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First U.S. Commissioner
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Abstract—Deepwater fisheries have become increasingly important over the past couple of decades, yet challenges in adequately characterizing relative abundance and population demographics of deepwater stocks have persisted for fishery-independent surveys. Consequently, in stock assessments of the complex of deepwater snapper and grouper species along the Atlantic coast of the southeastern United States, fishery-dependent data have been relied on to track population trends, which may be biased by management actions and fishing behavior. In this study, we investigated the effects of increasing the sampling intensity and spatial scale of a historical deepwater fishery-independent survey on estimates of abundance and population demographics and aimed to identify important habitat associations for snowy grouper (*Hyporthodus niveatus*) and blueline tilefish (*Caulolatilus microps*). Increased sampling intensity and spatial expansion of the survey did not significantly affect estimates of abundance for either of these species, but model uncertainty was reduced for snowy grouper. Length compositions differed significantly for snowy grouper. Inclusion of significant covariates related to habitat association into indices of abundance did not affect estimates of abundance or uncertainty for snowy grouper but increased the magnitude of abundance and improved model fit for blueline tilefish. Identifying and incorporating habitat association information into stock assessments are critical for improving the management of data-limited deepwater species in the region.

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Habitat associations and effects of survey expansion on abundance indices and population demographics for 2 deepwater fish species off the Atlantic coast of the southeastern United States

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Deepwater fisheries have become increasingly important over the past couple decades because of their economic value and because they provide an alternate resource when shallow-water stocks are depleted or access to those stocks is restricted by management (Large et al., 2013). Deepwater stocks, however, are difficult to manage because many desirable species have great longevity, slow growth and maturation, and high discard mortality, making them susceptible to overexploitation with a slow rate of recovery from a depleted status (Clark, 2001; Roberts, 2002; Clarke et al., 2003). Deepwater stocks also are difficult to monitor, as the depths and distance from shore at which these species occur often make it cost-prohibitive to adequately collect samples during traditional fishery-independent surveys for life history analyses, estimation of population demographics, and development of relative abundance trends.

Several deepwater species of importance to both commercial and recreational fisheries along the Atlantic coast of the southeastern United States (SEUSA) are included in the Snapper-Grouper Fishery Management Plan of the South Atlantic Fishery Management Council (SAFMC, 2023). Like that for species targeted in many other deepwater fisheries, demand for these species has increased in recent years, making adequate data for stock assessments essential to sustainably manage the increased demand. For example, commercial landings of blueline tilefish (*Caulolatilus microps*) in this region were never greater than 117 metric tons (t) prior to 2008 but exceeded 130 t in 5 of the 6 years from 2008 to 2014 (commercial landings, National Marine Fisheries Service, available from website). Recreational landings of blueline tilefish in the region totaled approximately 30,000 fish between 1993 and 2005 but averaged 39,000 fish/year from 2006 to 2014 (recreational landings, National Marine Fisheries Service, available from website).

For the complex of deepwater snapper and grouper species that are managed together, fishery-independent sampling with short bottom longline (SBLL) gear along the shelf break and in adjacent areas in the SEUSA was historically conducted as part of the Marine Resources Monitoring, Assessment, and Prediction (MARMAP) program beginning in 1996 (Smart et al.[1]). Data from these sampling efforts have been used in several Southeast Data, Assessment, and Review stock assessments for the snowy grouper (*Hyporthodus niveatus*), blueline tilefish, and greater amberjack (*Seriola dumerili*) (SEDAR, 2013a, 2013b, 2017, 2020). Although the SBLL survey of the MARMAP program has proved useful for population demographics and life history analysis, the limited spatial scope of the survey and low sample sizes due to funding restrictions have raised concerns about its utility for indexing abundance. Consequently, in past stock assessments of the species in the deepwater snapper-grouper complex, fishery-dependent data have been relied on heavily to track population trends, rather than the fishery-independent data source of the MARMAP program's SBLL survey. Fishery-dependent indices of abundance, however, may be biased because they are a function of management actions (e.g., regulations) and fishing behavior (Hilborn and Walters, 1992).

Hard-bottom habitats vary in overall footprint, size, structure, and attached biota along the coast in the SEUSA, and industry observations noted during a deepwater survey workshop indicate that these habitat characteristics differ with depth as well as latitude (Carmichael et al., 2015). Furthermore, habitat selection for many fish species is density dependent (Marshall and Frank, 1995), where populations may constrict to preferred habitats when overexploited and expand into less-preferred habitats when population sizes are high. Therefore, identification of which habitats are used (whether as preferred or marginal) is required for effective monitoring. Habitat use by many of the species encountered in sampling of the SBLL survey of the MARMAP program varies widely, although most species in the deepwater snapper-grouper complex are obligate or commonly associated with hard-bottom habitats (Powles and Barans, 1980; Sedberry et al., 2001). For example, blueline tilefish occur on both high-relief hard bottom and low-relief boulder or cobble fields, as well as on areas of mud or sand sediment where they are known to construct burrows (Struhsaker, 1969; Ross and Huntsman, 1982; Harris et al., 2004). Snowy grouper are found primarily on rocky ledges and cliffs but also have been observed in association with burrows of blueline tilefish (Parker and Ross, 1986; Matheson and Huntsman, 1984; Jones et al., 1989). The SBLL gear can be used to sample both high- and low-relief types of habitat, but habitat characterization in conjunction with sampling is not part of the design of the SBLL survey of the MARMAP program, limiting the use of this survey for identifying preferred and marginal habitats.

Because of the data limitations described previously herein, determinations of stock status for deepwater species in the SEUSA are often characterized as highly uncertain. The Magnuson-Stevens Fishery Conservation and Management Act (Magnuson-Stevens . . .2024) specifies that increased scientific uncertainty in stock status determinations requires greater management buffers to manage or reduce the risk of overfishing. Although effective tools for conservation, greater buffers can result in lower catch limits for the fishing industry and a higher likelihood that those limits will be met each year and that the fishery will close early, reducing fishing opportunities and profit and potentially leaving behind fish that could have been sustainably caught.

In this study, we investigated the effects of increasing sampling intensity and spatial scale above those of the historical SBLL survey of the MARMAP program on indices of abundance, uncertainty, and population demographics for snowy grouper and blueline tilefish. Additionally, we strove to identify significant habitat associations for these 2 commercially and recreationally important species using a novel underwater video camera system. Identifying and incorporating habitat association information into stock assessments are critical for improving the management of data-limited deepwater species in the SEUSA.

Materials and methods

From May through October during 1996–2020, SBLL sampling as part of the MARMAP program occurred annually, either with dedicated trips or in conjunction with routine chevron-trap sampling of the MARMAP program. Sampling was opportunistic and stations were selected from a universe of known hard-bottom locations. During 2021 and 2022, from May through October, an expanded effort of SBLL sampling utilizing the existing gear and method was conducted aboard the R/Vs *Palmetto* and *Lady Lisa* along the Atlantic coast between North Carolina and Florida (Fig. 1). This expanded effort was funded through a Marine Fisheries Initiative (MARFIN) grant from the National Marine Fisheries Service to the South Carolina Department of Natural Resources, and it specifically was designed to leverage the historical stations created through the efforts of the MARMAP program, to increase the coverage of SBLL sampling over the sampling universe of that program, and to increase annual sampling intensity beyond the numbers achieved in previous years. For example, during SBLL survey efforts of the MARMAP program in 2013, 41 stations were sampled along the coasts of South Carolina and North Carolina, a relatively common level of effort throughout the historical time series (Fig. 1). In contrast, 108 stations were sampled during MARFIN SBLL efforts in 2021 from Florida to North Carolina (Fig.1).

Individual SBLLs were made up of a 25.6-m length of 6.4-mm-diameter double-braided polyester groundline with up to 13.6 kg of weight attached to the terminal end and about 9 kg of weight attached to the buoyed end (Fig. 2). Groundlines were connected to marked surface buoys with a depth-dependent length of 8.0-mm-diameter

[1] Smart, T. I., M. J. M. Reichert, J. C. Ballenger, W. J. Bubley, and D. M. Wyanski. 2015. Overview of sampling gears and standard protocols used by the Southeast Reef Fish Survey and its partners. Mar. Resour. Monit. Assess. Predict. program, MARMAP Tech. Rep. 2015-005, 14 p. Southeast Data Assess. Rev., SEDAR Workshop Ref. Doc. SEDAR53-RD04. [Available from website.]

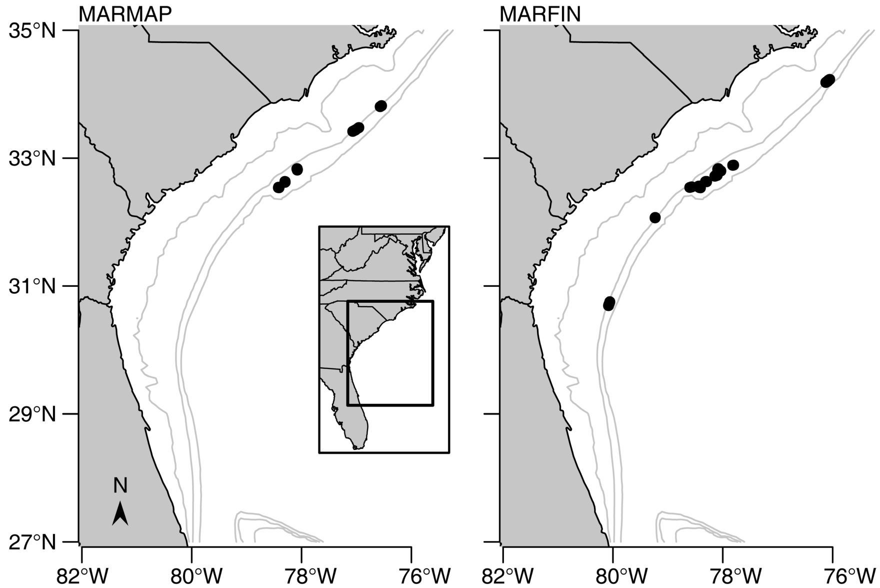

Figure 1

Maps of the average annual sampling efforts and spatial ranges of 2 surveys conducted off the Atlantic coast of the southeastern United States during which snowy grouper (*Hyporthodus niveatus*) and blueline tilefish (*Caulolatilus microps*) were caught in a representative year: Marine Resources Monitoring Assessment and Prediction (MARMAP) program short bottom longline (SBLL) deployments in 2013 (at 41 sampling stations) and Marine Fisheries Initiative (MARFIN) SBLL deployments in 2021 (at 108 stations). Black circles indicate locations of individual SBLL deployments. The gray lines indicate the 25-m, 100-m, and 300-m depth contours.

twisted polypropylene rope. Spaced evenly 1.2 m apart along the groundline were 20 gangions, consisting of a 6/0 swiveled longline snap crimped to a 0.5-m length of 1.5-mm-diameter clear monofilament (90-kg test) and a 14/0 circle hook (O. Mustad and Son AS[2], Gjøvik, Norway) baited with whole squid (*Illex* sp.). Up to 6 SBLLs were deployed in sequence from the stern of the research vessel while underway and fished concurrently, with each deployment being at least 200 m apart from any other deployment to reduce interactions among concurrently fished gear. After soaking for a target duration of 90 min during daylight hours only, SBLLs were retrieved by using a hydraulic pot hauler in the order they were deployed.

Bottom habitat type and system type at stations were characterized by collecting and analyzing 2 types of data: video footage and bathymetric data. Habitat information was collected by using a camera system designed at the South Carolina Department of Natural Resources and referred to as a *deepwater camera castle* (DCC). The DCC consisted of 3 unidirectional video cameras (GitUp, Git2, or Git2P, GitUp Ltd., Shenzhen, China, or HERO4, GoPro Inc., San Mateo, CA; capable of recording video in a resolution of 1080p at 30 fps) accompanied by underwater lights (GoBe 1000 Wide FC, Light and Motion, Marina, CA), all in deepwater housings (GPH-1750 or Benthic 2, Group B Distribution Inc., Ferndale, MI, or Golem deep housing with extended back, Golem Gear Inc., Brooksville, FL), and a temperature logger (Vemco Minilog II-T, InnovaSea Systems Inc., Boston, MA, or HOBO TidbiT v2, LI-COR Environmental, Bourne, MA) and mounted in a pyramidal steel cage (Fig. 2). Cameras and light groupings were in fixed positions, with 2 horizontally oriented cameras facing opposite directions and the third camera oriented for a nadir view. To help maintain the field-of-view orientation, a subsurface 100-mm float (Rosendahl and Co., Bergen, Norway) was secured to the top interior of the cage frame, and weights were attached at the base. During deployment, the DCC remained tethered to the ship. All DCC deployments followed the retrieval of SBLLs at each sampling station, to avoid lights affecting fish behavior.

At each sampling location, biota density, biota height, consolidated substrate, substrate size, and substrate relief were estimated on the basis of averaged values from analysis of video footage from all cameras on the DCC (Table 1). Habitat features recorded were within an estimated visibility range of approximately 5 m from the DCC; however, the line of sight varied depending on several factors, including ambient overhead light, turbidity,

[2] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

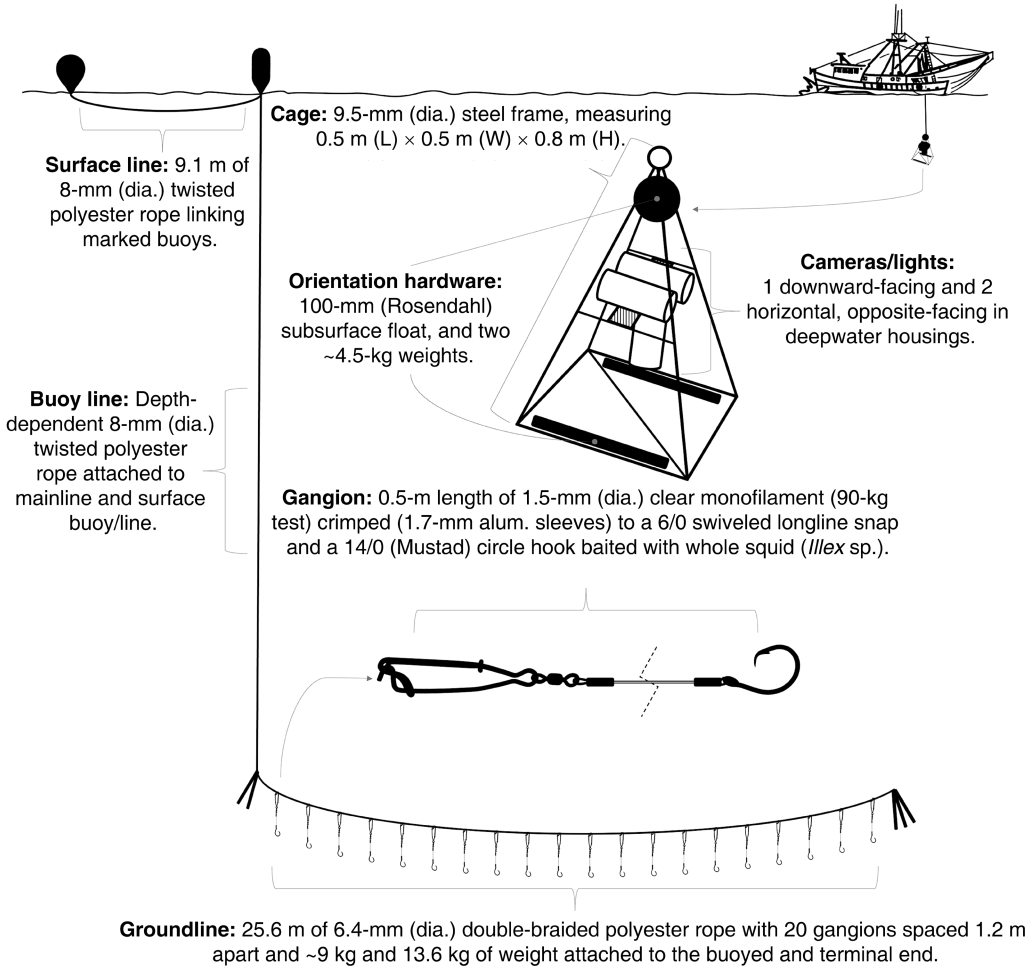

Figure 2

Schematic of short bottom longline (SBLL) gear used in fishery-independent sampling of deepwater fish stocks during 1996–2022 along the Atlantic coast of the southeastern United States and the deepwater camera castle deployed with SBLLs to collect information for habitat characterization. The fishing gear and the underwater video camera system were used in surveys conducted as part of the Marine Resources Monitoring Assessment and Prediction program and the Marine Fisheries Initiative. dia.=diameter; alum.=aluminum.

and obstruction from nearby structures. In addition, the structure at each sampling station was characterized as a system type (Table 1) by using bathymetric data collected with sonar equipment (DFF1-UHD [50/200 kHz] or FCV-295 [88/150 kHz], Furuno Electric Co., Ltd., Nishinomiya, Japan) from the ship's bridge (a transducer [Airmar IDT800-N2000 (235 kHz), Airmar Technology Corp., Milford, NH] was mounted on the hull of each ship). Maximum feature height for each station also was assigned by using sonar from the ship's bridge.

Several metrics routinely used in stock assessments were calculated for 2 scenarios: 1) the time series from SBLL sampling of the MARMAP program was used, except that data for 2021 and 2022 did not include expanded effort and spatial coverage to create a scenario in which sampling had continued at the typical levels of effort and coverage through 2022 and 2) the full time series was used for a scenario that included the increased effort and spatial coverage through 2022 supported as part of MARFIN. These metrics included encounter rate (proportion positive) for each species, standardized indices of abundance, and length and age compositions. Encounter rates were calculated as the number of SBLL deployments during which a species of interest was caught divided by the total number of SBLL deployments per year. For abundance indices, a zero-inflated negative binomial model for each species was constructed with included covariates and error distribution (negative binomial, Poission, or zero-inflated

Table 1

Metrics used to characterize habitat and system type on the basis of analysis of video footage from a deepwater camera castle, an underwater video camera system, or analysis of data from sonar equipment for surveys of the Marine Resources Monitoring Assessment and Prediction program in 1996–2020 and the Marine Fisheries Initiative in 2021–2022 off the Atlantic coast of the southeastern United States.

Metric	Description
Habitat characterization	
Biota density (%)	Estimate percentage
Biota height	Low: none; medium: maximum height of 0–0.5 m; and high: maximum height >0.5 m
Consolidated substrate (%)	Estimate percentage
Substrate size	Low: no consolidated sediment; medium: ≥50% of consolidated sediment ≤1.0 m in diameter; and high: ≥50% of consolidated sediment >1.0 m in diameter
Substrate relief	Low: maximum relief <0.3 m; medium: maximum relief of 0.3–1.0 m; and high: maximum relief >1.0 m
Characterization of system type	
Slope	No distinct feature, gradual change in depth
Roll	Extended low-relief, diffuse feature (hill)
Hump	Small, isolated feature
Single ledge	1 distinct ledge
Double ledge	2 distinct but closely related ledges or steps
Triple ledge	3 or more distinct but closely related ledges or steps

negative binomial and Poisson) selected according to Akaike information criterion (AIC; Akaike, 1973) by using the FishyR package (vers. 0.0.0.9001; Ballenger, 2022) in statistical software R, vers. 4.3.1 (R Core Team, 2023; Vecchio et al., 2023). Zero-inflated negative binomial models are often used for indices of abundance because of their ability to compensate for excessive zeros commonly observed in ecological count datasets (Zuur et al., 2009). *Abundance* (i.e., number of fish per species per SBLL) was used as a response variable and *year*, *temperature*, *depth*, and *latitude*, were predictor variables with *soak time* (i.e., effort) as an offset. *Longitude* was not included in the model used for abundance indices because of high correlation with *depth*. Variance inflation factor was calculated to test for multicollinearity among potential variables of the model for abundance indices, and none was found for the included covariates.

Ages were determined from otoliths for snowy grouper (SEDAR, 2013b; Wyanski et al.[3]) and blueline tilefish (SEDAR, 2013a; Spanik and Ballenger, 2023), and all fish were measured for length following capture. Length and age proportions were then calculated as the number of fish per species per 1-cm bin for total length (TL) or 1-year age bin per the total number of fish caught per species per year. Length and age compositions were compared between the 2 sampling scenarios, with and without the expanded MARFIN effort and coverage, by using Kolmogorov–Smirnov tests, and these comparisons were limited to 2021 and 2022 to negate any potential age or length truncation effects over the long time series.

Habitat association was investigated by using generalized additive models for each species with data from all gear deployments in sampling of both the MARMAP program and MARFIN for which habitat and structure were observed. We assumed that habitat and system type would be consistent over the time series for any given sampling station because of the likely low frequency of disturbance near the shelf edge. Model structures evaluated included Gaussian, negative binomial, and gamma, and negative binomial was selected on the basis of which model had the lowest AIC value. Smooth covariate effects modeled on *abundance* were *depth*, *latitude*, *bottom temperature*, *substrate size*, *biota height* (categorical), *system type*, *feature height* (continuous), *biota density*, and *consolidated substrate* (continuous). Factorial covariate effects modeled on *abundance* were *substrate size*, *biota height*, and *system type*. Variance inflation factor was calculated to test for multicollinearity among variables and did not indicate any strong correlations. All analyses were completed by using R and the R package mgcv (vers. 1.9-1; Wood, 2011, 2017).

On the basis of the habitat association analyses, new habitat indices of abundance were developed to include habitat covariates that were found to have a significant effect on *abundance*, in addition to the covariates used in the standardized index calculation. Habitat covariates were retroactively assigned to all SBLL sampling stations in the full time series that were previously sampled and characterized for habitat in this study, assuming that habitat at those stations had not changed over time. The resulting dataset including habitat covariates contained fewer records than the dataset used for the standardized abundance indices. Therefore, a new standardized abundance index was calculated with the same smaller dataset without habitat covariates, for comparison with the habitat abundance indices to eliminate any differences due to sample size.

Co-occurrence among snowy grouper and blueline tilefish in this study was evaluated by calculating the percentage of SBLL deployments that captured both species at each sampling location, excluding zero catches for both

[3] Wyanski, D. M., M. J. Reichert, J. C. Potts, D. B. White, and P. P. Mikell. 2013. Report on age determination workshops for snowy grouper, *Hyporthodus niveatus*, March 2009 and October 2012. Southeast Data Assess. Rev., SEDAR Work. Paper SEDAR36-WP09, 13 p. [Available from website.]

species from the full MARFIN dataset. Additionally, the Morisita–Horn index was calculated by using abundance (count) for both species at each sampling location as the response variable (Wolda, 1981). The Morisita–Horn index ranges from 0 to 1, with a value of 0 signifying no overlap in habitat and a value of 1 signifying complete overlap in habitat (Zaret and Rand, 1971).

Results

Annual SBLL survey effort of the MARMAP program from 1996 through 2020 ranged from 15 to 117 stations (mean: 48 stations) sampled at depths from 45 to 227 m, and annual MARFIN SBLL effort in 2021 and 2022 ranged from 108 to 163 stations (mean: 135 stations) sampled at depths from 85 to 219 m (Suppl. Table). A total of 113 new sampling stations either recommended by industry partners or located by reconnaissance were confirmed as having appropriate habitat type and depth for the survey. The addition of these new stations expanded the overall sampling universe from 216 to 329 available stations and resulted in a notable latitudinal range extension of the sampling universe in the study area from the southernmost station at 32°6′N to 29°0′N (Fig. 1). Of these 329 stations in the updated sampling universe, 210 stations were characterized for system type (64%), 188 stations were characterized for bottom habitat type (57%), and 184 stations were characterized for both (56%), greatly improving our ability to examine habitat associations for snowy grouper and blueline tilefish.

Increased sampling effort did not significantly affect the standardized indices of abundance for either snowy grouper or blueline tilefish, as evidenced by the overlap of 95% confidence intervals in most years of the abundance indices for the 2 sampling scenarios (Fig. 3). Standard errors associated with the standardized abundance indices were significantly lower with the level of sampling intensity of MARFIN relative to that of the MARMAP program for snowy grouper (P<0.001) but not for blueline tilefish (P=0.7).

By expanding sampling effort from the level of the MARMAP program to that of MARFIN, the average annual catch of snowy grouper increased from 43 to 135 fish and the average annual catch of blueline tilefish increased from 7 to 28 fish. Overall encounter rates increased from 42% to 53% for snowy grouper and from 12% to 28% for blueline tilefish. For snowy grouper, length compositions differed significantly between sampling of the MARMAP program (range: 44–94 cm TL, mean: 63 cm TL, sample size [n]=92) and that of MARFIN (range: 33–107 cm TL, mean: 62 cm TL, n=263) (P=0.006), but age compositions did not differ between MARMAP program (range: 2–14 years, mean: 6 years, n=92) and MARFIN (range: 1–25 years, mean: 7 years, n=263) sampling (P=0.6). For blueline tilefish, length compositions did not differ between sampling of the

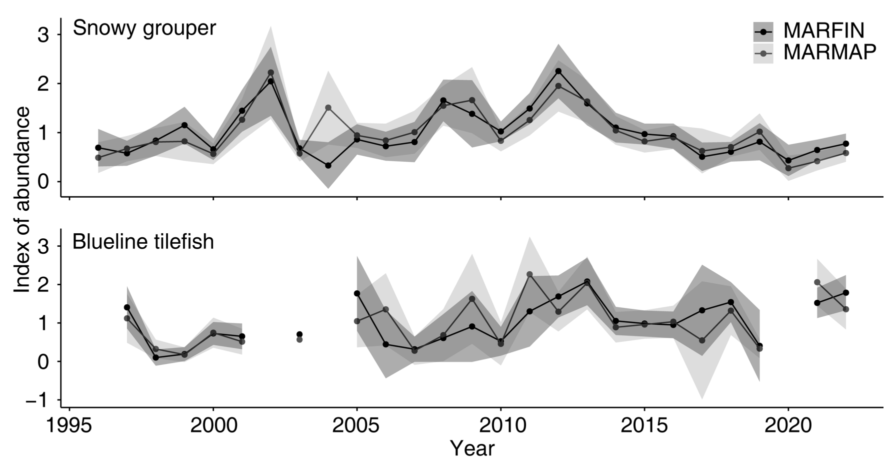

Figure 3

Indices of abundance for snowy grouper (*Hyporthodus niveatus*) and blueline tilefish (*Caulolatilus microps*) in 2 scenarios for sampling off the Atlantic coast of the southeastern United States during 1996–2022: a time series from surveys of the Marine Resources Monitoring Assessment and Prediction (MARMAP) program was used, without expanded survey effort and spatial coverage for 2021 and 2022, or the full time series that included the increased effort and coverage supported as part of the Marine Fisheries Initiative (MARFIN) was used. Index values were not calculated for blueline tilefish for 1996, 2002, 2004, or 2020 because that species was not captured on short bottom longline gear in those years. To calculate the indices for each species, a zero-inflated negative binomial model was constructed. The shaded areas represent 95% confidence intervals.

MARMAP program (range: 48–78 cm TL, mean: 61 cm TL, n=51) and that of MARFIN (range: 47–78 cm TL, mean: 61 cm TL, n=102) (P=0.4), and age compositions did not differ between MARMAP program (range: 3–25 years, mean: 9 years, n=51) and MARFIN (range: 3–25 years, mean: 8 years, n=102) sampling (P=0.8).

Habitat characteristics were not significantly related to abundance of snowy grouper, although sampling and water column characteristics were (Fig. 4). Significant continuous covariates in the generalized additive model were *depth* (P<0.001), *latitude* (P<0.001), and *temperature* (P<0.001), which have historically been included in calculation of indices of abundance and were collected throughout the time series. Optimal depth for snowy grouper was approximately 160 m. Peaks in abundance of snowy grouper in the survey region were observed around the latitudes 31°0′N and 33°30′N. A negative effect on abundance of snowy grouper was observed with bottom temperatures exceeding approximately 15°C. There were no statistically significant factorial covariate effects on abundance of snowy grouper; however, a positive trend with *biota height* was observed. Additionally, the effect on abundance of snowy grouper gradually trended more positively with increasing system type complexity (e.g., multiple closely related ledges). On the basis of these findings, we did not create a habitat abundance index for snowy grouper using additional bottom habitat covariates.

In contrast, habitat characteristics were significantly related to abundance of blueline tilefish (Fig. 5). The significant continuous habitat covariates were *depth* (P<0.001), *biota density* (P=0.006), and *consolidated substrate* (P<0.001). The optimal depth for blueline tilefish was approximately 190 m. Abundance was proportional to biota density and disproportional to consolidated substrate coverage. Although not statistically significant, a positive trend between temperature and abundance of blueline tilefish was observed when bottom temperatures exceeded approximately 17.5°C, and a negative trend was

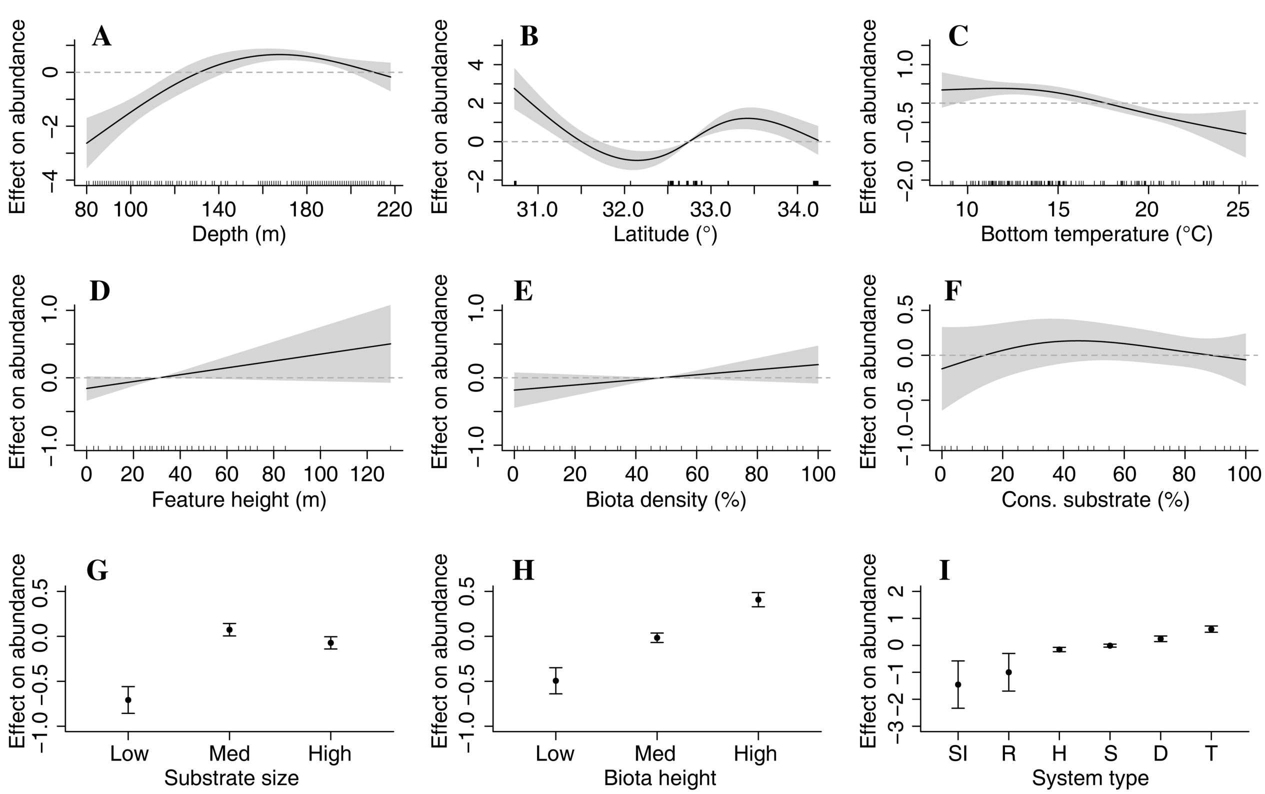

Figure 4

Results from habitat association modeling for (**A–F**) smooth and (**G–I**) factorial covariate effects on abundance of snowy grouper (*Hyporthodus niveatus*) caught during 1996–2022 off the Atlantic coast of the southeastern United States. The relationships of *abundance* with *depth*, *latitude*, and *bottom temperature* are statistically significant. *Substrate size* is categorized as low (no consolidated sediment), medium (≥50% of consolidated sediment ≤1.0 m in diameter), or high (≥50% of consolidated sediment >1.0 m in diameter). *Biota height* is classified as low (none), medium (maximum height of 0–0.5 m), or high (maximum height >0.5 m). The system types are slope (Sl), roll (R), hump (H), single ledge (S), double ledge (D), and triple ledge (T). The shaded areas represent 95% confidence intervals, and the error bars represent standard errors. In panels A–F, the gray dashed line separates where the effect of the covariate on abundance is positive or negative. Cons.=consolidated; Med=medium.

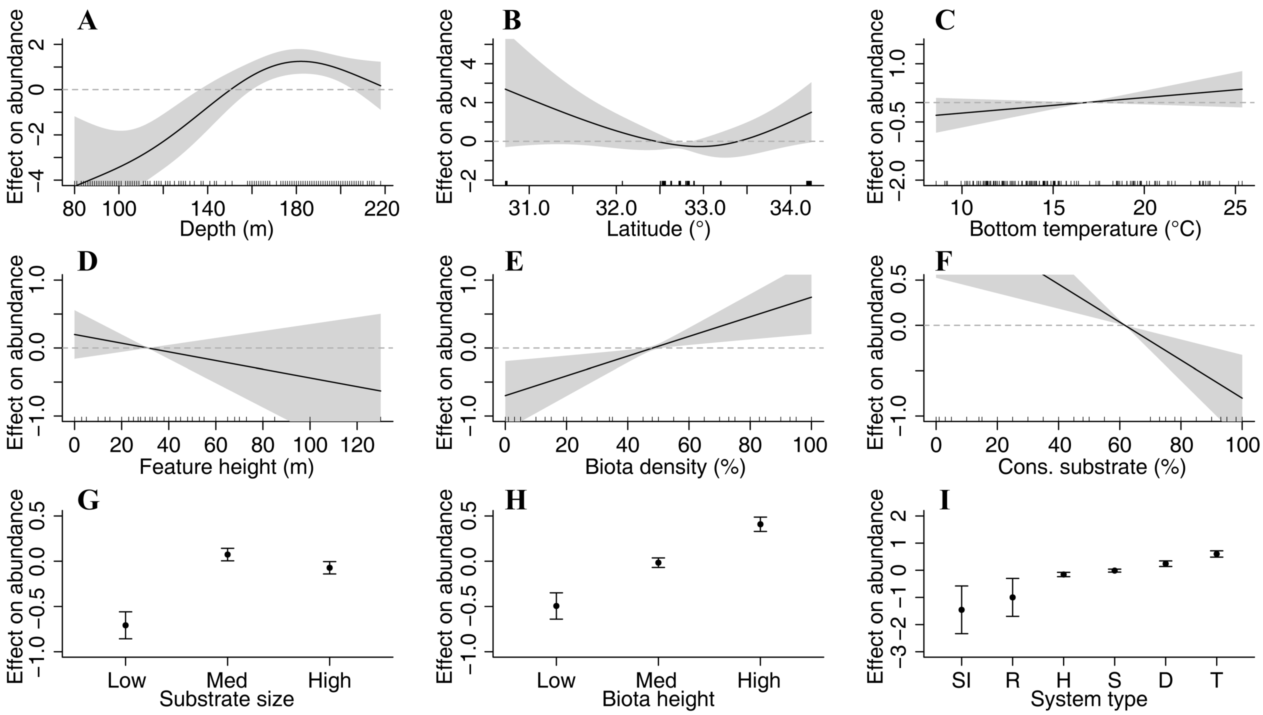

Figure 5

Results from habitat association modeling for (**A–F**) smooth and (**G–I**) factorial covariate effects on abundance of blueline tilefish (*Caulolatilus microps*) caught during 1996–2022 off the Atlantic coast of the southeastern United States. The relationships of *abundance* with *depth*, *biota density*, and *consolidated substrate* are statistically significant. *Substrate size* is categorized as low (no consolidated sediment), medium (≥50% of consolidated sediment ≤1.0 m in diameter), or high (≥50% of consolidated sediment >1.0 m in diameter). *Biota height* is classified as low (none), medium (maximum height of 0–0.5 m), or high (maximum height >0.5 m). The system types are slope (Sl), roll (R), hump (H), single ledge (S), double ledge (D), and triple ledge (T). The shaded areas represent 95% confidence intervals, and the error bars represent standard errors. In panels A–F, the gray dashed line separates where the effect of the covariate on abundance is positive or negative. Cons.=consolidated; Med=medium.

observed when bottom temperatures were below around 17.5°C. There were no statistically significant factorial habitat covariate effects on abundance of blueline tilefish; however, a positive trend between *abundance* and *biota height* was observed. On the basis of these findings, we developed a new habitat index of abundance for blueline tilefish using the sampling covariates included in the standardized index, as well as *biota density* and *consolidated substrate*. Including these significant habitat covariates for blueline tilefish greatly improved model fit, with AIC values decreasing from 1185.5 to 688.5. Moreover, incorporating these habitat covariates resulted in increased abundance estimates for 10 of 23 years throughout the time series (Fig. 6).

Both snowy grouper and blueline tilefish were captured simultaneously in 21% of the SBLL deployments during which either species was successfully captured. The Morisita–Horn index value was 0.3 for the evaluation of the co-occurrence of snowy grouper and blueline tilefish, indicating that these species did not significantly co-occur within microhabitats of the region sampled in this study. The low co-occurrence and Morisita–Horn index value support the differences observed in the habitat associations of snowy grouper and blueline tilefish.

Discussion

Increased intensity and spatial expansion of SBLL sampling resulted in an increase in total catch and encounter rate for both snowy grouper and blueline tilefish. Increased catch provides more biological samples to better describe life history and population demographics, and increased proportion positive reduces variability and uncertainty in abundance estimates. Survey expansion did not significantly affect the magnitude of the abundance indices for either snowy grouper or blueline tilefish despite the higher catch numbers and proportion positive for both species. It is likely that either the historical SBLL survey of the MARMAP program was already sampling within the core distributions of both snowy grouper and blueline tilefish or a more densely populated area was not encountered with the expansion of MARFIN sampling beyond that of the MARMAP program. In contrast, for another

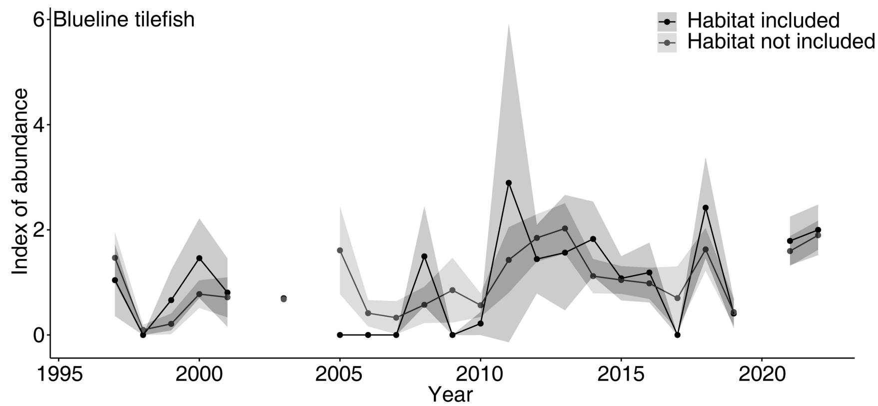

Figure 6

Indices of abundance for blueline tilefish (*Caulolatilus microps*) caught off the Atlantic coast of the southeastern United States during 1997–2001, 2003, 2005–2019, and 2021–2022, calculated with and without habitat covariates that had a statistically significant effect on abundance. Index values were not determined for 1996, 2002, 2004, or 2020 because no blueline tilefish were captured during sampling in those years. In some of the zero-inflated negative binomial models used to develop indices, the covariates *depth*, *latitude*, and *bottom temperature* were used because of their significant effects on abundance of this species. The shaded areas represent 95% confidence intervals.

fishery-independent survey in a similar geographic region, the sampling with chevron traps from North Carolina to Florida as part of the Southeast Reef Fish Survey, increased sampling effort and spatial expansion did affect abundance estimates for one of its commonly encountered species, the red snapper (*Lutjanus campechanus*) (Vecchio et al., 2023). The likely explanation for the net positive effects on the relative abundance index for red snapper was that the survey expansion increased the density of coverage in an area of core abundance for that species that was previously insufficiently sampled.

Survey expansion in our study did reduce the standard error around the standardized indices of abundance for snowy grouper but not the indices for blueline tilefish. Snowy grouper are known to orient over relatively small and isolated features, such as shipwrecks, artificial reefs, and rocky outcrops (Epperly and Dodrill, 1995; Paxton et al., 2021). Although both snowy grouper and blueline tilefish have what are considered small home ranges and high site fidelity, observed feeding habits of blueline tilefish indicate that they may occupy a more diverse array of substrates (Ross, 1982). In general, blueline tilefish may inhabit different microhabitats within the range of the SBLL sampling universe that include lower relief and more mixed substrates than the microhabitats sampled for snowy grouper, as indicated by the low habitat overlap between the 2 species. Increased sampling intensity and the inclusion of additional sampling locations may have increased the encounter rates at the more isolated habitats preferred by snowy grouper, and the increased proportion positive likely contributed to the reduction in model variability. Alternately, the diversity of habitats utilized by blueline tilefish may indicate that SBLL sampling and habitat characterization remained insufficient to improve model fit and reduce standard error. Including more sampling locations over a more diverse set of habitat types may also improve estimates of abundance for blueline tilefish because the SBLL sampling stations were initially chosen in an attempt to sample high-relief hard-bottom habitats and may not adequately overlap with the preferred habitat of blueline tilefish.

Length compositions varied significantly between the 2 sampling scenarios for snowy grouper, with a broader size range for fish collected during MARFIN efforts relative to that for fish collected in the efforts of the MARMAP program. Sampling the full range of sizes in a population is critical to understanding maturity schedules, fecundity, and the size and age at transition for protogynous hermaphrodites such as the snowy grouper. Although the snowy grouper collected in the MARFIN efforts were older than those caught in the MARMAP program efforts, this difference in age composition was not significant, potentially because of variability in the size-at-age relationship for this species (SEDAR, 2013b). Sampling the oldest individuals in the population is important for growth modeling and can affect estimates of natural mortality; therefore, even without a significant effect of sampling scenario, the MARFIN efforts represent an improvement in data availability for snowy grouper. Neither length nor age compositions for blueline tilefish differed significantly between the 2 scenarios, with length and age ranges between the 2 nearly identical. This similarity between the scenarios may be the result of the SBLL sampling universe not sufficiently covering all habitats utilized by blueline tilefish as mentioned in the previous paragraph. In many species in the study region, older, larger individuals tend to be found in deeper waters than younger, smaller individuals (Saul et al., 2012; Vecchio and Peebles, 2022), and larger or faster-growing individuals might be more likely to occupy preferred habitats than smaller or slower-growing individuals (Morris, 2003; Valvanis et al., 2008; Bartolino et al., 2011).

No significant associations of bottom habitat have been detected for snowy grouper by using camera deployments in the most recent sampling efforts. Paxton et al. (2021) reported that aggregations of snowy grouper were found at reefs with small spatial footprints surrounded by large areas of unconsolidated substrate in their study. The SBLL sampling of the MARMAP program was initially developed primarily to provide data for snowy grouper, and as such, the universe of sampling stations was targeted at bottom types thought to likely host this species (i.e., high-relief hard bottom). Because of this bias in the sampling universe, we may not be sampling a wide enough gradient of habitat types or may be lacking sufficient marginal habitats to observe habitat preferences for snowy grouper. Zero catches for snowy grouper may have been structural zeroes (i.e., zeroes outside of where snowy grouper could occur) or the result of the gear missing the targeted habitat because of the high likelihood of small habitat footprints, rather than the result of sampling marginal or unpreferred habitat that would have been useful in characterizing habitat associations (Gaston et al., 2000; Zuur et al., 2009; Paxton et al., 2021).

The habitat covariates that had a significant effect on abundance for blueline tilefish were *biota density* and *consolidated substrate*. Areas containing higher biota densities likely provide appropriate habitat for a wide range of benthic macroinvertebrates that are known to be dominant prey within the diverse diets of blueline tilefish (Ross, 1982; Bielsa and Labisky, 1987). In addition, *consolidated substrate* had a negative relationship with abundance of blueline tilefish. Able et al. (1987) reported that blueline tilefish build burrows for predator avoidance; therefore, it makes intuitive sense that abundance would be lower in areas of more consolidated substrate where burrows could not be constructed. Able et al. (1987) did observe a rare instance where blueline tilefish utilized a hole under a rock ledge and boulders to avoid predators, but they noted the difficulty fish had entering the hole and interactions fish had with individuals of other tilefish species competing for the space. Habitat data were pooled across the survey range for analysis; however, preferred habitat may differ geographically (Carmichael et al., 2015). Further habitat characterization and data analysis on a finer geographic scale may be warranted but was not feasible, given the sample size and incomplete sampling range throughout the entire region in our study. This limitation also may explain why the effect of *latitude* on *abundance* was not consistent across the survey range.

The inclusion of significant habitat association covariates into the habitat abundance indices for blueline tilefish had a positive effect on the magnitude of abundance in many years of the time series and greatly improved model fit according to AIC values. Thompson et al. (2022) also found that including habitat variables from cameras resulted in a decrease in AIC in their abundance models for other reef-associated species. The improvement in model fit for blueline tilefish when habitat characteristics were used may be attributable to an interaction between the diverse habitats occupied by this species and the increased ability to incorporate a previously unaccounted for source of variability. Improving uncertainty in stock assessments is a constant endeavor in fisheries science and can have implications for reducing management buffers, which may increase fishery yields.

Assessing deepwater habitats while simultaneously sampling fish presents unique challenges. For example, using underwater video camera systems in conjunction with baited fishing gear to determine habitat type has the potential to attract fish from nearby areas because they are drawn to the bait. The habitat characterized through analysis of video footage from the camera systems, therefore, may not reflect the actual habitat of the fish collected. Fish can detect bait from several hundred meters away (Løkkeborg et al., 2014); however, the chemical stimulus from bait must persist for long periods of time for fish to find the bait associated with a chemosensory plume. For example, Atlantic cod (*Gadus morhua*) can take 7 h to locate bait from a distance of 700 m (Løkkeborg, 1998). In our study, because the soak time was only 90 min, it seems likely that the habitat observations from the locations at which fish were captured are representative of natural habitat utilization, rather than indicative of a cumulative effect of being attracted by bait.

Another challenge is that limited visibility in deep waters necessitates the use of lights on underwater video gear, introducing another potential way that fish behavior can be affected (either attracting or repelling them) and ultimately impacting catchability. We separated the habitat cameras from the fish sampling gear in our study to prevent light from affecting catchability. Recognized limitations of the DCCs include 1) the field of view of only approximately 5 m directly in front of the camera or cameras allowed by the light sources and 2) the stationary nature of the gear. The cameras occasionally landed directly in front of a high-relief substrate, further limiting field of view in one direction. Although separating the cameras from the SBLL ensured that we maintained the SBLL time series, the limited field of view precluded the ability to characterize the bottom features along the entire length of the SBLL (25 m) and at the full range of available habitats in the greater vicinity where fish were captured.

The likelihood of damage from barotrauma for fish increases with depth of capture, resulting in higher mortality rates (Drumhiller et al., 2014; Bohaboy et al., 2020). Seasonal closures of commercial and recreational fisheries for both species examined in our study can be asynchronous in the SEUSA, meaning that targeting one species could result in mortalities of fish of the other species that were discarded because of regulations. Although both snowy grouper and blueline tilefish are found along the shelf edge in the SEUSA, values for 2 metrics in our study indicate that they inhabit different areas or microhabitats within their broad range: the low value of the Morisita–Horn index and the inconsistency in important habitat association covariates between the 2 species.

Results from our habitat association modeling indicate that blueline tilefish may utilize deeper waters, warmer waters, and areas of lower consolidated substrate (i.e., less hard) than snowy grouper. This lack of overlap in habitat utilization may alleviate concerns about bycatch in commercial and recreational fishing efforts targeting one species while the fishery for the other is closed for take. Ross (1982) found a wide diversity in the types of substrate occupied by blueline tilefish, although he postulated that individuals in the region could be restricted to a relatively narrow belt of warm water in the Florida Current. The lack of habitat overlap between the 2 species observed in our study may be due to thermal preferences, as the effect of bottom temperature on abundance had an inverse relationship beginning at a temperature of around 15°C for abundance of snowy grouper but abundance of blueline tilefish was positively related with temperature. However, the suggestion that blueline tilefish may prefer waters warmer than the temperatures preferred by snowy grouper is interesting considering the more northerly distribution of the blueline tilefish relative to that of the snowy grouper. Future research could investigate latitudinal variability in habitat and distinguish between identifying a potential range of suitable habitats versus identifying truly preferred habitats, but such work would likely require significantly higher sample sizes and a wider survey area than were achievable in this study.

The low level of co-occurrence between snowy grouper and blueline tilefish captured by using SBLL gear in our study is inconsistent with the high probability of co-occurrence of the 2 species estimated by Cao et al. (2024), who analyzed video footage from paired-chevron-trap sampling of the Southeast Reef Fish Survey in the same region. This contrast in results could reflect differences in selectivity between the sampling gears, an effect of deploying cameras in conjunction with bait versus deploying cameras independently, or it may be related to differences in geographic area and habitat sampled. The region surveyed in our study encompassed a more limited geographic area and deeper depths that may not be equivalent to the larger but shallower region examined by Cao at al. (2024). Furthermore, SBLL gear was frequently deployed in high-relief hard-bottom habitats, a type of habitat not typically sampled with the chevron-trap gear of the Southeast Reef Fish Survey.

Conclusions

In our study, increasing sampling intensity and expanding spatial distribution had little effect on the magnitude of relative abundance estimates for snowy grouper and blueline tilefish but did result in lower standard errors of the estimates, especially for snowy grouper. Increasing sampling intensity also affected observed length compositions for snowy grouper. We were able to use a novel underwater video camera system to characterize habitat and provide habitat association information for these 2 data-limited, commercially and recreationally valuable deepwater species. We found that incorporating habitat data can significantly improve both the magnitudes and the standard errors of indices of abundance in support of stock assessments for blueline tilefish. The use of habitat characterization in combination with catch data remains necessary because habitat type and utilization can vary widely in the SEUSA. Visual habitat information paired with high-resolution bottom mapping throughout the entirety of the region would be of high value to future management efforts, by further characterizing habitat distribution and utilization of species along the shelf edge in the region and by eliminating the limitations acknowledged here of low sample size and the constrained field of view of lighted drop-camera systems. Results from this study indicate that intensification of sampling and incorporation of habitat characterization and habitat association information can reduce uncertainty in stock assessments and may contribute to improving the subsequent management of deepwater species in the SEUSA.

Resumen

En interés en las pesquerías de aguas profundas ha crecido en importancia en las dos últimas décadas, aunque aun existen retos para caracterizar adecuadamente la abundancia relativa y la demografía de las poblaciones de profundidad en prospecciones independientes de la pesquería. Por consiguiente, en las evaluaciones de las poblaciones del complejo de especies de pargos y meros de aguas profundas de la costa atlántica del sureste de Estados Unidos, se ha confiado en datos de las pesquerías para seguir las tendencias de la población, las cuales pudieran estar sesgadas por las acciones de manejo y el comportamiento pesquero. En este estudio investigamos los efectos de aumentar la intensidad del muestreo y la escala espacial de una prospección histórica independiente de la pesquería de profundidad sobre las estimaciones de abundancia y la demografía de la población, y nos propusimos identificar asociaciones de hábitat importantes para la cherna pintada (*Hyporthodus niveatus*) y el blanquillo lucio (*Caulolatilus microps*). El aumento de la intensidad del muestreo y la ampliación espacial del estudio no afectaron significativamente a las estimaciones de abundancia de ninguna de estas especies, pero la incertidumbre del modelo se redujo en el caso de la cherna pintada. Las composiciones de tallas difirieron significativamente para la cherna pintada. La inclusión de covariables significativas relacionadas con la asociación de hábitats en los índices de abundancia no afectó a las estimaciones de abundancia ni a la incertidumbre para la cherna pintada, pero aumentó la magnitud de la abundancia y mejoró el ajuste del modelo para el blanquillo lucio. La

identificación e incorporación de información sobre asociaciones de hábitat en las evaluaciones stock es fundamental para mejorar el manejo regional de las especies de profundidad con datos limitados.

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