Working Paper: Black sea bass Ecosystem considerations and indicator development

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References

Overview

We reviewed the scientific literature to characterize ecosystem and climate influences on black sea bass (BSB) stock dynamics, such that these relationships could be considered, as appropriate, in addressing other Terms of Reference (TORs) in the black sea bass research track process.

Background

BSB are temperate reef fish that can be found throughout the Northwest Atlantic, from the Gulf of Mexico north to southern Nova Scotia (Drohan et al. 2007). Within this range, BSB are managed as three stocks: (1) the Gulf of Mexico stock, which includes southern Florida, (2) the South Atlantic stock, between Cape Kennedy, Florida and Cape Hatteras, North Carolina, and (3) the northern stock, which spans north of Cape Hatteras to the Gulf of Maine (GOM). Genetic analysis has found these stocks to be genetically distinct from one another, with the strongest separation occurring between the Gulf of Mexico population and the populations along the US continental shelf (Roy et al. 2012). The stocks along the Atlantic coast are distinct, but also display a limited degree of connectivity (McCartney et al. 2013).

BSB are seasonally migratory, occupying coastal habitats in warmer months and moving offshore to the continental shelf to overwinter. Fall offshore migration is triggered by bottom temperatures of 10-12°C, with the migration beginning in the north and proceeding south. There can be several months' difference in migration timing in the north (e.g., Massachusetts) and the south (e.g., Virginia).

The northern and South Atlantic stocks are further distinguished by differing migration patterns. While both stocks migrate from inshore locations in the warmer seasons to deeper, offshore habitats to overwinter, the northern stock migrates south as well as offshore, as they have stronger thermal constraints (Moser and Shepherd 2009). The northern stock has recently been subdivided into two regions split at the Hudson Canyon to better capture the spatial structure of the stock (NEFSC 2017).

BSB occupy a wide range of structurally complex habitats that offer refuge as well as access to epibenthic prey (Musick and Mercer 1977). Adult BSB can tolerate a wide range of salinities and temperatures for short times, but longer divergences from their preferred conditions can negatively impact growth and survival. Estimates of optimal bottom temperature for adults range from 8-10°C (Miller et al 2016, Cullen & Guida 2021). These temperature ranges were associated with salinity values ranging between 33–35 PSU.

The northern region of the northern stock is of particular interest as recent year classes have experienced successful recruitment and expansion into areas of the Gulf of Maine that previously had very low abundance of BSB (Bell et al. 2015). These individuals in the newly expanded habitats display differing life history traits such as size, diet, condition, maturity, and growth compared to the populations south of Massachusetts (McMahan et al. 2020).

Life history

Spawning

Mature BSB return to the inner continental shelf in late spring to spawn. Spawning in the Mid Atlantic Bight (MAB) occurs over sandy bottoms, or mixed sand and reef structures at depths of 20-50 m (Drohan et al 2007). Spawning occurs from April to October and initiates in the south and propagates northward (Musick & Mercer 1977). Estimates of length at 50% maturity (L50%) within the South Atlantic stock ranged from a mean of 108-145 mm in 1978-1998 (McGovern et al. 2002). L50% in the northern stock was observed to be larger than in the South Atlantic stock with 191 mm standard length (O'Brien et al. 1993). The aggregate estimate of L50% from NEFSC maturity data from spring and winter surveys since 1984 was 210 mm for fish in the northern stock (NEFSC 2017), while a study that collected fish in Massachusetts and Maine (a subset of the northern region) observed a L50% of 266 mm (McMahan et al. 2020).

BSB are atypical protogynous hermaphrodites. At hatching, the sex ratio skews female with the majority (~60%) of young-of-the-year (YOY) being female, with the remaining fish being roughly split between intersex individuals and males (Benton and Berlinsky 2006). There are some primary males at smaller size classes, which could be a resilience mechanism to ensure enough males to successfully spawn even when terminal males are rare (Blaylock & Shepherd 2016). When there are no terminal males in the local area, the largest female will transition to male (Benton and Berlinsky 2006).

Transition from female to terminal male generally begins after age 1, and reaches T50% of transition at ages 2-3 (O'Brien et al 1993). The size at transition is positively associated with latitude, with the Gulf of Mexico stock having the smallest size at transition (160–259 mm) and more northern stocks transitioning at larger sizes (McGovern et al. 2002). The T50% for the northern stock is 355 mm TL and occurs between the ages of 4–6 years.

Most sex transitions occur after the spawning window has ended in October (Provost et al. 2017). This clustering of transitions can impact estimates of fecundity, with egg production potentially being overestimated in the size classes subject to transitioning. This variable timing of transition and difficulty in estimating fecundity can be challenging for many common methods of population modeling.

Egg

Eggs arrive in the southern region in early May at sizes ranging from 0.8-1.1 mm (Berrien & Sibunka 1999). Spawning continues through the summer and into the fall and tapers out in October (Berrien & Sibunka 1999). The peak abundance of eggs begins in the south and advances northward. The peak egg densities are observed between July-September (Drohan et al 2007). Eggs are observed in temperatures ranging from 16-22°C at depths between 10-375 m (Drohan et al. 2007). The highest abundance occurs at 30 m. Eggs remain buoyant for their incubation period, which lasts for an average of 48 h but can extend up to 5 days with colder temperatures increasing the length of incubation (Able & Fahay 1998). Survival of fertilized eggs is also temperature dependent with the highest survival occurring at intermediate temperatures

of 20°C and lower survival at both low (15°C) and high (30°C) temperatures (Berlinsky et al. 2004). Water conditions of 12°C at 0 and 5 ppt salinity completely inhibit the growth and hatching of eggs. The pelagic stages of life are vulnerable to planktivore predators, with coelenterates potentially playing a role in distribution of teleost fish via predation of eggs and larvae (Arai, 1988).

Larva

Yolk-sack

BSB feed off of their yolk sac after hatching. This phase takes ~72 h at 21°C but can vary with temperature and salinity from 2-6 days (Berlinsky et al 2004). These individuals are ~2.1 mm in length and must use this time to develop structures to support exogenous feeding (Tucker 1989).

Feeding larvae

After yolk sac absorption, BSB larvae have a relatively long planktonic phase until they settle when they reach a size of 10-16 mm TL. Growth rates are estimated at 3.5 to 12.2 mm growth in 18 days at 22°C (Berlinsky et al. 2004). First diet items are likely microalgae or zooplanktonic prey, such as rotifers, in the 150-200 µm size range (Berlinsky et al. 2000). BSB larvae are found in temperatures between 12–24 °C and salinity levels of 30–35 ppt (Drohan et al. 2007). Larval abundance coincides with spawning and occurs throughout May-November with peaks in June-July. Larvae are pelagic and are found in a wide depth range of 0 to >2000 m, but peak abundance occurs at 20-30 m depth (Drohan et al. 2007). Male larvae have higher growth rates across temperature ranges during the first 280 days post hatch (Colburn et al 2009).

Juvenile

The location and timing of settlement is an important factor in the survival of juvenile BSB. Once reaching ~13-24 mm TL, BSB will settle into structurally complex habitats both onshore and offshore (Musick & Mercer 1977). Congregations of juveniles are observed around structured habitats like shell accumulations in marsh creeks and peat banks (Able et al. 1995). In the northern stock, BSB are associated with a diversity of benthic habitats, including both soft and hard structures in both shelf areas and estuaries (Drohan et al. 2007). Once settled, BSB have high site fidelity and limited home ranges (Able and Hales 1997, Fabrizio et al. 2014). Presence of juveniles in these habitats occurs between April-October (Peters and Chigbu 2017). During this early period, juveniles are estimated to grow at a rate of 0.32 to 1.22 mm per day during spring through fall of their first year (McBride et al. 2018).

The first year of life is the limiting factor in recruitment into the fishery (Miller et al. 2016). The disconnect between spawning biomass and recruitment into the fishery likely occurs due to high mortality rates in YOY BSB in their first winter post-hatch (Miller et al. 2016). The recently settled individuals have poor mobility and exposure to unfavorable conditions in their overwintering habitats can result in poor survival rates. These juveniles experience 100% mortality when exposed to winter temperatures below 2-3 °C (Hales & Able 2001). Salinity and

temperature have an interactive effect on overwinter survival resulting in a higher tolerance of colder temperatures at higher salinity levels (Younes et al. 2020).

Adult

Diet

Adult BSB are benthivorous generalist carnivores, with their diet being composed of a variety of epibenthic vertebrates and invertebrates, including crabs, amphipods, polychaetes, mollusks, and small fish (Sedberry 1988). BSB display an ontogenetic shift from polychaetes, miscellaneous arthropods, and decapod shrimp in early life stages to including more piscine prey as they increase in size (Byron and Link 2010). BSB are known to have food habit overlap with Atlantic cod (*Gadus morhua*), scup (*Stenotomus chrysops*), northern searobin (*Prionotus carolinus*), and striped searobin (*P. evolans*) (Byron and Link 2010, Santos 2020). Diet also varies within stock regions. For example, populations in the northern subunit have a decrease in quality of prey and a loss of diet diversity at higher latitudes, which is attributed to a lack of lipid-rich demersal and pelagic fish availability in the Gulf of Maine (McMahan et al. 2020). Similar latitudinal decreases in prey quality, from high quality fish prey to miscellaneous arthropods at more northern latitudes, was observed by Byron and Link (2010). Decapods are the dominant prey items throughout all size classes of BSB, from settlement through adulthood. BSB utilization of reef structure is not diet-driven (Steimle and Figley 1996).

Predators

Evidence of BSB predation is rare in the NEFSC Food Habits Database (<150 occurrences since 1973). When ordered by frequency of occurrence BSB predators include: demersal sharks, summer flounder, fourspot flounder, BSB, monkfish, spiny dogfish, skate, windowpane, little skate, bluefish, smooth dogfish, red hake, striped bass, silver hake, Atlantic cod, and winter skate (NEFSC 2017). Age-1+ weakfish have been observed to prey on juvenile BSB in the Chesapeake Bay (Hartman and Brandt 1995). Evidence of BSB predation by large pelagic and highly migratory species is slim. The NEFSC Apex Predator Program reported (C. McCandless and K. Duffy personal communication) that out of the entire time series of stomach contents of mako, thresher, porbeagle, and blue sharks, only one BSB was identified.

Competitors

Due to data limitations, we characterize potential competitors on the basis of species co-occurrence. Adult BSB in the summer share their benthic structure with tautog (*Tautoga onitis*), spotted hake (*Urophycis regia*), red hake (*U. chuss*), conger eel (*Conger oceanicus*), ocean pout (*Macrozoarces americanus*), pinfish (*Lagodon rhomboides*), and northern sea robin (*Prionotus carolinus*) (Drohan et al. 2007). Additionally, trawls that capture BSB also capture smooth dogfish (*Mustelus canis*), round herring (*Etrumeus teres*), and windowpane flounder (*Scophthalmus aquosus*) (Drohan et al. 2007). Santos (2020) examined the diet of Atlantic cod and BSB from Narragansett Bay and coastal southern Rhode Island and found a high degree of overlap in diet across sites and seasons.

Stock Assessment

Mortality

Temperature and salinity are strong constraints on BSB distribution and survival. BSB are sensitive to low winter temperatures, with activity dropping at temperatures below 6°C (Adams 1993). At these temperatures, minimal growth and feeding occur. Below 6°C, a high degree of mortality can occur with estimates of the lethal temperature ranging from 2-5°C based on fish size and exposure time (Hales & Able 2001, Younes et al. 2020). Exposure as short as 48h at <3°C is lethal even if temperatures return to milder (>10°C) conditions (Younes et al. 2020). In comparison, 5°C can be tolerated for much longer (>2 weeks) with limited mortality (Younes et al. 2020). Temperature tolerance directly interacts with salinity (Berlinsky et al. 2004). Marine teleosts must actively maintain homeostasis, and at salinities closer to the internal osmolality of estuarine fishes (8-12 PSU), osmoregulatory stress is minimized and starvation may be a primary driver of natural mortality at cold temperatures (Younes et al. 2020). Size selective mortality due to temperature in isolation was not observed in YOY BSB in laboratory experimentation (Younes et al. 2020). However, in situ observations indicate that size does influence mortality, and is hypothesized to be due to smaller individuals having a more diverse range of predators, or being more likely to leave refuge to forage in comparison to larger fish (Younes et al. 2020). This protective effect of lower salinity may play a role in the overwinter survival of BSB as estuarine environments may be more favorable in comparison to shelf habitats given similar thermal conditions (Younes et al. 2020).

Recruitment

Both male and female black sea bass begin to reach sexual maturity at approximately 19 cm (median length at maturity). This size occurs by ages 2-3 (O'Brien et al. 1993). Individuals >19 cm typically occupy a variety of structurally complex benthic habitats and exhibit strong site fidelity, and recruitment strength is strongly correlated with the availability of shelter (Drohan et al. 2007, Richards and Lindeman 1987). Depth and habitat utilization varies throughout the year. In winter, they are found at 50-200 m isobaths. Spring occurrences were observed over a wide depth range from 10-140 m with the most common occurrences between 11-40 m. Spring and fall NEFSC bottom trawl observations in the GOM to Cape Hatteras observed a wide range of temperatures from 4-18°C, and a peak in catch at 12°C (Drohan et al. 2007). In the summer, recruits travel inshore in bays and estuaries and reach peak inshore abundance in the fall (Drohan et al. 2007).

BSB are considered highly sensitive to climate change because their migration patterns allow multiple phases of their life history to be strongly influenced by environmental change (Hare et al 2016). One area of particular concern is the poor connection between spawning stock biomass and recruitment strength (Miller et al. 2016). This disconnect has been noted as a major limiting factor in understanding the population dynamics of BSB (NEFSC 2017). The abundance of YOY BSB in the fall surveys is poorly correlated with recruitment to the fishery, while spring indices of abundance of age 1 individuals display a higher correlation with recruitment into the fishery. These patterns indicate that overwintering is a strong filter of newly settled juveniles (Miller et al 2016, NEFSC 2017).

Temperature, bottom salinity, and to a lesser extent, shelf water volume (an approximation of winter habitat), all have significant effects on distribution and survival of YOY (Miller et al. 2016). The warmest years, with the lowest amount of shelf water volume, were correlated with the strongest survival of BSB. Shelf water volume was found to negatively affect catches of BSB, suggesting that the higher volume of water with unfavorable temperature and salinity may force BSB to migrate further offshore.

The recent trends of warming in the northwestern Atlantic are likely to have a positive effect on BSB in the northern region of the northern stock. BSB have recently been observed in areas that previously experienced lethal cold temperatures, such as the Gulf of Maine (McMahan et al. 2020). Fish in the newly expanded habitat have significantly different size, diet, condition, maturity and sex ratio in comparison to fish inhabiting historic habitats (McMahan et al. 2020). In these new habitats, fish had a longer length-at-age and lower maturity-at-age, which may be a result of improved food conversion ratios, or a phenotypic adaptation in response to the shorter growing season (McMahan et al. 2020).

While black sea bass are polyhaline, YOY BSB display peak growth at salinity ranges between 20 and 30 PSU (Cotton et al. 2003). YOY BSB in estuarine systems had higher recruitment years during years with higher average salinity. Other observations indicated that YOY BSB have a wide salinity tolerance, however salinities below their preference likely lowers their ability to survive their first winter. Observations of YOY survival in estuaries found higher catch per unit effort when the North Atlantic Oscillation index (NAO) was negative (Peters, & Chigbu 2017). Negative values in NAO indices were associated with colder temperatures, higher wind, and lower precipitation, and the decrease in freshwater input is hypothesized to be the causal factor in survival (Peters & Chigbu 2017).

Distribution

Changes in distribution of BSB have been linked to warming in the northwestern Atlantic. Howell and Auster (2012) identified a recent shift in fish assemblages in the northwest Atlantic from cold-adapted to warm-adapted species, including BSB. This trend of increasing presence of BSB in more northern locations can be attributed to both average temperature increases benefiting BSB, as well as a reduction in lethal low temperature events. The center of spring BSB biomass has shifted northward 150-200 km over the past 40 years (Bell et al 2015). Winter observations show that BSB are concentrated in locations with bottom temperatures >6 °C (Drohan et al. 2007; Moser and Shepherd, 2009). The 7°C isotherm, an indicator of tolerable habitat, now occurs at higher latitudes. Increases in temperature may improve overwintering survival of YOY, which could support BSB expansion to previously uninhabited areas (Bell et al 2015). High temperatures also constrain habitat use: the maximum tolerable temperature is 24°C (Slesinger et al. 2019), with prolonged exposure to higher temperatures (30°C) being unsustainable due to decreased oxygen saturation in conjunction with increased metabolic demands. This upper limit of temperature range may lead to a contraction of BSB in the southern region of the mid-Atlantic, as experimentation has demonstrated a poor ability to adapt to chronically warm conditions (Slesinger et al. 2019).

BSB display seasonal inshore-offshore patterns in direct response to environmental changes (Moser and Shepherd 2009). It is unknown if temperature is the ultimate cause of

migration, or if associated changes in food availability or salinity are stronger determinants of migration timing. Northern individuals display a latitudinal component to this annual migration pattern, with individuals migrating south in addition to offshore. The timing of these departures may be triggered by bottom water reaching temperatures between 10–12°C (Moser and Shepherd 2009). This important trigger arrives first in the northern latitudes and proceeds south. The southern component of the northern stock displays higher site fidelity to their overwintering locations, while the northern component of the northern stock has variable site fidelity that is inversely related to distance migrated (i.e., the farther the migration, the lower the probability of returning to the original location; Moser and Shepherd 2009).

Irregular and episodic storm events can drive rapid changes in temperature, dissolved oxygen, and salinity in the coastal environment, which can affect BSB behavior and distribution. Secor et al. (2019) observed water column destratification and complete dissipation of the cold pool resulting in a >10°C increase in bottom temperature within 10-20 h. Evacuation of shallow habitats as a response to storms was observed with 40% of BSB leaving temporarily, while a minority of individuals permanently emigrated (Secor et al. 2019). This migration can have implications for feeding, metabolic stress, and increased predation risks associated with additional required movement. These late season storms occur throughout the spawning season potentially impacting reproductive success (Secor et al. 2019). Depression of activity is another distinct strategy for enduring these conditions where individuals remain within the destratified conditions, but exhibit lower levels of movement. The primary driver in the decrease in activity was identified as rapid increases in bottom temperature, while turbulence played a relatively minor role (Wiernicki et al. 2020). In combination with long-term seasonal changes, these episodic disruptions to cold pool dynamics caused by increasing storm frequency may result in shifts in movement patterns, feeding, and reproductive behaviors of BSB (Wiernicki et al. 2020).

Indicator analysis

Background

Previous assessments have made research recommendations to investigate the climate drivers on BSB and the potential differences between regions. Two key sources of scientific uncertainty were identified for further exploration: overwintering survival and stock mixing.

Overwintering survival during the first year of life is hypothesized to be a strong determinant of recruitment and year class strength (Miller et al. 2016) In particular, Miller et al. (2016) indicated a lack of correlation between fall surveys of age-0 abundance and ultimate year class strength and identified several environmental factors that influenced the winter distribution of black sea bass on the shelf: salinity, temperature, and to a lesser extent, shelf water volume.

The current northern stock is divided and modeled as two separate regions divided at approximately the Hudson Canyon (Figure 1). Previous stock assessment models exhibited a strong retrospective pattern, particularly in the northern region. One potential source of this retrospective pattern could be the misattribution of both the survey and fishery catches between

the two regions. Due to their seasonal migration patterns, some proportion of fish caught in the southern region during the winter offshore trawl fishery or in the winter and spring NEFSC bottom trawl surveys are likely fish from the northern region. To further expand and explore these relationships, indicators were created and evaluated for their potential use to explain ecological drivers of stock dynamics.

Indicator selection

An in-depth literature review was conducted to identify appropriate ecosystem indicators. A literature search on the Web of Science using the terms 'TS=("Centropristis striata" OR "black sea bass") AND TS=("marin* environ*" OR ecolog* OR plankton* OR ecosystem* OR "estuarin* habitat*" OR "estuarin* nurseri*" OR "estuarin* system*" OR "small* pelag*" OR "surfac* temperatur*" OR "water* column*" OR "abiot* factor*" OR "climat* chang*" OR pollut* OR "advect* process*" OR "aquat* ecosystem*" OR "boundari* current*" OR "dissolv* oxygen*" OR "local* ecolog* knowledg*" OR "physic* factor*" OR "predat* pressur*" OR "trophic* dynam*" OR "water* gualiti*")' and a second more general search of the terms 'TS=("Centropristis striata" OR "black sea bass") AND TS=(Atlantic OR "United States")' identified 55 and 108 relevant papers, respectively. Based on content, these papers were further narrowed down and reviewed in depth. Information from the papers was used to develop a conceptual model of the life history of black sea bass, which identified the habitat and distribution, phenology, age, length, and growth patterns, energetics, diet, and predators and competitors of each BSB life stage from egg to adult (Table 1, Figure 2). This conceptual model was then used to determine relevant ecosystem linkages that could impact BSB, and these linkages were developed into a list of potential ecosystem indicators. Research recommendations from the prior BSB assessment were also considered and developed into potential indicators where possible. Final indicators were selected for analysis through discussion with the Working Group.

Overwinter survival: Winter bottom temperature

Data

BSB have an incipient lethal temperature threshold at 6°C, below which feeding ceases and temperature-induced death is the primary cause of mortality (Younes et al. 2020). The relationship between temperature and catches of BSB in the NEFSC Bottom Trawl Survey identified a preferred temperature of >8°C. (Miller et al. 2016). Regional annual winter bottom temperature is proposed as an ecosystem indicator of BSB recruitment; we hypothesize that colder winter bottom temperatures would cause higher YOY mortality and result in lower recruitment.

We identified two suitable data sources. The first is observed ocean temperature data from the Hydrographic Database maintained by the NEFSC Oceans and Climate Branch, which was used in the Miller et al. (2016) analyses. These are composed of CTD measurements concurrent with bottom trawl surveys and other deployed instruments. Quality assurance and control are performed on these sources to produce area weighted regional mean values as described in Fratantoni et al. (2013). Mean values were computed for each survey and a

reference annual cycle (fit to observations from 1981-2010) was removed to produce anomalies. The values in the dataset are anomalies plus expected mean value for each location and time of year based on this reference period. This time series is a representation of the interannual variability in temperature. To assess winter conditions, we averaged February and March data on the regional scale. January was excluded due to low in-situ data coverage.

The second data source is a high-resolution bottom temperature ocean reanalysis model output (du Pontavice et al. 2023). Bottom temperature data were aggregated from an ocean reanalysis that combined three products, a regional ocean model (ROMS) and two global ocean data assimilated models (GLORYS12v1 and PSY4V3R1) to build a high-resolution (1/12°), long-term bottom temperature product for the northeast U.S. continental shelf between 1959 and 2022 (du Pontavice et al. 2023). Mean winter (February and March) bottom temperature was calculated from daily gridded data assessed over the northern and southern Mid-Atlantic Bight regions. Spatio-temporal variation in mean winter bottom temperature was calculated as the standard error of the mean of each year.

The two bottom temperature datasets are statistically significantly correlated with one another (Figure 3). The Hydrographic Database is missing data coverage due to the timing and quality of in situ data collection, resulting in the Southern MAB time series missing three years of data, while Northern MAB time series is missing seven years of data. The reanalysis data is not missing any years of data because it uses numerical simulation to interpolate for areas and times where data are limited. The two sources differ in their range of values with the reanalysis product spanning 5.0-10.4°C (North) and 6.3-10.0°C (South) while NEFSC Hydrographic Database displays a higher range (North 6.7-12.6°C, South 9.5-13.2°C).

These temperature data sets were used to investigate the linkage between temperature and black sea bass overwinter survival and recruitment. We used log age-1 recruitment deviations from the ASAP model (NEFSC 2021) as a proxy for juvenile sea bass abundance. Because annual recruitment is estimated as the mean of the time series recruitment, log recruitment deviations with values greater than or less than 0 are years where recruitment was larger or smaller than the mean time series recruitment, respectively (Figure 4).

Correlation analysis

To assess the association between the proposed indicator and stock status, Pearson correlation testing was performed between the two annual regional mean winter temperature datasets and log recruitment deviations.

Both bottom temperature datasets were statistically significantly correlated with same-year log recruitment deviations in both BSB regions. Mean winter bottom temperature from the Fratantoni et al. (2013) dataset was significantly correlated with same-year estimates of recruitment in both regions (Figure 5; South: F =7.26, df = 26, p-value = 0.012 R² = 0.218, Adj R² = 0.188; North: F = 7.1, df = 24, p-value = 0.013, R² = 0.230, Adj R² = 0.199). The du Pontavice et al. (2023) dataset had similar results (Figure 6; South: R²= 0.173, Adj R²=0.144, F=6.06, df= 29, p-value= 0.019; North: R² = 0.27, Adj. R²= 0.25, F=11.18, df = 29, p-value: 0.002). This relationship shows that recruitment is higher than average in warmer years and lower than average in colder years.

Empirical Dynamic Modeling Analysis

To further understand the potential causal relationship between bottom temperature and recruitment of BSB, the two time series were analyzed using convergent cross mapping (CCM), a method of empirical dynamic modeling. CCM tests for causation by measuring the extent to which the time series for Y can reliably predict states of X. As the length of the time series for Y increases, the ability to predict X will increase if Y has a causal relationship with X (Sugihara et al. 2012).

We used the rEDM (Sugihara et al. 2019) and multispatialCCM (Clark 2014) R packages (R Core Team 2021) to assess causality between the du Pontavice et al. (2023) mean winter bottom temperature data and log recruitment deviations in both the northern and southern regions. While both regions showed the increasing trend in predictability with an increasing length of the time series (Figure 7), only the southern region had a marginally statistically significant p-value (0.08, α =0.1). This suggests that, at least in the southern region, bottom temperature has a causal relationship with black sea bass recruits.

Overwinter mixing

We evaluated the hypothesis that cold winters cause habitat contraction, which results in more northern BSB migrating south and being misattributed to the southern region via removals or spring trawl captures. Shelf water volume is used as a proxy for suitable winter habitat. Center of gravity and effective area occupied are used as proxies of stock mixing We assessed the correlation between habitat and mixing.

Data

The shelf slope front is an oceanographic feature that separates colder and less saline continental shelf waters from generally warmer and more saline slope waters over the continental slope. BSB congregate on the seaward edge of the slope front during winter and may use this oceanographic feature as a way point during the spring migration (Miller et al. 2016). The position of the front varies inter-annually, with the years with more fresh northern water resulting in the front being pushed further offshore. As this front moves towards or away from the coast, the available habitat can expand or contract as BSB may concentrate on the slope of the sharp thermohaline front. For example, when shelf water volumes are condensed BSB have a shorter distance to travel to return shoreward, which may give them an energetic advantage to surviving the migration (Miller et al. 2016). Miller et al. (2016) identified a negative impact on BSB catch when shelf water volume exceeded 4000 km³, which indicates that higher shelf water volumes could result in lower suitable habitat for BSB, and proposed that years with shelf water volume >4000 km³ could be used to identify possible mixing between the northern and southern subregions.

In this analysis, the shelf water is defined as all water having salinity <34, and shelf water volume (SHW) was calculated as a measure of the volume of water bound inshore of the shelf-slope front (Miller et al. 2016). This volume of water in the winter (February and March) is calculated for the north and south regions for each available time step.

A VAST (Vector Autoregressive Spatio-Temporal; Thorson 2019) model was fitted to spring fisheries independent data from both federal and state surveys to get density estimates across time and space (Hansell and Curti 2023). This model uses a spatial delta-generalized linear mixed model to generate standardized indexes of density and to estimate the geographic center of the population with the north and south regions over time. The upper quantiles of the centers of gravity are representative of biological limitations (Fredston-Hermann et al. 2020) and were used as a proxy of BSB distribution.

Correlation analysis

Shelf water volume was correlated with BSB distribution in the southern subregion only. There was a significant negative correlation association between upper 95% confidence interval of the southern MAB center of gravity and shelf water volume (Figure 8; r = -0.35 t = -2.80, df = 28, p-value = 0.007), and the effective area occupied by BSB was negatively correlated with shelf water volume in the southern MAB (Figure 9; r = -0.365, t = -2.07, df = 28, P-value = 0.047). In the northern MAB, no statistically significant correlations were found between shelf water volume and the center of gravity (Figure 8; r = 0.00, t = -0.014, df = 24, p-value = 0.98) or the effective area occupied (Figure 9; r = -0.333, t = -1.73, df = 24, P-value = 0.096).

Conclusions

Winter bottom temperature was positively correlated with log recruitment deviations in both the northern and southern subregions, with evidence of a causal relationship in the southern subregion. We suggest that winter bottom temperature be explored as an environmental covariate to inform recruitment in the assessment model.

Southern MAB BSB appear to occupy a smaller portion of the available habitat in years with higher shelf water volume. Further research is needed to determine the effects of overwintering conditions on the distribution of the northern subunit. We suggest that future efforts to reallocate removals and abundance indices between the northern and southern stock subunits focus on years with high potential stock mixing as determined by habitat indicators.

Tables

Table 1. Summary of ecosystem impacts on various life history and demographic stages

Environmental	Notes	
Impacts on:		References

Recruitment	 100% mortality when winter temperatures decreased below 2-3 °C ¹ 6°C Feeding stops and is the lethal temperature, with short exposures to 5 °C proving lethal even when returned to nominal temps ² a. Interaction with osmoregulation at lower salinity, lower temps were better tolerated. North Atlantic Oscillation index Correlated with age-0 CPUE but not age-1 ³ Strong recruitment correlated with the warmest years, higher salinity and lowest slope water volume ⁴ 	 Hales & Able 2001 Younes et al 2020 Peters & Chigbu 2016 Miller et al 2016
Natural Mortality	 Better indices of impairment can produce estimates of bycatch mortality² GOM fish may overwinter offshore and not following the southern shelf 6°C as the lower incipient lethal temperature ³ Temperature was not size selective for mortality in laboratory ³ Lethal range of 33.6°C and 2.7°C, respectively, when temperatures were increased or decreased at a rate of approximately 0.5°C per day a. thermal tolerances and preferences do not differ greatly between the northern and southern stocks of BSB.⁴ 	 Hales & Able 2001 Schweitzer et al 2020 Younes et al 2020 Sullivan and Tomasso 2010
Growth and Maturity	 Length-at-age was higher in northern areas then SAW 2016² Maturity at age significantly lower in Northern MA and GOM GOM less diverse diet and their condition was lower indicating still near metabolic limits Initial sex differentiation not strongly affected by temperature- stable ratios of ~60% female, ~20% intersex, ~ 20% male sex ratios between 17-25°C¹ Sex change induced for local conspecifics at only female ratios of F8:0M³ L50 for transition is 355 mm TL⁴ Transition occurs mostly between spawning seasons with peak in October Peak female fecundity occurs prior to sizes for transition to male ⁵ Implies a dome-shaped fecundity relationship for females to devalue the fecundity of large likely to transition females. 	 Colburn et al 2009 McMahan 2020 Benton and Berlinsky 2006 Provost et al 2017 Klibansky and Scharf 2018

Distribution and Habitat Use	 The stock north of Cape Hatteras is genetically distinct from the stock south of Cape Hatteras and Gulf of Mexico Adult maximum tolerable temperature is estimated to be ~24.°C. With chronic exposure to 30°C fish experienced reduced muscle function ² BSB thermal habitat may shrink considerably in the southern region of the MAB as bottom water temperatures reach >27°C Optimal temperature ~ 8°C with strong decline in habitat quality above 18°C ³ Late summer storms that cause destratification can cause decreased activity and fish evacuating reef habitats ⁴ Wind energy structures may provide additional habitat and refugia from some fishing gear types ⁵ Poleward shifts linked to warming trend in continental shelf waters but not expansion in area occupied ⁶	 McCartney et al 2013 Slesinger et al. 2019 Nazzaro et al. 2021 Wiernicki et al. 2020 Friedland et al. 2021 Bell et al. 2015 Secor et al. 2019 Fabrizio et al. 2013
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Figures

Figure 1. Northern stock area with NEFSC bottom trawl strata used in the black sea bass assessment from NEFSC 2017. Dividing line indicates a split between the northern subregion (Northern MAB) and southern subregion (Southern MAB) at the Hudson Canyon. Reproduced from Miller et al. 2016.



Figure 2. Conceptual model of ecosystem impacts on life history and demographic stages of black sea bass.



Figure 3. The association between regional mean winter bottom temperature (°C) from in situ measurements (Fratantoni et al. 2013) and ocean reanalysis model output (du Pontavice et al. 2023) (North r =0.81, P-value<0.001, South r =0.90, P-value<0.001).









Figure 5. The relationship between mean winter bottom temperature (Fratantoni et al. 2013) and log recruitment deviations (NEFSC 2021) across sub regions. Southern MAB: F =7.26, df = 26, p-value = 0.012 R² = 0.218, Adj R² = 0.188; Northern MAB: F = 7.1, df = 24, p-value = 0.013, R² = 0.230, Adj R² = 0.199.



Black sea bass Recrutment and bottom temperature southern MAB





Figure 6. The relationship between the reanalysis product winter bottom temperature (du Pontavice et al. 2023) and log recruitment deviations (NEFSC 2021) across sub regions (Southern MAB: $R^2 = 0.173$, Adj $R^2 = 0.144$, F=6.06, df= 29, p-value= 0.019; Northern MAB $R^2 = 0.27$, Adj. $R^2 = 0.25$, F=11.18, df =29, p-value: 0.002).





Black sea bass Recrutment and bottom temperature Northern MAB



Figure 7. Convergent Cross Mapping (CCM) analysis of log recruitment deviations (NEFSC 2021) and bottom temperature in the northern and southern regions. In both cases, the predictability (Rho) of bottom temperature increases as the length (L) of the time series for recruits increases, suggesting that information from bottom temperature is present in the recruits time series for both regions.



Figure 8. The association between winter shelf water volume and the upper 95% confidence interval of center of gravity of black sea bass distribution in the spring in both the southern (r = -0.35 t = -2.80, df = 28, p-value = 0.007) and northern MAB regions (r=0.00, t = -0.014, df = 24, p-value = 0.98)





Upper 95% CI Center of gravity and Winter shelf water volume Northern MAB



Figure 9. The association between winter shelf water volume and effective area occupied by black sea bass in the spring. The correlation was statistically significant in the southern MAB (r = -0.365,t = -2.07,df = 28, P-value = 0.047), but not in the northern MAB (r = -0.333, t = -1.73,df = 24, P-value = 0.096).



Effective area occupied (km²) and Winter shelf water volume

Effective area occupied (km⁴2) and Winter shelf water volume Northern MAB



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