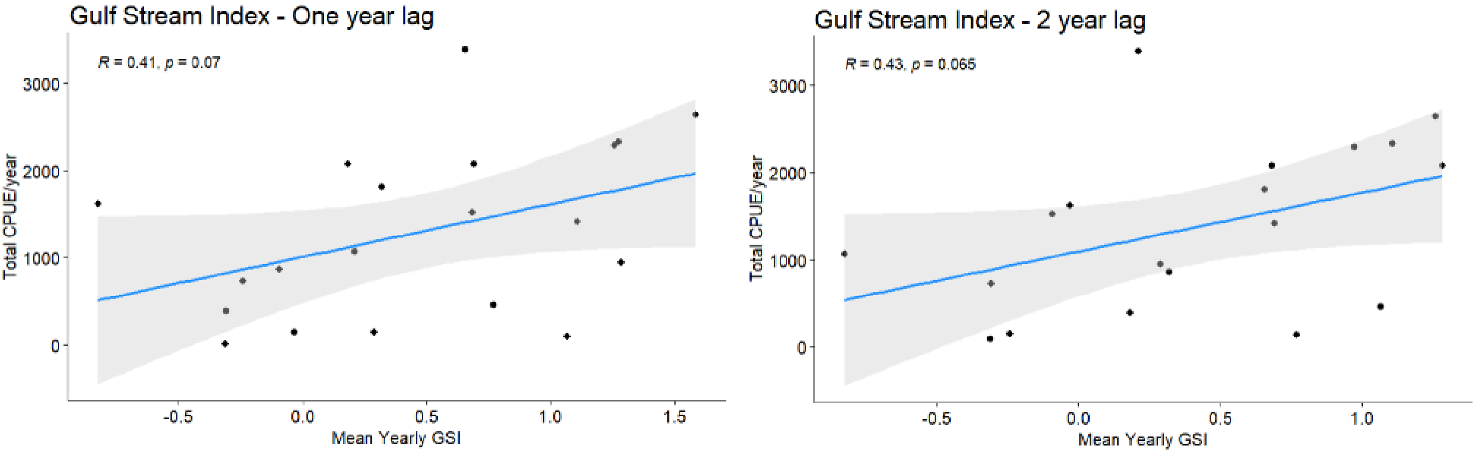


Figure 14. Model predictive ability. Predicted values calculated from the testing data set, comprised 30% of the complete data set. Actual values are CPUE values from the training dataset, which comprised 70% of the complete dataset. The ratio between the actual and predicted values was calculated, and the color bar represents those ratios along a gradient from warm colors, where 5 is total agreement to cooler colors, where 0 is no agreement.



Gulf Stream Index - One year lag

Gulf Stream Index - 2 year lag

Figure 15. Lags in Study Fleet and observer trawl CPUE with a yearly Gulf Stream Index by 1 and 2 years.

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Appendices

APPENDIX A. RECRUITMENT REGRESSIONS

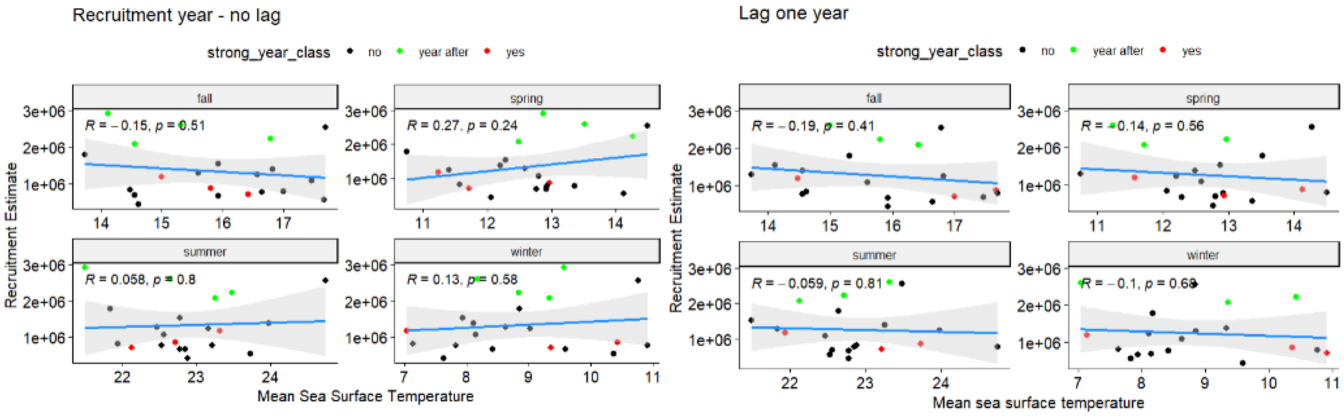


Figure A.1. Linear regressions of age-1 model recruitment estimate with average monthly sea surface temperature at time of recruitment (no lag) and birth (one year lag) separated by season. Strong year classes are denoted by red points, while the year after a recruitment pulse is denoted in green. All other years are in black. Pearson's correlation coefficient (R) and p-values are included for each season.

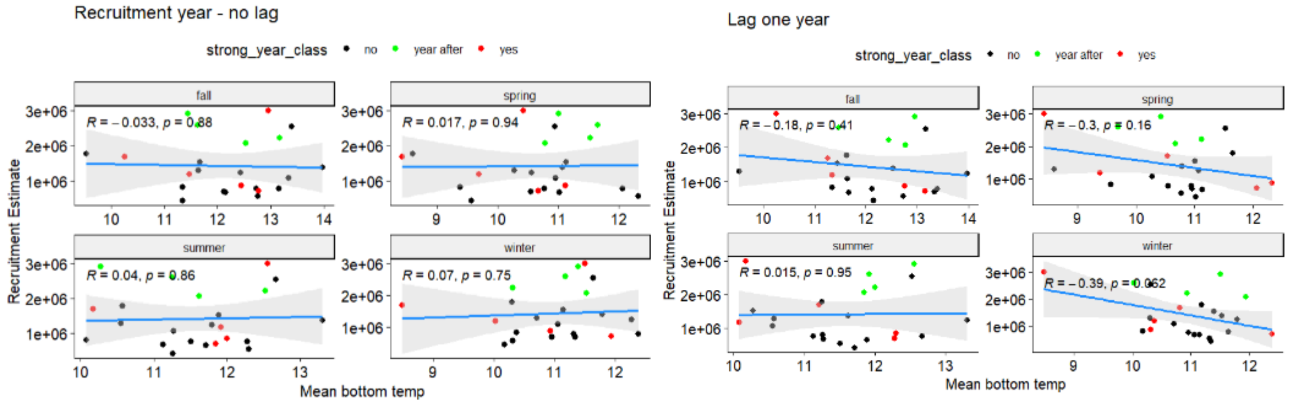


Figure A.2. Linear regressions of age-1 model recruitment estimate with average monthly bottom temperature at time of recruitment (no lag) and birth (one year lag) separated by season. Strong year classes are denoted by red points, while the year after a recruitment pulse is denoted in green. All other years are in black. Pearson's correlation coefficient (R) and p-values are included for each season.

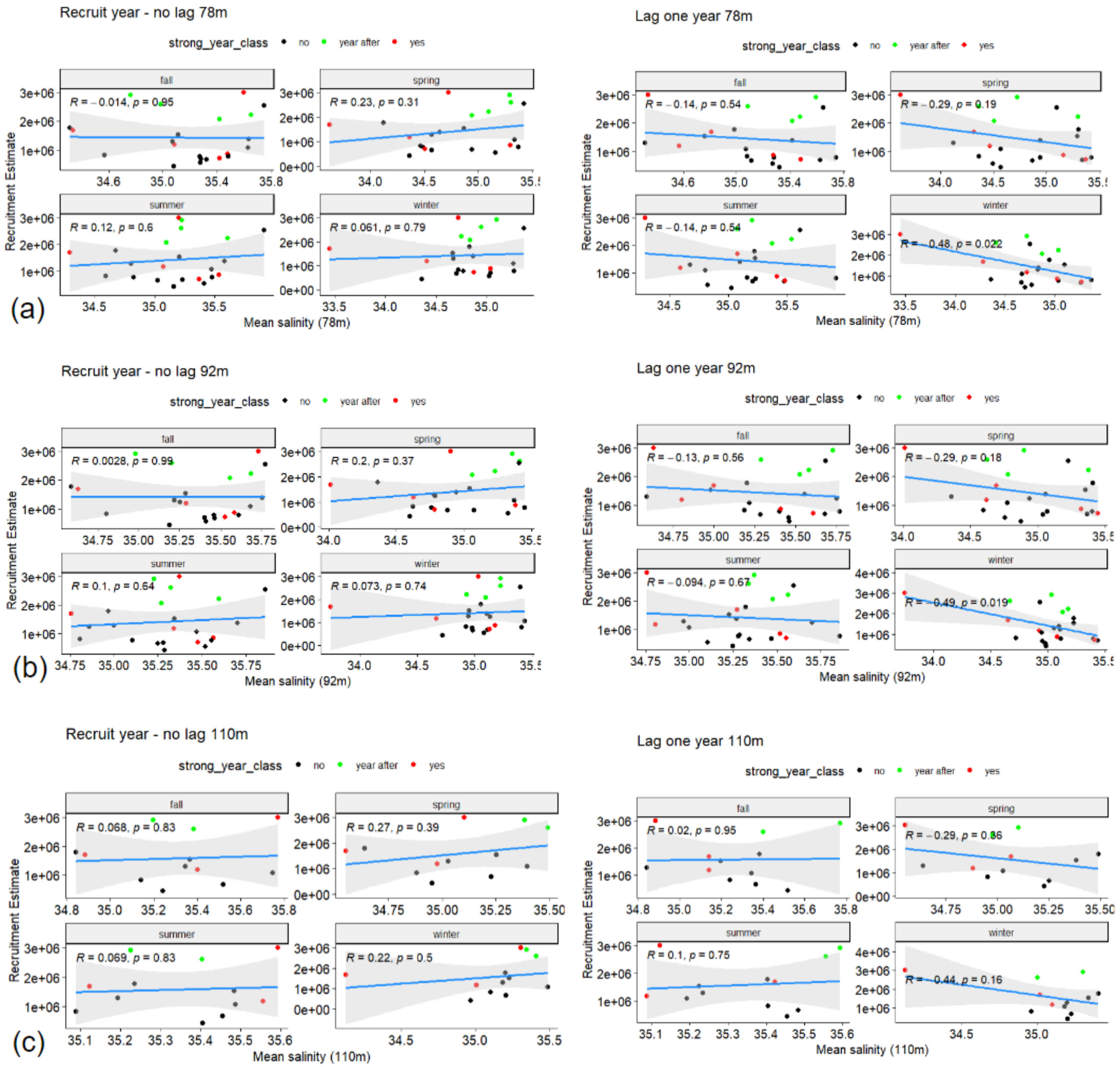


Figure A.3. Linear regressions of age-1 model recruitment estimate with average monthly salinity at 78m (a), 92m (b), and 110m (c) at time of recruitment (no lag) and birth (one year lag) separated by season. Strong year classes are denoted by red points, while the year after a recruitment pulse is denoted in green. All other years are in black. Pearson's correlation coefficient (R) and p-values are included for each season.

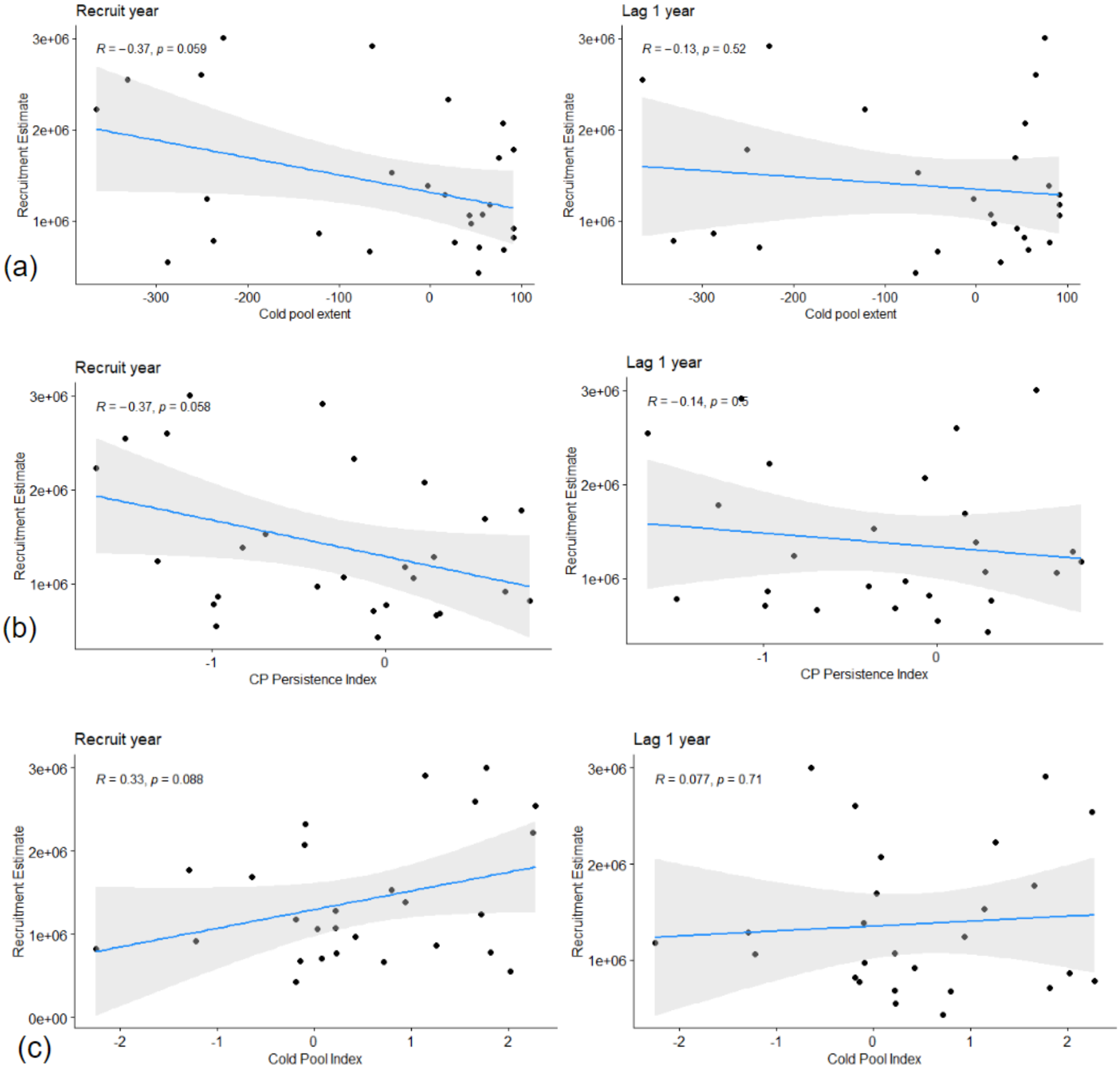


Figure A.4. Linear regressions of age-1 model recruitment estimate with annual cold pool extent (a), persistence (b), and index (c) at time of recruitment (no lag) and birth (one year lag). Pearson's correlation coefficient (R) and p-values are included for each season.

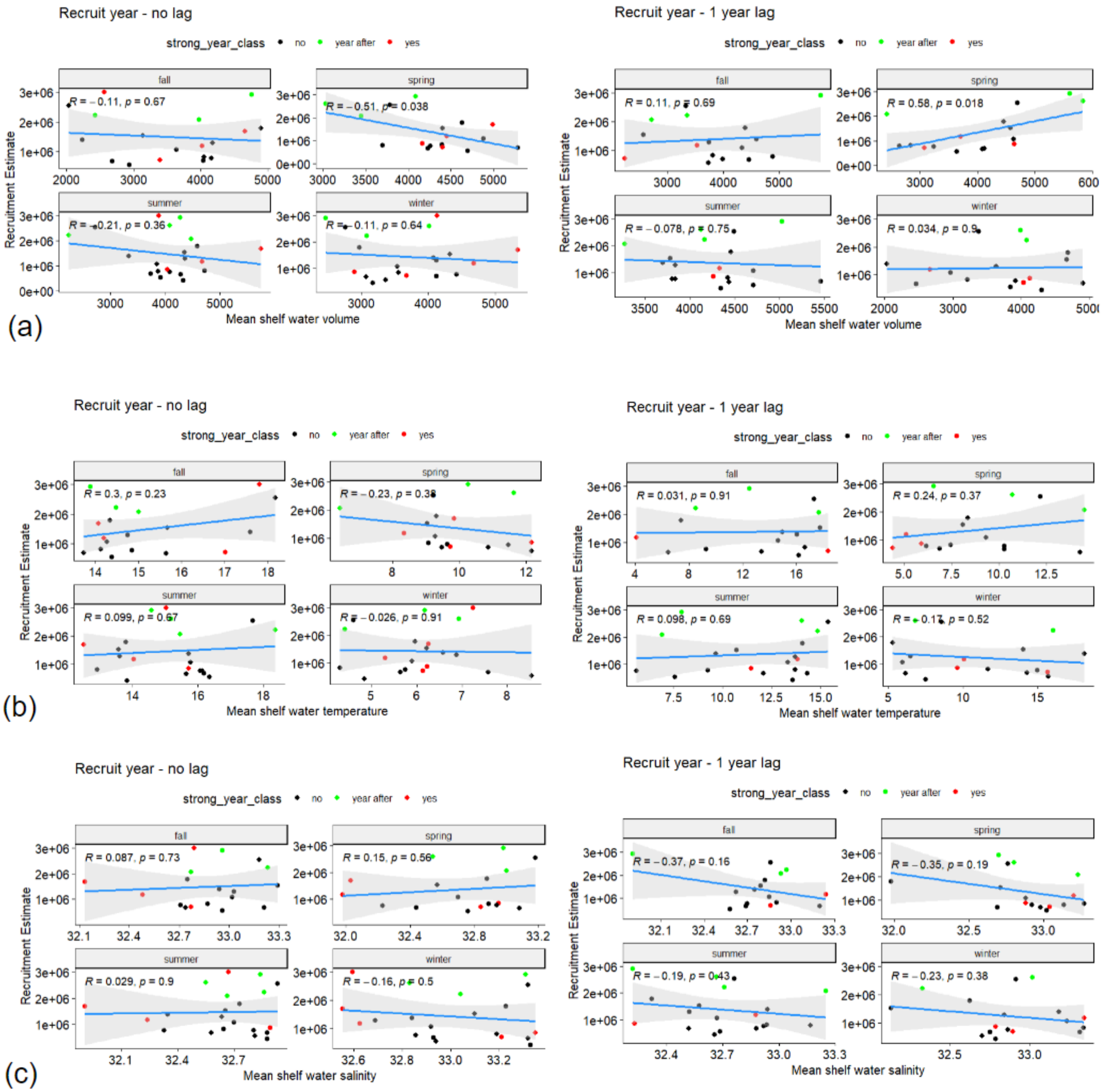


Figure A.5. Linear regressions of age-1 model recruitment estimate with average monthly shelf water volume (a), temperature (b), and salinity (c) at time of recruitment (no lag) and birth (one year lag) separated by season. Strong year classes are denoted by red points, while the year after a recruitment pulse is denoted in green. All other years are in black. Pearson's correlation coefficient (R) and p-values are included for each season.

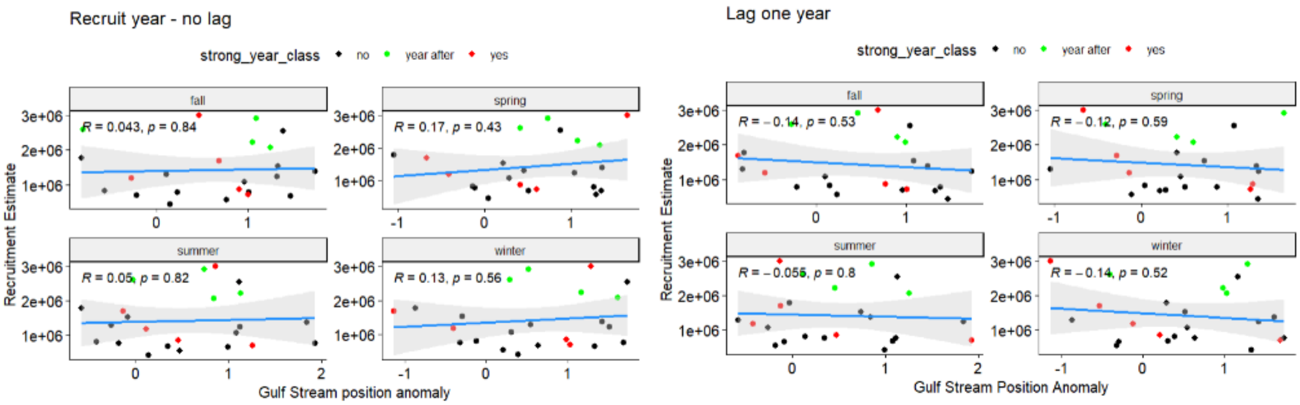


Figure A.6. Linear regressions of age-1 model recruitment estimate with average annual Gulf Stream position at time of recruitment (no lag) and birth (one year lag) separated by season. Strong year classes are denoted by red points, while the year after a recruitment pulse is denoted in green. All other years are in black. Pearson's correlation coefficient (R) and p-values are included for each season.

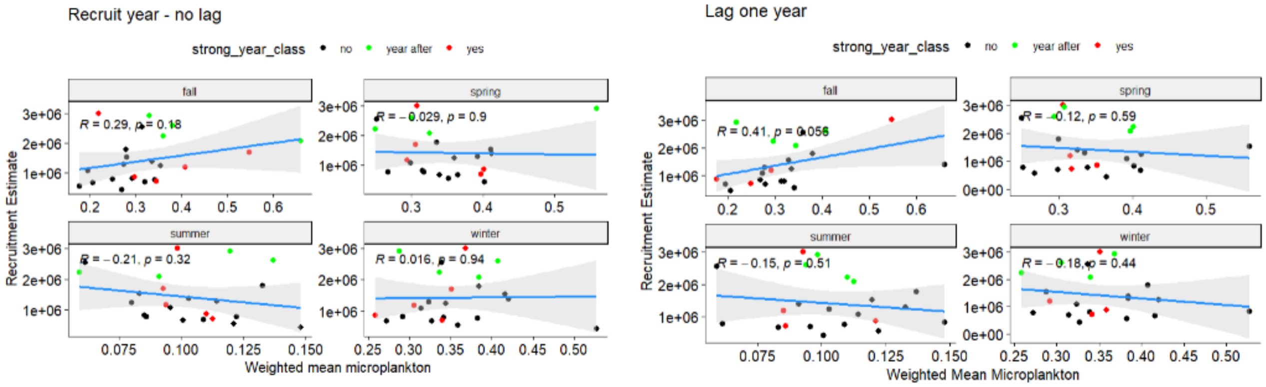


Figure A.7. Linear regressions of age-1 model recruitment estimate with weighted average monthly microplankton at time of recruitment (no lag) and birth (one year lag) separated by season. Strong year classes are denoted by red points, while the year after a recruitment pulse is denoted in green. All other years are in black. Pearson's correlation coefficient (R) and p-values are included for each season.

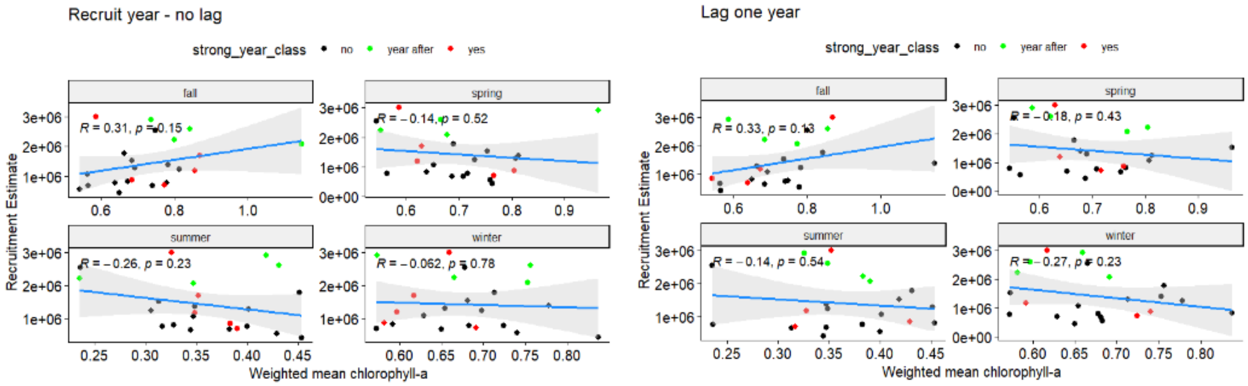


Figure A.8. Linear regressions of age-1 model recruitment estimate with weighted average monthly chlorophyll *a* at time of recruitment (no lag) and birth (one year lag) separated by season. Strong year classes are denoted by red points, while the year after a recruitment pulse is denoted in green. All other years are in black. Pearson's correlation coefficient (R) and p-values are included for each season.

APPENDIX B. STUDY FLEET/OBSERVER CPUE REGRESSIONS

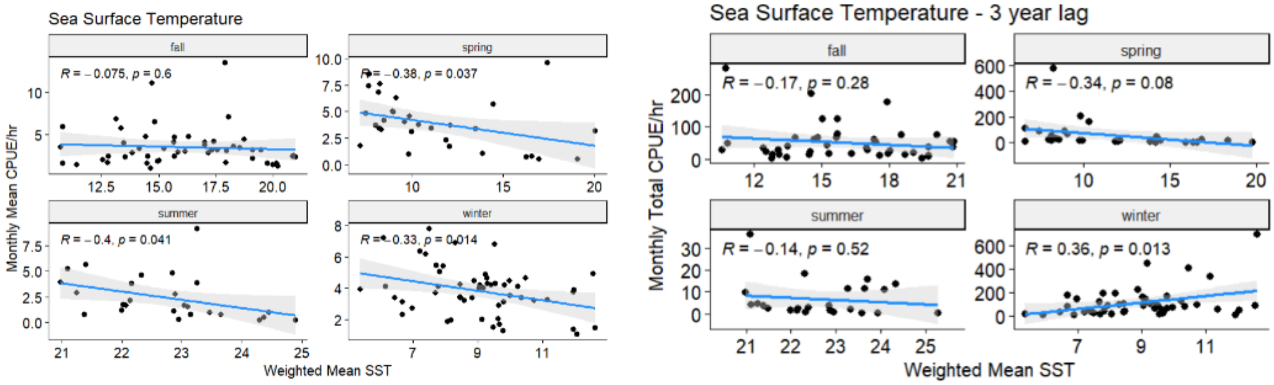


Figure B.1. Linear regressions of study fleet and observer trawl CPUE with weighted average monthly sea surface temperature at time of catch and at time of recruitment (3 year lag) separated by season. Pearson's correlation coefficient (R) and p-values are included for each season.

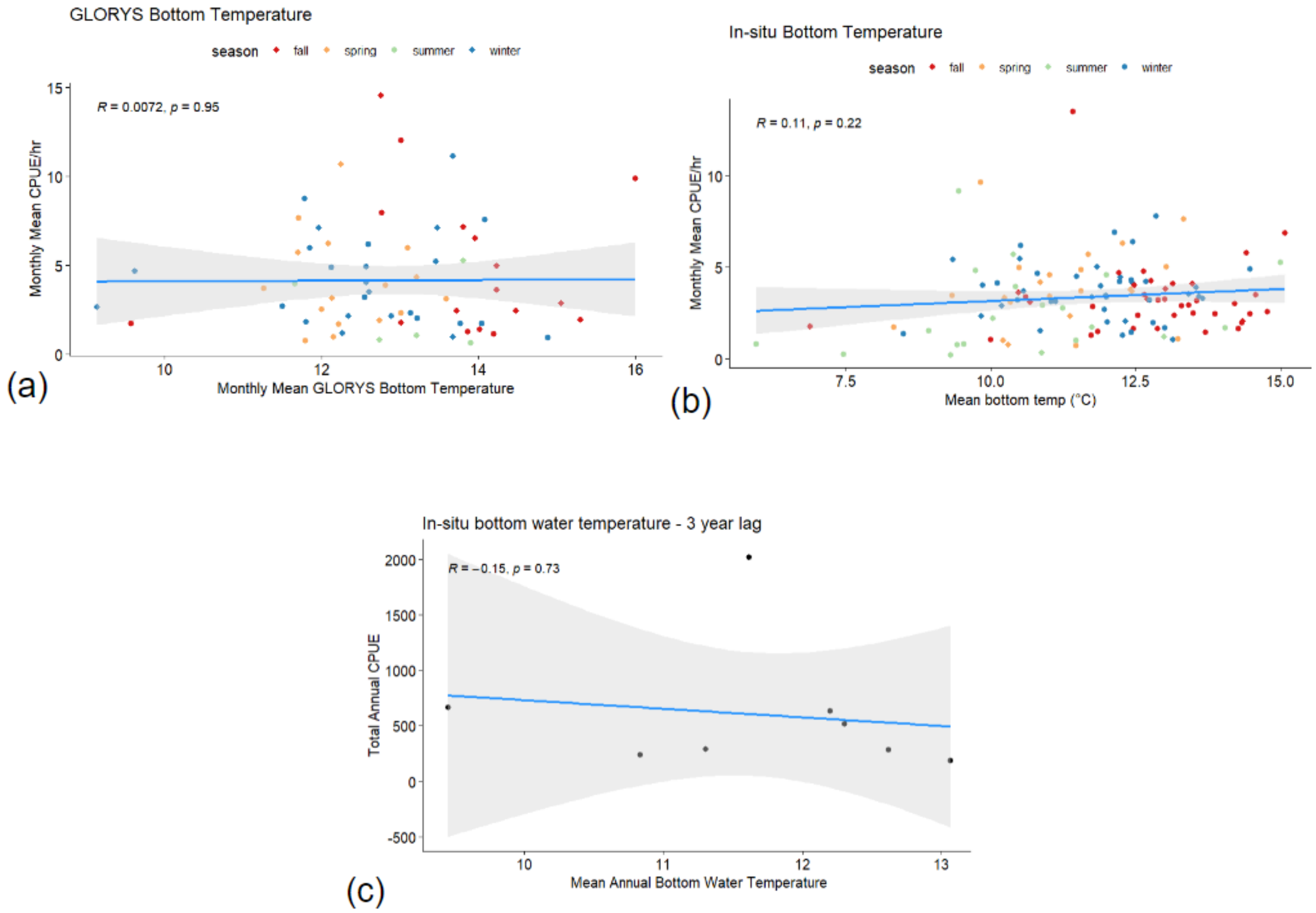


Figure B.2. Linear regressions of study fleet and observer trawl CPUE with weighted average monthly bottom temperature at time of catch using GLORYS bottom temperature (a), study fleet in-situ bottom temperature (b), and annual in-situ bottom water temperature at time of recruitment (3 year lag) (c). Plot values for GLORYS and in-situ bottom temperatures are distinguished by season: fall == red, spring == yellow, summer == green, winter == blue. Pearson's correlation coefficient (R) and p-values are included.

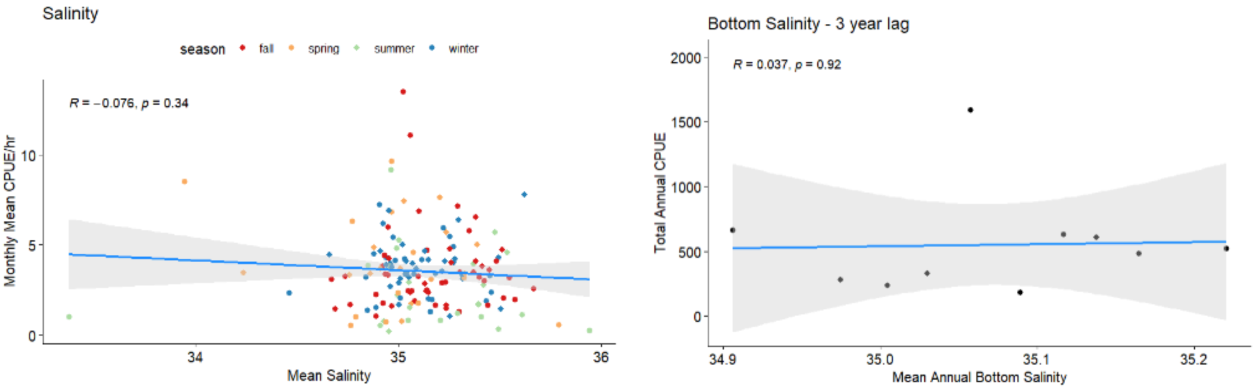


Figure B.3. Linear regressions of study fleet and observer trawl CPUE with weighted average monthly salinity at time of catch and annual CPUE at time of recruitment (3 year lag). Plot values for CPUE at time of catch are distinguished by season: fall == red, spring == yellow, summer == green, winter == blue. Pearson's correlation coefficient (R) and p-values are included.

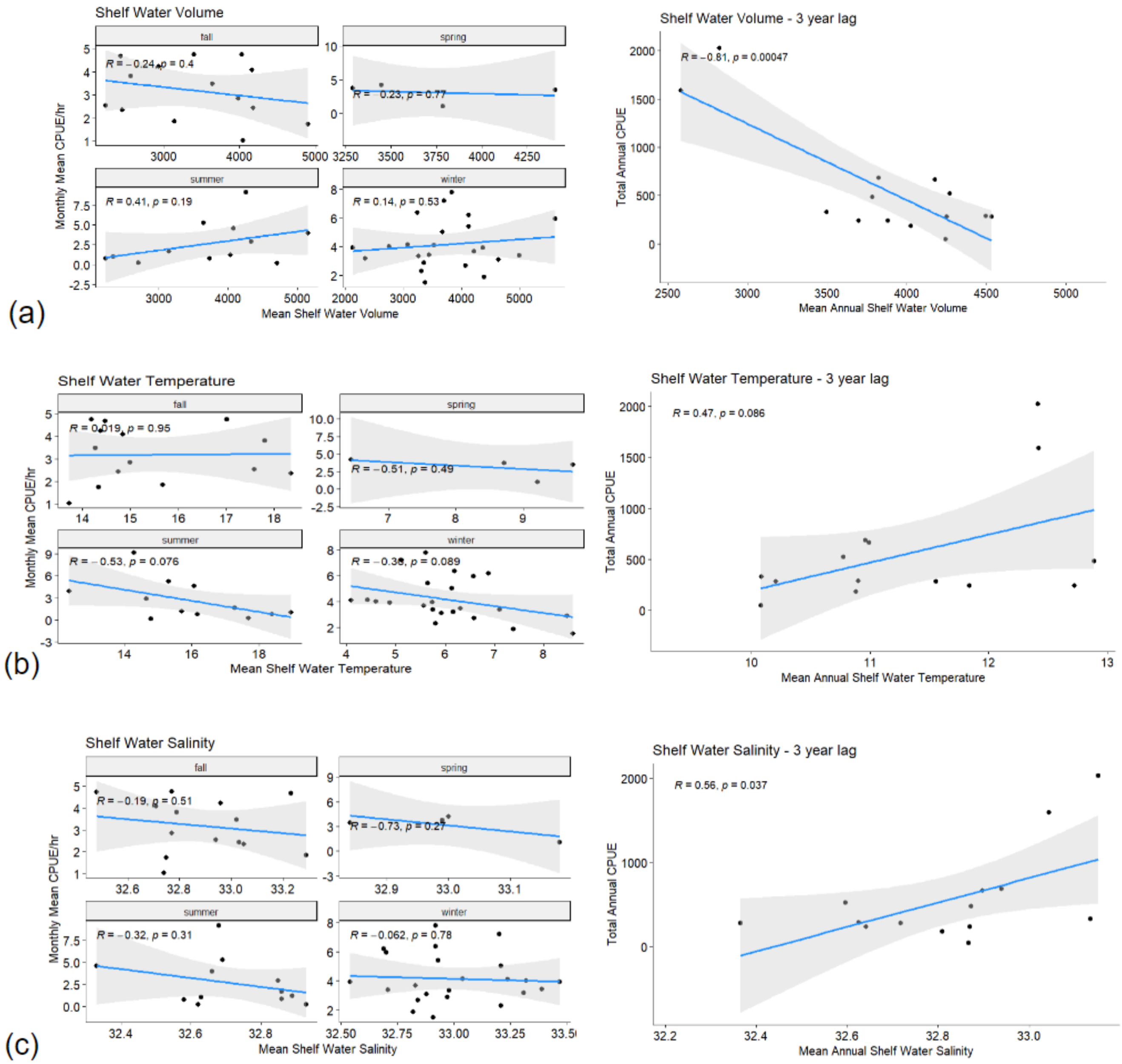


Figure B.4. Linear regressions of study fleet and observer trawl CPUE with weighted average monthly shelf water volume (a), temperature (b), and salinity (c) at time of catch and annual CPUE at time of recruitment (3 year lag). Pearson's correlation coefficient (R) and p-values are included.

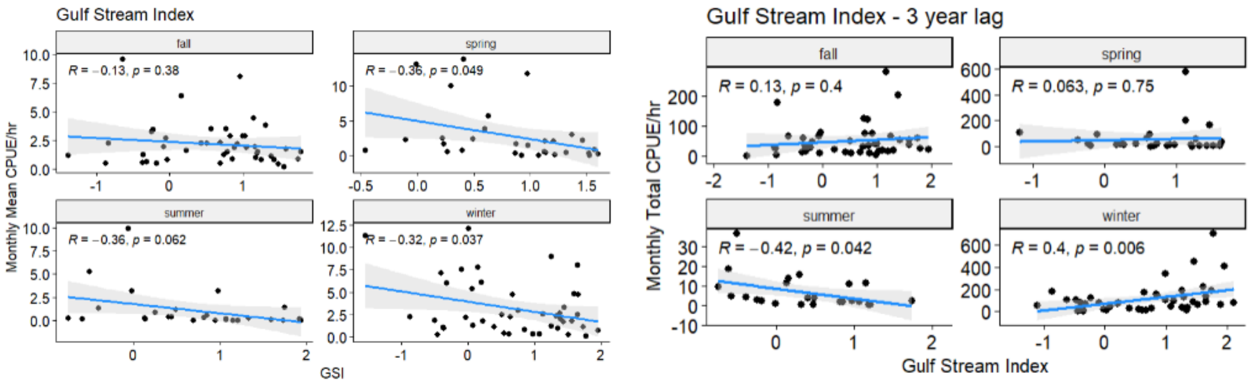


Figure B.5. Linear regressions of study fleet and observer trawl CPUE with average annual Gulf Stream position at time of catch and at time of recruitment (3 year lag) separated by season. Pearson's correlation coefficient (R) and p-values are included for each season.

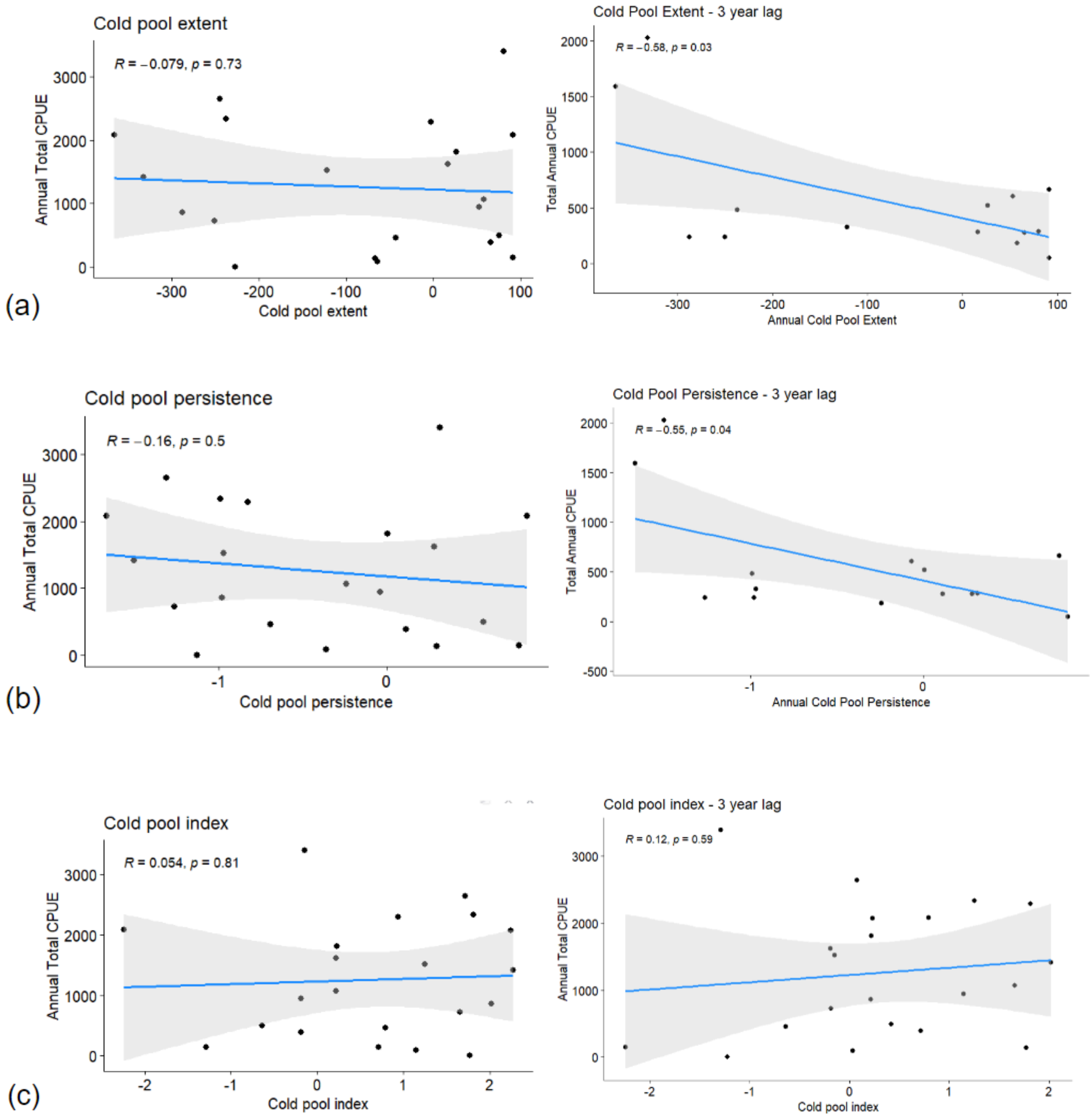


Figure B.6. Linear regressions of study fleet and observer trawl CPUE with annual cold pool extent (a), persistence (b), and index (c) at time of catch and and at time of recruitment (3 year lag). Pearson's correlation coefficient (R) and p-values are included.

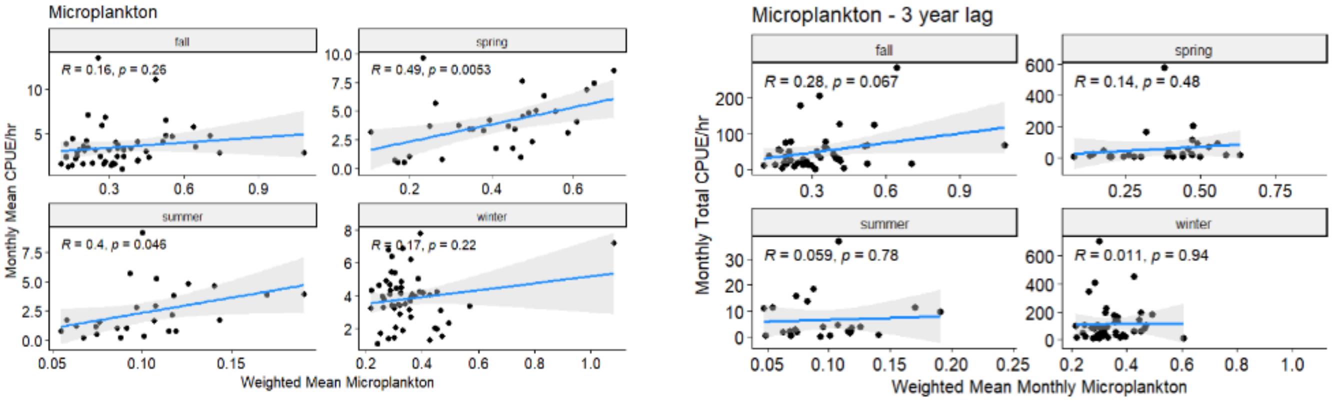


Figure B.7. Linear regressions of study fleet and observer trawl CPUE with average monthly microplankton at time of catch and at time of recruitment (3 year lag) separated by season. Pearson's correlation coefficient (R) and p-values are included for each season.

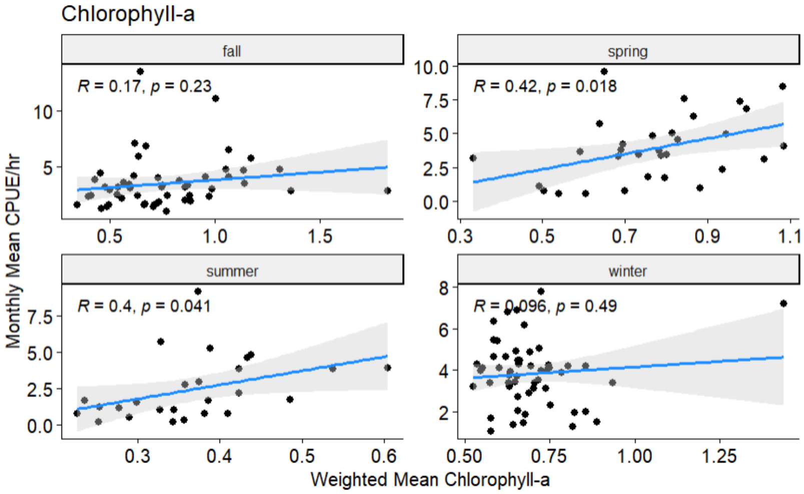


Figure B.8. Linear regressions of study fleet and observer trawl CPUE with average monthly chlorophyll-*a* at time of catch, separated by season. Pearson's correlation coefficient (R) and p-values are included for each season.

APPENDIX C. Variable selection, model diagnostics and evaluation

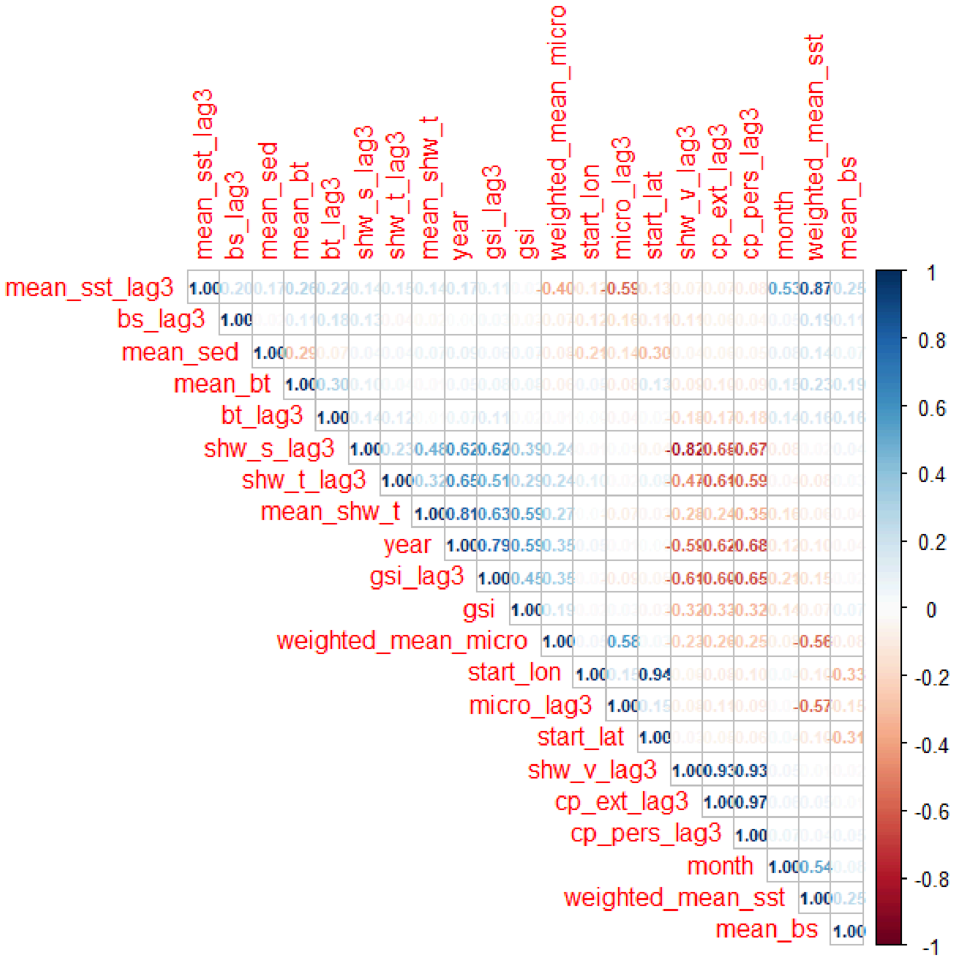
Variable selection

Table C.1. List of all candidate variables modeled. Columns indicate range of variable in dataset used, spatial scale of aggregation/extraction [Northeast Continental Shelf (NES), Golden Tilefish Strata (GTF), Fishing point location (FP)], and whether the variable was included in the final model as well as if they were added as splines (s) or factors (f). Note, Year and Month effects were modeled as tensor products to account for the effect of month across years. All splines (s) were modeled with basis type 'cr' (cubic regression spline), with a few exceptions. Year and Month were modeled as 'tp' and 'cc' (thin plate and cyclic cubic splines), respectively and Latitude and Longitude were modeled as a tensor product as 'ds' or Duchon splines.

Variable	**Range**	**Spatial Scale**	**Included**
CPUE	**2007-2021**	**FP**	**Yes (response)**
Year	**2007-2021**	**NA**	**Yes (s)**
Month	**1-12**	**NA**	**Yes (s)**
Longitude	**-74.85, -66.44**	**FP**	**Yes (s)**
Latitude	**35.94, 42.62**	**FP**	**Yes (s)**
CHL-A	0.19 - 1.82	GTF	No (s)
SST	6.68 - 25.62	GTF	No
Bottom temperature	**3.72 - 21.90**	**FP**	**Yes (s)**
Bottom Temperature, lag 3yrs	3.72 - 21.90	FP	No
Bottom salinity	**32.78 - 36.45**	**FP**	**Yes (s)**
Bottom salinity, lag 3yrs	32.78 - 36.45	FP	No
Shelf water volume, lag 3yrs	**2582.16-4532.92**	**NES**	**Yes (s)**
Shelf water temperature	**10.09 -14.80**	**NES**	**Yes (s)**
Shelf water temperature, lag 3yrs	10.09- 14.80	NES	No
Shelf water salinity, lag 3yrs	32.37 -33.15	NES	No
Gulf stream index	-1.39, 2.12	NES	No
Microplankton abundance	0.05 -1.09	GTF	No
Microplankton abundance, lag 3yrs	**0.05 -1.09**	**GTF**	**Yes (s)**
Sediment size	**8-73**	**NES**	**Yes (s)**
Gulf stream position	**Northerly, Southernly**	**NES**	**Yes (f)**

Gulf stream position, lag 3yrs	**Northerly, Southernly**	**NES**	**Yes (f)**
Cold pool size	Larger, Smaller	NES	No (f)
Cold pool size, lag 3yrs	Larger, Smaller	NES	No (f)
Cold pool length	Longer, Shorter	NES	No (f)
Cold pool length, lab 3yrs	Longer, Shorter	NES	No (f)

Table C.2. Correlation table of candidate variables.



	mean_sst_lag3	bs_lag3	mean_sed	mean_bt	bt_lag3	shw_s_lag3	shw_t_lag3	mean_shw_t	year	gsi_lag3	gsi	weighted_mean_micro	start_lon	micro_lag3	start_lat	shw_v_lag3	cp_ext_lag3	cp_pers_lag3	month	weighted_mean_sst	mean_bs
mean_sst_lag3	1.00	0.20	0.17	0.26	0.22	0.14	0.15	0.14	0.17	0.11	0.03	-0.40	0.12	-0.59	0.13	0.07	0.07	0.08	0.53	0.87	0.25
bs_lag3		1.00	0.02	0.11	0.18	0.13	0.04	0.02	0.00	0.03	0.03	0.07	0.12	0.16	0.11	0.11	0.06	0.04	0.05	0.19	0.11
mean_sed			1.00	0.29	0.07	0.04	0.04	0.07	0.09	0.06	0.07	0.08	0.21	0.14	0.30	0.04	0.06	0.05	0.08	0.14	0.07
mean_bt				1.00	0.30	0.10	0.04	0.01	0.05	0.08	0.09	0.06	0.09	0.08	0.13	0.09	0.10	0.09	0.15	0.23	0.19
bt_lag3					1.00	0.14	0.12	0.01	0.07	0.11	0.02	0.01	0.09	0.04	0.02	-0.18	0.17	0.18	0.14	0.16	0.16
shw_s_lag3						1.00	0.23	0.48	0.62	0.62	0.39	0.24	0.01	0.09	0.04	-0.82	0.69	0.67	0.08	0.02	0.04
shw_t_lag3							1.00	0.32	0.65	0.51	0.29	0.24	0.10	0.02	0.08	-0.47	0.61	0.59	0.04	0.08	0.03
mean_shw_t								1.00	0.81	0.63	0.59	0.27	0.04	0.07	0.03	-0.28	0.24	0.35	0.16	0.06	0.04
year									1.00	0.79	0.59	0.35	0.05	0.01	0.04	-0.59	0.62	0.68	0.12	0.10	0.04
gsi_lag3										1.00	0.45	0.35	0.03	0.09	0.05	-0.61	0.60	0.65	0.21	0.15	0.02
gsi											1.00	0.19	0.02	0.03	0.03	-0.32	0.33	0.32	0.14	0.07	0.07
weighted_mean_micro												1.00	0.05	0.58	0.03	-0.23	0.26	0.25	0.09	-0.56	0.08
start_lon													1.00	0.15	0.94	0.09	0.08	0.10	0.04	0.19	-0.33
micro_lag3														1.00	0.15	0.08	0.11	0.09	0.02	-0.57	0.15
start_lat															1.00	0.03	0.09	0.06	0.04	0.14	-0.31
shw_v_lag3																1.00	0.93	0.93	0.05	0.01	0.02
cp_ext_lag3																	1.00	0.97	0.06	0.05	0.01
cp_pers_lag3																		1.00	0.07	0.04	0.05
month																			1.00	0.54	0.08
weighted_mean_sst																				1.00	0.25
mean_bs																					1.00

Table C.3. Variance inflation factor (VIF) scores

Variable	VIF
cp_ext_lag3	83.75
cp_pers_lag3	60.13
weighted_mean_sst	25.07
shw_v_lag3	23.89
mean_sst_lag3	22.84
shw_t_lag3	12.3
shw_s_lag3	9.91
year	6.82
start_lat	5.42
start_lon	5.06
mean_shw_t	4.62
gsi_lag3	4.3
month	3.66
micro_lag3	3.01
gsi	2.71
weighted_mean_micro	2.59
mean_bt	1.39
bt_lag3	1.26
mean_bs	1.25
bs_lag3	1.12
mean_sed	1.11

Model diagnostics

Figure C.1. GAM concurvity

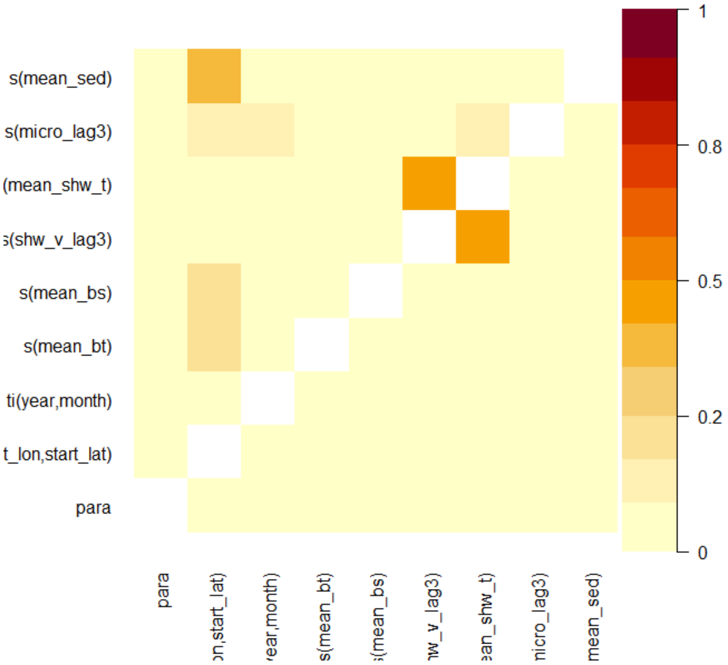
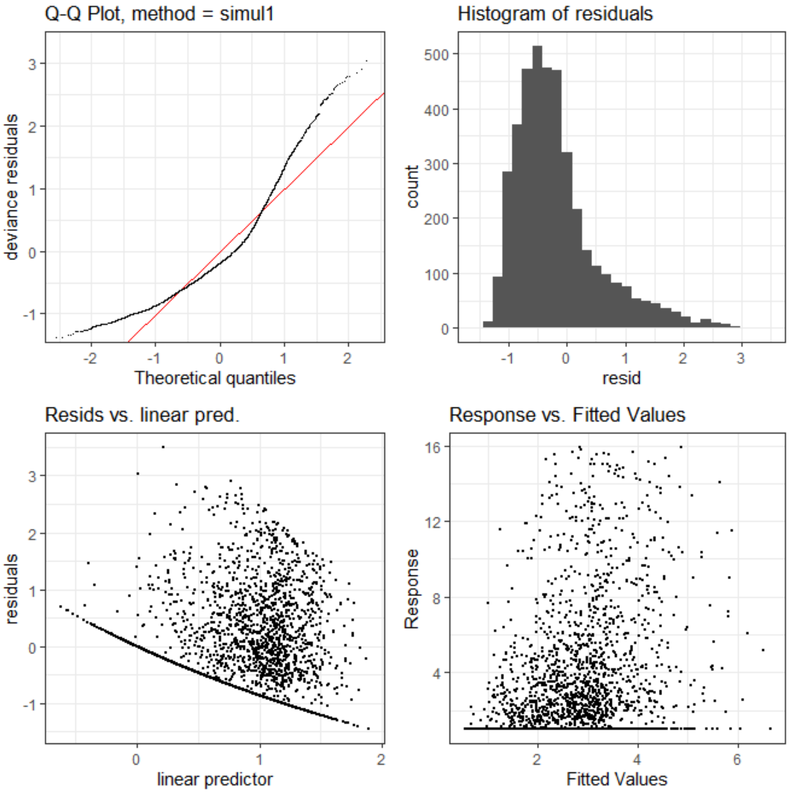


Figure C.2. GAM residual plot



APPENDIX D. Larval analyses

Table D.1.

Year	No. Cruises	No. Stations	No. Tows	No. Larval events
1971	7	127	233	0
1972	7	109	292	0
1973	6	131	330	0
1974	7	118	294	0
1975	6	100	235	0
1976	7	100	157	0
1977	20	325	1904	5
1978	17	334	2083	1
1979	14	219	1136	5
1980	10	175	1030	1
1981	11	378	1023	1
1982	8	406	897	1
1983	9	402	968	0
1984	9	410	1133	4
1985	11	514	1468	6
1986	10	370	1307	1
1987	10	383	1479	1
1988	7	337	779	2
1989	5	210	467	0
1990	8	262	861	0
1991	7	269	805	0
1992	11	337	917	0
1993	10	350	926	2

1994	7	246	486	0
1995	15	308	969	0
1996	14	294	941	0
1997	14	285	886	0
1998	13	247	982	0
1999	15	241	1038	1
2000	8	277	762	1
2001	8	270	721	6
2002	8	265	758	1
2003	7	222	481	1
2004	8	246	666	0
2005	7	253	674	1
2006	7	263	696	2
2007	8	261	663	1
2008	9	269	711	1
2009	7	265	714	7
2010	6	280	733	3
2011	7	290	910	1
2012	6	381	743	2
2013	7	405	685	0
2014	7	354	500	4
2015	5	353	454	2
2016	6	447	673	2
2017	7	277	614	4
2018	10	271	464	4
2019	7	338	595	1
2020	2	44	45	0
2021	12	411	813	6

2022	11	337	573	4
2023	7	230	384	0

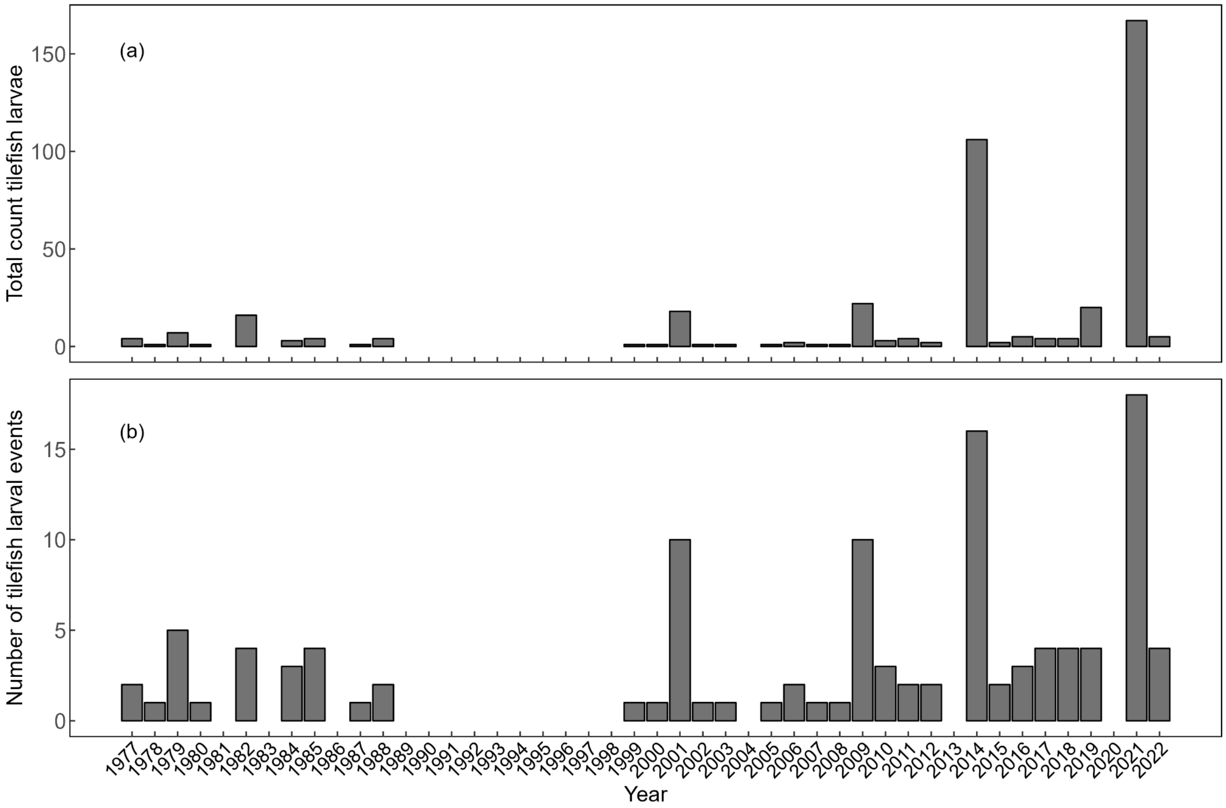


Figure D.1. Summary of positive golden tilefish larval events over time. (a) total number of tilefish larvae collected each year (b) number of tows where tilefish were caught.

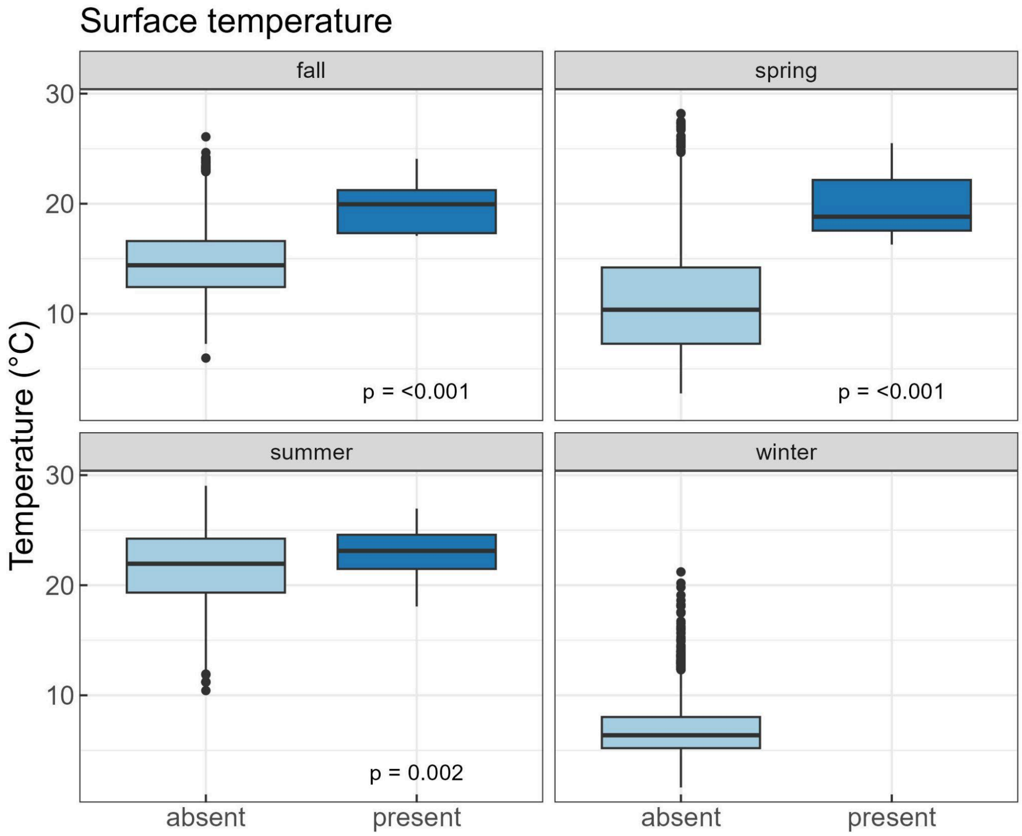


Figure D.2. The presence and absence of larvae collected across a range of surface temperatures. Light blue boxes represent the tows where golden tilefish larvae were absent and dark blue boxes represent the tows where golden tilefish larvae were present. The seasons were categorized as follows, Fall: October, November,December; Spring: April, May, June; Summer: July, August, September.

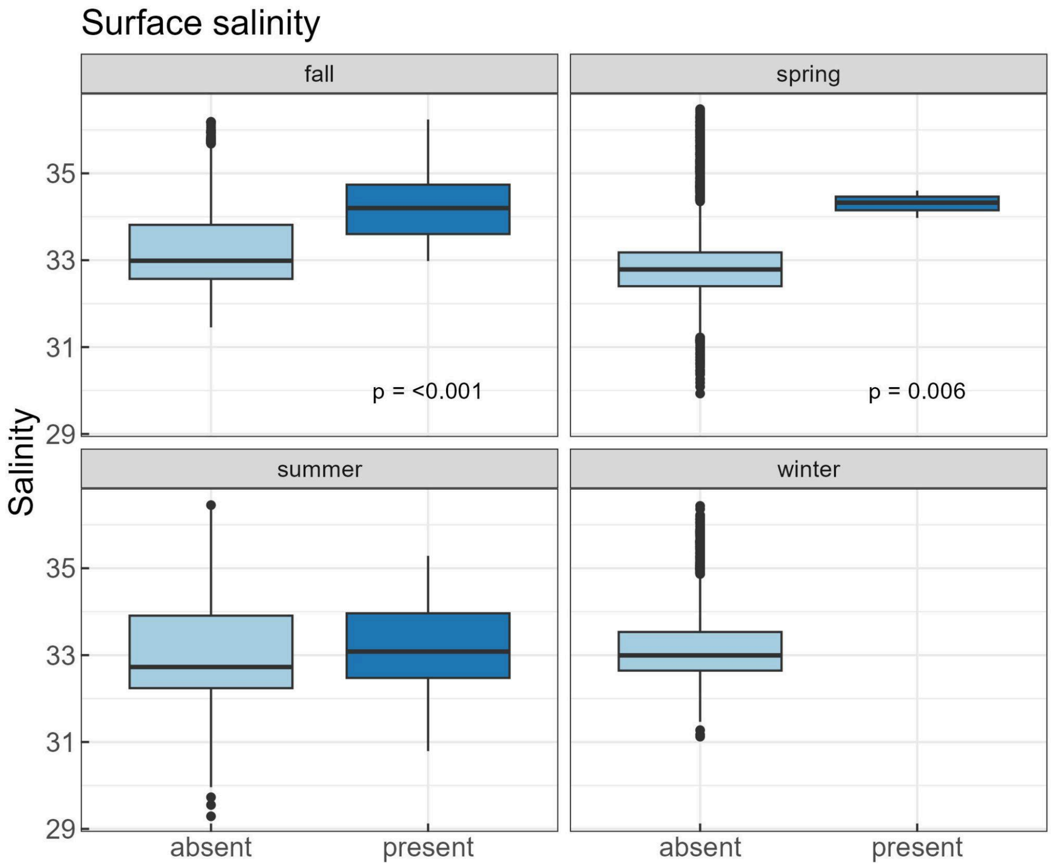
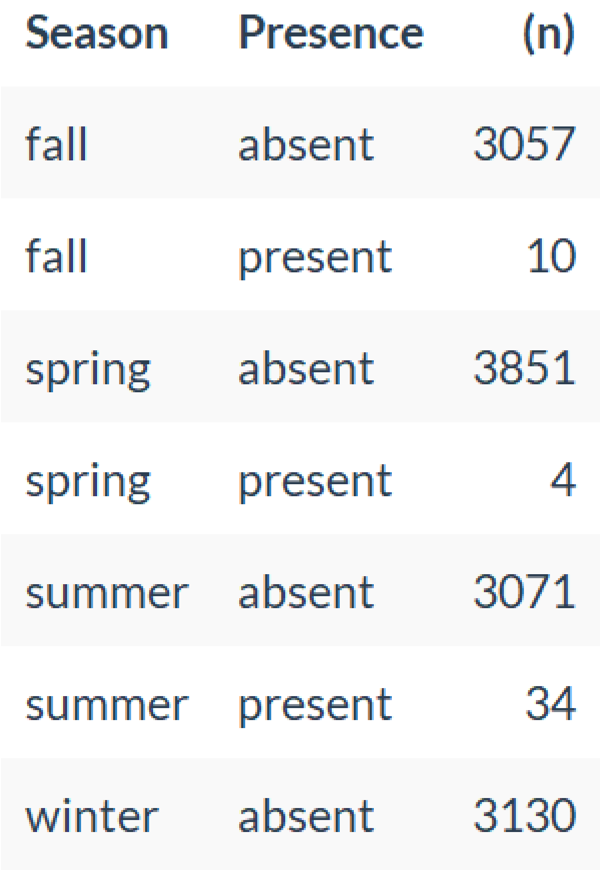


Figure D.3. The presence and absence of larvae collected across a range of surface salinities. Light blue boxes represent the tows where golden tilefish larvae were absent and dark blue boxes represent the tows where golden tilefish larvae were present. The seasons were categorized as follows, Fall: October, November,December; Spring: April, May, June; Summer: July, August, September.

Table D.2. Total counts of number of tows for presence and absence analyses across season.



Season	Presence	(n)
fall	absent	3057
fall	present	10
spring	absent	3851
spring	present	4
summer	absent	3071
summer	present	34
winter	absent	3130