BioOne COMPLETE

Diel Variations in Survey Catch Rates and Survey Catchability of Spiny Dogfish and their Pelagic Prey in the Northeast U.S. Continental Shelf Large Marine Ecosystem

Authors: Sagarese, Skyler R., Frisk, Michael G., and Cerrato, Robert M.

Source: Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science, 8(8) : 244-262

Published By: American Fisheries Society

URL: https://doi.org/10.1080/19425120.2015.1135219

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 8:244–262, 2016
Published with license by the American Fisheries Society
ISSN: 1942-5120 online
DOI: 10.1080/19425120.2015.1135219

ARTICLE

Diel Variations in Survey Catch Rates and Survey Catchability of Spiny Dogfish and their Pelagic Prey in the Northeast U.S. Continental Shelf Large Marine Ecosystem

Skyler R. Sagarese,*[1] Michael G. Frisk, and Robert M. Cerrato
School of Marine and Atmospheric Sciences, Stony Brook University, Stony Brook, New York 11794, USA

Kathy A. Sosebee
Northeast Fisheries Science Center, National Marine Fisheries Service, 166 Water Street, Woods Hole, Massachusetts 02543, USA

John A. Musick
Virginia Institute of Marine Science, Post Office Box 1346, Gloucester Point, Virginia 23062, USA

Paul J. Rago
Northeast Fisheries Science Center, National Marine Fisheries Service, 166 Water Street, Woods Hole, Massachusetts 02543, USA

Abstract

This study examines the potential uncertainty in survey biomass estimates of Spiny Dogfish *Squalus acanthias* in the Northeast U.S. Continental Shelf Large Marine Ecosystem (NES LME). Diel catch-per-unit-effort (CPUE) estimates are examined from the Northeast Fisheries Science Center bottom trawl surveys conducted during autumn (1963–2009) and spring (1968–2009). Influential environmental variables on survey catchability are identified for Spiny Dogfish life history stages and five pelagic prey species: Butterfish *Peprilus triacanthus*, Atlantic Herring *Clupea harengus*, shortfin squid *Illex* spp., longfin squid *Doryteuthis* spp., and Atlantic Mackerel *Scomber scombrus*. Daytime survey catchability was significantly higher than nighttime catchability for most species during autumn and for mature male Spiny Dogfish, shortfin squid, and longfin squid during spring in the NES LME. For most stages and species examined, breakpoint analyses identified significant increases in CPUE in the morning, peak CPUE during the day, and significant declines in CPUE in the late afternoon. Seasonal probabilities of daytime catch were largely driven by solar zenith angle for most species, with stronger trends identified during autumn. Unadjusted CPUE estimates appear to overestimate absolute abundance, with adjustments resulting in reductions in absolute abundance ranging from 41% for Spiny Dogfish to 91% for shortfin and longfin squids. These findings have important implications for Spiny Dogfish regarding estimates of population consumption of key pelagic prey species and their ecological footprint within the NES LME.

Subject editor: Donald Noakes, Vancouver Island University, Nanaimo, British Columbia

© Skyler R. Sagarese, Michael G. Frisk, Robert M. Cerrato, Kathy A. Sosebee, John A. Musick, and Paul J. Rago
This is an Open Access article distributed under the terms of the Creative Commons Attribution License (http://creativecommons.org/licenses/by/3.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited. The moral rights of the named author(s) have been asserted.

*Corresponding author: skyler.sagarese@noaa.gov
[1]Present address: National Marine Fisheries Service, Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, Florida 33149, USA.
Received February 25, 2015; accepted December 16, 2015

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Intensive foreign and domestic fishing effort during the 1970s reduced commercially important groundfish stocks (e.g., Atlantic Cod *Gadus morhua*), causing a hypothesized biomass "outburst" of less valuable small elasmobranchs during the 1980s, such as Spiny Dogfish *Squalus acanthias* (Link et al. 2002; Frisk et al. 2008). The National Marine Fisheries Service's Northeast Fisheries Science Center (NEFSC) bottom trawl surveys have collected Spiny Dogfish among other species from the Northeast U.S. Continental Shelf Large Marine Ecosystem (NES LME) since the 1960s. Highly variable survey catch and strong environmental associations of Spiny Dogfish have introduced uncertainty in the population trends derived from bottom trawl survey catches (Carlson et al. 2014; Sagarese et al. 2014a, 2014b). The utility of bottom trawl surveys in tracking Spiny Dogfish abundance has also been questioned by recent tagging studies that suggested a more pelagic existence than previously thought (Sulikowski et al. 2010; TRAC 2010; Carlson et al. 2014). While Spiny Dogfish survey catches are accompanied by uncertainties regarding population dynamics, NEFSC bottom trawl survey catches reflect the best available science for Spiny Dogfish and, as a result, contribute essential relative abundance inputs for stock assessment (NEFSC 2006; Rago and Sosebee 2013).

Ecologically, Spiny Dogfish have gained attention for their diverse feeding habits (Stehlik 2007) and potential predation on commercially important groundfish (Fogarty and Murawski 1998; Link et al. 2002; Morgan and Sulikowski 2015). Considered a key piscivore in the NES LME since the decline of Atlantic Cod (Link and Garrison 2002), Spiny Dogfish are opportunistic omnivores (Link and Ford 2006; Stehlik 2007) and have very few natural predators (Bowman et al. 2000; Stehlik 2007). In this species, piscivory increases with size as smaller individuals generally consume ctenophores, shrimps (order Decapoda), squids (order Teuthida), and small fishes (Garrison and Link 2000), whereas larger individuals feed upon pelagic prey, including clupeids, squids, scombrids, and other teleosts (Grosslein et al. 1980; Link and Almeida 2000; Overholtz et al. 2000). Spiny Dogfish distribution and abundance are tightly linked with prey distribution (Overholtz and Tyler 1985; Burgess 2002; Sagarese et al. 2014a). The species has been implicated in the suppressed recovery of commercially important groundfish stocks (Tallack and Mandelman 2009) and removals from the ecosystem have been suggested to boost the recovery of depleted groundfish stocks by relaxing predation and competition (Murawski 1991; Fogarty and Murawski 1998). However, Link et al. (2002) examined 40,756 Spiny Dogfish stomachs from the NES LME and declared a weak effect of elasmobranch predation on groundfish, as groundfish occurred in less than 1% of the stomachs examined (Link et al. 2002).

Quantifying predation that accurately reflects trophic dynamics is an essential step towards the application of multispecies models for ecosystem-based fisheries management (Tyrrell et al. 2011). Estimating consumption can pose a major challenge in quantifying such dynamics as this process requires comprehensive diet information and absolute predator abundances (Hollowed et al. 2000; Overholtz et al. 2008). Bottom trawl surveys conducted by the NEFSC have monitored long-term trends in the abundance of commercially important species since 1963 and have collected trophic interaction data since 1973 (Link and Almeida 2000; Link and Garrison 2002). Biases in the relative abundance estimates from the bottom trawl survey are assumed to be consistent from year to year when sampling is random with respect to the time of day and when relative stock size is robust to vertical migrations and therefore should not influence the utility of such estimates for monitoring population trends (Jacobson et al. 2015). In contrast, absolute biomass estimates from bottom trawl surveys unadjusted for diel effects may not accurately reflect population dynamics. As a result, absolute abundance estimates may skew estimates of consumption and misrepresent the trophic footprint of a species if it undertakes diel movements (i.e., becomes less available to trawl surveys at a particular time of day). Some fish and invertebrate surveys restrict sampling to daytime hours to remove the potential influence of diel movements on abundance estimates (discussed in Benoît and Swain 2003).

Survey-derived estimates of catch per unit effort (CPUE) are assumed proportional to both stock abundance and catchability (Godø et al. 1999; Salthaug and Aanes 2003; Ellis and Wang 2006). Survey catchability is defined as the proportion of a group (i.e., species or size-class) caught by one unit of effort, often the area swept by the trawl (Francis et al. 2003; Fraser et al. 2007). Catchability consists of three components: (1) presence in the area at the time of the survey (i.e., horizontal availability), (2) proportion encountered by the trawl (i.e., vertical availability), and (3) proportion caught by the trawl (i.e., efficiency) (Godø 1994; Michalsen et al. 1996; Francis et al. 2003; Trenkel et al. 2004). Stock assessment models often assume that survey catchability of a species remains constant both spatially and temporally; however, this situation rarely holds in nature (Godø et al. 1999; Trenkel et al. 2004; Gauthier and Rose 2005). If a species varies its position in the water column, thereby altering its availability to bottom trawls, large biases in the catchability coefficient can skew absolute abundance estimates (Francis and Williams 1995; Hjellvik et al. 2002).

Given the controversy surrounding Spiny Dogfish consumption of commercially important prey species (Link et al. 2002; Bangley and Rulifson 2014; Morgan and Sulikowski 2015), reliable estimates of absolute abundance are paramount in quantifying the ecological impact of Spiny Dogfish on other resources. Within the NES LME, past consumption estimates for Spiny Dogfish utilized unadjusted area-swept numbers from the NEFSC bottom trawl survey (Overholtz et al. 2000). Recognizing and adjusting for any biases (e.g., due to diel migrations) may remove unwanted variability surrounding catch indices (Petrakis et al. 2001) and enhance the

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

dependability of population-level estimates, the understanding of ecosystem processes, and the efficacy of management efforts. At present, no studies have addressed whether catchability of Spiny Dogfish by the NEFSC bottom trawl survey varies with time of day or with other environmental factors.

The objectives of this study were to (1) investigate how seasonal CPUE relates to time of day for Spiny Dogfish life history stages and key prey species, (2) test whether survey catchability changes with time of day and adjust CPUE where necessary, and (3) identify the influence of environmental and temporal factors on the probability of daytime survey catch. Understanding how Spiny Dogfish and their prey respond to diel and environmental factors will provide critical insight into ecological interactions, knowledge of which is required for ecosystem-based fisheries management in the NES LME.

METHODS

Data source.—Annual bottom trawl surveys have been conducted by the NEFSC during autumn and spring since 1963 and 1968, respectively. These surveys sampled the NES LME from Cape Hatteras, North Carolina, north to Georges Bank and the Gulf of Maine (Figure 1) using a stratified random survey design. The autumn survey has been conducted in offshore areas since 1963 with inshore strata added in 1972. The spring survey has sampled offshore areas since 1968 with inshore strata added in 1973. Survey strata comprised about 220,000 km^2. The number of stations sampled per stratum was proportional to its area, although inshore strata were sampled at approximately three times the sampling rate of offshore strata. Approximately 300–400 stations were visited during autumn (1963–2009; mean ± SE = 344 ± 13 stations; range = 183–644 stations) and spring (1968–2009; 346 ± 8 stations; range = 263–491 stations). Tow-specific data were analyzed after removing bad tows and excluding a small number of tows that did not have corresponding environmental measurements (i.e., bottom temperature). Standard tows are 30 min in duration at a towing speed of approximately 6.5 km/h. Detailed descriptions of the survey design and changes in survey protocols over time can be found in Despres-Patanjo et al. (1988) and Sosebee and Cadrin (2006).

Correction factors based on field experiments were applied for changes in vessels, gears, and doors when necessary to calibrate abundance estimates and are detailed elsewhere (Sissenwine and Bowman 1978; NEFSC 1991). The introduction of the National Oceanic and Atmospheric Administration (NOAA) ship *Henry B. Bigelow* in 2009 brought about changes to the trawling gear and survey protocol that are discussed in Brown et al. (2007). To ensure comparability of abundance estimates between vessels, a calibration study compared the catchability of the old vessel, the NOAA ship *Albatross IV*, with the new vessel and derived conversion factors (Miller et al. 2010).

Relative abundance data.—Indices of abundance were calculated from the spring and autumn NEFSC bottom trawl survey haul data for Spiny Dogfish and five key prey species: Butterfish *Peprilus triacanthus*, Atlantic Herring *Clupea harengus*, shortfin squid *Illex* spp., longfin squid *Doryteuthis* spp., and Atlantic Mackerel *Scomber scombrus*. These prey species were selected based on their importance in Spiny Dogfish diet according to the National Marine Fisheries Service's Food Webs Dynamic Program food habits database (Link and Almeida 2000). For both seasons, Spiny Dogfish indices were reported for five stages: aggregated male and female neonates (TL ≤ 26 cm), immature males (26 cm < TL < 60 cm), immature females (26 cm < TL < 80 cm), mature males (TL ≥ 60 cm), and mature females (TL ≥ 80 cm). For each species or stage, survey CPUE was defined as the number of individuals caught per tow and was assumed an appropriate index for abundance. Based on the standard tow duration and area swept by the trawl (0.034 km^2; NEFSC 2006), tow length was assumed to be constant. Prior to 1980, Spiny Dogfish were not sexed during the survey, and therefore stage analyses are restricted to the years 1980 through 2009. Spatial CPUE trends were examined to provide insight into the potential interactions between Spiny Dogfish and pelagic prey species using ArcGIS 10.2 (ESRI, Redlands, California). Due to the size of the NEFSC bottom trawl dataset and space constraints, only CPUE estimates equivalent to or exceeding the 95th percentile of CPUE (i.e., aggregations) were graphically displayed for each season.

Diel trends in CPUE.—Hourly CPUE was analyzed for each Spiny Dogfish stage and prey species to elucidate temporal trends over a diel time scale. Segmented regression and a breakpoint analysis on the hourly intervals (0000–0100 hours,…, 2200–2300 hours) revealed CPUE trends dependent upon the time of day and identified specific times when important shifts in CPUE occurred. A series of linear regressions was fitted between breakpoints parsimoniously to maximize the overall fit of the segmented regression while penalizing the number of breakpoints in the series using the Bayesian information criterion (Schwarz 1978; Frisk et al. 2011). The breakpoint(s) were considered the point or points that separated two significant linear regressions as derived from the data. All statistical analyses were conducted in R software version 2.14.0 (R Foundation for Statistical Computing, Vienna).

Day and night survey catchability.—Data were organized for survey catchability analyses so that each data row reflected an observation of $CPUE_{ys}$ for each year y and strata s combination (e.g., row-1 CPUE = CPUE in year 1963 and strata 1020, and so on) and not an individual tow. Offshore and inshore strata are defined by depth and latitude and depicted in Figures 1 and 2 of NEFSC (2006). The number of daytime (T_D) and nighttime tows (T_N), the proportion of catch caught during the day (C_{ysd}/C_{ys}), and the mean environmental values for depth (m), bottom temperature

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

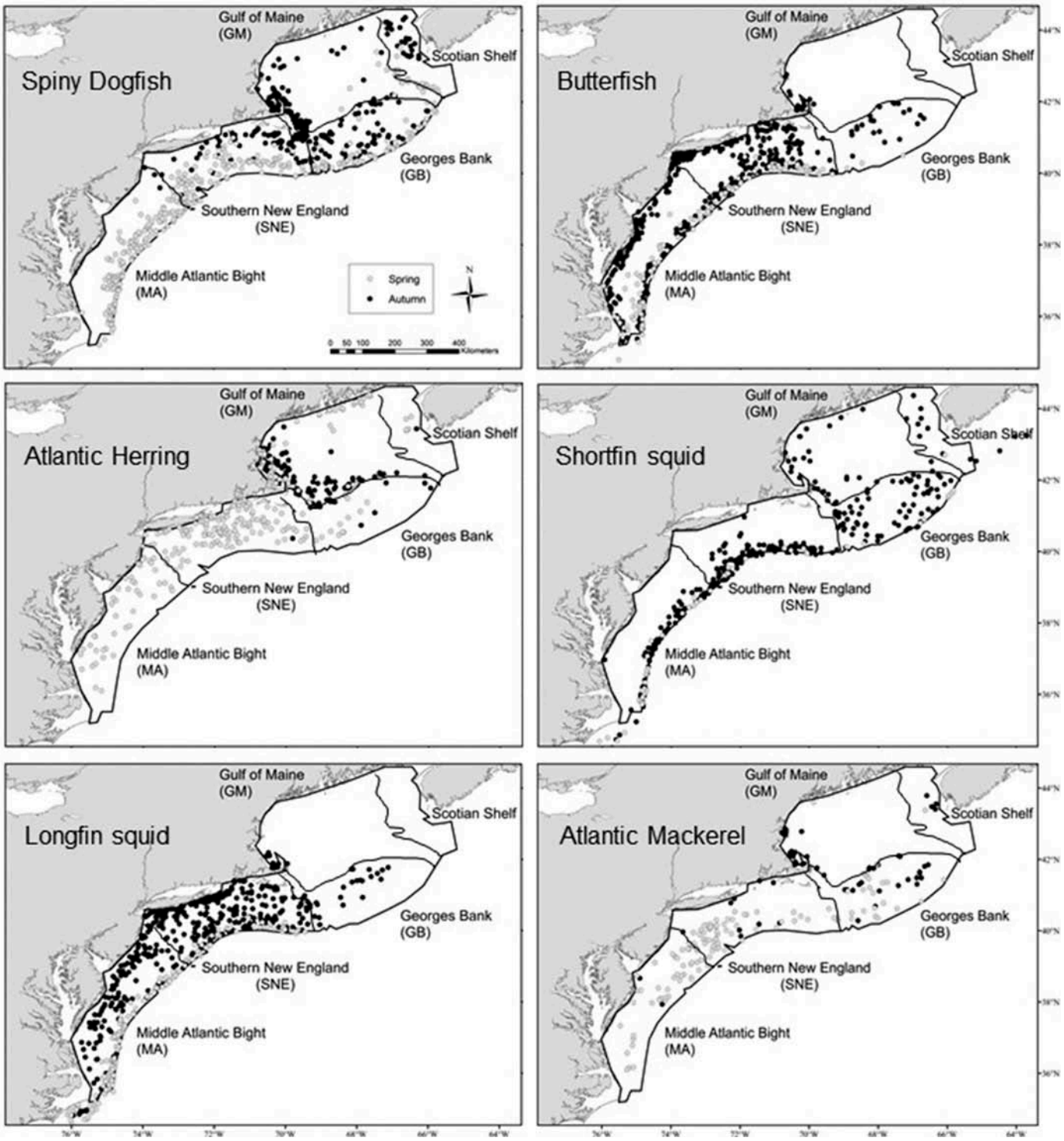


FIGURE 1. Locations of Spiny Dogfish and pelagic prey species aggregations during spring (gray circles) and autumn (black circles) in the Northeast U.S. Continental Shelf Large Marine Ecosystem (NES LME) between 1963 and 2009. The four regions are defined as follows: Gulf of Maine (GM), Georges Bank (GB), southern New England (SNE), and the Middle Atlantic Bight (MA). The black lines reflect the boundaries between each region. The gray shading indicates land masses. Aggregations were defined as CPUE estimates equal to or greater than the 95% percentile of the CPUE probability distribution each season. Note that only the largest CPUE estimates (i.e., aggregations) are displayed due to space constraints.

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

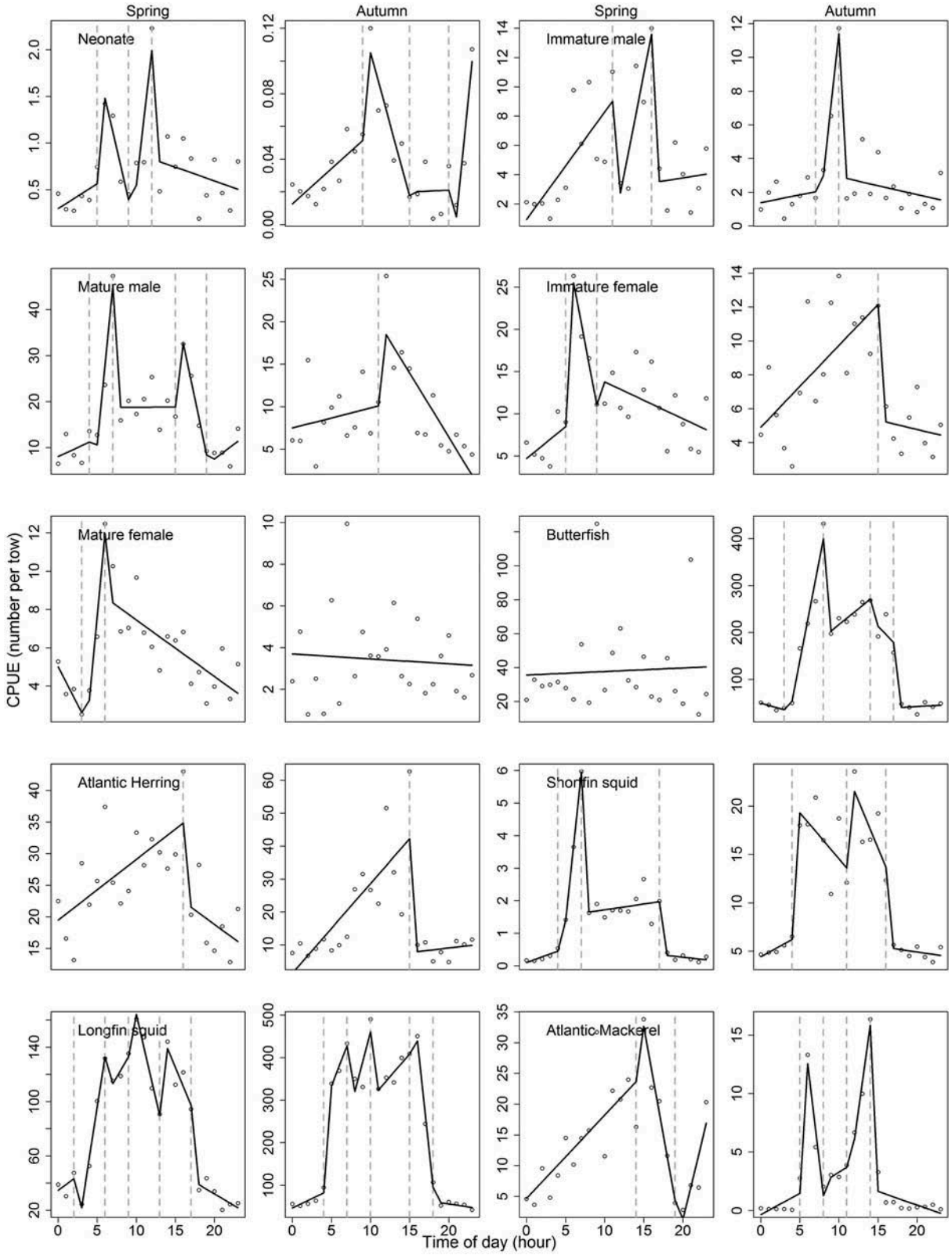


FIGURE 2. Breakpoint analysis of diel CPUE for Spiny Dogfish stages and pelagic prey species caught in the NES LME during spring and autumn between 1963 and 2009. The dots reflect the mean hourly CPUE by time of day across all years, the solid black lines reflect fitted segmented regression lines, and the dashed gray lines indicate significant breakpoints. Note that the scales differ among *y*-axes.

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

(°C), Julian day (d), and solar zenith angle (degrees) were reported for each observation. Analyses were conducted on all data combined (i.e., NES LME) and separately for four main regions within the survey domain: Georges Bank, the Gulf of Maine, southern New England, and the Middle Atlantic Bight (Figure 1).

For each Spiny Dogfish stage and prey species, the proportions of daytime survey catches were analyzed using generalized linear models (GLMs; McCullagh and Nelder 1989) to determine whether or not a different proportion was caught during the day and night (Casey and Myers 1998). Generalized linear modeling is an extension of linear modeling in which the response variable is portrayed in relation to the explanatory variables through a specified link function, where data are not forced into unnatural scales and where nonnormal data are not problematic (Hastie and Tibshirani 1990; Guisan et al. 2002). All GLMs were fit in R using a logit function to link the response with the predictor and a quasibinomial error distribution, which added an overdispersion parameter to the variance of the response (Zuur et al. 2009).

The logistic method of Casey and Myers (1998), later used by Benoît and Swain (2003), was employed to estimate the relative diel survey catchability (S_D) prior to the inclusion of environmental factors with the following equation:

$$\log\left(\frac{C_{ysd}}{C_{ys}}\right) = \log(S_D) + \log\left(\frac{T_D}{T_N}\right), \quad (1)$$

where an offset accounts for the relative number of T_D and T_N (McCullagh and Nelder 1989; Casey and Myers 1998; Benoît and Swain 2003). The intercept represents daytime survey catchability and was estimated within the GLM. An estimate for $\log(S_D)$ of 0 reflected no difference between day and night survey catchability, whereas a significant ($P < 0.05$) positive estimate represented higher daytime survey catchability. The reliability of significance tests and standard errors for estimated parameters was assessed using a randomization test with 1,000 replications (Manly 1991).

Adjusting CPUE for variable survey catchability.—When significant day–night effects were observed for Spiny Dogfish stages or prey species during each season, the unadjusted observed CPUE for each year i (CPUE_i) was converted to daytime equivalents using the estimated conversion factor, S_D, as follows:

$$\text{CPUE}_{adj,i} = \text{CPUE}_i / S_D, \quad (2)$$

under the assumption that the diel survey catchability estimated by the GLM approximated mean conditions. Changes in absolute abundance between CPUE_i and $\text{CPUE}_{adj,i}$ are reported as a percent to determine the relative change in abundance after adjusting for diel variations in survey catchability.

Environmental and temporal influences on survey catchability.—The influences of depth, bottom temperature (BT), Julian day (Julian), and solar zenith angle (Zenith) on the probability of daytime catch were assessed using generalized additive models (GAMs; Hastie and Tibshirani 1990; Wood 2006) with the following equation:

$$P_{ysd} = S_D + \text{offset}\left(\frac{T_D}{T_N}\right) + s(\text{Depth}) + s(\text{BT}) + s(\text{Julian}) + s(\text{Zenith}), \quad (3)$$

where $s()$ represents a smooth function and the remaining variables are as defined previously. For this analysis, GAMs were employed because the smoothing function can handle complex nonlinear relationships and uncover hidden structure between variables missed by traditional linear methods (Hastie and Tibshirani 1990; Guisan et al. 2002; Wintle et al. 2005). All GAMs were fit in version 1.8-4 of the mgcv package (Wood 2014) in R using a logit link function and a quasibinomial error distribution, which added an overdispersion parameter to the variance of the response (Zuur et al. 2009). Cubic regression splines were implemented with a maximum of five degrees of freedom (number of knots = 5). The number of knots was chosen based on expectations within explanatory variables and recommendations in the literature (Keele 2008; Zuur et al. 2009). In addition, each model formula included a "gamma = 1.4" to place a heavier penalty on each degree of freedom to counteract overfitting (Zuur et al. 2009; Wood 2014).

Variance inflation factors calculated for each explanatory variable were used to assess multicollinearity, with values below 3.0 deemed acceptable (Zuur et al. 2009). The percent of total deviance explained by each explanatory variable within the GAM was calculated with the following equations:

$$\text{Deviance}_{\text{Depth}}(\%) = \frac{\text{deviance(model excluding Depth)} - \text{deviance(full model)}}{\text{deviance(null model)}} \times 100, \quad (4)$$

$$\text{Deviance}_{\text{BT}}(\%) = \frac{\text{deviance(model excluding BT)} - \text{deviance(full model)}}{\text{deviance(null model)}} \times 100, \quad (5)$$

$$\text{Deviance}_{\text{Julian}}(\%) = \frac{\text{deviance(model excluding Julian)} - \text{deviance(full model)}}{\text{deviance(null model)}} \times 100, \quad (6)$$

$$\text{Deviance}_{\text{Zenith}}(\%) = \frac{\text{deviance(model excluding Zenith)} - \text{deviance(full model)}}{\text{deviance(null model)}} \times 100, \quad (7)$$

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

where the smoothing parameters of each reduced model (e.g., model excluding Depth) were equivalent to those estimated within the full model to maintain consistency among model parameters. The best models given the data were selected using stepwise backward selection (Harrell 2001; Wintle et al. 2005) and possessed the lowest generalized cross-validation score (Wood 2014). The implementation of a quasibinomial distribution prevented the calculation of Akaike or Bayesian information criterion scores to aid in model selection (Crawley 2007).

Models were validated using data sets internal to their development by comparing observed and predicted values of the probability of daytime catch using 1,000 bootstrapped data sets resampled with replacement (Grüss et al. 2014). Spearman's correlation coefficients (r_{sp}) between the probability of daytime catch predicted by the GAM and the observed probability of daytime catch in the bottom trawl survey data set were estimated and tested for significance (i.e., $\neq 0$) (Vaz et al. 2006; Loots et al. 2010; Grüss et al. 2014). Model performance was also assessed by examining residual plots for strong trends and by visually inspecting response curves for ecological realism (Wintle et al. 2005; Heinänen et al. 2008).

RESULTS

Relative Abundance Data

For Spiny Dogfish, aggregations were generally encountered offshore along the edge of the continental shelf from Cape Hatteras to Georges Bank during spring and on Georges Bank and in the western Gulf of Maine during autumn (Figure 1). The spatial extent of prey aggregations varied greatly between species and seasons. During spring, Butterfish, shortfin squid, and longfin squid primarily aggregated at the edge of the continental shelf in the Middle Atlantic Bight and southern New England (Figure 1). Aggregations of Atlantic Herring and Atlantic Mackerel were spread throughout the Middle Atlantic Bight and southern New England (Figure 1). Autumn trends were less consistent among prey species, with Butterfish aggregations identified both inshore and at the edge of the continental shelf in the Middle Atlantic Bight and southern New England (Figure 1). Atlantic Herring and, to a lesser extent, Atlantic Mackerel generally aggregated in the western and southern Gulf of Maine, whereas shortfin squid aggregated along the edge of the continental shelf throughout the region (Figure 1). Longfin squid were concentrated throughout the Middle Atlantic Bight and southern New England (Figure 1).

Diel Trends in CPUE

Spiny Dogfish stages exhibited highly variable diel CPUE during each season (Figure 2). Shifts in CPUE were evident for each Spiny Dogfish stage by the presence of at least one significant breakpoint, with an increasing trend occurring before 0900 hours during spring (Figure 2). Catch per unit effort peaked for both mature Spiny Dogfish (both sexes) and immature females around 0500 hours during spring, while the highest catches of neonates and immature males occurred around 1100 and 1500 hours, respectively (Figure 2). During autumn, CPUE of neonate and immature and mature male Spiny Dogfish peaked between 1000 and 1500 hours (Figure 2). Contrary to spring, no significant shifts in CPUE were detected for mature females due to consistently low CPUE (Figure 2).

Trends in CPUE for most prey species were relatively similar between seasons, with increasing trends in the morning, relatively high CPUE throughout the day (0500−1700 hours), and declining trends in the late afternoon (Figure 2). Exceptions were noted for Butterfish for which CPUE remained relatively low during spring (Figure 2). Atlantic Herring and Atlantic Mackerel CPUE increased to peak levels around 1500 hours and then declined sharply, whereas CPUE for the remaining prey species was generally dome shaped (Figure 2).

Day and Night Survey Catchability

Significantly higher daytime catchabilities were observed within the NES LME for all Spiny Dogfish combined, mature males, shortfin squid, longfin squid during spring, and most Spiny Dogfish stages and prey species during autumn ($P < 0.05$; Table 1). Regionally, trends for Spiny Dogfish stages were rarely significant during spring, with the exception of in the Middle Atlantic Bight (Table 1). Significantly higher daytime catchabilities were occasionally found for some prey species on Georges Bank, in southern New England, and in the Middle Atlantic Bight ($P < 0.05$; Table 1). Within the Gulf of Maine, regional daytime catchabilities were significantly higher for all Spiny Dogfish stages combined and mature males during autumn ($P < 0.05$). Significantly higher daytime catchabilities were estimated in all five regions for Butterfish, shortfin squid, and longfin squid. Although higher nighttime survey catchability was occasionally estimated, these trends were not significant (Table 1).

For some Spiny Dogfish stages and most prey species both regionally and seasonally, the probability of daytime capture deviated significantly from 50%, suggesting a significant difference between the proportions caught during the day and during the night ($P < 0.05$; Figure 3). Estimated probabilities of daytime capture ranged from 63% to 93% during spring and from 63% to 96% during autumn. The probability of daytime capture was significantly higher for all Spiny Dogfish combined and mature male Spiny Dogfish in the NES LME and Middle Atlantic Bight during spring, and also for immature female Spiny Dogfish in the Middle Atlantic Bight (Figure 3). During autumn, probabilities of daytime capture were relatively high for most Spiny Dogfish stages over the entire

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

TABLE 1. Seasonal and regional estimates with standard errors (Est ± SE) of diel survey catchability for Spiny Dogfish and prey species in the Northeast U.S. Continental Shelf Large Marine Ecosystem (NES LME) between 1963 and 2009. Positive estimates indicate higher daytime catchabilities. The *P*-values were estimated from the randomization test that assessed the reliability of confidence limits and significance tests for the day–night effect; *n* = number of data observations. Stages and species excluded from the table did not exhibit significant trends.

	Gulf of Maine			Georges Bank			Southern New England			Middle Atlantic Bight			NES LME		
Species and stage	*n*	Est ± SE	*P*	*n*	Est ± SE	*P*	*n*	Est ± SE	*P*	*n*	Est ± SE	*P*	*n*	Est ± SE	*P*
Spring															
Spiny Dogfish	333	0.3 ± 0.1	0.93	283	0.6 ± 0.1	0.41	330	0.4 ± 0.1	0.38	508	0.7 ± 0.1	0.00	1,454	0.5 ± 0.1	0.04
Mature male	182	0.7 ± 0.2	0.38	169	0.6 ± 0.2	0.45	191	0.4 ± 0.2	0.50	279	0.9 ± 0.1	0.00	821	0.7 ± 0.1	0.03
Immature female	211	0.4 ± 0.2	0.70	182	0.5 ± 0.2	0.41	219	0.2 ± 0.2	0.72	361	0.6 ± 0.1	0.01	973	0.4 ± 0.1	0.27
Butterfish	46	0.2 ± 0.3	0.97	83	1.5 ± 0.3	0.00	214	−0.1 ± 0.2	0.85	393	0.1 ± 0.1	0.89	736	0.1 ± 0.1	0.85
Shortfin squid	26	1.1 ± 0.5	0.51	109	2.5 ± 0.2	0.05	90	2.6 ± 0.3	0.02	166	2.4 ± 0.2	0.00	391	2.4 ± 0.1	0.00
Longfin squid	53	1.3 ± 0.3	0.51	146	1.2 ± 0.2	0.03	237	1.5 ± 0.2	0.00	479	1.1 ± 0.1	0.00	915	1.2 ± 0.1	0.00
Atlantic Mackerel	69	−1.3 ± 0.4	0.29	131	2.4 ± 0.2	0.25	227	0.6 ± 0.2	0.34	268	0.9 ± 0.1	0.02	695	0.8 ± 0.1	0.07
Autumn															
Spiny Dogfish	536	0.6 ± 0.1	0.03	288	0.9 ± 0.1	0.00	359	0.4 ± 0.1	0.07	107	0.2 ± 0.2	0.73	1,290	0.5 ± 0.1	0.00
Immature male	219	0.8 ± 0.2	0.21	167	0.8 ± 0.2	0.10	160	0.5 ± 0.2	0.24	51	0.9 ± 0.3	0.41	597	0.7 ± 0.1	0.02
Mature male	354	0.8 ± 0.1	0.01	133	0.3 ± 0.2	0.33	177	0.4 ± 0.2	0.14	6	0.3 ± 1.2	0.83	670	0.6 ± 0.1	0.00
Immature female	349	0.4 ± 0.1	0.40	193	0.6 ± 0.2	0.06	228	0.6 ± 0.2	0.05	59	0.8 ± 0.3	0.41	829	0.5 ± 0.1	0.02
Butterfish	250	2.4 ± 0.2	0.04	289	0.9 ± 0.1	0.04	525	1.6 ± 0.1	0.00	707	1.7 ± 0.1	0.00	1,771	1.6 ± 0.1	0.00
Atlantic Herring	435	0.5 ± 0.1	0.10	192	1.6 ± 0.2	0.07	94	0.3 ± 0.3	0.78	9	1.4 ± 0.8	0.41	730	0.9 ± 0.1	0.01
Shortfin squid	524	1.9 ± 0.1	0.00	363	1.3 ± 0.1	0.00	341	1.4 ± 0.1	0.00	329	0.5 ± 0.1	0.02	1,557	1.2 ± 0.1	0.00
Longfin squid	187	3.1 ± 0.2	0.00	267	1.4 ± 0.1	0.00	533	2.4 ± 0.1	0.00	767	1.5 ± 0.1	0.00	1,754	1.9 ± 0.1	0.00
Atlantic Mackerel	207	1.8 ± 0.2	0.05	172	2.0 ± 0.2	0.01	134	4.7 ± 10.0	0.54	10	5.7 ± 2.5	0.92	523	2.7 ± 0.1	0.00

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

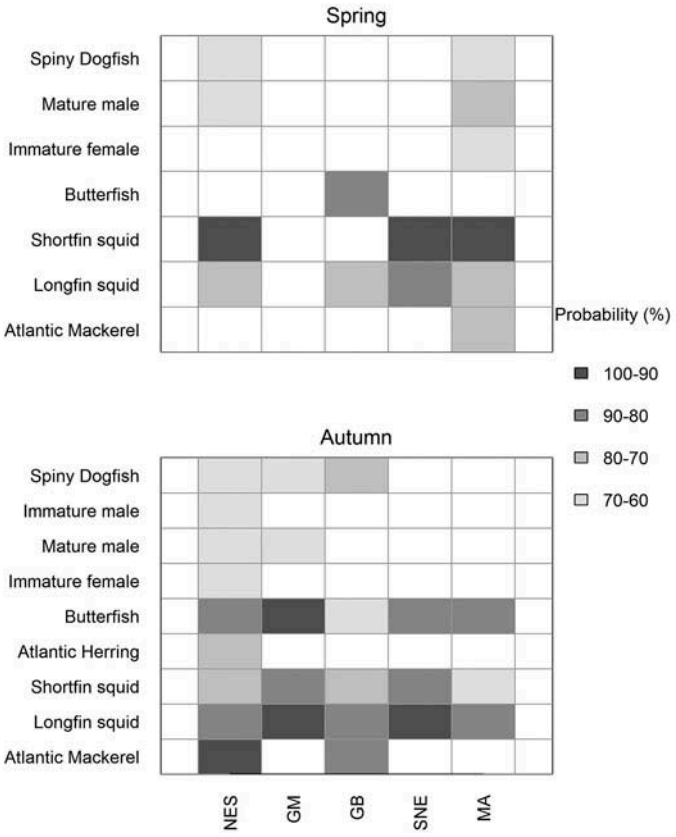


FIGURE 3. Regional probabilities of daytime capture for Spiny Dogfish stages and pelagic prey species in the NES LME during spring and autumn between 1963 and 2009. The shaded boxes reflect the results from significant GLMs (i.e., daytime probability of catch ≠ 50%). The white boxes reflect no significant difference in regional probabilities. Regions and their abbreviations are defined in Figure 1.

survey area but less so on a regional basis (Figure 3). The probability of daytime capture of prey species was frequently high across regions during both spring and autumn (Figure 3).

Adjusting CPUE for Higher Daytime Survey Catchability

Adjustments accounting for differences in day–night survey catchability resulted in lower absolute abundance for all Spiny Dogfish stages or species for which a significant day–night effect was detected, indicating that unadjusted CPUE estimates are overestimating absolute abundance (Figure 4). During spring, CPUE adjustments for day–night effects resulted in reductions in absolute CPUE for all Spiny Dogfish (41% reduction), mature male Spiny Dogfish (50% reduction), shortfin squid (91% reduction), and longfin squid (69% reduction). With the exceptions of neonate and mature female Spiny Dogfish, adjustments in CPUE were required for all Spiny Dogfish stages during autumn, with reductions in absolute CPUE ranging from 42% for all Spiny Dogfish and immature female Spiny Dogfish to 51% for immature male Spiny Dogfish (Figure 4). Catch-per-unit-effort values for all prey species were adjusted for day–night effects and resulted in reductions in absolute CPUE ranging from 61% for Atlantic Herring to 93% for Atlantic Mackerel (Figure 4).

Environmental and Temporal Influences on Survey Catchability

General modeling results.—This analysis focused on all Spiny Dogfish combined because of the lack of significant differences in diel survey catchability for many Spiny Dogfish stages. The percent of total deviance explained by the best GAMs ranged from 10.7% for Spiny Dogfish during spring to 52.9% for Atlantic Mackerel during autumn (Table 2). For all species examined, with the exception of Butterfish, a greater amount of deviance was explained during autumn than in spring.

Overall, the majority of GAMs revealed adequate agreement between the predicted and observed probabilities of daytime catch (Table 3) and residuals lacking both autocorrelation and strong trends. Poor correlations ($r_{sp} < 0.2$) were noted for Butterfish, shortfin squid, and Atlantic Mackerel GAMs during spring, and an $r_{sp} = -0.05$ was not significantly different from zero for shortfin squid (Table 3). Although most prey species revealed moderate correlations during autumn, the Atlantic Mackerel GAM resulted in an $r_{sp} = -0.38$, which indicates a negative relationship between predicted and observed probabilities of daytime catch, an undesirable outcome. As a result, care must be taken when interpreting GAM results that exhibited poor model validation.

Environmental and temporal trends.—During both seasons, the probabilities of daytime catch for Spiny Dogfish and prey species were frequently influenced by environmental and temporal factors, with the solar zenith angle identified as the most influential variable for all species and seasons (Table 2). Zenith explained at least 10% of the total deviance in almost all GAMs and ranged from 8.1% for Atlantic Mackerel during spring to 25.3% for Butterfish during spring (Table 2). For all species–seasons combinations, higher probabilities of daytime catch in the NES LME occurred at lower zenith angles during spring (Figure 5) and autumn (Figure 6).

Significant nonlinear relationships with environmental variables were frequently observed in GAMs during both autumn and spring in the NES LME. However, the percent of total deviance explained for each variable was generally below 5% (Table 2). The percent of total deviance explained by depth ranged from 0.2% for longfin squid during autumn to 6.4% for longfin squid during spring (Table 2). During spring, daytime catches were more likely to occur in shallow depths (< 75 m) for most prey species (Figure 5). During autumn, probabilities of daytime catch in the NES LME were higher at shallow depths (< 75 m) for Atlantic Herring and Atlantic Mackerel and at deeper depths for Spiny Dogfish, Butterfish, shortfin squid, and longfin squid (Figure 6). For bottom temperature, the percent of total deviance explained ranged from 0.2% for Spiny Dogfish during spring to 12.0% for Atlantic Mackerel during spring (Table 2). Higher

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

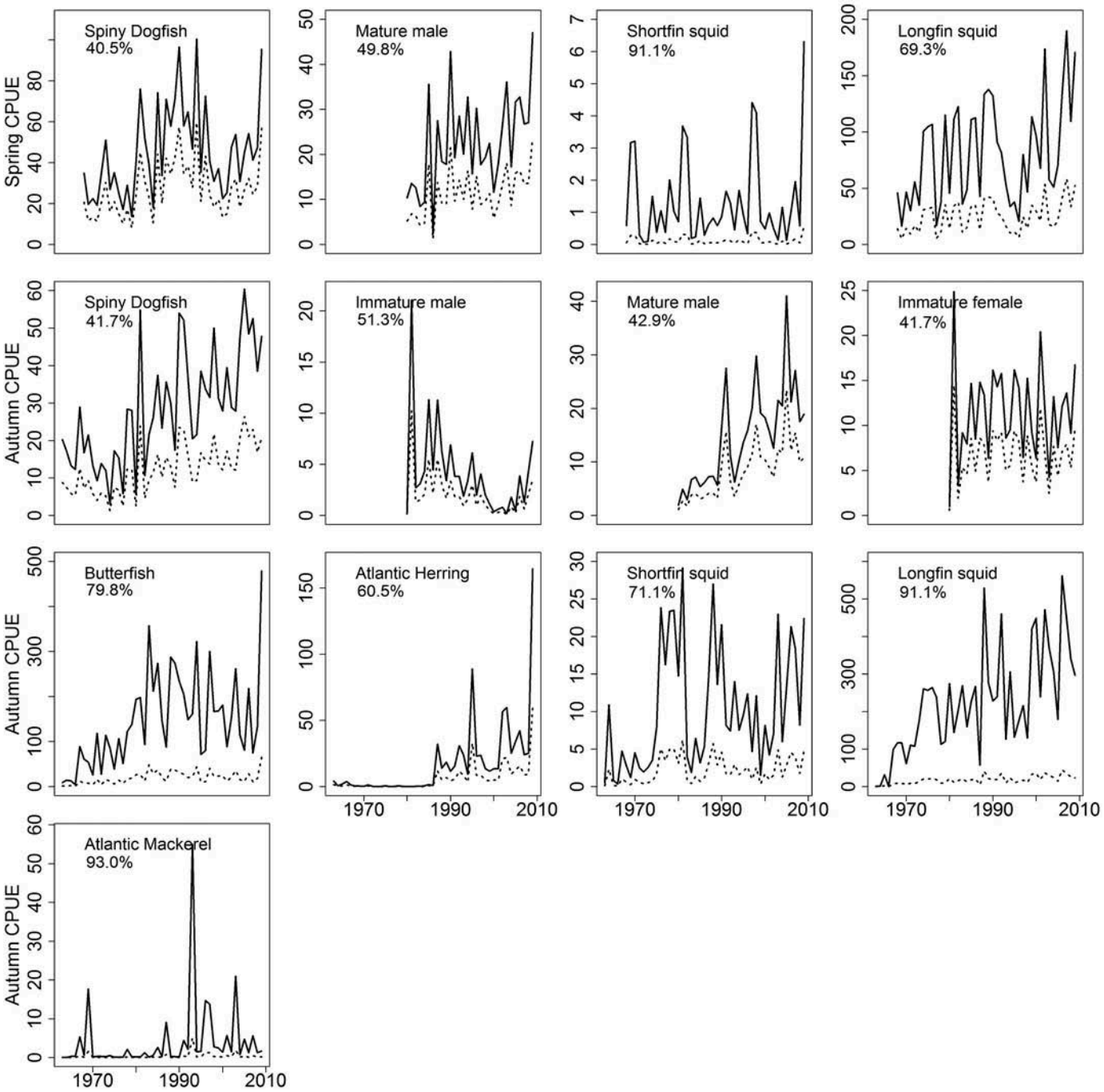


FIGURE 4. Plots of unadjusted (solid lines) and adjusted (dotted lines) CPUE for Spiny Dogfish stages and pelagic prey species in the NES LME when correction was warranted during autumn (1963–2009) and spring (1968–2009). The percentages shown reflect the average reductions in absolute abundance after accounting for the day–night effects on survey catchability. Note that the *y*-axes differ between panels.

probabilities of daytime catch generally occurred at cooler temperatures (< 6°C) during spring for all species (Figure 5). During autumn, daytime catches were more likely to occur below 10°C for most species and above 10°C for Atlantic Herring (Figure 6).

Significant nonlinear relationships with Julian day were also frequently observed in GAMs during both autumn and spring in the NES LME but explained minimal total deviance (Table 2). The percent of total deviance explained by Julian

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

TABLE 2. Generalized additive model results for the probability of daytime catches for Spiny Dogfish and prey species in the NES LME between 1963 and 2009 during spring and autumn. Abbreviations are as follows: n = the number of data observations, r^2 = the coefficient of determination, Dev = the percent of total deviance explained, Int ± SE = the intercept reflecting the day–night survey catchability estimate with SE (a positive estimate indicates higher daytime survey catchability), and EDF = the estimated degrees of freedom of the smoothing parameter for each respective explanatory variable. Significance (indicated with an asterisk) is based on an a priori α = 0.05. A blank cell indicates that the variable was not included in the best model.

					Depth (m)		Bottom temperature (°C)		Julian day		Zenith (°)	
Species	n	r^2	Dev (%)	Int ± SE	Dev (%)	EDF	Dev (%)	EDF	Dev (%)	EDF	Dev (%)	EDF
Spring												
Spiny Dogfish	1,454	0.11	10.7	0.95 ± 0.05*	0.4		0.2		0.5	1.0	10.3	3.9
Butterfish	736	0.53	46.6	1.02 ± 0.13*	1.4	3.9	3.5	1.7	1.3	2.9	25.3	2.1
Atlantic Herring	1,286	0.26	24.8	0.97 ± 0.08*	2.6	2.5	2.9	3.7	0.8	1.0	15.2	1.0
Shortfin squid	391	0.12	21.9	2.13 ± 0.11*	1.2	1.0	4.4	3.1	6.4	2.8	11.0	3.2
Longfin squid	915	0.32	30.6	1.95 ± 0.13*	6.4	3.4	1.0	2.2	2.6	1.0	11.5	3.3
Atlantic Mackerel	695	0.30	33.1	1.99 ± 0.15*	2.1	3.4	12.0	4.0	5.1	3.4	8.1	3.9
Autumn												
Spiny Dogfish	1,290	0.28	24.4	0.84 ± 0.07*	0.6	2.6	0.6	2.3	0.8	2.6	19.5	3.9
Butterfish	1,713	0.15	17.9	1.96 ± 0.08*	4.9	3.6	1.5	2.6	2.2	3.8	10.8	3.6
Atlantic Herring	714	0.35	34.6	1.08 ± 0.11*	2.3	1.0	4.8	3.2	5.7	3.7	10.4	3.9
Shortfin squid	1,522	0.27	28.6	1.51 ± 0.05*	5.1	2.6	1.4	2.9	4.5	3.7	13.2	1.0
Longfin squid	1,689	0.34	39.1	2.48 ± 0.08*	0.2	1.0	6.2	3.6	4.1	2.2	12.8	3.2
Atlantic Mackerel	512	0.41	52.9	2.09 ± 0.14*	3.2	2.3	2.9	2.8	5.7	1.0	24.2	3.9

day on the probability of daytime catch ranged from 0.5% for Spiny Dogfish during spring to 6.4% for shortfin squid during spring (Table 2). During spring, higher probabilities of daytime catch occurred earlier in the season for Spiny Dogfish and shortfin squid and towards the end of the season for the remaining species (Figure 5). During autumn, daytime catch was more likely to occur early in the season for longfin squid and Atlantic Mackerel and midseason for the remaining species (Figure 6).

TABLE 3. Spearman's correlation coefficients (r_{sp}) between the probabilities of daytime catch values predicted by GAMs and the observed probabilities of daytime catch values in the survey data for Spiny Dogfish and prey species in the NES LME between 1963 and 2009 during spring and autumn. The lower and upper confidence limits (CLs) define a 95% confidence interval. The significance of P-values is based on an a priori α = 0.05; significant values are indicated with an asterisk.

Species	r_{sp}	CL_{lower}	CL_{upper}	P
Spring				
Spiny Dogfish	0.43	0.39	0.47	0.000*
Butterfish	0.11	0.04	0.18	0.003*
Atlantic Herring	0.24	0.19	0.29	0.000*
Shortfin squid	−0.05	−0.16	0.07	0.308
Longfin squid	0.50	0.45	0.55	0.000*
Atlantic Mackerel	0.09	0.02	0.17	0.019*
Autumn				
Spiny Dogfish	0.42	0.38	0.47	0.000*
Butterfish	0.27	0.23	0.31	0.000*
Atlantic Herring	0.41	0.35	0.48	0.000*
Shortfin squid	0.33	0.29	0.38	0.000*
Longfin squid	0.44	0.40	0.48	0.000*
Atlantic Mackerel	−0.38	−0.47	−0.29	0.000*

DISCUSSION

Here we provide the first estimates of the influence of diel and environmental factors on seasonal CPUE and survey catchability during the NEFSC bottom trawl survey for Spiny Dogfish, Butterfish, and Atlantic Mackerel in the NES LME. Survey catchability estimates revealed higher daytime values for most Spiny Dogfish stages and prey species, highlighting the potential for bias in stage-specific or species-specific absolute abundance estimates. After accounting for day–night effects, reductions in absolute abundance ranged from 40.5% for Spiny Dogfish during spring to 93% for Atlantic Mackerel during autumn, suggesting that unadjusted CPUE was overestimating absolute abundances in the survey region. Higher probabilities of daytime catch corresponded to lower solar zenith angles, suggesting that bottom trawl catches were more likely during the day. Breakpoint analyses also supported higher catch rates during the day for most species and revealed significant increases in the early morning and decreases in the late afternoon. Although biases in day–night catchability should not impact relative abundance estimates used in stock assessments as discussed in the introduction, these

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

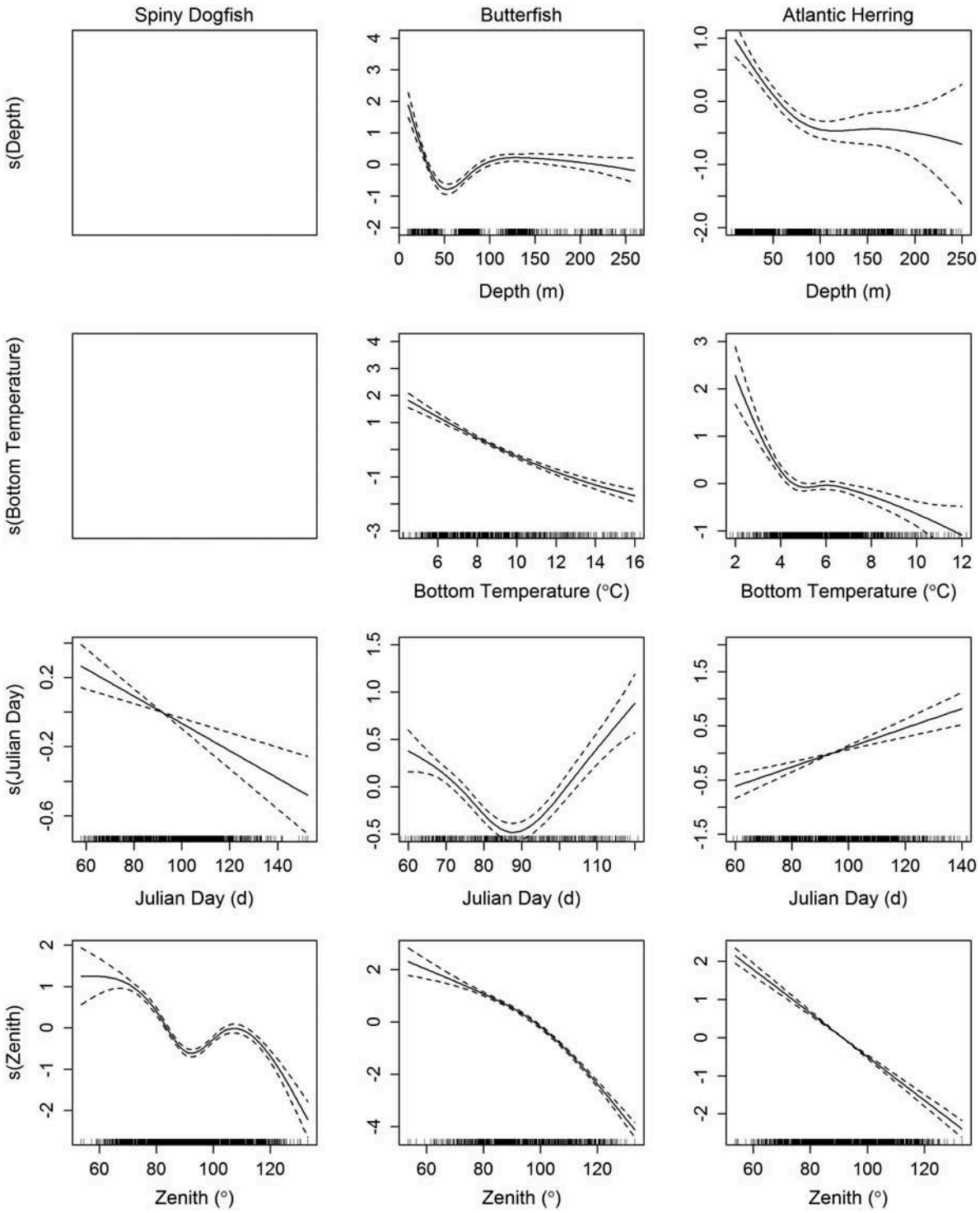


FIGURE 5. Partial GAM plots identifying the additive effect of each variable on the probability of daytime catch for Spiny Dogfish and pelagic prey species in the NES LME during spring between 1968 and 2009. The *y*-axis represents the degree of smoothing (and thus the probability of daytime catch), with its range indicative of the relative importance of each covariate. The *x*-axis reflects the relative density of data points as shown by the "rug." Some smoothes have been graphically abbreviated due to a lack of data at the endpoints. The dashed lines reflect the 95% confidence intervals around the response curves. An empty box indicates the absence of that term in the final model.

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

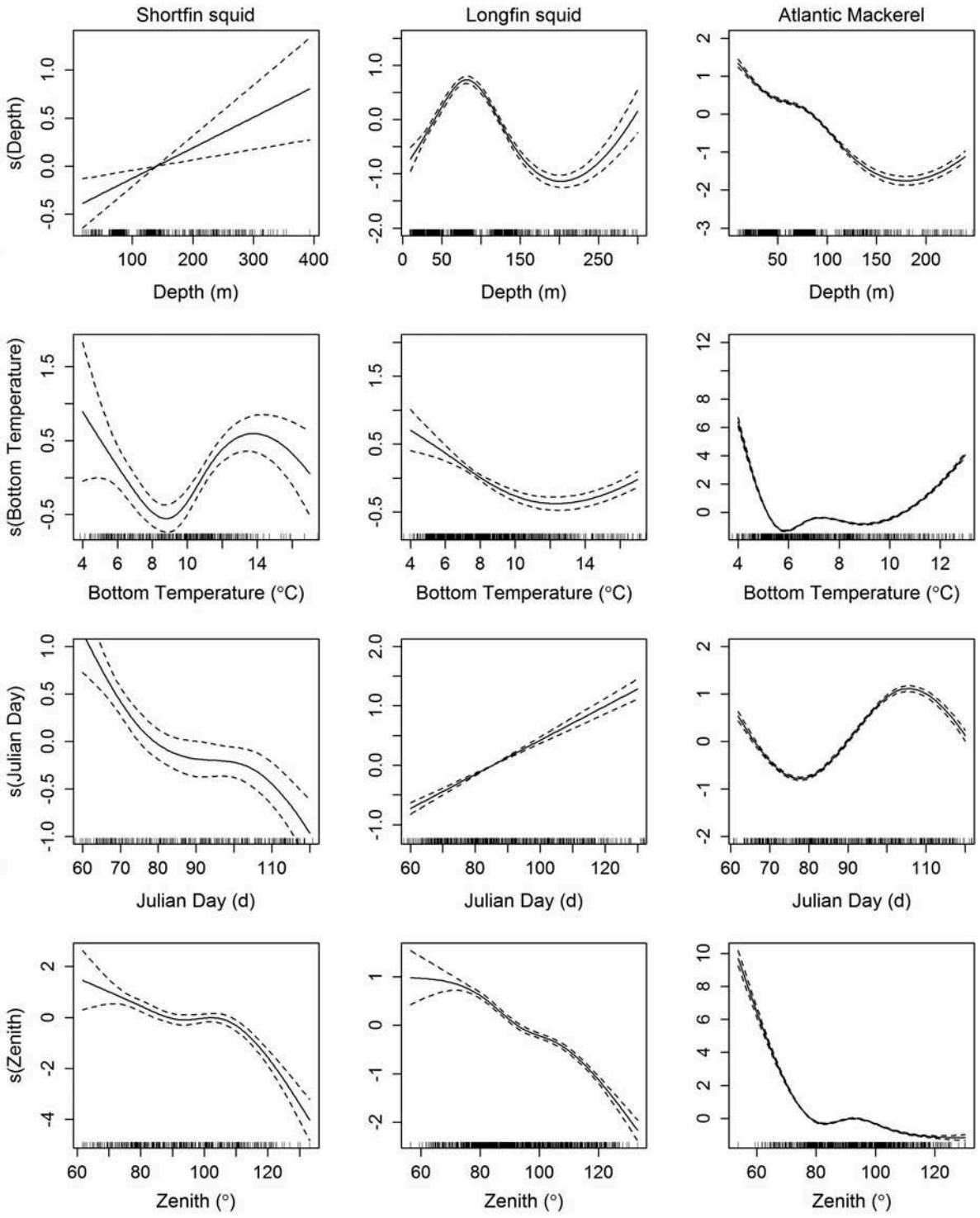


FIGURE 5. Continued.

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

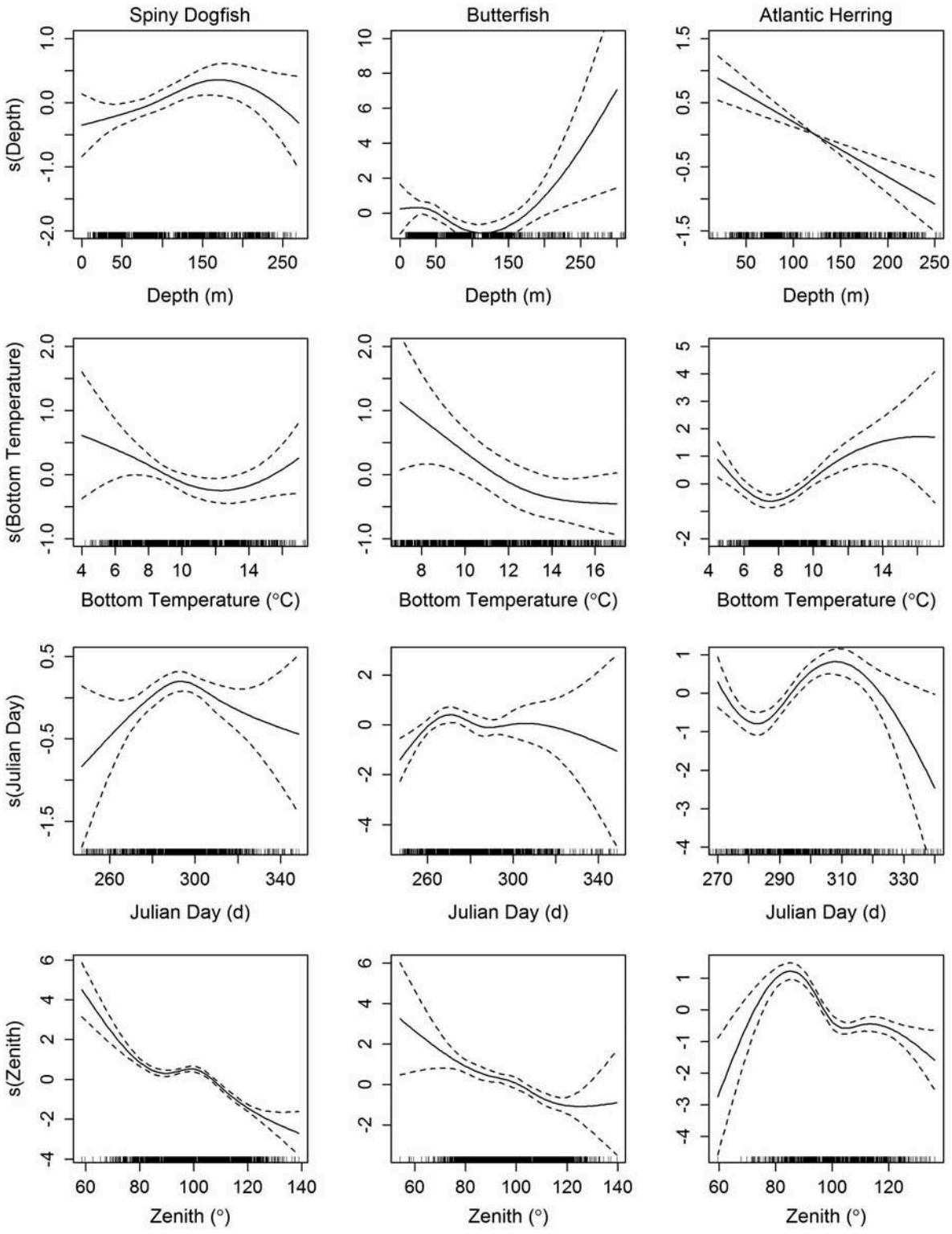


FIGURE 6. Partial GAM plots identifying the additive effect of each variable on the probability of daytime catch for Spiny Dogfish and pelagic prey species in the NES LME during autumn between 1963 and 2009. Further details are given in Figure 5.

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

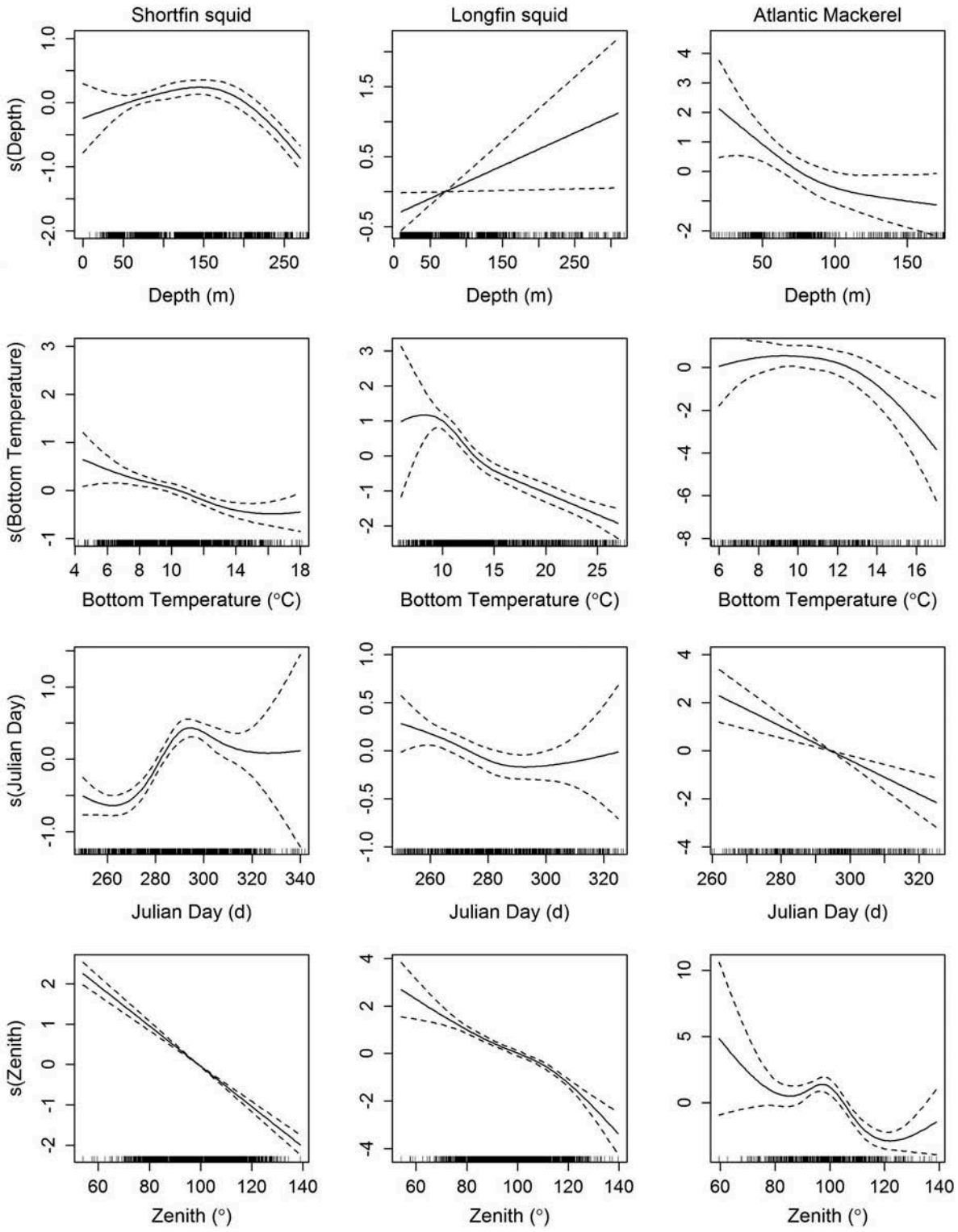


FIGURE 6. Continued.

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

results have immediate utility in quantifying absolute biomass and population consumption rates required for ecosystem-based fisheries management.

Changing survey catchability can have important implications for ecosystem modeling because bottom trawl estimates of abundance serve as direct model inputs (e.g., biomass) and assist in the estimation of consumption parameters that quantify predator–prey linkages. Adjusting CPUE estimates can help elucidate the role of Spiny Dogfish in the ecosystem, a research question that has already received considerable attention (Overholtz et al. 2000; Link et al. 2002; Bangley and Rulifson 2014; Morgan and Sulikowski 2015). Our results suggest that the NEFSC bottom trawl survey is overestimating the absolute abundance of Spiny Dogfish during both autumn and spring, possibly due to feeding, aggregating, or herding on the bottom, which could result in higher daytime survey catchability. Higher daytime survey catchability led to a 40% reduction in Spiny Dogfish abundance after converting all CPUE to daytime equivalents during both spring and autumn. Between 1977 and 1997, Spiny Dogfish were estimated to have consumed approximately 619,000 metric tons of prey species (Sand Lance *Ammodytes* sp. and the five prey species presented herein) (Overholtz et al. 2000). Although survey catchability was adjusted for the other predators examined, the area-swept numbers of Spiny Dogfish were not adjusted (Overholtz et al. 2000). Given the strong bias in CPUE of Spiny Dogfish, this consumption estimate likely overestimated their predatory impact in relation to fishery catches.

The suggestion that the NEFSC bottom trawl survey is overestimating absolute abundance based on our findings contradicts recent tagging study results for Spiny Dogfish that suggest that the survey is missing a substantial portion of the population (Sulikowski et al. 2010; Carlson et al. 2014). Our analysis assumed that lower nighttime catchability was reflective of Spiny Dogfish occupying more pelagic habitat rather than moving to depths outside the survey strata. The proportion of daytime catch, assumed a proxy for availability to the bottom trawl survey, was significantly related to solar zenith for Spiny Dogfish during both seasons. Preliminary tagging results along the U.S. East Coast suggest that Spiny Dogfish are more mobile both vertically and horizontally than previously thought and exhibit distinct diel patterns (Sulikowski et al. 2010; Carlson et al. 2014). However, it remains unclear how Spiny Dogfish are distributed beyond the depth range of the NEFSC trawl survey (NEFSC 2006). In 1999, a coastal field survey potentially identified a small contingent of Spiny Dogfish in waters south of Cape Hatteras (Rulifson and Moore 2009), suggesting that the survey may be missing a portion of the Spiny Dogfish population.

This study highlights the importance of estimating abundance as a precursor to ecosystem-based fisheries management (Godø and Walsh 1992; Hjellvik et al. 2002). Estimates of CPUE that account for known environmental or diel effects on survey catchability can better represent relative abundance trends in stock assessment models and absolute abundance trends for the more accurate consumption estimates required for ecosystem-based fisheries management. Given the enormous investment behind the NEFSC bottom trawl survey, any potential techniques capable of reducing bias in abundance estimation should be identified and applied. As suggested by Jacobson et al. (2015) for longfin squid, solar zenith angles could be used as priors on selectivity of the NEFSC bottom trawl survey in stock assessment models, which would allow changes in availability to the survey based on the time of day. Further, CPUE on a tow-by-tow basis could be standardized using the environmental variables identified as important drivers of Spiny Dogfish distribution, such as the solar zenith angle (Sagarese et al. 2014a), which also heavily influenced the probability of daytime catch by year and strata. Given the uncertainty regarding the availability of Spiny Dogfish to the NEFSC bottom trawl survey and recent tagging evidence that Spiny Dogfish do travel beyond the continental shelf based on satellite tags (Carlson et al. 2014), a specialized survey and/or additional tagging studies could provide insight into the distribution of Spiny Dogfish outside the NEFSC bottom trawl survey domain.

Various mechanisms linked to diel variations in survey catchability may partly explain the trends observed for Spiny Dogfish and their pelagic prey species. Although visual avoidance is commonly cited, this seems highly unlikely for any of the species examined since more individuals were captured during daylight when visibility is expected to be higher (Glass and Wardle 1989; Casey and Myers 1998; Petrakis et al. 2001). The observed change in the vertical availability of each species examined in the trawl survey strongly supports vertical migrations (Engås et al. 1988; Walsh 1992; Aglen et al. 1997; Aglen et al. 1999; Korsbrekke and Nakken 1999), which are well documented for both groundfish (e.g., Atlantic Cod) and pelagic species (e.g., Atlantic redfish *Sebastes* spp.) and generally balance predation risk with food availability (Michalsen et al. 1996; Aglen et al. 1999; Hjellvik et al. 2001; Gauthier and Rose 2005). Compared to temperature, depth, and Julian day, solar zenith angles explained the majority of the deviance explained regarding the probability of daytime catch for both squid species and Spiny Dogfish, particularly during autumn. Herding has been suggested to occur in both the northwestern Atlantic Ocean for Spiny Dogfish (NEFSC 2006) and in Puget Sound for Pacific Spiny Dogfish *Squalus suckleyi* (Palsson 2009), with its effect enhanced during the daylight when the sediment cloud is visible (Wardle 1993; Francis and Williams 1995; Michalsen et al. 1996; Fraser et al. 2007).

The majority of research addressing diel catchability has focused on commercially important species, such as Atlantic Cod (Rose 2004). Multiple studies have identified higher daytime catch rates and/or catchability for Atlantic Cod

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

(Michalsen et al. 1996; Casey and Myers 1998; Aglen et al. 1999; Korsbrekke and Nakken 1999; Petrakis et al. 2001) although regional differences were observed (e.g., subdivision 3P, Casey and Myers 1998). Length-dependent variations were often more pronounced for smaller Atlantic Cod (Michalsen et al. 1996; Aglen et al. 1999; Korsbrekke and Nakken 1999). Regional differences identified in survey catchability for mature male Spiny Dogfish and immature females in the Middle Atlantic Bight during spring and mature male Spiny Dogfish in the Gulf of Maine during autumn could relate to sex- and stage-specific movements related to environmental conditions or prey abundance (Sagarese et al. 2014a, 2014b). Our results for prey species agreed with previous findings in the northwestern Atlantic Ocean for longfin inshore squid *Doryteuthis pealeii* and northern shortfin squid *Illex illecebrosus* during autumn (Brodziak and Hendrickson 1999) and in Canadian waters for Atlantic Herring, Butterfish, Atlantic Mackerel, and northern shortfin squid (Casey and Myers 1998; Benoît and Swain 2003).

Trends in diel CPUE and spatial distribution were simultaneously investigated for the key prey species to enhance understanding of their availability and to facilitate hypothesized linkages between the dynamics of Spiny Dogfish and their prey. Spiny Dogfish commonly adapt their feeding habits to exploit abundant prey (Overholtz et al. 2000; Link and Garrison 2002; Moustahfid et al. 2010). During spring, relatively higher CPUE occurred between early morning (i.e., 0500 hours) and midafternoon (i.e., 1500 hours) for most Spiny Dogfish stages, shortfin squid, and longfin squid, implying greater numbers associated with the seafloor and increased potential for direct predation. Squid represent a major dietary component for Spiny Dogfish in all regions except the Middle Atlantic Bight (Bowman et al. 2000; Stehlik 2007). The observed overlap in vertical distribution may also be related to feeding similarity as both shortfin squid and Spiny Dogfish (10–60 cm) share a cephalopod- and fish-dominated diet (Garrison and Link 2000). These inferred vertical migrations may also be independent of feeding habits and, instead, cued internally by an endogenous rhythm (Fréon et al. 1993). Regardless of the mechanism, significant shifts in CPUE identified by the breakpoint analysis, specifically increased CPUE during the morning and decreased CPUE during the late afternoon, provide further evidence of higher catches during daytime hours for all species examined. Such shifts in CPUE could result from changes in fish behavior either directly due to vertical migrations or indirectly via prey or predator availability.

In reality, catchability is a complicated function of many factors and hence has earned a "nuisance" reputation (Francis et al. 2003). Additional variables, such as current speed or direction (Michalsen et al. 1996) and bottom topography (Casey and Myers 1998), may further contribute to the survey catchability of Spiny Dogfish and their prey species. In addition, the highly aggregated behavior of Spiny Dogfish warrants further research on the factors driving this behavior and the effects of density dependence on research survey catchability. Research on size-dependent escapement may prove fruitful for Spiny Dogfish, particularly for neonates because survey-derived abundance for this stage is used as a proxy for recruitment (NEFSC 2006). Midwater trawl or hydroacoustic surveys may also provide insight into the movements of Spiny Dogfish in the water column (Stehlik 2007) and whether the addition of these estimates could augment bottom trawl swept-area estimates when conducted simultaneously (Aglen et al. 1999).

ACKNOWLEDGMENTS

The authors thank all those individuals who have worked or volunteered aboard the NOAA RV *Albatross IV* and RV *Henry B. Bigelow*, Woods Hole, Massachusetts, for assistance with survey data collection. Two anonymous reviewers also helped improve the quality of this manuscript. This project was funded by the National Marine Fisheries Service Sea Grant Fellowship in Population Dynamics.

REFERENCES

Aglen, A., A. Engås, I. Huse, K. Michalsen, and B. Stensholt. 1997. Vertical distribution of cod, Haddock, and redfish: impact on bottom trawl and acoustic surveys in the Barents Sea. International Council for the Exploration of the Sea, CM 1997/Y:16, Copenhagen.

Aglen, A., A. Engås, I. Huse, K. Michalsen, and B. K. Stensholt. 1999. How vertical fish distribution may affect survey results. ICES Journal of Marine Science 56:345−360.

Bangley, C. W., and R. A. Rulifson. 2014. Feeding habits, daily ration, and potential predatory impact of mature female Spiny Dogfish in North Carolina coastal waters. North American Journal of Fisheries Management 34:668−677.

Benoît, H. P., and D. P. Swain. 2003. Accounting for length- and depth-dependent diel variation in catchability of fish and invertebrates in an annual bottom-trawl survey. ICES Journal of Marine Science 60:1298−1317.

Bowman, R. E., C. E. Stillwell, W. L. Michaels, and M. D. Grosslein. 2000. Food of northwest Atlantic fishes and two common species of squid. NOAA Technical Memorandum NMFS-NE-155.

Brodziak, J., and L. Hendrickson. 1999. An analysis of environmental effects on survey catches of squids *Loligo pealei* and *Illex illecebrosus* in the northwest Atlantic. U.S. National Marine Fisheries Service Fishery Bulletin 97:9−24.

Brown, R. W., M. Fogarty, C. Legault, T. Miller, V. Nordahl, P. Politis, and P. Rago. 2007. Survey transition and calibration of bottom trawl surveys along the northeastern continental shelf of the United States. International Council for the Exploration of the Sea, CM 2007/Q:20, Copenhagen.

Burgess, G. H. 2002. Spiny Dogfishes: family Squalidae. Pages 48–57 *in* B. B. Collette, and G. Klein-MacPhee, editors. Bigelow and Schroeder's fishes of the Gulf of Maine, 3rd edition. Smithsonian Institution Press, Washington, D.C.

Carlson, A. E., E. R. Hoffmayer, C. A. Tribuzio, and J. A. Sulikowski. 2014. The use of satellite tags to redefine movement patterns of Spiny Dogfish (*Squalus acanthias*) along the US East Coast: implications for fisheries management. PLoS (Public Library of Science) ONE [online serial] 9(7):e103384.

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Casey, J. M., and R. A. Myers. 1998. Diel variation in trawl catchability: is it as clear as day and night? Canadian Journal of Fisheries and Aquatic Sciences 55:2329–2340.

Crawley, M. J. 2007. The R book. Wiley, Chichester, UK.

Despres-Patanjo, L. I., T. R. Azarovitz, and C. J. Byrne. 1988. Twenty-five years of fish surveys in the northwest Atlantic: the NMFS Northeast Fisheries Center's bottom trawl survey program. Marine Fisheries Review 50:69–71.

Ellis, N., and Y. Wang. 2006. Effects of fish density distribution and effort distribution on catchability. ICES Journal of Marine Science 64:178–191.

Engås, A., J. A. Jacobsen, and A. V. Soldal. 1988. Diurnal changes in bottom trawl catches and vertical fish distribution. International Council for the Exploration of the Sea, CM 1988/B:32, Copenhagen.

Fogarty, M. J., and S. A. Murawski. 1998. Large-scale disturbance and the structure of marine systems: fishery impacts on Georges Bank. Ecological Applications 8:S6–S22.

Francis, M. P., and M. W. Williams. 1995. Diel variation in trawl catch rates of *Pagrus auratus* (Sparidae). Fisheries Research 24:301–310.

Francis, R. I. C. C., R. J. Hurst, and J. A. Renwick. 2003. Quantifying annual variation in catchability for commercial and research fishing. U.S. National Marine Fisheries Service Fishery Bulletin 101:293–304.

Fraser, H. M., S. P. R. Greenstreet, and G. J. Piet. 2007. Taking account of catchability in groundfish survey trawls: implications for estimating demersal fish biomass. ICES Journal of Marine Science 64:1800–1819.

Fréon, P., F. Gerlotto, and O. A. Misund. 1993. Consequences of fish behaviour for stock assessment. ICES Marine Science Symposia 196:190–195.

Frisk, M. G., D. E. Duplisea, and V. M. Trenkel. 2011. Exploring the abundance-occupancy relationships for the Georges Bank finfish and shellfish community from 1963 to 2006. Ecological Applications 21:227–240.

Frisk, M. G., T. J. Miller, S. J. D. Martell, and K. Sosebee. 2008. New hypothesis helps explain elasmobranch "outburst" on Georges Bank in the 1980s. Ecological Applications 18:234–245.

Garrison, L. P., and J. S. Link. 2000. Dietary guild structure of the fish community in the northeast United States continental shelf ecosystem. Marine Ecology Progress Series 202:231–240.

Gauthier, S., and G. A. Rose. 2005. Diel vertical migration and shoaling heterogeneity in Atlantic redfish: effects on acoustic and bottom-trawl surveys. ICES Journal of Marine Science 62:75–85.

Glass, C. W., and C. S. Wardle. 1989. Comparison of the reactions of fish to a trawl gear, at high and low light intensities. Fisheries Research 7:249–266.

Godø, O. R. 1994. Factors affecting the reliability of groundfish abundance estimates from bottom trawl surveys. Pages 166–195 *in* A. Fernö and S. Olsen, editors. Marine fish behaviour in capture and abundance estimation. Fishing News Books, Blackwell Scientific Books, London.

Godø, O. R., and S. J. Walsh. 1992. Escapement of fish during bottom trawl sampling: implications for resource assessment. Fisheries Research 13:281–292.

Godø, O. R., S. J. Walsh, and A. Engås. 1999. Investigating density-dependent catchability in bottom-trawl surveys. ICES Journal of Marine Science 56:292–298.

Grosslein, M. D., R. W. Langton, and M. P. Sissenwine. 1980. Recent fluctuations in pelagic fish stocks of the northwest Atlantic, Georges Bank region, in relation to species interactions. Rapports et Proces-Verbaux des Reunions Conseil International pour l'Exploration de la Mer 177:374–404.

Grüss, A., M. Drexler, and C. H. Ainsworth. 2014. Using delta generalized additive models to produce distribution maps for spatially explicit ecosystem models. Fisheries Research 159:11–24.

Guisan, A., T. C. Edwards, and T. Hastie. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecological Modelling 157:89–100.

Harrell, F. E. 2001. Regression modeling strategies: with application to linear models, logistic regression, and survival analysis. Springer-Verlag, New York.

Hastie, T. J., and R. J. Tibshirani. 1990. Generalized additive models. Chapman and Hall, New York.

Heinänen, S., M. Rönkä, and M. Von Numers. 2008. Modelling the occurrence and abundance of a colonial species, the Arctic tern *Sterna paradisaea* in the archipelago of SW Finland. Ecography 31:601–611.

Hjellvik, V., O. R. Godø, and D. Tjøstheim. 2001. Modeling diurnal variation of marine populations. Biometrics 57:189–196.

Hjellvik, V., O. R. Godø, and D. Tjøstheim. 2002. Diurnal variation in bottom trawl survey catches: does it pay to adjust? Canadian Journal of Fisheries and Aquatic Sciences 59:33–48.

Hollowed, A. B., N. Bax, R. Beamish, J. Collie, M. Fogarty, P. Livingston, J. Pope, and J. C. Rice. 2000. Are multispecies models an improvement on single-species models for measuring fishing impacts on marine ecosystems? ICES Journal of Marine Science 57:707–719.

Jacobson, L. D., L. C. Hendrickson, and J. Tang. 2015. Solar zenith angles for biological research and an expected catch model for diel vertical migration patterns that affect stock size estimates for longfin inshore squid, *Doryteuthis pealeii*. Canadian Journal of Fisheries and Aquatic Sciences 72:1329–1338.

Keele, L. J. 2008. Semiparametric regression for the social sciences. Wiley, Chichester, UK.

Korsbrekke, K., and O. Nakken. 1999. Length and species-dependent diurnal variation of catch rates in the Norwegian Barents Sea bottom-trawl surveys. ICES Journal of Marine Science 56:284–291.

Link, J. S., and F. P. Almeida. 2000. An overview and history of the food web dynamics program of the Northeast Fisheries Science Center, Woods Hole, Massachusetts. NOAA Technical Memorandum NMFS-NE-159.

Link, J. S., and M. D. Ford. 2006. Widespread and persistent increase of Ctenophora in the continental shelf ecosystem off NE USA. Marine Ecology Progress Series 320:153–159.

Link, J. S., and L. P. Garrison. 2002. Changes in piscivory associated with fishing induced changes to the finfish community on Georges Bank. Fisheries Research 55:71–86.

Link, J. S., L. P. Garrison, and F. P. Almeida. 2002. Interactions between elasmobranchs and groundfish species (Gadidae and Pleuronectidae) on the northeast U.S. shelf. I: evaluating predation. North American Journal of Fisheries Management 22:550–562.

Loots, C., S. Vaz, B. Planque, and P. Koubbi. 2010. What controls the spatial distribution of the North Sea plaice spawning population? Confronting ecological hypotheses through a model selection framework. ICES Journal of Marine Science 67:244–257.

Manly, B. F. J. 1991. Randomization and Monte Carlo methods in biology. Chapman and Hall, London.

McCullagh, P., and J. A. Nelder. 1989. Generalized linear models, 2nd edition. Chapman and Hall, London.

Michalsen, K., O. R. Godø, and A. Fernō. 1996. Diel variation in the catchability of gadoids and its influence on the reliability of abundance indices. ICES Journal of Marine Science 53:389–395.

Miller, T. J., C. Das, P. J. Politis, A. S. Miller, S. M. Lucey, C. M. Legault, R. W. Brown, and P. J. Rago. 2010. Estimation of *Albatross IV* to *Henry B. Bigelow* calibration factors. National Marine Fisheries Service, Northeast Fisheries Science Center Reference Document 10-05, Woods Hole, Massachusetts.

Morgan, A. C., and J. A. Sulikowski. 2015. The role of Spiny Dogfish in the northeast United States continental shelf ecosystem: how it has changed over time and potential interspecific competition for resources. Fisheries Research 167:260–277.

Moustahfid, H., M. C. Tyrrell, J. S. Link, J. A. Nye, B. E. Smith, and R. J. Gamble. 2010. Functional feeding responses of piscivorous fishes from the northeast US continental shelf. Oecologia 163:1059–1067.

Murawski, S. A. 1991. Can we manage our multispecies fisheries? Fisheries 16(5):5–13.

NEFSC (Northeast Fisheries Science Center). 1991. Report of the twelfth northeast regional stock assessment workshop (12th SAW), spring 1991.

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

National Marine Fisheries Service, NEFSC Reference Document 91-03, Woods Hole, Massachusetts.

NEFSC (Northeast Fisheries Science Center). 2006. Report of the 43rd northeast regional stock assessment workshop (43rd SAW), Stock Assessment Review Committee (SARC) consensus summary of assessments. National Marine Fisheries Service, NEFSC Reference Document 06-25, Woods Hole, Massachusetts.

Overholtz, W. J., L. D. Jacobson, and J. S. Link. 2008. An ecosystem approach for assessment advice and biological reference points for the Gulf of Maine–Georges Bank Atlantic Herring complex. North American Journal of Fisheries Management 28:247−257.

Overholtz, W. J., J. S. Link, and L. E. Suslowicz. 2000. Consumption of important pelagic fish and squid by predatory fish in the northeastern USA shelf ecosystem with some fishery comparisons. ICES Journal of Marine Science 57:1147−1159.

Overholtz, W. J., and A. V. Tyler. 1985. Long-term responses of the demersal fish assemblages of Georges Bank. U.S. National Marine Fisheries Service Fishery Bulletin 83:507−520.

Palsson, W. A. 2009. The status of Spiny Dogfish in Puget Sound. Pages 53–65 *in* V. F. Gallucci, G. A. McFarlane, and G. G. Bargmann, editors. Biology and management of dogfish sharks. American Fisheries Society, Bethesda, Maryland.

Petrakis, G., D. N. MacLennan, and A. W. Newton. 2001. Day-night and depth effects on catch rates during trawl surveys in the North Sea. ICES Journal of Marine Science 58:50−60.

Rago, P. J., and K. A. Sosebee. 2013. Update on the status of Spiny Dogfish in 2013 and projected harvests at the Fmsy proxy and Pstar of 40%. Report to the Mid-Atlantic Fishery Management Council Scientific and Statistical Committee. Available: http://www.nefsc.noaa.gov/program_review/background2014/TOR3TerceiroDogfish2013%20Status%20Report%20and%20Projections.pdf. (April 2016).

Rose, G. A. 2004. Reconciling overfishing and climate change with stock dynamics of Atlantic Cod (*Gadus morhua*) over 500 years. Canadian Journal of Fisheries and Aquatic Sciences 61:1553−1557.

Rulifson, R. A., and T. M. Moore. 2009. Population estimates of Spiny Dogfish aggregations overwintering south of Cape Hatteras, North Carolina, using an area density method. Pages 133–138 *in* V. F. Gallucci, G. A. McFarlane, and G. G. Bargmann, editors. Biology and management of dogfish sharks. American Fisheries Society, Bethesda, Maryland.

Sagarese, S. R., M. G. Frisk, R. M. Cerrato, K. A. Sosebee, J. A. Musick, and P. J. Rago. 2014a. Application of generalized additive models to examine ontogenetic and seasonal distributions of Spiny Dogfish (*Squalus acanthias*) in the northeast (US) shelf large marine ecosystem. Canadian Journal of Fisheries and Aquatic Sciences 71:847−877.

Sagarese, S. R., M. G. Frisk, T. J. Miller, K. A. Sosebee, J. A. Musick, and P. J. Rago. 2014b. Influence of environmental, spatial, and ontogenetic variables on habitat selection and management of Spiny Dogfish in the northeast (US) shelf large marine ecosystem. Canadian Journal of Fisheries and Aquatic Sciences 71:567−580.

Salthaug, A., and S. Aanes. 2003. Catchability and the spatial distribution of fishing vessels. Canadian Journal of Fisheries and Aquatic Sciences 60:259−268.

Schwarz, G. 1978. Estimating the dimension of a model. Annals of Statistics 6:461−464.

Sissenwine, M. P., and E. W. Bowman. 1978. An analysis of some factors affecting the catchability of fish by bottom trawls. International Commission for the Northwest Atlantic Fisheries Research Bulletin 13:81–87.

Sosebee, K. A., and S. X. Cadrin. 2006. A historical perspective on the abundance and biomass of northeast demersal complex stocks from NMFS and Massachusetts inshore bottom trawl surveys, 1963–2002. National Marine Fisheries Service, Northeast Fisheries Science Center, Reference Document 06-05, Woods Hole, Massachusetts.

Stehlik, L. L. 2007. Essential fish habitat source document: Spiny Dogfish, *Squalus acanthias*, life history and habitat characteristics, 2nd edition. NOAA Technical Memorandum NMFS-NE-203.

Sulikowski, J. A., B. Galuardi, W. Bubley, N. B. Furey, W. B. Driggers, G. W. Ingram, and P. C. W. Tsang. 2010. Use of satellite tags to reveal the movements of Spiny Dogfish *Squalus acanthias* in the western North Atlantic Ocean. Marine Ecology Progress Series 418:249−254.

Tallack, S. M. L., and J. W. Mandelman. 2009. Do rare-earth metals deter Spiny Dogfish? A feasibility study on the use of electropositive "mischmetal" to reduce the bycatch of *Squalus acanthias* by hook gear in the Gulf of Maine. ICES Journal of Marine Science 66:315−322.

TRAC (Transboundary Resources Assessment Committee). 2010. Northwest Atlantic Spiny Dogfish. Fisheries and Oceans Canada, TRAC Status Report 2010/02. Available: http://www.asmfc.org/uploads/file/2010SpinyDogfishTRAC.pdf. (April 2016).

Trenkel, V. M., R. I. C. C. Francis, P. Lorance, S. Mahévas, M. Rochet, and D. M. Tracey. 2004. Availability of deep-water fish to trawling and visual observation from a remotely operated vehicle (ROV). Marine Ecology Progress Series 284:293−303.

Tyrrell, M. C., J. S. Link, and H. Moustahfid. 2011. The importance of including predation in fish population models: implications for biological reference points. Fisheries Research 108:1−8.

Vaz, S., S. Pavoine, P. Koubbi, C. Loots, and F. Coppin. 2006. Spatio-temporal characteristics of fish populations in relation to environmental forcing functions as a component of ecosystem-based assessment: effects on catchability. International Council for the Exploration of the Sea, CM 2006/O:06, Copenhagen.

Walsh, S. J. 1992. Size-dependent selection at the footgear of a groundfish survey trawl. North American Journal of Fisheries Management 12:625−633.

Wardle, C. S. 1993. Fish behaviour and fishing gear. Pages 609–644 *in* T. J. Pitcher, editor. Behaviour of teleost fishes, 2nd edition. Chapman and Hall, London.

Wintle, B. A., J. Elith, and J. M. Potts. 2005. Fauna habitat modelling and mapping: a review and case study in the lower Hunter central coast region of NSW. Austral Ecology 30:719−738.

Wood, S. N. 2006. Generalized additive models: an introduction with R. Chapman and Hall/CRC, Boca Raton, Florida.

Wood, S. N. 2014. Package 'mgcv.' Available: http://cran.r-project.org/web/packages/mgcv/index.html. (September 2014).

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York.

Downloaded From: https://complete.bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use