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**The population ecology of the spiny dogfish in the Northeast (US) shelf large marine
ecosystem: Implications for the status of the stock**

A Dissertation Presented

by

Skyler Rose Sagarese

to

The Graduate School

in Partial Fulfillment of the

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Doctor of Philosophy

in

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Abstract of the Dissertation

The population ecology of the spiny dogfish in the Northeast (US) shelf large marine ecosystem: Implications for the status of the stock

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In this dissertation, statistical and modeling approaches were undertaken to increase the knowledge of spiny dogfish distribution, habitat, and population dynamics including: (1), environmental preference (2), habitat modeling (3), assessing diel variation in survey catchability of spiny dogfish and key prey species and (4), elucidating how spiny dogfish distributional shifts influenced their availability to commercial fisheries. For objective (1), I estimated habitat preference for neonate (total length, $TL \leq 26$ cm), immature (male: $26 \text{ cm} < TL < 60$ cm; female: $26 \text{ cm} < TL < 80$ cm), and mature (male: $TL \geq 60$ cm; female: $TL \geq 80$ cm) spiny dogfish using Northeast Fisheries Science Center (NEFSC) annual bottom trawl survey data from 1963 through 2009. Preferences were compared between dogfish stages to relate movements and distribution to environmental and reproductive behavior. In addition, I explored the influence of density-dependence on distribution. For objective (2), I analyzed the quantitative relationship between spiny dogfish occurrence and abundance with ambient environmental and temporal factors, and

ecological factors (i.e., prey abundance, presence of conspecifics) in the NES LME using NEFSC survey data and generalized additive models (GAMs) to elucidate potential mechanisms underlying distributions of dogfish stages. For objective (3), I investigated diel variation on NEFSC survey catch rates and catchability and assessed the influence of temperature, depth, and Julian day on day-time capture probability. Lastly, for objective (4), I examined the spatio-temporal interactions between spiny dogfish distribution (derived from NEFSC survey data) and commercial fishers (derived from NEFSC Observer data) in the NES LME to elucidate how spiny dogfish distributional changes have impacted their availability to the fishery.

I found strong ontogenetic differences in seasonal and decadal distribution and habitat preference for spiny dogfish. All dogfish stages occupied warmer, more saline, and more southerly locations in autumn compared to those available during spring. In contrast, during autumn larger spiny dogfish occupied warmer, shallower, and less saline waters whereas neonates preferred more saline waters than those surveyed. In addition, spiny dogfish appeared more aggregated during autumn than spring. Dogfish stages differed considerably regarding preferred habitat during both seasons. Density appeared related to geographic range when all dogfish stages were combined during autumn.

Generalized additive modeling resulted in widespread significant nonlinear relationships throughout dogfish stages and seasons. Generally, seasonal occurrence was tightly linked to environmental properties (e.g., bottom temperature and depth) with temporal variables (e.g., year and Julian day) influential for some dogfish stages. Prey species considered for analyses included Atlantic butterfish (*Peprilus triacanthus*), Atlantic herring (*Clupea harengus*), shortfin squid (*Illex* sp.), longfin squid (*Loligo* sp.), and Atlantic mackerel (*Scomber scombrus*). While environment (e.g., bottom temperature and depth) and temporal (e.g., year and Julian day)

variables also influenced the abundances of most dogfish stages, ecological factors (e.g., *Loligo* sp. and *Illex* sp. abundances) significantly contributed to the abundances of mature females and neonates. Spring trends in abundance identified bottom temperature as highly influential for most dogfish stages whereas during autumn ecological factors predominantly controlled abundance. Forecasted distributions under different temperature scenarios during spring generally revealed higher probabilities of spiny dogfish occurrence throughout the range during a "warmer" ($BT_{avg} + 1^{\circ}C$) year but lower probabilities in northern regions during a "cooler" ($BT_{avg} + 1^{\circ}C$) year.

Day and night catch distributions differed significantly ($p_{adj} < 0.0045$) for spiny dogfish during spring and most prey species during both seasons, with larger day-time catches evident. Annual day-time catch rates exceeded night rates for most prey during both seasons, for spiny dogfish during autumn, and for both neonate and mature male spiny dogfish during spring. While larger and more frequent day-time aggregations were frequently observed for all species examined, only autumn-captured *Illex* sp. revealed a significant ($p_{adj} < 0.0045$) difference in the distribution of day and night aggregations. Most species revealed highly variable temporal *CPUE* during both seasons, often with higher rates during day-time. Significantly ($p < 0.05$) higher day-time catchability was observed for most dogfish stages and prey species during autumn but solely for mature male spiny dogfish and squid during spring. *CPUE* estimates adjusted for higher day-time catchability when appropriate resulted in lower *CPUE* estimates, suggesting the NEFSC survey is overestimating the overall and regional abundances of most species. Environmental factors frequently influenced the seasonal probability of day-time catch for all species and seasons.

Fishery-dependent analyses focused on the sink gill net and otter trawl fisheries, two of the largest domestic fisheries landing spiny dogfish since 1989. While both fisheries encountered

spiny dogfish throughout the NES LME during most calendar months, summer catches primarily occurred in the north whereas winter catches predominated in the south. During both seasons, spiny dogfish *CPUE* was more clustered ($I \sim 0.3$) in the SGN fishery compared to both the OT fishery ($I \sim 0.15$) and the survey ($I \sim 0.18$). Centers of spiny dogfish abundance differed significantly ($p < 0.05$) during each season and often differed among fisheries and the survey ($p_{adj} < 0.0167$). The spatial overlap between fisher effort and spiny dogfish distribution (SO_E) increased with time for the SGN fishery during spring and the OT fishery during autumn, suggesting a growing portion of the stock was available to each fishery. Direct spatial overlap of spiny dogfish distribution inferred from both survey and fishery catch (SO_C) revealed variable seasonal trends with interpolated overlap (SO_I) often exceeding but matching trends derived directly. Vulnerability of spiny dogfish to each fishery was generally higher during autumn and has increased recently for many dogfish stages.

Dedication

I'd like to dedicate this work to my family, friends, and the many teachers and mentors along the way for their inspiration, support, and help throughout my academic career. I'd especially like to thank my mom and dad for raising me as a nature lover and for supporting my pursuit of marine science.

Table of Contents

List of Figures.....	xiii
List of Tables.....	xvi
Acknowledgements.....	xviii
I. Introduction.....	1
Life history and management challenges.....	2
Elucidating drivers behind habitat preference, abundance, and distribution.....	6
Investigating survey catchability of spiny dogfish and key prey species.....	8
Assessing availability to the commercial fishery.....	9
Tables.....	12
Figures.....	17
II. Influence of environmental, spatial, and ontogenetic variables on habitat selection and management of spiny dogfish in the Northeast (US) shelf large marine ecosystem.....	20
Introduction.....	20
Methods.....	23
Data.....	23
Species distribution.....	24
Habitat preference and the degree of aggregation.....	24
Comparison of habitat preference.....	27
Decadal habitat preference and comparison.....	27
Density-dependence analysis.....	28
Results.....	29
Spatiotemporal distributions of spiny dogfish.....	29
Spatiotemporal distributions of spiny dogfish stages.....	30
Spatiotemporal abundance of spiny dogfish stages.....	32
Habitat preference and degree of aggregation.....	33
Survey conditions.....	33
Temperature.....	33
Salinity.....	34
Depth.....	35
Latitude.....	36
Degree of aggregation.....	37
Density-dependence.....	38
Discussion.....	39
Tables.....	45
Figures.....	51
III. Application of generalized additive models to examine ontogenetic and seasonal distributions of spiny dogfish in the Northeast (US) shelf large marine ecosystem.....	59

Introduction.....	59
Methods.....	62
Data source.....	62
Data.....	63
Variable selection.....	63
Spatial overlap with prey and conspecifics.....	64
Statistical analysis.....	65
Model fitting.....	65
Model selection.....	66
Model evaluation.....	67
Forecasting of occurrence under various temperature regimes.....	69
Results.....	69
Data.....	69
Spatial overlap with prey and conspecifics.....	70
GIC.....	70
LIC.....	71
Statistical analysis.....	71
General modeling results.....	71
Temporal trends.....	73
Environmental trends.....	73
Ecological trends.....	74
Model validation.....	74
Forecasting of occurrence under various temperature regimes.....	75
Discussion.....	76
Tables.....	84
Figures.....	94

IV. Is diel variation in catchability skewing survey-derived abundance estimates of spiny dogfish and their prey?.....	103
Introduction.....	103
Methods.....	105
Data source.....	106
Data.....	106
Distributional Analyses.....	107
<i>CPUE</i> Analyses.....	108
Day Night Catchability.....	109
Environmental Influences on Catchability.....	112
Results.....	112
Distributional Trends.....	113
Catches.....	113
Aggregations.....	113
Annual Trends.....	114
Catch rates.....	114
Temporal Trends.....	116
<i>CPUE</i>	116

Frequencies by Julian day.....	117
Day Night Catchability.....	117
Environmental Influences on Catchability.....	119
General Modeling Results.....	119
Environmental and Temporal Trends.....	120
Discussion.....	121
Tables.....	127
Figures.....	133
V. Spatio-temporal interactions between spiny dogfish and commercial fishers in the Northeast (US) shelf large marine ecosystem.....	143
Introduction.....	143
Methods.....	146
Data sources.....	146
Fisheries-dependent.....	146
Fisheries-independent.....	147
Data.....	147
Spatial distribution.....	148
Spatial autocorrelation.....	148
Center of abundance.....	149
Spatial analyses.....	150
Semivariograms.....	150
Grid determination.....	152
Spatial overlap.....	152
Vulnerability to fishery.....	155
Map-correlation analysis.....	155
Results.....	156
Commercial catch distributions.....	156
Overall catch.....	156
Monthly catch distribution.....	156
Spatial autocorrelation.....	157
Center of abundance.....	157
Spatial analysis.....	158
Semivariogram trends.....	158
Grid size.....	160
Spatial overlap of spiny dogfish distribution with fishery effort.....	161
Spatial overlap of spiny dogfish distribution with fishery catch.....	162
Vulnerability to fishery.....	164
Map-correlation analysis.....	165
Spiny dogfish distribution and fishery effort.....	165
Spiny dogfish distribution and fishery catch.....	166
Discussion.....	166
Tables.....	173
Figures.....	178

VI. Summary.....	190
References.....	195
Appendix.....	216
1A. Summary of stock assessment efforts put forth by the Northeast Fisheries Science Center (NEFSC) on marine resources within the NES LME.....	216
2A. Decadal distributions and regional catch of spiny dogfish.....	218
2B. Spiny dogfish abundance.....	228
2C. Decadal habitat preference and degree of aggregation for spiny dogfish.....	231
2D. Density-dependence.....	246
3A. Boosted regression tree analysis.....	249
3B. Model selection.....	251
3C. Full GAM modeling results.....	255
3D. Occurrence (PA) models for autumn.....	267
3E. Occurrence (PA) models for spring.....	284
3F. Abundance (PRES) models for autumn.....	297
3G. Abundance (PRES) models for spring.....	314
3H. Projected distributions under different temperature scenarios.....	332
4A. Factors considered influential on survey catchability.....	340
4B. Tow classification of NEFSC survey stations.....	342
4C. Aggregations of spiny dogfish and prey species.....	343
4D. Diel- and depth-dependent catch rates of spiny dogfish and prey species.....	344
4E. Diel habitat preference for spiny dogfish and prey species.....	355
4F. Regional <i>CPUE</i> estimates adjusted for diel variation.....	371
4G. Full GAM results for probability of day-time catch during spring.....	380

4H. Full GAM results for probability of day-time catch during autumn.....	392
4I. Comparison of <i>CPUE</i> from NEFSC bottom trawl survey and fishery-dependent mid-water trawl survey.....	404
5A. Summary of commercial fishery statistics.....	405
5B. Statistics for Moran's I.....	407
5C. Statistics for center of spiny dogfish abundance.....	409
5D. Semivariogram modeling.....	412
5E. Spatial distribution of fishery effort.....	436
5F. Spatial distribution of spiny dogfish catch by fisheries and the NEFSC survey.....	457

List of Figures

Figure 1.1: Map of the Northeast (US) shelf large marine ecosystem (NES LME) where the Northeast Fisheries Science Center (NEFSC) annual bottom trawl survey is conducted during autumn and spring.....	17
Figure 1.2: Annual commercial landings of Atlantic cod (<i>Gadus morhua</i>) and spiny dogfish (<i>Squalus acanthias</i>) for the Atlantic region in metric tons and price per metric ton.....	18
Figure 1.3: Summary of stock assessment efforts within the NES LME conducted by the NEFSC on marine resources since the first Stock Assessment Workshop (SAW) in 1985.....	19
Figure 2.1: Annual seasonal movements of spiny dogfish within the NES LME.....	51
Figure 2.2: Decadal distribution and regional survey catch of spiny dogfish in the NES LME during spring (1968 – 2009).....	52
Figure 2.3: Decadal distribution and regional survey catch of spiny dogfish in the NES LME during autumn (1963 – 2009).....	53
Figure 2.4: Regional relative abundance of spiny dogfish in the NES LME during spring (1968 – 2009) and autumn (1963 – 2009).....	54
Figure 2.5: Cumulative distributions of available and occupied habitat for spiny dogfish in the NES LME during spring between 1968 and 2009.....	55
Figure 2.6: Cumulative distributions of available and occupied habitat for spiny dogfish in the NES LME during autumn between 1963 and 2009.....	56
Figure 2.7: Annual variation in the distribution index D_{95} , or minimum area over which 95% of the spiny dogfish population is spread, during autumn and spring in the NES LME from 1963 to 2009	57
Figure 2.8: Relationship between annual $CPUE$ of all spiny dogfish and the distribution index for autumn and spring in the NES LME.....	58
Figure 3.1: Map of the Northeast (US) shelf large marine ecosystem (NES LME) where the NEFSC annual bottom trawl survey is conducted during autumn and spring.....	94
Figure 3.2: Partial GAM plots for the occurrence of mature males during autumn identifying the additive effect of each variable on the response.....	95
Figure 3.3: Partial GAM plots for the occurrence of immature males during spring identifying the additive effect of each variable on the response.....	96
Figure 3.4: Partial GAM plots for the abundance of mature females during autumn identifying	

the additive effect of each variable on the response.....	97
Figure 3.5: Partial GAM plots for the abundance of immature males during spring identifying the additive effect of each variable on the response.....	98
Figure 3.6: Partial GAM derived effects of important interactions on the occurrence of mature males during autumn and immature males during spring and on the abundance of mature females during autumn and immature males during spring.....	99
Figure 3.7: Comparison of the predicted probability of occurrence as determined by inverse distance weighting interpolation versus observed occurrence in the NES LME during spring for spiny dogfish stages.....	100
Figure 3.8: Hypothetical predicted probability of mature female spiny dogfish occurrence during spring in the NES LME for a year exhibiting average, warmer, and cooler bottom temperatures.....	101
Figure 3.9: Hypothetical predicted probability of neonate spiny dogfish occurrence during spring in the NES LME for a year exhibiting average, warmer, and cooler bottom temperatures.....	102
Figure 4.1: Map of the Northeast (US) shelf large marine ecosystem where the NEFSC annual bottom trawl survey is conducted during spring and autumn.....	133
Figure 4.2: Illustration of the concept behind the logistic model used in Casey and Myers (1998) where the y-intercept is an estimate of the relative diel catchability.....	134
Figure 4.3: Locations of spiny dogfish aggregations during spring and autumn in the NES LME between 1963 and 2009 during the day and night.....	135
Figure 4.4: Locations of prey species aggregations during spring and autumn in the NES LME between 1963 and 2009 during the day and night.....	136
Figure 4.5: Breakpoint analysis of temporal <i>CPUE</i> for spiny dogfish stages and prey species during spring in the NES LME.....	137
Figure 4.6: Breakpoint analysis of temporal <i>CPUE</i> for spiny dogfish stages and prey species during autumn in the NES LME.....	138
Figure 4.7: Probability of day-time capture for spiny dogfish stages and prey species during spring and autumn in the NES LME.....	139
Figure 4.8: Unadjusted <i>CPUE</i> and day-night adjusted <i>CPUE</i> when necessary for All Regions during the autumn NEFSC bottom trawl survey for spiny dogfish and prey species.....	140

Figure 4.9: Partial GAM plots for the probability of day-time catch for spiny dogfish and prey species for All Regions combined during autumn identifying the additive effect of each variable on the response.....	141
Figure 4.10: Partial GAM plots for the probability of day-time catch for spiny dogfish and prey species for All Regions combined during spring identifying the additive effect of each variable on the response.....	142
Figure 5.1: Spiny dogfish commercial catch since 1989 according to NESFC fisheries observer data during autumn and spring in the NES LME.....	178
Figure 5.2: Monthly <i>CPUE</i> of spiny dogfish by the commercial sink gill net fishery based on fishery observer records in the NES LME.....	179
Figure 5.3: Monthly <i>CPUE</i> of spiny dogfish by the commercial otter trawl fishery based on fishery observer records in the NES LME.....	181
Figure 5.4: Annual degree of clustering of spiny dogfish <i>CPUE</i> for the sink gill net fishery, otter trawl fishery, and NEFSC bottom trawl survey during autumn and spring.....	183
Figure 5.5: Seasonal degree of clustering of spiny dogfish <i>CPUE</i> for the sink gill net fishery, otter trawl fishery, and NEFSC bottom trawl survey during autumn and spring.....	184
Figure 5.6: Annual centers of spiny dogfish abundance observed by the sink gill net fishery, otter trawl fishery, and NEFSC bottom trawl survey during autumn and spring between 1989 and 2009 in the NES LME.....	185
Figure 5.7: Sample and fitted variograms of spiny dogfish <i>CPUE</i> for the overall time series (1989 – 2009) in the NES LME for the sink gill net and otter trawl fisheries and the NEFSC bottom trawl survey during autumn and spring.....	186
Figure 5.8: Percent spatial overlap of spiny dogfish distribution derived from the NEFSC trawl survey with commercial fisher effort from the sink gill net and otter trawl fisheries during autumn and spring in the NES LME.....	187
Figure 5.9: Percent spatial overlap of spiny dogfish distribution derived from the NESFC trawl survey with commercial fisher catch for the sink gill net and otter trawl fisheries during autumn and spring in the NES LME.....	188
Figure 5.10: Proportion of the spiny dogfish stock vulnerable to the sink gill net and otter trawl fisheries during autumn and spring in the NES LME.....	189

List of Tables

Table 1.1: Summary of major findings and research recommended by spiny dogfish stock assessments conducted by the Northeast Fisheries Science Center (NEFSC) Stock Assessment Workshops (SAW).....	12
Table 1.2: Summary of major findings and research recommended by spiny dogfish stock assessments conducted by the joint United States and Canadian Transboundary Resources Assessment Committee (TRAC).....	16
Table 2.1: Habitat associations of spiny dogfish in the Northeast (US) shelf large marine ecosystem (NES LME) during autumn (1963 – 2009) and spring (1968 -2009).....	45
Table 2.2: Seasonal habitat comparisons for spiny dogfish in the NES LME by stage during autumn (1963 – 2009) and spring (1968 – 2009).....	46
Table 2.3: Decadal habitat associations of spiny dogfish in the NES LME during autumn (1963 – 2009) and spring (1968 – 2009).....	47
Table 2.4: Gini index quantifying the degree of aggregation for spiny dogfish in the NES LME during autumn (1963 – 2009) and spring (1968 – 2009).....	50
Table 3.1: Summarization of spiny dogfish occurrence and abundance used in generalized additive models (GAMs).....	84
Table 3.2: Variables identified as potential explanatory variables for modeling spiny dogfish occurrence and abundance after preliminary exploratory data analyses on both spring and autumn NEFSC bottom trawl datasets.....	85
Table 3.3: Pearson correlation matrix for variables of interest derived from the NEFSC bottom trawl survey spanning the NES LME for autumn and spring.....	86
Table 3.4: Average annual global and local indices of collocation for spiny dogfish life-history stages with prey species and other stages based on swept-area density estimates during autumn and spring in the NES LME.....	87
Table 3.5: Abbreviated GAM results describing the occurrence and abundance of mature female and male spiny dogfish during autumn and spring in the NES LME since 1980	88
Table 3.6: Abbreviated GAM results describing the occurrence and abundance of immature female and male spiny dogfish during autumn and spring in the NES LME since 1980..	90
Table 3.7: Abbreviated GAM results for the occurrence and abundance of neonate spiny dogfish during autumn and spring in the NES LME since 1963.....	92

Table 3.8: Validation measures for the optimal occurrence and abundance models for spiny dogfish in the NES LME based on independent test datasets for autumn and spring.....	93
Table 4.1: Night and day catch distributions for spiny dogfish and prey species during spring and autumn in the NES LME.....	127
Table 4.2: Annual bottom trawl catch ratios for spiny dogfish and prey species at different times of the day and water depths from the NEFSC annual bottom trawl survey conducted in the NES LME during spring and autumn.....	128
Table 4.3: Frequency analysis of the number of Julian days dominated by <i>CPUE</i> trends for spiny dogfish and prey species in the NES LME during spring and autumn.....	129
Table 4.4: Seasonal and regional estimates of diel catchability for spiny dogfish and prey species in the NES LME during spring and autumn.....	130
Table 4.5: GAM results for the probability of day-time catches for spiny dogfish and prey species during spring.....	131
Table 4.6: GAM results for the probability of day-time catches for spiny dogfish and prey species during autumn.....	132
Table 5.1: Permutational MANOVA on Bray-Curtis distances for the center of spiny dogfish abundance based on three modes of fishing during autumn and spring.....	173
Table 5.2: Best-fit semivariogram models and parameters for the spatial distributions of spiny dogfish <i>CPUE</i> derived from the sink gill net and other trawl fisheries and the NEFSC bottom trawl survey for the overall time series (1989 – 2009) during autumn and spring in the NES LME.....	174
Table 5.3: Spatial overlap and map-correlation of spiny dogfish distribution and commercial fisher effort during autumn and spring between 1989 and 2009 in the NES LME.....	175
Table 5.4: Spatial overlap and map-correlation of spiny dogfish catch in the sink gill net fishery and the NEFSC bottom trawl survey during autumn and spring between 1989 and 2009 in the NES LME.....	176
Table 5.5: Spatial overlap and map-correlation of spiny dogfish catch in the otter trawl fishery and the NEFSC bottom trawl survey during autumn and spring between 1989 and 2009 in the NES LME.....	177

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Chapter 1:

INTRODUCTION

Continental shelf waters off the northeastern United States have supported lucrative commercial fisheries since at least the 16th century (German 1987, Fogarty & Murawski 1998). Historically, fishers targeted highly profitable and abundant groundfish including cod and flounder throughout the Gulf of Maine, Georges Bank and Southern New England (Figure 1.1) (Fogarty & Murawski 1998). However, intensive foreign and domestic fishing effort during the 1970s reduced these stocks, causing an indirect biomass "outburst" of less valuable small elasmobranchs during the 1980s (Link et al. 2002, Frisk et al. 2008). While these changes greatly altered ecosystem structure, they also presented new challenges to both fishers and resource managers. To maintain their livelihood, commercial fishers were forced to target previously undesirable skates and dogfish (Figure 1.2A) (Rago et al. 1998, McMillan & Morse 1999). Beginning in 1976, resource managers were required by the Magnuson-Stevens Fishery Conservation and Management Act to manage fishery resources as sustainably as possible. Unfortunately, a paucity of knowledge and data concerning population dynamics, particularly for elasmobranchs (NEFC 1985, 1990), has complicated both past and present management.

As fisheries ecology shifts towards ecosystem-based fisheries management (EBFM) (Link et al. 2011), it is imperative to elucidate the population dynamics and ecological roles of low valued (Figure 1.2B) and lesser studied species. This work focuses on one such species, the spiny dogfish (*Squalus acanthias*), previously underutilized and historically considered a

nuisance (Jensen 1965). Since the inception of federal stock assessments within the northeastern US, most have focused on commercially important fishes (Figure 1.3; Table 1A.1). Originally assigned low assessment priority in 1985, few federal (Table 1.1) and international (Table 1.2) spiny dogfish assessments have been conducted and, when they are, often cite data limitations and uncertainties in key population parameters. The main goals of this dissertation are to provide vital information on habitat, environmental and ecological factors (i.e., prey abundance) driving seasonal distributions, diel catchability of trawl surveys, and how distributional changes alter their availability to commercial fisheries within the Northeast (US) shelf large marine ecosystem (NES LME) (Figure 1.1). Ultimately, these findings will help reduce variability surrounding survey estimates of abundance, thereby enhancing the reliability of stock assessments for spiny dogfish.

Life history and management challenges

Spiny dogfish is a small, slow growing, long-lived elasmobranch present in both oceanic and coastal environments throughout the Atlantic (Templeman 1984, Nammack et al. 1985, Henderson et al. 2002, Stenberg 2005, Campana et al. 2006), Pacific (Saunders & McFarlane 1993, McFarlane & King 2003, Brodeur et al. 2009), and Mediterranean/Black Seas (Avsar 2001, Chatzisprou & Megalofonou 2005, Demirhan & Seyhan 2007). Recent morphological and molecular evidence has distinguished the Atlantic population (*S. acanthias*) from the North Pacific population (*S. suckleyi*) (Ebert et al. 2010, Veríssimo et al. 2010), increasing the demands for stock-specific data collection. In the Northwest Atlantic, spatial structuring of the population is suggested by the presence of a resident component in the Gulf of St. Lawrence and a trans-boundary component migrating seasonally between US and Canadian waters (Campana et al.

2007, TRAC 2010a). For management purposes within the NES LME, spiny dogfish is considered a single unit stock (NEFSC 1994).

Like many elasmobranchs, their life-history characteristics make spiny dogfish extremely vulnerable to overfishing (Stevens et al. 2000). While spiny dogfish in the Pacific can live up to 100 years (Tribuzio & Kruse 2011), longevity within the northwest Atlantic is estimated at 45 years (Campana et al. 2006). Females and males mature late in life at approximately 12 years (80 cm total length, TL) and 6 years (60 cm TL), respectively (Burgess 2002, Sosebee 2005). Spiny dogfish possess one of the longest gestation periods (18-22 months) (Hisaw & Albert 1947, Burgess 2002), rivaling that of the African elephant (*Loxodonta africana*) (22 months) (Laws et al. 1975, Foley et al. 2001). Spiny dogfish are yolk-sac viviparous and produce small litters ranging from 1 to 15 individuals and average 4.4 free-living embryos per year (Sosebee 2005). Females are available to breed anytime (Verissimo et al. 2011) with parturition occurring every other year (Gauld 1979, Stenberg 2005). Reportedly, mating occurs in offshore waters during summer (Henderson et al. 2002) and parturition occurs during winter (Holden & Meadows 1962, Nammack et al. 1985, Jones & Ugland 2001, Henderson et al. 2002). Recruitment is believed to be strongly related to spawning stock biomass (i.e., mature female (TL \geq 80 cm) abundance) (ASMFC 2002). Based on these factors, spiny dogfish is considered one of the least productive elasmobranchs (Hisaw & Albert 1947, Smith et al. 1998, Cortés 2000, Stevens et al. 2000, Burgess 2002, Campana et al. 2006), a taxon already known for low productivity.

For spiny dogfish within the NES LME, complexities relating to behavior have also hindered commonly employed virtual population analysis (VPA) to model stock dynamics. Large-scale trans-boundary seasonal movements are undertaken by spiny dogfish, with a majority of the population spending colder months in the Mid-Atlantic and traveling north to the

Georges Bank/ Gulf of Maine during summer (Burgess 2002). Although rare, trans-Atlantic movements have been observed (Templeman 1976, Overholtz & Tyler 1985, Burgess 2002). As such, surveys tend to capture a high degree of (biologically unrealistic) variability (NEFSC 2006) in seasonal and decadal distributional trends (Overholtz & Tyler 1985, Rago et al. 1998, Rago & Sosebee 2009). These fluctuations in survey abundance are thought to result from variability in the timing of movement and not necessarily related to population abundance (Overholtz & Tyler 1985). In summary, this unpredictable timing can prove challenging when trying to decipher between population fluxes and seasonal movements (Overholtz and Tyler 1985).

Over the last decade, spiny dogfish has been recognized as a species of ecological importance within the NES LME. Ecologically, they have gained attention for their diverse feeding habits (Stehlik 2007) and potential predation on commercially important groundfish (Fogarty & Murawski 1998, Link et al. 2002). Considered a key piscivore since the decline of Atlantic cod (*Gadus morhua*) (Link & Garrison 2002), spiny dogfish are opportunistic predators (Link & Ford 2006, Stehlik 2007) and have very few natural predators (Bowman et al. 2000, Stehlik 2007). The amount of prey consumed often parallels the relative abundance of their prey items (Moustahfid et al. 2010). In this species, piscivory increases with size as smaller individuals generally consume ctenophores, shrimp, squid and small fishes (Garrison & Link 2000) while larger individuals feed upon pelagic prey such as clupeids, squid, scombrids, and other teleosts (Grosslein et al. 1980, Link & Almeida 2000, Overholtz et al. 2000). The presence of ctenophores within spiny dogfish stomach contents has been used to elucidate abundance trends for this difficult to sample gelatinous species (Link & Ford 2006). Removals of spiny dogfish from the ecosystem have been suggested to boost the recovery of groundfish stocks by

relaxing predation and competition on these depleted stocks (Murawski 1991, Fogarty & Murawski 1998). However, Link et al. (2002) found groundfish in less than 1% of the 40,756 spiny dogfish stomachs examined and declared a weak effect of elasmobranch predation on groundfish recruitment (Link et al. 2002).

In recent years, intense debate surrounding the stock status of spiny dogfish has occurred between the fishing and scientific communities. While fishermen report spiny dogfish in overwhelming abundance, often destroying gear or consuming catch, evidence of declining trends in size, fecundity and recruitment have been observed in monitoring surveys from multiple agencies: Northeast Fisheries Science Center (NEFSC), Massachusetts Division of Marine Fisheries (MADMF), and Atlantic States Marine Fisheries Commission (ASMFC) (Rago et al. 1998, Sosebee 2005, NEFSC 2006, Rago & Sosebee 2009). Selective harvest of large fecund females has amplified concerns regarding the ability of this stock to recover from overexploitation (Rago & Sosebee 2009). While the rebuild was expected by 2020 (ASMFC 2002), target reference points were met in 2010 (Rago & Sosebee 2010), partly the result of an abnormally large spawning stock estimate (i.e., mature female abundance) in the 2006 spring bottom trawl survey (NEFSC 2006). This nearly five-fold increase in estimated stock size compared to previous years was biologically unrealistic given the life history characteristics of this species (NEFSC 2006).

In the remainder of this introduction and thereafter, I will highlight my approaches that enhance our understanding of spiny dogfish distribution, movements, catchability and ecology. Ultimately, these results will contribute vital information enhancing the reliability of stock assessments necessary for management.

Elucidating drivers behind habitat preference, abundance, and distribution

Stock assessment of spiny dogfish draws heavily on relative abundance indices derived from fishery-independent trawl surveys, with neonate ($TL \leq 26$ cm) and mature female abundance serving as proxies for recruitment and spawning stock biomass (SSB), respectively (NEFSC 2003). As a result, assessment models can be extremely sensitive to deviations and errors within these estimates. Environmental conditions have the potential to change the local distribution and abundance of a species and/or introduce variability into catch (O'Brien & Rago 1996, Bigelow et al. 1999). If survey catchability fluctuates with the environment, skewed estimates can misrepresent actual trends (Murawski & Finn 1988, Perry & Smith 1994, Swain & Sinclair 1994, Smith & Page 1996, Tomkiewicz et al. 1998, Shepherd et al. 2002). As an example, higher relative trawl catches of Atlantic cod were associated with more cold-intermediate water on the seafloor, thereby altering the availability of this species (Smith & Page 1996). Prey distribution, an ecological driver, can also influence a species' spatial pattern by concentrating predators in prey-dense areas (Stoner et al. 2001).

Preferred habitat, a factor of the drivers discussed above, can vary by life-history stage, resulting in differences in stage-specific abundance and distribution at broad spatial scales (Methratta & Link 2007). Understanding how dogfish stages respond to various drivers will help reduce uncertainty in survey estimates of stock size and composition thereby enhancing trend monitoring. Representing these relationships, particularly in the face of climate change (Hedger et al. 2004, Nye et al. 2009), will improve assessment models and enable better prediction of sustainable fishing limits for a changing environment (Maravelias 1999, Begg & Marteinsdottir 2002, Brodeur et al. 2009, Murase et al. 2009, Damalas et al. 2010). In my dissertation I will analyze ontogenetic spiny dogfish habitat and distribution to elucidate the effects of

environmental influences and interspecific relationships (i.e., predator/prey) on seasonal distributions.

In the second chapter, I present results on seasonal and decadal habitat preference for neonate, immature (male: $26 \text{ cm} < \text{TL} < 60 \text{ cm}$; female: $26 \text{ cm} < \text{TL} < 80 \text{ cm}$), and mature (male: $\text{TL} \geq 60 \text{ cm}$; female: $\text{TL} \geq 80 \text{ cm}$) spiny dogfish in the NES LME during autumn and spring. Habitat variables of interest include bottom temperature, bottom salinity, depth, and latitude. The analyses are based on data collected by the NEFSC annual bottom trawl survey conducted since 1963 and 1968 during autumn and spring, respectively, and the methods of Perry and Smith (1994). Subsequently, I compare habitat preference among dogfish stages to elucidate distribution patterns in relation to reproductive behavior. I also present results on the influence of density-dependence on distribution and abundance. The paper will be authored by myself and my advisor Dr. Michael Frisk, Dr. Tom Miller from the University of Maryland Center for Environmental Science (UMCES), Dr. Paul Rago and Kathy Sosebee from the NEFSC, and Dr. Jack Musick from the Virginia Institute of Marine Science (VIMS).

In the third chapter, I present a second analysis aimed at describing spiny dogfish habitat and distribution in the NES LME. Using two-stage generalized additive models (GAMs) and the same NEFSC dataset described above, I analyze the quantitative relationship between both spiny dogfish occurrence and abundance with ambient environmental, temporal, spatial, and ecological (i.e., prey abundance, conspecific presence) factors. Few studies simultaneously link predator and prey abundances due to a lack of appropriate data (Stoner et al. 2001). Based on my results, I propose potential mechanisms driving the distributions of each dogfish stage and forecast their distributions under various temperature scenarios. The paper will be authored by myself, my

advisor Dr. Michael Frisk, my committee chair Dr. Robert Cerrato, Dr. Paul Rago and Kathy Sosebee from the NEFSC, and Dr. Jack Musick from VIMS.

Investigating survey catchability of spiny dogfish and key prey species

Usage of abundance indices from scientific surveys for stock assessment often requires numerous assumptions, one of the most common citing that catchability, or the fraction of the population caught by one unit of effort (e.g. area swept by bottom trawl), remains constant in space and time (Francis et al. 2003, Fraser et al. 2007). Catchability combines with local abundance and fishing effort to generate catch rates (Michalsen et al. 1996, Ward & Myers 2005). Therefore, the accuracy of many stock assessments generally depends heavily on the reliability of this assumption (Hjellvik et al. 2002). Diurnal migrations have the potential to reduce the reliability of bottom trawl catch rates by influencing their availability at the bottom (Michalsen et al. 1996, Casey & Myers 1998, Petrakis et al. 2001, Adlerstein & Ehrich 2003). In addition, assessing diel-dependent migrations of predators and their respective prey can expose the potential for ecological interactions.

Although the position of an individual in the water column may seem trivial, the resultant biases in catchability can mislead abundance estimates derived from monitoring surveys (Francis & Williams 1995, Hjellvik et al. 2002). For spiny dogfish, this issue was raised at the Transboundary Resources Assessment Committee (TRAC) benchmark modeling meeting held in Woods Hole, MA, during January 2010. Attendees suggested that differences in day versus night catch rates may contribute to the unexplainable oscillations in biomass, either through year effects or an operational effect via diel migrations. While long-term data exists for this elasmobranch, many uncertainties remain; it is unclear whether their catchability in fishery-

independent surveys is influenced by the time of day (i.e., day versus night), depth of the survey, and/or is stage-dependent.

In the fourth chapter, I explore catch rate distributions, variability in catchability of dogfish stages, and their relationships with important prey species in the spring and autumn NEFSC bottom trawl surveys to improve the reliability of abundance estimates. Prey species include Atlantic butterfish (*Peprilus triacanthus*), Atlantic herring (*Clupea harengus*), shortfin squid (*Illex* sp.), longfin squid (*Loligo* sp.), and Atlantic mackerel (*Scomber scombrus*) and are chosen based on trends within the NEFSC Food Web Dynamics Program (FWDP) food habits database (Link & Almeida 2000). Catch rates are examined for diel (day vs. night) and depth (shallow vs. deep) effects while the effects of environmental factors (depth, bottom temperature, Julian day) on day-time catch probability are explored using GAMs. Simultaneous collection by the NEFSC survey enables a detailed investigation of how various factors influence the catchability of both predator and prey and how this may influence multi-species interactions. *CPUE* estimates adjusted for diel variation are presented where necessary. Understanding how spiny dogfish and their prey species respond to diel and environmental factors will benefit not only single-species assessment but will provide vital information concerning multi-species interactions for EBFM. The paper will be authored by myself, my advisor Dr. Michael Frisk, my committee chair Dr. Robert Cerrato, Dr. Paul Rago and Kathy Sosebee from the NEFSC, and Dr. Jack Musick from VIMS.

Assessing availability to the commercial fishery

Stock assessments can benefit from an increased understanding of fleet dynamics and the behavior of individual fishers (Salas & Gaertner 2004, Branch et al. 2006). Fishery-dependent

surveys offer an inexpensive opportunity to obtain highly detailed data on commercially exploited species over large temporal and spatial scales (Bertrand et al. 2004, Hilborn 2007). While these surveys provide estimates of relative abundance, their reliability is often questioned due to variations in catchability between different gears (Arreguín-Sánchez 1996, Harley & Myers 2001, Salthaug & Aanes 2003) and non-random fishing patterns (Paloheimo & Dickie 1964, Salthaug & Aanes 2003, Ellis & Wang 2007). In addition, improvements in technology and social networking have made fishermen highly capable of targeting and capturing stocks, further altering their catchability over time (Hilborn & Walters 1992).

Changes in the spatial distribution of a species within fishing grounds can greatly impact their availability to and the catchability of a fishery (Fréon et al. 1993, Pennington & Godø 1995, Smith & Page 1996, Godø et al. 1999). If fleets target high abundance areas, the catchability and resulting fishery-dependent biomass estimates may be artificially high due to hyperaggregation, or the aggregation of fish at low abundance (Rose & Kulka 1999). Spiny dogfish is a species of great concern for hyperaggregation because of its demographics and high potential for non-linearity of the catchability coefficient (Frisk et al. 2011). In addition, the large-scale seasonal movements and resultant changes in spatial and temporal distribution have the potential to greatly influence their availability to the fishery. To this date, little effort has been expended to explore how fishery catchability of spiny dogfish has varied with their distribution.

In the final chapter of the dissertation, I use the NEFSC trawl survey data and data derived from the large-scale NEFSC observer program (Anderson 1992) to describe the spatio-temporal interactions among spiny dogfish and commercial fishers throughout the NES LME between 1989 and 2009. This time period covers the many phases of the directed spiny dogfish fishery: commencement, development, overexploitation, and recovery. I analyze fisher and

survey behavior in terms of effort distribution and track changes in annual centers of spiny dogfish abundance. Semivariogram modeling provides an appropriate and identical cell size enabling the comparison of spatial overlap between fisher effort or catch and spiny dogfish distribution as derived from the survey. I estimate both direct and interpolated spatial overlap to explore changes in distribution and availability to two major commercial fisheries: sink gill net (SGN) and otter trawl (OT). Lastly, I quantify the proportion of the spiny dogfish population vulnerable to each fishery to elucidate changes in the availability or catchability of this stock over time. The paper will be authored by myself, my advisor Dr. Michael Frisk, my committee chair Dr. Robert Cerrato, Dr. Paul Rago and Kathy Sosebee from the NEFSC, and Dr. Jack Musick from VIMS.

Table 1.1. Summary of major findings and research recommended by spiny dogfish stock assessments conducted by the Northeast Fisheries Science Center (NEFSC) through Stock Assessment Workshops (SAW).

SAW (Year)	
1 st (1985)	<p><u>Major findings:</u></p> <ul style="list-style-type: none"> • Low assessment priority based on federal/other agency needs <p><u>Suggestions:</u></p> <ul style="list-style-type: none"> • Bycatch, discard mortality, & predator/prey relationships likely important • Uncertainty/variability surrounding growth rates & survey abundance indices
11 th (1990)	<p><u>Major findings:</u></p> <ul style="list-style-type: none"> • Large discard component in shrimp & groundfish fisheries • New assessment/analysis using yield-per-recruit approach • Current stock biomass appears at record high level; survey indices have ↑d steadily over the decade • Recommend sustainable annual exploitation rate of 10% <p><u>Suggestions:</u></p> <ul style="list-style-type: none"> • Use caution if exploitation rate ↑d; life history characteristics suggest high degree of vulnerability • Assessments require more precision • Improve survey indices of abundance/biomass & estimate absolute population size • Examine changes in population demographics (size, age, sex composition) over time • Determine stock recruitment relationships from survey • Explore trophic dynamics & role in ecosystem • Estimate removals from the stock through discards
18 th (1994)	<p><u>Major findings:</u></p> <ul style="list-style-type: none"> • 1st formal assessment in spite of poor data • High biomass level but spawning portion has not ↑d since the 1980s; ↑ in biomass cannot be fully explained • Beginning to see ↓s in landings per-unit-of-effort, mean length in commercial landings & in NEFSC survey • Still uncertainty in maximum age (50 years?) & natural mortality rate (0.092?) • Recruitment estimated by individuals ≤ 35 cm in spring catches, depends on evaluation of incomplete vulnerability to survey gear & sampling variability • Fishable & spawning stock biomass will continue to ↓ given the current level of exploitation <p><u>Suggestions:</u></p> <ul style="list-style-type: none"> • Coordinate US & Canadian assessment/management • Need to evaluate role in ecosystem & ecological impact on other species

SAW

(Year)

-
- 18th
(cont'd)
- Additional sampling, analysis, & research required to reduce uncertainty in population biology, landings & discard data

- 37th
(2003)
- Major findings:
- ↑ in total landings (1990 – 1996) accompanied by a 311% ↑ in numbers landed
 - Estimated discard mortality based on sea sampling (observer) data still uncertain
 - Swept-area estimates of stock biomass exhibit annual variation that exceeds biologically realistic changes for such a long-lived species
 - Average size of mature females has ↓d from about 95 to 85 cm in NEFSC, MADMF, NC SeaMap surveys
 - Pup weight & average pup weight ↑s with maternal length; larger females produce larger clutches of eggs & larger average-sized pups
 - 1997-2003: number of pups produced lower than expected even when accounting for reduced abundance of mature females; ↓ in pup size in smaller females potential mechanism?
 - Median size of retained dogfish in MA fisheries has ↓d from 77 cm in 2000 to 65 cm in 2002
 - Scenarios reveal rebuilt population by 2020 using F status quo (F of 2002), F = 0.03, or no commercial quota (no landings in US)
 - Scenario with US landings (3992 *mt*) & Canadian landings (3400 *mt*) fails to rebuild over 30 yr
 - Nominal footprint assumption adequately characterizes true size of population
 - Biomass dynamics model from 1994 poor, not pursued further

Suggestions:

- Estimate post-capture survival & discard mortality rates
- More detailed analyses (GLM, GAM) to identify the association between effort & discards
- Additional work necessary to understand differences between abundance patterns in US & Canadian surveys
- Additional analyses of Canadian data regarding ↓ing mature female size
- Allocate landings to statistical area using Vessel Trip Reports data from 1994+
- Evaluate utility of length frequency from NEFSC Observer Program from 2001+
- Incorporate 2000+ MADMF Observer data into the NEFSC database
- Conduct tagging & genetic studies in US & Canadian waters to investigate stock structure
- Study herding properties of gear for spiny dogfish & other demersal groundfish
- Investigate distribution of spiny dogfish in regions beyond current NEFSC trawl surveys
- Initiate ageing studies, additional age validation, & age structure exchanges
- Explore an alternative assessment using standard statistical fisheries modeling approach
- Analyze the effects of environmental conditions on survey catch rates

SAW
(Year)

- 37th
(cont'd)
- Explore stock-recruitment relationships to estimate intrinsic rate of population \uparrow
 - \uparrow biological sampling, particularly maturation & fecundity estimates
 - Review of environmental variables associated with encounter during trawl survey, like temperature & depth
 - Availability of the resource assumed to be constant over entire survey area
 - Investigation into use of a fecundity index

- 43rd
(2006)
- Major findings:
- Stock not currently overfished (current stock size of mature females = 106,000 *mt*), exceeds $B_{\text{threshold}}$ (100,000 *mt*) & overfishing not occurring
 - Shifts in length frequencies toward smaller sizes
 - Mortality from gillnets may be much lower than previously assumed (0.3)
 - 1997 to 2006, incidence of pups in survey almost nonexistent
 - Progressive loss of smaller dogfish < 70cm
 - Frequency of large female schools \downarrow d b/w 1982 & 2006 concomitant with reduction in average length of fish in the schools
 - Sex ratios of mature males (> 60 cm) to mature females (>80 cm) averaged about 2:1 before 1992 to 7:1 in 2001
 - Variance (stratum numbers per tow) is increasing faster than the mean, the ability to detect moderate true changes will \downarrow as population size \uparrow s
 - 2006 NEFSC spring survey - average weight per tow \uparrow d by two-fold after more than a decade of consistent \downarrow s or no appreciable \uparrow s
 - Neither survey represents a significant improvement over a simple random sample for spiny dogfish (survey designed to accommodate many species; optimal allocation suggests redirection of effort to strata with highest densities; these can change over time)
 - Fall survey more variable over time, less useful as a measure of a closed population (~50% of dogfish catch in 'large' tows during autumn)
 - Fall: Inshore movement by males of nearly 60km (females ~20km closer) between mid 1980s & 2000s; spring: males moved 50km closer, females no trend
 - Model based only on accumulated stock biomass may be inadequate to predict recruitment for a population currently experiencing strong truncated size distribution, reduced average size of females, smaller than average size pups, & skewed sex ratio
 - ~50% of dogfish (efficiency) captured by trawl
 - Biomass of mature females will \uparrow thru 2008-09 as fish < 80cm grow into mature size range; then will \downarrow due to low recruitment
 - Length Tuned Model had difficulty producing sufficient amounts of larger fish to match observed length frequency data

Suggestions:

- More detailed consideration of reproductive biology necessary
- Additional analyses required to assess contemporary F rates

SAW
(Year)

43rd

(cont'd)

- Intensive investigation of the variability of the survey data & consideration of alternative hypotheses
 - Selection function needs work due to mixture of component fleets constituting composite size frequency distribution & uncertainty of size compositions for 1994 or earlier
 - Conduct tagging & genetic studies in US & Canadian waters to clarify current assumptions about stock structure
 - Conduct experimental work on NEFSC trawl survey gear performance, with focus on video work to study the fish herding properties of the gear for species like dogfish & other demersal groundfish
 - Investigate their distribution beyond depth range of current NEFSC trawl surveys, possibly using experimental research or supplemental surveys
 - Conduct aging workshop for spiny dogfish
 - Examine observer data to calculate weighted average discard mortality rate based on assumption that rate ↑s with catch size
 - Develop experimental estimates of discard mortality in New England & Mid-Atlantic commercial & recreational fisheries
 - Conduct coast-wide tagging study to explore stock structure, migration patterns & mixing rates
-

Table 1.2. Summary of major findings and research recommended by spiny dogfish stock assessments conducted by the joint United States and Canadian Transboundary Resources Assessment Committee (TRAC).

TRAC (Year)	<u>Major findings:</u>
1 st (2010)	<ul style="list-style-type: none"> • Consensus trans-boundary stock assessment not developed • Resident components in northern part of range, overlaid by migratory, trans-boundary component; seasonal N-S migrations in US, inshore-offshore in Canadian waters • Two models represented progress but comparing performance was difficult due to differences in data used in model fitting & widely divergent assumptions in each model, unacceptable levels of uncertainty in model outputs • Low abundance of pups during 1997-2003, consistent ↓ in US commercial and survey of mature females, average pup size in survey has ↓d • SSB will ↓ between 2011 and 2017 as low # of 1997-2003 recruits mature • Magnitude of total discard & estimated mortality of discarded fish highly uncertain • Consumption is a function of stock abundance, sexual dimorphism, seasonality, and stock size composition; annual total estimated consumption ~ 230,000 <i>mt</i> over time series
	<u>Suggestions:</u>
	<ul style="list-style-type: none"> • More detailed examination of time-at-large & the general patterns of fishing effort in areas of release are necessary before tag recapture data can be used to quantify movement flux among release areas • Address influence of fishing effort & reporting rates on recapture probabilities • Further exploration of stock recruitment models • Further exploration of both projection models • Tagging studies to help clarify movement patterns & migration rates; then formation of spatially structured models

Figure 1.1. Map of the Northeast (US) shelf large marine ecosystem (NES LME) where the NEFSC annual bottom trawl survey was conducted during autumn and spring. The four regions are defined as follows: Gulf of Maine (GM), Georges Bank (GB), Southern New England (SNE), and the Middle Atlantic Bight (MA). Filled gray shapes indicate land masses. Lines reflect depth contours in meters.

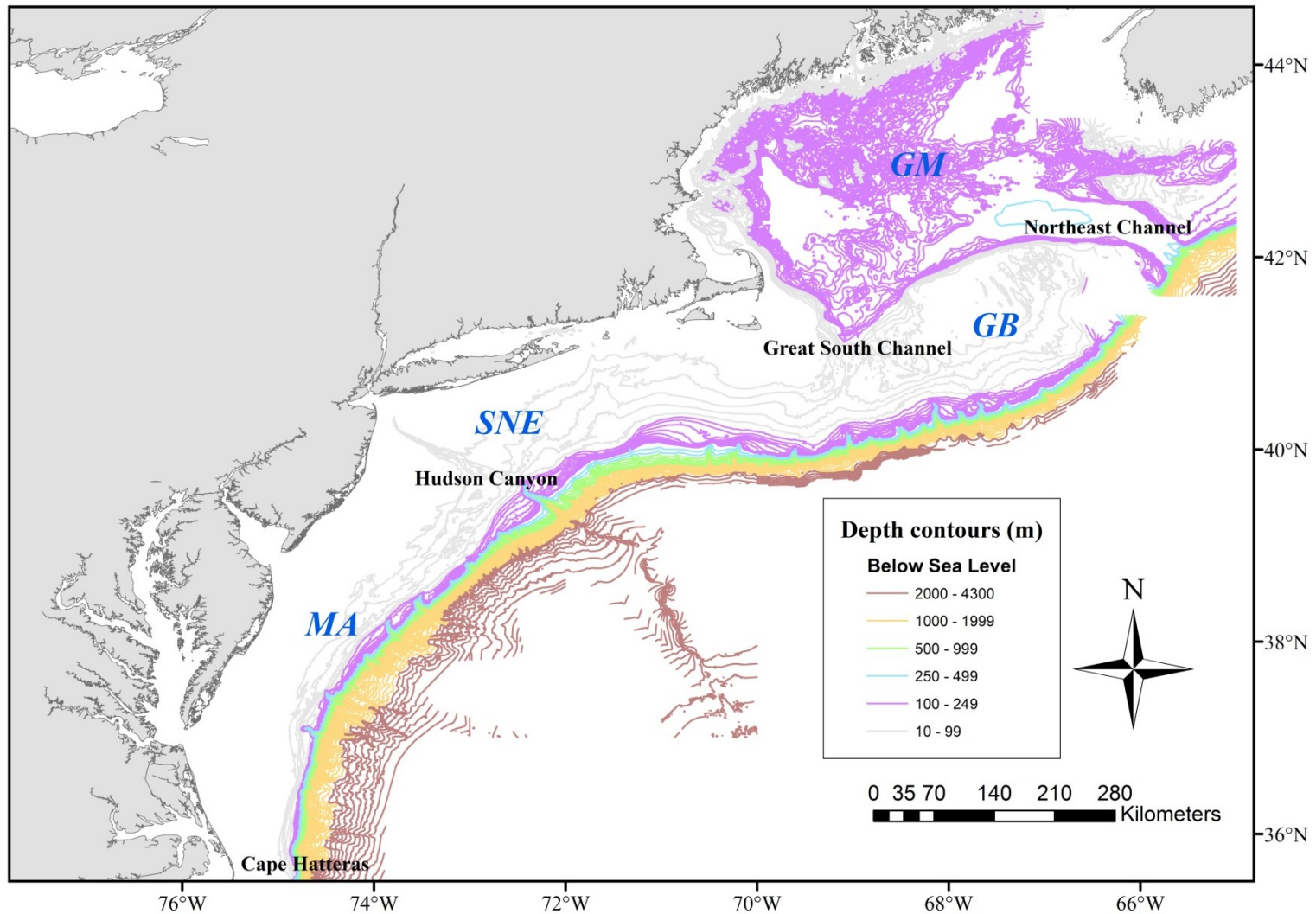


Figure 1.2. Annual commercial landings of Atlantic cod (*Gadus morhua*) (gray) and spiny dogfish (*Squalus acanthias*) (black) throughout the Atlantic region as derived from the Annual Commercial Landings Statistics for "cod" and "shark, spiny dogfish" at http://www.st.nmfs.noaa.gov/st1/commercial/landings/annual_landings.html). A) Landings in metric tons *mt* (x 1000) and B) value (\$) per *mt*.

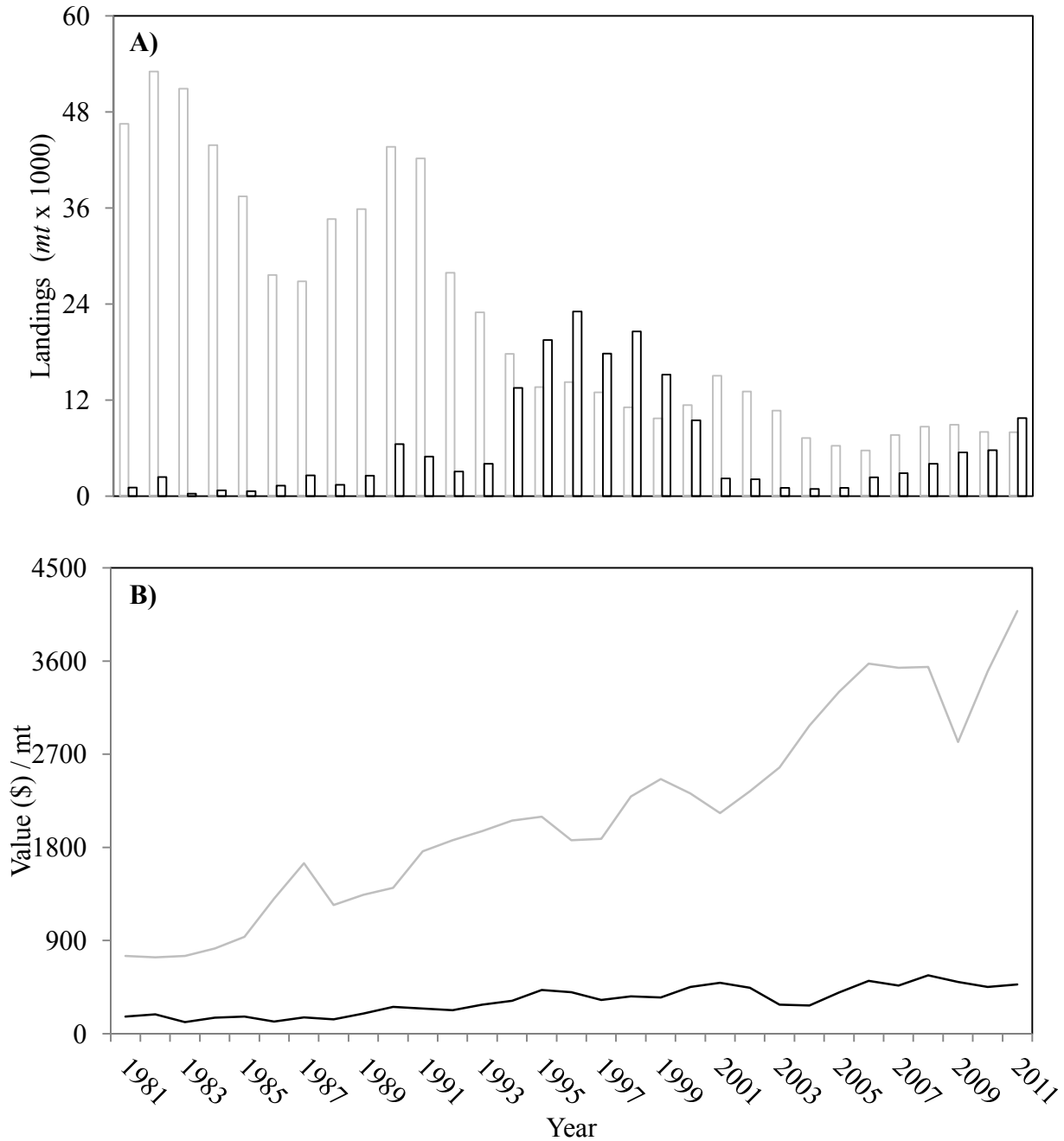
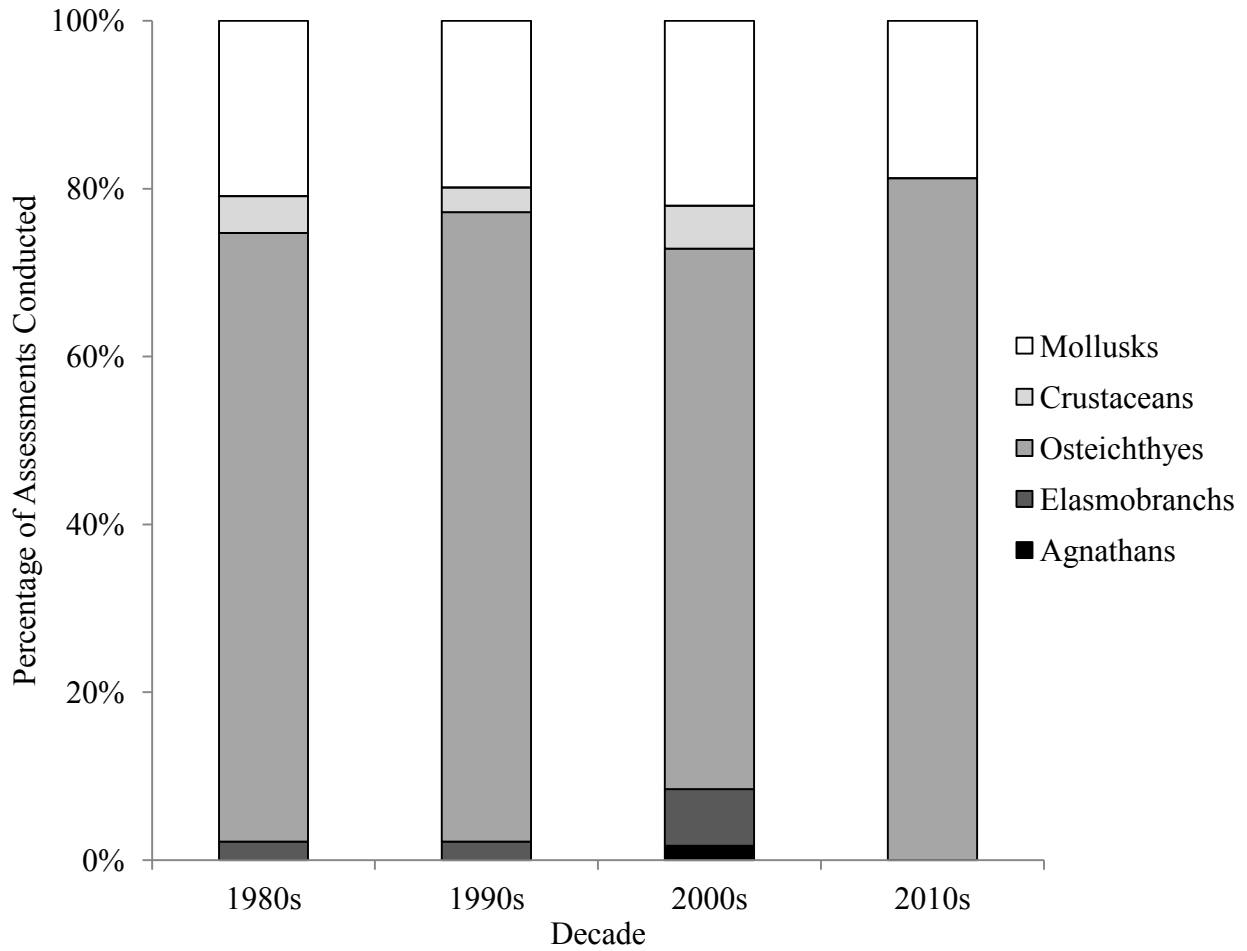


Figure 1.3. Summary of stock assessment efforts on marine resources within the Northeast (US) shelf large marine ecosystem put forth by the Northeast Fisheries Science Center (NEFSC) since the first Stock Assessment Workshop (SAW) in 1985.



Chapter 2:
**INFLUENCE OF ENVIRONMENTAL, SPATIAL, AND ONTOGENETIC VARIABLES
ON HABITAT SELECTION AND MANAGEMENT OF SPINY DOGFISH IN THE
NORTHEAST (US) SHELF LARGE MARINE ECOSYSTEM**

Introduction

Understanding the habitat preferences of marine fishes is important when describing their spatial distribution and ecology (Perry & Smith 1994, Smith & Page 1996, Shepherd et al. 2002) and is a prerequisite for effective fisheries management (Reynolds 2003). If distribution varies in response to environmental conditions, then fisheries-independent survey-based estimates of abundance may mislead stock assessments (Murawski & Finn 1988, Perry & Smith 1994, Smith & Page 1996, Tomkiewicz et al. 1998, Shepherd et al. 2002). Moreover, a species' environmental preference may also vary with life-history stage, resulting in diverse population distributional patterns at broad spatial scales (Methratta & Link 2007). Ontogenetic shifts in habitat use, resulting from either change in morphology, physiology, ecological function and/or predation risk, are frequently documented in marine fishes (Fry 1971, Werner & Gilliam 1984, Swain 1993, Swain et al. 1998, Methratta & Link 2007). Density-dependent effects can also influence habitat selection (Swain & Kramer 1995, Swain 1999, Spencer 2008, Persohn et al. 2009).

In the northwest Atlantic, the rising harvest of elasmobranchs to supplement fisher income has necessitated research to enhance stock assessment of these understudied species, particularly for the spiny dogfish (*Squalus acanthias*) (Rago et al. 1998, McMillan & Morse 1999). Research concerning habitat preference in this region has focused mainly on

commercially important teleosts including Atlantic cod (*Gadus morhua*) (Scott 1982; many others), haddock (*Melanogrammus aeglefinus*) (Scott 1982, Perry & Smith 1994, Methratta & Link 2007), American plaice (*Hippoglossoides platessoides*) (Scott 1982; many others), yellowtail flounder (*Limanda ferruginea*) (Scott 1982, Perry & Smith 1994), and silver hake (*Merluccius bilinearis*) (Murawski & Finn 1988, Perry & Smith 1994, Methratta & Link 2007). Globally, many variables have proven influential in determining the distribution and abundance of various elasmobranchs including temperature, salinity, depth, dissolved oxygen concentration, and surface chlorophyll (Hopkins & Cech Jr 2003, Vogler et al. 2008, Persohn et al. 2009, Craig et al. 2010, Cortés et al. 2011).

Spiny dogfish is a small, slow growing, long-lived elasmobranch that occurs in oceanic and coastal environments throughout the world (Compagno et al. 2005, Veríssimo et al. 2010). In the northwest Atlantic, maturity occurs at age 6 (~60 cm total length, TL) for males and age 12 (~80 cm TL) for females (Burgess 2002, Sosebee 2005) with longevity estimated at 45 years (Campana et al. 2006). Traditionally, spiny dogfish was a species of low commercial value and knowledge of its habitat preference was limited, particularly regarding different life-history stages. The available evidence suggests that in the Gulf of Maine (GM) and Georges Bank (GB) regions, spiny dogfish preferred shallow, warm waters in autumn and deep, warm waters in spring (Methratta & Link 2007). Large spiny dogfish catches occurred in warm waters on the Scotian Shelf (Scott 1982) with warmer (6.6 – 9.2°C), saltier (32.7 – 34.4), and deeper (89 – 185 m) bottom habitat occupied than that available (Shepherd et al. 2002). In addition, differences between sexes and length classes were acknowledged (Shepherd et al. 2002).

Spiny dogfish is a highly migratory species that displays variable distributional trends at seasonal and decadal scales (Templeman 1984, Overholtz & Tyler 1985, Rago et al. 1998, Rago

& Sosebee 2009) in the Northeast (US) shelf large marine ecosystem (NES LME). The classic depiction of the spiny dogfish life cycle involves seasonal movements between wintering areas in the Middle Atlantic Bight (MA) and summer feeding grounds in the northwest Atlantic. In early spring, females lead the population north (Templeman 1944, Hisaw & Albert 1947), reaching GB in March and April (Figure 2.1) (Hisaw & Albert 1947, Burgess 2002). Between May and June the population spreads into the GM or onto the Scotian Shelf (Burgess 2002). During summer, some spiny dogfish move inshore into Canadian bays and estuaries (Rago et al. 1998, Campana et al. 2007) with females arriving first (Burgess 2002). Reportedly, parturition occurs during winter (Holden & Meadows 1962, Nammack et al. 1985, Jones & Ugland 2001, Henderson et al. 2002) after an approximate two year gestation period (Hisaw & Albert 1947, Jones & Ugland 2001). Spiny dogfish habitat utilization and migration is hypothesized to be driven by seasonal changes in temperature (Burgess 2002, Shepherd et al. 2002, Methratta & Link 2007).

During seasonal migrations spiny dogfish are often locally abundant for several months at a time and display large interannual variations. Local concentrations have been blamed for the declines or suppressed recovery of important commercial species. Thus distinguishing changes in true abundance from variations in seasonal movements can be challenging. The slow life history and interannual distributional shifts by spiny dogfish in fishery-independent surveys emphasize the need to investigate the relationships between spiny dogfish distribution and environmental variables when estimating relative abundance. In addition, it is important that both density-dependent and density-independent mechanisms are considered to further understand distributional shifts (Spencer 2008). Here, we examine the influences of environmental variables (bottom temperature, bottom salinity, and depth) and a spatial variable (latitude) on the

distribution of neonate (sexes combined), immature (male and female separately), and mature (male and female separately) spiny dogfish during autumn and spring. We also investigate how density-dependent factors influenced their distribution and abundance.

Methods

Data

All analyses utilized fisheries-independent data obtained from NOAA's Northeast Fisheries Science Center (NEFSC) annual autumn and spring bottom trawl surveys. These surveys sample the NES LME from Cape Hatteras, NC, to GB and the GM using a stratified random design. Offshore and inshore strata are depicted in Figures 1 and 2 of NEFSC (2006). The autumn survey has been conducted in offshore areas since 1963 and inshore strata were added in 1972. The spring survey began sampling offshore areas in 1968 and inshore strata were added in 1973. Survey strata comprise about 64,000 nm². The number of stations sampled per stratum was proportional to its area but inshore strata were sampled at approximately three times the sampling rate of offshore strata. Approximately 300 – 400 stations were visited during autumn (mean ± SE = 344 ± 13 stations) and spring (mean ± SE = 346 ± 8 stations). Detailed descriptions of the survey design and changes in survey protocols over time can be found in Azarovitz (1981) and Azarovitz et al. (1997).

Correction factors based on field experiments were applied for changes in vessels, gear and doors when necessary. The introduction of the *Henry B. Bigelow* in 2009 brought about changes to the trawling gear and survey protocol (Brown et al. 2007). In addition, a calibration study compared the catchability of the old vessel, the *Albatross IV*, with the new vessel (Miller et

al. 2010). Catchability, defined as the proportion of a stock caught by one unit of fishing effort (e.g., area swept by trawl) (Francis et al. 2003, Fraser et al. 2007), consists of three components: (1) the horizontal or areal availability which describes the probability of presence in the area at the time of the survey (Francis et al. 2003, Trenkel et al. 2004); (2) the vertical availability which conveys the proportion in the area which could be encountered by the trawl (Francis et al. 2003, Trenkel et al. 2004); and (3) the efficiency or proportion of available fish caught in the trawl (Godø 1994, Michalsen et al. 1996, Trenkel et al. 2004).

Species distribution

Tow duration was standardized and represented by the survey catch of spiny dogfish per unit effort (*CPUE*; number of spiny dogfish/tow). Average values were calculated for all spiny dogfish combined and separately for each dogfish stage and season. Dogfish stages have been consistently reported since 1980 and were defined as follows: aggregated male and female neonates ($TL \leq 26$ cm), immature males ($26 \text{ cm} < TL < 60$ cm), immature females ($26 \text{ cm} < TL < 80$ cm), mature males ($TL \geq 60$ cm), and mature females ($TL \geq 80$ cm). Neonate size was chosen based on a total length at birth of 26-27 cm (Hisaw & Albert 1947, Burgess 2002). Four regions were recognized within the survey domain: GB, GM, Southern New England (SNE), and the MA (Figure 2.1).

Distributional maps of spiny dogfish for autumn and spring, reflective of survey trends, were produced using ArcMap (v10. ESRI Corp). Decadal patterns of distributional trends were provided for the following decades: 1963-9, 1970-9, 1980-9, 1990-9, and 2000-9.

Habitat preference and the degree of aggregation

Habitat preference for each dogfish stage was estimated following the nonparametric method developed by Perry and Smith (1994) using R (R Core Development 2010). First, the empirical cumulative distribution function (CDF) of the available habitat $f(t)$ adjusted for unequal sampling effort within strata ($\frac{W_h}{n_h}$) was estimated with the following function:

$$(2.1) \quad f(t) = \sum_h \sum_i \frac{W_h}{n_h} I(x_{hi}) \quad \text{where } I(x_{hi}) = \begin{cases} 1, & \text{if } x_{hi} \leq t \\ 0, & \text{otherwise} \end{cases}$$

where W_h = proportion of the survey in stratum h , $h=1, \dots, L$, n_h = number of trawls in stratum h , x_{hi} = measurement for a habitat variable (e.g., temperature) in trawl i of stratum h , $i=1, \dots, n_h$ and I = indicator function where t represents an index ranging from the lowest to the highest value of the habitat variable. Eq. 2.1 was calculated over all values of t for each habitat measurement (x_{hi}) available. Second, the CDF of occupied habitat $g(t)$ was estimated with the following function:

$$(2.2) \quad g(t) = \sum_h \sum_i \frac{W_h}{n_h} \frac{y_{hi}}{\bar{y}_{st}} I(x_{hi})$$

where y_{hi} = number of spiny dogfish caught in trawl i and stratum h and \bar{y}_{st} = stratified mean catch. Note that Eq. 2.2 specifies the catch-weighted distribution of the habitat variable. For each habitat variable, the 5th, 50th (median), and 95th percentiles were determined. If spiny dogfish are randomly distributed with respect to the habitat covariate, x_{hi} , $f(t)$ and $g(t)$ would be identical. Thus, the strength of association between catch and habitat could be determined as the degree of difference between occupied, $g(t)$, and available habitat, $f(t)$, with a Kolmogorov-Smirnov type test statistic (TS) for the absolute maximum vertical difference (D) between the two CDFs:

$$(2.3) \quad \max |g(t) - f(t)| = \max \left| \sum_h \sum_i \frac{W_h}{n_h} \left(\frac{y_{hi} - \bar{y}_{st}}{\bar{y}_{st}} \right) I(x_{hi}) \right|.$$

The estimated TS was then compared to a pseudo-population of 10,000 randomized test statistics ($PPTS$) obtained by randomizing pairings of $\frac{W_h}{n_h} \left(\frac{y_{hi} - \bar{y}_{st}}{\bar{y}_{st}} \right)$ and (x_{hi}) for all h and i across the entire survey (Perry & Smith 1994). Significance was estimated as $p = \frac{\# PPTS > TS}{Total PPTS}$.

The degree of spiny dogfish aggregation was explored using Lorenz curves (Dagum 1985) which express the potential influence of aggregations on the power of randomization tests (Swain et al. 1998). When randomizing pairs of catch and habitat variables, large jumps in the catch-weighted CDF of occupied habitat may result from uncommonly large catches and the resulting associations between spiny dogfish and habitat variables may reflect either habitat selection or chance (Swain et al. 1998). If the degree of aggregation interferes with the power of detecting a significant association, a given value of D will appear less significant compared to a more evenly distributed population (Swain et al. 1998). Following Swain et al. (1998), the estimated percentage of the stock associated with each tow ($\Phi_{i,h}$) was calculated with the following function:

$$(2.4) \quad \Phi_{i,h} = \frac{100 w_i y_{hi}}{\bar{y}_{st}}$$

where w_i = proportion of the survey area associated with trawl i and the remaining symbols defined as above. The percentage of area associated with each tow (A_i) was calculated with the following function:

$$(2.5) \quad A_i = 100 w_i.$$

The Lorenz curve was obtained by plotting the cumulative A_i (abscissa) against the cumulative Φ_i (ordinate). The degree of concentration was quantified by the Gini index of inequality (Gini 1912) which measures the deviation of the Lorenz curve from a 45° line and ranges from 0 (equal distribution) to 1 (maximum heterogeneity) (Gini 1912, Temming et al. 2007). The higher the index, the stronger the curvature (Temming et al. 2007) and therefore the more aggregated the distribution (Swain et al. 1998, Swain & Morgan 2001). The Gini index was calculated using the 'RELDIST' package (Handcock 2013) in R (R Core Development 2010).

Comparison of habitat preference

Cumulative distributions of occupied habitat were calculated for all dogfish stages and compared using a Kolmogorov-Smirnov type of statistic (Swain et al. 1998). We tested whether dogfish stages occupied statistically different habitat. Eq. 2.2 was used to estimate the CDF of occupied habitat for each dogfish stage while Eq. 2.3 was used to estimate the statistic for significance testing with one slight difference. Here, D was calculated using the $g(t)$ for each dogfish stage. We evaluated the null hypothesis that differences in habitat distribution were due to chance alone.

Decadal habitat preference and comparison

Decadal habitat preferences were also explored for all dogfish stages during both autumn and spring and were calculated as above. Comparisons of occupied habitat between decades were made for each dogfish stage during both seasons. Catches for decadal periods were randomized

and CDFs were calculated for each decade. Since CDFs between decades differed in sample sizes, comparisons required the creation of common intervals of each independent variable (e.g. temperature intervals of 0.0, 0.1... 32.0) and their respective value for each randomized CDF. Significance was estimated as above. Abundance and distributional maps for each decade were created in ArcMap (v10. ESRI Corp) and compared visually for each dogfish stage. The degree of aggregation described above was also investigated for each dogfish stage and decade.

Density-dependent analysis

The relationship between stock area and abundance was examined for density-dependence using an index of geographic range, the minimum area containing 95% of the target species (D_{95}) (Swain & Sinclair 1994). This index was calculated for all spiny dogfish combined and separately for each dogfish stage during both seasons. The cumulative frequencies of spiny dogfish catch in each year was determined with the following function:

$$(2.6) \quad F(c) = 100 \frac{\sum_{h=1}^L \sum_{i=1}^{n_h} \frac{A_h}{n_h} y_{hi} I(y_{hi})}{\sum_{h=1}^L \sum_{i=1}^{n_h} \frac{A_h}{n_h} y_{hi}} \quad \text{where} \quad I(y_{hi}) = \begin{cases} 1 & \text{if } y_{hi} \leq c \\ 0 & \text{otherwise} \end{cases}$$

where y_{hi} = spiny dogfish catch in trawl i of stratum h , L = total number of strata, A_h = area of stratum h , c = level of spiny dogfish density (i.e., 5th percentile of density (c_{05})) and the remaining symbols as described above. Next, the cumulative area in relation to spiny dogfish catch was calculated with the following function:

$$(2.7) \quad G(c) = \sum_{h=1}^L \sum_{i=1}^{n_h} \frac{A_h}{n_h} I(y_{hi}) \quad \text{where} \quad I(y_{hi}) = \begin{cases} 1 & \text{if } y_{hi} \leq c \\ 0 & \text{otherwise.} \end{cases}$$

D_{95} was calculated with the following equation:

$$(2.8) \quad D_{95} = A_T - G(c_{05})$$

where A_T = total survey area (n mi²) and $G(c_{05})$ = area over which density was \leq the 5th percentile level. D_{95} increases as a population's spatial distribution spreads out and decreases as its distribution becomes more concentrated. D_{95} can remain constant if abundance changes at the same rate in all areas (Swain & Sinclair 1994, Swain & Benoit 2006). The relationship between annual D_{95} and \log_e transformed abundance (survey CPUE) was explored using regression and correlation (r). The power (β) of each correlation was estimated as a function of sample size (N) and a significance level of $\alpha = 0.05$ in the 'PWR' package (Champely 2009) of R (R Core Development 2010).

Results

Spatiotemporal distribution of spiny dogfish

Spring surveys generally encountered spiny dogfish in the MA and SNE with these regions accounting for 62 – 92% of the total survey catch depending upon the decade (Figure 2.2). Though limited by effort, less than 8% of the 1960s catch occurred in the GM and on GB (Figure 2.2). During the 1970s, this proportion increased to 20% (Figure 2.2). The 1980s and 1990s revealed a different pattern as the proportion caught solely on GB (28%) rivaled that from the MA (31 – 34%) and SNE (28 – 37%) (Figure 2.2). In contrast, during the 2000s the majority of spiny dogfish (62%) were captured in the MA (Figure 2.2).

Survey trends in distribution during autumn were highly variable for all regions with the exception of the MA where spiny dogfish were rarely encountered (0 – 10%) (Figure 2.3). During the 1960s, spiny dogfish were predominantly caught in SNE (71%) (Figure 2.3). In contrast, the 1970s and the 1980s revealed large portions of the population on GB (37 – 39%) and in SNE (43 – 44%) (Figure 2.3). In both the 1990s and 2000s, a smaller portion of the population occurred on GB (9 – 15%) while the majority of catches occurred in the GM (47 – 52%) and SNE (33 – 44%) (Figure 2.3). It is important to recognize that some spiny dogfish are present in Canadian waters during autumn and therefore outside the area surveyed. As a result, slight changes in the fraction occurring north and east of the NEFSC survey area could greatly alter the fractions elsewhere.

Spatiotemporal distribution of spiny dogfish stages

Neonate. Decadal distributional trends were similar during spring with the exception of the 1960s where most neonates were caught in the MA (88%) (Figure 2A.1). In general, the majority were captured along the shelf's edge in the MA and SNE with proportions ranging from 21 – 51% and 42 – 76%, respectively. During autumn, neonates were rarely encountered and therefore distribution was highly variable (Figure 2A.2). During the 1960s, the majority were captured sporadically throughout SNE (54%) and the MA (43%). Both the 1970s and 1980s revealed catches primarily on GB (44 – 46%) and in SNE (42 – 48%). In the 1990s, neonates were widely distributed along the shelf's edge from the MA (42%) to GB (28%). Most recently, neonates have primarily concentrated along the shelf's edge in SNE (50%) and the MA (27%).

Immature. While immature spiny dogfish were present throughout the MA, SNE, and GB during spring of the 1980s and 1990s, differences were observed between sexes. Males

generally inhabited the shelf's edge with the majority of catches occurring on GB (41 – 52%) and in SNE (33 – 36%) (Figure 2A.3). In contrast, females were common both inshore and along the shelf's edge with relatively consistent catches (~30%) among GB, the MA, and SNE (Figure 2A.5). During the 2000s, their distributions diverged further as males were predominantly encountered in SNE (78%) while females occurred throughout the MA (48%) and SNE (29%). During autumn, immature spiny dogfish were predominantly encountered in SNE, on GB, and in the GM. During the 1980s and 2000s, males were caught primarily on GB (44 – 56%) and in SNE (37%) (Figure 2A.4) whereas during the 1990s most were encountered on GB (40%) and in the GM (34%). While large proportions of females were consistent throughout the time series in SNE (36 – 48%) (Figure 2A.6), considerable catches occurred on GB (43%) during the 1980s and in the GM (38 – 41%) during subsequent decades.

Mature. Mature spiny dogfish were common throughout the MA and SNE during spring of the 1980s and 1990s. Males were mostly caught in SNE (46%) and the MA (27%) during the 1980s and in the MA (37%) and on GB (28%) in the 1990s (Figure 2A.7). In contrast, MA catches of females remained high during both decades (57-61%) (Figure 2A.9). The 2000s revealed an overwhelming proportion of MA catch for both males (69%) and females (78%). During autumn, mature spiny dogfish were mostly collected from SNE and the GM during all decades. During the 1980s, most males were encountered in SNE (40%) and in the GM (39%) (Figure 2A.8) whereas females were prominent in SNE (71%) (Figure 2A.10). A shift in distribution occurred for mature dogfish during subsequent decades as GM catches encompassed a greater portion (males: 56 – 61%; females 40 – 48%).

Spatiotemporal abundance of spiny dogfish stages

Neonate. Neonate *CPUE* varied considerably between regions and years during both seasons (Figure 2.4). Relatively high *CPUE* occurred in the 1980s and early 1990s on GB, in the 2000s in the GM, and sporadically throughout both SNE and the MA. Combined across regions, neonate abundance was generally below the time series mean during both spring (Figure 2B.1) and autumn (Figure 2B.2), especially during the 1990s and 2000s.

Immature. During spring, *CPUE* trends for immature spiny dogfish were highly variable between regions and years but remained similar between sexes (Figure 2.4). On this figure, the lack of survey catches from 1973-79 stems from inconsistent reporting of sex and is not necessarily reflective of abundance trends. During spring, high *CPUE* was observed in the 1980s on GB, in the 1980s and 1990s in the MA, in the 1990s in the GM, and in the late 2000s in SNE (Figure 2.4). Combined across regions, abundances of immature spiny dogfish were generally above the time series mean from 1980-1996 and then consistently below mean *CPUE* (Figure 2B.1). Unique to immature males during spring, *CPUE* between GB and the MA was highly correlated ($r = 0.65$) (Table 2B.1).

During autumn, immature dogfish revealed relatively high *CPUE* on GB in the 1980s whereas GM *CPUE* remained high throughout the early 1990s for males and after 1990 for females (Figure 2.4). *CPUE* remained low in both SNE and the MA with the exception of the late 1960s. Combined across regions, immature male abundance was generally below the time series mean whereas no pattern was observed for immature females (Figure 2B.2).

Mature. *CPUE* of mature spiny dogfish was inconsistent between regions and years but tended to remain similar between sexes. During spring, *CPUE* of both sexes peaked on GB in

1990, remained relatively high throughout the 1980s in SNE, and gradually increased after the late 1990s in the MA (Figure 2.4). In the GM, *CPUE* was high during the 1980s and late 2000s for females and the 1990s for males. Combined across regions, mature male abundance revealed no consistent trend (Figure 2B.1). In contrast, mature female abundance was generally above the time series mean prior to 1993 but consistently below throughout the remainder of the time series (Figure 2B.1).

During autumn, *CPUE* increased throughout the 2000s for both sexes on GB and in the GM while MA *CPUE* remained low (Figure 2.4). In contrast, SNE *CPUE* of mature dogfish remained relatively consistent throughout the time series. Combined across regions, mature male abundance was generally below the time series mean until the mid 1990s and then above thereafter (Figure 2B.2). In contrast, mature female abundance was primarily below the time series mean with the exception of 2004 – 2008 (Figure 2B.2).

Habitat preference and degree of aggregation

Survey conditions. The range of environmental and spatial (i.e., latitude) conditions sampled remained relatively similar between years for both seasons (Figure 2C.1). Exceptions occurred during the 1960s and early 1970s when only offshore strata were sampled.

Temperature. Associations with temperature were common throughout both seasons for most dogfish stages examined (Table 2.1). During spring, all dogfish stages avoided temperatures below 5°C or above 14°C (Figure 2.5A). Within these limits, the distributions of all dogfish stages indicated that spiny dogfish were selecting significantly warmer waters (i.e., $g(t) - f(t) > 0$) (Table 2.1; Figure 2.5A). Immature males inhabited significantly warmer waters (10.0°C

[median], 5.3 – 13.4°C [90% Confidence Interval]) compared to immature female (8.3°C, 5.1 – 12.9°C) and mature spiny dogfish (male: 8.2°C, 5.2 – 11.7°C; female: 7.7°C, 5.0 – 11.2°C) (Table 2.2; Figure 2.5A). In addition, neonates exhibited a warmer preference (8.8°C, 5.0 – 13.4°C) than mature females. During autumn, spiny dogfish were absent at stations where temperatures fell below 5°C or exceeded 17°C (Figure 2.6A). Mature spiny dogfish and immature females significantly ($p < 0.05$) associated with warmer waters than those available (i.e., surveyed) (Table 2.1; Figure 2.6A). Mature females occupied significantly warmer waters (12.9°C, 7.8 – 15.6°C) compared to both males (immature: 11.0°C, 7.8 – 14.4°C; mature: 10.8°C, 7.0 – 14.8°C) and neonates (11.0°C, 7.3 – 13.9°C) (Table 2.2; Figure 2.6A).

Throughout each decade during spring, all dogfish stages selected significantly ($p < 0.05$) warmer waters than those available (Figure 2C.2) with the exception of neonates in the 1970s (Table 2.3). In contrast, during autumn, decadal analysis revealed fewer significant ($p < 0.05$) associations with bottom temperature for all dogfish stages examined (Table 2.3; Figure 2C.3). While decadal habitat preferences concerning temperature were compared within dogfish stages (Table 2C.1), results are not discussed due to a lack of statistical power.

Salinity. Associations with salinity were also common throughout both seasons for most dogfish stages (Table 2.1). During spring, all dogfish stages occupied significantly ($p < 0.05$) higher salinities than those available (Table 2.1; Figure 2.5B). Immature males exhibited a higher salinity preference (34.6, 32.6 – 35.6) compared to mature spiny dogfish (male: 34.0, 32.4 – 35.1; female: 33.8, 32.0 – 35.0) (Table 2.2; Figure 2.5B). During autumn, neonates and mature spiny dogfish showed significant ($p < 0.05$) salinity associations compared to those available (Table 2.1; Figure 2.6B). Neonates occupied more saline environments (34.5, 31.8 – 35.5) while

lower salinity preferences were displayed by mature spiny dogfish (male: 32.3, 31.6 – 34.2; female: 32.3, 31.5 – 33.6). Both neonates and immature males (33.6, 31.9 – 35.3) preferred higher salinities compared to immature females (32.5, 31.6 – 34.9) and mature spiny dogfish (Table 2.2; Figure 2.6B).

Throughout the 2000s during spring, all dogfish stages occupied significantly ($p < 0.05$) higher salinities than those available (Table 2.3; Figure 2C.4). During autumn, mature males and immature females preferred significantly lower salinities than those available during the 1990s (Table 2.3; Figure 2C.5). During the 2000s, neonates and immature males occupied more saline environments while the remaining dogfish stages occupied less saline environments than those available (Table 2.3; Figure 2C.5). While decadal habitat preferences concerning salinity were compared within dogfish stages (Table 2C.1), results are not discussed due to a lack of statistical power.

Depth. Associations with depth were prevalent throughout both seasons with the exception of immature spiny dogfish (Table 2.1). During spring, immature males and mature females occupied significantly deeper (123 m, 65 – 252 m) and shallower (59 m, 26 – 202 m) depths, respectively, than those available (Table 2.1; Figure 2.5C). All dogfish stages revealed significantly ($p < 0.05$) different depth preferences with the exception of immature females and mature males (Table 2.2). During autumn, mature spiny dogfish and immature females occupied significantly shallower depths than those available (Table 2.1; Figure 2.6C). As observed during spring, most dogfish stages revealed significantly ($p < 0.05$) different depth preferences. Mature females occupied shallower depths (42 m, 22 – 108 m) whereas deeper depths were occupied by

both neonates (89 m, 42 – 165 m) and immature males (88 m, 42 – 208 m) (Table 2.2; Figure 2.6C).

Throughout the 1980s during spring, significant ($p < 0.05$) depth associations were found for all dogfish stages whereas only immature males and mature females exhibited preferences during the 1990s and 2000s (Table 2.3; Figure 2C.6). These trends generally matched overall trends with younger spiny dogfish deeper and mature females shallower than surveyed depths. Fewer significant ($p < 0.05$) associations with depth occurred during autumn (Table 2.3). With the exception of immature males, all significant associations resulted from a shallower depth preference compared to depths available (Figure 2C.7). While decadal habitat preferences concerning depth were compared within dogfish stages (Table 2C.1), results are not discussed due to a lack of statistical power.

Latitude. Associations with latitude were common throughout both seasons with the exception of immature males (Table 2.1). During spring, all dogfish stages occupied significantly ($p < 0.05$) lower latitudes than those available (Table 2.1; Figure 2.5D). Neonates exhibited the shortest latitudinal preference (40.06°N, 37.52 – 40.57°N) while mature females displayed the largest (38.80°N, 35.87 – 42.26°N). All dogfish stages exhibited significantly ($p < 0.05$) different latitudinal distributions except for immature females and mature males (Table 2.2). Mature females preferred more southerly areas compared to the other dogfish stages (Figure 2.5D). During autumn, mature males occupied significantly higher latitudes than those available while the distributions of neonates and female spiny dogfish were more diverse (Table 2.1; Figure 2.6D). Mature females occupied a smaller range (41.10°N, 40.42 – 42.96°N). Mature males significantly ($p < 0.05$) preferred more northerly locations (41.78°N, 40.59 – 43.90°N) compared

to all dogfish stages while neonates occupied more southerly regions (40.23°N, 38.47 – 41.78°N) compared to immature females (41.07°N, 40.03 – 43.62°N) and mature spiny dogfish (Table 2.2; Figure 2.6D).

During each decade, all dogfish stages selected significantly ($p < 0.05$) lower latitudes during spring than those surveyed with the exception of immature males during the 2000s (Table 2.3; Figure 2C.8). In contrast, fewer significant ($p < 0.05$) associations with latitude were detected during autumn (Table 2.3; Figure 2C.9). While decadal habitat preferences concerning latitude were compared within dogfish stages (Table 2C.1), results are not discussed due to a lack of statistical power.

Degree of aggregation. Overall, all dogfish stages were more aggregated in distribution during autumn than spring, as evident by higher Gini indices (Table 2.4) and increased concavity (Figure 2C.10). Males and neonates revealed a relatively similar degree of aggregation between seasons (Figure 2C.10) as reflected by small deviations in Gini indices (0.004 – 0.01) (Table 2.4). In contrast, the degree of female aggregations changed at least two-fold between seasons compared to the other dogfish stages (Table 2.4). Upon examination of D values, non-significant values during autumn were as great or greater than those deemed significant during spring, suggesting that the degree of aggregation was interfering with the power of detecting a significant association (Table 2.1). As an example, an identical range of D (0.04 – 0.43) for neonates during both seasons was significant during spring ($p = 0.000$) but not autumn ($p = 0.091$). Similar trends in aggregation and interference were also present on a decadal basis for many dogfish stages (Table 2.3) during spring (Figure 2C.11) and autumn (Figure 2C.12).

However, higher Gini indices during spring indicated greater aggregation of mature males during the 1980s and immature males during the 1990s and 2000s (Table 2C.2).

Density-dependence

Based on collections from the NEFSC surveys, D_{95} of spiny dogfish in the NES LME varied noticeably throughout the time series during both seasons (Figure 2.7). The area occupied by neonates during spring generally increased whereas during autumn D_{95} remained low throughout most of the time series (Figure 2.7). During spring, D_{95} for immature spiny dogfish increased steadily until the early 2000s and then declined (Figure 2.7). In contrast, D_{95} trends diverged during autumn as larger values occurred during the late 1980s and the 1990s for immature males and after the late 1990s for immature females (Figure 2.7). During spring, the area occupied by mature males increased to peak levels in the early 2000s while D_{95} remained relatively high throughout the time series for mature females (Figure 2.7). For mature males, D_{95} generally increased after 1990 during autumn whereas D_{95} for mature females remained low between 1980 and 1995, peaked in the late 1990s, and has since declined (Figure 2.7).

No strong relationships between geographic range (D_{95}) and abundance (survey $CPUE$) were detected for any dogfish stage during either spring or autumn (Table 2D.1; Figure 2D.1). However, significant negative relationships were found for all spiny dogfish combined during autumn through both regression analysis ($y = -3520.8x + 21433.8$; $R^2 = 0.22$, $p < 0.05$) (Table 2D.1; Figure 2.8) and correlation analysis ($N = 47$; $r = -0.47$, $p < 0.05$, $\beta = 0.92$) (Table 2D.2). Unfortunately the ability to detect significant relationships for dogfish stages appeared to be limited by low statistical power ($\beta < 0.70$) (Table 2D.2).

Discussion

The quantification of environmental preference is an essential step towards effective management and enhances modeling the dynamics of a stock's distribution, trend monitoring and forecasting ability (Perry & Smith 1994, Smith & Page 1996). We presented stage-specific movement and abundance patterns that have implications for the assessment of spiny dogfish and ecosystem dynamics within the NES LME. During spring, preference for warmer, more saline, southerly regions was common among dogfish stages. In contrast, trends were more diverse during autumn, a season when some spiny dogfish enter Canadian waters and therefore are unavailable to the NEFSC survey. During this season, larger spiny dogfish generally occupied warmer, shallower, and less saline waters compared to those surveyed. Comparisons of preference concerning temperature, salinity, depth, and latitude revealed strong ontogenetic differences, highlighting the importance of recognizing stage-dependence, particularly when assessing distribution and abundance trends. We provided the first quantitative evidence via latitudinal associations of a general spiny dogfish movement pattern of overwintering in southern regions with northerly movements during summer (Templeman 1984).

The distinct seasonal ontogenetic latitudinal preferences displayed by spiny dogfish may increase vulnerability of certain dogfish stages to harvest, thereby disproportionately impacting reproductive potential. During autumn, mature females inhabited significantly lower latitudes than mature males, potentially as a way to ensure a higher degree of pup survival by minimizing intra-specific predation by males (Henderson et al. 2002). Currently, data deficiencies limit direct measures of agonistic and cannibalistic behavior in male and female spiny dogfish. While all dogfish stages preferred southerly regions during spring, ranges were highly variable. Neonates displayed a narrow latitudinal range along the relatively warmer offshore waters of the

eastern shores of Virginia and Georges Bank suggesting this locality may be of importance to the survival and growth of young. In contrast, the largest latitudinal range was exhibited by mature females and may result from different associations resulting from the species' complex reproductive cycle. Spiny dogfish give birth every other year (Hisaw & Albert 1947) and are capable of mating anytime (Verissimo et al. 2011). During this season, recently-impregnated females (Stage A; Hisaw & Albert 1947) may inhabit different latitudes than females possessing more developed young (Stage C; Hisaw & Albert 1947) or reproductively-dormant females searching for mates.

Wide latitudinal ranges have previously been identified for many families of viviparous or live-bearing elasmobranchs (Goodwin et al. 2005). It has been postulated that rates of colonization remain high for viviparous species for taxa ranging from reptiles to teleosts due to *in utero* transport of offspring across environmental extremes (Clutton-Brock 1991, Pope et al. 1994, Shine 1995, Qualls & Shine 1998, Goodwin et al. 2005). Spiny dogfish carry young for almost two years, traversing enormous distances and environments before returning to release pups in habitats similar to their neonate origins. This behavior conveys an evolutionary advantage for bearing young in warm protected habitat where survival and growth are maximized, at the adult's energetic expense, and has been linked to the selective pressure of competition, predation and physiological trade-offs (Cushing 1975, 1976, Helfman 1978, Macpherson & Duarte 1991). During autumn, mature females actively seek shallow warm waters where growth rates of internal embryos may be enhanced (Moore 1998). The utilization of low temperatures by mature spiny dogfish during spring may help reduce energetic costs while enabling maximum reproductive potential for spawning events. Research is needed to connect habitat selection and *in utero* development to determine trade-offs between occupied habitat and

reproductive success during the extended gestation period of spiny dogfish. The species 'slow' life history (Musick 1999) and medium size combined with an iteroparous reproductive strategy (Frisk et al. 2002, Frisk et al. 2005) highlights the potential for strong mature female habitat selection related to *in utero* growth (Moore 1998) to optimize lifetime fitness. Producing larger pups in protected environments likely contributes more towards first year survivability than would producing larger litter sizes.

Ontogenetic movements related to habitat selection are widespread throughout the marine environment for a broad range of taxa (Roff 2002, Jorgensen et al. 2008). Often, larval and juvenile stages inhabit shallow warm waters where food supply and growth rates are enhanced while older fish occupy deeper colder depths for lower metabolic costs and an increased life-span (Love 1970, 1980, Macpherson & Duarte 1991). Interestingly, spiny dogfish display an opposing pattern in that the species shifts from deeper depths during early life to shallower regions throughout adulthood (Shepherd et al. 2002, Methratta & Link 2007). Within the northwest Atlantic, both goosefish (*Lophius americanus*) (Caruso 2002) and witch flounder (*Glyptocephalus cynoglossus*) (Markle 1975, Smith et al. 1975) also utilize continental slope waters as nursery grounds. For these species, this pattern likely reduces resource competition or intra-specific predation between stages and may relate to differences in dietary preferences (Shepherd et al. 2002).

Environmental factors have been recognized as important parameters for predicting the distribution and abundance of both teleosts (Scott 1982; many others) and elasmobranchs (Shepherd et al. 2002; many others). While less described than temperature (Shepherd et al. 2002), salinity relationships stem from associations with water masses and/or mixing fronts (Brodeur et al. 2009). In our study, male spiny dogfish inhabited more saline environments

during spring, a result also described in Canadian waters (Shepherd et al. 2002). During autumn, neonates preferred higher salinities while mature females selected lower salinity regions. These results likely relate to physical locations as neonates settle offshore in deeper, higher salinity waters while mature females populate shallow inshore regions influenced by land-derived runoff (Shepherd et al. 2002). It is also possible that ontogenetic salinity preference may relate to body size as suggested for the angular angel shark (*Squatina guggenheim*) in the southwest Atlantic (Vogler et al. 2008).

The complex life history, seasonal movements, and apparent ubiquitous abundance of spiny dogfish poses a challenge for understanding catchability and developing robust estimates of stock trends for development of single-species and ecosystem-based management. Unfavorable environmental conditions (e.g., impinging cold water masses) may reduce the availability of a species to trawls and bias derived abundance estimates (Smith & Page 1996, Shepherd et al. 2002). It is commonly assumed that catchability and its subcomponents are fixed in time (Walters & Martell 2004). However, for a species like spiny dogfish whose range shifts seasonally, timing of sampling and interannual variation in environmental drivers may bias results. An increase in exploitation necessitated the development of the Interstate Fishery Management Plan (FMP) in 2000 to rebuild female spawning stock biomass (ASMFC 2002). While the rebuild was expected by 2020 (ASMFC 2002), target reference points were met in 2010 (Rago & Sosebee 2010), partly the result of an abnormally large spawning stock estimate from the 2006 spring bottom trawl survey (NEFSC 2006). Upon closer inspection, mature female abundance was consistently high between days 2 through 4 of the 2006 survey in relatively warmer temperatures, highlighting the importance and sensitivity of the survey to timing. This anomaly underlines the challenge of obtaining reliable abundance estimates from bottom trawl

surveys when catchability varies with the environment (e.g., Smith and Page 1996) and with changes in population size (Frisk et al. 2011).

Current US management recognizes a single continuous population of spiny dogfish within the northwest Atlantic with individuals traveling between US and Canadian waters (Campana et al. 2007). Driven by environmental conditions, these seasonal north-south movements determine when spiny dogfish are vulnerable to survey gear. Recent increases in estimated spiny dogfish abundance, particularly in the western Gulf of Maine, have resulted in increased quotas for fishermen. However, the large removals of mature females by the fishery and low recruitment from 1997 to 2003 (NEFSC 2006, Rago & Sosebee 2009) will likely affect spiny dogfish population dynamics and potential harvest for decades to come. Our research suggests that recent increases are likely influenced by variation in movements of mature and immature spiny dogfish. While broad-scale movement in the northwest Atlantic appears to be strongly dependent upon physical properties, food availability and/or competition (Shepherd et al. 2002, Methratta & Link 2007) may also contribute towards observed trends in distribution and abundance. Although attempts to investigate density-dependence within dogfish stage abundances were limited by statistical power, overall relative abundance increased as the geographic range contracted during autumn. This issue should be further investigated to determine the validity of this trend since density-dependence has important implications for stock assessment, specifically by influencing catchability (Swain & Benoit 2006).

The effectiveness of fisheries management generally relies on the validity of assumptions underlying abundance estimation and the magnitude of removals by the fishery and other sources. Future investigation of abundance indices in relation to survey variability and environmental influences can reduce uncertainty and provide valuable information for

management at the species and ecosystem level. Investigating ecological factors such as predator or prey distributions may help to connect foraging behavior with population dynamics. These investigations can help improve our understanding of the joint effects of environmental factors, population biology and harvests on the dynamics of exploited populations. In addition, further work should investigate how density-independent and density-dependent factors influence catchability. As an aggregating species, behavioral responses of solitary versus aggregated spiny dogfish to bottom trawls likely affects survey catchability as was observed for cod (Godø et al. 1999). Further research aimed at quantifying this in addition to hypothesized herding behavior (NEFSC 2006) is necessary to elucidate potential influences of density-dependence on bottom trawl catch rates.

Table 2.1. Habitat associations of spiny dogfish life-history stages in the Northeast (US) shelf large marine ecosystem during spring (1968 – 2009) and autumn (1963 – 2009). Habitat variables include bottom temperature (BT), bottom salinity (BS), depth, and latitude (Lat). Stages include neonate (Neo; TL ≤ 26 cm), immature male (ImmM; 26 cm < TL < 60 cm) and female (ImmF; 26 cm < TL < 80 cm), and mature male (MatM; TL ≥ 60 cm) and female (MatF; TL ≥ 80 cm). Habitat percentiles (5th, 50th[median], 95th), *D* = range of absolute vertical distances between distributions, *TS* = test statistic, and *p* = probability. Significance (bolded) based on an *a priori* $\alpha = 0.05$. Notes: spiny dogfish not sexed consistently until 1980 and *p* = 0.000 does not mean *p* = 0.

Variable	Stage	SPRING						AUTUMN					
		5th	50th	95th	<i>D</i>	<i>TS</i>	<i>p</i>	5th	50th	95th	<i>D</i>	<i>TS</i>	<i>p</i>
BT (°C)	Survey	3.5	6.0	11.2	-	-	-	5.9	10.2	20.1	-	-	-
	Neo	5.0	8.8	13.4	0.04 - 0.43	0.475	0.000	7.3	11.0	13.9	0.04 - 0.43	0.221	0.093
	ImmM	5.3	10.0	13.4	0.04 - 0.35	0.581	0.000	7.8	11.0	14.4	0.04 - 0.47	0.284	0.071
	MatM	5.2	8.2	11.7	0.02 - 0.22	0.424	0.000	7.0	10.8	14.8	0.03 - 0.23	0.144	0.021
	ImmF	5.1	8.3	12.9	0.03 - 0.25	0.414	0.000	7.4	11.4	15.8	0.03 - 0.27	0.267	0.000
	MatF	5.0	7.7	11.2	0.02 - 0.19	0.360	0.000	7.8	12.9	15.6	0.04 - 0.27	0.354	0.000
BS	Survey	31.7	33.2	35.0	-	-	-	31.4	33.1	35.2	-	-	-
	Neo	32.6	34.1	35.4	0.06 - 0.47	0.331	0.030	31.8	34.5	35.5	0.07 - 0.57	0.417	0.026
	ImmM	32.6	34.6	35.6	0.05 - 0.48	0.498	0.000	31.9	33.6	35.3	0.05 - 0.68	0.238	0.322
	MatM	32.4	34.0	35.1	0.04 - 0.32	0.357	0.000	31.6	32.3	34.2	0.05 - 0.34	0.308	0.001
	ImmF	32.1	34.0	35.5	0.04 - 0.32	0.304	0.000	31.6	32.5	34.9	0.04 - 0.45	0.245	0.052
	MatF	32.0	33.8	35.0	0.02 - 0.34	0.267	0.003	31.5	32.3	33.6	0.05 - 0.41	0.428	0.000
Depth (m)	Survey	20.2	77.3	234.8	-	-	-	20.3	77.8	231.5	-	-	-
	Neo	54.6	89.6	184.2	0.04 - 0.36	0.307	0.000	42.2	88.8	165.3	0.04 - 0.39	0.264	0.016
	ImmM	65.3	123.2	252.3	0.04 - 0.35	0.397	0.000	42.0	88.2	207.6	0.04 - 0.45	0.211	0.216
	MatM	37.8	77.2	226.4	0.02 - 0.18	0.157	0.001	22.9	58.3	204.3	0.02 - 0.20	0.168	0.003
	ImmF	29.9	94.1	239.3	0.02 - 0.20	0.098	0.131	25.9	65.2	200.3	0.03 - 0.26	0.149	0.034
	MatF	26.1	59.0	201.9	0.02 - 0.21	0.239	0.000	22.3	42.0	108.3	0.03 - 0.28	0.439	0.000
Lat (°N)	Survey	36.69	40.95	43.69	-	-	-	36.72	40.99	43.69	-	-	-
	Neo	37.52	40.06	40.57	0.04 - 0.35	0.555	0.000	38.47	40.23	41.78	0.04 - 0.38	0.407	0.000
	ImmM	38.46	40.29	42.40	0.04 - 0.29	0.393	0.000	39.99	40.81	43.44	0.04 - 0.50	0.240	0.131
	MatM	36.78	39.95	42.60	0.02 - 0.32	0.370	0.000	40.59	41.78	43.90	0.03 - 0.21	0.369	0.000
	ImmF	36.20	40.19	42.57	0.02 - 0.21	0.341	0.000	40.03	41.07	43.62	0.03 - 0.25	0.256	0.000
	MatF	35.87	38.80	42.26	0.02 - 0.26	0.465	0.000	40.42	41.10	42.96	0.04 - 0.26	0.330	0.000

Table 2.2. Seasonal habitat comparisons for spiny dogfish life-history stages in the Northeast (US) shelf large marine ecosystem during spring (1968 – 2009) and autumn (1963 – 2009). Habitat variables include bottom temperature (BT), bottom salinity (BS), depth, and latitude (Lat). Stages as defined in Table 2.1. *D* = range of absolute vertical distance between distributions, *TS* = test statistic, and *p* = probability. Significance (bolded) based on an *a priori* $\alpha = 0.05$. Notes: spiny dogfish not sexed consistently until 1980 and *p* = 0.000 does not mean *p* = 0.

		BT (°C)			BS			Depth (m)			Lat (°N)		
		<i>D</i>	<i>TS</i>	<i>p</i>	<i>D</i>	<i>TS</i>	<i>p</i>	<i>D</i>	<i>TS</i>	<i>p</i>	<i>D</i>	<i>TS</i>	<i>p</i>
<u>SPRING</u>													
ImmF vs.	ImmM	0.04 - 0.36	0.266	0.003	0.07 - 0.50	0.311	0.058	0.04 - 0.34	0.307	0.000	0.04 - 0.31	0.239	0.003
	MatM	0.04 - 0.32	0.123	0.269	0.05 - 0.42	0.073	0.994	0.03 - 0.24	0.151	0.073	0.03 - 0.34	0.119	0.254
	MatF	0.03 - 0.31	0.164	0.068	0.05 - 0.46	0.119	0.845	0.04 - 0.25	0.328	0.000	0.04 - 0.29	0.295	0.000
	Neo	0.05 - 0.37	0.110	0.689	0.06 - 0.54	0.126	0.919	0.04 - 0.35	0.222	0.030	0.05 - 0.41	0.235	0.019
ImmM vs.	MatM	0.04 - 0.31	0.357	0.000	0.06 - 0.51	0.377	0.011	0.03 - 0.30	0.388	0.000	0.04 - 0.30	0.353	0.000
	MatF	0.05 - 0.32	0.422	0.000	0.07 - 0.55	0.400	0.013	0.05 - 0.36	0.620	0.000	0.04 - 0.39	0.532	0.000
	Neo	0.07 - 0.48	0.246	0.217	0.09 - 0.70	0.345	0.307	0.06 - 0.48	0.389	0.005	0.06 - 0.59	0.318	0.039
MatM vs.	MatF	0.03 - 0.34	0.131	0.277	0.06 - 0.47	0.122	0.812	0.03 - 0.29	0.254	0.001	0.03 - 0.29	0.231	0.003
	Neo	0.05 - 0.34	0.191	0.118	0.07 - 0.54	0.118	0.935	0.04 - 0.44	0.274	0.003	0.04 - 0.34	0.212	0.046
MatF vs.	Neo	0.04 - 0.37	0.249	0.013	0.06 - 0.55	0.218	0.374	0.04 - 0.32	0.511	0.000	0.04 - 0.41	0.364	0.000
<u>AUTUMN</u>													
ImmF vs.	ImmM	0.05 - 0.44	0.186	0.298	0.07 - 0.63	0.422	0.034	0.05 - 0.37	0.258	0.031	0.05 - 0.40	0.220	0.110
	MatM	0.04 - 0.34	0.191	0.064	0.06 - 0.55	0.132	0.840	0.04 - 0.30	0.110	0.491	0.04 - 0.31	0.277	0.001
	MatF	0.04 - 0.37	0.198	0.122	0.07 - 0.54	0.213	0.436	0.04 - 0.35	0.357	0.000	0.04 - 0.35	0.165	0.214
	Neo	0.06 - 0.48	0.227	0.180	0.08 - 0.64	0.520	0.009	0.06 - 0.41	0.343	0.003	0.05 - 0.43	0.575	0.000
ImmM vs.	MatM	0.05 - 0.39	0.215	0.099	0.07 - 0.56	0.459	0.007	0.05 - 0.41	0.355	0.000	0.05 - 0.37	0.408	0.000
	MatF	0.06 - 0.47	0.351	0.018	0.08 - 0.71	0.635	0.002	0.05 - 0.45	0.582	0.000	0.05 - 0.53	0.342	0.013
	Neo	0.08 - 0.70	0.083	1.000	0.10 - 0.85	0.237	0.808	0.08 - 0.68	0.129	0.969	0.07 - 0.64	0.363	0.199
MatM vs.	MatF	0.05 - 0.36	0.301	0.001	0.06 - 0.54	0.192	0.560	0.04 - 0.38	0.303	0.001	0.04 - 0.35	0.367	0.000
	Neo	0.06 - 0.43	0.151	0.506	0.08 - 0.61	0.566	0.000	0.05 - 0.41	0.396	0.000	0.05 - 0.40	0.753	0.000
MatF vs.	Neo	0.06 - 0.48	0.379	0.007	0.10 - 0.71	0.707	0.000	0.07 - 0.48	0.696	0.000	0.05 - 0.52	0.690	0.000

Table 2.3. Decadal habitat associations of spiny dogfish life-history stages in the Northeast (US) shelf large marine ecosystem during spring (1968 – 2009) and autumn (1963 – 2009). Habitat variables include bottom temperature (BT), bottom salinity (BS), depth, and latitude (Lat). Stages as defined in Table 2.1. Habitat percentiles (5th, 50th [median], 95th), *D* = range of absolute vertical distances between distributions, *TS* = the test statistic, and *p* = probability. Significance (bolded) based on an *a priori* $\alpha = 0.05$. Notes: spiny dogfish not sexed consistently until 1980 and *p* = 0.000 does not mean *p* = 0.

Variable	Stage	Decade	SPRING						AUTUMN					
			5th	50th	95th	<i>D</i>	<i>TS</i>	<i>p</i>	5th	50th	95th	<i>D</i>	<i>TS</i>	<i>p</i>
BT (°C)	Survey	1960s	2.2	4.9	9.9	-	-	-	5.0	8.4	14.5	-	-	-
		1970s	3.7	6.2	11.2	-	-	-	6.4	10.6	18.7	-	-	-
		1980s	3.7	5.8	10.9	-	-	-	6.1	10.3	20.0	-	-	-
		1990s	3.4	6.0	11.7	-	-	-	6.3	10.6	21.3	-	-	-
		2000s	3.6	6.1	11.0	-	-	-	6.2	10.4	21.2	-	-	-
	Neo	1960s	6.4	9.6	10.4	0.10 - 0.82	0.748	0.002	7.2	8.8	13.6	0.09 - 0.61	0.333	0.209
		1970s	5.0	8.0	12.2	0.06 - 0.70	0.356	0.093	7.2	11.3	15.2	0.08 - 0.58	0.214	0.520
		1980s	6.9	9.4	12.0	0.06 - 0.54	0.703	0.000	9.2	10.9	13.0	0.09 - 0.81	0.403	0.316
		1990s	5.6	10.0	14.2	0.06 - 0.57	0.519	0.001	7.6	12.3	12.5	0.08 - 0.65	0.333	0.272
		2000s	4.6	8.7	11.0	0.06 - 0.51	0.413	0.005	7.2	11.8	13.4	0.07 - 0.60	0.249	0.324
	ImmM	1980s	5.6	9.5	12.2	0.06 - 0.49	0.621	0.000	8.3	10.9	14.3	0.06 - 0.73	0.348	0.278
		1990s	5.8	11.2	14.2	0.05 - 0.46	0.636	0.000	8.0	12.0	15.5	0.05 - 0.36	0.235	0.043
		2000s	4.9	9.0	12.5	0.07 - 0.64	0.485	0.017	7.4	11.1	14.5	0.08 - 0.53	0.198	0.587
	MatM	1980s	5.5	8.3	11.6	0.05 - 0.52	0.557	0.000	7.4	11.8	14.2	0.05 - 0.44	0.212	0.114
		1990s	4.9	8.1	12.2	0.04 - 0.32	0.360	0.000	7.1	11.1	14.4	0.05 - 0.37	0.189	0.204
		2000s	5.5	8.1	11.4	0.03 - 0.26	0.454	0.000	6.9	10.4	14.9	0.04 - 0.27	0.166	0.048
	ImmF	1980s	5.3	9.2	12.1	0.05 - 0.45	0.528	0.000	7.9	10.9	14.4	0.05 - 0.58	0.332	0.112
		1990s	4.9	8.2	14.1	0.03 - 0.27	0.370	0.000	7.9	11.9	15.5	0.04 - 0.36	0.233	0.017
2000s		5.4	8.1	12.3	0.03 - 0.29	0.422	0.000	7.3	11.9	16.2	0.04 - 0.31	0.231	0.007	
MatF	1980s	4.8	7.7	11.4	0.05 - 0.42	0.380	0.000	9.0	12.3	16.3	0.07 - 0.54	0.458	0.002	
	1990s	4.9	7.3	11.2	0.04 - 0.33	0.339	0.000	8.4	14.0	15.9	0.07 - 0.53	0.313	0.054	
	2000s	5.4	8.0	10.9	0.03 - 0.25	0.414	0.000	7.4	12.7	15.7	0.05 - 0.35	0.297	0.002	
BS	Survey	1990s	31.1	32.7	35.0	-	-	-	31.2	33.1	35.3	-	-	-
		2000s	32.0	33.3	35.1	-	-	-	31.5	33.1	35.2	-	-	-
	Neo	1990s	31.4	32.5	34.1	0.08 - 0.80	0.227	0.734	31.7	35.3	35.6	0.11 - 0.87	0.474	0.222

Depth (m)	ImmM	2000s	32.7	34.2	35.4	0.07 - 0.52	0.345	0.032	32.3	34.5	35.6	0.07 - 0.55	0.425	0.008
		1990s	32.1	33.9	35.1	0.06 - 0.69	0.333	0.285	31.6	33.0	34.6	0.07 - 0.54	0.305	0.079
		2000s	32.8	35.2	35.6	0.08 - 0.62	0.557	0.002	32.5	34.4	35.3	0.07 - 0.54	0.422	0.006
	MatM	1990s	32.0	33.4	34.9	0.05 - 0.58	0.188	0.374	31.5	32.1	34.1	0.06 - 0.58	0.501	0.001
		2000s	32.9	34.1	35.2	0.03 - 0.24	0.414	0.000	31.6	32.5	34.2	0.04 - 0.30	0.277	0.000
	ImmF	1990s	31.9	33.4	34.9	0.04 - 0.49	0.179	0.412	31.6	32.2	34.3	0.06 - 0.46	0.365	0.007
		2000s	32.8	34.2	35.5	0.04 - 0.31	0.383	0.000	31.7	32.6	35.0	0.04 - 0.29	0.227	0.007
	MatF	1990s	31.4	32.9	34.9	0.04 - 0.52	0.128	0.781	31.4	32.2	34.0	0.08 - 0.75	0.398	0.102
		2000s	32.3	33.8	35.1	0.03 - 0.27	0.282	0.000	31.5	32.4	33.6	0.04 - 0.36	0.447	0.000
	Survey	1960s	27.4	84.5	232.3	-	-	-	33.5	91.3	234.3	-	-	-
		1970s	20.5	81.8	233.8	-	-	-	20.1	78.4	229.6	-	-	-
		1980s	20.3	76.2	235.5	-	-	-	19.8	75.2	233.0	-	-	-
		1990s	18.7	74.5	233.0	-	-	-	18.8	73.9	235.7	-	-	-
		2000s	19.8	75.3	237.8	-	-	-	19.9	73.9	228.0	-	-	-
	Neo	1960s	46.6	86.8	151.9	0.10 - 0.82	0.335	0.627	38.6	73.6	110.2	0.09 - 0.63	0.432	0.032
		1970s	66.4	91.4	127.5	0.06 - 0.68	0.377	0.068	31.5	74.6	102.4	0.07 - 0.57	0.345	0.066
		1980s	51.1	85.5	204.0	0.06 - 0.44	0.304	0.031	63.5	143.1	150.5	0.10 - 0.73	0.392	0.273
		1990s	45.2	87.4	220.4	0.07 - 0.53	0.309	0.129	49.1	98.5	258.3	0.09 - 0.68	0.375	0.133
		2000s	54.1	90.1	140.4	0.06 - 0.49	0.317	0.065	44.4	87.3	265.4	0.07 - 0.53	0.341	0.073
	ImmM	1980s	70.1	107.5	264.8	0.05 - 0.38	0.425	0.000	42.3	90.8	189.3	0.07 - 0.74	0.243	0.557
		1990s	63.2	134.3	236.1	0.06 - 0.49	0.418	0.002	41.1	83.1	201.9	0.04 - 0.33	0.285	0.003
2000s		61.9	136.9	260.3	0.07 - 0.61	0.441	0.046	64.9	114.1	221.2	0.08 - 0.52	0.393	0.014	
MatM	1980s	51.5	93.1	226.2	0.04 - 0.41	0.277	0.009	22.3	51.5	209.3	0.04 - 0.36	0.209	0.044	
	1990s	37.1	84.3	242.0	0.03 - 0.31	0.155	0.207	24.7	53.3	198.9	0.05 - 0.37	0.211	0.083	
ImmF	2000s	35.9	63.2	216.5	0.03 - 0.26	0.157	0.053	22.9	64.6	200.0	0.04 - 0.26	0.144	0.113	
	1980s	33.0	101.2	254.3	0.04 - 0.34	0.220	0.029	29.7	72.3	204.3	0.05 - 0.53	0.170	0.565	
	1990s	31.1	91.0	235.8	0.04 - 0.29	0.104	0.501	25.1	64.6	197.0	0.04 - 0.34	0.155	0.205	
MatF	2000s	25.4	69.2	241.5	0.03 - 0.31	0.082	0.765	25.8	57.1	199.9	0.04 - 0.30	0.167	0.095	
	1980s	27.4	64.1	187.6	0.04 - 0.37	0.256	0.016	25.3	39.4	81.4	0.06 - 0.50	0.485	0.000	
	1990s	26.5	53.9	195.9	0.04 - 0.29	0.240	0.002	17.3	39.5	87.2	0.06 - 0.51	0.505	0.000	
Survey	2000s	22.0	44.0	200.2	0.03 - 0.28	0.375	0.000	21.6	41.9	136.0	0.04 - 0.32	0.391	0.000	
	1960s	36.90	41.05	43.85	-	-	-	37.84	41.48	43.88	-	-	-	
	1970s	36.84	40.99	43.75	-	-	-	36.64	40.92	43.79	-	-	-	
Lat (°N)														

	1980s	36.64	40.94	43.72	-	-	-	36.67	40.96	43.67	-	-	-
	1990s	36.63	40.92	43.60	-	-	-	36.56	40.92	43.64	-	-	-
	2000s	36.64	40.92	43.68	-	-	-	36.61	40.91	43.64	-	-	-
Neo	1960s	36.24	39.01	40.30	0.10 - 0.79	0.685	0.015	38.54	39.88	40.88	0.09 - 0.57	0.627	0.000
	1970s	38.43	39.78	40.41	0.06 - 0.76	0.615	0.000	39.47	40.54	41.75	0.08 - 0.59	0.384	0.029
	1980s	37.02	40.22	40.59	0.06 - 0.49	0.558	0.000	39.91	40.18	41.37	0.09 - 0.74	0.410	0.236
	1990s	36.72	39.99	40.45	0.06 - 0.61	0.585	0.000	37.40	40.35	41.71	0.09 - 0.63	0.462	0.027
	2000s	38.54	40.12	40.69	0.07 - 0.50	0.530	0.000	37.37	40.21	43.22	0.06 - 0.58	0.415	0.015
ImmM	1980s	38.65	40.34	41.27	0.05 - 0.40	0.418	0.000	40.00	40.79	42.61	0.06 - 0.67	0.291	0.374
	1990s	38.36	40.29	42.51	0.06 - 0.47	0.361	0.010	40.33	41.16	43.65	0.05 - 0.39	0.330	0.001
	2000s	38.66	40.12	42.73	0.06 - 0.64	0.391	0.119	39.93	40.46	44.02	0.08 - 0.58	0.267	0.219
MatM	1980s	37.82	40.32	42.47	0.05 - 0.40	0.403	0.000	40.72	41.51	43.76	0.05 - 0.36	0.444	0.000
	1990s	36.82	40.23	42.83	0.03 - 0.32	0.262	0.005	40.58	41.84	43.69	0.05 - 0.37	0.400	0.000
	2000s	36.23	38.74	42.58	0.03 - 0.30	0.498	0.000	40.64	41.95	44.01	0.04 - 0.28	0.395	0.000
ImmF	1980s	36.35	40.26	42.35	0.04 - 0.35	0.416	0.000	40.01	41.09	43.24	0.05 - 0.52	0.291	0.113
	1990s	36.80	40.24	42.59	0.03 - 0.32	0.303	0.000	40.45	41.07	43.70	0.04 - 0.33	0.352	0.000
	2000s	35.96	39.24	42.65	0.03 - 0.31	0.386	0.000	40.24	41.09	43.46	0.03 - 0.32	0.302	0.000
MatF	1980s	35.90	39.13	42.25	0.04 - 0.40	0.465	0.000	40.78	41.10	42.29	0.06 - 0.49	0.438	0.001
	1990s	35.89	38.89	42.18	0.04 - 0.28	0.449	0.000	40.59	41.09	42.83	0.07 - 0.49	0.394	0.005
	2000s	35.79	38.01	42.25	0.03 - 0.23	0.542	0.000	40.43	41.23	43.22	0.05 - 0.37	0.369	0.000

Table 2.4. Gini index quantifying the degree of aggregation for spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring (1968 – 2009) and autumn (1963 – 2009). Stages as defined in Table 2.1. DOM refers to which season exhibited a higher aggregation index (Aut = autumn, Spr = spring). DIFF quantifies the deviation between seasonal Gini indices. Note: spiny dogfish not sexed consistently until 1980.

Stage	Gini Index		DOM	DIFF
	<u>SPRING</u>	<u>AUTUMN</u>		
All	0.925	0.951	Aut	0.026
Neo	0.987	0.994	Aut	0.007
ImmM	0.984	0.988	Aut	0.004
MatM	0.965	0.976	Aut	0.011
ImmF	0.950	0.973	Aut	0.022
MatF	0.950	0.983	Aut	0.033

Figure 2.1. Annual seasonal movements of spiny dogfish within the Northeast (US) shelf large marine ecosystem (NES LME). Legend reflects average depth contours within the Northeast Fisheries Science Center (NEFSC) bottom trawl survey domain. Regions are as follows: Gulf of Maine (GM), Georges Bank (GB), Southern New England (SNE), and the Middle Atlantic Bight (MA). Distinctive features include: (1) Cape Hatteras, (2) Hudson Canyon, (3) Great South Channel, and (4) Northeast Channel.

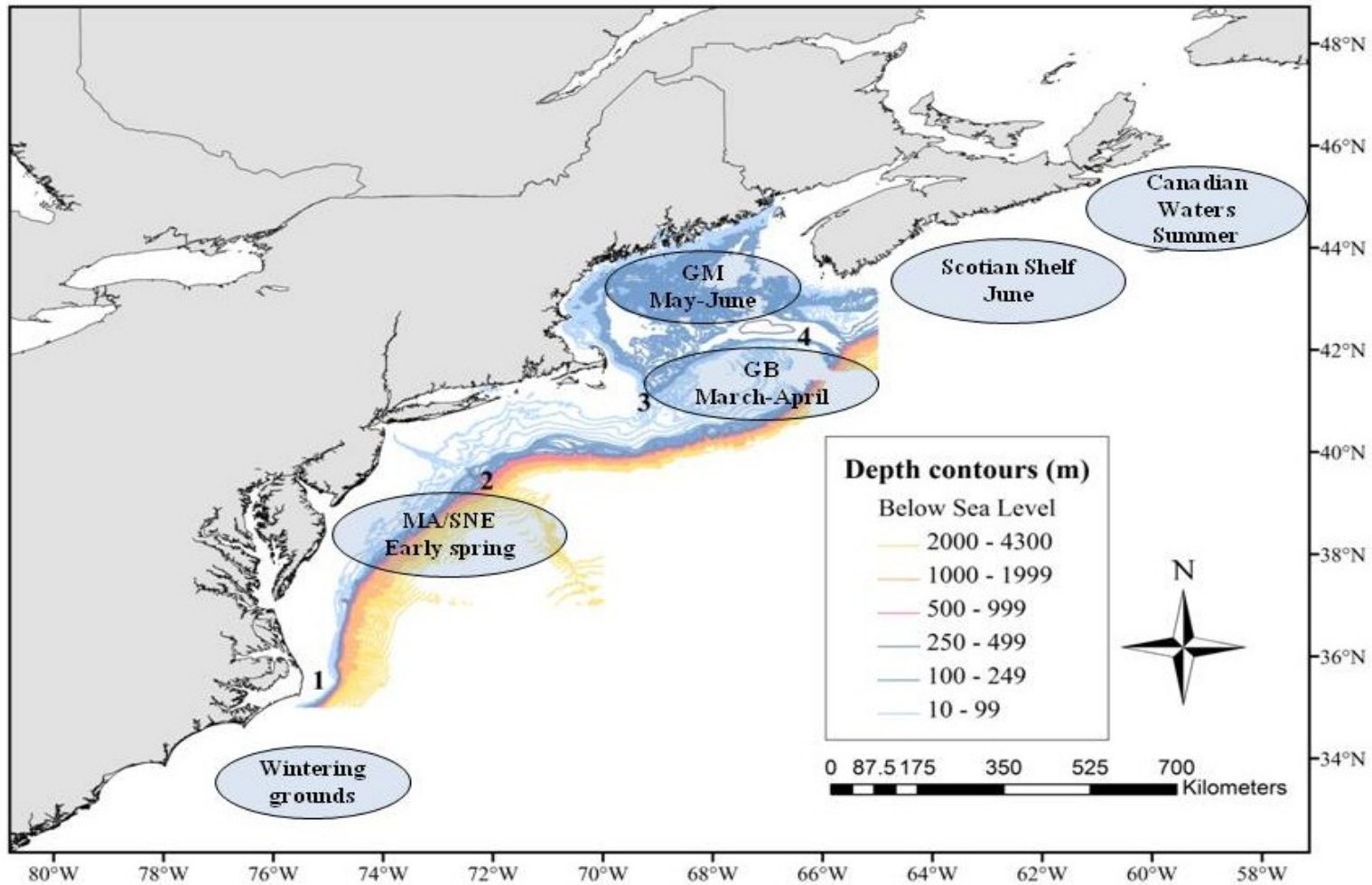


Figure 2.2. Decadal distribution and regional survey catch of spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring (1968 – 2009). Plotted are the number of dogfish per tow (dark green = 0, green = 1 – 50, light green = 51 – 100, yellow = 101 – 250, orange = 251 – 1000, red > 1001). Pie charts show regional proportion of survey catch from the Middle Atlantic Bight (white), Southern New England (light gray), Georges Bank (gray), and the Gulf of Maine (dark gray). Notes: Inshore sampling began in 1973 and data collection was limited during the 1960s.

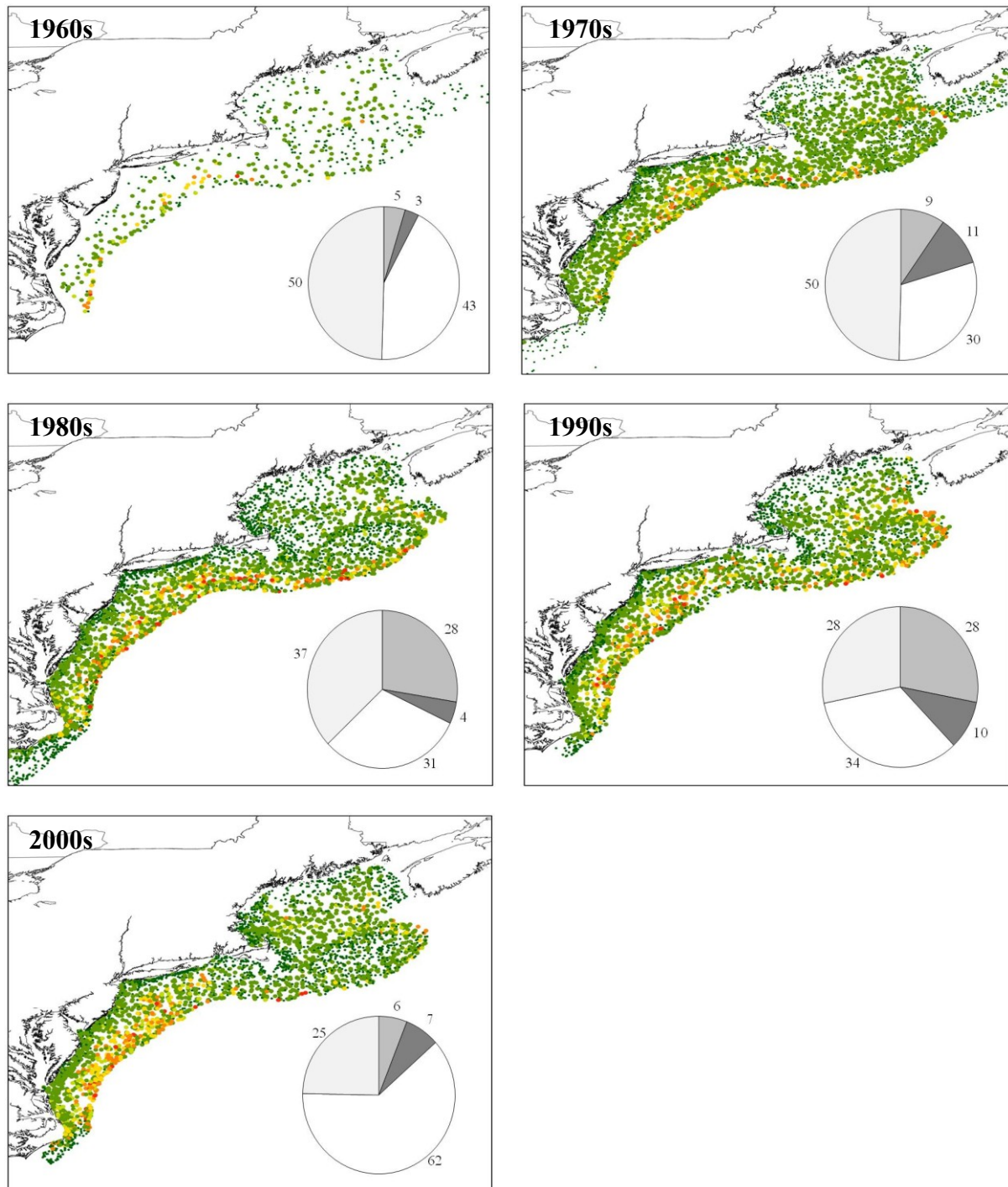


Figure 2.3. Decadal distribution and regional survey catch of spiny dogfish in the Northeast (US) shelf large marine ecosystem during autumn (1963 – 2009). Plotted are the number of dogfish per tow (dark green = 0, green = 1 – 50, light green = 51 – 100, yellow = 101 – 250, orange = 251 – 1000, red > 1001). Pie charts show regional proportion of survey catch from the Middle Atlantic Bight (white), Southern New England (light gray), Georges Bank (gray), and the Gulf of Maine (dark gray). Notes: Inshore sampling began in 1972 and data collection was limited during the 1960s.

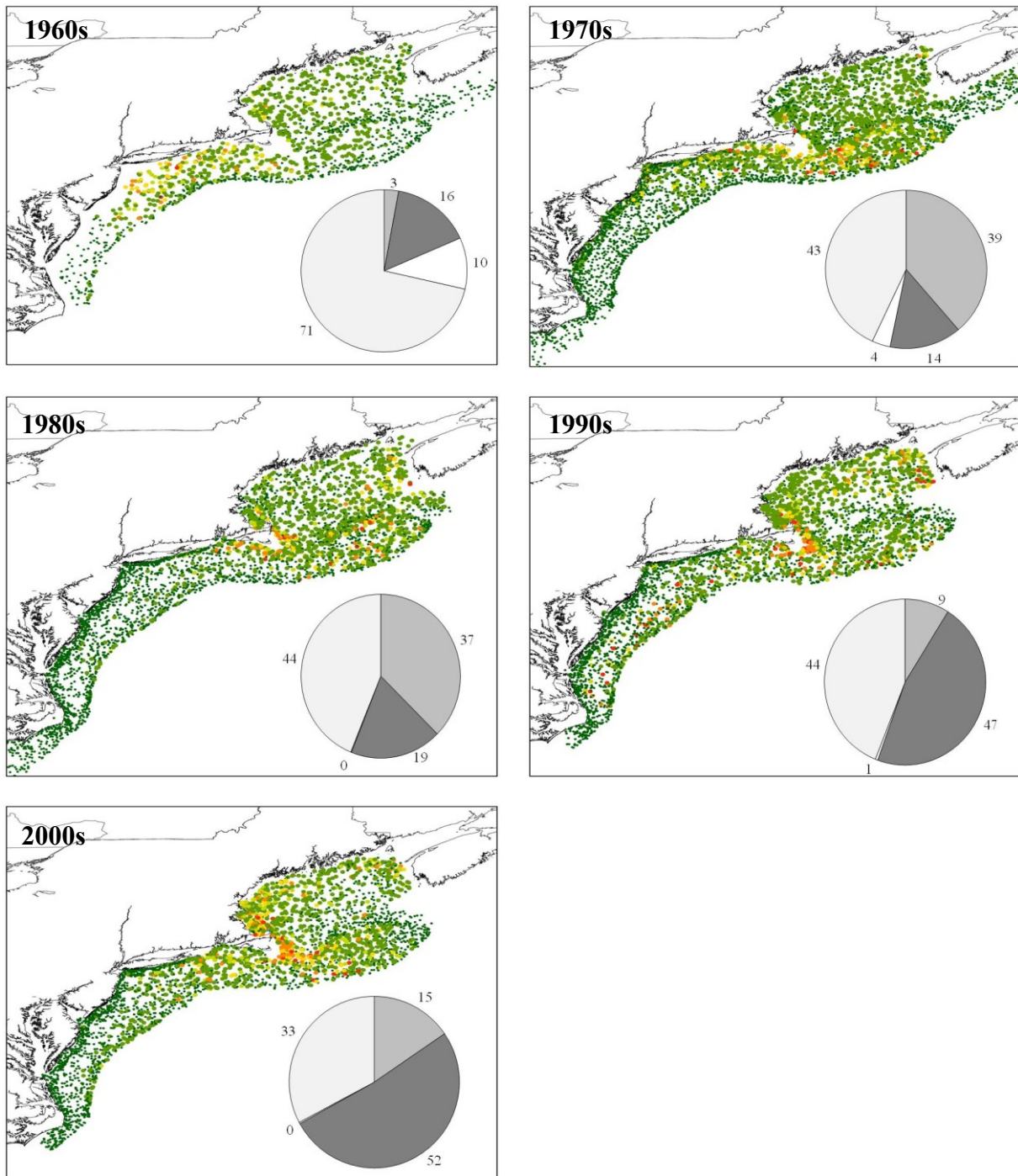


Figure 2.4. Regional relative abundance of spiny dogfish life-history stages in the Northeast (US) shelf large marine ecosystem during spring (1968 – 2009) (left panel) and autumn (1963 – 2009) (right panel). Regions include Georges Bank (black), Gulf of Maine (blue), Southern New England (orange), and the Middle Atlantic Bight (green). Notes: gap between 1973-79 is due to inconsistencies in sexing of spiny dogfish, y-axes differ between panels, and *CPUE* estimates have been normalized ($CPUE / \Sigma(CPUE)$).

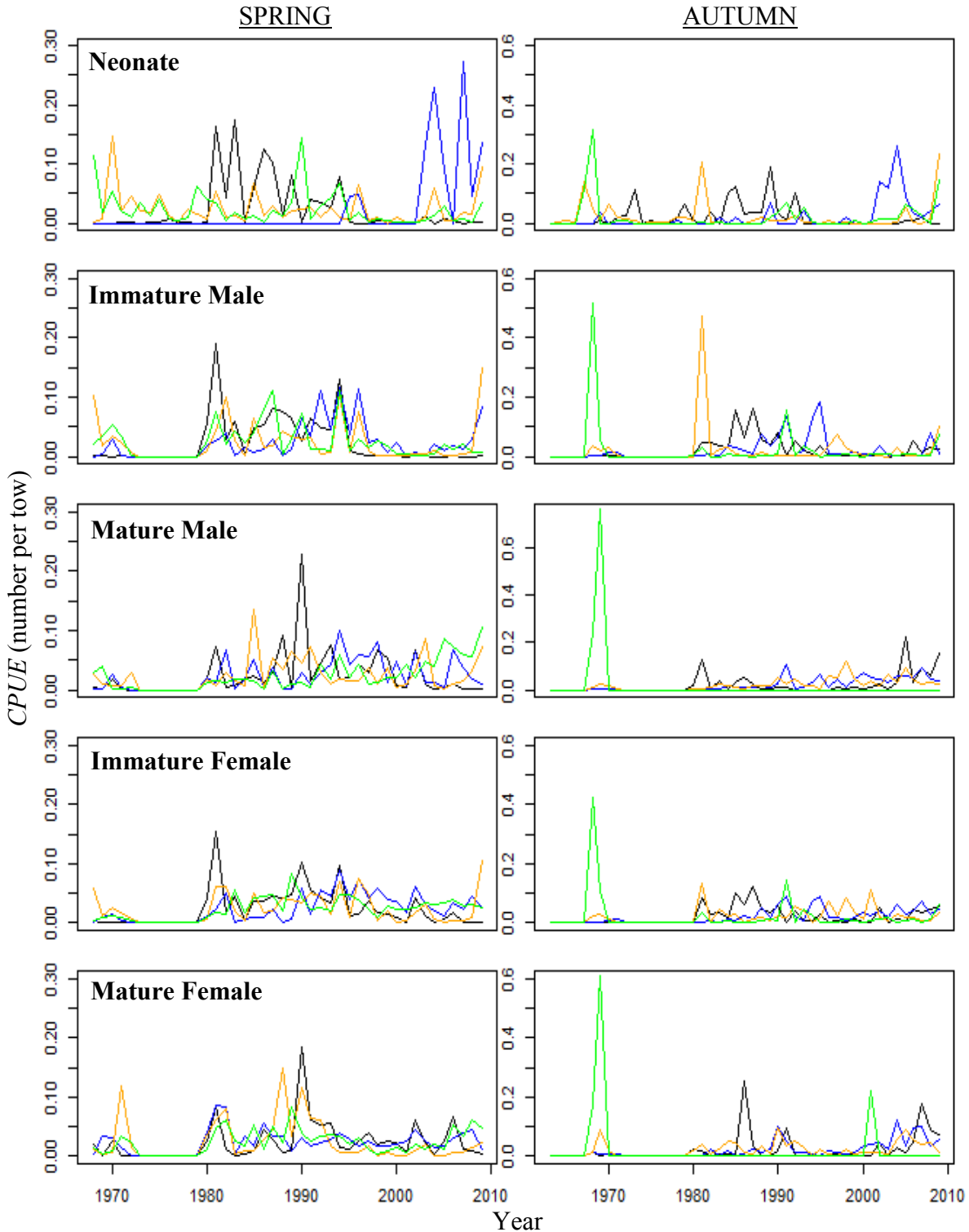


Figure 2.5. Cumulative distributions of available and occupied habitat for spiny dogfish life-history stages in the Northeast (US) shelf large marine ecosystem during spring between 1968 and 2009. Habitat variables include: A) bottom temperature, B) bottom salinity, C) depth, and D) latitude. CDFs shown include survey (thick black), neonate (orange), immature male (red), mature male (green), immature female (blue), and mature female (purple). Notes: spiny dogfish not sexed consistently until 1980 and salinity data has been collected consistently since 1996.

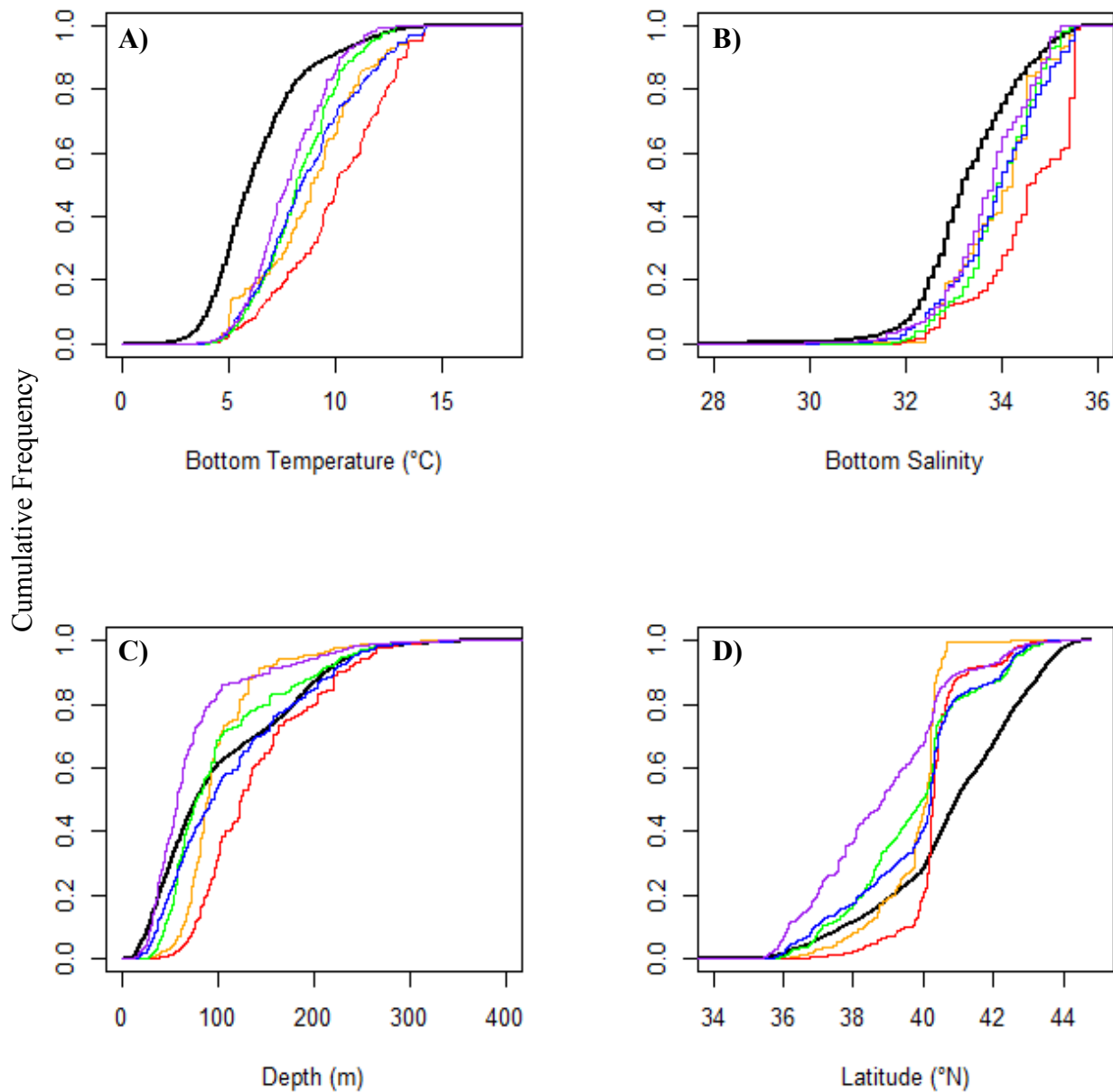


Figure 2.6. Cumulative distributions of available and occupied habitat for spiny dogfish life-history stages in the Northeast (US) shelf large marine ecosystem during autumn between 1963 and 2009. Habitat variables include: A) bottom temperature, B) bottom salinity, C) depth, and D) latitude. CDFs shown include survey (thick black), neonate (orange), immature male (red), mature male (green), immature female (blue), and mature female (purple). Notes: spiny dogfish not sexed consistently until 1980, salinity data has been collected consistently since 1996, temperature range on the x-axis differs from previous figure.

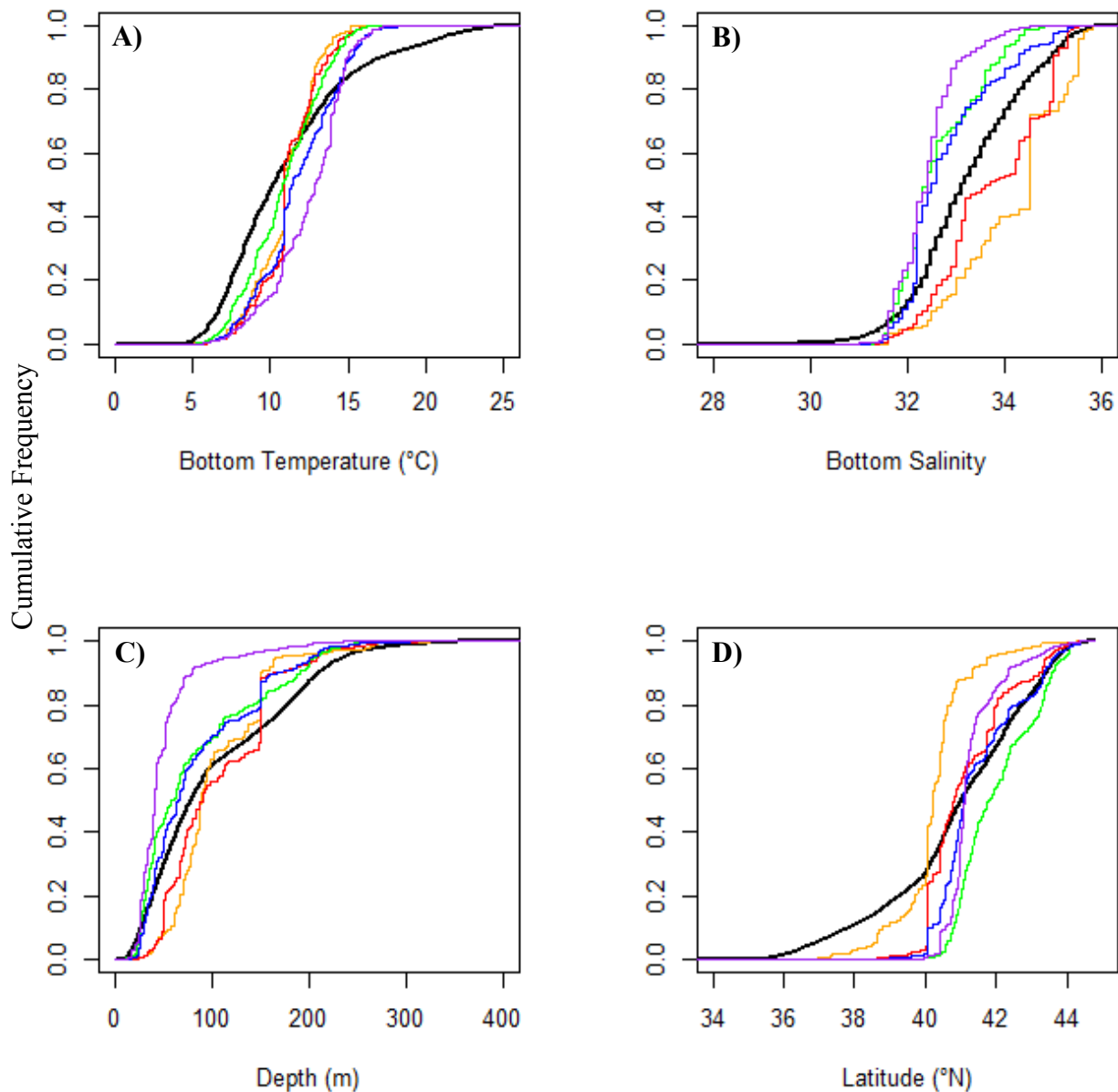


Figure 2.7. Annual variation in the distribution index D_{95} , or minimum area over which 95% of the spiny dogfish population is spread, during spring (gray) and autumn (black) in the Northeast (US) shelf large marine ecosystem from 1963 to 2009. Notes: y-axes differ between panels and gap between 1973-79 is due to inconsistencies in sexing of spiny dogfish.

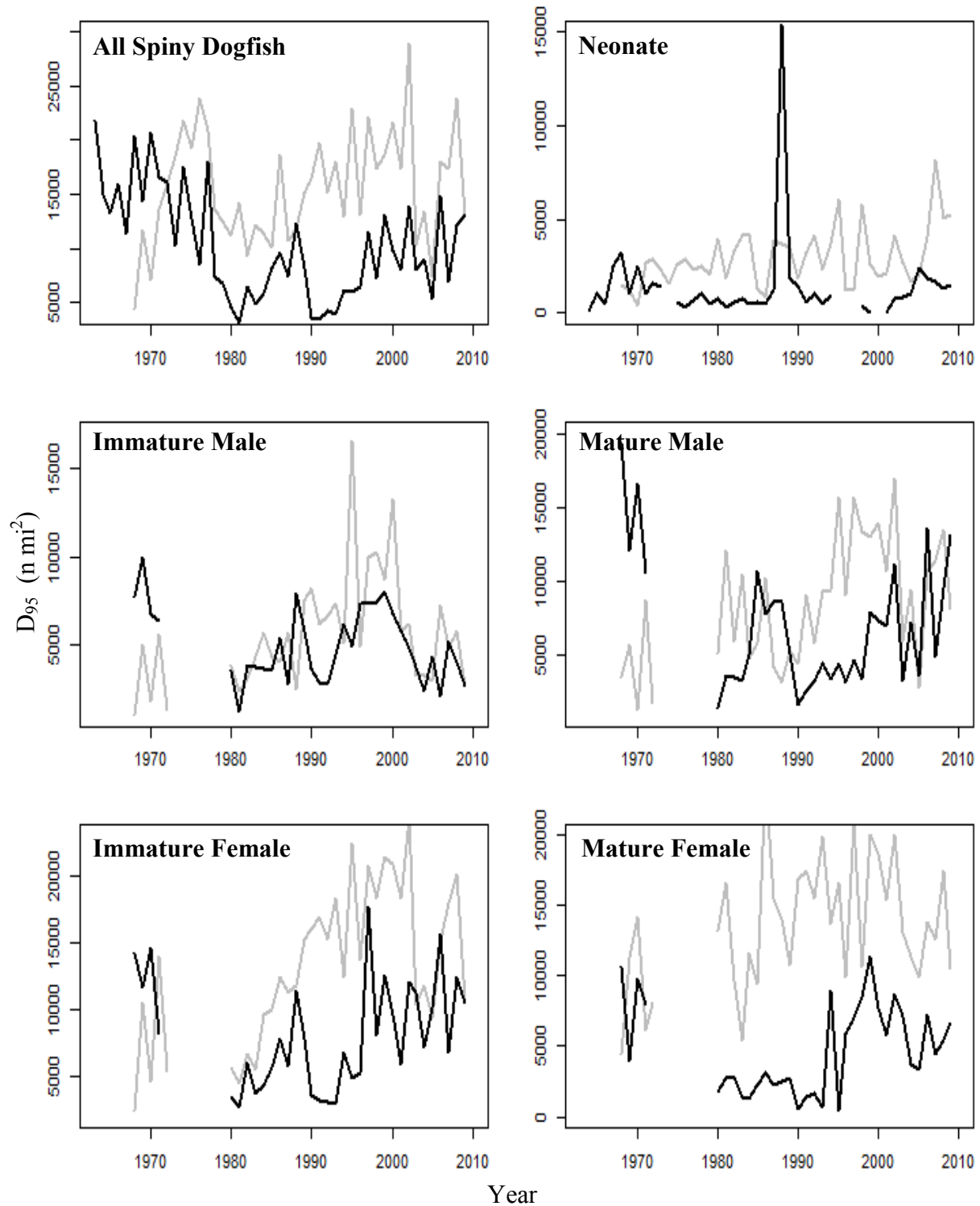
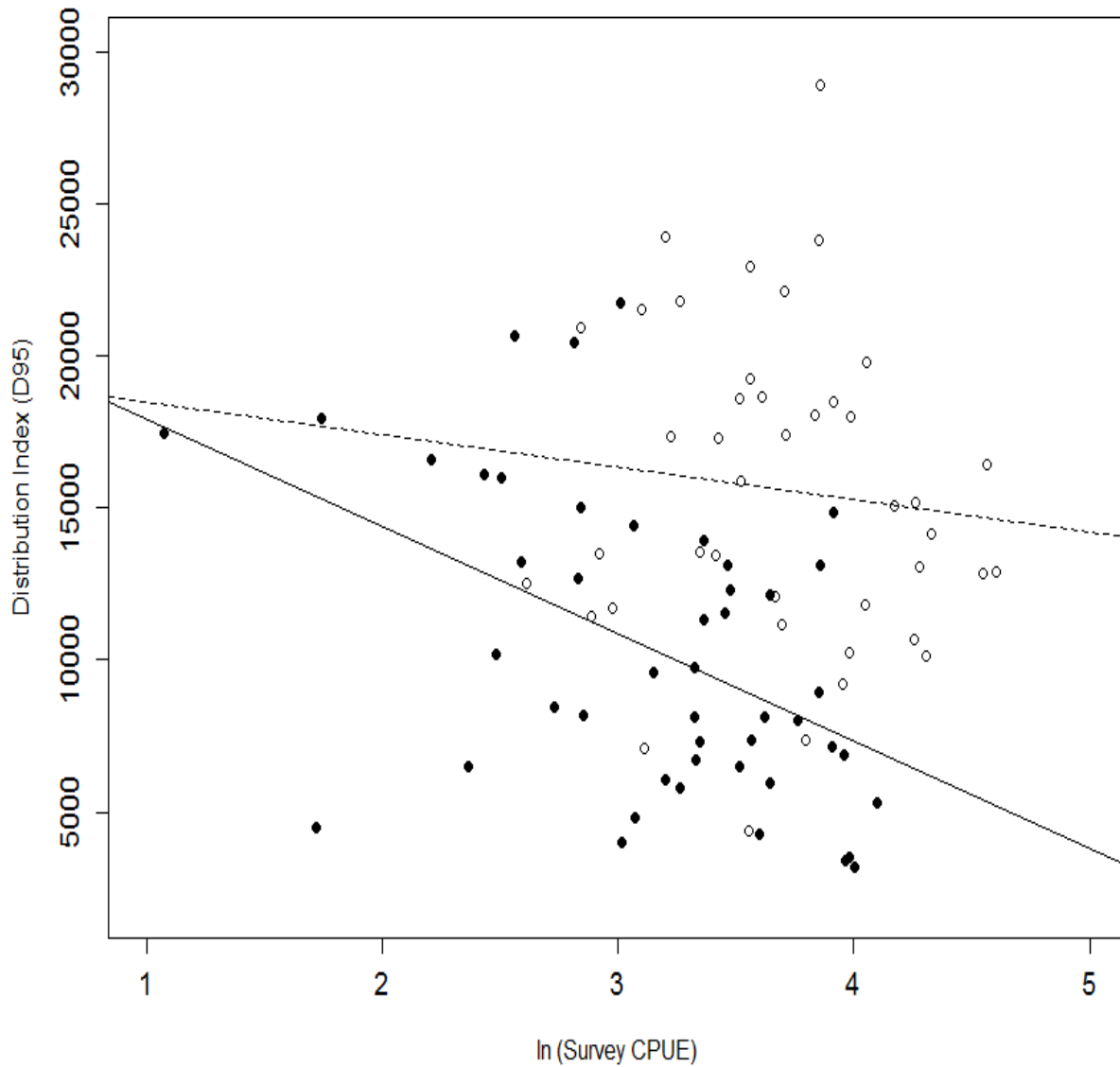


Figure 2.8. Relationship between annual abundance (survey *CPUE*) of all spiny dogfish and the distribution index (D_{95}) for spring (open circle) and autumn (black circle) in the Northeast (US) shelf large marine ecosystem. The distribution index D_{95} (n mi²), or minimum area over which 95% of the population is spread, was regressed against the log_e transformed index of abundance (*CPUE*). Linear regression lines are shown for autumn (solid; $y = -3520.8x + 21433.8$; $R^2 = 0.22$, $p < 0.05$) and spring (dashed; $y = -1071.0x + 19540$; $R^2 = 0.01$, $p > 0.05$).



Chapter 3:
**APPLICATION OF GENERALIZED ADDITIVE MODELS TO EXAMINE
ONTOGENETIC AND SEASONAL DISTRIBUTIONS OF SPINY DOGFISH IN THE
NORTHEAST (US) SHELF LARGE MARINE ECOSYSTEM**

Introduction

The Magnuson-Stevens Fishery Conservation and Management Act of the United States emphasizes the integration of ecosystem considerations into assessment methods (Link et al. 2011) consistent with a move towards ecosystem-based fisheries management (EBFM) (Pikitch et al. 2004). In the Northeast (US) shelf large marine ecosystem (NES LME) (Figure 3.1), spiny dogfish (*Squalus acanthias*) play a key role in the structure and function of marine fisheries ecosystems (Fogarty & Murawski 1998, Link & Garrison 2002, Link & Ford 2006) drawing concern as both a consumer, potentially competing with commercial fisheries, and as a species of conservation interest due to its vulnerable life history (Frisk et al. 2005, Frisk et al. 2011). Yet, the species' response to environmental and ecological drivers remains unknown leaving a critical gap in the science needed to understand the species' population dynamics. Unlike many regions of their range, spiny dogfish remain abundant in the NES LME and often display large fluctuations in local distribution and abundance (Rago & Sosebee 2009). A better understanding of the environmental and ecological drivers of changes in distribution may elucidate the mechanisms explaining large, and often biologically unrealistic, temporal changes in survey estimates of abundance and biomass. Estimation of these relationships, especially in the face of climate change (Hedger et al. 2004, Nye et al. 2009), will enhance forecasting ability (Link et al.

2011) and provide insight into species responses under both anthropogenic and natural alterations to the ecosystem.

A major focus of fisheries ecology is to define and understand the association of a species' abundance with time, space and the environment (Denis et al. 2002). Habitat conditions have the potential to influence local abundance and introduce variability into indices of abundance complicating trend monitoring (O'Brien & Rago 1996, Bigelow et al. 1999). Unfavorable water masses can reduce the availability of a species to trawls and skew survey-derived abundance estimates (Smith & Page 1996, Shepherd et al. 2002). Prey distributions are also capable of shaping a species' spatial pattern by concentrating predators in prey-dense areas (Perry & Smith 1994, Campana & Joyce 2004) although direct investigation is usually hindered by a lack of appropriate data (Stoner et al. 2001). While fundamental to the traditional study of single species population dynamics (Feyrer et al. 2007, Brodeur et al. 2009, Damalas et al. 2010), understanding how a species relates to the environment and their prey is critical for developing ecosystem analyses.

The majority of research relating fish distributions to the environment and other ecosystem characteristics has concerned commercial species including Atlantic cod (*Gadus morhua*) (O'Brien & Rago 1996), winter flounder (*Pseudopleuronectes americanus*) (Stoner et al. 2001), and yellowtail flounder (*Limanda ferruginea*) (Simpson & Walsh 2004). In the northwest Atlantic, decades of intensive foreign and domestic fishing effort reduced principal groundfish stocks in the 1970-80s, altering not only the ecosystem structure but also the objectives of fishery and management targets (Murawski 1991, Fogarty & Murawski 1998). Species such as skates and dogfish that were traditionally discarded became commercially important as a means to offset the low catches of high valued groundfish (Murawski 1991,

Fogarty & Murawski 1998, Link et al. 2002, Frisk et al. 2008). This increased harvest created the need to understand the population dynamics of these elasmobranchs and to develop management strategies to prevent overexploitation (Rago et al. 1998). infer

The recent increased commercial importance of spiny dogfish coupled with biologically unrealistic fluctuations in abundance and assessment uncertainty (NEFSC 2006) highlights the need to understand the species' drivers of distribution and abundance. In addition, long-term sustainability remains uncertain as recent monitoring surveys (Northeast Fisheries Science Center (NEFSC), Massachusetts Division of Marine Fisheries (MADMF), Atlantic States Marine Fisheries Commission (ASMFC)) have revealed reductions in size, fecundity and recruitment (Rago et al. 1998, Sosebee 2005, NEFSC 2006, Rago & Sosebee 2009). Many factors complicate the assessment of this species including seasonal trans-boundary movements and inconsistencies in both seasonal and decadal trends (Overholtz & Tyler 1985, Rago et al. 1998, Rago & Sosebee 2009). Spiny dogfish movement is hypothesized to reflect the distribution of prey, particularly during spring (Overholtz & Tyler 1985, Burgess 2002). Common prey items include squids, clupeids, scombrids, and other fishes (Fogarty & Murawski 1998, Link & Almeida 2000, Link & Garrison 2002). With a better understanding of the influence of distributional variation on survey estimates (Frisk et al. 2008, Frisk 2010), improved abundance indices may be obtained (Rago et al. 1998, McMillan & Morse 1999, Stevens et al. 2000, NEFSC 2006) that benefit both traditional single species stock assessments and ecosystem based management.

Habitat modeling identifies a species' habitat preference and predicts their abundance or occupancy based on an inferred response to environmental conditions (Brotons et al. 2004, Wintle et al. 2005, Heinänen et al. 2008). In this study, we analyzed habitat preferences of spiny dogfish using generalized additive models (GAMs) and focused on the relationships of

occupancy and abundance with ambient environmental, temporal, spatial, and ecological factors in the NES LME. Factors driving the distributions of spiny dogfish life-history stages were identified and potential mechanisms discussed. As in Feyrer et al. (2007), our study highlights the utility of long-term datasets as a valuable monitoring tool in describing fish habitat. Ultimately, our findings will help elucidate trend inconsistencies encountered in stock assessments, provide insight into how spiny dogfish will respond to climate change and contribute to the growing data demands for EBFM.

Methods

Data source

Data were collected from the NEFSC annual bottom trawl surveys conducted on the NES LME during autumn and spring (Figure 3.1). These surveys sample the NES LME from Cape Hatteras, NC, to GB and the GM using a stratified random design. Offshore and inshore strata are depicted in Figures 1 and 2 of NEFSC (2006). The autumn survey has been conducted in offshore areas since 1963 and inshore strata were added in 1972. The spring survey began sampling offshore areas in 1968 and inshore strata were added in 1973. The number of stations sampled per stratum was proportional to its area but inshore strata were sampled at approximately three times the sampling rate of offshore strata. Approximately 300 – 400 stations were visited each season ($N_{AUTUMN} = 344 \pm 13$ stations, S.E.; $N_{SPRING} = 346 \pm 8$ stations). Detailed descriptions of the survey design, protocol, execution and efficiency can be found in previous literature (Azarovitz 1981, Azarovitz et al. 1997).

Correction factors based on field experiments were applied for changes in vessels, gear and doors when necessary. The introduction of the NOAA ship *Henry B. Bigelow* in 2009 brought about changes to the trawling gear and survey protocol, details of which are described (Brown et al. 2007). In addition, a calibration study enabled comparison of the catchability of the old vessel, the *Albatross IV*, with that of the new vessel (Miller et al. 2010).

Data

Indices of spiny dogfish abundance were extracted from the NEFSC trawl survey data for five groups: aggregated male and female neonates (total length, $TL \leq 26$ cm), immature males ($26 \text{ cm} < TL < 60$ cm), immature females ($26 \text{ cm} < TL < 80$ cm), mature males ($TL \geq 60$ cm), and mature females ($TL \geq 80$ cm). Tow duration was standardized and represented by the number of dogfish caught per tow (*CPUE*). To account for zero-inflation, the distribution of each dogfish stage was reported in two separate datasets: (1) occurrence (PA: 1 = present, 0 = absent) and (2) abundance or zero-truncated presence (PRES) (Table 3.1). Each dataset was randomly divided into a training set (70% of observations) for model fitting with the remainder used as an independent test set (remaining 30% of observations) for model validation (Miller & Franklin 2002, Brotons et al. 2004).

Variable selection

Exploratory data analyses were conducted to identify candidate explanatory variables for inclusion in modeling exercises. Ecological factors (i.e., prey abundance) were selected based on their importance in spiny dogfish diet as reported from the NMFS Food Webs Dynamic Program food habits database (Link & Almeida 2000). Prey species chosen included: Atlantic butterfish

(*Peprilus triacanthus*), Atlantic herring (*Clupea harengus*), shortfin squid (*Illex* sp.), longfin squid (*Loligo* sp.), and Atlantic mackerel (*Scomber scombrus*). As for spiny dogfish, *CPUE* from the NEFSC survey was considered an appropriate proxy for prey abundance. Large correlations ($r > 0.6$) resulted in the inclusion of only one variable to minimize collinearity (Wintle et al. 2005). In addition, variance inflation factors were calculated using the AED package (Zuur 2010) in R (R Core Development 2010) with values below 3.0 acceptable (Zuur et al. 2009).

Spatial overlap with prey and conspecifics

The potential for spatial overlap between predator and prey and also between dogfish stages was characterized using two survey-based spatial indicators: the global index of collocation (*GIC*) which reflects the geographical collocation of two distinct populations (Wuillez et al. 2007, Wuillez et al. 2009) and the local index of collocation (*LIC*) which reflects the local overlap at sampling stations (Bez & Rivoirard 2000). Annual *GIC* for each dogfish stage and prey species required estimates of the center of gravity (*CG*), or the mean location of a surveyed population, and the inertia (*I*), or the dispersion of the population around its *CG* (see Wuillez et al. 2009 for equations) and was calculated as:

$$(3.1) \quad GIC = 1 - \frac{\Delta CG^2}{\Delta CG^2 + I_{dogfish\ stage} + I_{prey\ or\ conspecific}}$$

where ΔCG separates the *CG* of a dogfish stage (i.e., predator or conspecific) and prey species or conspecific stage. Areas of influence, required for both *CG* and *I* calculations, were estimated from Voronoi plots using the 'tripack' package (Renka et al. 2009) of R (R Core Development

2010). The *GIC* index ranges from 0 (each population occupies a distinct location) to 1 (two *CGs* completely coincide) (Woillez et al. 2007, Woillez et al. 2009).

The *LIC* was calculated for each predator-prey and conspecific combination during each year (t) with the following:

$$(3.2) \quad LIC(t) = \frac{\sum_{i=1}^N z_i^{prey \text{ or } conspecific}(t) z_i^{dogfish \text{ stage}}(t)}{\sqrt{\sum_{i=1}^N (z_i^{prey \text{ or } conspecific}(t))^2 \sum_{i=1}^N (z_i^{dogfish \text{ stage}}(t))^2}}.$$

This index represents the non-centered correlation between fish densities, z , between stations and ranges from 0 (no overlap) to 1 (densities are proportional to each other at sampled stations) (Bez & Rivoirard 2000).

Statistical analysis

Model fitting

The distributions of spiny dogfish were modeled separately for each stage and season using generalized additive models (GAM) (Hastie & Tibshirani 1990, Wood 2006), a semi-parametric extension of the generalized linear model (GLM) commonly applied to the spatial distributions of fishes (Guisan et al. 2002, Leathwick et al. 2006, Heinänen et al. 2008, Damalas et al. 2010). While GLMs use a linear predictor to define the relationship between the response and explanatory variables, GAMs utilize a smoothing function (Wintle et al. 2005) that can easily handle non-linear relationships and uncover hidden structure between variables missed by traditional linear methods (Hastie & Tibshirani 1990, Guisan et al. 2002). GAM analyses are

often data-driven and can be either explanatory or predictive in nature (Yee & Mitchell 1991, Fewster et al. 2000, Guisan et al. 2002, Feyrer et al. 2007).

Two stage (i.e., hurdle) models were constructed to account for zero-inflation and overdispersion (Potts & Elith 2006, Heinänen et al. 2008, Zuur et al. 2009). The first stage predicted the probability of occurrence using a logit link function and a binomial error distribution. The second stage predicted the conditional presence using a log link function and a negative binomial error distribution (Gotway & Stroup 1997, Link & Sauer 1997, Fewster et al. 2000, Martin et al. 2005). This method allowed for the independent identification of driving forces behind both occurrence and abundance which may differ (Potts & Elith 2006). All GAMs were built in R (R Core Development 2010) with the package 'mgcv' (Wood 2011) using cubic regression splines and a maximum of 5 degrees of freedom ($k = 5$).

Model selection

Due to the vast number of potential combinations of explanatory variables, GAMs were built in steps. The first sub-model (abiotic) was a function of the temporal, spatial, and environmental variables while the second sub-model (biotic) was solely a function of ecological variables. Step-wise backward selection was implemented (Harrell 2001, Wintle et al. 2005) and the optimal sub-model was chosen based on the lowest Akaike's information criterion (AIC) (Fielding & Bell 1997, Pearce & Ferrier 2000, Zuur et al. 2009).

To reduce model complexity and computation time, the five largest two-way interactions were identified by boosted regression tree (BRT) analysis and later incorporated into GAMs. BRT analysis combines a large number of simple decision trees into a single model and results in strong predictive performance and good descriptions of modeled relationships (Elith et al. 2008).

Following Elith et al. (2008), we tested a range of tree complexities (*tc*; additive model = 1, 2-way interactions = 2, etc.) and learning rates (*lr*; determines contribution of each tree to growing model) to resolve which combination minimized predictive deviance and maximized predictive performance and validated this combination using ten-fold cross validation on training data (Elith et al. 2008, Froeschke et al. 2010). Model performance was assessed by the predictive deviance between test data and predicted values (De'ath 2007, Elith et al. 2008, Leathwick et al. 2008, Froeschke et al. 2010) and through examination of the area under the receiver operator characteristic curve (AUC) solely for occurrence models (Hanley & McNeil 1982). AUC represents the ability of a model to discriminate between presence and absence sites and ranges from 0.5 (no better than random) to 1.0 (perfect discrimination) (Brotons et al. 2004, Leathwick et al. 2006, Heinänen et al. 2008). All BRTs were carried out in R (R Core Development 2010) using the 'gbm' package (Ridgeway 2010) supplemented with functions from Elith et al. (2008).

After sub-model selection and identification of interactions, all were combined into a single model. In situations where a variable was present as part of an interaction but was excluded from either sub-model, the variable was added to the combined model to honor the hierarchy principle (Faraway 2006). Each combined model was further simplified if possible by removing terms (those not part of an interaction) based on approximate *p* values and re-examining the AIC, with the lowest AIC identifying the optimal model. Response curves were visually inspected for ecological realism (Wintle et al. 2005, Heinänen et al. 2008).

Model evaluation

Unbiased estimates of each optimal model's predictive performance were obtained by evaluating a test dataset (Fielding & Bell 1997, Pearce & Ferrier 2000). PA models were tested

for discrimination and accuracy in R (R Core Development 2010) using the packages 'pROC' (Robin et al. 2011) and 'PresenceAbsence' (Freeman 2007), respectively, and for model behavior via bias using Bland-Altman plots (Bland & Altman 1986). The ability of the model to discriminate between presence and absence sites was described using AUC (Brotons et al. 2004, Leathwick et al. 2006) with values between 0.7 and 0.9 considered reasonable and values > 0.9 good as the true positive rate was high relative to the false positive rate (Swets 1988, Pearce & Ferrier 2000). The ability to correctly predict the proportion of sites with a spiny dogfish given an occupied environmental profile was determined by calibration plots with perfect calibration indicated by a line with a slope = 1 and an intercept = 0 (Wintle et al. 2005, Heinänen et al. 2008). Model behavior was further assessed using a Bland-Altman plot, which compares the binary responses across a gradient of bins and identifies bias by examining the relationship between the difference and mean (Bland & Altman 1986).

Validation of PRES models was assessed using typical model performance estimators including calibration, correlations and mean error (Potts & Elith 2006, Heinänen et al. 2008), and Bland-Altman plots (Bland & Altman 1986). Calibration was measured with a simple linear regression between observed and predicted values with the intercept term indicative of bias and the slope reflective of the consistency in the predictions (Potts & Elith 2006). The strength of the relationship between observed and predicted values was assessed using Pearson's correlation coefficient (r), although a perfect correlation ($r = 1.0$) may still display bias in a consistent direction (Potts & Elith 2006, Heinänen et al. 2008). The similarity between ranks of observed and predicted values was assessed using Spearman's rank correlation (r_{sp}) with a high value indicating a correct order of predictions (Potts & Elith 2006). As misleading results are often obtained when relying solely on correlation coefficients (Bland & Altman 1986), model behavior

was assessed using a Bland-Altman plot by binning the values and identifying bias as described above. Lastly, both root mean square error of prediction (*RMSE*) and average error (*AVE*) were calculated as in Potts and Elith (2006).

Forecasting of occurrence under various temperature regimes

To further investigate occurrence in relation to temperature, we created a hypothetical dataset ($n = 344$ stations) covering spring (Julian days 59 to 128) and autumn (Julian days 247 - 305) with the frequency of tows per day similar to previous surveys. For each hypothetical observation, average bottom temperature (BT_{avg}), depth, and zenith were assigned based on the averages throughout the time series for each Julian day. Occurrence was predicted solely using optimal abiotic models due to the uncertainty of how prey species would respond to the temperature changes. Different temperature scenarios were investigated by two bottom temperature variables, one to reflect a "warmer" than average year ($BT_{avg} + 1^{\circ}C$) and one a "cooler" than average year ($BT_{avg} - 1^{\circ}C$). Prediction maps were created by interpolating the predicted occurrence at hypothetical latitude and longitudes based on the 2009 survey using inverse-distance weighted methods in the spatial analyst package extension of ArcMap (v10. ESRI Corp).

Results

Data

Stations missing BT were excluded from all analyses. Occurrence and abundance of all dogfish stages were greater during spring compared to autumn (Table 3.1). During both seasons,

the highest percentage of positive tows was displayed for immature females (autumn: 26.08%; spring: 37.74%) and the lowest for neonates (autumn: 1.22%; spring: 5.82%) (Table 3.1).

Six biotic and six abiotic variables were chosen as candidate explanatory variables for describing occurrence and abundance of each dogfish stage based on perceived importance and data availability (Table 3.2). High correlations ($r > 0.6$) in both PA (Table 3.3) and PRES training datasets led to the exclusion of latitude and PAR in all analyses. While depth and BT were occasionally highly correlated, both were retained due to their expected importance. Neither PA nor PRES models for any dogfish stage or season contained variables with large (> 3.0) variance inflation factors and, therefore, collinearity was assumed negligible.

Spatial overlap with prey and conspecifics

GIC

Most dogfish stages had relatively high global co-occurrence with prey species and conspecifics during both spring and autumn (Table 3.4). For prey species, the lowest *GIC* was displayed between neonates and herring during autumn ($GIC = 0.22$) and spring ($GIC = 0.46$) and mature females and herring during spring ($GIC = 0.46$) (Table 3.4A). For conspecifics, the lowest *GIC* was displayed between neonates and mature males during autumn ($GIC = 0.26$) and neonates and mature females during spring ($GIC = 0.61$) (Table 3.4B). In contrast, the highest *GIC* was found for mature males and herring during autumn ($GIC = 0.81$) and between all spiny dogfish combined and mackerel during spring ($GIC = 0.73$) (Table 3.4A). For conspecifics, the highest *GIC* was exhibited by immature and mature females during autumn ($GIC = 0.88$) and for immature males and females during spring ($GIC = 0.92$) (Table 3.4B).

LIC

Locally, very little co-occurrence between spiny dogfish and prey species was observed during either season (Table 3.4A) in contrast to higher co-occurrence of dogfish stages (Table 3.4B). *LIC* with prey species remained low during autumn for most predator-prey combinations and ranged from 0.01 (mackerel with neonates, mature females with *Illex* sp.) to 0.07 (females with *Loligo* sp.) (Table 3.4A). Minimum *LIC* was displayed between neonates and mature dogfish during autumn ($LIC = 0.01$) and neonates and mature females during spring ($LIC = 0.05$) (Table 3.4B). Compared to autumn, relatively higher *LICs* were observed with prey species during spring and ranged from 0.01 (herring with both neonate and immature males) to 0.11 (all spiny dogfish combined with *Loligo* sp.) (Table 3.4A). Maximum *LIC* was observed for immature males and immature females during both autumn ($LIC = 0.64$) and spring ($LIC = 0.69$) (Table 3.4B).

Statistical analysis

General modeling results

Influential variables varied for both BRT (Table 3A.1) and GAM analyses. During autumn, both PA and PRES GAMs explained more deviance for mature dogfish (Table 3.5) and immature females whereas more error was explained during spring for immature males (Table 3.6) and neonates (Table 3.7). The addition of important two-way interactions identified by BRT analysis reduced AIC values in both PA (range: 19 – 473) (Tables 3B.1-2) and PRES GAMs (range: 78 – 467) (Tables 3B.3-4) and increased deviance explained during both autumn (PA: $\leq 5\%$, PRES: $\leq 18\%$) and spring (PA: $\leq 7\%$, PRES: $\leq 10\%$). While the addition of interactions to

the neonate PRES model during autumn increased the AIC by 1 point, they were retained as the deviance explained more than doubled.

PA models for all dogfish stages identified depth, BT, and/or their interactions with region or the co-occurrence of the corresponding stage as highly influential during both seasons (Tables 3.5-7). Full PA modeling results are presented in Table 3C.1 for autumn and Table 3C.2 for spring. Temporal factors (i.e., Julian day, year, or interactions) contributed greatly to mature male occurrence during autumn (Table 3.5), immature female and neonate occurrence during autumn and immature male and neonate occurrence during spring (Tables 3.6-7). During autumn, *Loligo* sp. abundance was also important to immature males although the smooth was not significant (Table 3C.1). PRES models also revealed an importance of depth, BT, and/or their associated interactions for most dogfish stages during both seasons (Tables 3.5-7). However, variable influence was more diverse within PRES models. Full PRES modeling results are presented in Table 3C.3 for autumn and Table 3C.4 for spring. During autumn, zenith was highly influential on the abundance of mature dogfish, temporal variables (i.e., Julian day, year, or interactions) on all dogfish stages except neonates, *Loligo* sp. abundances on mature females, and *Illex* sp. on neonates (Tables 3.5-7). During spring, important variables were zenith for neonate abundance, temporal (Julian day or year) for females, and *Illex* sp. and *Loligo* sp. abundance for mature females (Tables 3.5-7).

During both seasons, the probabilities of occurrence and increasing abundance for all dogfish stages were influenced by abiotic and biotic factors and their interactions (Tables 3.5-7, 3C.1-4). In addition, most PA and PRES models revealed significant regional and/or co-occurrence patterns. Overall, probabilities of female dogfish were generally higher in the presence of male dogfish and vice versa. In both PA (Figures 3.2-3) and PRES models (Figures

3.4-5), region and/or co-occurrence frequently interacted with environmental and/or temporal variables (Tables 3.5-7). Full modeling results for PA and PRES models are displayed in Appendices 3D (autumn PA), 3E (spring PA), 3F (autumn PRES), and 3G (spring PRES). Unique to PRES models during autumn, the probability of increasing abundance for mature females (Table 3.5; Figure 3.4) and neonates (Table 3.7) was significantly influenced by regional interactions with prey abundances. Many of the PA models displayed significant interactions between environmental and temporal variables during both autumn (Figures 3.6A, 3D.1-7) and spring (Figures 3.6B, 3E.1-8). Although similar interactions were present in PRES models (Figure 3.6C), prey abundances also contributed to significant interactions during both seasons (Figures 3.6D, 3F.1-7, 3G.1-8).

Temporal trends

Many dogfish stages showed significantly higher probabilities of occurrence throughout the 1980s and/or 2000s during autumn (Tables 3.5-6; Figures 3.2, 3D.1-7) or spring (Tables 3.5-7; Figures 3E.1-8). In terms of increasing abundance, most dogfish stages displayed higher probabilities in the 2000s during autumn (Tables 3.5-6; Figure 3.4; Figures 3F.1-7) and throughout the 1980-90s during spring (Tables 3.5-7; Figure 3.5; Figures 3G.1-8). Significant nonlinear relationships with Julian day were frequently observed in both PA and PRES models during both seasons (Tables 3.5-7).

Environmental trends

Higher probabilities of both occurrence and increasing abundance were generally affiliated with specific depths for most dogfish stages during both autumn (Tables 3.5-7; Figure

3.2) and spring (Tables 3.5-7; Figures 3.3, 3.5). Temperatures around 14°C produced higher probabilities of occurrence for all dogfish stages except neonates during autumn (Figure 3.2; Figures 3D.1-7) but solely for immature males during spring (Table 3.6; Figure 3.3). For most dogfish stages, the probability of increasing abundance revealed significant relationships with temperature during both seasons (Tables 3.5-7; Figures 3.4-5). Male dogfish generally possessed a greater probability of occurrence at low-to-moderate zenith angles during both seasons (Tables 3.5-6; Figures 3.2-3). Higher probabilities of increasing abundance generally occurred at low zenith angles for many dogfish stages during both seasons (Tables 3.5-7).

Ecological trends

The importance of prey abundance was more pronounced in PRES models compared to PA models (Tables 3C.1-4). Prey abundance occasionally influenced the probability of occurrence whereas it frequently affected the probability of increasing abundance (Tables 3.5-7). During autumn, herring and *Loligo* sp. influenced the occurrence of mature females and neonates (Tables 3.5, 3.7) and mature males (Table 3.5; Figure 3.2), respectively, while PA models during spring revealed an importance of mackerel abundance to immature females and neonates (Tables 3.6-7), *Loligo* sp. to immature males (Table 3.6; Figure 3.3), and butterfish to neonates (Table 3.7). Multiple significant relationships concerning prey abundances were observed in PRES models for most dogfish stages during both autumn and spring (Tables 3C.3-4).

Model validation

Generally, PA models displayed reasonable validation in terms of discrimination, calibration and/or bias (Table 3.8) and lacked autocorrelated and/or spatially correlated residuals.

In some instances, weak spatial correlation was identified as either more frequent negative residuals throughout the region (autumn: ImmM; spring: ImmM, Neo) or small residuals outnumbering large in the southern region (autumn: ImmF; spring: MatM). The residuals of most models revealed heterogeneous spreads when graphed against the explanatory variables, mostly a result of sparse large observations, during both autumn (Figures 3D.8-12) and spring (Figures 3E.9-13). Most predicted probabilities of occurrence agreed with observed patterns (Figures 3.7, 3D.13-17) with the exception of neonates during both seasons.

The majority of PRES models also exhibited reasonable validation for most measures (Table 3.8) and displayed residuals lacking autocorrelation. However, many models did reveal contradictory agreement, poor calibration, moderate to strong bias (Table 3.8), and/or spatial correlation in the form of slightly more frequent negative residuals throughout a specific region (autumn: MatF, ImmF; spring: MatF, MatM, ImmF). As seen above, most models revealed heterogeneous spreads in residuals when compared to explanatory variables during both autumn (Figures 3F.8-12) and spring (Figures 3G.9-13). While many models underestimated the magnitude of abundance, most reasonably predicted where higher abundances were likely to occur (Figures 3F.13-17, 3G.14-18) with the exception of neonates during autumn.

Forecasting of occurrence under various temperature regimes

Occurrence trends were less pronounced during autumn (Figures 3H.1 – 3H.5). However, mature dogfish and immature females were more likely to occur in the northern range during the warmer year (Figures 3H.1-3). In contrast, trends during spring revealed noticeable differences for all dogfish stages. Compared to an average year, mature dogfish and immature females were more likely to occur (0.6 – 0.9) throughout the range during the warmer year but less likely to

occur (< 0.5) in northern regions during the cooler year (Figures 3.8, 3H.6-7). While the probabilities of neonate and immature occurrence were generally low (< 0.5) throughout the range, there was a visible difference between the cooler and warmer years (Figures 3.9, 3H.8). Temperatures below average revealed a relatively high probability (0.5 – 0.7) of neonate occurrence south of the Hudson Canyon. In contrast, during the warmer year, similar probabilities spread into eastern SNE and mimicked occurrence during the average temperature year. These changes in availability with temperature may have a large impact on perceived trends from the NEFSC survey, especially since the abundances of mature females and neonates serve as proxies for spawning stock biomass and recruitment, respectively.

Discussion

An understanding of the relationship between local abundance, environmental and ecological drivers of distribution can reduce potential bias in survey metrics, forecast the response of a population to climate change (Perry et al. 2005, Brander 2007, Nye et al. 2009), and help explain variation in commercial catchability (Jackson et al. 2001, Link & Garrison 2002). This study identified mechanisms behind the distribution of an understudied elasmobranch using a two-stage generalized additive model (GAM). The utilization of boosted regression tree (BRT) analysis allowed for assessment of potentially important interactions and greatly enhanced GAM validation and descriptive power, particularly by enabling the modeling of environmental drivers, predator and prey abundances, and key interactions. Significant nonlinear relationships between spiny dogfish and their environment or prey were common throughout the various dogfish stages and seasons. Environmental factors significantly influenced the occurrence and abundance of most dogfish stages and are discussed below in

relation to movement and behavior. These results can be used to better understand the relationship between sampling periods and movement drivers to the catchability of the spiny dogfish stock in the NES LME.

While two-stage GAMs frequently describe spatial distributions of commercially important fishes (Maravelias 1997, 1999, Bellido et al. 2001, Sacau et al. 2005, Murase et al. 2009), this method also proved suitable for spiny dogfish showing that seasonal occurrence and abundance of most dogfish stages were driven by different processes. The importance of bottom temperature on occurrence during both seasons supports temperature as a migratory cue (Murawski & Finn 1988, McMillan & Morse 1999, Collette & Klein-MacPhee 2002, Methratta & Link 2007). The strong temporal signal in occurrence estimated for younger dogfish and mature males may relate to the timing of movements which varied with season, Julian day, and/or year. Contrary to occurrence, abundance trends showed more variability between dogfish stages and seasons. Greater abundances may indicate food-rich frontal systems, preferred habitat, or aggregate behavior for protection from predators. Environmental variables were still of significance for many dogfish stages but, during autumn, ecological factors overwhelmingly influenced neonate and mature female abundance suggesting a partial dependency on prey abundance, potentially for direct predation or indirectly through mutual prey or similar habitat preference.

Stage-dependent habitat selection is supported by the dominance of environmental factors on the occurrence of various dogfish stages, particularly mature dogfish. These patterns most likely result from differences in sex, maturity, reproductive behavior, and/or any interconnected trade-offs. In the north Atlantic, fertilization is thought to occur year-round whereas offshore waters are the site of mating during summer (Henderson et al. 2002) and parturition during

winter (Holden & Meadows 1964, Nammack et al. 1985, Jones & Ugland 2001, Henderson et al. 2002) after an approximate two year gestation period (Hisaw & Albert 1947, Jones & Ugland 2001). During autumn, GAMs revealed a greater chance of encountering mature females around 240 m in SNE, a region which may contain optimal conditions for growth and development of pups; potentially representing pupping grounds. During spring, mature females were more likely present in one of two depth zones: shallow (~85 m) shelf waters and deep (~375 m) SNE waters. Shelf females may be impregnated individuals inhabiting cooler environments to slow embryonic development (Jones & Ugland 2001) whereas those at greater depths may be pre- or post-mated (Burgess 2002, Henderson et al. 2002) or searching for summer pupping grounds (Latham 1921, Hisaw & Albert 1947, Chatzisprou & Megalofonou 2005). During spring, mature males also revealed a bimodal encounter probability with depth. The higher chance of presence overall in shelf waters (~130 m) may reflect distributions of prey not studied herein and is consistent with a documented shoreward shift in distribution (NEFSC 2006, Rago & Sosebee 2009). In contrast, the occurrence in the deep (~380 m) MA may reflect either an effort to lower metabolic demands in colder waters or an attempt to minimize spatial overlap with younger intraspecifics to reduce resource competition and cannibalism (Stenberg 2005). Further research on specifying locations of breeding and pupping is encouraged to pinpoint essential habitat necessary to maximize recruitment and conserve spawning stock biomass.

Examination of seasonal spiny dogfish occurrence also offers some insight into stage- and sex-dependent movements and aggregating behavior. Spiny dogfish aggregations generally consist of either small immature males and females, medium-sized mature males or immature females, or large mature females (Jensen 1965). In the GM, greater probabilities of occurrence for mature dogfish and immature females during autumn support the theory that larger dogfish

migrate northward during warmer months (Hisaw & Albert 1947, Campana et al. 2007). In contrast, immature males and neonates were more likely encountered on GB and in SNE, respectively, corresponding to the findings of Methratta and Link (2007). During spring, more probable occurrence of females and neonates in the MA may be linked to parturition events whereas the greater chance of encountering males on GB may relate to avoidance of pupping grounds to reduce spatial overlap between dogfish stages. During both seasons, all dogfish stages examined revealed higher probabilities of occurrence when the corresponding stage also co-occurred (e.g. mature male occurrence higher in the presence of mature females), an effect which was more pronounced during autumn. While this finding contradicts the previous notion of mature dogfish aggregating by sex, this co-occurrence may reflect an attempt to maintain proximity for reproduction. For immature dogfish which often aggregate together, co-occurrence may result from an overlap of resources between dogfish stages or enhanced protection from predators.

Environmental drivers of distribution and abundance varied greatly among dogfish stages and between seasons. During spring, greater abundances of males and neonates were usually associated with relatively warmer and deeper waters in agreement with previous observations (Shepherd et al. 2002, Methratta & Link 2007). Mature female abundance was greater at shallow depths, early in the season, and at low *Loligo* sp. abundance. While this suggests a strong predatory relationship (assuming female consumption is driving low abundances), squid only contributed ~5% by weight to the diet of mature female dogfish in the NES LME between 1973-2001 (Link & Almeida 2000, Stehlik 2007) and instead may be exhibiting predator avoidance. Important links to prey abundances were also observed during autumn as greater abundances of both mature females and neonates occurred on GB at low *Loligo* sp. abundance and high *Illex* sp.

abundance, respectively. Recent dietary evidence supports increased consumption of both ctenophores (Link & Ford 2006) and squid (Belleggia et al. 2012) by spiny dogfish in the Atlantic. The abundance of mature males was greater earlier in autumn in the GM and later on GB and in SNE and also at low zenith angles. This timing probably relates to their seasonal movements and may be triggered by photoperiod. In addition, sensitivity to zenith may convey diel migratory patterns, a topic which requires further study for this species.

The perplexing behavior of spiny dogfish has attracted considerable skepticism regarding the utility of survey metrics to estimate population indices, especially those obtained from bottom trawls (Sulikowski et al. 2010). Management of this resource is based on stock assessment models which assume that survey abundance estimates reflect actual population trends (NEFSC 2006). Trans-boundary seasonal movements and highly variable interannual distribution and abundance trends contribute further to management uncertainty (Overholtz & Tyler 1985, Rago & Sosebee 2009). During their annual movements, spiny dogfish become vulnerable to the NEFSC bottom trawl as they pass through the surveyed area. However, slight variations in either the timing of the survey or environmental cues may modify their response and change the availability or catchability of the stock to the survey. We showed that even slightly above or below average temperatures during spring can result in large changes to the probability of capturing spiny dogfish throughout the survey range. For both mature females and neonates, a warmer year would result in a greater proportion of the survey area occupied, while a cooler year would result in occurrence primarily south of the Hudson Canyon. It is difficult to estimate the impact on survey catchability, but it is likely that availability of the stock to the survey will vary considerably.

Neonate GAMs represent a step towards identifying essential habitat and understanding spiny dogfish population dynamics. It is important to recognize that our neonate definition, spiny dogfish 26 cm or less, specifies newly-born individuals and not first-year recruits. Therefore, conditions deemed significant by GAMs may depict optimal environment or prey conditions for pupping success. During spring, neonates were more likely to occur in deep, relatively warmer waters, particularly off GB, where their growth and metabolism may be enhanced. Interestingly, the higher probability of neonate occurrence in early spring suggests that survey metrics may be highly sensitive to the timing of the survey. Given the relatively low numbers of neonates sampled in the survey, slight changes in the timing will likely lead to a bias in survey derived metrics, particularly recruitment indices. While informative, caution should be exercised due to small sample sizes, especially during autumn where neonates were rarely encountered. Future work should focus on neonate distribution, possibly through mid-water trawls better adapted at collecting neonates to provide more accurate estimates of neonate abundance and recruitment potential.

Models displayed deviance and validation values comparable, and in some cases better, than previous GAM studies (Bigelow et al. 1999, Cardinale & Arrhenius 2000, Sacau et al. 2005, Feyrer et al. 2007); however, we were unable to remove weak residual patterns in about half of the occurrence and abundance models. Our results are based on assumptions regarding identification and inclusion of variables and interactions, representation of the smoothing functions, and model selection. In particular, the inclusion of the abundances of known prey species can complicate matters if their catchabilities vary throughout the survey and adds to the number of estimated parameters. Previous research has highlighted the need to understand predator/prey dynamics in spring, justifying the added model complexity (Overholtz & Tyler

1985). Strong relationships were identified by the GAMs between some dogfish stages and prey species. Global indices of collocation supported these findings; however, local overlap on a tow by tow basis did not, possibly due to vertical migrations of either predator or prey. The relationship between spiny dogfish and prey may be overemphasized in our models, particularly if they are competing for similar prey items that were missed. Further research should assess the relationship between observed diet and predator/prey dynamics on a smaller time-scale. In addition, the inclusion of other potentially important variables such as salinity (fronts) or chlorophyll may further improve model performance. Strong relationships between *Squalus suckleyi* abundance in NMFS/Oregon State University (OSU) surveys conducted in the Pacific were found with temperature, chlorophyll, and salinity of the Columbia river plume (Brodeur et al. 2009).

The first detailed federal single-species stock assessment for spiny dogfish, conducted in 1994, highlighted the challenges of assessing this data-poor species (NEFSC 1994). Effective fisheries management is generally hampered by a lack of information concerning habitat, predators and prey of the managed species, and other ecosystem components and interactions (Pikitch et al. 2004). Here we provided vital information concerning spiny dogfish habitat, stage co-occurrence, and ecological interactions for integration into management initiatives. By incorporating our findings into assessment models, variability surrounding spiny dogfish abundance indices can be reduced along with the potential for misinterpretation of their population dynamics. Habitat modeling is a useful tool in the standardization of survey indices and can forecast the distributions of managed stocks from environmental and ecological variables. In addition, GAMs provide the framework to examine how climate change and other ecosystem alterations will influence distributions. Realization of EBFM will require the

contribution of research efforts, such as this one, supplying vital information for traditionally less-studied species like spiny dogfish.

Table 3.1. Summarization of spiny dogfish occurrence (PA) and abundance (PRES) used in GAM analyses for neonates (Neo; $TL \leq 26$ cm), immature males (ImmM; $26 \text{ cm} < TL < 60$ cm), immature females (ImmF; $26 \text{ cm} < TL < 80$ cm), mature males (MatM; $TL \geq 60$ cm), and mature females (MatF; $TL \geq 80$ cm). Data were obtained from the National Marine Fisheries Service (NMFS) Northeast Fisheries Science Center (NEFSC) annual bottom trawl surveys conducted during autumn and spring since 1963 and 1968, respectively. * depicts the number of observations after missing bottom temperatures were removed. + Tows = overall percentage of tows where each dogfish stage was present (i.e., $CPUE > 0$).

Stage	PA			PRES			+ Tows (%)
	N _{PA} *	Training	Test	N _{PRES} *	Training	Test	
<u>AUTUMN</u>							
Neo	14395	10077	4319	175	123	53	1.22
ImmM	8714	6100	2614	1107	775	332	12.57
ImmF	8714	6100	2614	2299	1609	690	26.08
MatM	8714	6100	2614	1994	1396	598	22.88
MatF	8714	6100	2614	1413	989	424	16.22
<u>SPRING</u>							
Neo	12814	8970	3844	746	522	224	5.82
ImmM	8869	6208	2661	1420	994	426	16.22
ImmF	8869	6208	2661	3301	2311	990	37.74
MatM	8869	6208	2661	2764	1935	829	31.16
MatF	8869	6208	2661	3126	2188	938	35.25

Table 3.2. Variables identified as potential explanatory variables for each generalized additive model describing the occurrence and abundance of spiny dogfish life-history stages after preliminary exploratory data analyses on both spring and autumn NEFSC bottom trawl survey datasets.

Variable (units)	Type	Explanation
BFN (# butterfish/tow)	Biotic	Relative abundance of butterfish (<i>Peprilus triacanthus</i>) captured per tow
HERN (# Atlantic herring/tow)	Biotic	Relative abundance of Atlantic herring (<i>Clupea harengus</i>) captured per tow
ILLN (# <i>Illex</i> sp./tow)	Biotic	Relative abundance of <i>Illex</i> sp. captured per tow
LOLN (# <i>Loligo</i> sp./tow)	Biotic	Relative abundance of <i>Loligo</i> sp. captured per tow
MACN (# Atlantic mackerel/tow)	Biotic	Relative abundance of Atlantic mackerel (<i>Scomber scombrus</i>) captured per tow
Co	Biotic	Co-occurrence of specified stage; 0 = absent, 1 = present
Depth (m)	Environmental	Measurement of depth where trawl was conducted
BT (°C)	Environmental	Measurement of bottom temperature where trawl was conducted
Zenith (°)	Environmental	Estimated solar zenith angle at trawl location
Year	Temporal	Year trawl was conducted
Julian (d)	Temporal	Julian day trawl was conducted
Region	Spatial	Georges Bank (GB), Gulf of Maine (GM), Southern New England (SNE), or Middle Atlantic Bight (MA)

Table 3.3. Pearson correlation matrix for variables of interest derived from the NEFSC bottom trawl survey spanning the Northeast (US) shelf large marine ecosystem during autumn (upper panel) and spring (lower panel). **Note:** Matrices below are based on the occurrence (PA) training datasets for autumn ($n = 6100$ observations) and spring ($n = 6208$ observations). Lat: latitude, PAR: photosynthetically active radiation. See Table 3.2 for other definitions. Boldness indicates large correlations ($r > 0.6$).

	Year	Depth	BT	Lat	Julian	Zenith	PAR	BFN	HERN	ILLN	LOLN	MACN
Year	-	-0.02	-0.01	0.11	-0.14	-0.02	0.02	0.00	0.05	0.02	0.07	0.00
Depth		-	-0.63	0.37	0.40	0.06	-0.07	-0.05	0.01	0.09	-0.15	-0.01
BT			-	-0.68	-0.58	-0.10	0.11	0.04	-0.07	-0.05	0.10	-0.01
Lat				-	0.77	0.12	-0.15	-0.05	0.06	-0.04	-0.04	0.00
Julian					-	0.16	-0.17	-0.07	0.08	-0.05	-0.13	-0.01
Zenith						-	-0.87	-0.10	-0.03	-0.06	-0.21	-0.02
PAR							-	0.10	0.03	0.05	0.18	0.01
BFN								-	0.00	0.13	0.14	0.00
HERN									-	0.01	-0.01	0.00
ILLN										-	0.01	0.01
LOLN											-	0.00
MACN												-
Year	-	-0.02	-0.10	0.09	-0.15	0.02	-0.02	0.00	0.08	-0.01	0.04	0.07
Depth		-	0.21	0.38	0.40	-0.06	0.04	0.02	-0.08	0.11	0.05	-0.04
BT			-	-0.58	-0.33	0.03	0.00	0.11	-0.10	0.11	0.28	-0.01
Lat				-	0.77	-0.11	0.05	-0.07	0.05	-0.08	-0.2	-0.01
Julian					-	-0.14	0.08	-0.06	-0.02	-0.05	-0.16	-0.04
Zenith						-	-0.91	-0.01	-0.03	-0.04	-0.06	-0.06
PAR							-	0.02	0.02	0.02	0.06	0.06
BFN								-	-0.01	0.10	0.20	0.00
HERN									-	-0.02	-0.03	0.11
ILLN										-	0.27	-0.01
LOLN											-	-0.01
MACN												-

Table 3.4. Average annual global (*GIC*) and local (*LIC*) indices of collocation for spiny dogfish life-history stages with A) prey species and B) other spiny dogfish stages based on swept-area density estimates in the Northeast (US) shelf large marine ecosystem during autumn and spring. Stages as defined in Table 3.1. Prey species include: butterflyfish (BF), Atlantic herring (HER), *Illex* sp. (ILL), *Loligo* sp. (LOL), and Atlantic mackerel (MAC). In B), numbers above the diagonal reflect *GIC* while numbers below reflect *LIC*.

A)

	BF	HER	ILL	LOL	MAC	BF	HER	ILL	LOL	MAC
<i>GIC</i>						<i>LIC</i>				
<u>AUTUMN</u>										
All	0.41	0.69	0.52	0.42	0.74	0.05	0.04	0.03	0.05	0.04
Neo	0.58	0.22	0.63	0.61	0.35	0.02	0.02	0.06	0.02	0.01
ImmM	0.57	0.46	0.61	0.56	0.61	0.02	0.02	0.04	0.05	0.02
MatM	0.32	0.81	0.42	0.33	0.72	0.02	0.02	0.02	0.04	0.02
ImmF	0.42	0.65	0.50	0.43	0.71	0.03	0.04	0.04	0.07	0.03
MatF	0.35	0.59	0.45	0.38	0.68	0.06	0.03	0.01	0.07	0.05
<u>SPRING</u>										
All	0.63	0.56	0.57	0.60	0.73	0.08	0.03	0.08	0.11	0.10
Neo	0.56	0.46	0.59	0.52	0.69	0.09	0.01	0.08	0.09	0.06
ImmM	0.57	0.60	0.50	0.49	0.62	0.08	0.01	0.07	0.09	0.06
MatM	0.60	0.55	0.52	0.59	0.64	0.09	0.03	0.07	0.10	0.09
ImmF	0.61	0.61	0.55	0.55	0.66	0.07	0.03	0.06	0.10	0.07
MatF	0.65	0.46	0.60	0.68	0.62	0.05	0.04	0.03	0.07	0.09

B)

	Neo	ImmM	MatM	ImmF	MatF	Neo	ImmM	MatM	ImmF	MatF
<u>AUTUMN</u>						<u>SPRING</u>				
Neo	-	0.53	0.26	0.39	0.30	-	0.80	0.72	0.77	0.61
ImmM	0.18	-	0.61	0.82	0.67	0.36	-	0.83	0.92	0.62
MatM	0.01	0.20	-	0.83	0.79	0.11	0.30	-	0.88	0.75
ImmF	0.13	0.64	0.39	-	0.88	0.24	0.69	0.46	-	0.73
MatF	0.01	0.07	0.41	0.38	-	0.05	0.08	0.33	0.43	-

Table 3.5. Abbreviated GAM results describing the occurrence (PA) and abundance (PRES) of mature female (MatF) and male (MatM) spiny dogfish during autumn (Aut) and spring (Spr) in the Northeast (US) shelf large marine ecosystem since 1980. DEV = percent deviance explained by the optimal model, AIC = Akaike's Information Criterion. Variables and their respective units are defined in Table 3.2. Regions include GM = Gulf of Maine, GB = Georges Bank, SNE = Southern New England, and MA = Middle Atlantic Bight. Values in table display the rank and trend (in parentheses: ↑ = linear increase, ↓ = linear decrease, number = maximal peak) for each respective variable. ⁺ identifies parametric terms with (+) or (-) indicative of a higher or lower trend compared to either GB (for region) or to CoA (for co-occurrence). - = not applicable. C = complex trend for specified two-way interaction. Only variables exhibiting significant trends ($p < 0.05$) are shown for brevity.

	MatF				MatM			
	PA Aut	PA Spr	PRES Aut	PRES Spr	PA Aut	PA Spr	PRES Aut	PRES Spr
DEV (%)	52.1	32.4	56.9	48.8	53.0	43.0	45.6	39.4
AIC	2645	5520	6946	14820	3206	4508	12433	17803
<u>Main Effect:</u>								
Year	7('04)	11('88)	1('09)	5(↓)	6('89)	6(↑)	8('09)	15('98)
Depth	-	3(85m)	-	2(100m)	3(70m)	3(130m)	4(↓)	7(135m)
BT	2 (13.5°C)	-	5(14.5°C)	-	2(13°C)	4(9°C)	5(12°C)	3(↓)
Julian	6(308d)	9(↑)	6(254d)	3(57d)	1(120d)	8(58d)	-	10(88d)
Zenith	-	13(150°)	3(150°)	10(25°)	11(80°)	10(22°)	2(37°)	-
BFN	-	-	-	9(0)	-	-	13(0)	17(185)
HERN	10(275)	-	10(400)	7(400)	-	-	12(200)	-
ILLN	-	-	8(0)	4(0)	-	-	11(15)	-
LOLN	-	-	-	1(0)	8(↓)	-	9(250)	14(0)
MACN	-	-	-	6(225)	-	-	15(0)	13(250)
RegionGM ⁺	(+)1.93	-	(+)1.22	-	(+)1.54	(-)1.43	(+)1.18	(-)1.67
RegionSNE ⁺	-	(-)0.41	(+)1.47	(+)0.34	(-)0.55	(-)0.52	(+)1.01	-
RegionMA ⁺	-	(+)1.87	-	(+)0.67	-	-	-	(+)0.87
CoP ⁺	(+)2.87	(+)1.99	(+)1.15	(+)1.09	(+)2.94	(+)1.99	(+)1.01	(+)0.96
<u>Interaction:</u>								
Year,GB	-	-	-	-	5('80)	-	-	-
Depth,Year	-	-	-	-	C	C	-	-

	MatF				MatM			
	PA Aut	PA Spr	PRES Aut	PRES Spr	PA Aut	PA Spr	PRES Aut	PRES Spr
Depth,GM	-	5(375m)	-	-	-	-	-	-
Depth,GB	-	-	-	-	-	-	-	9(130m)
Depth,SNE	1(240m)	2(375m)	-	-	-	5(300m)	-	8(400m)
Depth,MA	-	8(40m)	-	-	-	1(380m)	-	6(170m)
Depth,CoP	-	-	4(↓)	-	-	-	10(85m)	-
BT,Year	-	-	-	C	-	-	-	-
BT,Depth	-	C	-	C	-	C	-	-
BT,GM	-	1(↑)	-	-	-	-	-	5(11.5°C)
BT,GB	-	-	-	-	-	-	-	1(14°C)
BT,SNE	-	-	-	-	-	-	-	4(14°C)
BT,MA	-	-	-	-	-	-	-	2(14°C)
Julian,Year	-	-	C	-	-	C	-	-
Julian,Depth	-	C	-	-	C	-	-	C
Julian,GM	-	-	-	-	-	-	3(256d)	-
Julian,GB	-	-	-	-	-	-	1(296d)	-
Julian,SNE	-	-	-	-	-	-	6(302d)	-
Julian,CoP	-	-	-	-	4(245d)	-	-	-
Zenith,Year	-	-	C	-	-	-	-	-
Zenith,Depth	-	-	C	-	-	-	C	-
Zenith,BT	-	-	-	-	-	-	-	C
Zenith,CoP	8(↓)	-	-	-	-	-	-	-
LOLN,BT	-	-	-	C	-	-	-	-
LOLN,GB	-	-	2(0)	-	-	-	-	-
LOLN,SNE	-	-	7(0)	-	-	-	-	-
HERN,BT	-	-	-	-	-	-	-	C

Table 3.6. Abbreviated GAM results describing the occurrence (PA) and abundance (PRES) of immature female (ImmF) and male (ImmM) spiny dogfish during autumn (Aut) and spring (Spr) in the Northeast (US) shelf large marine ecosystem since 1980. DEV = percent deviance explained by the optimal model, AIC = Akaike's Information Criterion. Variables and their respective units are defined in Table 3.2. Regions include GM = Gulf of Maine, GB = Georges Bank, SNE = Southern New England, and MA = Middle Atlantic Bight. Values in table display the rank and trend (in parentheses; ↑ = linear increase, ↓ = linear decrease, number = maximal peak) for each respective variable. ⁺ identifies parametric terms with (+) or (-) indicative of a higher or lower trend compared to either GB (for region) or to CoA (for co-occurrence). - = not applicable. C = complex trend for specified two-way interaction. Only variables exhibiting significant trends ($p < 0.05$) are shown for brevity.

	ImmF				ImmM			
	PA Aut	PA Spr	PRES Aut	PRES Spr	PA Aut	PA Spr	PRES Aut	PRES Spr
DEV (%)	43.4	37.9	45.4	43.7	39.7	46.1	54.9	59.0
AIC	4045	5222	12524	18878	2835	3043	5377	7294
<u>Main Effect:</u>								
Year	2('01)	8('09)	10('05)	15('88)	-	-	4('09)	7('94)
Depth	-	-	6(↓)	4(↓)	2(380m)	2(90m)	9(300m)	6(0m)
BT	1(13°C)	2(1-6°C)	2(14°C)	-	1(13°C)	1(13.5°C)	3(5°C)	3(3°C)
Julian	-	-	5(320d)	2(122d)	-	3(↓)	6(286d)	-
Zenith	-	-	11(40°)	11(65°)	10(↓)	8(20°)	8(40°)	9(75°)
BFN	-	-	-	13(0)	-	-	12(↓)	11(250)
HERN	-	-	15(1000)	10(1300)	-	-	-	-
ILLN	-	-	14(40)	16(0)	-	-	-	12(↓)
LOLN	-	-	9(250)	14(2400)	-	7(3500)	7(0)	-
MACN	-	9(200)	18(↓)	12(300)	-	-	-	-
RegionGM ⁺	(+)1.36	(-)0.74	(+)0.79	(-)1.65	(-)1.12	(-)0.69	(-)0.68	(-)2.60
RegionSNE ⁺	(+)0.45	-	-	(-)0.53	-	-	-	-
RegionMA ⁺	(-)0.85	(+)1.00	(-)1.52	(-)0.27	-	-	-	(-)0.44
CoP ⁺	(+)3.31	(+)2.22	(+)1.80	(+)1.18	(+)3.57	(+)2.54	(+)1.99	(+)1.92
<u>Interaction:</u>								
Year,GB	4('09)	-	-	-	-	-	-	-
Year,GM	3('03)	-	-	-	-	-	-	-

	ImmF				ImmM			
	PA Aut	PA Spr	PRES Aut	PRES Spr	PA Aut	PA Spr	PRES Aut	PRES Spr
Year,SNE	6(↑)	-	-	-	-	-	-	-
Year,MA	-	-	-	-	-	-	-	-
Year,CoP	-	-	-	-	6('80)	6('80)	-	-
Depth,GM	-	5(↑)	-	-	-	-	-	-
Depth,SNE	-	7(280m)	-	-	-	-	-	-
Depth,MA	-	4(380m)	-	-	-	-	-	-
Depth,CoA	-	3(290m)	-	-	4(0m)	-	-	-
Depth,CoP	-	1(↑)	-	-	-	5(160m)	-	-
Depth,Year	C	C	-	-	-	-	-	-
BT,GM	-	-	-	1(3°C)	-	-	2(13°C)	5(11.5°C)
BT,GB	-	-	3(18°C)	-	-	-	-	1(14°C)
BT,SNE	-	-	-	-	-	-	1(7.5°C)	4(14°C)
BT,MA	-	-	1(4°)	-	-	-	-	2(↑)
BT,CoA	-	-	-	3(11.5°C)	3(↓)	-	-	-
BT,Year	-	-	-	C	-	-	C	C
BT,Depth	-	C	-	C	-	-	-	-
Julian,CoP	-	-	7(290d)	-	-	-	-	-
Julian,Depth	C	C	C	-	-	-	-	-
Julian,BT	-	-	-	C	-	C	-	C
BFN,BT	-	-	-	-	-	-	-	-
BFN,Julian	-	-	-	-	-	-	-	-
ILLN,GB	-	-	-	-	-	-	-	-
ILLN,Depth	-	-	-	-	-	-	-	C
ILLN,BT	-	-	-	-	-	-	C	-
MACN,ILLN	-	-	-	-	-	-	C	-

Table 3.7. Abbreviated GAM results describing the occurrence (PA) and abundance (PRES) of neonate (Neo) spiny dogfish during autumn (Aut) and spring (Spr) in the Northeast (US) shelf large marine ecosystem since 1963. DEV = percent deviance explained by the optimal model, AIC = Akaike's Information Criterion. Variables and their respective units are defined in Table 3.2. Regions include GM = Gulf of Maine, GB = Georges Bank, SNE = Southern New England, and MA = Middle Atlantic Bight. Values in table display the rank and trend (in parentheses; ↑ = linear increase, number = maximal peak) for each respective variable. ⁺ identifies parametric terms with (+) or (-) indicative of a higher or lower trend compared to GB (for region). - = not applicable. C = complex trend for specified two-way interaction. Only variables exhibiting significant trends ($p < 0.05$) are shown for brevity.

	PA Aut	PA Spr	PRES Aut	PRES Spr		PA Aut	PA Spr	PRES Aut	PRES Spr
DEV (%)	21.8	34.3	33.0	50.4	Year,SNE	-	-	-	-
AIC	1152	2706	514	3182	Year,MA	2('63)	-	-	-
					Depth,GM	-	-	-	-
<u>Main Effect:</u>					Depth,SNE	-	-	-	-
Year	-	6('09)	-	6('83)	Depth,MA	-	-	-	-
Depth	-	3(240m)	5(↑)	5(175m)	Depth,Year	C	-	-	-
BT	1(3°C)	-	-	-	BT,GM	-	-	-	-
Julian	-	4(57d)	-	-	BT,GB	-	1(↑)	-	-
Zenith	-	8(60°)	-	4(34°)	BT,SNE	-	-	-	-
BFN	-	7(350)	-	7(0)	BT,MA	-	-	-	3(10.5°C)
HERN	7(850)	-	-	-	BT,Year	-	-	-	C
ILLN	-	-	-	-	BT,Depth	-	C	-	-
LOLN	-	-	-	11(2000)	Julian,Depth	-	-	-	-
MACN	-	10(1500)	-	9(250)	Julian,BT	-	-	-	-
RegionGM ⁺	(-)1.18	-	(-)3.01	(-)2.88	BFN,BT	C	-	-	-
RegionSNE ⁺	(+)0.68	(+)2.78	(-)1.97	(+)0.63	BFN,Julian	-	-	-	C
RegionMA ⁺	-	(+)3.03	(-)2.38	-	ILLN,GB	-	-	1(↑)	-
					ILLN,Depth	-	-	-	-
<u>Interaction:</u>					ILLN,BT	-	-	-	C
Year,GB	-	-	-	-	MACN,ILLN	-	-	-	-
Year,GM	-	-	-	-					

Table 3.8. Validation measures for the optimal occurrence (PA) and abundance (PRES) models for spiny dogfish life-history stages in the Northeast (US) shelf large marine ecosystem based on independent test datasets for autumn and spring. Stages as defined in Table 3.1. AUC = area under the receiver operating characteristic curve \pm standard error, m = slope and b = y-intercept of the fitted calibration line: observed = $m(\text{predicted}) + b$, BA R^2 = coefficient of determination from a Bland-Altman plot with (+) indicative of an increasing slope, r = Pearson's correlation coefficient, r_{sp} = Spearman's rank correlation coefficient, $RSME$ = root mean square error of prediction and AVE = average error. See text for equations and further details.

Stage	PA				PRES						
	AUC (%)	m	b	BA R^2	r_p	r_s	m	b	$RMSE$	AVE	BA R^2
<u>AUTUMN</u>											
Neo	87.2 \pm 2.8	1.72	-0.13	0.60 (+)	0.61	0.35	1.27	-0.73	7.86	-0.28	0.96 (+)
ImmM	90.9 \pm 1.5	1.01	-0.01	0.02 (+)	0.56	0.47	1.52	-5.83	67.98	-5.00	0.97 (+)
ImmF	92.0 \pm 1.1	1.00	0.01	0.02 (+)	0.27	0.50	0.71	21.89	320.37	-6.21	0.99 (+)
MatM	94.4 \pm 0.9	1.02	0.00	0.04 (+)	0.48	0.57	0.84	8.85	126.22	-0.85	0.90 (+)
MatF	94.0 \pm 1.1	1.01	0.00	0.01 (+)	0.67	0.64	1.04	0.99	43.69	-1.72	0.54 (+)
<u>SPRING</u>											
Neo	90.1 \pm 1.7	1.28	-0.06	0.33 (+)	0.57	0.50	1.06	0.56	20.19	-1.21	0.47 (+)
ImmM	92.7 \pm 1.2	0.95	0.02	0.06 (+)	0.81	0.57	2.39	-31.17	135.54	-8.14	0.98 (+)
ImmF	90.3 \pm 1.2	1.03	0.00	0.11 (+)	0.59	0.52	1.65	-18.17	115.97	-2.68	0.95 (+)
MatM	90.3 \pm 1.2	1.01	0.00	0.01 (+)	0.28	0.55	0.49	36.88	271.43	4.38	0.99 (+)
MatF	85.8 \pm 1.5	1.00	0.00	0.00 (+)	0.38	0.46	1.15	-1.35	64.33	-1.52	0.96 (+)

Figure 3.1. Map of the Northeast (US) shelf large marine ecosystem (NES LME) where the NEFSC annual bottom trawl survey is conducted during autumn and spring. The four regions are defined as follows: Gulf of Maine (GM), Georges Bank (GB), Southern New England (SNE), and the Middle Atlantic Bight (MA). Solid gray indicates land masses. Lines reflect depth contours in meters.

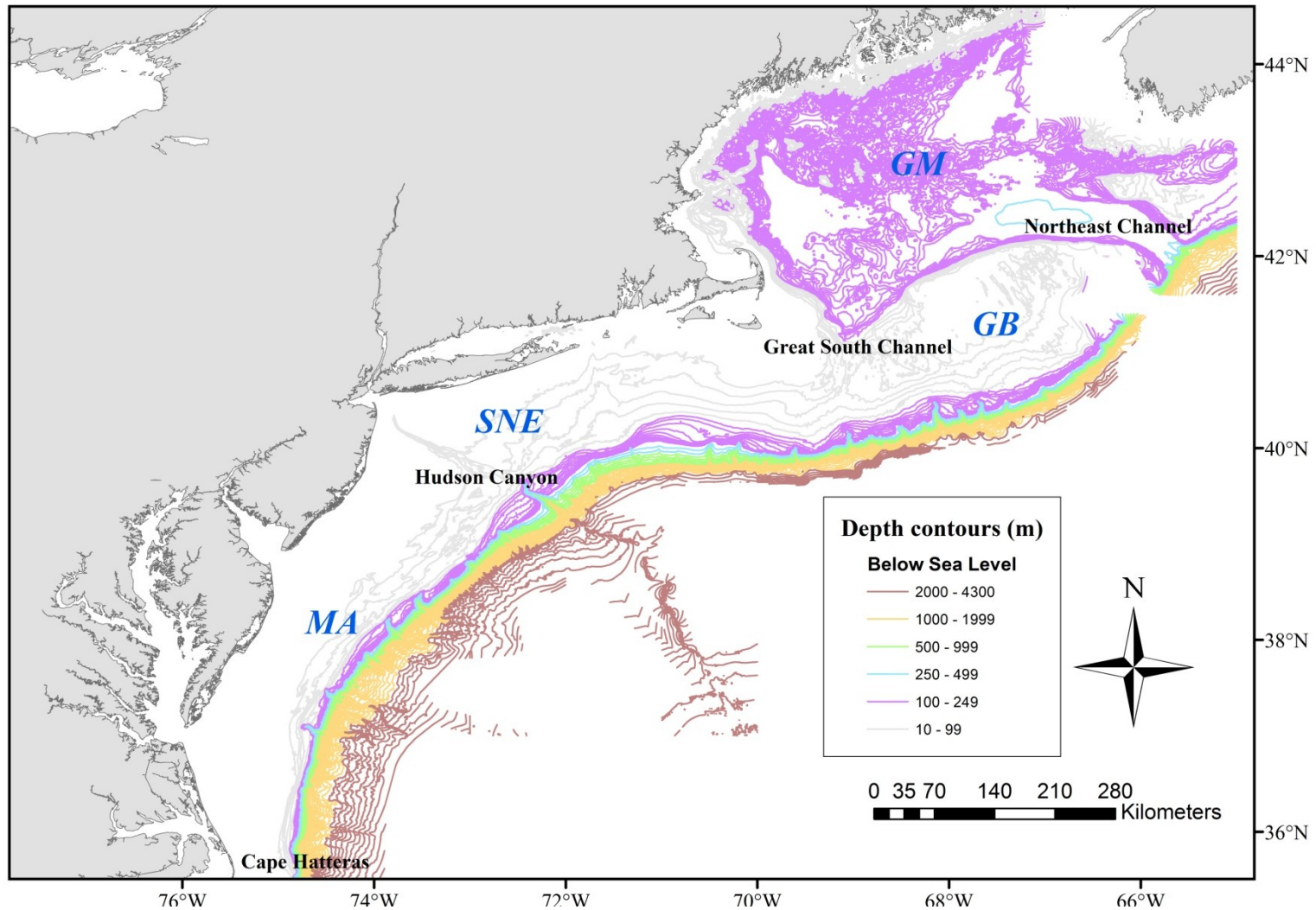


Figure 3.2. Partial GAM plots identifying the additive effect of each variable on the probability of occurrence of mature male spiny dogfish during autumn. Variables as defined in Table 3.2. The y-axis represents the degree of smoothing (variable, estimated degrees of freedom) with its range indicative of the relative importance of each covariate. The x-axis reflects the relative density of data points as shown by the 'rug'. Range estimates exclude extreme values where rugs are sparse. Some smoothes have been graphically abbreviated due to a lack of data at the endpoints. The gray region reflects the 95% confidence intervals around the response curves. NS = not significant.

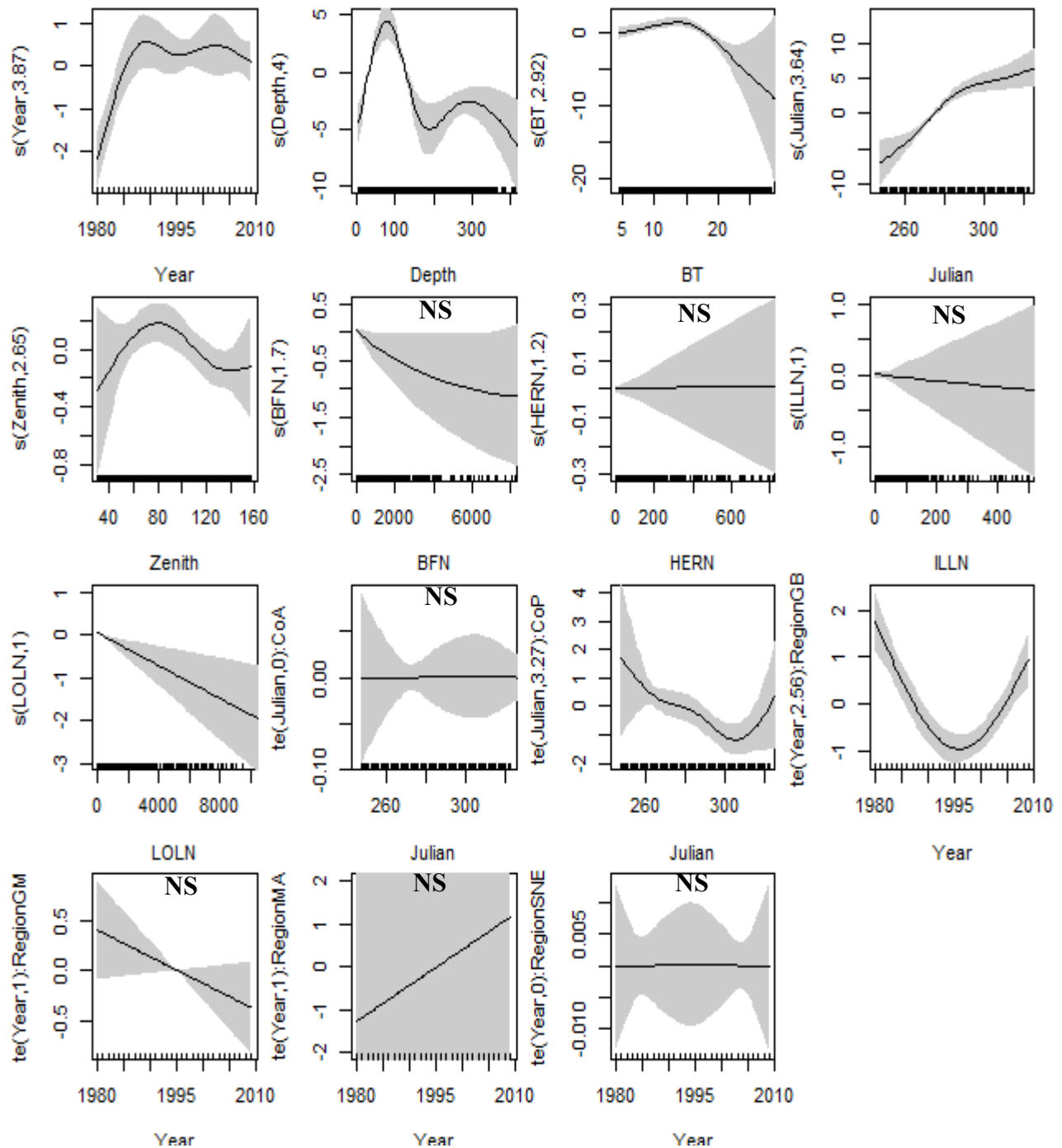


Figure 3.3. Partial GAM plots identifying the additive effect of each variable on the probability of occurrence of immature male spiny dogfish during spring. Variables as defined in Table 3.2. The y-axis represents the degree of smoothing (variable, estimated degrees of freedom) with its range indicative of the relative importance of each covariate. The x-axis reflects the relative density of data points as shown by the 'rug'. Range estimates exclude extreme values where rugs are sparse. Some smoothes have been graphically abbreviated due to a lack of data at the endpoints. The gray region reflects the 95% confidence intervals around the response curves. NS = not significant.

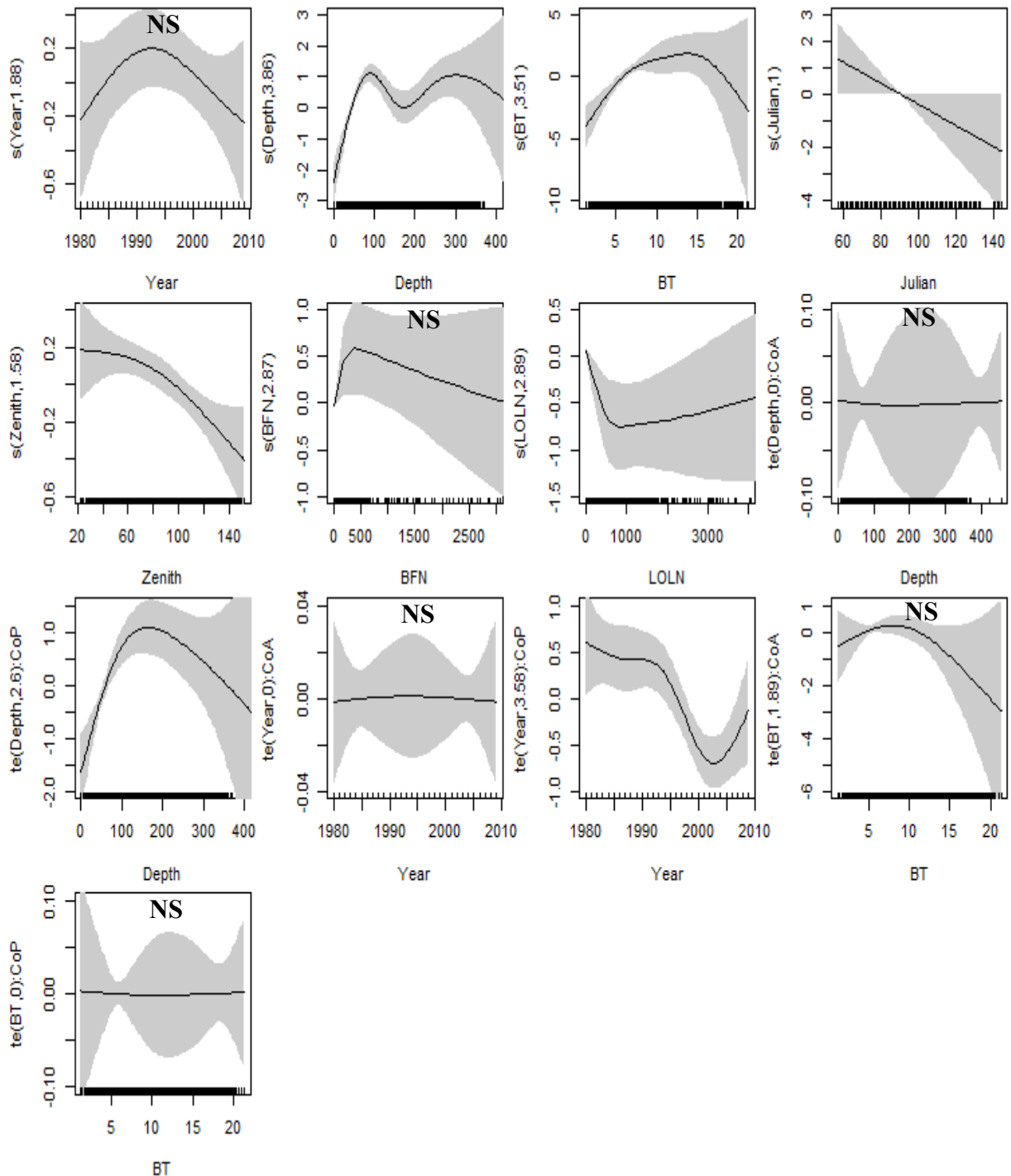


Figure 3.4. Partial GAM plots identifying the additive effect of each variable on the probability of increasing abundance of mature female spiny dogfish during autumn. Variables as defined in Table 3.2. The y-axis represents the degree of smoothing (variable, estimated degrees of freedom) with its range indicative of the relative importance of each covariate. The x-axis reflects the relative density of data points as shown by the 'rug'. Range estimates exclude extreme values where rugs are sparse. Some smoothes have been graphically abbreviated due to a lack of data at the endpoints. The gray region reflects the 95% confidence intervals around the response curves. NS = not significant.

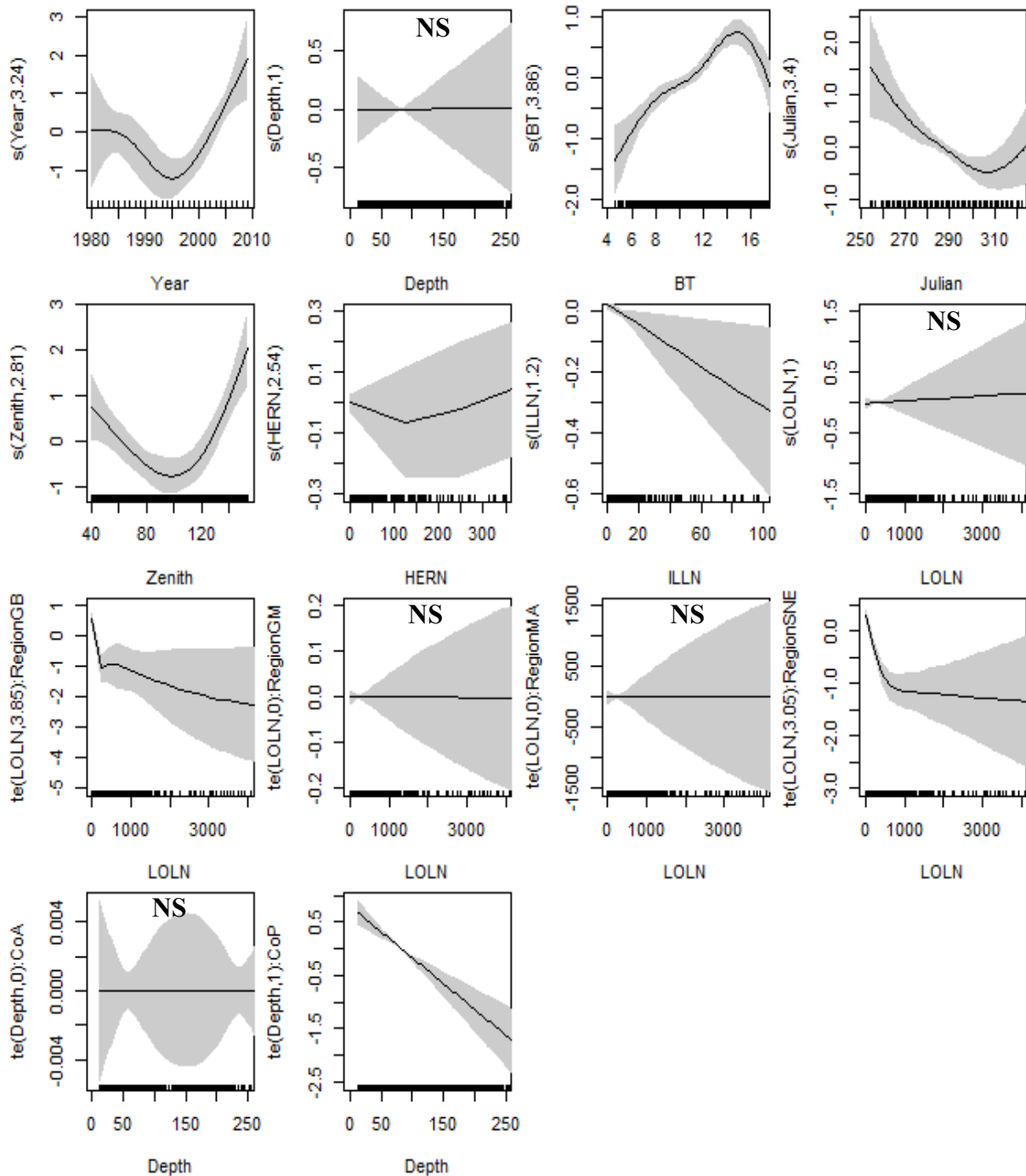


Figure 3.5. Partial GAM plots identifying the additive effect of each variable on the probability of increasing abundance of immature male spiny dogfish during spring. Variables as defined in Table 3.2. The y-axis represents the degree of smoothing (variable, estimated degrees of freedom) with its range indicative of the relative importance of each covariate. The x-axis reflects the relative density of data points as shown by the 'rug'. Range estimates exclude extreme values where rugs are sparse. Some smoothes have been graphically abbreviated due to a lack of data at the endpoints. The gray region reflects the 95% confidence intervals around the response curves. NS = not significant.

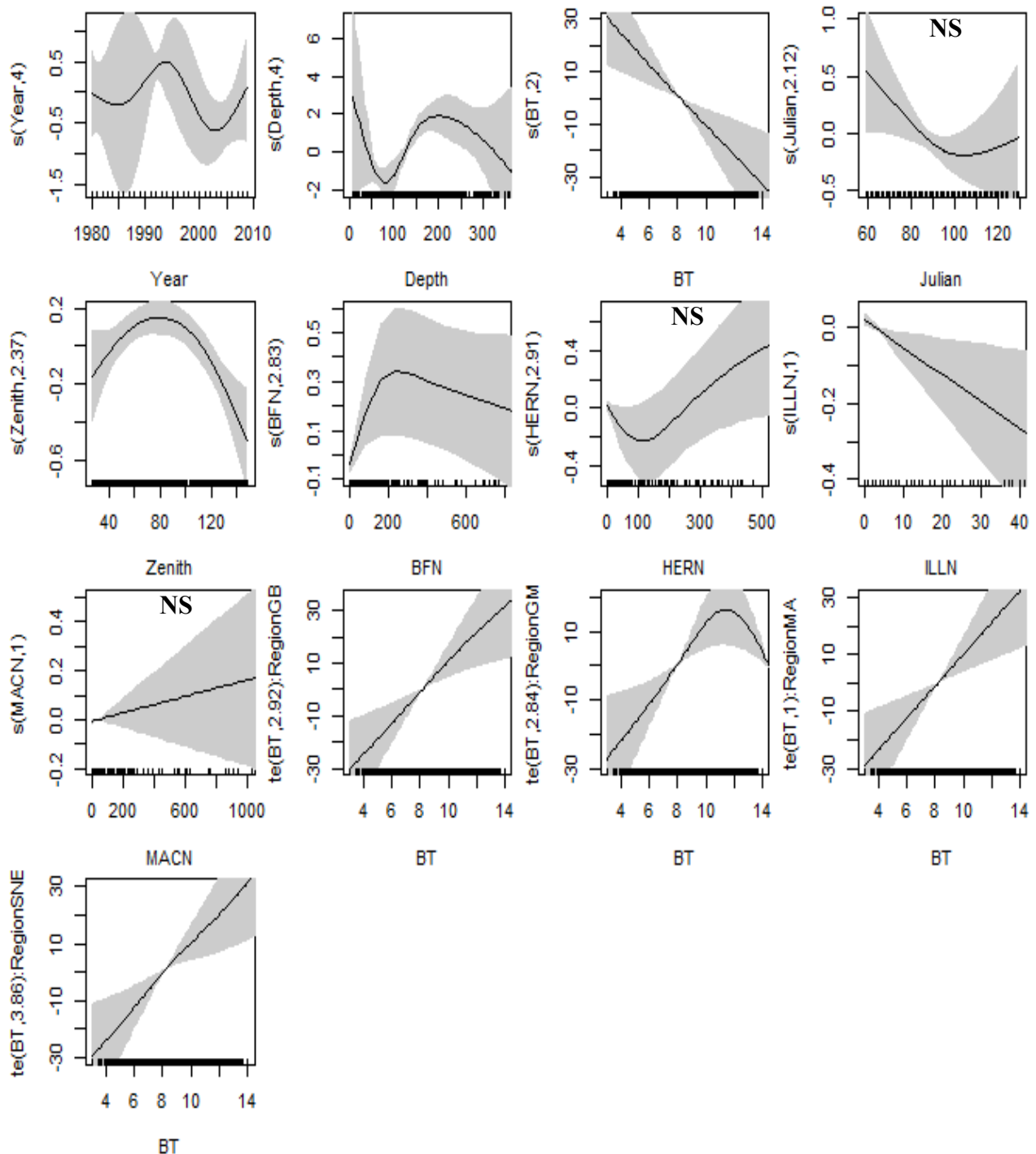


Figure 3.6. Partial GAM derived effects of important interactions on the occurrence of (A) mature male spiny dogfish during autumn and (B) immature male spiny dogfish during spring and on the abundance of (C) mature female spiny dogfish during autumn and (D) immature male spiny dogfish during spring. Variables as defined in Table 3.2. Interaction effects are shown as perspective plots without error bounds. The response on the z-axis reflects the tensor smooth (variable 1, variable 2, estimated degrees of freedom).

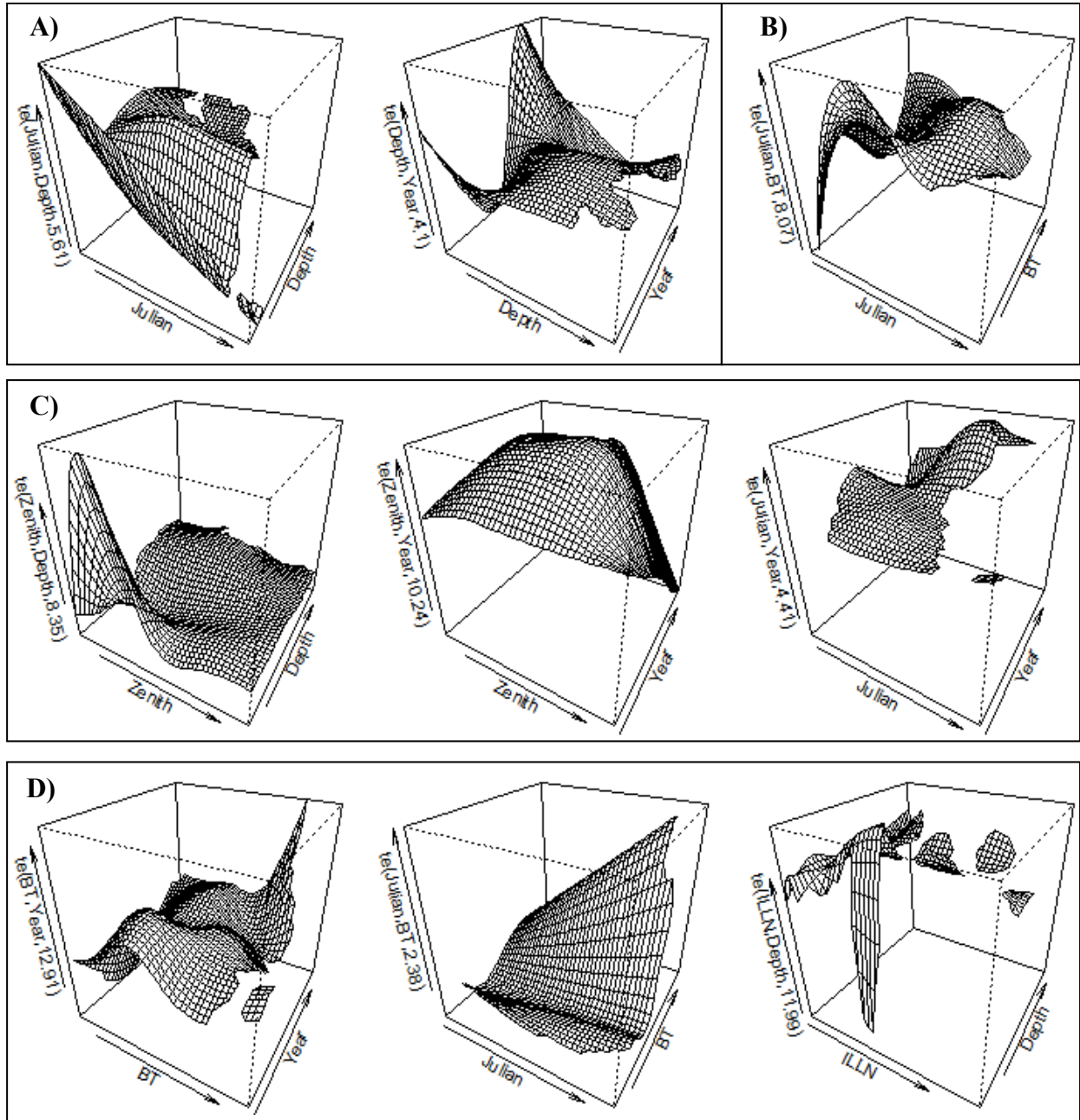


Figure 3.7. Comparison of the predicted probability of occurrence (filled contours) as determined by inverse distance weighted interpolation versus observed occurrence (points) in the Northeast (US) shelf large marine ecosystem for spiny dogfish life-history stages during spring. MA = Middle Atlantic Bight, SNE = Southern New England, GB = Georges Bank, and GM = Gulf of Maine. Solid gray indicates land masses. Probabilities include 0 – 0.2 (white), 0.3 – 0.4 (blue), 0.5 – 0.6 (green), 0.7 – 0.8 (yellow), 0.9 – 1.0 (red). Note: interpolation carried out in ArcGIS using spatial analyst.

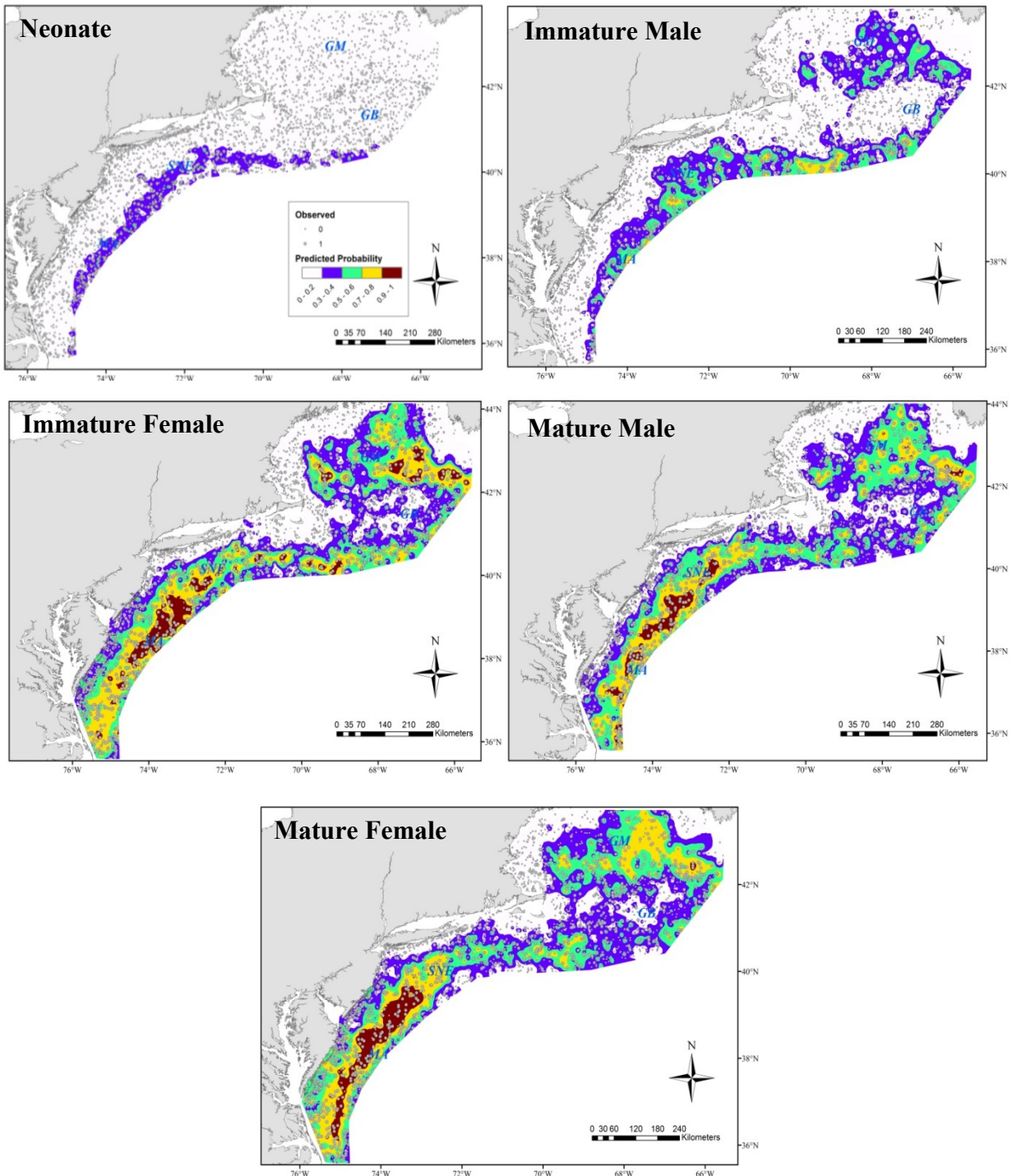


Figure 3.8. Hypothetical predicted probability of mature female spiny dogfish occurrence during spring in the Northeast (US) shelf large marine ecosystem for a year exhibiting average (BT_{avg}), warmer ($BT_{avg} + 1^\circ C$), and cooler ($BT_{avg} - 1^\circ C$) bottom temperatures. Probabilities include < 0.5 (red), $0.5 - 0.6$ (orange), $0.6 - 0.7$ (yellow), $0.7 - 0.8$ (green), $0.8 - 0.9$ (light blue), and $0.9 - 1.0$ (dark blue). MA = Middle Atlantic Bight, SNE = Southern New England, GB = Georges Bank, and GM = Gulf of Maine. Note: only the abiotic sub-model was used for prediction due to uncertainty regarding how prey species would respond to temperature changes.

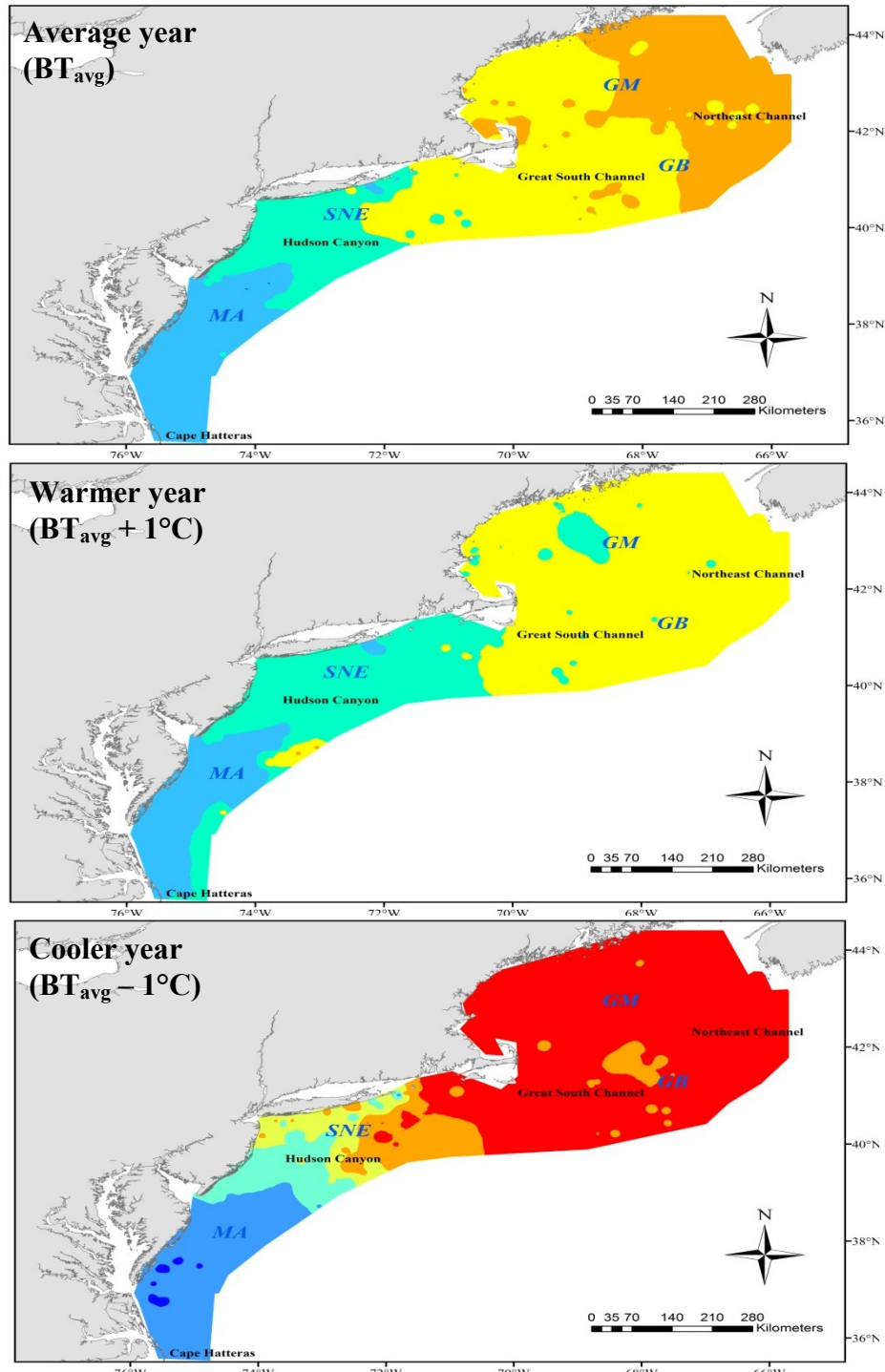
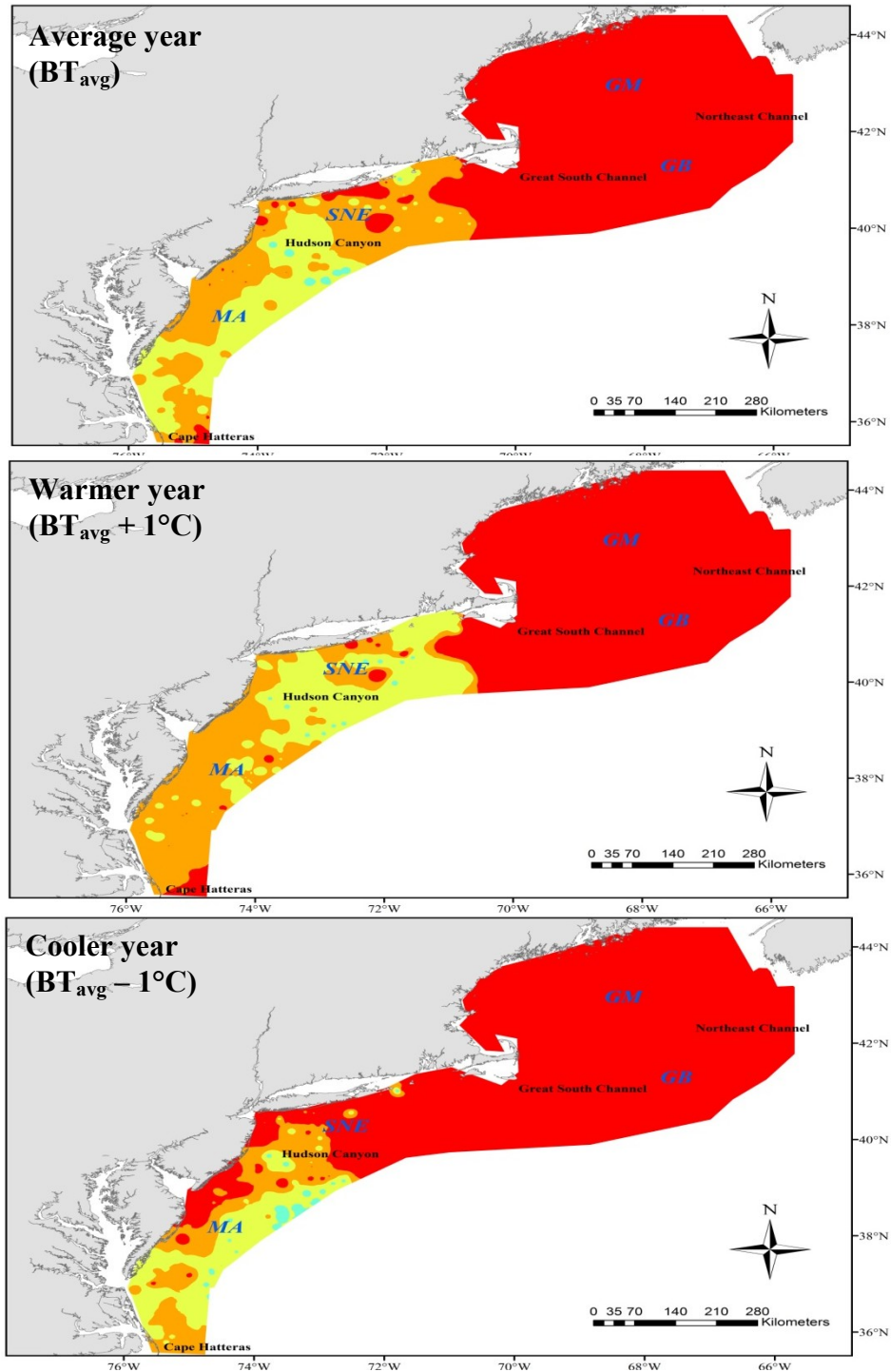


Figure 3.9. Hypothetical predicted probability of neonate spiny dogfish occurrence during spring in the Northeast (US) shelf large marine ecosystem for a year exhibiting average (BT_{avg}), warmer ($BT_{avg} + 1^{\circ}C$), and cooler ($BT_{avg} - 1^{\circ}C$) bottom temperatures. Probabilities include < 0.5 (red), $0.5 - 0.6$ (orange), $0.6 - 0.7$ (yellow), $0.7 - 0.8$ (green), $0.8 - 0.9$ (light blue), and $0.9 - 1.0$ (dark blue). MA = Middle Atlantic Bight, SNE = Southern New England, GB = Georges Bank, and GM = Gulf of Maine. Note: only the abiotic sub-model was used for prediction due to uncertainty regarding how prey species would respond to temperature changes.



Chapter 4:

IS DIEL VARIATION IN CATCHABILITY SKEWING SURVEY-DERIVED ABUNDANCE ESTIMATES OF SPINY DOGFISH AND THEIR PREY?

Introduction

Quantifying predation on prey fishes that adequately reflects ecosystem dynamics is an essential step towards the application of multispecies models for ecosystem based fisheries management (EBFM) (Tyrrell et al. 2011). Unfortunately, estimating consumption can pose a major challenge in quantifying such dynamics (Hollowed et al. 2000, Overholtz et al. 2008). The Northeast (US) shelf large marine ecosystem (NES LME), once dominated by commercially important groundfish such as Atlantic cod (*Gadus morhua*), is now populated by predatory spiny dogfish (*Squalus acanthias*) and pelagic forage fishes (e.g., herring and mackerel). While Northeast Fisheries Science Center (NEFSC) bottom trawl surveys have monitored abundance trends since 1963 during autumn and 1968 during spring, high variability highlights the uncertainty inherent within population estimates such as consumption. In recent years, commercial fishermen have reported overwhelming local abundance of spiny dogfish and have expressed concern that the stock threatens the recovery of commercially valuable species.

Spiny dogfish feed upon pelagic prey including squids, clupeids, scombrids, and other fishes (Fogarty & Murawski 1998, Link & Almeida 2000, Link & Garrison 2002). Their distribution and abundance is thought to be tightly linked with prey distribution (Overholtz & Tyler 1985, Burgess 2002), highlighting the potential for ecological interactions. While the perceived discrepancy in stock size and status between the scientific and fishing communities

may be an artifact of increased fisher success (e.g., improved technology and communication), it could also indicate changing availability of spiny dogfish to the survey which is impacting abundance estimates. Recently a more pelagic (TRAC 2010b) and mobile (Sulikowski et al. 2010) existence than presently accepted has been suggested for patterns observed in survey trends.

Survey-derived estimates of catch per unit of effort (*CPUE*), a relative abundance index, are assumed proportional to both stock abundance and catchability (Godø et al. 1999, Salthaug & Aanes 2003, Ellis & Wang 2007). Catchability, defined as the proportion of a group (e.g., species or size class) caught by one unit of effort (e.g., area swept by trawl) (Francis et al. 2003, Fraser et al. 2007), consists of three components: (1) the horizontal or areal availability which describes the probability of presence in the area at the time of the survey (Francis et al. 2003, Trenkel et al. 2004); (2) the vertical availability which conveys the proportion of the stock in the area which could be encountered by the trawl (Francis et al. 2003, Trenkel et al. 2004); and (3) the efficiency or proportion of available stock caught in the trawl (Godø 1994, Michalsen et al. 1996, Trenkel et al. 2004). While assessment models often assume that a species' catchability remains constant both spatially and temporally, this situation rarely holds in nature (Somarakis et al. 1998, Godø et al. 1999, Salthaug & Aanes 2003, Trenkel et al. 2004, Gauthier & Rose 2005).

Catchability frequently varies with environmental conditions and therefore derived abundance estimates assuming constant catchability may misrepresent species density and ecosystem dynamics (Francis & Williams 1995, Hjellvik et al. 2002, Benoît & Swain 2003, Salthaug & Aanes 2003). While many factors ranging from environmental (e.g., temperature) to anthropogenic (e.g., vessel, skipper knowledge) may influence catchability (Table 4A.1), vertical movements or diel migrations are frequently examined using survey-derived abundance

estimates (Michalsen et al. 1996, Casey & Myers 1998, Petrakis et al. 2001, Benoît & Swain 2003, Gauthier & 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 abundance estimates (Francis & Williams 1995, Hjellvik et al. 2002). Recognizing and adjusting for biases can remove unwanted variability within catch indices (Petrakis et al. 2001), thereby enhancing the dependability of stock assessments and population-level estimates in addition to the effectiveness of management efforts. Further, biased abundances of mature female or neonate spiny dogfish could negatively impact estimates of spawning stock biomass and recruitment, respectively.

Past scientific interest and management were heavily biased towards economically valuable groundfish; now, with important commercial fisheries supported by previously underutilized spiny dogfish (Rago et al. 1998, Stevens et al. 2000) and forage fish (Tacon & Metian 2009), it is imperative research is conducted to evaluate and adjust for biases within the data for more accurate stock assessment (Godø & Walsh 1992) and consumption estimates. In this study, we assessed catch rates and estimated catchability of spiny dogfish and important prey species in the NES LME. NEFSC bottom trawl survey data enabled investigation of both predator and prey catchability and of how diel variations may influence ecological interactions. Abundance estimates adjusted for day-night effects are reported where necessary. Understanding how spiny dogfish and their prey respond to diel and environmental factors will benefit not only single-species assessment, it will provide vital information on ecological interactions for EBFM.

Methods

Data Source

Annual bottom trawl surveys have been conducted by the NEFSC during autumn and spring since 1963 and 1968, respectively. These surveys sample the NES LME from Cape Hatteras, NC, to Georges Bank (GB) and the Gulf of Maine (GM) (Figure 4.1) using a stratified random design. Offshore and inshore strata are depicted in Figures 1 and 2 of NEFSC (2006). The autumn survey has been conducted in offshore areas since 1963 and inshore strata were added in 1972. The spring survey began sampling offshore areas in 1968 and inshore strata were added in 1973. Survey strata comprise about 64,000 nm². The number of stations sampled per stratum was proportional to its area but inshore strata were sampled at approximately three times the sampling rate of offshore strata. Approximately 300 – 400 stations were visited during autumn (mean ± SE = 344 ± 13 stations) and spring (mean ± SE = 346 ± 8 stations). Detailed descriptions of the survey design and changes in survey protocols over time can be found in Azarovitz (1981) and Azarovitz et al. (1997).

Correction factors based on field experiments were applied for changes in vessels, gear and doors when necessary. The introduction of the *Henry B. Bigelow* in 2009 brought about changes to the trawling gear and survey protocol (Brown et al. 2007). In addition, a calibration study compared the catchability of the old vessel, the *Albatross IV*, with the new vessel (Miller et al. 2010).

Data

Indices of relative abundance were extracted from the NEFSC bottom trawl survey during both spring and autumn for spiny dogfish and five important prey species: Atlantic butterfish (*Peprilus triacanthus*), Atlantic herring (*Clupea harengus*), shortfin squid (*Illex* sp.),

longfin squid (*Loligo* sp.), 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 (NMFS) Food Webs Dynamic Program food habits database (Link & Almeida 2000). Spiny dogfish indices were reported for five life-history stages: aggregated male and female neonates (total length (TL) ≤ 26 cm), immature males (26 cm $<$ TL $<$ 60 cm) and females (26 cm $<$ TL $<$ 80 cm), and mature males (TL ≥ 60 cm) and females (TL ≥ 80 cm). *CPUE* was defined as the number of each species or dogfish stage caught per tow and was assumed an appropriate proxy for abundance.

For all species and dogfish stages examined, *CPUE* was further dissected into both day (D) and night (N) and shallow (SH) and deep (DE) components (i.e., $CPUE_N = \text{number captured at N divided by number of N tows}$). Tows where the solar zenith was $\geq 108^\circ$ were classified as night whereas tows with angles $< 108^\circ$ were day-time tows. Based on these classifications, 66% and 59% of tows occurred during the day for spring and autumn, respectively (Table 4B.1). Following Petrakis et al. (2001), depth zones were identified as SH (< 75 m) and DE (≥ 75 m) and provided an approximate equal division of hauls, with SH tows totaling 54% during spring and 53% during autumn (Table 4B.1).

Distribution Analyses

For each species and season, two different distributions were inspected for diel differences: 1) catches and 2) aggregations. Catch distributions consisted of catches (zero included) reported for individual stations each year. Aggregations were defined as those catches $\geq 95^{\text{th}}$ percentile and were mapped in ArcMap (v10. ESRI Corp) for visual inspection. Nonparametric methods were utilized due to the non-normal nature of the data and the failure of

transformation efforts (Sokal & Rohlf 1995). Day and night distributions of both catch and aggregations were compared using the Kolmogorov-Smirnov two-sample test (Sokal & Rohlf 1995) under the null hypothesis that the two samples (e.g. N and D) were drawn from the same distribution. The location of each sample was tested using the Mann-Whitney U-test or Wilcoxon two-sample test under the null hypothesis that the two samples originated from populations having the same location. Similar analyses have analyzed diurnal catch rates in bottom trawl catches within European waters (Aglen et al. 1999, Petrakis et al. 2001). All *a priori* significance levels ($\alpha = 0.05$) were adjusted using the Bonferroni correction method ($\alpha_{\text{adj}} = 0.0045$) to reduce the potential for type I errors during multiple comparisons. All statistical analyses were performed in R (R Core Development 2010).

CPUE Analyses

Annual catch ratios (N/D and SH/DE) were calculated to display trends for each year and season (Petrakis et al. 2001). These ratios were based on mean *CPUE* reported for each dogfish stage and prey species. Each ratio was graphically inspected and characterized by summary statistics. Differences in catch rates (i.e., N versus D, SH versus DE) were tested using the Mann-Whitney U-test with significance determined using adjusted *p*-values (Sokal & Rohlf 1995).

CPUE was also analyzed on an hourly basis to elucidate temporal trends over a smaller time scale for each dogfish stage and prey species. Segmented regression and a breakpoint analysis on the hourly intervals provided trends and identified times where important changes in *CPUE* occurred. In breakpoint analysis, a series of linear regressions were 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 (BIC). The breakpoint(s) were considered the point or points which separated two significantly differing linear regressions as derived from the data (Frisk et al. 2011).

A frequency analysis examined the dominance (i.e., more frequent than expected) of time of day and depth on *CPUE* trends for each dogfish stage, prey species and season. For this analysis, the data were organized so each row reflected an observation of the mean *CPUE* for each year and Julian day combination (e.g., row 1 = year 1963, day 317; row 2 = year 1963, day 318, etc.). For each year, all days lacking catches were excluded from this analysis. A 2x2 contingency table displayed the number of Julian days which revealed temporal (D or N) and depth dominance (SH or DE) (i.e., $CPUE_D > CPUE_N = D$ dominant). Four observed dominance classes were possible: day-deep (DDE), day-shallow (DSH), night-deep (NDE), and night-shallow (NSH). Observed frequencies were compared with expected frequencies (0.25, 0.25, 0.25, 0.25) using the Chi-square test when sample sizes were appropriate. When sample sizes were too small ($n < 5$), Fisher's exact test was used (Crawley 2007).

Day Night Catchability

For each dogfish stage and prey species, the proportion of day-time catches was explored using generalized linear models (GLMs) (McCullagh & Nelder 1989) to determine whether or not a different proportion was caught during the day and night (Casey & Myers 1998). An extension of linear modeling, GLMs portray the response variable in relation to the explanatory variables through a specified link function, do not force data into unnatural scales, and allow for non-normality (Hastie & Tibshirani 1990, Guisan et al. 2002). This method is commonly used to relate catch rates to environmental or other explanatory variables (Smith 1990, Adlerstein &

Ehrich 2003, Benoît & Swain 2003, Campbell 2004, Ward & Myers 2005). All GLM models were fit in R (R Core Development 2010) using a quasi-binomial distribution which added an overdispersion parameter to the variance of the response and a logit function to link the response with the predictor (Zuur et al. 2009).

For catchability analyses, the data were organized so each row reflected an observation of *CPUE* for each year and strata combination (e.g., row 1 = year 1963, strata 1020; row 2 = year 1963, strata 1030, etc.). Analyses were conducted on all data combined (i.e., All Regions) and separately for four regions (Figure 4.1) within the survey domain: GB, GM, Southern New England (SNE), and the Middle Atlantic Bight (MA).

For each observation the number of day (T_{ysd}) and night tows (T_{ysn}) in year y and stratum s , the proportion of catch caught during the day (C_{ysd}/C_{yst}), and the mean environmental value (depth, bottom temperature, Julian day) were reported. The logistic method of Casey and Myers (1998) and Benoît and Swain (2003) was employed to first estimate the relative diel catchability (S_d) prior to the inclusion of environmental factors. This method is based off the expectation that no difference between day and night catchability (i.e., $S_d = 1$) would give the following:

$$(4.1) \quad \frac{p_{ys}}{1-p_{ys}} = S_d \times \frac{T_{ysd}}{T_{ysn}}$$

where p_{ys} is the probability that a fish is caught in year y and stratum s during the day (Casey & Myers 1998). A log transformation results in the final equation:

$$(4.2) \quad \log\left(\frac{p_{ys}}{1-p_{ys}}\right) = \log(S_d) + \log\left(\frac{T_{ysd}}{T_{ysn}}\right)$$

where an offset accounts for the relative number of day and night tows (McCullagh & Nelder 1989, Casey & Myers 1998, Benoît & Swain 2003). The probability of catching a fish during the day in a particular year and stratum, given the total number of fish caught in that year and stratum, follows a binomial distribution assuming fish are captured independently and the probability of capture during the day is constant for individuals of that species (Casey & Myers 1998). Here, the intercept represented the natural logarithm of the catchability during the day and was estimated by the model. An estimate $[\log(S_d)]$ of 0 reflected no difference between day and night catchability whereas a positive estimate represented higher catchability during the day (Figure 4.2). After the intercept was estimated, the probability of day-time capture was back-calculated (from the logit scale) and compared relative to 50% where day and night capture probability would be equal. The reliability of significance tests and standard errors for estimated parameters was assessed using 1000 randomizations (Manly 1991).

One limitation of this logistic model is it assumes that the same proportion of fish will remain in a stratum during the survey period for a given year (Casey & Myers 1998). For a species like spiny dogfish, which displays north-south seasonal movements and highly variable local abundance (NEFSC 2006), the validity of this assumption may be problematic.

Where significant day-night effects were observed for dogfish stages or prey species, $CPUE$ was converted to daytime equivalents using estimated conversion factors (i.e., S_d):

$$(4.3) \quad CPUE_{adj} = \frac{CPUE}{S_d}$$

under the assumption that diel catchability estimates approximated mean conditions.

Environmental and Temporal Influences on Catchability

The influences of depth, bottom temperature, and Julian day on the proportion of day-time catch were assessed using generalized additive models (GAMs) (Hastie & Tibshirani 1990, Wood 2006). This method enabled removal of the assumption inherent within the logistic model described above (Casey & Myers 1998). GAMs utilize a smoothing function (Wintle et al. 2005) that can easily handle complex non-linear relationships and uncover hidden structure between variables missed by traditional linear methods (Hastie & Tibshirani 1990, Guisan et al. 2002). Collinearity between potential variables was explored and variance inflation factors with values < 3.0 were deemed acceptable (Zuur et al. 2009). All GAMs were built in the R package 'mgcv' (Wood 2011) using cubic regression splines, a maximum of 5 degrees of freedom ($k = 5$), and a quasi-binomial distribution. Optimal models contained important variables identified using step-wise backward selection (Harrell 2001, Wintle et al. 2005) and possessed the lowest generalized cross-validation (GCV) score (Wood 2011). Low sample sizes for some species and/or regions prevented the inclusion of interaction terms (e.g., depth:temperature) and the formulation of both training and testing datasets to enable rigorous model validation. Therefore, model performance was 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). The robustness of smoothness selection for each model, originally based on GCV, was checked by refitting each model using "maximum likelihood" and assessing the agreement between estimated degrees of freedom (Wood 2011). The potential for concurvity, a generalization of co-linearity, was also explored for each optimal model (Wood 2011).

Results

Distributional Trends

Catches

While the percentage of positive catches (i.e., catch > 0) were generally similar across day and night for most species, mean catch rates often differed during both seasons (Table 4.1). Day and night distributions differed significantly ($p_{adj} < 0.0045$) for most prey species during each season and for all dogfish stages combined during spring (Table 4.1). These species all exhibited significantly ($p_{adj} < 0.0045$) larger mean day-time catches. While other dogfish stages and prey species revealed significantly larger mean day-time catches (e.g., immature males), distributional differences were not detected.

Aggregations

During both spring and autumn, quantified aggregations for prey species (range: 57 – 1825 individuals) were generally larger than those for spiny dogfish stages (range: 11 – 336 individuals). *Loligo* sp. comprised the largest aggregation during each season (spring: 1494, autumn: 1825). In contrast, smallest aggregations were displayed by *Illex* sp. (57) during spring, and mackerel (86) during autumn. While most dogfish stages and prey species displayed larger and more frequent day-time aggregations during each season, only autumn-captured *Illex* sp. revealed a significant ($p_{adj} < 0.0045$) difference in the distribution of day and night aggregations (Table 4C.1).

During spring, most spiny dogfish aggregations during both day and night were encountered offshore along the edge of the continental shelf from Cape Hatteras to GB (Figure 4.3). However, differences in aggregation locations between sexes and stages were observed. Males generally aggregated along the shelf's edge whereas female aggregations spread further

inshore (Figure 4.3). While all dogfish stages aggregated throughout the MA and SNE, aggregations of immature spiny dogfish were more common on GB (Figure 4.3). The majority of spiny dogfish aggregations during autumn were encountered on GB and inshore around Massachusetts during both times of day (Figure 4.3). As observed during spring, locations of aggregations generally differed between sexes and stages. Mature dogfish primarily aggregated inshore around Massachusetts (Figure 4.3). While immature dogfish generally amassed offshore on GB or in the GM, female aggregations were also present inshore around Cape Cod (Figure 4.3). Although rare, neonate aggregations were documented along the shelf's edge during both seasons (Figure 4.3).

The spatial extent of prey aggregations varied greatly between species and seasons. During spring, butterfish, *Illlex* sp. and *Loligo* sp. mainly aggregated at the shelf's edge in the MA and SNE (Figure 4.4). In contrast, aggregations of herring and mackerel were spread throughout the MA and SNE with herring also prevalent inshore in the GM and mackerel on GB (Figure 4.4). Compared to spring, autumn trends were less consistent among prey species. Butterfish aggregated both inshore and at the shelf's edge in the MA and SNE (Figure 4.4). Herring generally amassed in the western GM whereas *Illlex* sp. remained along the shelf's edge throughout the region (Figure 4.4). *Loligo* sp. were concentrated throughout the MA and SNE (Figure 4.4). Lastly, mackerel sporadically aggregated throughout the GM and GB (Figure 4.4).

Annual Trends

Catch Rates

Spiny dogfish. Most years displayed higher catch rates during the day for all spiny dogfish combined (Figure 4D.1) and individual stages (Figures 4D.2-6) during both seasons. For

all dogfish stages combined, day-time catch rates differed significantly ($p_{adj} < 0.0045$) from night-time catch rates during both seasons (Table 4.2). However, when analyzed by dogfish stage, significance ($p_{adj} < 0.0045$) was found solely for neonate and mature male spiny dogfish during spring (Table 4.2). In general, night catches were on average <1 times day catches for most dogfish stages examined during each season (Table 4.2). Annual catch ratios derived from depth revealed more variation among dogfish stages and seasons (Table 4.2). During spring, the majority of years revealed higher catch rates in deep compared to shallow depths for most dogfish stages (Figures 4D.1-6). In addition, most dogfish stages revealed significantly different catch rates ($p_{adj} < 0.0045$) with shallow catches on average <1 times deep catches with the exception of mature female spiny dogfish (Table 4.2). In contrast, during autumn, significantly ($p_{adj} < 0.0045$) higher catch rates occurred in shallow regions for mature spiny dogfish and all dogfish stages combined and in deep regions for neonate spiny dogfish (Table 4.2). Shallow catches were on average >1 times deep catches for all dogfish stages except neonates (Table 4.2).

Prey species. During both seasons, the majority of years displayed higher day-time catch rates for all prey species examined (Figures 4D.7-11). Day and night catch rates differed significantly ($p_{adj} < 0.0045$) for most prey species during each season (Table 4.2). Both seasons generally displayed night catches <1 times on average day catches for most species examined (Table 4.2). Seasonal trends in depth-dependent catch rates were highly significant ($p_{adj} < 0.0045$) but variable, particularly during spring (Table 4.2). During this season, most years revealed higher deep catch rates for butterfish and both squid species (Figures 4D.7-11). While shallow catches were on average <1 times deep catches for both *Illex* sp. and *Loligo* sp., an unusually large shallow catch of butterfish inflated its annual ratio to > 1 (Table 4.2). Upon removal of this outlier, the mean annual ratio reinforced predominant deep water catches. In

contrast, herring displayed an annual ratio > 1 indicating higher shallow catches during this season (Table 4.2). During autumn, significantly ($p_{adj} < 0.0045$) higher catch rates occurred in shallow waters for butterfish, *Loligo* sp., and mackerel and in deep waters for *Illex* sp. (Table 4.2).

Temporal Trends

CPUE

Both dogfish stages and prey species revealed highly variable temporal *CPUE* during both spring (Figure 4.5) and autumn (Figure 4.6). Peak *CPUE* during spring occurred around 5AM for both mature spiny dogfish and immature females whereas the highest catches of neonates and immature males occurred around 11AM and 3PM, respectively (Figure 4.5). Most dogfish stages revealed two estimated breakpoints with the exception of neonates (3 breakpoints) and mature males (4 breakpoints) (Figure 4.5). All dogfish stages except immature male spiny dogfish revealed at least one significant breakpoint in the morning between 12 and 9AM (Figure 4.5). For male spiny dogfish, *CPUE* trends also diverged between 3 and 7PM (Figure 4.5). In contrast to spiny dogfish, both *CPUE* trends and estimated breakpoints regarding prey species during spring were more diverse (Figure 4.5). *CPUE* remained relatively high throughout the day (6AM – 5PM) for herring, *Loligo* sp., and mackerel (Figure 4.5). In contrast, *CPUE* was relatively consistent for butterfish and remained low for *Illex* sp. with the exception of 7AM when peak *CPUE* occurred (Figure 4.5). The numbers and locations of estimated breakpoints varied greatly, with the most (5) exhibited by *Loligo* sp. and the least (0) by butterfish (Figure 4.5).

During autumn, peak *CPUE* of neonate and male spiny dogfish occurred around 10AM and around 3PM for immature females (Figure 4.6). In contrast, *CPUE* of mature females remained relatively low (Figure 4.6). Diverging trends in *CPUE* were less obvious during autumn as evident by fewer estimated breakpoints (0 to 3) for most dogfish stages (Figure 4.6). At 10AM, *CPUE* trends diverged for neonate and male spiny dogfish whereas 3PM served as a breakpoint for neonate and immature females (Figure 4.6). In contrast to spring, all prey species revealed relatively consistent *CPUE* patterns with relatively higher values between 7AM and 3PM (Figure 4.6). The majority of estimated breakpoints occurred within this range.

Frequencies by Julian Day

During spring, time of day and depth were highly interdependent for all dogfish stages and species examined with the exception of *Illex* sp. (Table 4.3). Trends during spring were variable. The most common trend observed overall, more Julian days displaying both DDE and DSH *CPUE*, was exhibited by mature spiny dogfish and mackerel (Table 4.3). DDE *CPUE* was more frequent than expected for all spiny dogfish combined, neonates, immature females, and *Loligo* sp. (Table 4.3). Herring were more frequently encountered DSH whereas more days displayed both DDE and NDE *CPUE* for immature males and butterfish (Table 4.3).

During autumn, most dogfish stages and prey species displayed both dominant DDE and DSH *CPUE* trends (Table 4.3). DDE *CPUE* was more frequent for neonates and *Illex* sp. whereas more days revealed both DDE and NDE *CPUE* for herring and both DSH and NSH *CPUE* for mature spiny dogfish (Table 4.3).

Day Night Catchability

For each dogfish stage and prey species, estimates of diel catchability were obtained for the entire survey area (i.e., All Regions combined) and for each region during both spring and autumn (Table 4.4). Over the entire survey area, significantly ($p < 0.05$) higher day-time catchabilities were displayed by all dogfish stages combined, mature males and both squid species during spring and by all dogfish stages and prey species except neonate and mature female spiny dogfish during autumn (Table 4.4). While regional trends for dogfish stages were rarely significant during spring with the exception of the MA, significantly higher day-time catchabilities were found for some prey species on GB, in SNE, and in the MA (Table 4.4). In contrast, during autumn regional day-time catchabilities were higher for all dogfish stages combined in the GM and on GB and for mature males in the GM. Significantly higher day-time catchabilities were widespread throughout all regions for butterflyfish and both squid species. While higher night-time catchability was occasionally estimated, these trends were not significant (Table 4.4).

The probability of day-time capture, as estimated by fitted GLMs with significant diel catchability (i.e., intercepts), deviated from 50% for many dogfish stages and prey species both regionally and seasonally, indicating a difference in catch between day and night (Figure 4.7). Estimates ranged from 63 to 93% during spring and from 63 to 96% during autumn. Probability of day-time capture was high in the MA during spring for all dogfish stages combined, mature males, and immature females. Over the entire survey area, high probability was observed for all stages combined and mature males (Figure 4.7A). During autumn, probabilities were high for most dogfish stages over the entire survey area, for all dogfish stages combined in the GM and on GB, and for mature males in the GM (Figure 4.7B). In contrast, the probability of day-time

capture for prey species was frequently high across regions for *Illex* sp. and *Loligo* sp. During spring and most species during autumn (Figure 4.7).

Adjusted abundance estimates taking into account differences in day-night catchability revealed lower *CPUE*, suggesting that unadjusted *CPUE* was overestimating overall and regional abundance for many dogfish stages and prey species during spring (Figures 4F.1-5) and autumn (Figures 4.8, 4F.6-9).

Environmental and Temporal Influences on Catchability

General modeling results

Based on the previous finding of few significant differences in diel catchability for dogfish stages, the remaining analysis focuses on all dogfish stages combined. The majority of GAMs spanning species and regions utilized 50 or more data points, with sample sizes ranging from 26 – 1454 during spring (Table 4.5) and from 92 – 1713 during autumn (Table 4.6). Low sample sizes (<50) plagued models for butterfish and *Illex* sp. in the GM during spring. During autumn, more deviance was generally explained for spiny dogfish in southern regions, butterfish in northern regions, and herring throughout the range. In contrast, more error was explained during spring for most prey species throughout the range (Tables 4.5-6). During both seasons, roughly half of the models analyzed explained at least 20% deviance (Tables 4.5-6). Of these models, most occurred in the GM and SNE during autumn and in the GM, GB, and MA during spring. Full modeling results can be found in Appendices 4G (Figures 4G.1-6) for spring and 4H (Figures 4H.1-6) for autumn.

Overall, the majority of models revealed residuals lacking both autocorrelation and strong trends. Degrees of freedom estimated by maximum likelihood were generally similar to those

obtained by GCV, indicating a robust selection of smoothing. Estimates of concurvity did not reveal concerning collinearity. However, some models displayed residuals revealing heterogeneous spreads when graphed against the explanatory variables during spring (Figures 4G.7-12) and autumn (Figures 4H.7-12), mostly a result of sparse large observations. Those models generally revealed small sample sizes (<50), poor fits via residuals and, as a result, were excluded from our discussion.

During both seasons, the probability of day-time catch was frequently influenced by environmental and temporal factors (Tables 4.5-6). Most regional models for spiny dogfish and prey species identified at least one variable as significantly influential on the probability of daytime catch during spring (Table 4.5) and autumn (Table 4.6). During spring, both depth and bottom temperature were frequently selected while Julian day was less common (Table 4.5). In contrast, during autumn, depth was the most frequently selected variable followed closely by bottom temperature and Julian day (Table 4.6).

Environmental and Temporal Trends

Significant nonlinear relationships with depth and bottom temperature were frequently observed during both seasons (Tables 4.5-6). For all regions combined during autumn, probabilities of daytime catch were higher at shallow depths (<75m) for herring and mackerel and at moderate depths for spiny dogfish, butterfish, *Illex* sp. and *Loligo* sp. (Table 4.6; Figure 4.9). In contrast, during spring, day-time catches were more likely in shallow depths (<75m) for most prey species (Table 4.5; Figure 4.10). During autumn, higher probabilities of day-time catch generally occurred at cooler (<10°C) temperatures for butterfish, *Loligo* sp. and mackerel and at warmer temperatures for spiny dogfish, herring, and *Illex* sp. (Table 4.6; Figure 4.9).

During spring, higher probabilities of day-time catch generally occurred at cooler temperatures (<8°C) for all species (Table 4.5; Figure 4.10).

Significant nonlinear relationships with Julian day were also frequently observed in models during both autumn and spring (Tables 4.5-6). During autumn, day-time catch was more likely early in the season for *Loligo* sp. and mackerel and in the middle of the season for most other species (Table 4.6; Figure 4.9). During spring, higher probabilities of day-time catch occurred earlier in the season for *Illex* sp. and towards the end of the season for the remaining species (Table 4.5; Figure 4.10).

Discussion

Research surveys enable the quantification of a species' population dynamics by simplifying assumptions concerning gear efficiency, catchability, and consistency across various environmental gradients (Godø 1994, Godø et al. 1999, Francis et al. 2003). Here we documented influential diel and environmental factors on seasonal catch rates and catchability of spiny dogfish and key prey species throughout the NES LME. Both revealed higher day-time estimates for some dogfish stages and most prey species, highlighting the potential for bias within stage-specific or species-specific abundance estimates. Current methods appear to be overestimating abundances of both spiny dogfish and prey species, a bias which has important implications towards stock sustainability and quantification of population consumption rates.

In addition to improving our ability to adequately capture population trends, adjusting abundance estimates can help elucidate the role of spiny dogfish within the ecosystem. Our results suggest that the NEFSC trawl survey is overestimating the abundances of spiny dogfish and their prey during the day, possibly due to feeding/aggregating or herding on the bottom. This

has important implications regarding the ecological role of spiny dogfish, principally concerning consumption. Between 1977 and 1997, spiny dogfish consumed an estimated 619,000 metric tons (*mt*) of prey species (sand lance *Ammodytes* sp. and the 5 presented herein) (Overholtz et al. 2000). While survey catchability was adjusted for most other predators examined, area swept numbers of spiny dogfish were not adjusted (Overholtz et al. 2000). Given the strong bias in *CPUE*, this consumption estimate likely overestimated their predatory impact in relation to fishery catches. In addition, mass balance models based on inaccurate consumption estimates can lead to biased representations and estimates of ecosystem dynamics. Adjusted *CPUE* estimates will better represent actual abundance trends for single-species stock assessment and provide more accurate consumption estimates needed for EBFM.

Although representing one of the longest time series in the world, few studies have thoroughly explored how the catchability of the NEFSC annual bottom trawl survey varies with the environment. Overall, higher day-time catchabilities were documented for all spiny dogfish combined, mature males, and squid during spring and for most species during autumn. The majority of these relationships were characterized by large sample sizes and small associated errors, implying precise estimates. Similar results were found in the North Sea for herring (Petrakis et al. 2001) and in the northwest Atlantic for *Loligo pealei* and *Illex illecebrosus* during autumn (Brodziak & Hendrickson 1999). In Canadian waters, catchability was higher during the night for thorny, smooth, and winter skates and during the day for herring, butterfish, mackerel, and *Illex illecebrosus* (Casey & Myers 1998, Benoît & Swain 2003). High uncertainty (i.e., large standard errors surrounding diel catchability estimates) hindered analyses for spiny dogfish and black dogfish (*Centroscyllium fabricii*) (Casey & Myers 1998, Benoît & Swain 2003).

Many mechanisms linked to diel variations in catchability may partly explain these observed trends. While visual avoidance is commonly cited, this seems highly unlikely for any species examined since more individuals were captured during daylight when visibility is expected to be higher (Glass & Wardle 1989, Casey & Myers 1998, Petrakis et al. 2001). The observed change in availability of the stock to the trawl survey strongly supports vertical migrations (Engås et al. 1988, Walsh 1992, Aglen et al. 1997, Aglen et al. 1999, Korsbrekke & Nakken 1999) which are well-documented for both groundfish (e.g. Atlantic cod) and pelagic species (e.g. redfish) and generally balance predation risk with food availability (Michalsen et al. 1996, Aglen et al. 1999, Hjellvik et al. 2001, Gauthier & Rose 2005). For spiny dogfish, herding has been proposed in both the northwest Atlantic (NEFSC 2006) and in Puget Sound (Palsson 2009). Generally its effect may be enhanced during daylight when the sediment cloud is visible (Wardle 1993, Francis & Williams 1995, Michalsen et al. 1996, Fraser et al. 2007). Day-time catches likely overestimated biomass and resultant consumption estimates because a higher percentage was available to the trawl. In contrast, night-time catches may underestimate true biomass since spiny dogfish may spread more evenly throughout the water column. Therefore, night-time catches may provide a more conservative indicator of biomass and in turn consumption estimates.

Historically, both fishery and research interests have been tightly linked, with research efforts focused on commercially important species such as Atlantic cod (Rose 2004). Cod catches are generally higher during the day (Michalsen et al. 1996, Casey & Myers 1998, Aglen et al. 1999, Korsbrekke & Nakken 1999, Petrakis et al. 2001) although exceptions have been noted in certain areas (e.g., subdivision 3P, Casey & Myers 1998). In addition, length-dependent variations are often more pronounced for smaller fish (Michalsen et al. 1996, Aglen et al. 1999,

Korsbrekke & Nakken 1999). The highly aggregated behavior of spiny dogfish warrants further research on factors influencing this behavior and the effects density dependence may have on both research survey and fishery-dependent catchability. Studies concerning size-dependent escapement may prove fruitful for spiny dogfish, particularly for neonates whose survey-derived abundance is used as a proxy for recruitment (NEFSC 2006). In addition, mid-water trawl or acoustic surveys may provide additional insight into species' movements within the water column. While preliminary analyses revealed no relationship between annual *CPUE* estimates from bottom trawls (fishery-independent) and mid-water trawls (fishery-dependent) (Figure 4I.1), field studies are encouraged to determine if bottom trawl swept area estimates should be combined with simultaneous acoustic or mid-water trawl estimates (Aglen et al. 1999).

In the present study, trends for important prey species were reported to enhance understanding of their availability and to facilitate hypothesized linkages between the dynamics of spiny dogfish and their prey. As opportunistic predators (Stehlik 2007), spiny dogfish commonly adapt their feeding habits to exploit abundant prey (Overholtz et al. 2000, Link & Garrison 2002, Moustahfid et al. 2010) and display an ontogenetic shift towards increased piscivory (Garrison & Link 2000, Laptikhovsky et al. 2001, Alonso et al. 2002, Link & Garrison 2002). During spring, relatively higher *CPUE* occurred between early morning (i.e., 5:00am) and mid-afternoon (i.e., 3:00pm) for most dogfish stages and for 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 MA (Bowman et al. 2000, Stehlik 2007). However, the observed overlap in vertical distribution may also be related to feeding similarity as both *Illex* sp. and spiny dogfish (10 – 60 cm) share a cephalopod and fish-dominated diet (Garrison & 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). During autumn, spiny dogfish *CPUE* peaked between 9:00am and noon for most dogfish stages whereas *CPUE* of most prey species remained high between 5:00am and 3:00pm. Inspection of predator and prey distributions on a smaller spatial and temporal scale may elucidate drivers behind their changing vertical availability.

Depth-dependent catch rates were highly variable for most dogfish stages and prey species examined with many of these patterns linked to inshore and offshore seasonal migrations and/or preferred habitat. Greater shallow-water catch rates for mature female spiny dogfish likely relate to increased reproductive benefit of maximized internal embryo growth in certain environmental conditions (Moore 1998). In contrast, higher deep-water catch rates for younger dogfish (Shepherd et al. 2002, Stehlik 2007) and *Illlex* sp. (Brodziak & Hendrickson 1999, Hendrickson & Holmes 2004) may reflect preferred offshore habitat either for dietary purposes or as refuge from predation (Shepherd et al. 2002). Mature male and immature female spiny dogfish overwinter in deep offshore waters during the spring survey with mature males traveling inshore to warm coastal waters during autumn (Methratta & Link 2007). Depth trends for prey species were less consistent with known migratory paths. Deep-water catches were more common for *Loligo* sp. during spring when the species is supposedly inshore while shallow-water catches were greater during autumn when the stock is present offshore (Jacobson 2005). These inconsistencies may stem from our classifications and treatment of the data. Interannual variability within catch rates may provide further insight into patterns as our analyses only considered annual mean trends. Further investigation is warranted as movements between shallow and deep regions can greatly alter the horizontal availability of each species to the survey.

This study highlights the importance of examining the quality of survey data and adjusting for biased estimates of abundance when necessary to more accurately reflect actual trends (Godø & Walsh 1992, Hjellvik et al. 2002). 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. Changing catchability has important implications for stock assessment, particularly for spiny dogfish, where bottom trawl estimates provide relative abundance indices. 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 & Myers 1998) may further contribute to the catchability of spiny dogfish and their prey species. Gaining a better understanding of survey catchability will not only improve biological reference point estimates, it will help provide insight into ecological interactions for EBFM.

Table 4.1. Night (N) and day (D) distributions of catch for spiny dogfish life-history stages and prey species during spring (1968 – 2009) and autumn (1963 – 2009) in the Northeast (US) shelf large marine ecosystem. Stages include all dogfish combined (All), neonate (Neo; TL ≤ 26 cm), immature male (ImmM; 26 cm < TL < 60 cm) and female (ImmF; 26 cm < TL < 80 cm), mature male (MatM; TL ≥ 60 cm) and female (MatF; TL ≥ 80 cm). Prey species include butterfish (BF), Atlantic herring (HER), *Illex* sp. (ILL) and *Loligo* sp. (LOL) squids, and Atlantic mackerel (MAC). % Catch ≥ 1 refers to the percentage of tows containing spiny dogfish. *TS* = Kolmogorov-Smirnov (KS) test statistic, *p* = probability, *C* = mean catch for specified period (N or D) for Mann-Whitney U (MWU) test. Significance (bolded) based on an adjusted α of 0.0045 ($\alpha = 0.05$ corrected for 11 comparisons between stages/species). Note: spiny dogfish not sexed consistently until 1980.

Stage/Species	% Catch ≥ 1		KS		MWU		
	N	D	<i>TS</i>	<i>p</i>	<i>C_N</i>	<i>C_D</i>	<i>p</i>
<u>SPRING</u>							
All	40	43	0.03	0.0042	31.26	51.89	0.0001
Neo	3	4	0.02	0.2568	0.51	0.84	0.0000
ImmM	8	9	0.02	0.2755	3.28	6.07	0.0022
MatM	17	18	0.01	0.5717	10.20	19.68	0.0421
ImmF	21	22	0.01	0.4946	8.08	12.23	0.1370
MatF	19	20	0.02	0.3896	4.48	6.25	0.0596
BF	15	15	0.01	0.9957	33.84	37.11	0.9153
HER	26	33	0.07	0.0000	17.67	27.61	0.0000
ILL	3	7	0.03	0.0015	0.23	1.89	0.0000
LOL	22	25	0.05	0.0000	38.56	102.99	0.0000
MAC	10	13	0.03	0.0072	7.82	17.76	0.0001
<u>AUTUMN</u>							
All	29	29	0.02	0.0268	19.54	34.07	0.2430
Neo	0	1	0.00	1.0000	0.03	0.05	0.0154
ImmM	5	7	0.02	0.0535	1.45	3.74	0.0000
MatM	12	14	0.02	0.0280	6.21	11.78	0.0279
ImmF	13	15	0.02	0.0337	4.98	9.26	0.0003
MatF	7	8	0.01	0.4371	2.96	3.52	0.0059
BF	38	48	0.14	0.0000	39.02	222.89	0.0000
HER	13	12	0.01	0.3629	8.24	21.26	0.0233
ILL	24	38	0.14	0.0000	4.64	15.33	0.0000
LOL	43	61	0.24	0.0000	54.03	350.82	0.0000
MAC	2	5	0.04	0.0001	0.21	6.11	0.0000

Table 4.2. Annual bottom trawl catch ratios for spiny dogfish life-history stages and prey species at different times of the day (N = night [zenith $\geq 108^\circ$], D = day [zenith $< 108^\circ$]) and depths (SH = shallow [depth < 75 m], DE = deep [depth ≥ 75 m]) from the NEFSC annual bottom trawl survey conducted in the Northeast (US) shelf large marine ecosystem during spring (1968 – 2009) and autumn (1963 – 2009). Stages and species as defined in Table 4.1. Range = range of annual ratios which were calculated from the mean catch rates, *SE* = standard error, *p* = probability derived from nonparametric Mann-Whitney U-test. Significance (bolded) based on an adjusted α of 0.0045 ($\alpha = 0.05$ corrected for 11 comparisons between stages/species).

Stage/ Species	SPRING			AUTUMN		
	Range	Mean \pm SE	<i>p</i>	Range	Mean \pm SE	<i>p</i>
N/D Annual Ratio						
All	0.07 - 1.62	0.64 \pm 0.05	0.0000	0.07 - 4.86	0.77 \pm 0.11	0.0002
Neo	0.01 - 16.01	1.18 \pm 0.40	0.0022	0.00 - 3.22	0.64 \pm 0.15	0.0094
ImmM	0.06 - 5.68	0.79 \pm 0.18	0.1017	0.03 - 5.29	0.86 \pm 0.19	0.0701
MatM	0.02 - 1.48	0.59 \pm 0.06	0.0037	0.00 - 3.66	0.69 \pm 0.11	0.0563
ImmF	0.07 - 3.73	0.80 \pm 0.12	0.0230	0.08 - 8.63	0.95 \pm 0.27	0.0317
MatF	0.08 - 3.68	0.83 \pm 0.11	0.1426	0.04 - 16.25	2.31 \pm 0.73	0.8927
BF	0.05 - 81.38	3.09 \pm 1.93	0.0423	0.02 - 5.06	0.32 \pm 0.11	0.0000
HER	0.01 - 2.65	0.68 \pm 0.10	0.0158	0.04 - 21.17	1.47 \pm 0.45	0.3198
ILL	0.00 - 0.79	0.18 \pm 0.02	0.0000	0.01 - 2.84	0.35 \pm 0.06	0.0000
LOL	0.05 - 1.54	0.41 \pm 0.05	0.0000	0.00 - 0.80	0.17 \pm 0.02	0.0000
MAC	0.02 - 5.76	0.62 \pm 0.18	0.0000	0.00 - 3.43	0.38 \pm 0.11	0.0002
SH/DE Annual Ratio						
All	0.09 - 2.12	0.55 \pm 0.07	0.0000	0.32 - 18.91	4.10 \pm 0.63	0.0000
Neo	0.00 - 18.79	0.86 \pm 0.45	0.0000	0.00 - 7.36	0.75 \pm 0.24	0.0018
ImmM	0.00 - 0.82	0.15 \pm 0.03	0.0000	0.02 - 12.02	1.98 \pm 0.52	0.3836
MatM	0.05 - 2.09	0.58 \pm 0.08	0.0030	0.00 - 19.27	4.19 \pm 0.74	0.0015
ImmF	0.02 - 2.10	0.57 \pm 0.09	0.0011	0.18 - 18.95	3.48 \pm 0.74	0.0522
MatF	0.17 - 622.29	19.70 \pm 17.74	0.1501	0.38 - 168.81	27.28 \pm 6.51	0.0000
BF	0.01 - 52.49	1.81 \pm 1.24	0.0000	0.23 - 213.36	12.78 \pm 5.15	0.0001
HER	0.61 - 79.58	9.05 \pm 2.38	0.0000	0.01 - 7.95	0.79 \pm 0.20	0.0379
ILL	0.00 - 3.85	0.16 \pm 0.10	0.0000	0.03 - 5.47	0.29 \pm 0.11	0.0000
LOL	0.00 - 1.81	0.34 \pm 0.05	0.0000	0.53 - 29.01	4.32 \pm 0.66	0.0000
MAC	0.03 - 612.79	24.96 \pm 15.03	0.0170	0.08 - 704.02	39.87 \pm 19.06	0.0025

Table 4.3. Frequency analysis of the number of Julian days dominated by *CPUE* trends (N = night, D = day, SH = shallow, DE = deep) for spiny dogfish life-history stages and prey species in the Northeast (US) shelf large marine ecosystem during spring (1968 – 2009) and autumn (1963 – 2009). Stages and species as defined in Table 4.1. X^2 = Chi-square test statistic, p = probability. Significance (bolded) based on an $\alpha = 0.05$. Dominant = trends more frequent than expected. Notes: spiny dogfish not sexed consistently until 1980 and *Spring *Illlex* sp. analyzed using Fisher's exact test due to small sample size (Odds ratio given in X^2 column).

Stage/ Species	Observed				Expected				X^2	p	Dominant Trend(s)
	DDE	DSH	NDE	NSH	DDE	DSH	NDE	NSH			
<u>SPRING</u>											
All	308	180	161	88	184	184	184	184	136.4	0.000	DDE
Neo	129	73	62	20	71	71	71	71	85.2	0.000	DDE
ImmM	192	63	117	21	98	98	98	98	166.4	0.000	DDE, NDE
ImmF	218	123	126	54	130	130	130	130	104.3	0.000	DDE
MatM	191	148	100	50	122	122	122	122	90.8	0.000	DDE, DSH
MatF	158	170	103	80	128	128	128	128	43.8	0.000	DDE, DSH
BF	227	71	164	26	122	122	122	122	201.7	0.000	DDE, NDE
HER	143	286	71	139	160	160	160	160	153.5	0.000	DSH
ILL	257	16	81	2	89	89	89	89	0.4*	0.264*	-
LOL	300	86	121	13	130	130	130	130	343.1	0.000	DDE
MAC	160	155	54	56	106	106	106	106	99.0	0.000	DDE, DSH
<u>AUTUMN</u>											
All	183	233	87	201	176	176	176	176	67.3	0.000	DDE, DSH
Neo	54	21	25	14	29	29	29	29	32.6	0.000	DDE
ImmM	133	107	70	79	97	97	97	97	25.2	0.000	DDE, DSH
ImmF	130	156	62	118	117	117	117	117	40.4	0.000	DDE, DSH
MatM	59	138	29	115	85	85	85	85	88.2	0.000	DSH, NSH
MatF	46	126	15	102	72	72	72	72	107.1	0.000	DSH, NSH
BF	238	312	84	162	199	199	199	199	145.1	0.000	DDE, DSH
HER	142	89	124	51	102	102	102	102	47.8	0.000	DDE, NDE
ILL	460	187	136	52	209	209	209	209	447.7	0.000	DDE
LOL	231	424	11	108	194	194	194	194	491.7	0.000	DDE, DSH
MAC	113	157	42	50	91	91	91	91	98.6	0.000	DDE, DSH

Table 4.4. Seasonal and regional estimates (Est \pm SE, standard error) of diel catchability for spiny dogfish life-history stages and prey species in the Northeast (US) shelf large marine ecosystem during spring (1968 – 2009) and autumn (1963 – 2009) following Casey and Myers (1998). Stages and species as defined in Table 4.1. n = number of observations. Positive estimates (Est) indicate higher daytime catchabilities. Significance (bolded) based on an *a priori* $\alpha = 0.05$ through randomization. GM = Gulf of Maine, GB = Georges Bank, SNE = Southern New England, MA = Middle Atlantic Bight, All = All Regions combined.

Stage/Species	GM		GB		SNE		MA		All	
	n	Est	n	Est	n	Est	n	Est	n	Est
<u>SPRING</u>										
All	333	0.25 (0.12)	283	0.61 (0.14)	330	0.39 (0.13)	508	0.68 (0.09)	1454	0.52 (0.06)
Neo	9	0.20 (0.85)	28	3.37 (0.46)	147	0.54 (0.20)	142	-0.11 (0.18)	326	0.44 (0.13)
ImmM	121	0.47 (0.20)	122	0.94 (0.21)	167	0.11 (0.19)	148	-0.07 (0.18)	558	0.36 (0.10)
MatM	182	0.68 (0.17)	169	0.64 (0.18)	191	0.43 (0.17)	279	0.89 (0.12)	821	0.69 (0.08)
ImmF	211	0.39 (0.16)	182	0.53 (0.17)	219	0.18 (0.16)	361	0.61 (0.10)	973	0.41 (0.07)
MatF	215	0.45 (0.14)	171	0.11 (0.16)	192	1.12 (0.17)	366	0.42 (0.11)	944	0.60 (0.07)
BF	46	0.19 (0.28)	83	1.52 (0.28)	214	-0.09 (0.16)	393	0.10 (0.11)	736	0.07 (0.09)
HER	417	0.82 (0.12)	225	0.95 (0.15)	338	0.11 (0.12)	306	0.44 (0.12)	1286	0.37 (0.06)
ILL	26	1.05 (0.51)	109	2.53 (0.22)	90	2.64 (0.26)	166	2.37 (0.16)	391	2.42 (0.11)
LOL	53	1.28 (0.30)	146	1.20 (0.18)	237	1.53 (0.15)	479	1.11 (0.09)	915	1.18 (0.07)
MAC	69	-1.30 (0.36)	131	2.35 (0.21)	227	0.55 (0.16)	268	0.88 (0.14)	695	0.77 (0.09)
<u>AUTUMN</u>										
All	536	0.61 (0.10)	288	0.87 (0.14)	359	0.36 (0.12)	107	-0.22 (0.22)	1290	0.54 (0.06)
Neo	14	0.78 (0.47)	31	1.31 (0.41)	54	-0.27 (0.28)	28	0.77 (0.35)	127	0.38 (0.18)
ImmM	219	0.81 (0.16)	167	0.76 (0.19)	160	0.54 (0.20)	51	0.93 (0.32)	597	0.72 (0.10)
MatM	354	0.81 (0.12)	133	0.33 (0.21)	177	0.43 (0.18)	6	0.33 (1.15)	670	0.56 (0.09)
ImmF	349	0.39 (0.12)	193	0.64 (0.17)	228	0.57 (0.15)	59	0.84 (0.30)	829	0.54 (0.08)
MatF	282	0.30 (0.13)	93	0.72 (0.26)	172	-0.04 (0.18)	4	1.19 (1.05)	551	0.07 (0.10)
BF	250	2.40 (0.16)	289	0.85 (0.14)	525	1.61 (0.10)	707	1.71 (0.08)	1771	1.60 (0.05)
HER	435	0.45 (0.11)	192	1.56 (0.18)	94	0.16 (0.25)	9	1.44 (0.75)	730	0.93 (0.09)
ILL	524	1.89 (0.10)	363	1.32 (0.12)	341	1.43 (0.12)	329	0.52 (0.11)	1557	1.24 (0.06)
LOL	187	3.13 (0.17)	267	1.43 (0.14)	533	2.37 (0.09)	767	1.51 (0.07)	1754	1.90 (0.05)
MAC	207	1.78 (0.17)	172	1.95 (0.19)	134	4.67 (10)	10	5.69 (2.46)	523	2.66 (0.11)

Table 4.5. GAM results describing the probability of day-time catches for spiny dogfish (SD) and prey species during spring (1968 – 2009). Species as defined in Table 4.1. All = All Regions combined, GM = Gulf of Maine, GB = Georges Bank, SNE = Southern New England, MA = Middle Atlantic Bight. n = number of observations, Dev = percent deviance explained, Int (SE) = intercept reflecting the day-night catchability estimate with standard error (significance [bolded] based on an *a priori* $\alpha = 0.05$); positive estimate indicates higher daytime catchabilities. Trends include: ↓ = decreasing, ↑ = increasing, symbols (U, ∩, U∩, ∩U, w, m) reflect nonlinear significant trends with the number in parentheses indicative of the peak value. NS = not significant, - = not applicable.

Species: Region	n	Dev (%)	Int (SE)	Depth	Trends BT	Julian
SD: All	1454	1.1	0.95 (0.06)	NS	↓	-
GM	333	34.0	1.45 (0.13)	∩(250m)	U(4°C)	w(135d)
GB	283	12.8	0.82 (0.14)	↓	↑	NS
SNE	330	1.9	0.97 (0.12)	-	NS	-
MA	508	7.2	0.65 (0.12)	∩(60m)	∩U(6°C)	NS
BF: All	736	23.2	1.26 (0.15)	U∩(10m)	U(5°C)	U(118d)
GM	46	5.9	1.17 (0.34)	-	NS	-
GB	83	8.2	2.24 (0.23)	↓	-	-
SNE	214	26.5	1.17 (0.27)	↓	NS	∩U(72d)
MA	393	39.5	0.73 (0.17)	U(10m)	∩U(7°C)	U(60d)
HER: All	1286	9.5	0.96 (0.07)	↓	U∩(2°C)	↑
GM	417	20.1	0.96 (0.15)	NS	U(3°C)	m(102d)
GB	225	39.0	2.04 (0.19)	U(45m)	↓	U∩(110d)
SNE	338	14.0	0.91 (0.15)	↓	NS	w(110d)
MA	306	12.6	0.35 (0.20)	U∩(10m)	m(8.5°C)	-
ILL: All	391	10.0	2.14 (0.10)	-	U(4°C)	↓
GM	26	40.3	3.26 (0.61)	-	-	↓
GB	109	2.2	2.13 (0.19)	-	-	NS
SNE	90	33.1	2.25 (0.25)	↑	U(13°C)	m(77d)
MA	166	20.1	2.20 (0.16)	-	U(14°C)	U(60d)
LOL: All	915	19.1	2.01 (0.13)	∩U(300m)	U(4°C)	↑
GM	53	35.2	2.25 (0.37)	↑	∩(5.7°C)	-
GB	146	26.7	2.39 (0.35)	NS	∩(9.5°C)	NS
SNE	237	15.7	2.54 (0.22)	↓	NS	-
MA	479	21.8	1.51 (0.14)	w(80m)	U(5°C)	↑
MAC: All	695	24.1	1.98 (0.14)	U(20m)	w(4°C)	U∩(105d)
GM	69	83.2	0.92 (0.65)	U∩(90m)	↑	↓
GB	131	62.9	3.76 (0.40)	U∩(45m)	NS	↑
SNE	227	31.8	2.06 (0.29)	U∩(25m)	w(4°C)	U∩(95d)
MA	268	36.5	1.92 (0.31)	U∩(15m)	U∩(8°C)	w(65d)

Table 4.6. GAM results describing the probability of day-time catches for spiny dogfish (SD) and prey species during autumn (1963 – 2009). Species as defined in Table 4.1. All = All Regions combined, GM = Gulf of Maine, GB = Georges Bank, SNE = Southern New England, MA = Middle Atlantic Bight. *n* = number of observations, Dev = percent deviance explained, Int (SE) = intercept reflecting the day-night catchability estimate with standard error (significance [bolded] based on an *a priori* $\alpha = 0.05$); positive estimate indicates higher daytime catchabilities. Trends include: ↓ = decreasing, ↑ = increasing, symbols (U, ∩, U∩, ∩U, w, m) reflect nonlinear significant trends with the number in parentheses indicative of the peak value. NS = not significant, - = not applicable.

Species: Region	<i>n</i>	Dev (%)	Int (SE)	Depth	Trends BT	Julian
SD: All	1290	5.6	0.83 (0.08)	m(180m)	U(17°C)	∩(290d)
GM	536	14.9	1.01 (0.10)	∩(160m)	↓	∩U(295d)
GB	288	2.0	0.96 (0.12)	-	↑	-
SNE	359	15.5	0.82 (0.15)	∩(80m)	U(8°C)	U∩(255d)
MA	107	67.0	-0.13 (0.23)	U∩(80m)	U∩ (8°C)	-
BF: All	1713	7.0	2.00 (0.08)	U(280m)	↓	∩(270d)
GM	243	50.0	2.07 (0.26)	U∩(50m)	∩(8.5°C)	m(290d)
GB	280	17.5	1.62 (0.52)	NS	w(7°C)	U∩(275d)
SNE	510	5.1	1.92 (0.09)	↓	↓	-
MA	680	14.4	1.87 (0.11)	∩U(150m)	U∩(9°C)	-
HER: All	714	24.1	1.00 (0.11)	↓	U(16°C)	U∩(310d)
GM	427	22.1	0.48 (0.10)	↓	U∩(5°C)	↑
GB	186	45.4	1.49 (0.28)	-	U(6°C)	U(275d)
SNE	92	48.4	0.58 (0.40)	∩(60m)	U(13°C)	↓
MA	-	-	-	-	-	-
ILL: All	1522	14.6	1.55 (0.05)	m(175m)	U(18°C)	∩(290d)
GM	516	21.6	2.04 (0.08)	∩(175m)	↓	∩U(295d)
GB	350	6.43	1.56 (0.09)	↑	↑	-
SNE	336	30.0	1.36 (0.10)	∩(80m)	U(8°C)	U∩(255d)
MA	320	14.2	0.58 (0.13)	U∩(80m)	-	w(250d)
LOL: All	1689	22.4	2.55 (0.07)	↑	↓	↓
GM	181	30.7	3.51 (0.35)	m(75m)	NS	↓
GB	258	12.2	2.78 (0.36)	↑	-	w(308d)
SNE	518	35.1	3.32 (0.12)	↑	↓	↓
MA	732	19.0	1.74 (0.08)	∩(50m)	↓	U∩(250d)
MAC: All	512	28.7	2.39 (0.14)	↓	∩(9°C)	↓
GM	204	35.6	1.56 (0.31)	m(70m)	∩(8.5°C)	U∩(290d)
GB	168	30.2	1.54 (0.44)	U(40m)	↓	↓
SNE	130	44.2	4.85 (0.33)	-	↓	U∩(260d)
MA	-	-	-	-	-	-

Figure 4.1. Map of the Northeast (US) shelf large marine ecosystem (NES LME) where the NEFSC annual bottom trawl survey is conducted during autumn and spring. The four regions are defined as follows: Gulf of Maine (GM), Georges Bank (GB), Southern New England (SNE), and the Middle Atlantic Bight (MA). Solid gray indicates land masses. Lines reflect depth contours in meters.

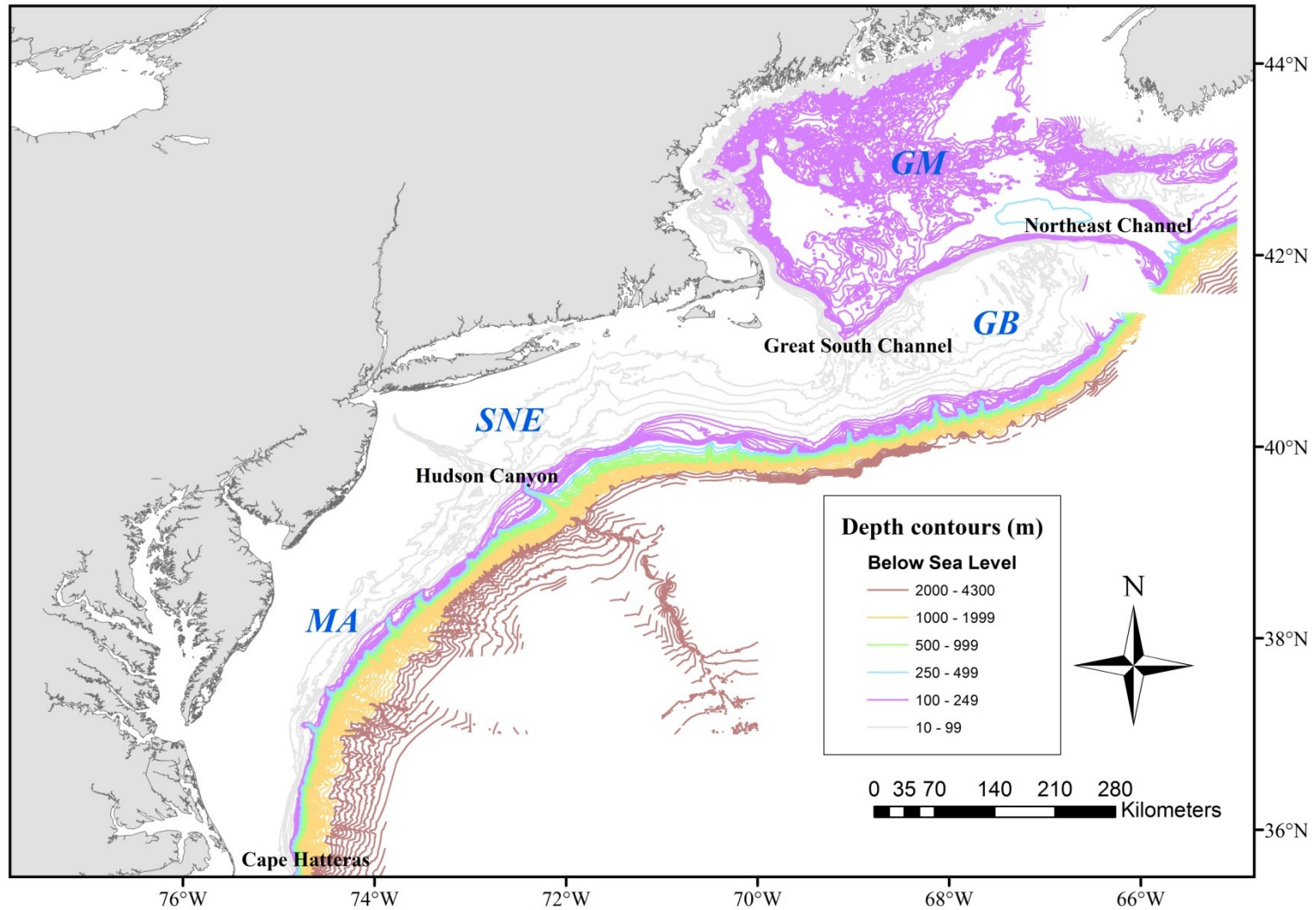


Figure 4.2. Illustration of the concept behind the logistic model used in Casey and Myers (1998) where the y-intercept [i.e., $\log(S_d)$] serves as an estimate of the relative diel catchability. T_{ysn} = number of night-time (zenith $\geq 108^\circ$) tows, T_{ysd} = number of day-time (zenith $< 108^\circ$) tows. The dotted line displays $\log(S_d) = 0$ and reflects no difference between day and night catchability. The gray line displays $\log(S_d) > 0$ and represents higher catchability during the day. The black line displays $\log(S_d) < 0$ and represents higher catchability during the night.

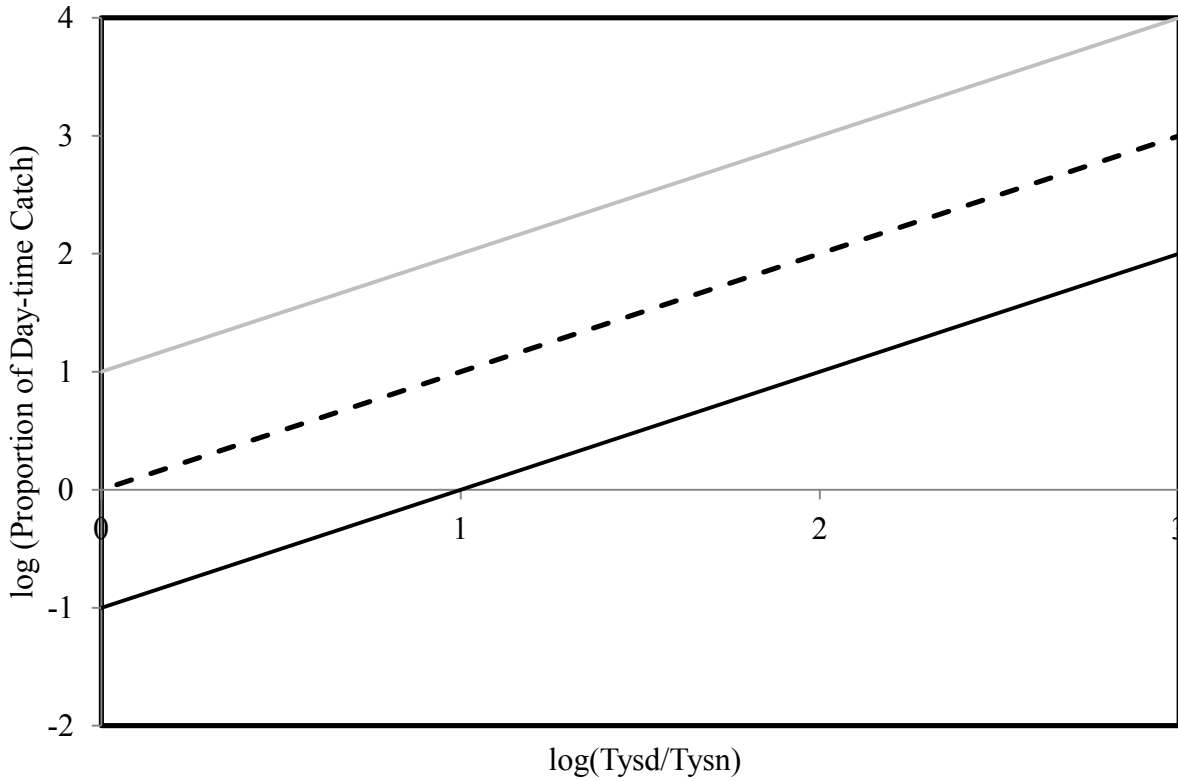


Figure 4.3. Locations of aggregations for spiny dogfish life-history stages during spring (1968 – 2009) (light hue) and autumn (1963 – 2009) (dark hue) in the Northeast (US) shelf large marine ecosystem during the day (orange) and night (black). Aggregations are defined as the top 5th percentile of the catch distribution. Note: spiny dogfish not sexed consistently until 1980.

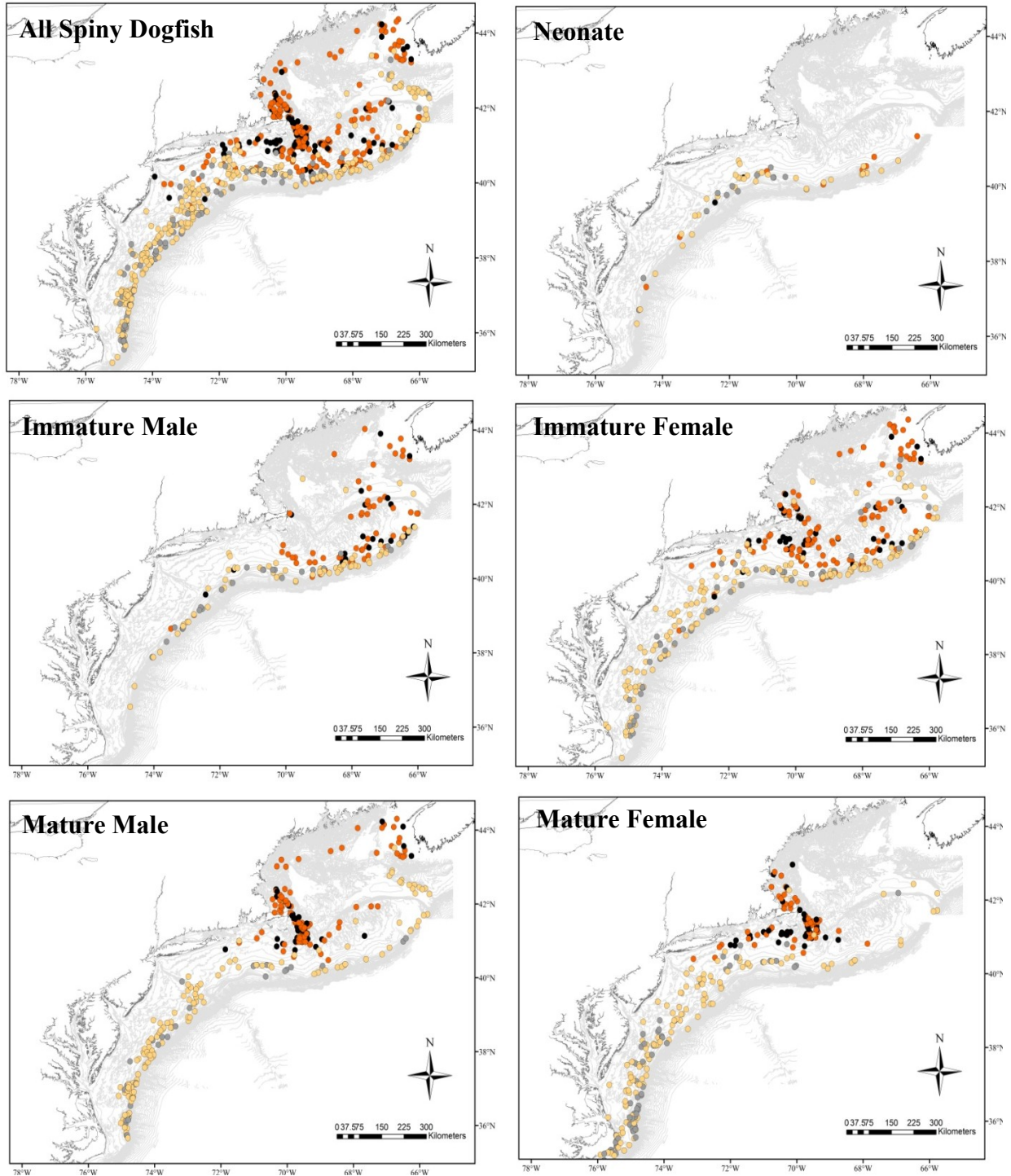


Figure 4.4. Locations of aggregations for prey species during spring (1968 – 2009) (light hue) and autumn (1963 – 2009) (dark hue) in the Northeast (US) shelf large marine ecosystem during the day (orange) and night (black). Aggregations are defined as the top 5th percentile of the catch distribution.

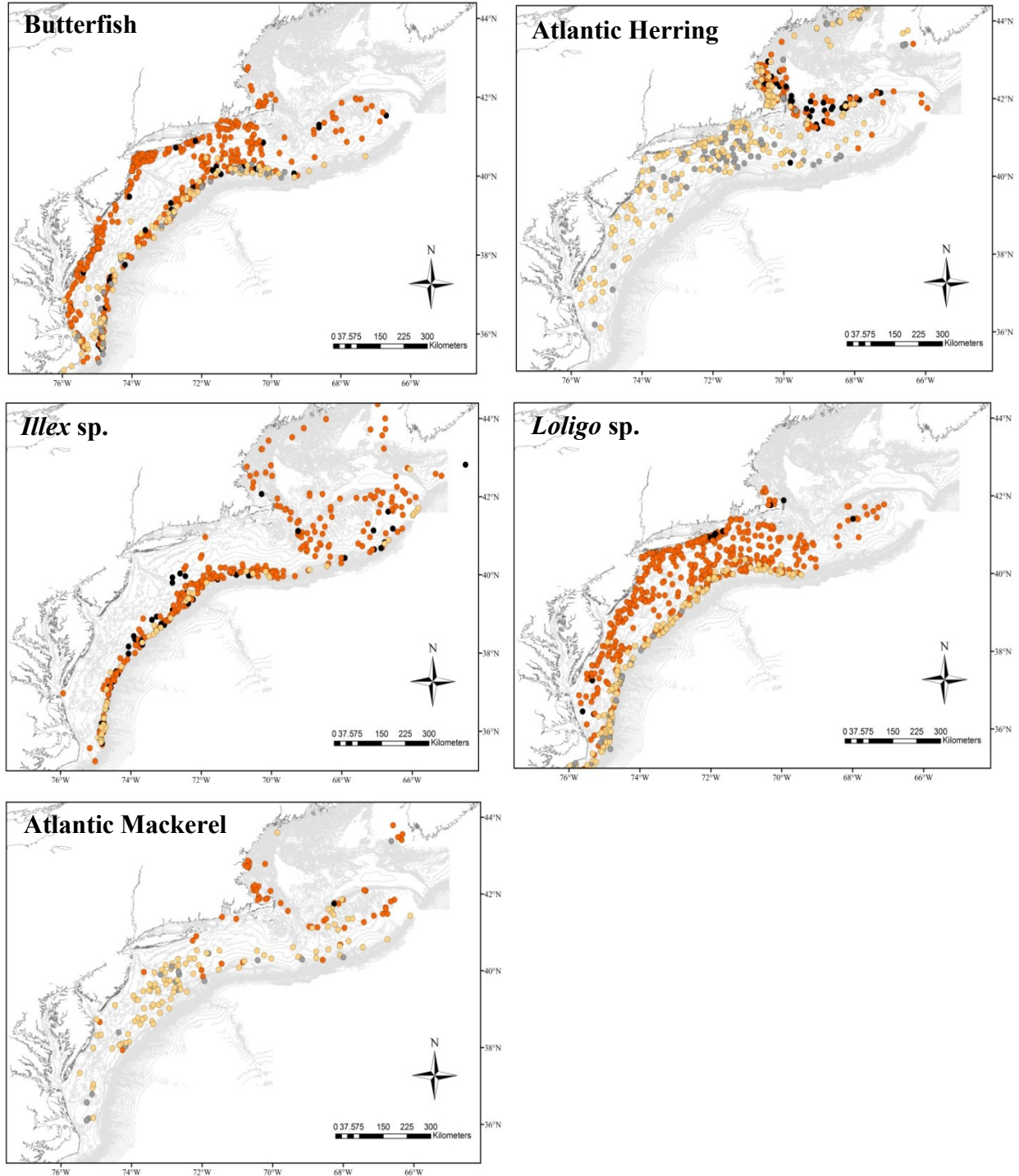


Figure 4.5. Breakpoint analysis of temporal CPUE for spiny dogfish life-history stages and prey species during spring (1968 – 2009) in the Northeast (US) shelf large marine ecosystem. Dots reflect mean hourly CPUE by time of day (0 = 12AM, 23 = 11PM), solid lines reflects fitted segmented regression lines, and dashed lines indicate significant breakpoints. Notes: spiny dogfish not sexed consistently until 1980 and scales differ among y-axes.

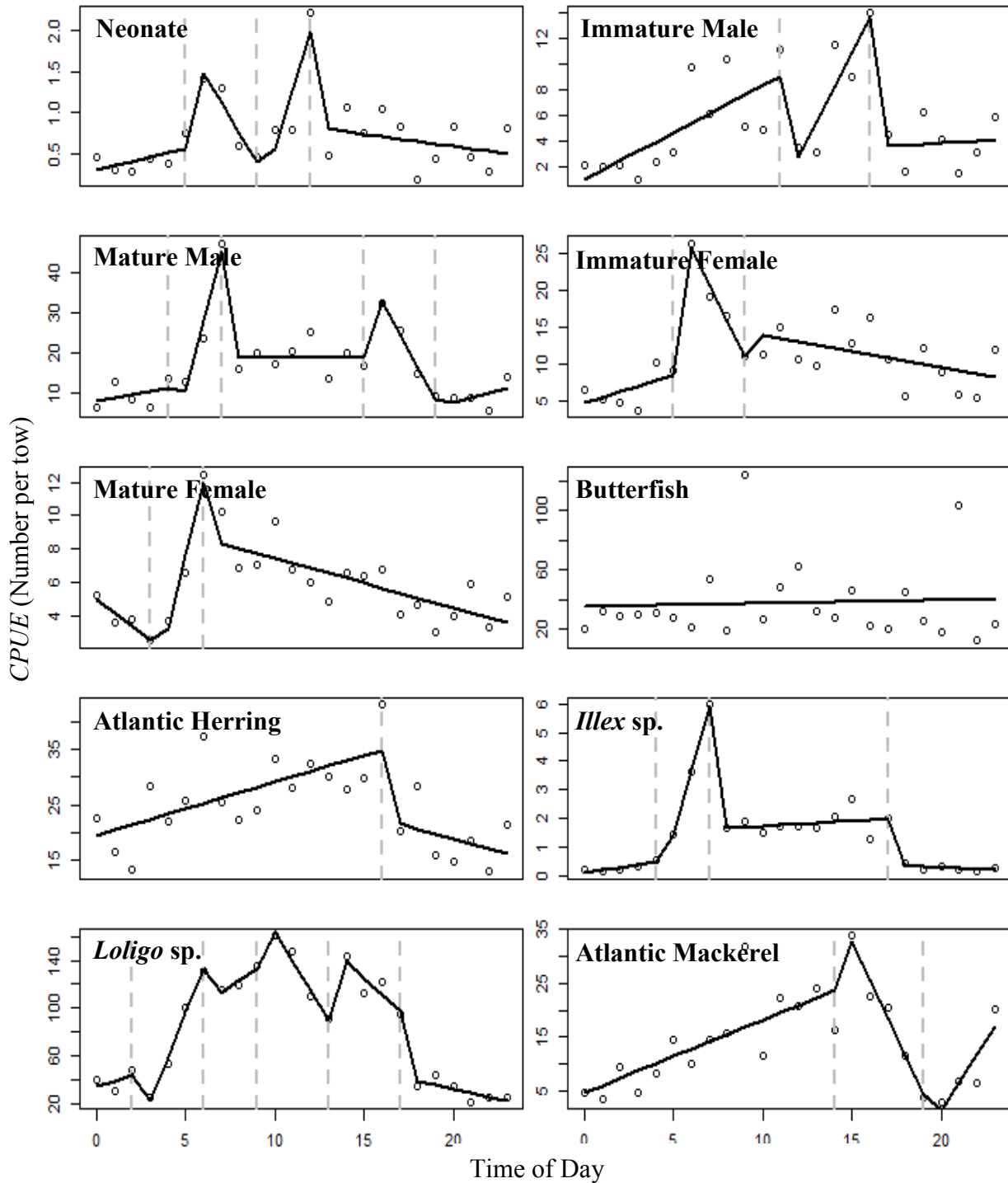


Figure 4.6. Breakpoint analysis of temporal *CPUE* for spiny dogfish life-history stages and prey species during autumn (1963 – 2009) in the Northeast (US) shelf large marine ecosystem. Dots reflect mean hourly *CPUE* by time of day (0 = 12AM, 23 = 11PM), solid lines reflects fitted segmented regression lines, and dashed lines indicate significant breakpoints. Notes: spiny dogfish not sexed consistently until 1980 and scales differ among y-axes.

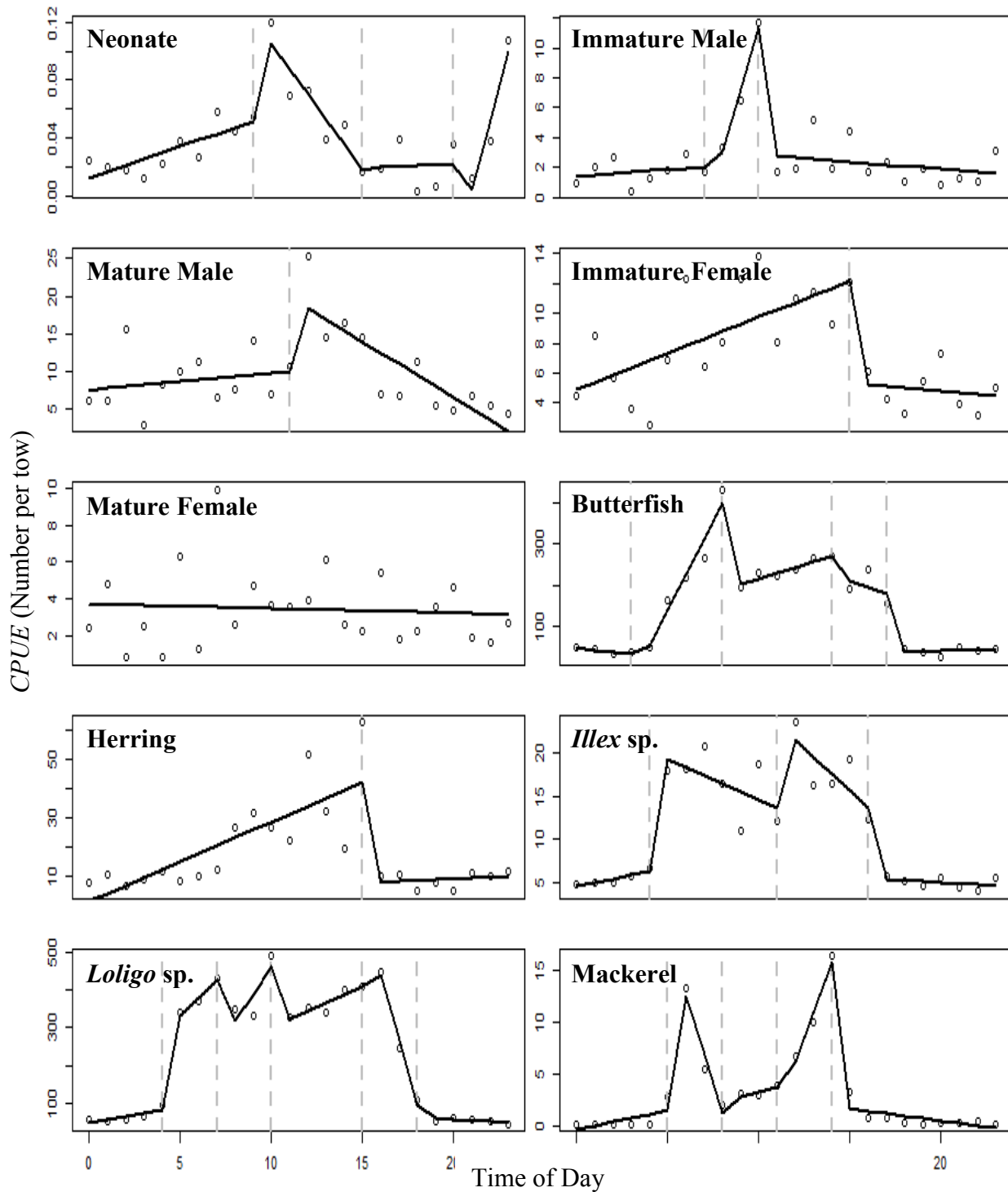


Figure 4.7. Probability of day-time capture for spiny dogfish life-history stages and prey species during (A) spring (1968 – 2009) and (B) autumn (1963 – 2009) in the Northeast (US) shelf large marine ecosystem. Stages and species as defined in Table 4.1. All = All Regions combined, GM = Gulf of Maine, GB = Georges Bank, SNE = Southern New England, MA = Middle Atlantic Bight. Dashed line reflects 50% where there would be no difference between day and night. Only results from significant GLMs are shown. Note: spiny dogfish not sexed consistently until 1980.

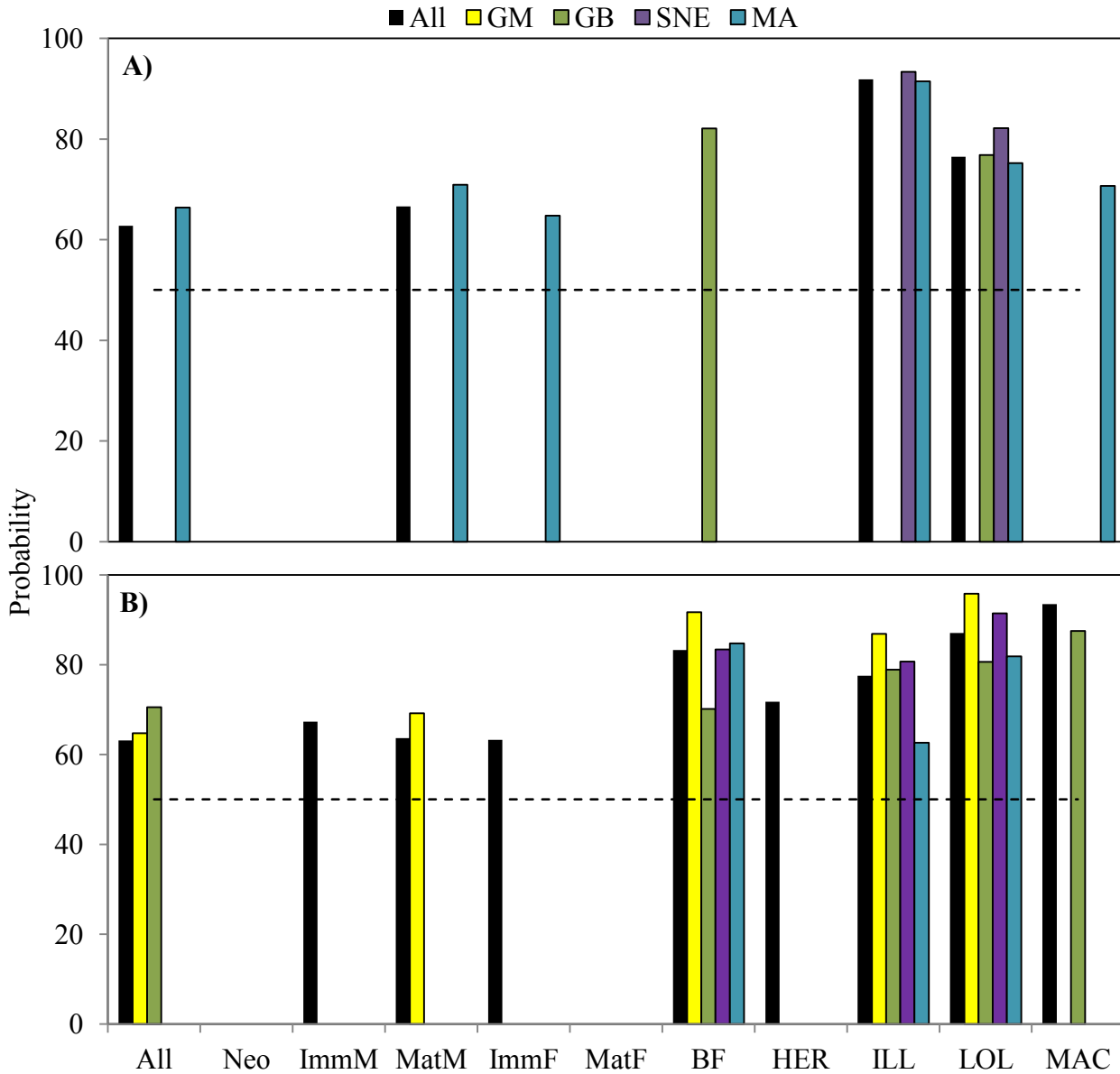


Figure 4.8. Unadjusted *CPUE* (solid) and day-night adjusted *CPUE* (dotted) when appropriate for All Regions (Gulf of Maine, Georges Bank, Southern New England, Middle Atlantic Bight) derived from the NEFSC bottom trawl survey during autumn (1963 – 2009). Notes: spiny dogfish not sexed consistently until 1980 and y-axes differ between panels.

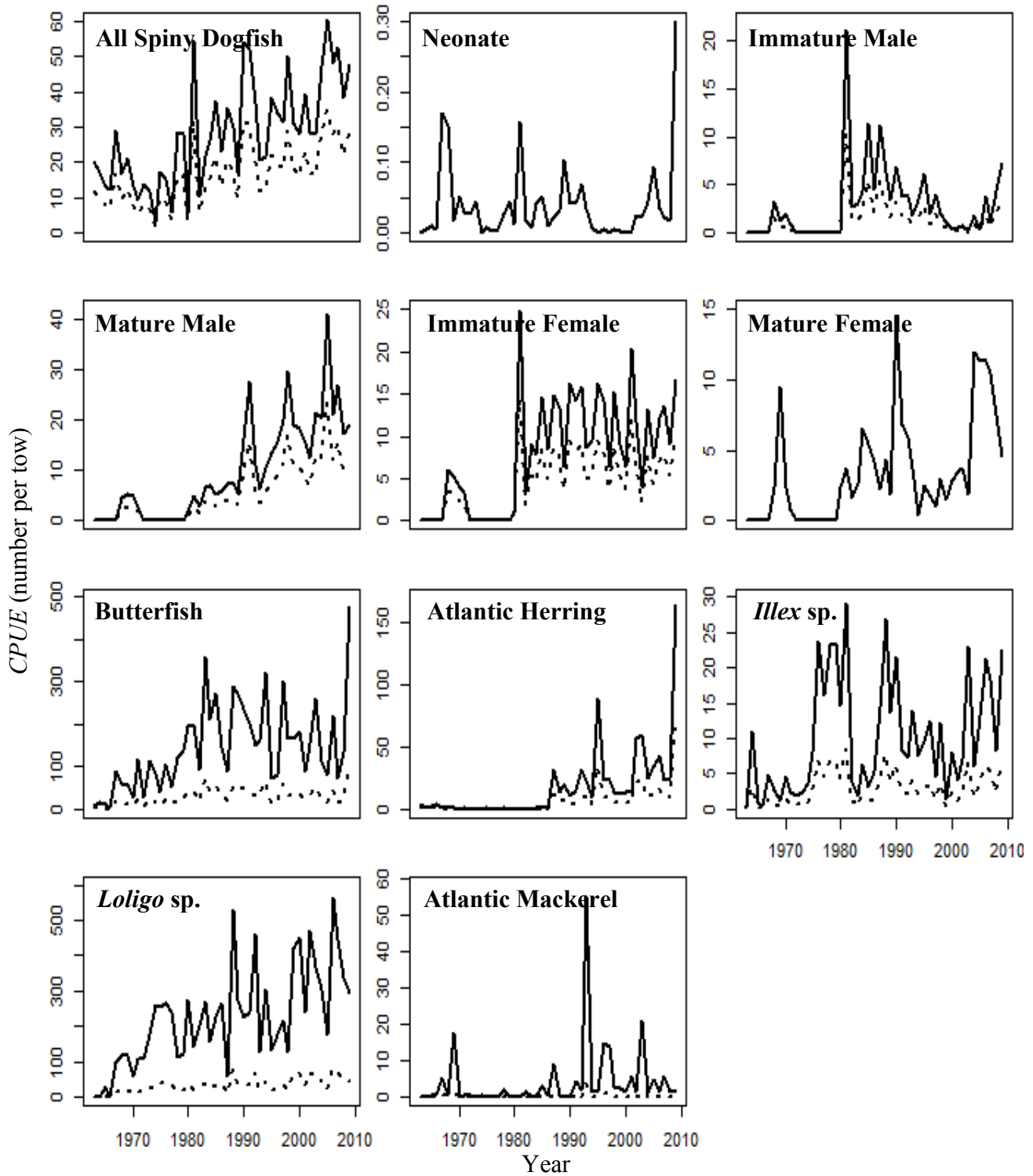


Figure 4.9. Partial GAM plots identifying the additive effect of each variable on the probability of day-time catch for spiny dogfish and prey species in All Regions combined during autumn (1963 – 2009). The y-axis represents the degree of smoothing (variable, estimated degrees of freedom) with its range 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 gray region reflects the 95% confidence intervals around the response curves. Absence of term within the optimum model represented by empty box.

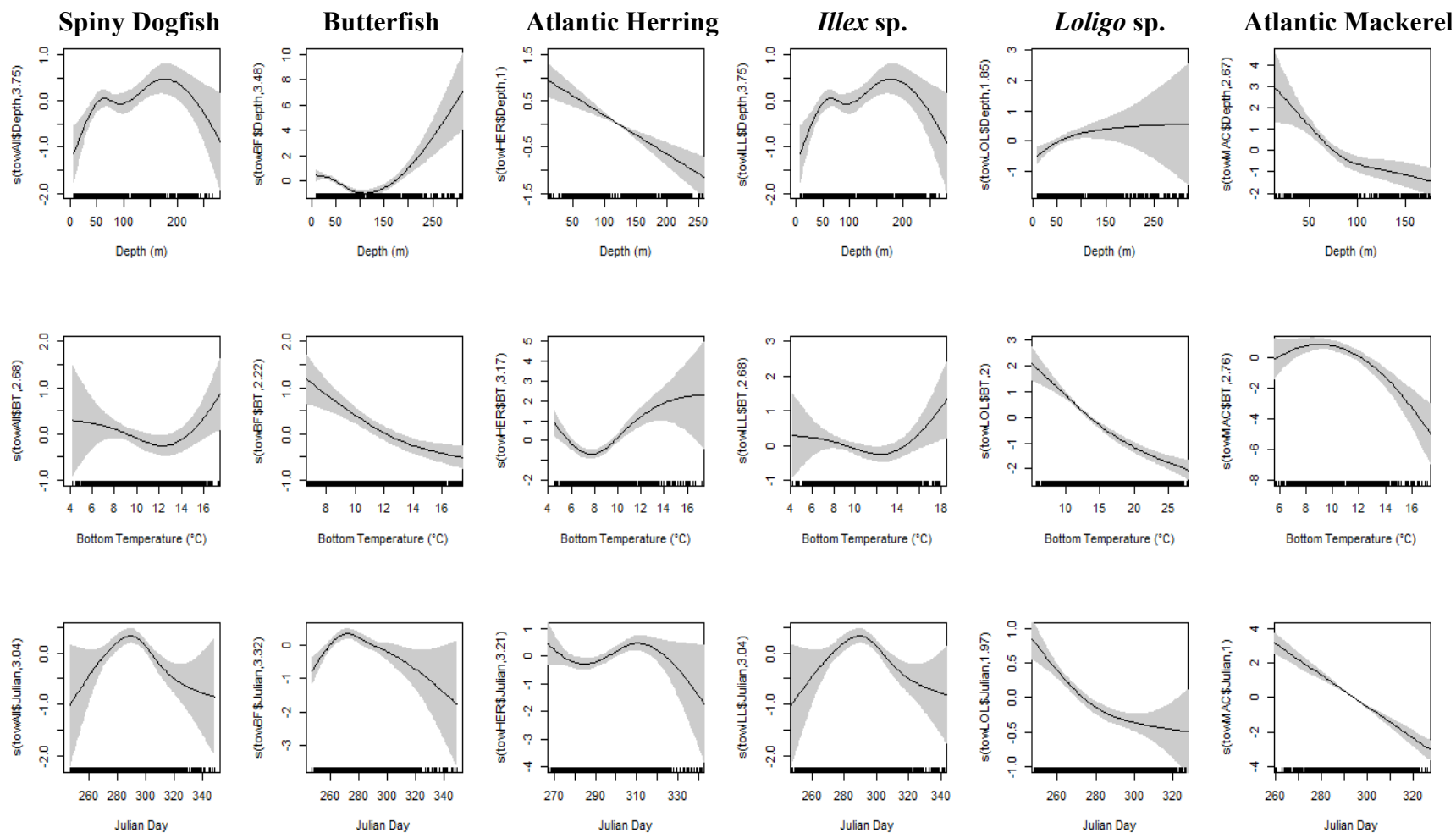
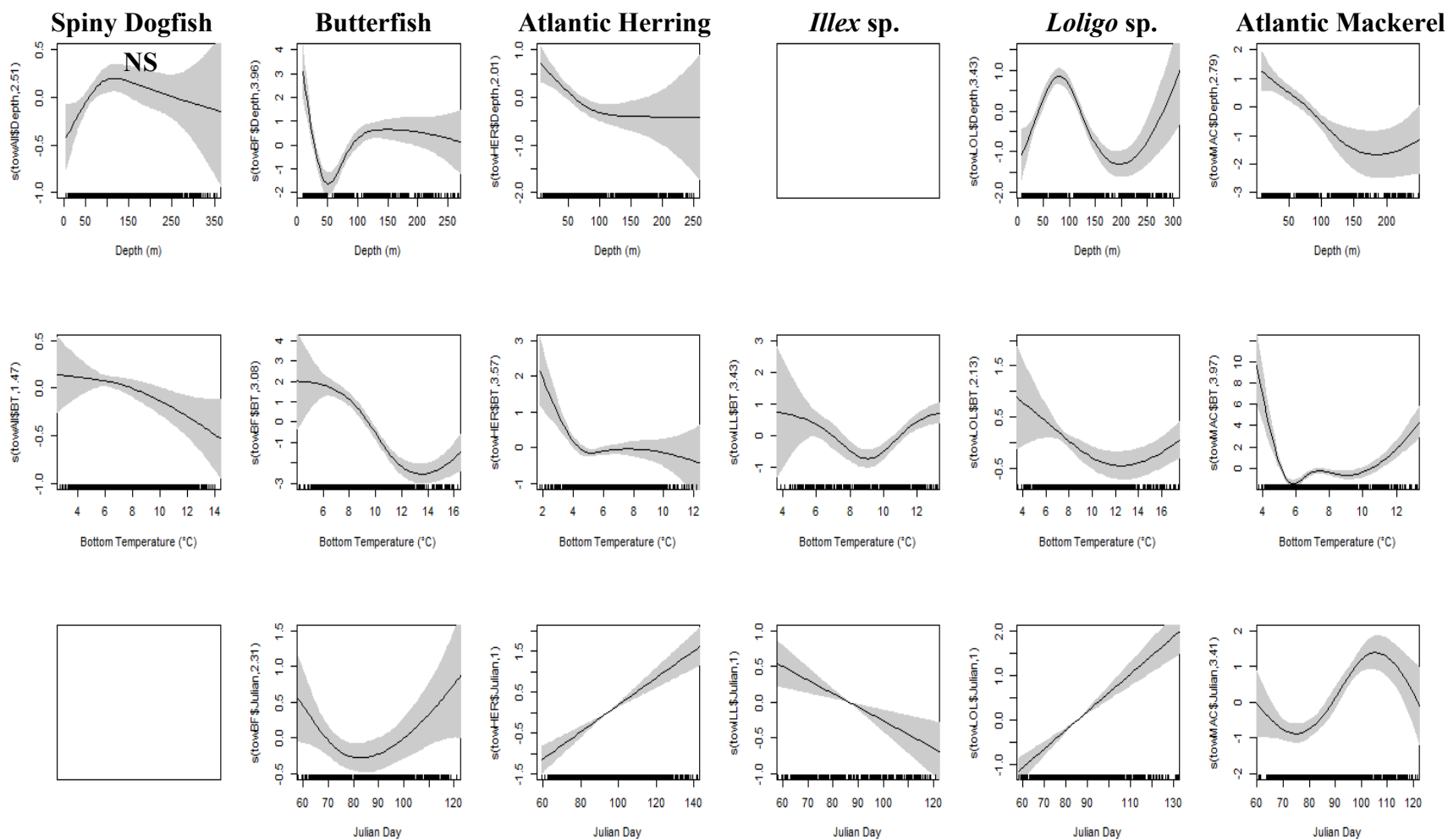


Figure 4.10. Partial GAM plots identifying the additive effect of each variable on the probability of day-time catch for spiny dogfish and prey species in All Regions combined during spring (1968 – 2009). The y-axis represents the degree of smoothing (variable, estimated degrees of freedom) with its 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 gray region reflects the 95% confidence intervals around the response curves. Absence of term within the optimum model represented by empty box. NS = not significant.



Chapter 5:
**SPATIO-TEMPORAL INTERACTIONS BETWEEN SPINY DOGFISH AND
COMMERCIAL FISHERS IN THE NORTHEAST (US) SHELF LARGE MARINE
ECOSYSTEM**

Introduction

A reduction in both landings and abundance of traditionally important commercial species (e.g., Atlantic cod *Gadus morhua*) within the Northeast (US) shelf large marine ecosystem (NES LME) has increased both the fishery and ecological importance of spiny dogfish (*Squalus acanthias*) (Fogarty & Murawski 1998, Rago et al. 1998). Ecologically, spiny dogfish is an opportunistic predator and has been associated with the suppressed recovery of valuable groundfish (Fogarty & Murawski 1998, Link et al. 2002). Spiny dogfish may also serve as an essential scavenger within the ecosystem (Beamish et al. 2009). Management of spiny dogfish requires balancing fisheries productivity with protecting both the resource and the ecosystem (Branch et al. 2006). However, the species' slow life history and complex migratory behavior have contributed to a mismatch in survey derived abundance estimates and observations by the fishing industry (NEFSC 2006, Rago & Sosebee 2009). Understanding commercial fisher behavior through effort delineation in comparison to spatial patterns observed in scientific surveys is critical to the development of robust abundance estimation and effective management objectives (Salas & Gaertner 2004).

Fishery-dependent surveys offer an inexpensive opportunity to obtain highly detailed data on commercially exploited species over large temporal and spatial scales (Bertrand et al. 2004,

Hilborn 2007). An important metric derived from such surveys is the catch per unit of effort (*CPUE*):

$$CPUE \left(\frac{C}{E} \right) = A \times q$$

where C = catch, E = fishing effort (e.g., number of hours fished), A = stock abundance, and q = catchability coefficient. *CPUE* is assumed proportional to A (Hilborn & Walters 1992, Rose & Kulka 1999, Salthaug & Aanes 2003) and E is assumed to be randomly distributed over the fishing grounds (Paloheimo & Dickie 1964, Ellis & Wang 2007). In nature, these assumptions rarely hold as nonlinear relationships often arise between *CPUE* and A (Arreguín-Sánchez 1996, Harley & Myers 2001, Salthaug & Aanes 2003) and fishers frequently target fish aggregations (i.e., E non-random) (Paloheimo & Dickie 1964, Salthaug & Aanes 2003, Ellis & Wang 2007).

Nonlinearity between *CPUE* and A is often caused by variability in q , or catchability. Defined as the proportion of the population biomass caught by one unit of effort (Hilborn & Walters 1992), catchability incorporates both the proportion of the stock available (i.e., availability) and the proportion actually caught or vulnerable to the gear (i.e., efficiency) (Michalsen et al. 1996, Francis et al. 2003, Trenkel et al. 2004). Catchability is parsimoniously assumed constant in both space and time (Godø 1994, Pennington & Godø 1995, Aglen et al. 1999, Salthaug & Aanes 2003) but can vary with the environment (Swain et al. 2000), fish behavior (Frisk et al. 2011), and fleet dynamics (Bertrand et al. 2004) among others. As a result, the reliability of stock assessment can be diminished by discounting catchability and its various influences and can ultimately misrepresent ecosystem dynamics (Francis & Williams 1995).

Changes in the spatial distribution of a species within fishing grounds can affect their catchability, either by increasing or decreasing their availability or vulnerability to the fishery

(Fréon et al. 1993, Pennington & Godø 1995, Smith & Page 1996, Godø et al. 1999). Fishing within high density areas can result in artificially high biomass estimates due to hyperaggregation, or the aggregation of fish at low abundances (Rose & Kulka 1999). The risk of hyperaggregation relates to a species' temporal and spatial behavior and varies among species (Frisk et al. 2011). Hyperstable relationships can occur if *CPUE* remains high while *A* declines (Hilborn & Walters 1992, Rose & Kulka 1999). Atlantic cod was a prime example of this concept as biased *CPUE* estimates misrepresented stock status and led to stock collapse off eastern Canada (Hutchings 1996, Rose & Kulka 1999, Salthaug & Aanes 2003). In addition, a southward shift in distribution during the 1990s increased their vulnerability to domestic and foreign fishing fleets outside the Exclusive Economic Zone (EEZ), thereby altering their catchability (Rose et al. 1994, Rose & Kulka 1999).

For spiny dogfish, high potential for non-linearity of *q* combined with their demographics identified this elasmobranch as a species of greatest concern (Frisk et al. 2011). In addition, large-scale seasonal movements and distributional changes both spatially and temporally likely modify their availability to commercial fishers. To explore how such changes have impacted commercial fisheries in the NES LME, and to elucidate mechanisms behind incompatible stock estimates, we investigated their spatio-temporal interactions between 1989 and 2009 using data collected from the large-scale Northeast Fisheries Science Center (NEFSC) fisheries observer program. Distributions of commercial fisher effort and catch of spiny dogfish were analyzed for to the two largest commercial fisheries: sink gill net (SGN) and otter trawl (OT). Their spatio-temporal overlap with spiny dogfish distribution derived from NEFSC trawl surveys was quantified to assess changes in availability using both direct (i.e., rasterized station data) and geostatistical (i.e., interpolated) techniques.

Methods

Data Sources

Fisheries-dependent

Spiny dogfish have experienced varying levels of exploitation since the consistent documentation of commercial landings in the 1960s. Substantial aggregated landings (estimates >20,000 metric tons, *mt*) occurred in the 1960-70s by foreign fishing fleets before the establishment of the EEZ (ASMFC 2002, NEFSC 2006). Domestically, landings remained low (<1,000 *mt*) until commercially valuable groundfish stocks declined in the 1980s, leading to a directed spiny dogfish fishery in 1990 (Rago et al. 1998). During the 1990s, domestic landings were roughly 6 times higher than the previous decade and peaked in 1996 (27,000 *mt*) (Camhi 1998, ASMFC 2002). In 1998, the National Marine Fisheries Service (NMFS) declared the stock overfished as a result of rapid expansion of the fishery and overharvest of large fecund females (ASMFC 2002). Regulatory measures including trip quotas and strict regulations were implemented in the early 2000s to reduce commercial landings, harvest, and possession of spiny dogfish (ASMFC 2002). With the exception of the targeted fishery in the 1990s, spiny dogfish were indirectly caught as bycatch in groundfish and other fisheries (Rago & Sosebee 2009).

For the purpose of this study, data collected by the large-scale NEFSC fisheries observer program (Anderson 1992) were assumed representative of commercial fisher distribution and behavior between 1989 and 2009. At-sea sampling provided catch (total, kept, discarded), effort, location, and associated biological and fishery data (e.g., gear) on a tow by tow basis with a high spatial resolution (Anderson 1992, Murawski et al. 1995).

Fisheries-independent

Spiny dogfish distribution and abundance was derived from annual NEFSC bottom trawl surveys conducted during autumn and spring. These stratified random sampling surveys sample the NES LME from Cape Hatteras, NC north to the Gulf of Maine (GM). Offshore and inshore strata are depicted in Figures 1 and 2 of NEFSC (2006). Four regions were surveyed including the GM, Georges Bank (GB), Southern New England (SNE), and the Middle Atlantic Bight (MA). The autumn survey has been conducted in offshore areas since 1963 and inshore strata were added in 1972. The spring survey began sampling offshore areas in 1968 and inshore strata were added in 1973. Survey strata comprise about 64,000 nm². The number of stations sampled per stratum was proportional to its area but inshore strata were sampled at approximately three times the sampling rate of offshore strata. Approximately 300 – 400 stations were visited during autumn (mean ± SE = 344 ± 13 stations) and spring (mean ± SE = 346 ± 8 stations). Detailed descriptions of the survey design and changes in survey protocols over time can be found in Azarovitz (1981) and Azarovitz et al. (1997). Correction factors based on field experiments were applied for changes in vessels, gear and doors when necessary. The introduction of the *Henry B. Bigelow* in 2009 brought about changes to the trawling gear and survey protocol (Brown et al. 2007). In addition, a calibration study compared the catchability of the old vessel, the *Albatross IV*, with the new vessel (Miller et al. 2010).

Data

CPUE was utilized as an index of relative spiny dogfish abundance for both survey and fishery data. For the survey, *CPUE* was defined as the number of spiny dogfish caught per tow. *CPUE* for each fishery was defined as the number of spiny dogfish caught per hour fished. It is

important to note that survey and fishery *CPUE* are not comparable due to differences in effort allocation, gear configuration, catchability, etc. For the purpose of this study, we were solely interested in where spiny dogfish were encountered (i.e., $CPUE > 0$). No attempts were made to standardize *CPUE* between gear types or compare magnitudes directly. Spatial locations were provided by latitude and longitude measurements.

NEFSC trawl surveys typically occur over an eight week period and proceed from Cape Hatteras, NC, north to the GM (Rago 2005). The survey samples from September through November during autumn and from March through May during spring. To enable temporal comparisons of spiny dogfish occurrence in the survey and each fishery, only fishery-dependent data collected during these time periods were utilized.

Spatial Distribution

Spatial Autocorrelation

To determine the magnitude and range of spatial correlation, or the dependency among spiny dogfish *CPUE* observations in geographic space, spatial autocorrelation was investigated for each fishery and the survey using Moran's *I* statistic (Moran 1948, Goodchild 1986). This method assumed spiny dogfish were captured at random. Moran's *I* detects the degree of clustering for points within a given distance (d) using the following equation:

$$(5.1) \quad I_d = \frac{n \sum_{ij} w_{ij} (x_i - \bar{x})(x_j - \bar{x})}{(\sum w_{ij}) \sum_{i=1}^n (x_i - \bar{x})^2}$$

where n = number of observations, x_i and x_j = attribute values (*CPUE*), \bar{x} = mean *CPUE*, and w_{ij} = weighting function ($w_{ij} = 1$ if points are within d , otherwise 0) (Nielsen et al. 2007), and $\sum_{ij} =$

sum over i and j with $i \neq j$. Moran's I values range from -1 (dispersed) to +1 (clustered) with values of 0 reflecting a random spatial pattern. Moran's I was calculated in R (R Core Development 2010) using the 'spdep' package and a spatial weights matrix based upon the 5-nearest neighbors (Bivand 2012).

Center of Abundance

To provide insight into annual distributional shifts of spiny dogfish derived from each fishery and the survey, annual centers of spiny dogfish abundance were estimated (Marino et al. 2009). This parameter was calculated with the following equation:

$$(5.2) \quad X_j = \frac{\sum_{i=1}^n b_i X_{ij}}{\sum b_i}$$

where X = parameter of interest (latitude, longitude), j = year, and b_i = log-transformed abundance ($\log_e (CPUE + 0.05)$) for each station i (Nye et al. 2009). Annual centers of spiny dogfish abundance were mapped in ArcGIS (v10. ESRI Corp) for visual examination and standard deviation, covariance, and correlation coefficients were calculated (Marino et al. 2009).

Centers of spiny dogfish abundance between the survey and each fishery were compared to determine whether their spatial locations differed for each season. Despite transformation efforts, non-normality and highly correlated dependent variables prevented parametric techniques (Quinn & Keough 2002). Instead, a one-way permutational multivariate analysis of variance (formerly NP-MANOVA) for a balanced ANOVA design based on Bray Curtis distances was used to test for differences in location using PERMANOVA v.1.6 (Anderson 2001). This method assumed that observation units were changeable under a true null hypothesis

and tested for the multivariate null hypothesis of no relationship between groups (i.e., modes of fishing: survey trawl, fisher OT, fisher SGN) (Anderson 2001). The test statistic was a multivariate analogue to Fisher's F -ratio and was calculated directly from a dissimilarity matrix with the p -value obtained by permutation and Monte Carlo randomization (Anderson 2001).

For comparisons between the survey and each fishery, the mode of fishing was treated as a fixed factor with the latitude and longitude identifying centers of spiny dogfish abundance as the dependent variables and annual values as observations. For spring, 1989 was excluded from this analysis to keep the sample size consistent among modes of fishing. Significance was determined by 9,999 permutations of the raw data and an *a priori* significance level of $\alpha = 0.05$. Given a significant result, *a posteriori* pairwise-comparisons were conducted using 9,999 permutations to determine which modes of fishing differed significantly (Anderson 2001). All *a posteriori* significance levels ($\alpha = 0.05$) were adjusted using the Bonferroni correction method ($\alpha_{\text{adj}} = 0.0167$) to reduce the potential for type I errors during multiple comparisons (Crawley 2007).

Spatial Analyses

Semivariograms

Quantification of the spatial overlap between spiny dogfish distribution and commercial fishers required a comparable grid scheme of spatially identical cells before geostatistical modeling was feasible. Spatial dependence, or the tendency for sample values closer to be more similar than values further apart, was assessed using semivariogram modeling. Empirical semivariograms ($\gamma(h)$) were calculated using the following semivariance equation:

$$(5.3) \quad \gamma(h) = \frac{1}{2n(h)} \sum [Z(x_i) - Z(x_{i+h})]^2$$

where $Z(x_i)$ and $Z(x_{i+h})$ = measured *CPUE* values at sample points x_i and x_{i+h} , respectively, and $n(h)$ = total number of sample pairs for any separation distance h (Matheron 1971). Each semivariogram was used to estimate three parameters: (1) the range (a) or the asymptotic distance beyond which samples were spatially independent; (2) the sill (C_S) or the value of the semivariance at any distance $\geq a$; and (3) the nugget (C_0) or the value where the semivariance = 0. In situations where autocorrelation between two locations changed with both direction and distance, a condition known as anisotropy, two additional parameters were estimated: the ratio of the minor to major axis lengths and the angle of the principal direction of continuity (Pebesma et al. 2010).

For each year, survey and fishery *CPUE* of spiny dogfish were log transformed ($\log_e(CPUE) + 0.05$) to meet the normality requirement for semivariogram modeling and to account for zero values. Semivariograms were fitted annually and overall (i.e., all years combined). All models were run in the 'gstat' package (Pebesma 2004) in R (R Core Development 2010) with anisotropic parameters estimated via the 'intamap' package (Pebesma et al. 2010). Multiple initial parameters (C_S, C_0, a) in combination with various theoretical models were tested including the following:

$$(5.4) \quad \text{Nugget: } \gamma(h) = C_0 = C_S$$

$$(5.5) \quad \text{Gaussian: } \gamma(h) = C_0 + (C_S - C_0) \times \left[1 - \exp\left(-\frac{h^2}{a^2}\right)\right]$$

$$(5.6) \quad \text{Exponential: } \gamma(h) = C_0 + (C_S - C_0) \times \left[1 - \exp\left(-\frac{h}{a}\right)\right]$$

$$(5.7) \quad \text{Spherical: } \gamma(h) = C_0 + (C_S - C_0) \times \left[1.5 \times \left(\frac{h}{a} \right) - 0.5 \times \left(\frac{h}{a} \right)^3 \right].$$

Optimal semivariogram models were selected based on the lowest Akaike's Information Criterion (*AIC*) calculated with the following equation:

$$(5.8) \quad AIC = n \ln(R) + 2p$$

where n = number of experimental points on the semivariogram, R = residual sum of squares, and p = number of parameters in the model (Webster & McBratney 1989). In the absence of spatial dependence ($a = 0$), a nearly horizontal semivariogram was obtained and characterized by the 'nugget' model (Park & Obrycki 2004).

Grid Determination

Ranges identified from each optimal annual and overall semivariogram model for the survey and each fishery were compiled and used to determine an appropriate cell size for spatial analyses. Annual range estimates were averaged across years and compared to range estimates obtained overall. An appropriate range was desired to ensure that the cell size was large enough to minimize the influence of autocorrelation but small enough to track fine-scale trends (Santora et al. 2010).

Spatial Overlap

To examine how spiny dogfish distributional changes have altered their availability to each fishery, we quantified annual spatial overlap during each season. Station data for the survey

and each fishery were converted into rasters to reflect mean *CPUE* for each grid cell using the 'raster' package (Hijmans & van Etten 2012) in R (R Core Development 2010). For the purpose of this study, absolute *CPUE* was not of importance as we were strictly interested in the occurrence of spiny dogfish. Once the data were rasterized into identical spatial resolutions, the amount of direct spatial overlap (Brodeur et al. 2008) of spiny dogfish distribution derived from the survey was compared with: 1) commercial fisher effort indicative of presence and 2) commercial fisher catch indicative of spiny dogfish distribution (as explained below).

The percent spatial overlap concerning commercial fisher effort (SO_E) was calculated with the following equation:

$$(5.9) \quad SO_E(\%) = \frac{N_{SF,E}}{N_{F,E}} \times 100$$

where $N_{SF,E}$ = number of cells containing both survey spiny dogfish catch and commercial fisher effort and $N_{F,E}$ = number of cells where commercial fishers fished. This metric provided insight into where the fishery was operating in relation to survey-derived spiny dogfish distribution and related to the availability of the spiny dogfish stock to the fishery. Low overlap reflected reduced availability to the fishery.

The percent spatial overlap concerning commercial fisher spiny dogfish catch (SO_C) was calculated with the following equation:

$$(5.10) \quad SO_C(\%) = \frac{N_{SF,C}}{N_{F,C}} \times 100$$

where $N_{SF,C}$ = number of cells containing both survey catch and commercial fisher catch of spiny dogfish and $N_{F,C}$ = number of cells where commercial fishers caught spiny dogfish. This metric provided insight into where both the fishery and the survey were catching spiny dogfish and served as an estimate of the overlap between the distributions derived from each source. Here, a low overlap indicated a high spatial mismatch between where the fishery and the survey were catching spiny dogfish.

Spatial overlap was also investigated for interpolated values obtained through kriging (Oliver & Webster 1990, Reese & Brodeur 2006, Brodeur et al. 2008). Ordinary kriging was chosen as this technique is easier to implement and possesses stronger prediction strength (Lloyd & Atkinson 2001). Kriging model performance and predictions were checked using diagnostics including the mean prediction variance and standard error, root mean square error of prediction (*RMSE*), the average error (*AVE*), and 100-fold cross-validation (Cressie 1993). All analyses were carried out in the 'gstat' package (Pebesma 2004) of R (R Core Development 2010).

After interpolation, the spatial overlap concerning predicted spiny dogfish distribution (SO_I) via the survey and each fishery was calculated with the following equation:

$$(5.11) \quad SO_I (\%) = \frac{N_{SF,I}}{N_{F,I}} \times 100$$

where $N_{SF,I}$ = number of cells predicting both survey catch and commercial fisher catch of spiny dogfish and $N_{F,I}$ = number of cells predicting commercial fisher catch. This metric provided insight into where both the fishery and survey were predicted to catch spiny dogfish throughout the NES LME and served as an estimate of the overlap between the distributions derived from

each source. Here, a low overlap indicated that the fishery was catching spiny dogfish not accounted for by the survey.

Vulnerability to Fishery

The proportion of the survey-derived spiny dogfish stock vulnerable or available to each fishery was used to infer changes in catchability of the population. This quantity was reported as a percentage and estimated annually with the following equation:

$$(5.12) \quad Vul = \frac{C_F}{C_T} \times 100$$

where C_F = sum of survey spiny dogfish catch in cells where commercial fishing occurred and C_T = total sum of survey spiny dogfish catch. Vulnerability was reported for spiny dogfish as a species and separately for each life-history stage based on the following classifications of survey catches: aggregated male and female neonates (total length, $TL \leq 26$ cm), immature males ($26 \text{ cm} < TL < 60$ cm), immature females ($26 \text{ cm} < TL < 80$ cm), mature males ($TL \geq 60$ cm), and mature females ($TL \geq 80$ cm). This vulnerability analysis assumed that survey catch accurately reflected trends for the entire spiny dogfish stock throughout the NES LME. High values indicated that a large portion of the spiny dogfish stock was present in cells where commercial fisheries were operating.

Map-Correlation Analysis

Map-correlation analysis (Park & Obrycki 2004) investigated annual correlations between survey-derived spiny dogfish distribution and fishery effort and between spiny dogfish

distributions derived from the survey and each fishery. Map-correlation coefficients were calculated based on sample-to-sample correlations with cells treated as samples. Pearson's correlation (r) measured the 'strength' of the relationship whereas Spearman's rank correlation (r_s) measured the similarity between ranks of observed and predicted values (Quinn & Keough 2002).

Results

Commercial Catch Distributions

Overall Catch

During both autumn and spring, the majority of spiny dogfish were captured by SGN (autumn: 57%; spring: 47%) and OT (autumn: 29%; spring: 45%) (Figure 5.1). Other gears contributed 8% and 15% during spring and autumn, respectively. In addition to providing the largest catches, these two commercial fisheries also exhibited the longest and most consistent time series (Table 5A.1). During both seasons, the SGN fishery expended more effort and kept a larger percentage of spiny dogfish catch (autumn: 61%; spring: 82%) compared to the OT fishery (autumn: 8%; spring: 6%) (Table 5A.1). As a result, spatial analyses focused on these two fisheries.

Monthly Catch Distribution by the Otter Trawl and Sink Gill Net Fisheries

Both commercial fisheries operated year-round in all four regions surveyed by the NEFSC and generally encountered spiny dogfish in each region during most calendar months

(Figures 5.2-3). Exceptions occurred solely in the SGN fishery during July and September where positive catches were absent south of Cape May, NJ. This fishery generally operated on the continental shelf (Figure 5.2) whereas the OT fishery operated both on the shelf and along its edge (Figure 5.3). Both fisheries exhibited similar monthly *CPUE* patterns. During cooler months (November through April), spiny dogfish were abundant off Cape Hatteras, NC in both the SGN (Figure 5.2) and OT (Figure 5.3) fisheries. In contrast, during warmer months (May through October) spiny dogfish were common throughout the GM in the SGN (Figure 5.2) fishery and also on GB in the OT (Figure 5.3) fishery.

Spatial Autocorrelation

The degree of clustering of spiny dogfish *CPUE* revealed annual (Figure 5.4) and seasonal (Figure 5.5) variability in both fisheries and the survey (Table 5B.1). In the SGN fishery, the degree of clustering over time revealed a slight decrease, particularly during autumn (Figure 5.4). In contrast, the OT was predominantly characterized by low I (< 0.2) throughout the time series, indicating a fairly random spatial association of spiny dogfish *CPUE* (Figure 5.4). Similarly, the degree of clustering from the survey remained relatively low ($I < 0.2$) during both seasons but revealed higher clusters in the mid 2000s during autumn and in the late 2000s during spring (Figure 5.4). The paucity of negative I 's indicated that these distributions were rarely dispersed. Overall, spiny dogfish were more clustered in the SGN fishery ($I \sim 0.35$) during both seasons compared to the OT fishery ($I \sim 0.1$) and the survey ($I \sim 0.15$) (Figure 5.5). Seasonal medians in I did not appear to differ significantly for either fishery or the survey (Figure 5.5).

Center of Abundance

Annual centers of spiny dogfish abundance differed significantly during both seasons ($p < 0.05$; Table 5.1). In addition, the locations of these centers differed significantly among modes of fishing ($p_{adj} < 0.0167$; Table 5.1) with the exception of the survey versus SGN fishery during spring.

The locations of these centers of spiny dogfish abundance generally varied with season for each fishery (Figure 5.6; Table 5C.1) and the survey (Figure 5.6; Table 5C.2). During autumn, most annual centers from the SGN and OT fisheries occurred in the southwest GM and throughout SNE, respectively (Figure 5.6A). The early 1990s displayed the northernmost locations for the SGN fishery. Centers of abundance based on the survey generally occurred in the southern GM and were located furthest offshore from the early to mid 1990s (Figure 5.6A).

During spring, the annual centers of spiny dogfish abundance for both the SGN fishery and the survey frequently occurred along the shelf's edge (Figure 5.6B). Centers based on the SGN fishery have shifted from the GM (early 1990s) to SNE and the MA in recent years (Figure 5.6B). Centers of abundance derived from the survey have consistently occurred around the Hudson Canyon with the late 1990s displaying the northernmost values. The OT fishery revealed centers of abundance along the northern edge of GB and SNE (Figure 5.6B).

Spatial Analysis

Semivariogram Trends

Overall. Optimal semivariogram models for each fishery and the survey incorporated anisotropy and varied seasonally in structure (Table 5.2). For the SGN fishery, the spatial correlation of spiny dogfish *CPUE* was best fit by a complex exponential ($C_S = 5$, $C_0 = 10$, $a = 1$)

model during autumn and a simple Gaussian ($C_S = 3$, $C_0 = 5$, $a = 1$) model during spring (Table 5.2). For the OT fishery, simple Gaussian and exponential models were selected for autumn and spring, respectively. The spatial correlation of spiny dogfish *CPUE* for the survey was best fit by simple exponential and spherical models during autumn and spring, respectively.

Ranges obtained from all optimal semivariogram models varied from 0.1 km to 20.19 km and rarely exceeded 2 km overall (Table 5.2). During both seasons, the smallest range was displayed by the SGN fishery whereas the OT fishery possessed the largest. Overall, optimal semivariogram models were at least adequate in capturing the overall trend indicated by the sample variograms (Figure 5.7).

Annual. Optimal semivariogram trends were investigated across modes of fishing and seasons (Figures 5D.1-21) and generally revealed similar model structure and range estimates to those obtained overall across years (Tables 5D.1-3). Optimal semivariogram models were highly diverse for both SGN and OT fisheries during both seasons. For the SGN fishery, a majority of the years revealed simple spherical and Gaussian models during autumn and spring, respectively (Table 5D.1). Both seasons also displayed 4 less common optimal models, each of which differed either in model type or input parameters. During spring, nugget models were selected for 2003, 2004, and 2006, indicating a lack of spatial autocorrelation. For the OT fishery, 6 different models were selected at least once as optimal during autumn with the simple Gaussian model most frequent (Table 5D.2). Out of 8 optimal models identified during spring, the simple spherical model was most common. Three years lacked spatial autocorrelation and revealed an optimal nugget model: 1994, 1998, and 1999.

Optimal semivariograms for the NEFSC survey were either simple spherical or exponential models during both seasons (Table 5D.3). During autumn, exponential models were consistently selected after 1993. In contrast, spherical models were optimal for the majority of the time series during spring.

Variogram ranges for all modes of fishing rarely exceeded 10 km on an annual basis. The SGN fishery revealed the smallest range and rarely exceeded 3 km during either season (Table 5D.1). The ranges displayed by the OT fishery were generally larger but seldomly exceeded 10 km (Table 5D.2). Three exceptionally large ranges (> 400 km) were identified, two during autumn (1995, 2003) and one during spring (2007). For the survey, variogram ranges rarely exceeded 5 km (Table 5D.3).

For all modes of fishing, the majority of semivariogram models were at least adequate in matching the overall trend indicated by empirical variograms (Figures 5D.1-21). The SGN fishery revealed highly scattered semivariance values and consequently poor fits during both autumn (2000, 2002) (Figures 5D.12,14) and spring (2000, 2002-06) (Figures 5D.12,14-18). For the OT fishery, similarly poor fits were identified during autumn (1997-99) (Figures 5D.9-11). Survey semivariograms did not display poor modeling behavior and generally fit the data points well.

Grid Size

A size of 15 minute-spatial cells spanning 0.25° latitude x 0.25° longitude was selected based on the estimated ranges (≤ 20 km) from both overall and annual semivariograms. A total of 468 grid cells were identified, with grid areas ranging from 532 to 644 km² in the northernmost and southernmost grids, respectively. While three annual range estimates (2.4% of

the total) from the OT fishery exceeded the specified size (Table 5D.2), this cell size was retained as it was large enough to cover multiple stations per cell while small enough to permit processing and enable tracking of fine-scale changes (Santora et al. 2010).

Spatial Overlap of Spiny Dogfish Distribution with Fishery Effort

Survey: Based on the number of cells where spiny dogfish were caught, the survey generally encountered spiny dogfish over a wider range during spring (109 – 152 cells [range], 132 ± 14 [mean \pm SD]) than autumn (62 – 128 cells, 92 ± 17).

Sink Gill Net: The number of cells fished by SGN was generally similar between autumn (27 – 76 cells, 52 ± 14) and spring (23 – 76 cells, 55 ± 16) (Figures 5E.1A-21A). Both seasons also displayed comparable quantities of cells containing both SGN effort and survey catch (autumn: 10 – 27 cells, 18 ± 5 ; spring: 0 – 32 cells, 16 ± 10). The spatial overlap of SGN effort and survey catch was generally higher during autumn than spring (Table 5.3; Figure 5.8), indicating that a greater portion of the spiny dogfish stock as derived from the survey was available to the fishery. During autumn, the overlap ranged from 17.5% in 1993 to 53.0% in 2006 (mean \pm SD = 35 ± 9) but lacked a strong trend (Table 5.3; Figure 5.8). In contrast, the overlap during spring gradually increased over time, building from 0% in 1990-91 to ~ 40% in 2008-09 (mean \pm SD = 27 ± 15) (Table 5.3; Figure 5.8).

Otter Trawl: The number of cells fished by OT varied substantially during both autumn (22 – 244 cells, 118 ± 64) and spring (48 – 219 cells, 122 ± 59) (Figures 5E.1B-21B). As above, this fishery displayed similar numbers of cells containing both OT effort and survey catch

between seasons (autumn: 4 – 67 cells, 31 ± 21 ; spring: 9 – 75 cells, 37 ± 20). While the spatial overlap during spring generally exceeded overlap during autumn between 1989 and 1996, this dominance disappeared after 1997 (Table 5.3; Figure 5.8). During autumn, the spatial overlap between OT effort and survey catch showed a slight increasing trend over time, ranging from ~18% in the 1990s to ~30% in the 2000s (mean \pm SD = 25 ± 8) (Table 5.3; Figure 5.8). In contrast, the spatial overlap during spring did not reveal any noticeable patterns and ranged from 18.8% in 1999 to 40.6% in 1995 (mean \pm SD = 30 ± 6) (Table 5.3; Figure 5.8).

Spatial Overlap of Spiny Dogfish Distribution with Fishery Catch

Sink Gill Net: The number of cells where SGNs encountered spiny dogfish were generally few but tended to be more numerous during autumn (12 – 63 cells, 36 ± 13) compared to spring (6 – 54 cells, 27 ± 16). In addition, more cells displayed both SGN and survey catch during autumn (7 – 22 cells, 14 ± 5) than spring (0 – 22 cells, 8 ± 6). The predominantly lower SO_C during spring compared to autumn was indicative of less overlap between spiny dogfish distributions derived from the SGN fishery and survey (Table 5.4; Figure 5.9). During autumn, SO_C was lowest during 1993 (20.8%), increased to peak values in 2001 (66.7%), and then declined (mean \pm SD = 43 ± 12) (Table 5.4; Figure 5.9). During spring, no direct overlap during 1990 and 1991 was followed by higher values (~40%) during the late 1990s and 2000s (mean \pm SD = 26 ± 14) (Table 5.4; Figure 5.9).

Ordinary kriging adequately predicted the spatial distributions of spiny dogfish for the sink gill net fishery (Table 5F.1) and the NEFSC bottom trawl survey (Table 5F.2). Positive cells (i.e., those containing spiny dogfish) based on interpolated survey catch were less numerous during autumn (117 – 283 cells, 205 ± 44) (Figures 5F.1-21) than spring (171 – 358 cells, $287 \pm$

45) (Figures 5F.22-42). In contrast, the number of positive cells based on interpolated SGN catch was generally greater during autumn (1 – 467 cells, 179 ± 175) (Figures 5F.1-21) than spring (0 – 95 cells, 27 ± 27) (Figures 5F.22-42). As a result, more cells containing both interpolated SGN catch and survey catch occurred during autumn (1 – 217 cells, 86 ± 81) than spring (0 – 82 cells, 19 ± 22). Spatial overlap obtained by interpolation (SO_I) yielded similar trends to SO_C but often exceeded SO_C estimates during both seasons (Figure 5.9). During autumn, SO_I was relatively low during the early 1990s then increased to maximum values throughout the 2000s (mean \pm SD = 65 ± 27) (Table 5.4; Figure 5.9). The maximum values (100%) of SO_I during 2000-02 were artifacts of very low sample sizes (< 10 cells) used during interpolation. During spring, SO_I was relatively high with the exception of the mid 2000s (mean \pm SD = 48 ± 34) (Table 5.4; Figure 5.9).

Otter Trawl: The number of cells where OTs encountered spiny dogfish was highly variable during both seasons (autumn: 11 – 185 cells, 78 ± 51 ; spring: 21 – 167 cells, 81 ± 49). The quantity of cells containing spiny dogfish catch by both the OT fishery and survey was similar among seasons (autumn: 2 – 58 cells, 24 ± 19 ; spring: 4 – 60 cells, 27 ± 15). SO_C was fairly similar in magnitude between seasons but revealed different trends (Table 5.5; Figure 5.9). During autumn, 1998 appeared to separate a period of relatively low overlap (~20%) between 1990-97 from a period of higher overlap (>30%) from 1999 to 2009 (mean \pm SD = 31 ± 10) (Table 5.5; Figure 5.9). In contrast, no strong pattern was displayed during spring as SO_C remained variable and ranged from 19.0% in 1999 to 48.7% in 2001 (mean \pm SD = 33 ± 7) (Table 5.5; Figure 5.9).

Ordinary kriging adequately predicted the spatial distributions of spiny dogfish for the OT fishery (Table 5F.1). As observed for the SGN fishery, spatial overlap derived from

interpolated OT data was generally greater but displayed similar patterns to those obtained directly (Figure 5.9). Positive cells (i.e., those containing spiny dogfish) based on interpolated OT catch were more numerous during autumn (28 – 399 cells, 161 ± 96) (Figures 5F.1-21) compared to spring (19 – 287 cells, 135 ± 92) (Figures 5F.22 – 5F.42). However, the number of cells containing both interpolated OT catch and survey catch was generally greater during spring (16 – 281 cells, 107 ± 65) compared to autumn (5 – 175 cells, 78 ± 48). While the pattern displayed by SO_I during autumn was similar to SO_C as above, the magnitude of each trend was more pronounced (Figure 5.9). SO_I ranged from 6.7% in 1997 to 90.4% in 1999 (mean \pm SD = 51 ± 27) (Table 5.5; Figure 5.9). During spring, SO_I was consistently high throughout the time series but did reveal a trough during the early 2000s (mean \pm SD = 81 ± 9) (Table 5.5; Figure 5.9).

Vulnerability to Fishery

Aggregated: The proportion of the spiny dogfish stock vulnerable to both fisheries was generally higher during autumn than spring (Figure 5.10), indicating that a greater portion as derived from the survey was available to each fishery during the former season. During both seasons, the proportion vulnerable to the SGN fishery remained below 30% with the exception of the mid to late 2000s (Figure 5.10). While the OT fishery during spring revealed a similar trend, the proportion vulnerable increased dramatically in 2001 during autumn and remained relatively high thereafter (Figure 5.10).

Stage-dependent: The proportions vulnerable by stage were highly variable between fisheries and seasons (Figure 5.10). Sporadic survey catches of neonates, particularly during

autumn, resulted in erratic trends for both seasons and fisheries (Figure 5.10). A common trend of higher vulnerability to the OT fishery during the 2000s was displayed for most stages (Figure 5.10). During both seasons, the vulnerability of immature males to the OT fishery has recently increased while it has remained relatively stable to the SGN fishery with the exception of the late 2000s during spring (Figure 5.10). Mature males were generally more vulnerable to each fishery during autumn compared to spring and displayed relatively high vulnerability to both fisheries during the mid to late 2000s (Figure 5.10). Immature females were generally more vulnerable to both fisheries during autumn, particularly during the 2000s, whereas trends during spring remained variable (Figure 5.10). Vulnerability of mature females to both fisheries remained relatively low during spring (Figure 5.10). In contrast, during autumn, their vulnerability to the SGN and OT fisheries has remained relatively high since 1996 and 2000, respectively (Figure 5.10).

Map Correlation Analysis

Spiny Dogfish Distribution and Fishery Effort

For both fisheries, survey-derived spiny dogfish distribution was not highly correlated with commercial fisher effort (Table 5.3). For the SGN fishery, r values fluctuated around zero during both autumn (0 – 0.23) and spring (-0.01 – 0.22) (Table 5.3). Slightly larger r_{sp} values were observed (autumn: 0.14 – 0.32; spring: -0.03 – 0.27) but still resulted in weak relationships (Table 5.3). For the OT fishery, r values were also close to zero during autumn (-0.01 – 0.20) and spring (-0.01 – 0.12) (Table 5.3). In addition, relatively higher but weak r_{sp} were obtained during both seasons (autumn: 0.04 – 0.43; spring: 0.07 – 0.36) (Table 5.3).

Spiny Dogfish Distribution and Fishery Catch

For the SGN fishery, low r values were displayed by both SO_C (autumn: 0 – 0.20; spring: -0.34 – 0.13) and SO_I (autumn: -0.06 – 0.39; spring: -0.23 – 0.08) (Table 5.4). In contrast, slightly larger r_{sp} values were observed for both SO_C (autumn: 0.14 – 0.33; spring: -0.02 – 0.22) and SO_I (autumn: -0.02 – 0.75; spring: -0.54 – 0.33) with some values indicating moderate to high correlations (Table 5.4). For the OT fishery, low to moderate r values were displayed by both SO_C (autumn: 0 – 0.50; spring: 0 – 0.26) and SO_I (autumn: 0.09 – 0.53; spring: -0.01 – 0.44) (Table 5.5). Again, r_{sp} values were slightly larger for both SO_C (autumn: 0.03 – 0.44; spring: 0.05 – 0.33) and SO_I (autumn: -0.57 – 0.64; spring: 0.03 – 0.66) (Table 5.5).

Discussion

Uncertain biomass projections, stemming partially from inconsistent and biologically-unrealistic trends in survey-derived abundance, have recently invited skepticism throughout the scientific and fishing communities pertaining to spiny dogfish stock status within the NES LME (Fogarty & Murawski 1998, Link et al. 2002, NEFSC 2006, Sulikowski et al. 2010). Here we documented changes in the availability of the stock to provide insight into inherent variability within abundance and biomass estimates. Central locations of spiny dogfish abundance varied both seasonally and annually and revealed temporal shifts. Spatial overlap of spiny dogfish distribution and commercial fisher effort (SO_E) quantified interaction potential and availability to both SGN and OT fisheries. Recent increases in availability were observed for the SGN fishery during spring and the OT fishery during autumn. Direct spatial overlap of spiny dogfish catch from both the survey and each fishery (SO_C) revealed variable seasonal trends with interpolated patterns (SO_I) generally exceeding but complimenting those trends derived directly.

Vulnerability analyses revealed stage-dependent trends and recent increases, particularly during autumn.

Seasonal NEFSC survey tracks have remained relatively consistent both spatially and temporally and thereby provide a snapshot of the spiny dogfish stock. Survey-derived abundance estimates capture a majority (90%) of the spiny dogfish stock during spring but are more variable due to emigration into Canadian waters during autumn (NEFSC 2003). During each survey, stations are assigned at random within strata (Despres-Patanjo et al. 1988) to provide unbiased estimates of relative stock biomass and abundance of encountered fishes (Rago 2005). However, many factors can affect the survey track and potentially bias the estimation of indices including unanticipated events such as inclement weather or foreseen events such as untrawlable areas. Since stock assessment of spiny dogfish relies heavily on survey-derived trends in spawning stock biomass and recruitment, their stock status can be highly sensitive to potential bias within the survey. Further, their deterministic seasonal movements, unpredictable distributional shifts, and hypothesized herding behavior may amplify changes in survey catchability and introduce uncertainty into management (NEFSC 2006). Assessment of spiny dogfish will benefit from an understanding of trends derived from fishery-dependent sources augmenting those from trawl surveys.

Often avoided due to biased fishing patterns (Branch et al. 2006), analysis of fishery-dependent data provided a unique vantage point of spiny dogfish distribution, tracking presence throughout the NES LME during all calendar months. The central location of spiny dogfish abundance was highly variable between seasons and differed significantly between fisheries and the survey. While NEFSC has conducted sporadic summer and winter surveys, these surveys are usually special-purpose trawls (Despres-Patanjo et al. 1988) or display incomplete spatial

coverage (Wigley et al. 2003). The migratory behavior of spiny dogfish has spawned a highly seasonal fishery, greatly complicating management success (ASMFC 2002). Fisheries generally operate in New England during the summer and migrate south with spiny dogfish during winter as waters become cooler, concentrating off North Carolina (Camhi 1998). In the late 1990s, semi-annual quota periods (I: May 1 – Oct 31, 600 pound possession limit; II: Nov 1 – Apr 30, 300 pound possession limit) led to the landing of the entire quota during the first period off New England, preventing southern fishermen from harvesting spiny dogfish during winter. While our monthly assessment of fisher distribution generally matched these trends, both fisheries caught spiny dogfish throughout the range, implying that not all spiny dogfish migrate seasonally. Future research targeting these resident spiny dogfish should investigate their behavior and potential reasons for residency.

Empirical investigations of spatial distribution in relation to vulnerability or availability are a recent development in fisheries science (Salthaug & Aanes 2003, Bertrand et al. 2004, Ellis & Wang 2007). Off the coast of Peru, anchovy (*Engraulis ringens*) became more vulnerable due to high densities coupled with improved detection ability through sonar and radar (Bertrand et al. 2004). Here, the quantification of predatory behavior by commercial fishers using spatial overlap provided valuable insight into potential spatial interactions both seasonally and annually. Catchability is a function of the fishers' success (Salthaug & Aanes 2003) and depends upon trip duration (Salas & Gaertner 2004), gear (Charles 1995, Ruttan 1998, Salas 2000, Salthaug 2001, Salas & Gaertner 2004), information sharing or cooperation (Salas & Gaertner 2004, Branch et al. 2006), and/or learning (Salthaug & Aanes 2003, Bertrand et al. 2004). Off Venezuela, vulnerability of tuna schools was linked to skipper's skill, fishing equipment used (e.g., radar), features of the school (e.g., size), and environmental factors (Gaertner et al. 1999). The observed

increase in SO_E throughout the time series for the SGN fishery during spring and the OT fishery during autumn suggested a concomitant increase in the portion of the spiny dogfish stock available. In addition, the proportion vulnerable estimated using survey catches in fished versus all cells also increased recently for all spiny dogfish combined and most stages. This may reflect technological advancements and/or social networking which can increase the efficiency of fishers at locating and capturing schools of either spiny dogfish directly or indirectly via targeting their prey, thereby improving their catchability of the encountered species (Hilborn & Walters 1992).

Spatial analyses of spiny dogfish distribution derived from the survey and each fishery revealed seasonal and annual differences in both direct (SO_C) and interpolated (SO_I) overlap, offering insight into the portion of the stock encountered by both fishers and monitoring surveys. Generally, interpolated overlap was larger than direct overlap. Lower direct overlap values for pelagic fishes and jellyfish off California were thought a result of either avoidance or patchy behavior and, therefore, geostatistical estimates were preferred (Brodeur et al. 2008). Highly variable survey catches of spiny dogfish (NEFSC 2006) support an unpredictable and patchy distribution throughout the NES LME. After years of declining abundances during spring, the survey index for mature females spiked to the 5th highest estimate (39.4 kg/tow) in 2006, owing to maximal average catches in 5 separate strata and shifts in concentrations from SNE and GB to the GM and MA (NEFSC 2006). During autumn, when spiny dogfish are primarily located in the northern NES LME or in Canadian waters, survey indices are even more variable with approximately 50% of the catch attributed to 'large' (> 1,000 kg) tows (NEFSC 2006). Often, these wide swings in abundance are greater than expected given the life history of this slow growing, less fecund species. Estimates of spatial overlap (SO_C and SO_I) for the OT fishery

displayed two periods of contrasting overlap: 1) a low period prior to 1998 where spiny dogfish were uncommonly caught by both the fishery and the survey; and 2) a high period thereafter reflecting more area where spiny dogfish were captured by both the survey and the fishery. The SGN fishery during autumn also displayed a similar trend. Reduced overlap in the early 1990s may correspond with the 'elasmobranch outburst' where spiny dogfish were highly abundant throughout the region (Fogarty & Murawski 1998, Frisk et al. 2008). Interestingly, the year separating the two distinct periods, 1998, was also the year in which the stock was declared overfished (ASMFC 2002). Relatively higher spatial overlap after this year suggests increased vulnerability of the stock to each fishery. While this seems counterintuitive given that the 2000s were strictly a bycatch fishery, it is possible this increased overlap relates to distributions of species targeted by both fishers and spiny dogfish (i.e., predation).

The reliability of commercial statistics is often plagued by fisher behavior, particularly when vessels search for concentrations of fish rather than fishing at random (Paloheimo & Dickie 1964, Salthaug & Aanes 2003). During both seasons the SGN fishery *CPUE* of spiny dogfish was generally more clustered than either the OT fishery or the survey. This finding suggests that this passive fishery may target spiny dogfish directly whereas OT catches are likely bycatch. Further support is provided by the higher percentage of catch kept by the SGN fishery (autumn: 61%; spring: 81%) compared to the OT fishery (autumn: 8%; spring: 5%). The observed fishing patterns for the OT fishery may be more tightly linked to target species distributions. For the SGN fishery, the 1990s often displayed relatively high clustering of *CPUE* as fishing efforts spread inshore within SNE and MA. During this same time frame, a shoreward shift in distribution, predominantly of mature males, was documented by the survey (NEFSC 2006). For spiny dogfish, this shift was more pronounced for mature males during both seasons.

Inshore shifts in distribution increased the vulnerability of cod stocks in the 1990s (Atkinson et al. 1997, Rose & Kulka 1999, Rose et al. 2000) and anchovy schools off Peru (Bertrand et al. 2004). While one could expect increased spatial overlap in inshore regions of both fisher effort and spiny dogfish distribution, this was not evident in either fishery.

Non-random fishing patterns may relate to the restructuring of fishing effort due to area closures within the NES LME (Murawski et al. 2005). Closures of fishing grounds have increased in an attempt to limit exploitation and reduce fishing mortality on depleted groundfish stocks (Murawski et al. 2000). Year-round closures allocated to GB (Areas I & II) and SNE (Nantucket Lightship Area) in 1994 covered ~ 17,000 km with additional closures in the GM during 1996 and 1998 covering ~ 5,000 km (Murawski et al. 2005). In addition, rolling closures in the GM were implemented to reduce exploitation seasonally (Murawski et al. 2005). While these closures reduce the area available for fishing, year-round closures can invite 'fishing the line' (Kellner et al. 2007) or the concentration of fishing effort at the boundary whereas seasonal closures can attract more fishing effort after opening (Murawski et al. 2005). As a result, the displacement of fishing effort may alter their ability to fish and reduce the potential effectiveness of such area-based management (Branch et al. 2006) or MPAs (Auster & Shackell 2000, Murawski et al. 2000).

The spatial analyses presented herein relied heavily on numerous assumptions and extensive manipulation of each dataset. Trends within NEFSC fisheries observer data were assumed to represent those of domestic fishing fleets since 1989. While this restricted analyses to more recent years, this time period encompassed the development of the directed domestic fishery (1990), its collapse (late 1990s), and the onset of recovery (late 2000s). Spatial analyses utilized a cell size of ~560 km² which removed spatial autocorrelation in 98% of observations.

These analyses assumed that this grid size was appropriate for both the rasterization and interpolation of station data. Compared to our cell size, much smaller sizes (185 – 261 km²) have been utilized in other distributional studies using the same fishery-independent dataset within the same geographic region (Methratta & Link 2007, Nye et al. 2009). Our larger estimate was likely the result of the incorporation of fisheries data due to their more clustered fishing patterns during both seasons. For the majority of our analyses, results were not available on a stage-specific basis due to limited reporting of sex within fisheries data. Further investigation of spiny dogfish-fisher interactions at the life-history stage level could provide insight into stage-dependent vulnerability, elucidating the potential influence of fishers on spawning stock biomass (i.e., mature female abundance) and recruitment (i.e., neonate abundance).

Table 5.1. Permutational MANOVA on Bray-Curtis distances for the center of spiny dogfish abundance based on three modes of fishing (SGN = sink gill net, OT = otter trawl, Surv = NEFSC bottom trawl survey) during autumn and spring since 1989. df = degrees of freedom, SS = sums of squares, MS = mean square, F = pseudo- F ratio test statistic, p (perm) = permuted p -value, MC = Monte Carlo asymptotic p -value. Overall significance (bolded) based on an *a priori* $\alpha = 0.05$, comparison significance based on an adjusted α of 0.0167 ($\alpha = 0.05$ corrected for 3 comparisons between modes of fishing). ⁺pair-wise *a posteriori* tests where t is the multivariate version of the t -statistic based on distances. Note: 1989 excluded from analysis during spring to keep the sample size consistent among modes of fishing

Source	df	SS	MS	F	p (perm)	p (MC)
<u>AUTUMN</u>						
Modes of fishing	2	166.71	83.35	22.14	0.0001	0.0001
Residual	60	225.89	3.76			
Total	62	392.60				
<u>SPRING</u>						
Modes of fishing	2	321.83	160.92	15.62	0.0001	0.0001
Residual	57	587.04	10.30			
Total	59	908.88				

Comparison ⁺	t	p (perm)	p (MC)
<u>AUTUMN</u>			
SGN vs OT	3.739	0.0003	0.0002
SGN vs Surv	5.190	0.0001	0.0001
OT vs Surv	5.338	0.0001	0.0001
<u>SPRING</u>			
SGN vs OT	2.899	0.0053	0.0048
SGN vs Surv	2.101	0.0394	0.0411
OT vs Surv	8.299	0.0001	0.0001

Table 5.2. Best-fit semivariogram models and parameters for the spatial distribution of spiny dogfish *CPUE* derived from the sink gill net (SGN) and other trawl (OT) fisheries and the NEFSC bottom trawl survey (Surv) between 1989 and 2009 during autumn and spring in the Northeast (US) shelf large marine ecosystem. Semivariogram parameters include the sill (C_s), the nugget (C_0), and the range (a). Anisotropy parameters include the ratio of the minor to major lengths (Ratio) and the angle for the principal direction of continuity (Angle). Models include exponential (Exp), gaussian (Gau), and spherical (Sph) with the numbers in parentheses reflective of initial parameters (C_s, C_0, a).

Gear	Model	C_s	C_0	a (km)	Ratio	Angle (°)
<u>AUTUMN</u>						
SGN	Exp(5,10, 1)	6.74	0.00	0.10	0.93	54
OT	Gau(3, 5, 1)	4.94	6.16	1.79	0.93	141
Surv	Exp(3, 5, 1)	3.45	4.94	1.57	0.91	130
<u>SPRING</u>						
SGN	Gau(3, 5, 1)	2.30	1.90	1.31	0.73	30
OT	Exp(3, 5, 1)	12.02	4.80	20.19	0.98	39
Surv	Sph(3, 5, 1)	4.37	4.76	1.38	0.76	37

Table 5.3. Spatial overlap (SO_E) and map-correlation of spiny dogfish distribution derived from the NEFSC trawl survey and commercial fisher effort between 1989 and 2009 during autumn and spring in the Northeast (US) shelf large marine ecosystem. SO_E for each fishery calculated as the number of grid cells containing both survey catch of spiny dogfish and commercial fisher effort divided by the number of grid cells where commercial fishers fished. r = Pearson's correlation coefficient, r_{sp} = Spearman's coefficient. - = not applicable.

Year	Sink Gill Net						Otter Trawl					
	AUTUMN			SPRING			AUTUMN			SPRING		
	SO_E (%)	r	r_{sp}	SO_E (%)	r	r_{sp}	SO_E (%)	r	r_{sp}	SO_E (%)	r	r_{sp}
1989	32.3	0.08	0.17	-	-	-	23.2	0.08	0.20	26.8	0.06	0.23
1990	37.0	0.13	0.21	0.0	0.00	-0.03	23.3	0.08	0.19	30.8	0.04	0.22
1991	27.8	0.01	0.27	0.0	-0.01	-0.03	11.4	0.01	0.14	25.3	0.04	0.15
1992	29.6	0.00	0.22	3.6	-0.01	-0.01	21.6	0.06	0.21	20.0	0.12	0.17
1993	17.5	0.02	0.15	7.8	-0.01	0.01	14.3	0.04	0.14	29.7	0.04	0.18
1994	25.0	0.06	0.17	15.2	0.01	0.06	24.2	0.00	0.13	30.1	0.07	0.22
1995	34.5	0.14	0.27	27.7	0.01	0.14	16.3	0.06	0.13	40.6	0.05	0.33
1996	36.4	0.03	0.28	25.0	0.01	0.13	23.6	0.01	0.17	30.4	0.03	0.22
1997	47.3	0.05	0.31	29.2	0.06	0.16	11.4	-0.01	0.04	25.9	0.03	0.12
1998	41.1	0.07	0.28	34.7	0.03	0.21	40.9	0.01	0.17	32.8	0.01	0.18
1999	31.5	0.06	0.19	42.7	0.00	0.27	30.8	0.08	0.20	18.8	0.02	0.07
2000	39.5	0.07	0.28	31.1	0.01	0.17	23.2	0.05	0.23	38.2	0.06	0.27
2001	40.6	0.05	0.22	41.2	0.02	0.19	22.3	0.01	0.21	37.9	0.04	0.24
2002	40.0	0.06	0.22	37.5	0.02	0.17	32.1	0.20	0.31	31.4	0.00	0.15
2003	50.0	0.02	0.32	26.5	0.00	0.11	27.7	0.08	0.32	32.4	0.01	0.34
2004	30.3	0.23	0.26	27.5	0.00	0.18	26.2	0.13	0.34	22.6	0.03	0.23
2005	31.4	0.06	0.24	29.1	0.00	0.17	29.0	0.08	0.40	25.9	0.00	0.30
2006	52.9	0.12	0.32	46.8	0.03	0.26	42.3	0.15	0.43	35.2	-0.01	0.30
2007	29.5	0.10	0.21	39.5	0.05	0.25	33.3	0.10	0.43	33.0	0.06	0.35
2008	29.6	0.23	0.18	39.3	0.22	0.21	28.1	0.11	0.32	28.4	0.09	0.28
2009	27.9	0.07	0.14	43.8	0.10	0.25	27.5	0.07	0.35	34.2	0.09	0.36

Table 5.4. Spatial overlap (SO_C , SO_I) and map-correlation of spiny dogfish catch by the sink gill net fishery and the NEFSC bottom trawl survey between 1989 and 2009 during autumn and spring in the Northeast (US) shelf large marine ecosystem. SO_C is the percent spatial overlap calculated directly as the number of cells where both commercial fishers and the survey caught spiny dogfish divided by the number of cells where commercial fishers caught spiny dogfish. SO_I is the percent spatial overlap calculated using interpolated values. r = Pearson's correlation coefficient; r_{sp} = Spearman's coefficient. ΔSO is the difference in spatial overlap between direct and interpolated methods.

Year	AUTUMN							SPRING							
	Direct			Interpolated				ΔSO	Direct			Interpolated			
	SO_C (%)	r	r_{sp}	SO_I (%)	r	r_{sp}	SO_C (%)		r	r_{sp}	SO_I (%)	r	r_{sp}	ΔSO	
1989	32.1	0.04	0.16	41.1	-0.06	0.24	9	-	-	-	-	-	-	-	
1990	36.0	0.01	0.19	41.5	0.01	0.62	6	0.0	0.00	-0.02	0.0	-0.01	-0.13	0	
1991	30.2	0.04	0.28	28.4	0.00	0.42	2	0.0	0.00	-0.02	12.5	-0.07	0.01	13	
1992	30.2	0.00	0.22	53.0	0.00	0.30	23	4.8	-0.01	0.00	63.0	-0.05	-0.02	58	
1993	20.8	0.00	0.17	26.9	0.03	-0.02	6	11.4	0.01	0.03	73.7	0.00	0.13	62	
1994	27.3	0.00	0.15	66.7	-0.03	0.16	39	25.0	0.01	0.08	77.3	0.08	0.15	52	
1995	41.0	0.00	0.27	20.3	-0.01	0.24	21	28.6	0.02	0.13	74.2	0.04	0.24	46	
1996	37.2	0.01	0.23	50.5	0.05	0.11	13	37.5	0.02	0.14	75.5	0.06	0.10	38	
1997	59.3	0.11	0.28	95.5	0.08	0.46	36	27.7	0.02	0.12	86.3	0.05	0.31	59	
1998	56.4	0.10	0.33	51.9	0.06	0.53	5	40.7	0.04	0.22	78.8	0.01	0.33	38	
1999	51.7	0.13	0.25	71.3	0.18	0.55	20	45.5	0.01	0.22	53.1	0.04	-0.12	8	
2000	43.8	0.00	0.19	100.0	0.09	0.53	56	14.3	0.13	0.03	70.0	-0.02	-0.24	56	
2001	66.7	0.01	0.23	100.0	0.14	0.63	33	36.4	0.00	0.09	50.0	0.01	0.05	14	
2002	52.9	0.08	0.21	100.0	0.39	0.75	47	22.2	0.00	0.04	14.3	-0.02	-0.54	8	
2003	58.6	0.06	0.32	85.7	0.01	0.48	27	16.7	0.00	0.02	0.0	-0.23	-0.08	17	
2004	39.6	0.20	0.29	57.8	0.21	0.60	18	19.0	0.00	0.06	0.0	-0.20	-0.38	19	
2005	38.0	0.07	0.25	55.8	0.11	0.51	18	28.0	0.00	0.11	0.0	-0.13	-0.22	28	
2006	54.5	0.05	0.26	100.0	0.09	0.55	45	34.8	0.00	0.11	0.0	-0.18	-0.45	35	
2007	50.0	0.05	0.28	100.0	0.27	0.65	50	34.3	-0.34	0.14	66.7	-0.04	-0.35	32	
2008	37.8	0.05	0.20	58.8	0.17	0.50	21	40.0	0.01	0.15	75.0	-0.02	-0.32	35	
2009	30.3	0.04	0.14	58.2	0.01	0.21	28	46.7	0.00	0.19	82.1	-0.11	-0.37	35	

Table 5.5. Spatial overlap (SO_C , SO_I) and map-correlation of spiny dogfish catch by the otter trawl fishery and the NEFSC bottom trawl survey between 1989 and 2009 during autumn and spring in the Northeast (US) shelf large marine ecosystem. SO_C is the percent spatial overlap calculated directly as the number of cells where both commercial fishers and the survey caught spiny dogfish divided by the number of cells where commercial fishers caught spiny dogfish. SO_I is the percent spatial overlap calculated using interpolated values. r = Pearson's correlation coefficient; r_{sp} = Spearman's coefficient. ΔSO is the difference in spatial overlap between direct and interpolated methods.

Year	AUTUMN							SPRING						
	Direct			Interpolated				ΔSO	Direct			Interpolated		
SO_C (%)	r	r_{sp}	SO_I (%)	r	r_{sp}	r_{sp}	SO_C (%)		r	r_{sp}	SO_I (%)	r	r_{sp}	r_{sp}
1989	30.3	0.06	0.23	52.7	0.06	0.28	22	34.7	0.07	0.25	82.1	0.01	0.64	47
1990	23.1	0.47	0.15	25.0	-0.03	-0.57	2	30.7	0.01	0.18	63.3	0.07	0.37	33
1991	14.2	0.03	0.15	31.9	-0.01	-0.19	18	31.4	0.06	0.16	88.4	0.04	0.52	57
1992	24.6	0.28	0.20	42.7	0.00	0.11	18	24.2	0.02	0.18	73.0	-0.01	0.32	49
1993	17.9	0.02	0.15	27.1	0.03	0.24	9	30.4	0.01	0.11	80.6	0.01	0.17	50
1994	33.3	0.00	0.14	16.0	-0.01	0.23	17	38.9	0.02	0.19	95.5	0.13	0.37	57
1995	29.0	0.00	0.16	16.1	-0.01	0.16	13	45.3	0.01	0.28	83.3	0.01	0.17	38
1996	17.4	0.00	0.09	16.5	-0.02	-0.33	1	35.5	0.08	0.21	81.5	0.09	0.03	46
1997	12.5	0.00	0.03	6.7	-0.09	-0.55	6	24.2	0.02	0.09	86.0	0.02	0.20	62
1998	54.5	0.00	0.17	30.8	-0.03	-0.22	24	34.6	0.00	0.13	84.2	0.02	0.28	50
1999	40.0	0.11	0.17	90.4	0.10	0.61	50	19.0	0.00	0.05	96.9	-0.01	0.41	78
2000	36.6	0.01	0.25	78.6	0.05	0.38	42	40.7	0.26	0.23	77.1	0.44	0.27	36
2001	29.0	0.03	0.21	66.7	-0.01	0.37	38	48.7	0.07	0.24	69.7	0.13	0.27	21
2002	34.4	0.50	0.31	45.1	0.01	-0.03	11	32.6	0.00	0.15	72.6	0.10	0.34	40
2003	34.0	0.07	0.34	69.4	0.01	0.35	35	36.8	0.01	0.33	76.8	0.35	0.30	40
2004	28.5	0.40	0.32	66.4	0.53	0.53	38	24.8	0.08	0.21	73.5	0.11	0.51	49
2005	32.7	0.06	0.38	74.4	0.08	0.57	42	27.8	0.01	0.26	76.9	0.21	0.52	49
2006	47.5	0.14	0.43	74.2	0.15	0.50	27	38.3	0.00	0.28	73.0	0.00	0.38	35
2007	39.6	0.18	0.44	78.9	0.31	0.64	39	31.5	0.01	0.29	91.6	0.13	0.66	60
2008	32.3	0.12	0.32	67.8	0.06	0.29	35	30.5	0.10	0.28	91.3	0.32	0.66	61
2009	30.3	0.07	0.34	84.0	0.02	0.51	54	35.9	0.05	0.33	89.9	0.05	0.62	54

Figure 5.1. Commercial catch of spiny dogfish since 1989 according to NEFSC fisheries observer data during autumn and spring in the Northeast (US) shelf large marine ecosystem. Dark gray = sink gill net, gray = otter trawl, and light gray = other gears. Other gears included longline, drift gillnet, scallop dredge, and other trawls (haddock separator, mid-water, mid-water pair, pair, ruhle, scallop, shrimp, and twin).

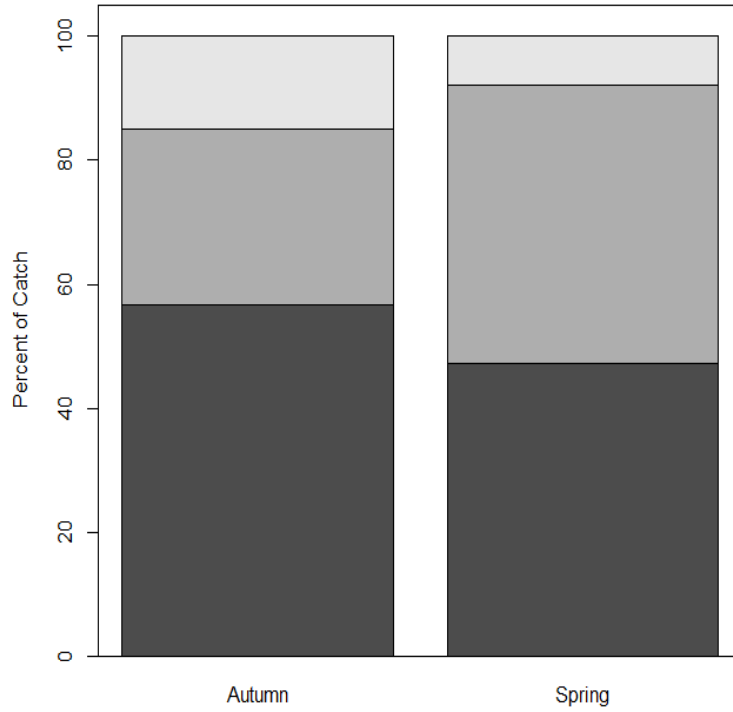
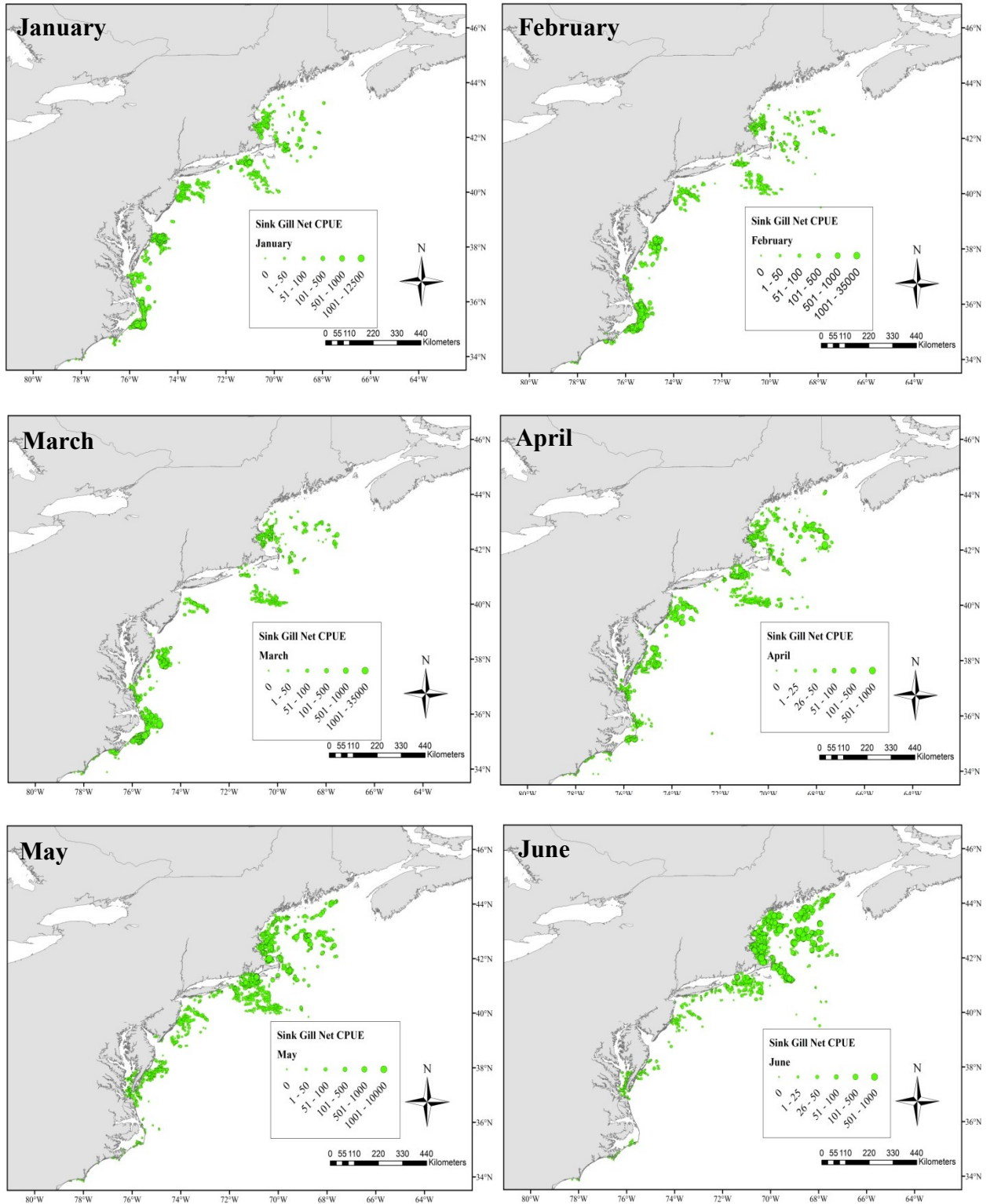


Figure 5.2. Monthly CPUE of spiny dogfish by the commercial sink gill net fishery based on fishery observer records in the Northeast (US) shelf large marine ecosystem. CPUE reflects the number of spiny dogfish caught per hour fished. Shaded gray reflects land masses.



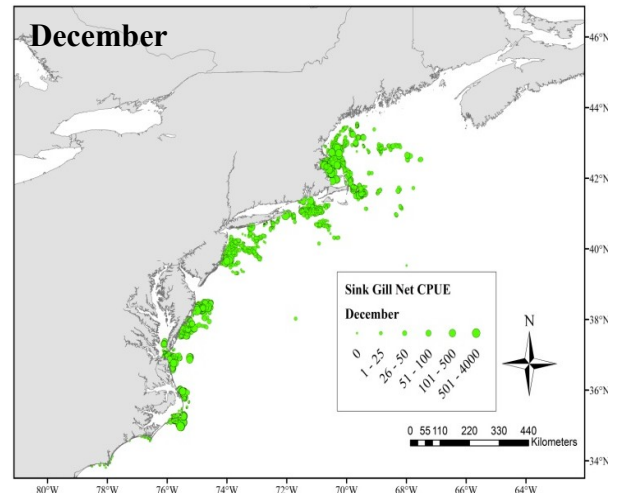
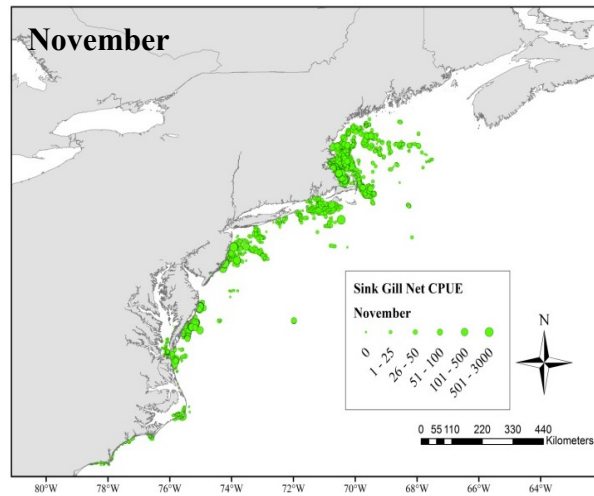
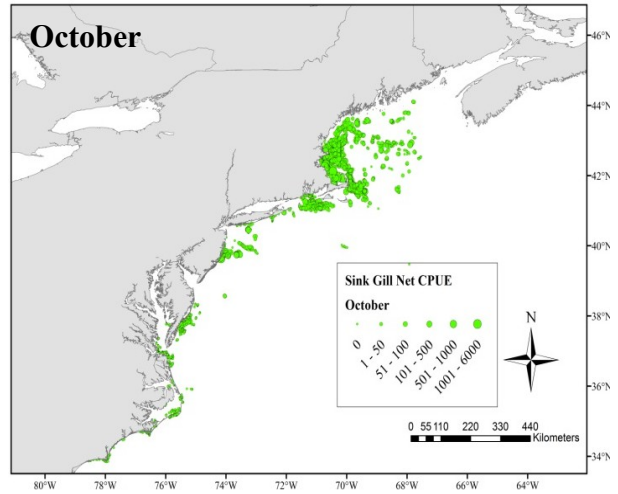
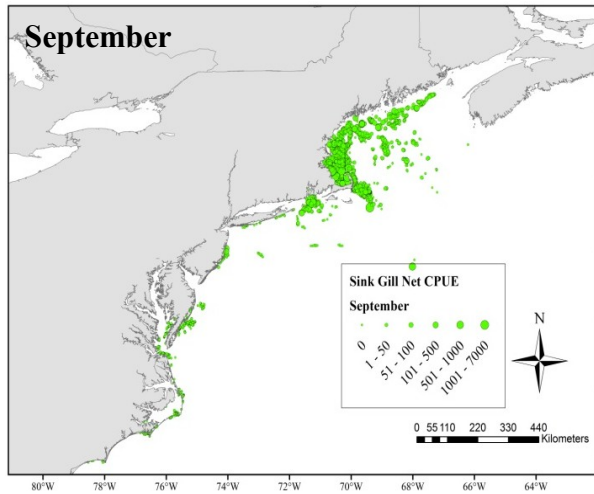
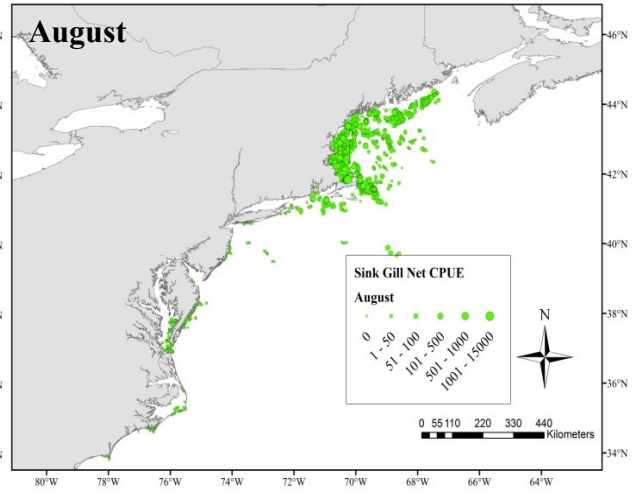
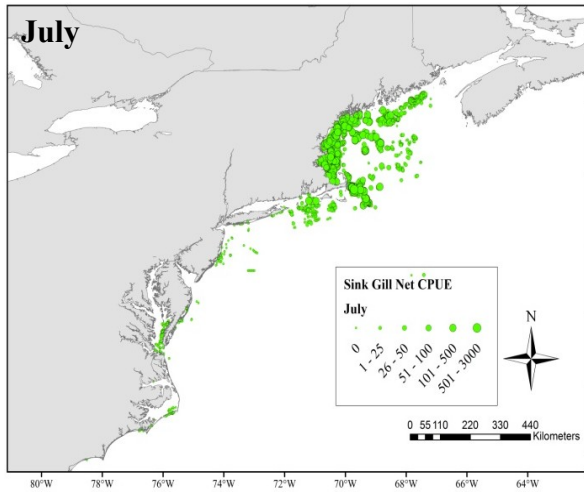
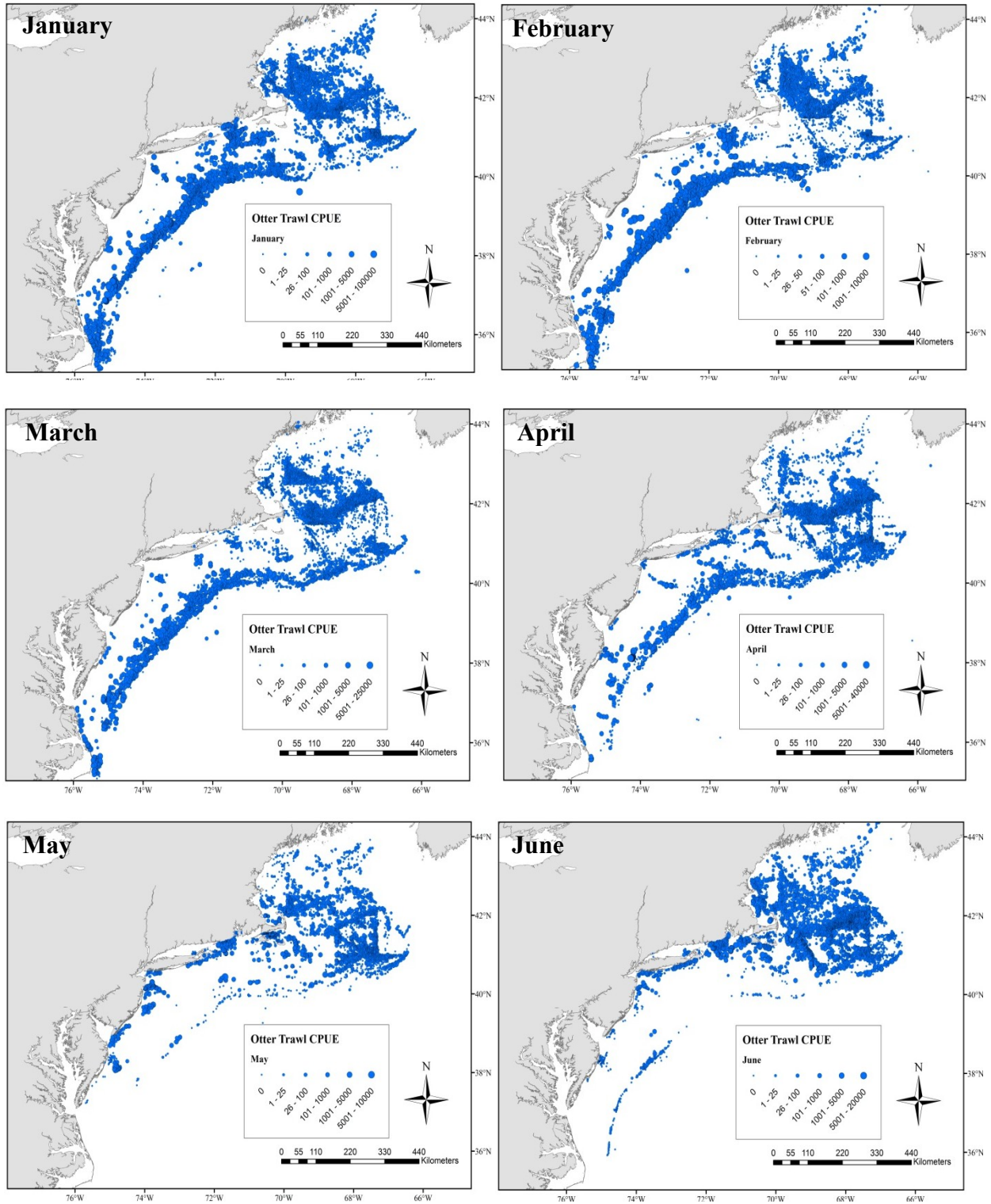


Figure 5.3. Monthly CPUE of spiny dogfish by the commercial otter trawl fishery based on fishery observer records in the Northeast (US) shelf large marine ecosystem. CPUE reflects the number of spiny dogfish caught per hour fished. Shaded gray reflects land masses.



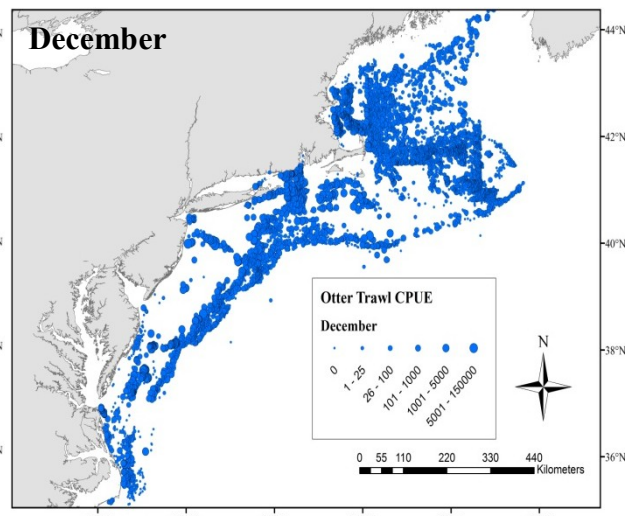
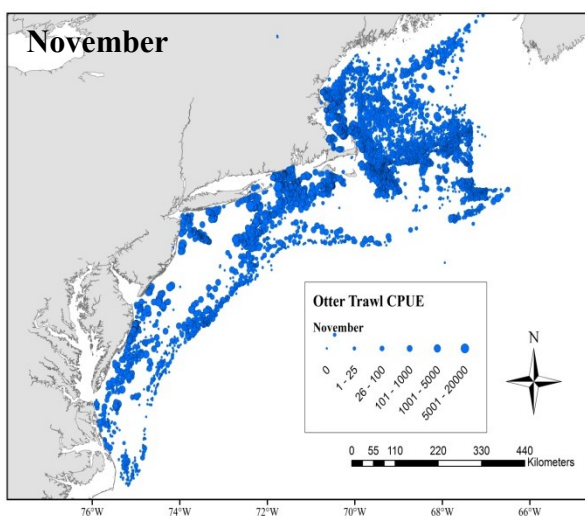
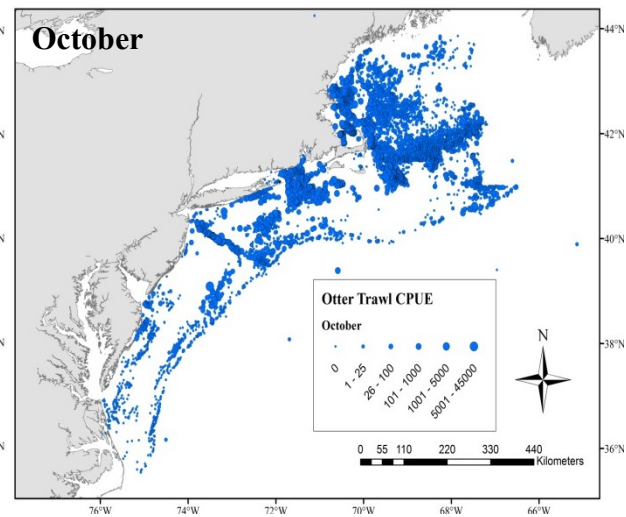
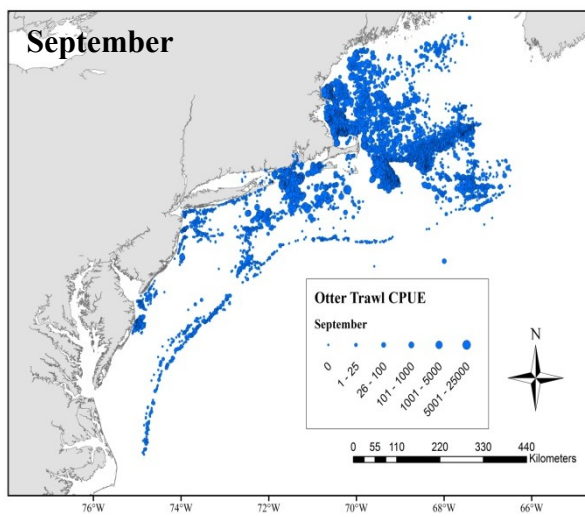
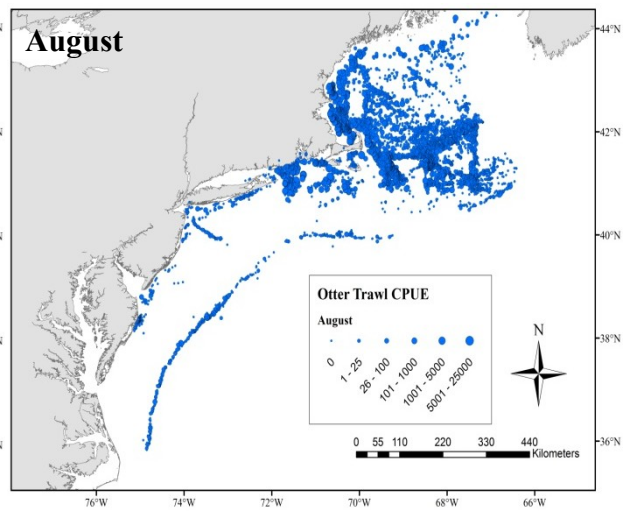
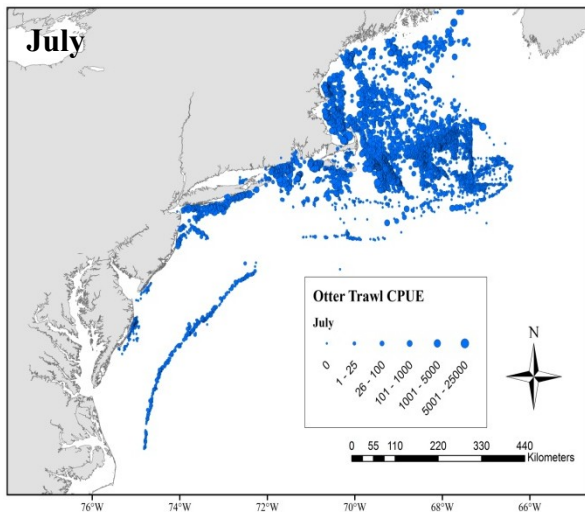


Figure 5.4. Annual degree of clustering in spiny dogfish *CPUE* for the sink gill net and otter trawl fisheries and the NEFSC bottom trawl survey between 1989 and 2009 during autumn (black) and spring (gray). Moran's *I* statistic ranges from +1.0 (clustered) to -1.0 (dispersed) with values = 0 indicative of a random spatial association.

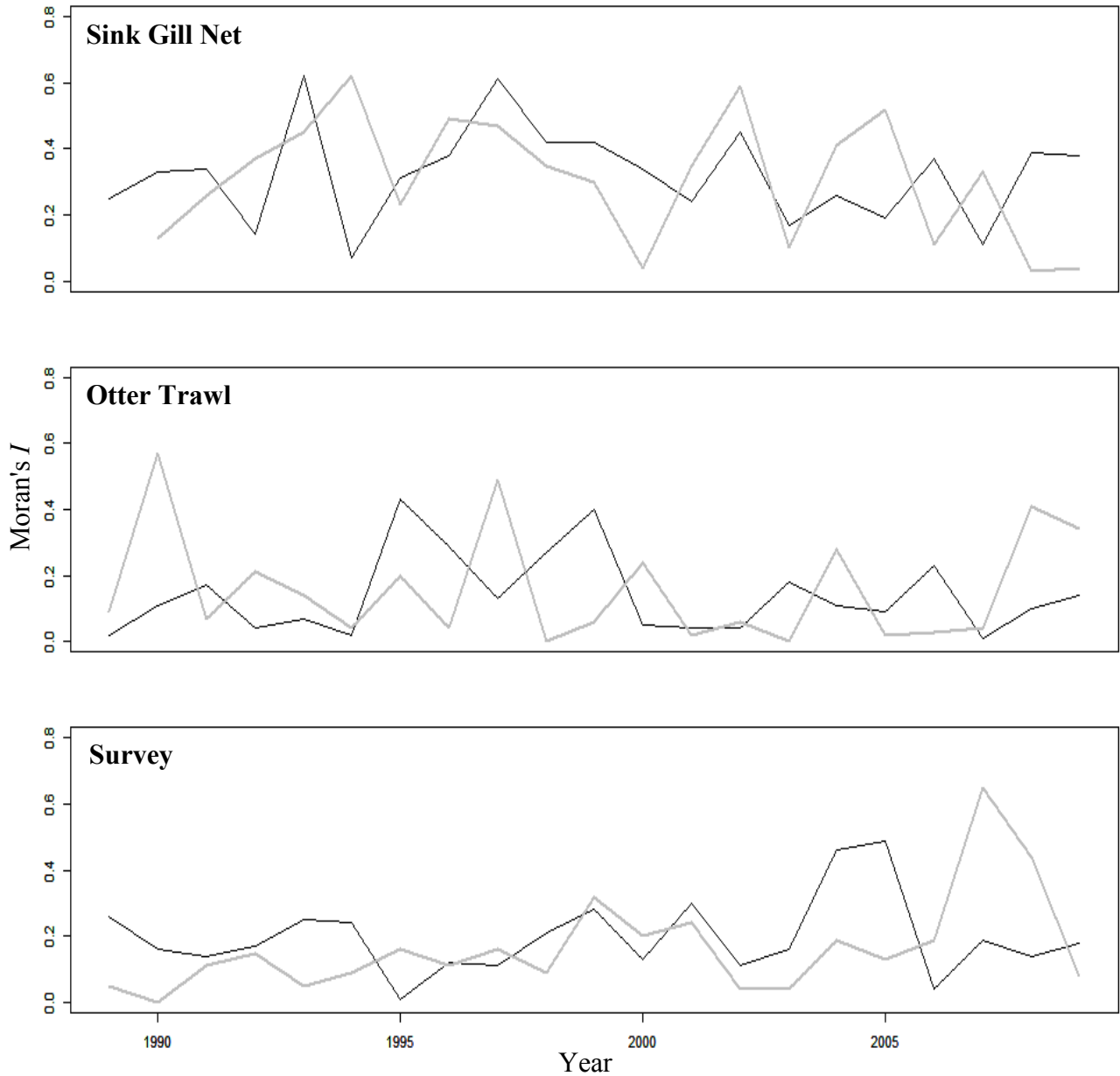


Figure 5.5. Seasonal degree of clustering in spiny dogfish *CPUE* for the sink gill net fishery (SGN), otter trawl fishery (OT), and NEFSC bottom trawl survey (Surv) between 1989 and 2009 during autumn (FALL) and spring (SPR). Moran's *I* statistic ranges from +1.0 (clustered) to -1.0 (dispersed) with values = 0 indicative of a random spatial association. The thick horizontal line reflects the median, the notched box represents the interquartile range and the 25th (bottom) and 75th (top) percentiles, and the whiskers reflect either the maximum value or 1.5 times the interquartile range. Notches provide a rough impression of the significance of the differences between medians.

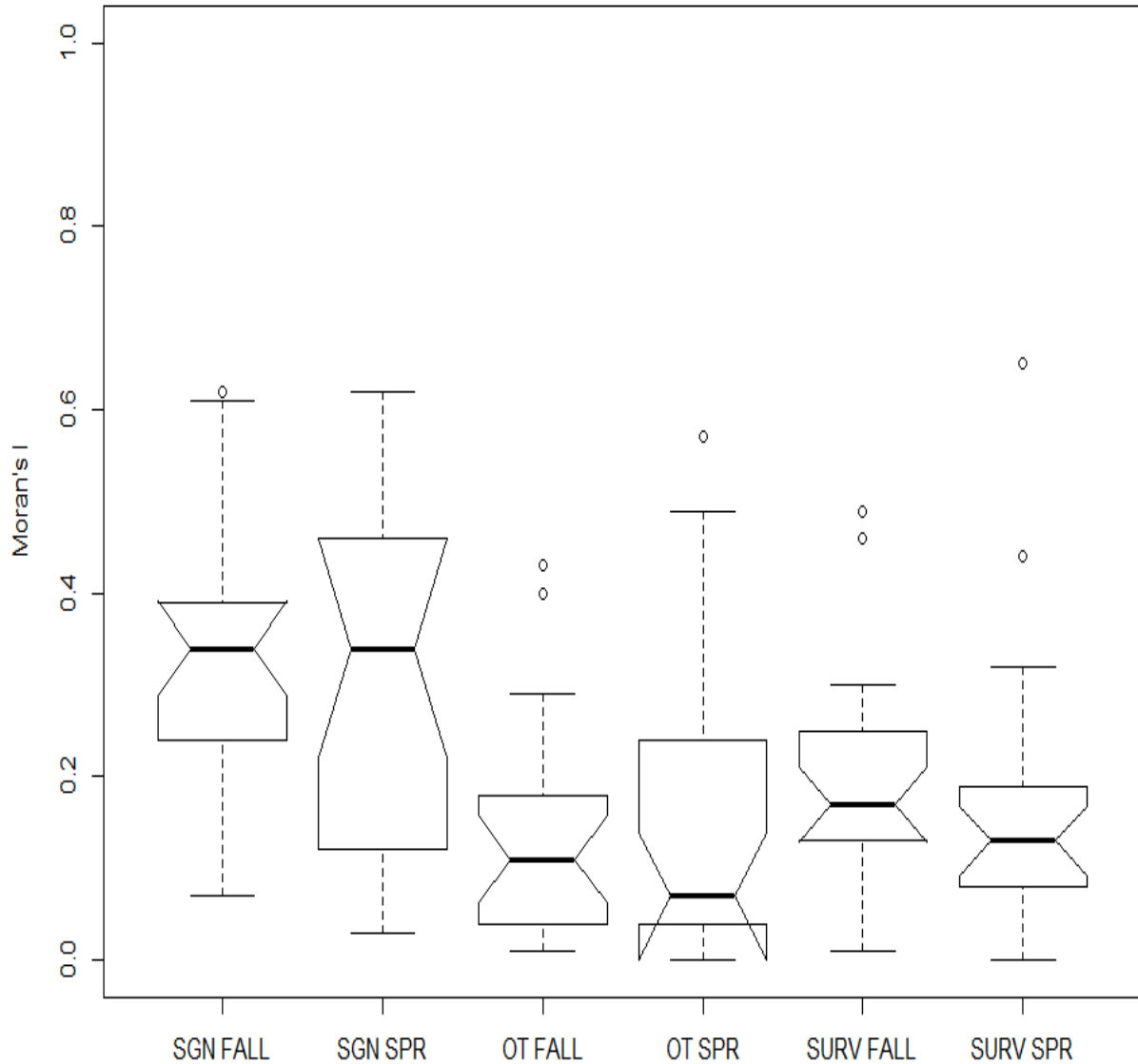


Figure 5.6. Annual centers of spiny dogfish abundance observed by the sink gill net fishery (red), otter trawl fishery (green), and NEFSC bottom trawl survey (black) between 1989 and 2009 during (A) autumn and (B) spring in the Northeast (US) shelf large marine ecosystem. Shaded gray reflects land masses. Gray lines represent depth contours throughout the region.

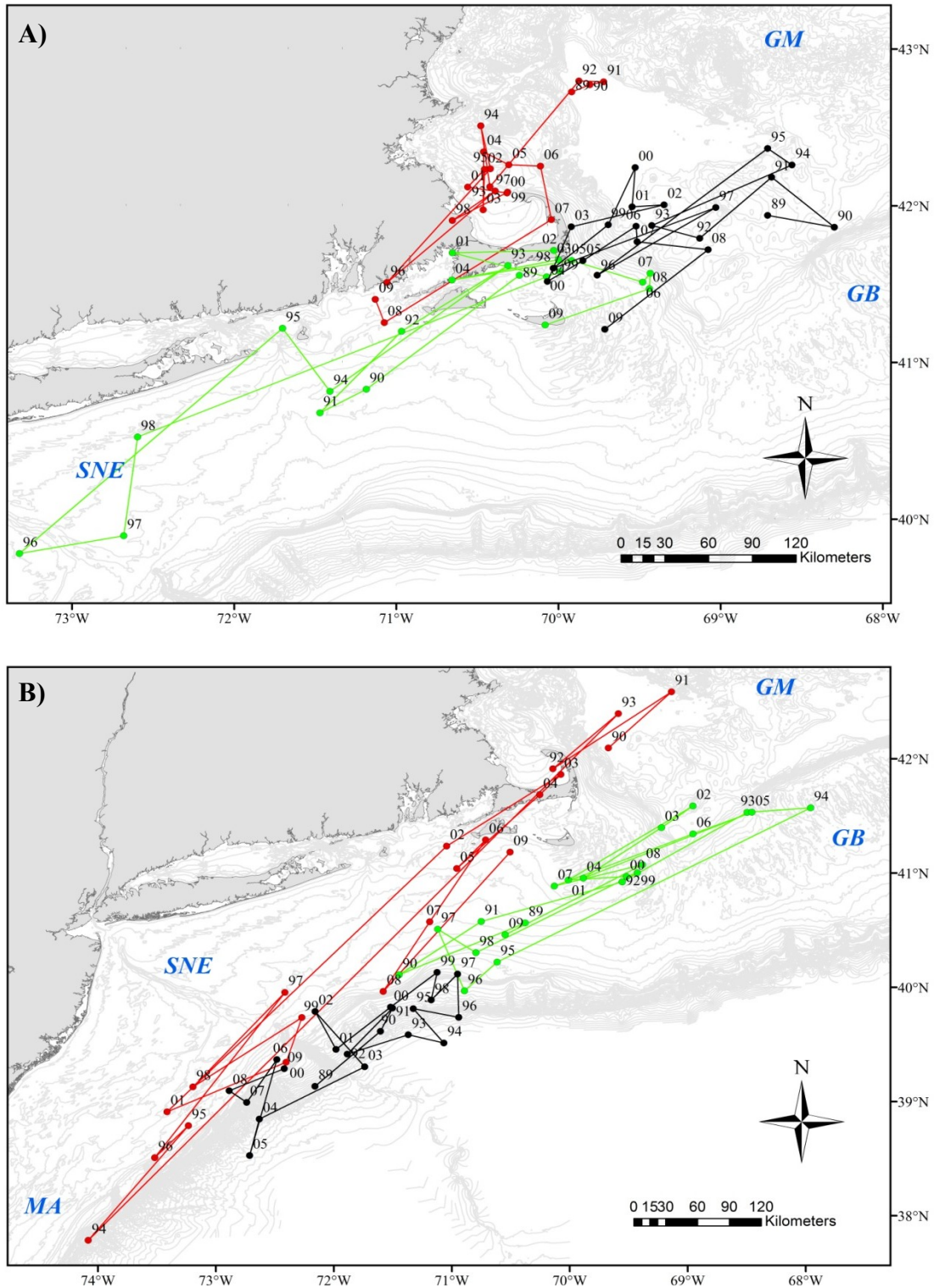


Figure 5.7. Sample (points) and fitted (line) variograms of spiny dogfish *CPUE* for the sink gill net and otter trawl fisheries and the NEFSC bottom trawl survey over the entire time series (1989 – 2009) during autumn (left panel) and spring (right panel) in the Northeast (US) shelf large marine ecosystem. Notes: ranges on x- and y-axes differ between panels.

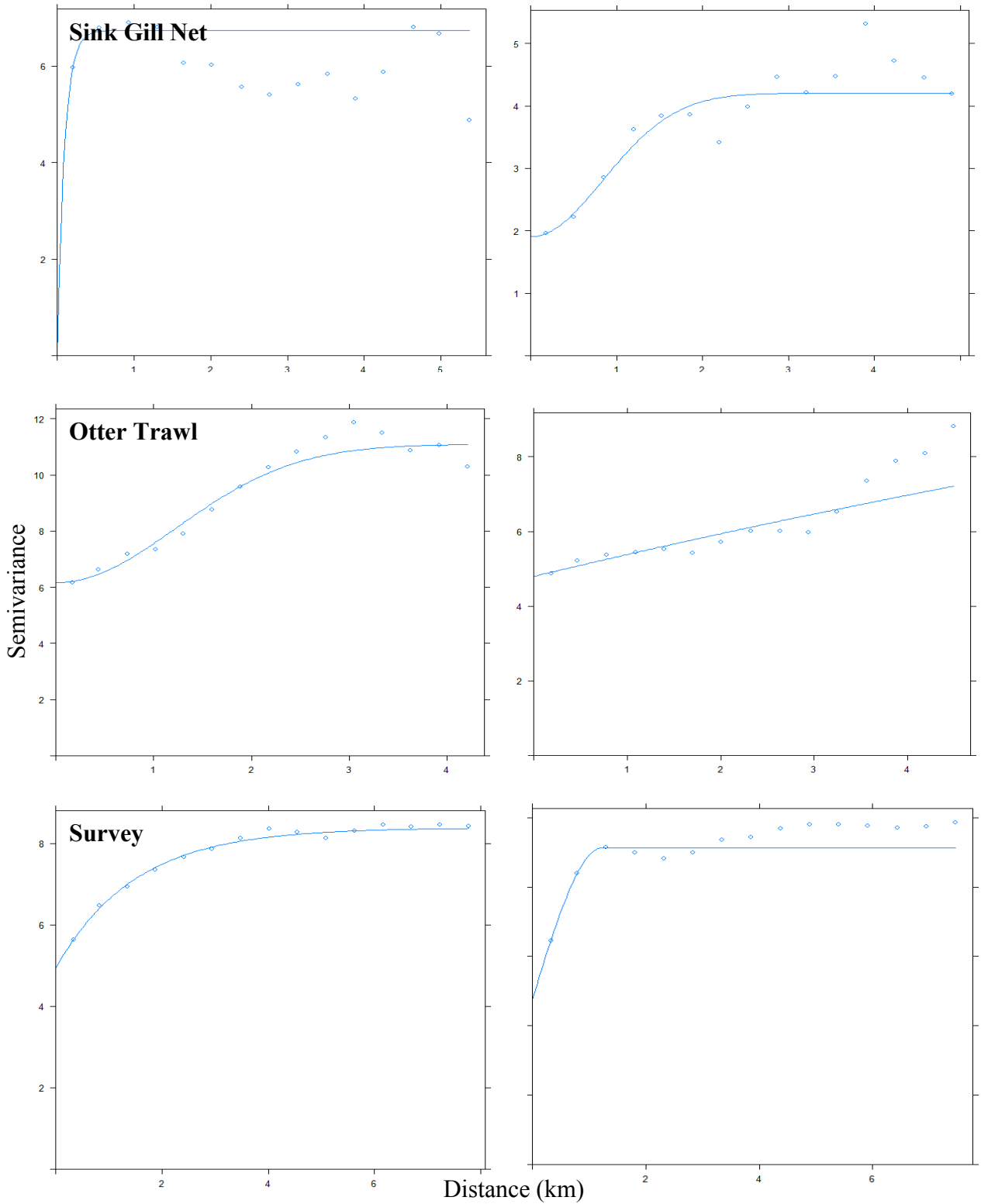


Figure 5.8. Percent spatial overlap (SO_E) of spiny dogfish distribution derived from the NEFSC trawl survey with commercial fisher effort from the sink gill net and otter trawl fisheries between 1989 and 2009 during autumn (black) and spring (gray) in the Northeast (US) shelf large marine ecosystem. SO_E was calculated as the number of grid cells containing both survey catch and commercial fisher effort divided by the number of grid cells where commercial fishers fished. Higher overlap indicates increased vulnerability of spiny dogfish to the fishery.

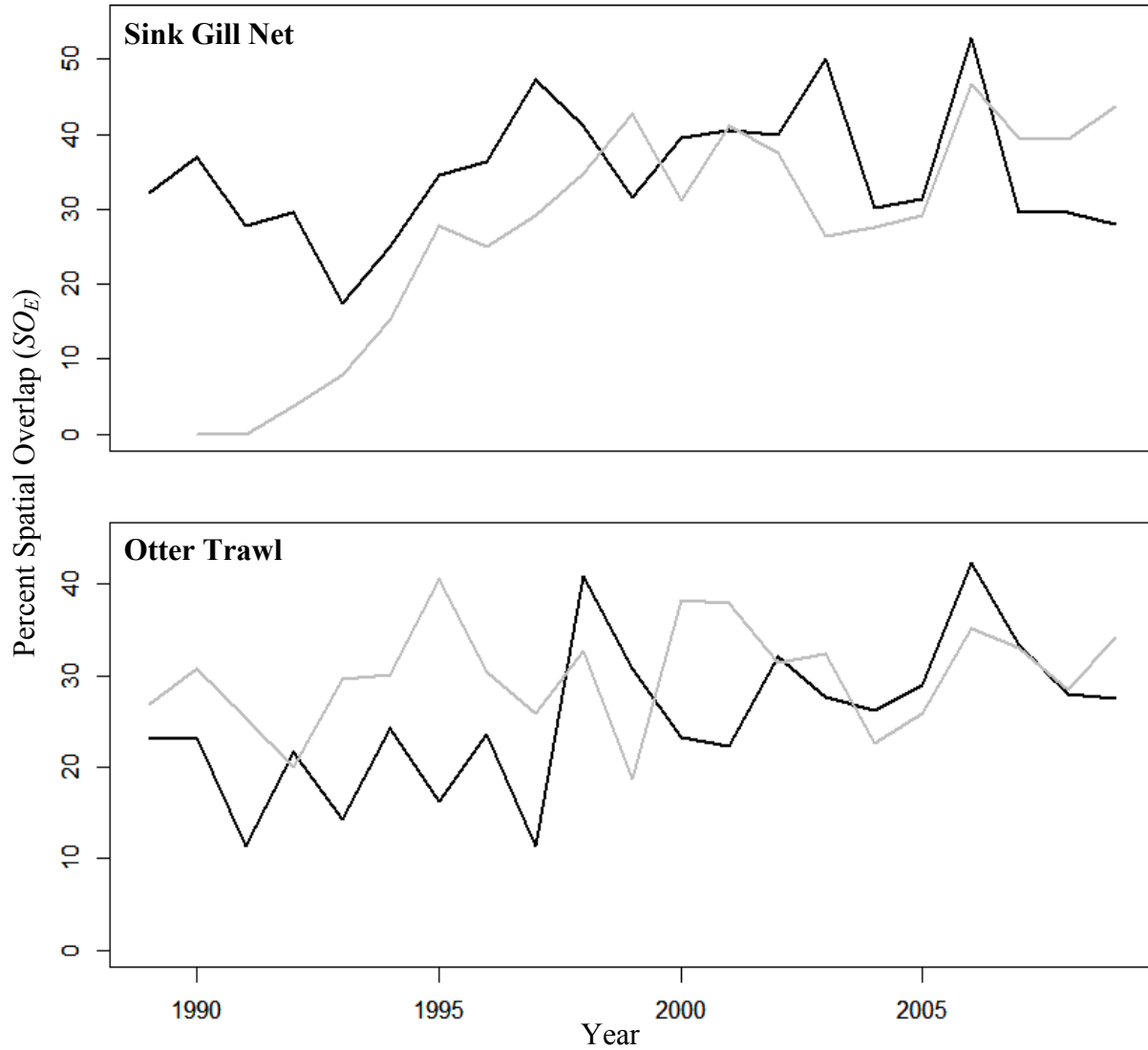


Figure 5.9. Percent spatial overlap (SO_C , SO_I) of spiny dogfish distribution derived from the NEFSC trawl survey with commercial fisher catch for the sink gill net and otter trawl fisheries between 1989 and 2009 during autumn (left panel) and spring (right panel) in the Northeast (US) shelf large marine ecosystem. Solid lines reflect direct spatial overlap (SO_C) whereas dashed lines reflect spatial overlap using interpolated values (SO_I). Higher values indicate increased overlap between spiny dogfish distribution derived from the survey and each fishery.

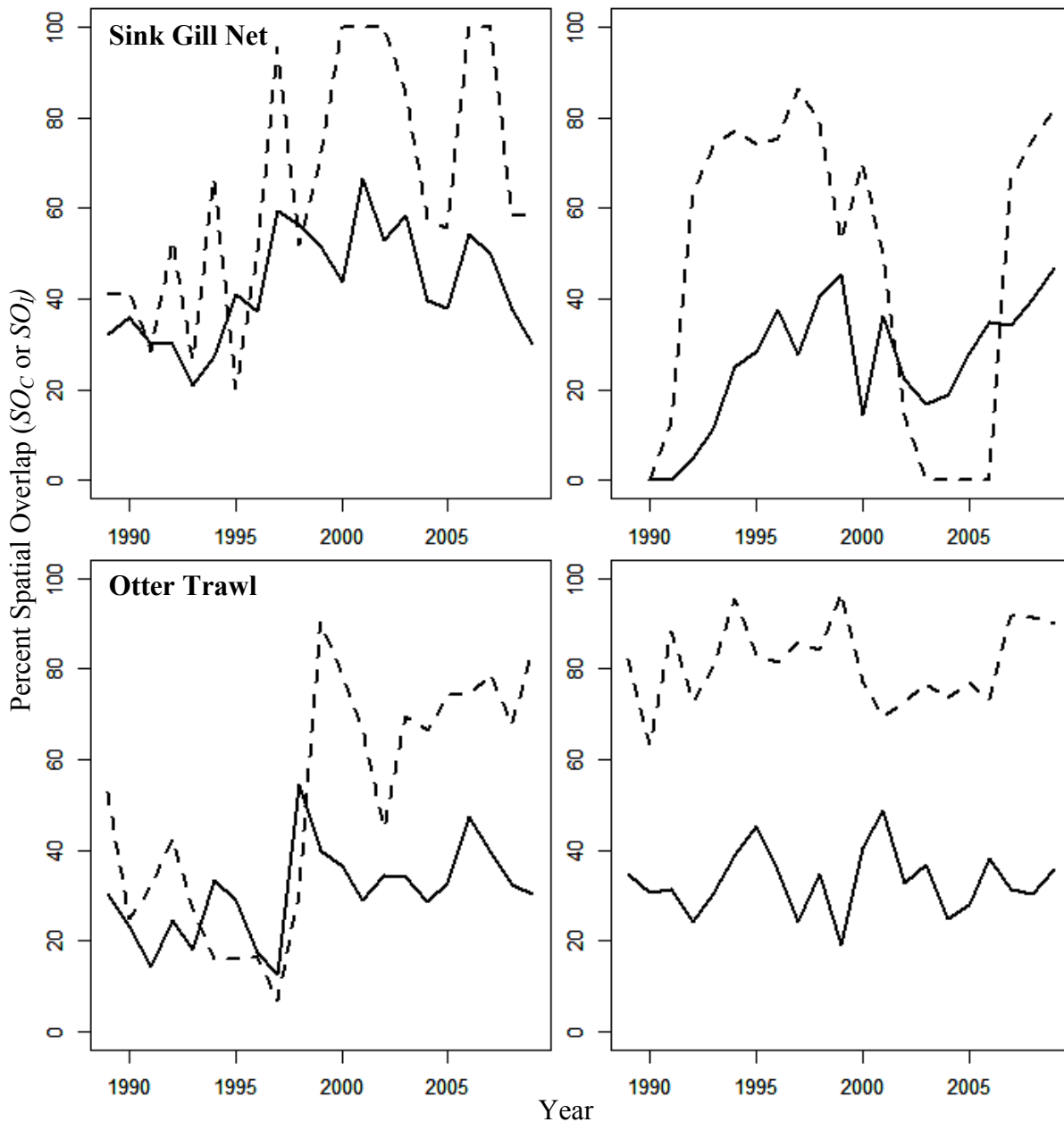
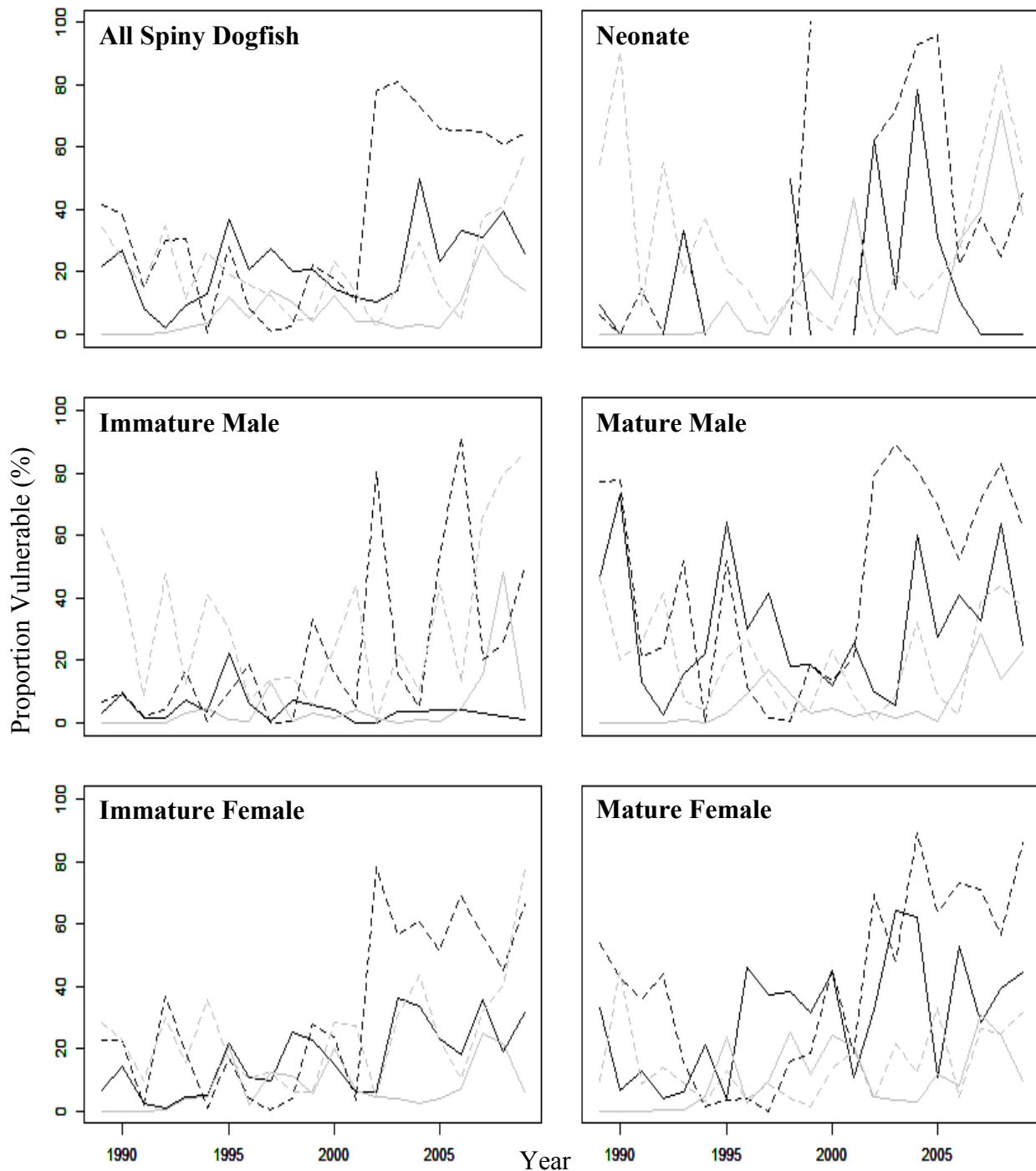


Figure 5.10. Proportion of the spiny dogfish stock vulnerable to the sink gill net (solid line) and otter trawl (dashed line) fisheries between 1989 and 2009 during autumn (black) and spring (gray) in the Northeast (US) shelf large marine ecosystem. The proportion vulnerable was estimated as the total survey catch of each spiny dogfish life-history stage in cells where commercial fishers fished divided by the entire survey catch of each stage. Stages include neonate (total length, TL \leq 26 cm), immature male (26 cm $<$ TL $<$ 60 cm), mature male (TL \geq 60 cm), immature female (26 cm $<$ TL $<$ 80 cm) and mature female (TL \geq 80 cm).



Chapter 6:

SUMMARY

Recent declines of principal groundfish stocks in the northwest Atlantic have promoted harvest of the previously undesirable spiny dogfish (Rago et al. 1998, McMillan & Morse 1999). However, the sustainability of this resource has been questioned due to intensive harvest of large fecund females, declining trends in survey-derived indices of mature female size, neonate size, and recruitment in combination with male-skewed sex ratios (Rago et al. 1998, NEFSC 2006, Rago & Sosebee 2009). In addition, their complex seasonal movements, high variability in distributional trends, and ubiquitous abundance have introduced uncertainty into survey-derived indices of abundance, therefore complicating stock assessment (NEFSC 2006, Rago & Sosebee 2009). Their commercial and ecological importance warrants sustainable management, which has unfortunately been challenged by a paucity of information on stage-specific distribution, abundance, ecological role, and survey catchability in relation to the environment.

The goals of my dissertation aimed at improving the stock assessment of spiny dogfish through assessing habitat and distribution in relation to environmental and/or ecological factors and by elucidating how distributional changes and seasonal movements can influence survey catchability and availability to commercial fishers. In the habitat approach, I identified preferred habitat and modeled spiny dogfish occurrence and abundance using Northeast Fisheries Science Center (NEFSC) survey data in order to better understand how environmental and ecological factors influence ontogenetic distributions. This was achieved in chapter 2 "Influence of

environmental, spatial, and ontogenetic variables on habitat selection and management of spiny dogfish in the Northeast (US) shelf large marine ecosystem" and chapter 3 "Application of generalized additive models to examine ontogenetic and seasonal distributions of spiny dogfish (*Squalus acanthias*) in the Northeast (US) shelf large marine ecosystem".

In the second part of my dissertation I focus on catchability of spiny dogfish and key prey species. First, I investigated the catchability of the NEFSC bottom trawl survey to assess diel and environmental influences on catch rates of both predator (i.e., spiny dogfish) and prey (Atlantic butterfish, Atlantic herring, *Illex* sp., *Loligo* sp., Atlantic mackerel) to elucidate the potential for multi-species interactions. In addition, I reported *CPUE* estimates adjusted for diel variation when necessary in chapter 4 "Is diel variation in catchability skewing survey-derived abundance estimates of spiny dogfish and their prey within the Northeast (US) shelf large marine ecosystem?" Lastly, in chapter 5 "Spatio-temporal interactions between spiny dogfish and commercial fishers in the Northeast (US) shelf large marine ecosystem", I examined how changes in spiny dogfish distribution have impacted their availability to commercial fisheries to provide insight into fish-fisher spatio-temporal dynamics.

In chapter 2, I presented seasonal movement and abundance patterns that have implications for the assessment of spiny dogfish and ecosystem dynamics of the NES LME. I identified seasonal ontogenetic habitat preferences in order to better understand how dogfish stages associate with environmental conditions and how this can influence survey estimates of relative abundance. My analyses, which built upon previous habitat knowledge of spiny dogfish collected from Canadian waters (Scott 1982, Shepherd et al. 2002), highlighted the importance of recognizing sex- and stage-dependence. Latitudinal trends provided quantitative evidence of a general spiny dogfish movement pattern of overwintering in southern regions with northerly

movements during summer. In addition, investigation of neonate (total length, TL \leq 26 cm) trends revealed a narrow latitudinal range which may serve as important nursery grounds. Specifically, these findings suggest that environmental conditions influence the availability of spiny dogfish to bottom trawls. For a species like spiny dogfish whose range shifts seasonally, timing of sampling and interannual variation in environmental drivers may bias survey-derived abundance estimates.

In chapter 3, I provided vital information concerning spiny dogfish habitat, stage co-occurrence, and inter-species interactions by generalized additive modeling. This approach enabled the investigation of mechanisms behind distributional changes and forecasted future distributions under different environmental scenarios (i.e., climate change). Significant nonlinear relationships were widespread throughout dogfish stages and seasons. Environmental factors were significantly related to the occurrence and abundance of most dogfish stages. The importance of bottom temperature on occurrence supports the previous notion that temperature is a migratory cue (Murawski & Finn 1988, McMillan & Morse 1999, Collette & Klein-MacPhee 2002, Methratta & Link 2007). During autumn, ecological factors also played an important role in shaping abundance, particularly for mature female and neonate spiny dogfish. Forecasted occurrence during spring revealed that even slightly above or below average temperatures can result in large changes to the probability of capturing spiny dogfish throughout the survey range.

In chapter 4, I examined catch rates and catchability for spiny dogfish and key prey species for diel variation and environmental influences to provide insight into survey catchability and potential ecological interactions (i.e., predator-prey). Catch rates and survey catchability revealed higher day-time estimates for many dogfish stages and prey species, highlighting the potential for bias within stage-specific or species-specific abundance estimates. Current methods

appear to be overestimating abundances of both spiny dogfish and prey species, a bias which has important implications towards stock sustainability and quantification of population consumption rates. Night-time catches may provide a better indicator of true biomass since spiny dogfish are spread more evenly throughout the water column. Environmental factors frequently influenced the seasonal probability of day-time catch for all species. These results have important implications regarding the usage of survey estimates for stock assessment and encourage further efforts to enhance our understanding of both single-species population dynamics and ecological interactions.

In chapter 5, I quantified the spatio-temporal interactions among spiny dogfish and two commercial fisheries (otter trawl, OT; sink gill net, SGN) in the NES LME using NEFSC observer data between 1989 to 2009. I utilized survey and fisher behavior to document changes in the availability of the stock to provide insight into inherent variability in abundance estimates. Fishers encountered spiny dogfish throughout the region during most calendar months with summer catches primarily north and winter catches predominantly south. During both seasons, spiny dogfish *CPUE* was more clustered ($I \sim 0.3$) in the SGN fishery compared to both the OT ($I \sim 0.15$) and survey ($I \sim 0.18$). Central locations of spiny dogfish abundance varied both seasonally and annually. Increased spatial overlap and availability was observed for the SGN fishery during spring and the OT fishery during autumn, suggesting a growing portion of the stock available to each fishery. Vulnerability analyses revealed stage-dependent trends and recent increases, particularly during autumn.

Overall, my results will enhance assessment of this species by contributing stage-specific information on habitat selection, population ecology, and catchability, thereby reducing inconsistencies in trend monitoring. From chapter 2, increased knowledge of behavior in relation

to the environment will reduce variability associated with survey indices and improves measures of trend. In addition to providing a foundation for hypothesis-driven studies aimed at forecasting the response of spiny dogfish to a changing climate, results from Chapter 3 can be used to better understand the relationship between sampling periods and movement drivers to catchability of the population in the NES LME. Chapter 4 provides critical insight into the usage of survey estimates for stock assessment and reports adjustments to account for variations in catchability. Lastly, Chapter 5 enhances our understanding of fisher distribution and elucidates how changes in the availability of a stock may mask mechanisms behind inherent variability within survey estimates.

During their seasonal migrations spiny dogfish often appear highly abundant in local areas for several months at a time. In these locations, they are often blamed for the declines or suppressed recovery of important commercial species and, as a result, few animals attract more disdain from commercial fishermen and anglers. The nuisance and controversial reputations of spiny dogfish seem undeserved; while their ubiquitous abundance can pose a challenge to fishers, their life-history characteristics and aggregated behavior warn of high vulnerability to heavy exploitation. Reproductively, spiny dogfish boasts one of the slowest gestation periods with mature females traveling enormous distances across environmental gradients. In addition, their ecological importance to the NES LME remains relatively unknown. Additional research is needed to better manage and understand the population dynamics of the spiny dogfish.

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Appendix 1A. Stock Assessment Efforts Put Forth by the Northeast Fisheries Science Center (NEFSC) on Marine Resources within the Northeast (US) shelf Large Marine Ecosystem

Table 1A.1. Stock assessments conducted on marine resources in the Northeast (US) shelf large marine ecosystem since the first Stock Assessment Workshop (SAW) in 1985 by the NEFSC. Data obtained from <http://www.nefsc.noaa.gov/saw/>. Regions assessed are listed in parentheses when necessary and include Gulf of Maine (GM), Georges Bank (GB), Southern New England (SNE), and the Middle Atlantic Bight (MA).

Species	Total	Species	Total
<u>Crustaceans</u>		<u>Osteichthyes (cont'd)</u>	
American lobster	5	Red hake	3
Northern shrimp	5	Red hake (GM/northern GB)	2
Deep sea red crab	1	Red hake (southern GB/MA)	2
<u>Mollusks</u>		Redfish	4
Ocean quahog	11	Redfish (GM/GB)	2
Sea scallops	14	River herring/shad	1
Atlantic surfclam	11	Salmon	1
<i>Illex</i> squid	13	Scup	8
<i>Loligo</i> squid	13	Scup (SNE)	1
<u>Agnathans</u>		Silver hake	8
Atlantic hagfish	1	Silver hake (GM/northern GB)	2
<u>Osteichthyes</u>		Silver hake (southern GB/MA)	2
American plaice	6	Striped bass	4
American plaice (GB)	1	Summer flounder	13
American plaice (GM)	1	Tautog (Blackfish)	2
Atlantic cod	2	Tilefish	5
Atlantic cod (GB)	9	Weakfish	3
Atlantic cod (GM)	10	White hake	5
Atlantic herring	7	White hake (GB/GM)	2
Atlantic herring (GM)	1	Windowpane flounder (northern)	1
Black sea bass	9	Windowpane flounder (southern)	1
Black sea bass (northern stock)	1	Winter flounder	3
Bluefish	8	Winter flounder (inshore)	1
Butterfish	9	Winter flounder (GB)	4
Butterfish (GM/MA)	1	Winter flounder (GM)	3
Cusk	2	Winter flounder (SNE/MA)	4
Haddock	3	Witch flounder	5
Haddock (GB)	5	Witch flounder (GB/GM)	1
Haddock (GM)	4	Atlantic wolffish	2
Atlantic mackerel	10	Yellowtail flounder	3
<u>Osteichthyes (cont'd)</u>			

Monkfish (Goosefish)	7	Yellowtail flounder (SNE/MA)	7
Ocean pout	3	Yellowtail flounder (GB)	5
Offshore hake	1	Yellowtail flounder (Cape Cod/GM)	3
Pollock	6		
<u>Elasmobranchs</u>			
NE skate complex	2		
Skates	1		
Spiny dogfish	5		
Small elasmobranchs	1		

Appendix 2A. Decadal Distributions and Regional Survey Catch of Spiny Dogfish

Figure 2A.1. Decadal distribution and regional survey catch of neonate (TL \leq 26 cm) spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring. Plotted are the number per tow (dark green = 0, green = 1, light green = 2-5, yellow = 6-10, orange = 11-100, red $>$ 101). Pie charts show regional proportion of survey catch from the Middle Atlantic Bight (white), Southern New England (light gray), Georges Bank (gray), and the Gulf of Maine (dark gray). Notes: Inshore sampling began in 1973 and data collection was limited during the 1960s.

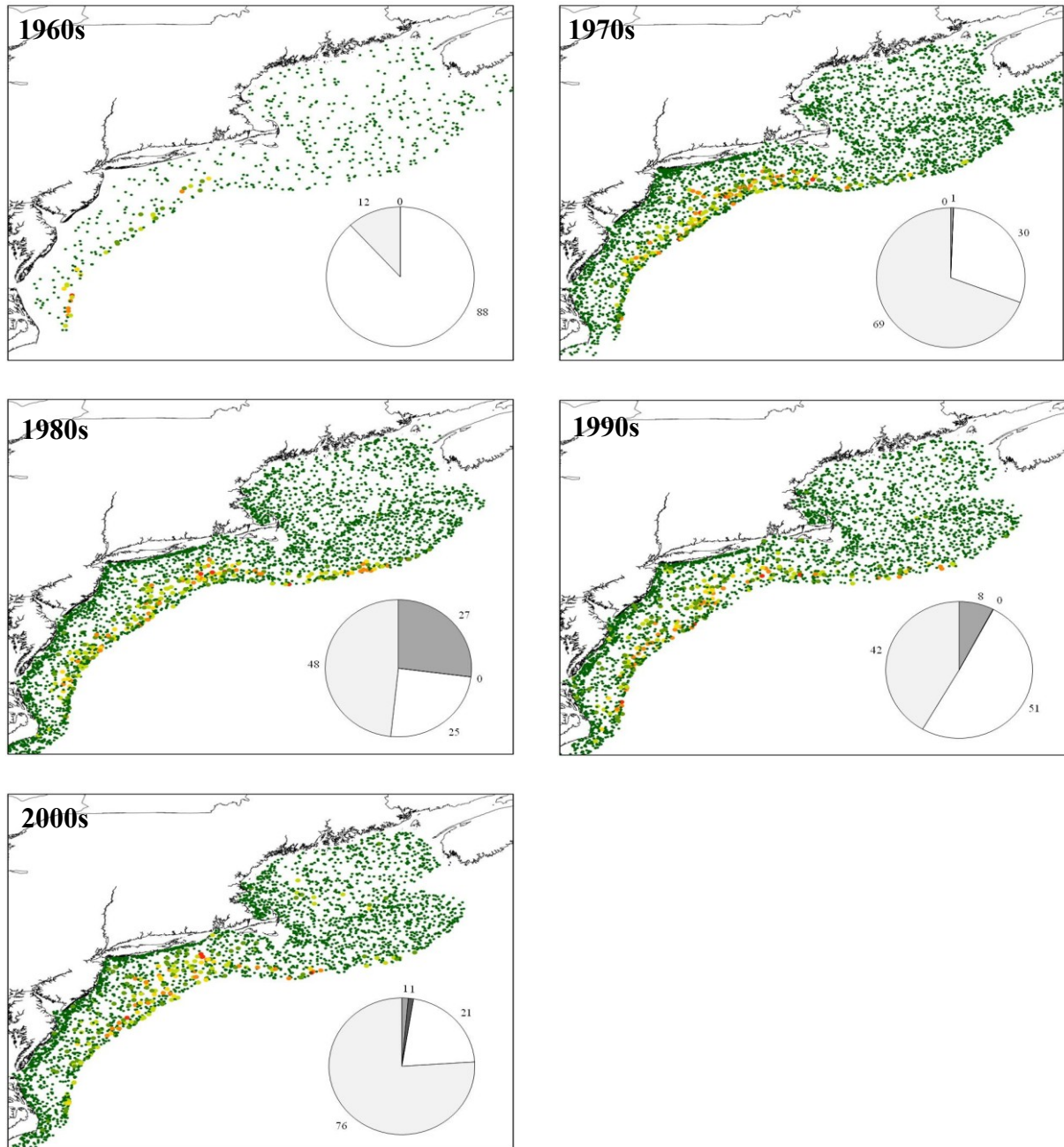


Figure 2A.2. Decadal distribution and regional survey catch of neonate (TL \leq 26 cm) spiny dogfish in the Northeast (US) shelf large marine ecosystem during autumn. Plotted are the number per tow (dark green = 0, green = 1, light green = 2-5, yellow = 6-10, orange = 11-15, red $>$ 16). Pie charts show regional proportion of survey catch from the Middle Atlantic Bight (white), Southern New England (light gray), Georges Bank (gray), and the Gulf of Maine (dark gray). Notes: Inshore sampling began in 1972 and data collection was limited during the 1960s.

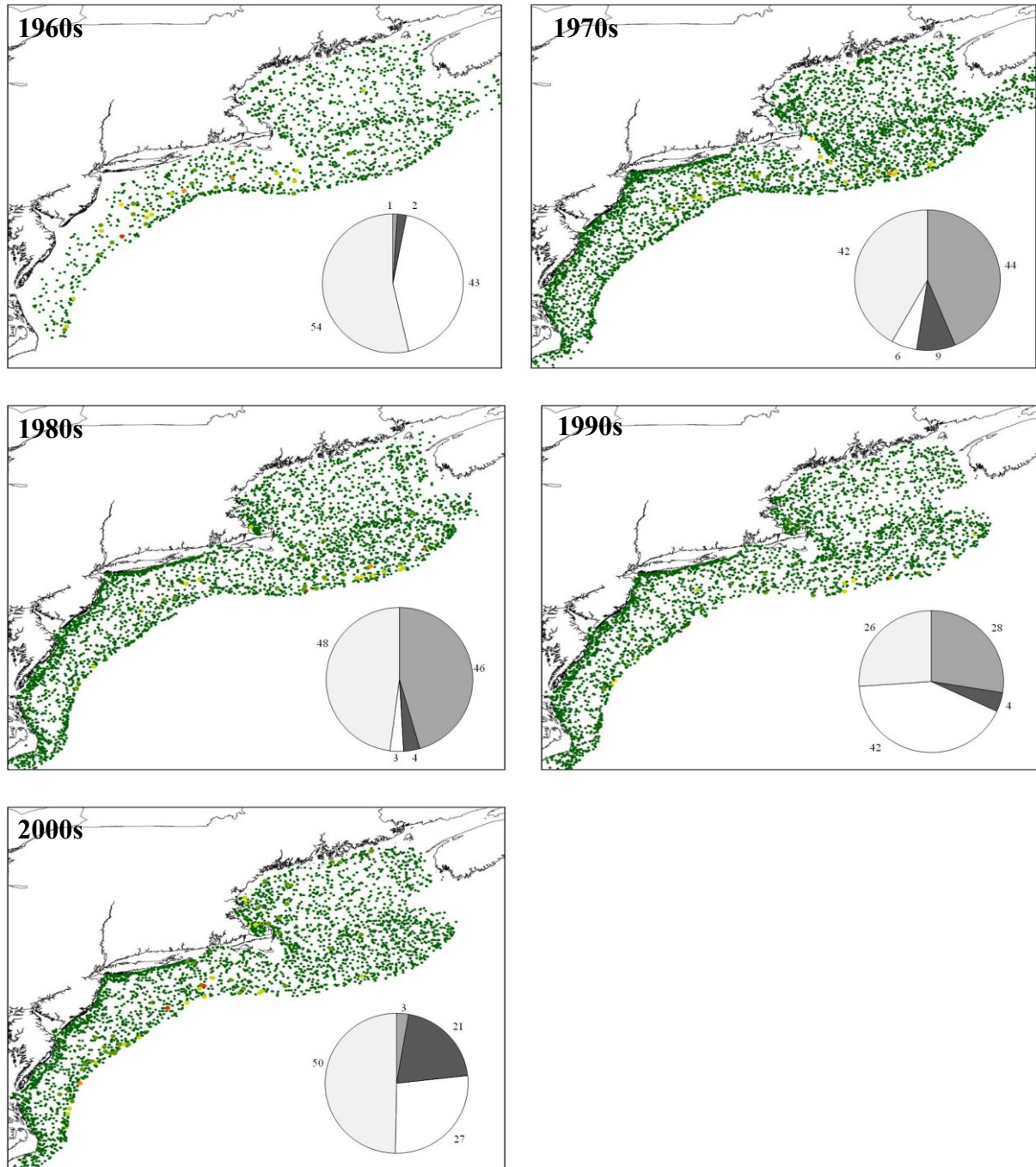


Figure 2A.3. Decadal distribution and regional survey catch of immature male (26 cm < TL < 60 cm) spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring. Plotted are the number per tow (dark green = 0, green = 1-50, light green = 51-100, yellow = 101-250, orange = 251-1000, red > 1001). Pie charts show regional proportion of survey catch from the Middle Atlantic Bight (white), Southern New England (light gray), Georges Bank (gray), and the Gulf of Maine (dark gray). Note: spiny dogfish not sexed consistently until 1980.

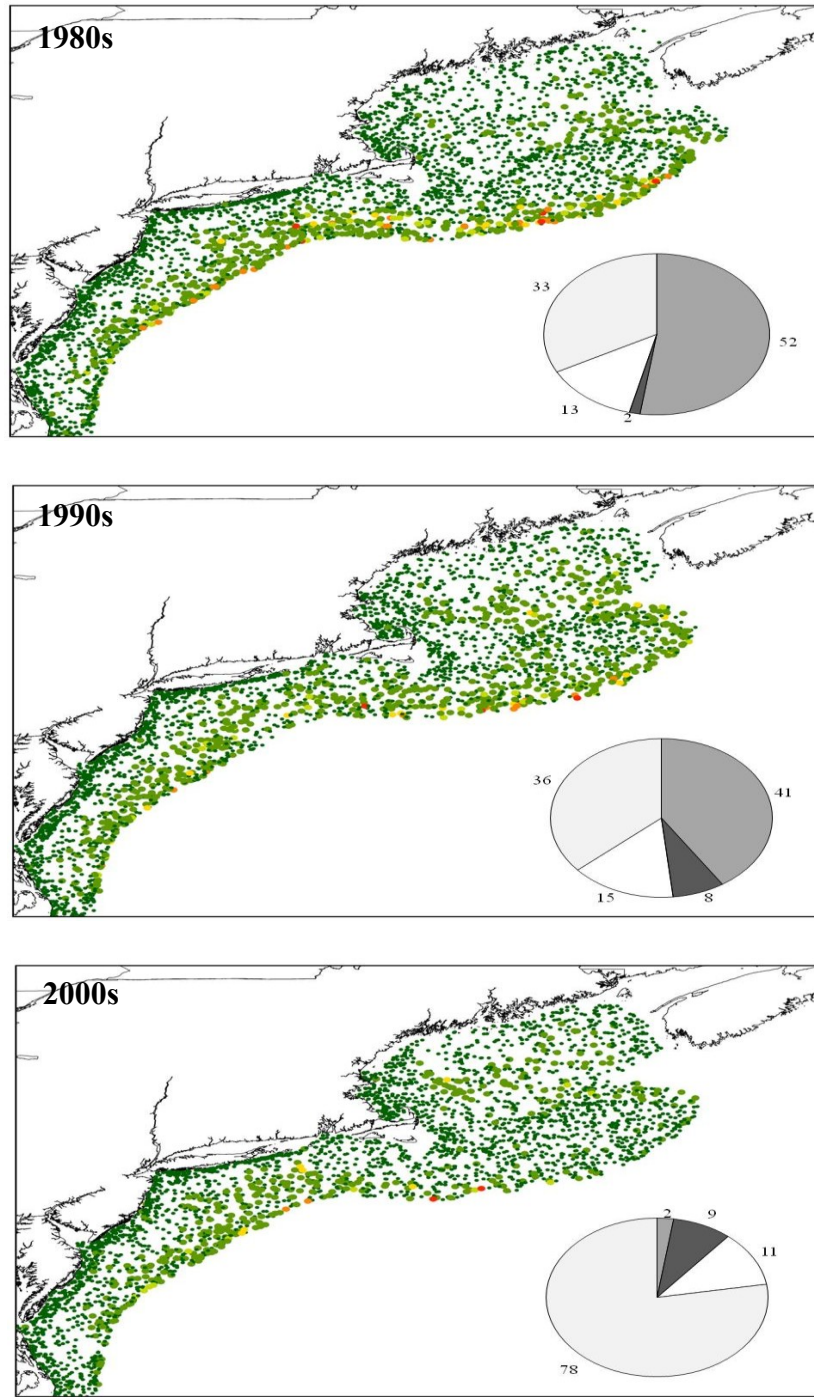


Figure 2A.4. Decadal distribution and regional survey catch of immature male (26 cm < TL < 60 cm) spiny dogfish in the Northeast (US) shelf large marine ecosystem during autumn. Plotted are the number per tow (dark green = 0, green = 1-50, light green = 51-100, yellow = 101-250, orange = 251-1000, red > 1001). Pie charts show regional proportion of survey catch from the Middle Atlantic Bight (white), Southern New England (light gray), Georges Bank (gray), and the Gulf of Maine (dark gray). Note: spiny dogfish not sexed consistently until 1980.

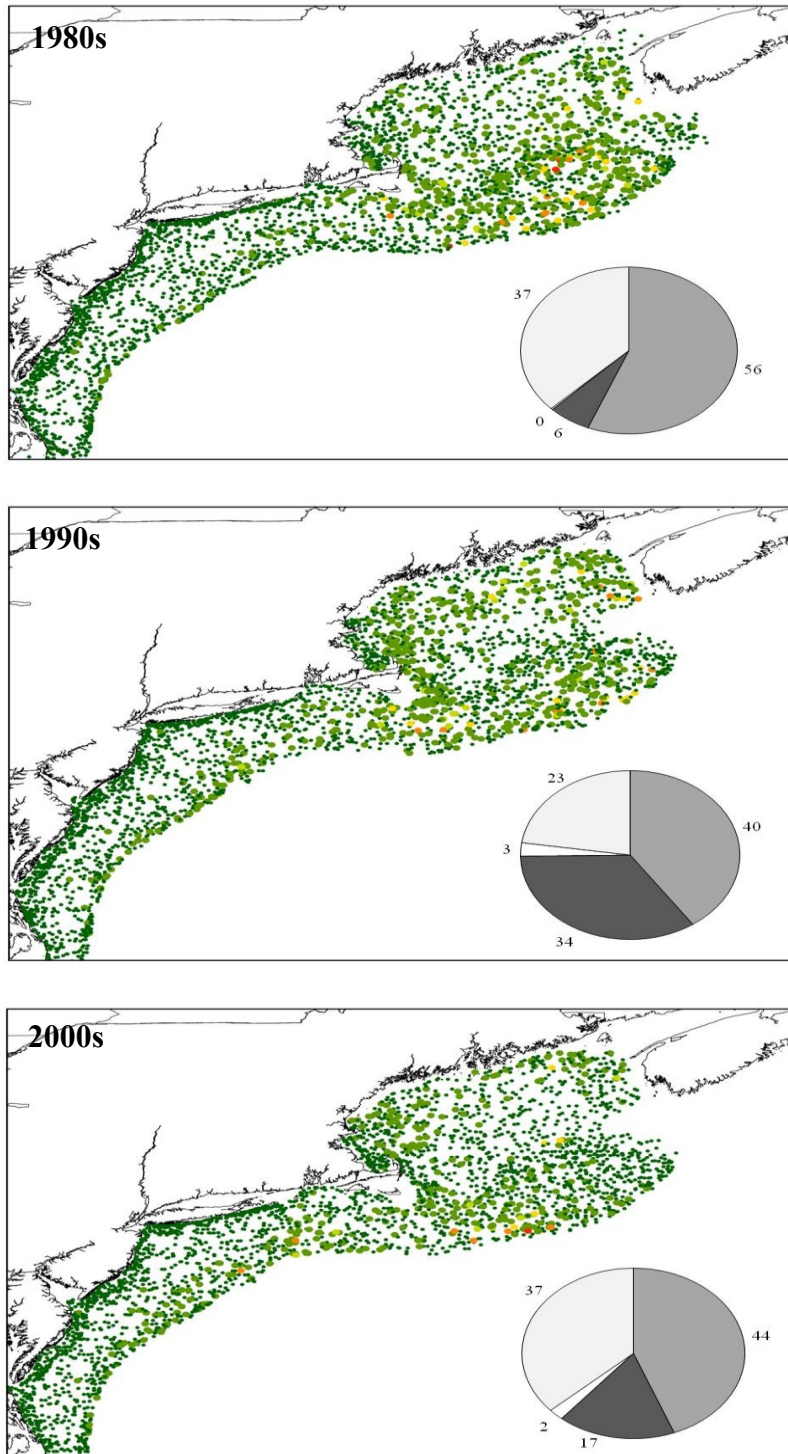


Figure 2A.5. Decadal distribution and regional survey catch of immature female (26 cm < TL < 80 cm) spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring. Plotted are the number per tow (dark green = 0, green = 1-50, light green = 51-100, yellow = 101-250, orange = 251-1000, red > 1001). Pie charts show regional proportion of survey catch from the Middle Atlantic Bight (white), Southern New England (light gray), Georges Bank (gray), and the Gulf of Maine (dark gray). Note: spiny dogfish not sexed consistently until 1980.

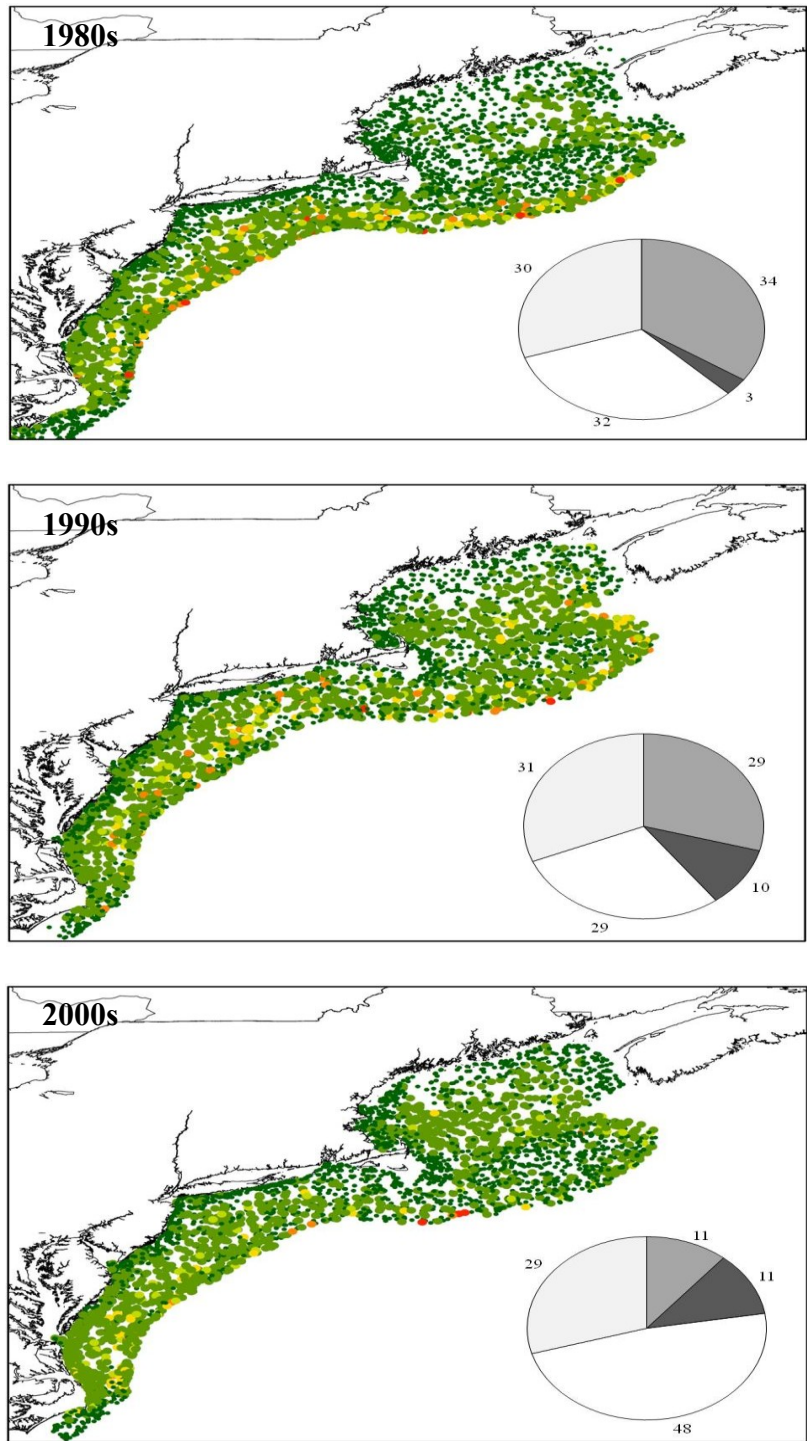


Figure 2A.6. Decadal distribution and regional survey catch of immature female (26 cm < TL < 80 cm) spiny dogfish in the Northeast (US) shelf large marine ecosystem during autumn. Plotted are the number per tow (dark green = 0, green = 1-50, light green = 51-100, yellow = 101-250, orange = 251-1000, red > 1001). Pie charts show regional proportion of survey catch from the Middle Atlantic Bight (white), Southern New England (light gray), Georges Bank (gray), and the Gulf of Maine (dark gray). Note: spiny dogfish not sexed consistently until 1980.

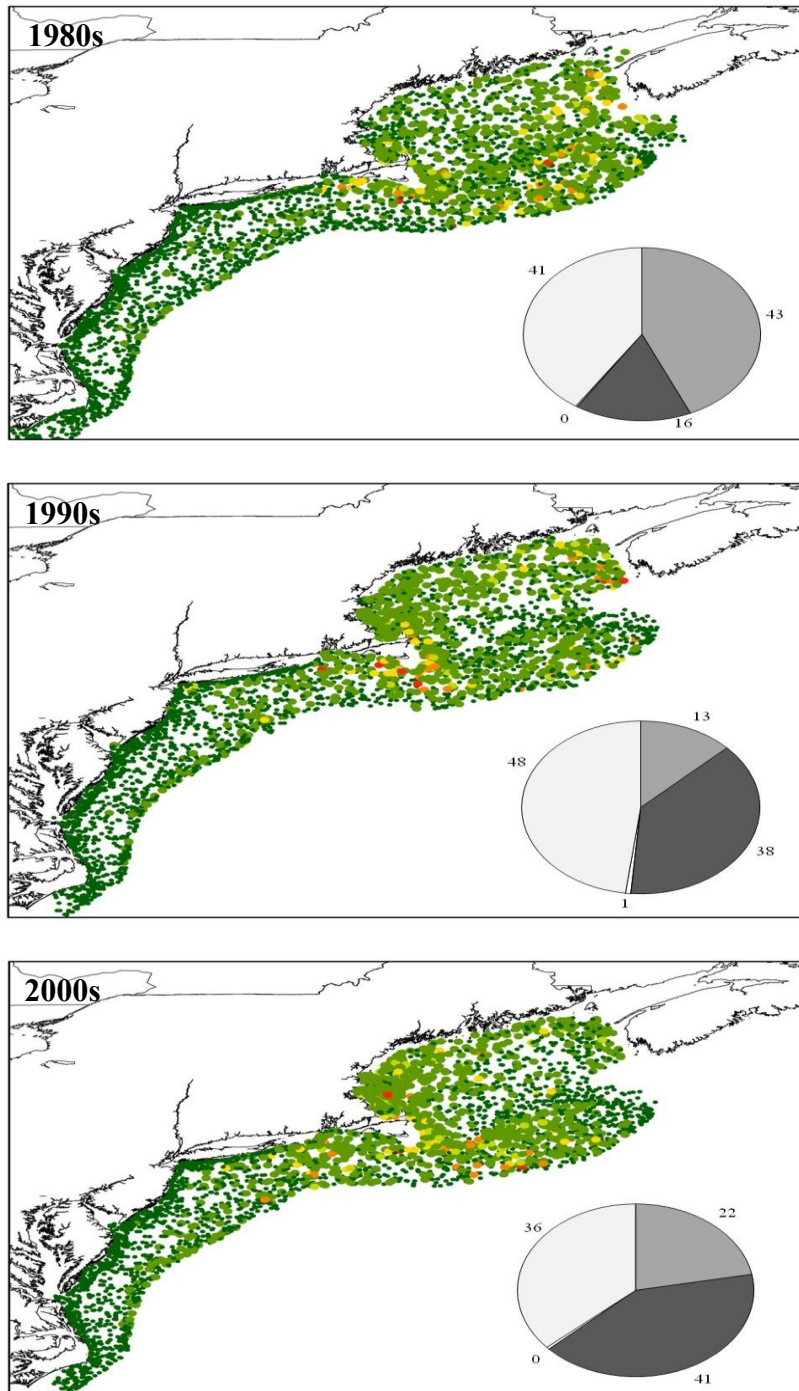


Figure 2A.7. Decadal distribution and regional survey catch of mature male (TL \geq 60 cm) spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring. Plotted are the number per tow (dark green = 0, green = 1-50, light green = 51-100, yellow = 101-250, orange = 251-1000, red $>$ 1001). Pie charts show regional proportion of survey catch from the Middle Atlantic Bight (white), Southern New England (light gray), Georges Bank (gray), and the Gulf of Maine (dark gray). Note: spiny dogfish not sexed consistently until 1980.

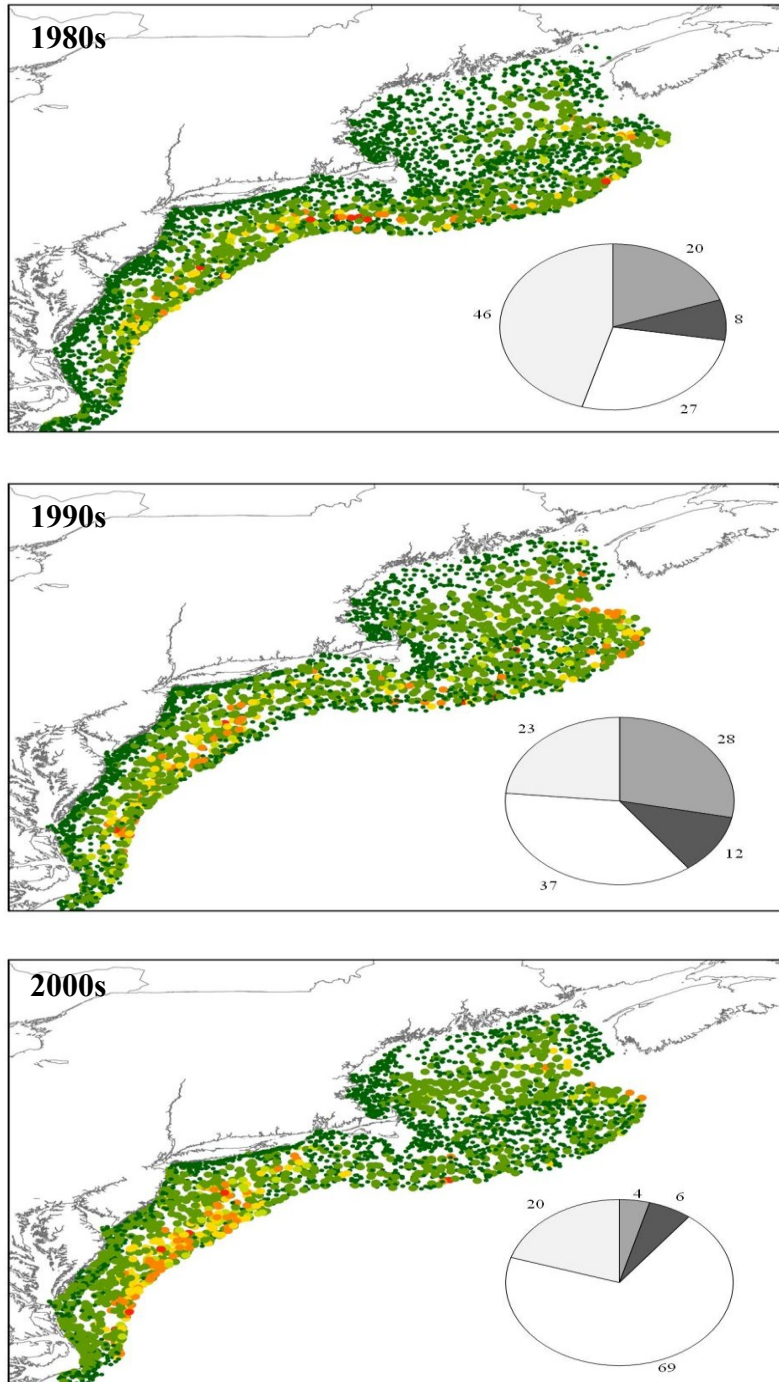


Figure 2A.8. Decadal distribution and regional survey catch of mature male (TL \geq 60 cm) spiny dogfish in the Northeast (US) shelf large marine ecosystem during autumn. Plotted are the number per tow (dark green = 0, green = 1-50, light green = 51-100, yellow = 101-250, orange = 251-1000, red > 1001). Pie charts show regional proportion of survey catch from the Middle Atlantic Bight (white), Southern New England (light gray), Georges Bank (gray), and the Gulf of Maine (dark gray). Note: spiny dogfish not sexed consistently until 1980.

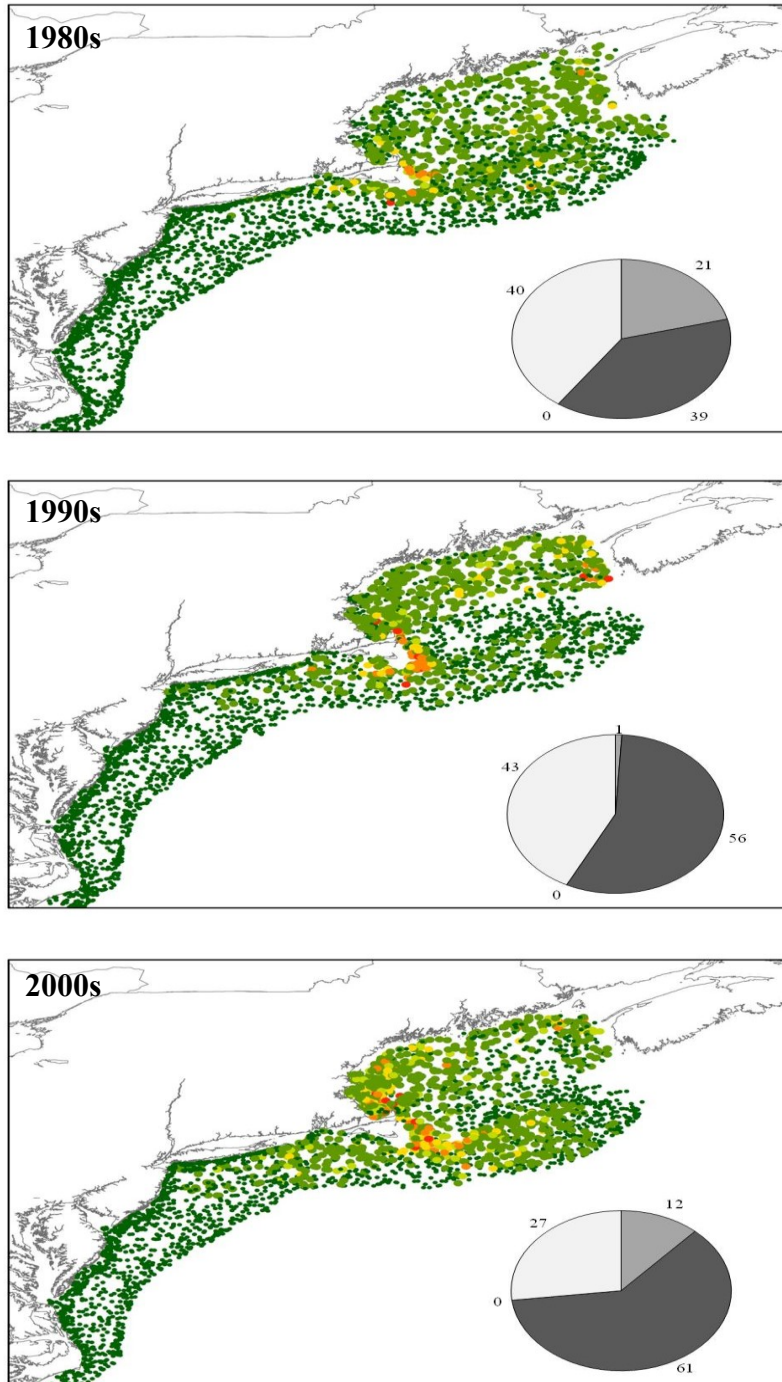


Figure 2A.9. Decadal distribution and regional survey catch of mature female (TL \geq 80 cm) spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring. Plotted are the number per tow (dark green = 0, green = 1-50, light green = 51-100, yellow = 101-250, orange = 251-1000, red > 1001). Pie charts show regional proportion of survey catch from the Middle Atlantic Bight (white), Southern New England (light gray), Georges Bank (gray), and the Gulf of Maine (dark gray). Note: spiny dogfish not sexed consistently until 1980.

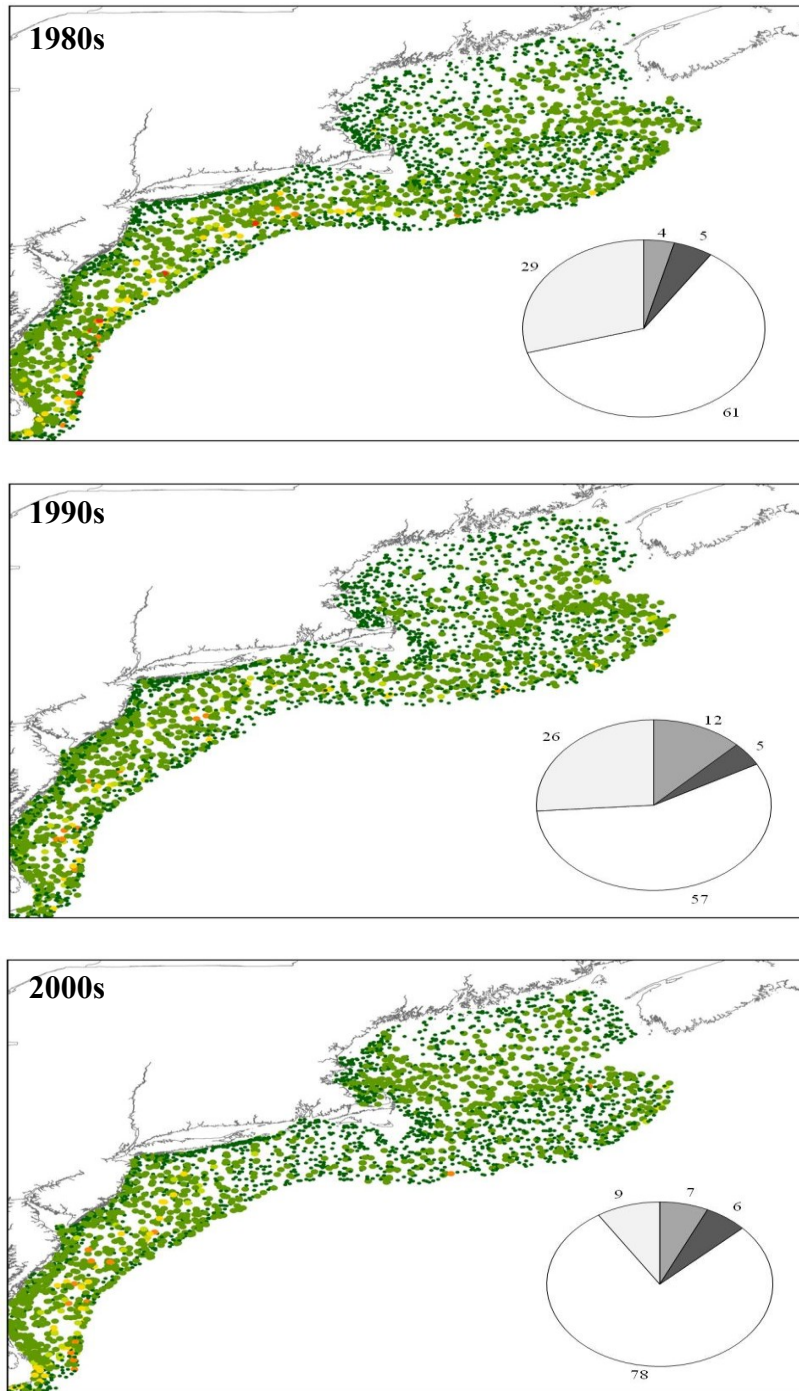
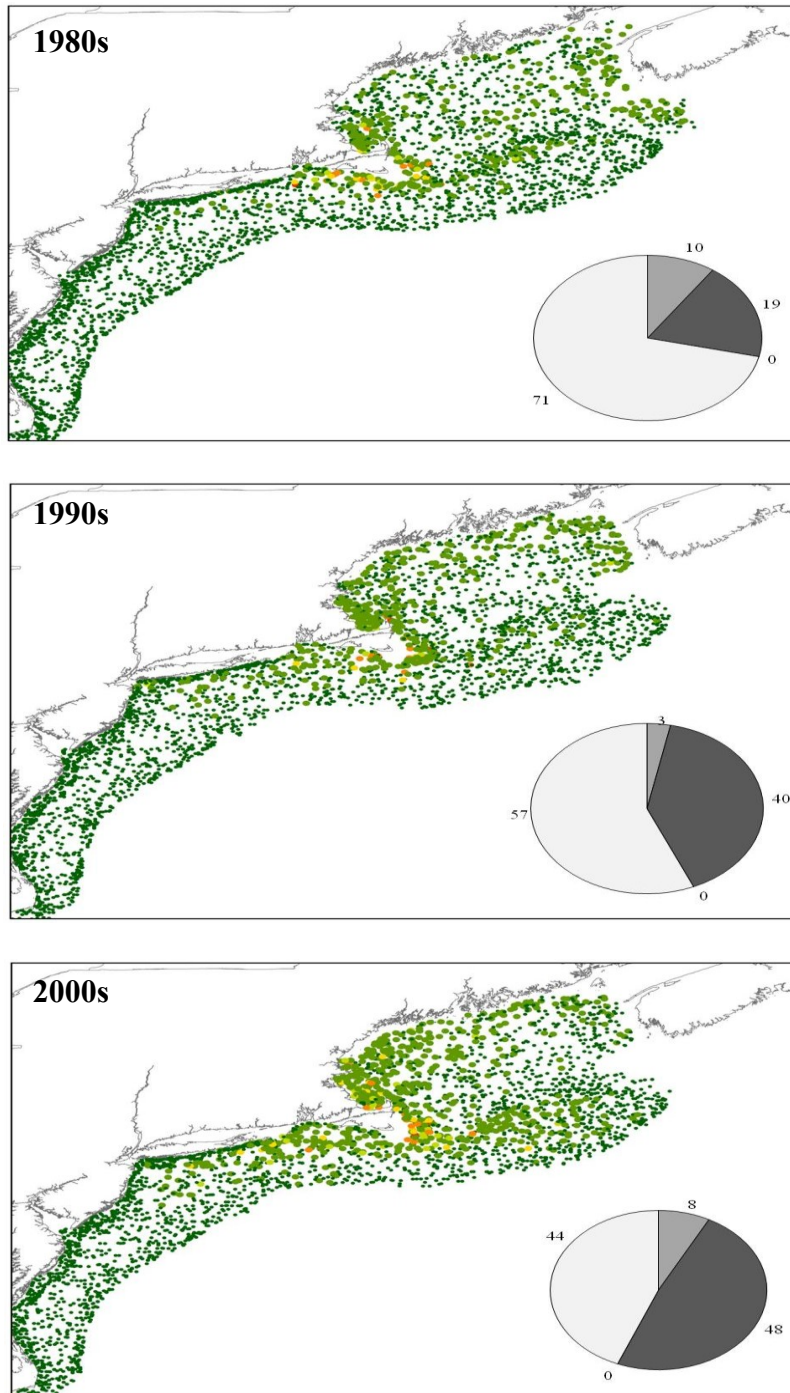


Figure 2A.10. Decadal distribution and regional survey catch of mature female (TL \geq 80 cm) spiny dogfish in the Northeast (US) shelf large marine ecosystem during autumn. Plotted are the number per tow (dark green = 0, green = 1-50, light green = 51-100, yellow = 101-250, orange = 251-1000, red > 1001). Pie charts show regional proportion of survey catch from the Middle Atlantic Bight (white), Southern New England (light gray), Georges Bank (gray), and the Gulf of Maine (dark gray). Note: spiny dogfish not sexed consistently until 1980.



Appendix 2B. Spiny Dogfish Abundance

Table 2B.1. Correlations between z-score transformed regional abundances of spiny dogfish life history stages during spring (1968 – 2009) and autumn (1963 – 2009) in the Northeast (US) shelf large marine ecosystem. GB = Georges Bank, GM = Gulf of Maine, SNE = Southern New England, and MA = Middle Atlantic Bight. Stages as defined in Table 2.1. Note: spiny dogfish not sexed consistently until 1980.

	SPRING				AUTUMN			
	GB	GM	SNE	MA	GB	GM	SNE	MA
All								
GB	1.00	0.26	0.25	0.05	1.00	0.03	0.12	-0.18
GM	-	1.00	0.06	0.22	-	1.00	0.04	-0.16
SNE	-	-	1.00	0.20	-	-	1.00	0.04
MA	-	-	-	1.00	-	-	-	1.00
Neo								
GB	1.00	-0.19	0.03	0.00	1.00	-0.04	-0.13	-0.13
GM	-	1.00	0.19	-0.13	-	1.00	0.01	0.06
SNE	-	-	1.00	0.17	-	-	1.00	0.43
MA	-	-	-	1.00	-	-	-	1.00
ImmM								
GB	1.00	0.30	0.30	0.65	1.00	0.17	0.09	-0.09
GM	-	1.00	0.50	0.36	-	1.00	-0.10	0.05
SNE	-	-	1.00	0.33	-	-	1.00	0.10
MA	-	-	-	1.00	-	-	-	1.00
MatM								
GB	1.00	0.25	0.15	-0.13	1.00	0.32	0.31	-0.09
GM	-	1.00	0.14	0.25	-	1.00	0.34	-0.13
SNE	-	-	1.00	0.18	-	-	1.00	-0.01
MA	-	-	-	1.00	-	-	-	1.00
ImmF								
GB	1.00	0.37	0.45	0.41	1.00	0.23	0.25	-0.07
GM	-	1.00	0.40	0.37	-	1.00	0.03	0.05
SNE	-	-	1.00	0.32	-	-	1.00	0.10
MA	-	-	-	1.00	-	-	-	1.00
MatF								
GB	1.00	0.38	0.42	0.26	1.00	0.40	0.15	-0.08
GM	-	1.00	0.36	0.43	-	1.00	0.54	-0.04
SNE	-	-	1.00	0.38	-	-	1.00	0.35
MA	-	-	-	1.00	-	-	-	1.00

Figure 2B.1. Deviations in mean annual abundance (*CPUE*) for spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring (1968 – 2009). Residuals calculated as annual *CPUE* subtracted from overall mean *CPUE*. Note: spiny dogfish not sexed consistently until 1980.

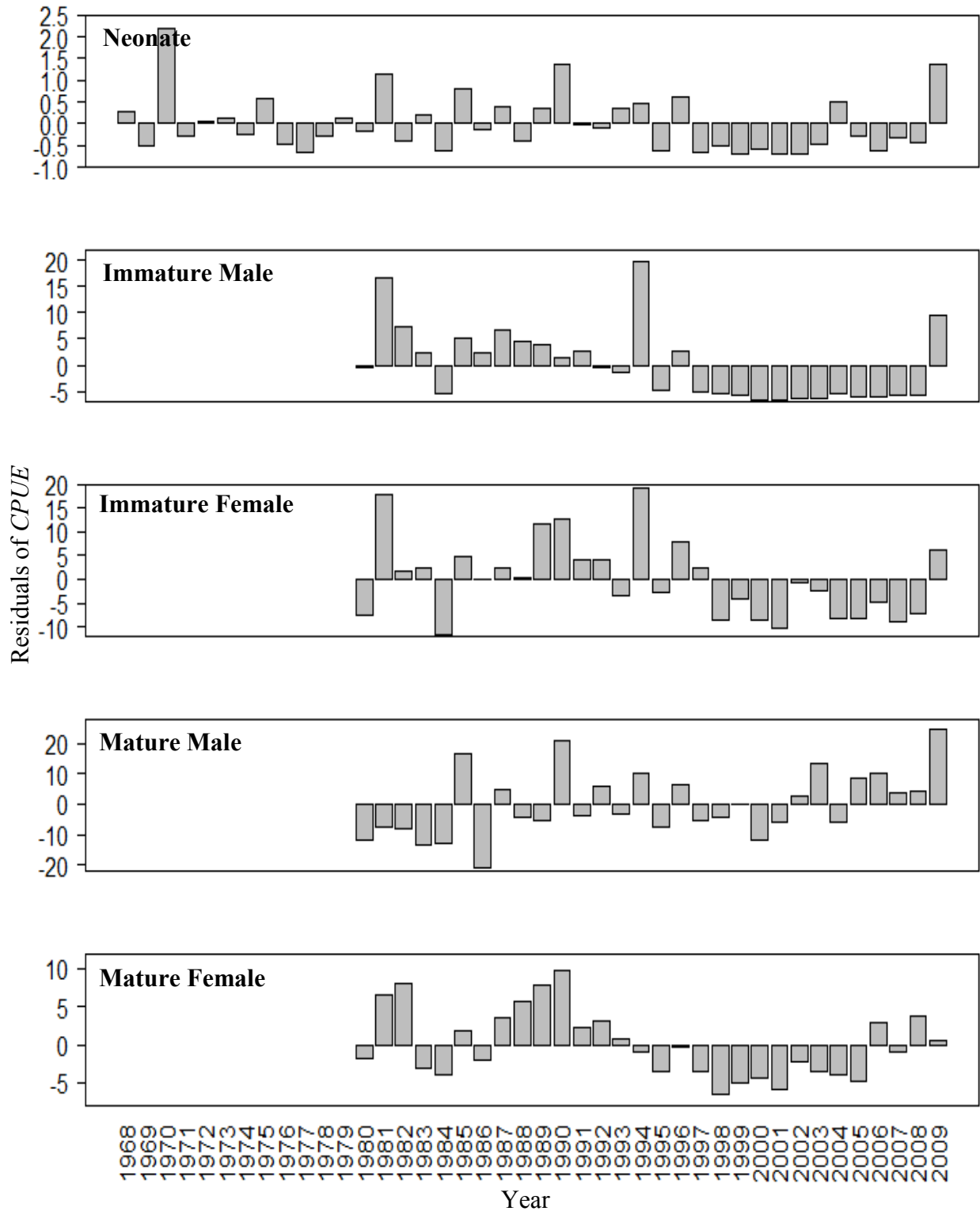
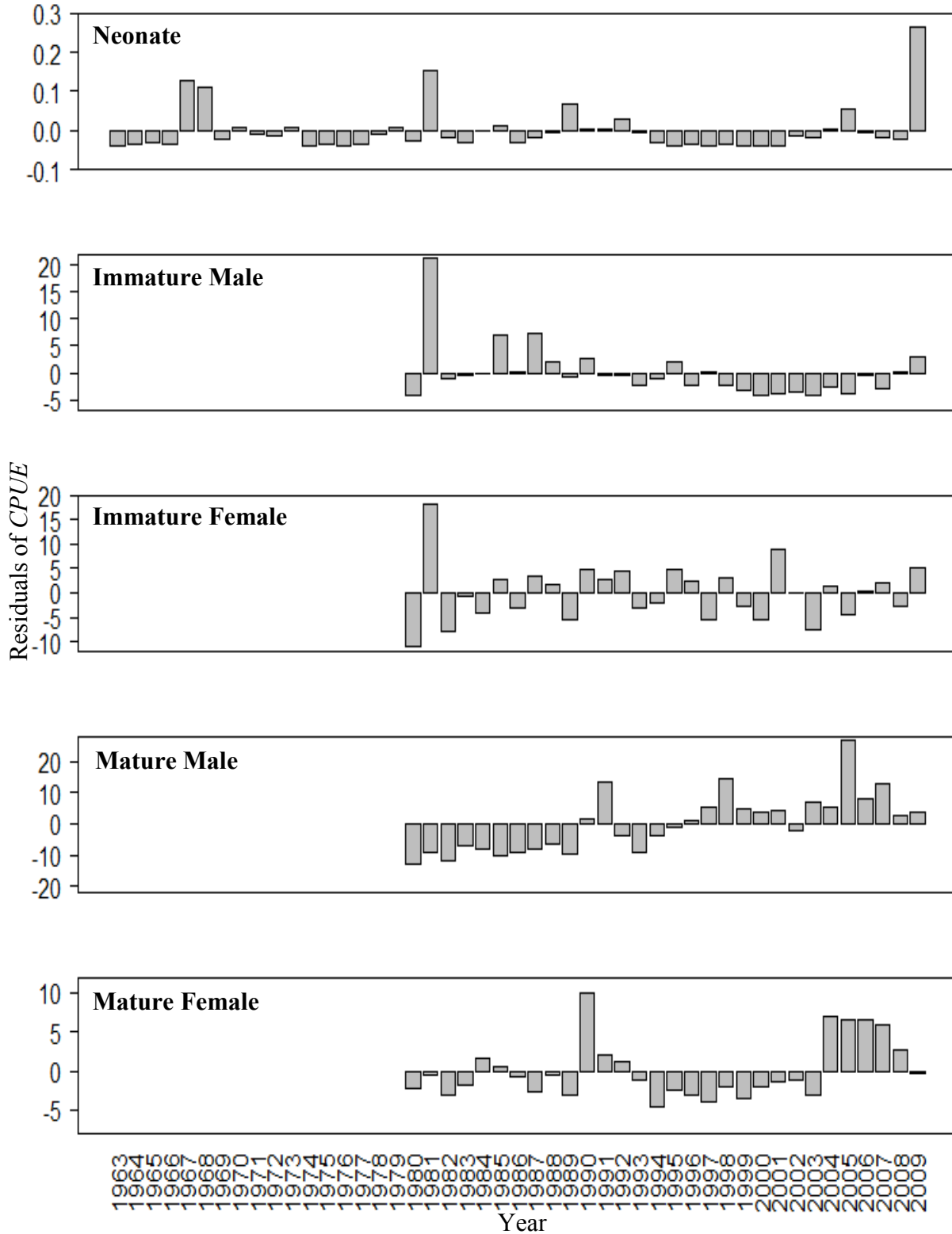


Figure 2B.2. Deviations in mean annual abundance (*CPUE*) for spiny dogfish in the Northeast (US) shelf large marine ecosystem during autumn (1963 – 2009). Residuals calculated as annual *CPUE* subtracted from overall mean *CPUE*. Note: spiny dogfish not sexed consistently until 1980.



Appendix 2C. Decadal Habitat Preference and Degree of Aggregation for Spiny Dogfish

Table 2C.1. Decadal habitat comparisons for spiny dogfish life-history stages in the Northeast (US) shelf large marine ecosystem during spring (1968 – 2009) and autumn (1963 – 2009). Habitat variables include bottom temperature (BT), bottom salinity (BS), depth, and latitude (Lat). Stages as defined in Table 2.1. *D* = range of absolute vertical distance between distributions, *TS* = test statistic, and *p* = probability. Significance (bolded) based on an *a priori* $\alpha = 0.05$. - indicates data constraints. Notes: spiny dogfish not sexed consistently until 1980 and *p* = 0.000 does not mean *p* = 0.

Stage	Decades	BT (°C)			BS			Depth (m)			Lat (°N)		
		<i>D</i>	<i>TS</i>	<i>p</i>	<i>D</i>	<i>TS</i>	<i>p</i>	<i>D</i>	<i>TS</i>	<i>p</i>	<i>D</i>	<i>TS</i>	<i>p</i>
SPRING													
Neo	60vs70	0.11 - 0.98	0.347	0.809	-	-	-	0.10 - 0.93	0.270	0.886	0.11 - 0.94	0.465	0.384
	60vs80	0.11 - 0.95	0.235	0.955	-	-	-	0.12 - 0.86	0.152	0.997	0.12 - 0.90	0.538	0.135
	60vs90	0.12 - 0.96	0.362	0.727	-	-	-	0.12 - 0.87	0.344	0.669	0.12 - 0.94	0.393	0.524
	60vs00	0.11 - 0.95	0.399	0.642	-	-	-	0.12 - 0.89	0.322	0.710	0.12 - 0.93	0.565	0.141
	70vs80	0.08 - 0.70	0.336	0.345	-	-	-	0.08 - 0.68	0.195	0.827	0.08 - 0.83	0.406	0.109
	70vs90	0.09 - 0.70	0.297	0.493	-	-	-	0.07 - 0.70	0.369	0.280	0.09 - 0.77	0.228	0.795
	70vs00	0.08 - 0.74	0.244	0.668	-	-	-	0.09 - 0.77	0.336	0.354	0.09 - 0.81	0.382	0.235
	80vs90	0.07 - 0.71	0.259	0.596	-	-	-	0.09 - 0.63	0.246	0.579	0.07 - 0.62	0.316	0.297
	80vs00	0.08 - 0.67	0.365	0.171	-	-	-	0.08 - 0.60	0.246	0.503	0.07 - 0.64	0.344	0.171
	90vs00	0.08 - 0.64	0.424	0.096	0.08 - 0.89	0.595	0.161	0.09 - 0.67	0.130	0.993	0.10 - 0.65	0.244	0.690
ImmM	80vs90	0.06 - 0.67	0.370	0.102	-	-	-	0.07 - 0.55	0.246	0.396	0.08 - 0.56	0.190	0.707
	80vs00	0.08 - 0.66	0.277	0.453	-	-	-	0.08 - 0.65	0.360	0.141	0.07 - 0.64	0.498	0.010
	90vs00	0.08 - 0.69	0.347	0.278	0.07 - 0.89	0.484	0.382	0.07 - 0.71	0.200	0.868	0.09 - 0.66	0.402	0.164
MatM	80vs90	0.04 - 0.47	0.140	0.808	-	-	-	0.06 - 0.45	0.186	0.406	0.06 - 0.42	0.181	0.446
	80vs00	0.05 - 0.55	0.127	0.800	-	-	-	0.05 - 0.43	0.374	0.001	0.05 - 0.41	0.509	0.000
	90vs00	0.04 - 0.38	0.141	0.508	0.08 - 0.70	0.403	0.253	0.04 - 0.39	0.202	0.165	0.05 - 0.41	0.393	0.000
ImmF	80vs90	0.05 - 0.45	0.160	0.607	-	-	-	0.06 - 0.44	0.161	0.463	0.05 - 0.42	0.124	0.771
	80vs00	0.05 - 0.51	0.241	0.214	-	-	-	0.05 - 0.45	0.275	0.053	0.06 - 0.45	0.311	0.020
	90vs00	0.05 - 0.41	0.146	0.513	0.09 - 0.66	0.351	0.430	0.05 - 0.42	0.137	0.610	0.05 - 0.38	0.294	0.011

Stage	Decades	BT (°C)			BS			Depth (m)			Lat (°N)		
		<i>D</i>	<i>TS</i>	<i>p</i>	<i>D</i>	<i>TS</i>	<i>p</i>	<i>D</i>	<i>TS</i>	<i>p</i>	<i>D</i>	<i>TS</i>	<i>p</i>
MatF	80vs90	0.05 - 0.48	0.113	0.929	-	-	-	0.05 - 0.44	0.268	0.072	0.06 - 0.44	0.155	0.618
	80vs00	0.05 - 0.49	0.150	0.706	-	-	-	0.05 - 0.47	0.455	0.000	0.05 - 0.42	0.291	0.041
	90vs00	0.04 - 0.38	0.202	0.098	0.08 - 0.68	0.395	0.263	0.04 - 0.36	0.212	0.074	0.05 - 0.34	0.226	0.049
<u>AUTUMN</u>													
Neo	60vs70	0.13 - 0.94	0.440	0.516	-	-	-	0.12 - 0.88	0.227	0.905	0.12 - 0.85	0.585	0.057
	60vs80	0.14 - 0.96	0.615	0.265	-	-	-	0.12 - 0.91	0.686	0.049	0.13 - 0.90	0.597	0.149
	60vs90	0.14 - 0.93	0.537	0.335	-	-	-	0.12 - 0.88	0.545	0.147	0.13 - 0.88	0.362	0.571
	60vs00	0.11 - 0.86	0.466	0.386	-	-	-	0.11 - 0.78	0.471	0.185	0.11 - 0.81	0.283	0.714
	70vs80	0.10 - 0.88	0.369	0.574	-	-	-	0.10 - 0.87	0.577	0.094	0.10 - 0.84	0.334	0.636
	70vs90	0.11 - 0.82	0.498	0.300	-	-	-	0.12 - 0.77	0.471	0.122	0.10 - 0.73	0.530	0.050
	70vs00	0.10 - 0.74	0.339	0.367	-	-	-	0.10 - 0.71	0.390	0.221	0.09 - 0.69	0.516	0.042
	80vs90	0.11 - 0.90	0.543	0.263	-	-	-	0.12 - 0.87	0.323	0.765	0.12 - 0.85	0.248	0.926
	80vs00	0.11 - 0.81	0.432	0.331	-	-	-	0.08 - 0.76	0.395	0.382	0.11 - 0.77	0.314	0.647
90vs00	0.08 - 0.75	0.404	0.257	0.09 - 0.87	0.449	0.312	0.10 - 0.81	0.398	0.250	0.10 - 0.77	0.417	0.212	
ImmM	80vs90	0.08 - 0.76	0.361	0.403	-	-	-	0.08 - 0.72	0.217	0.824	0.09 - 0.77	0.333	0.440
	80vs00	0.09 - 0.81	0.289	0.724	-	-	-	0.09 - 0.78	0.310	0.626	0.10 - 0.78	0.279	0.736
	90vs00	0.08 - 0.55	0.217	0.565	0.08 - 0.73	0.552	0.014	0.07 - 0.55	0.349	0.082	0.07 - 0.60	0.484	0.003
MatM	80vs90	0.07 - 0.59	0.181	0.767	-	-	-	0.07 - 0.53	0.146	0.857	0.07 - 0.53	0.196	0.575
	80vs00	0.05 - 0.51	0.211	0.284	-	-	-	0.05 - 0.43	0.116	0.841	0.06 - 0.45	0.155	0.549
	90vs00	0.05 - 0.45	0.157	0.535	0.06 - 0.63	0.392	0.032	0.06 - 0.43	0.149	0.578	0.06 - 0.48	0.153	0.566
ImmF	80vs90	0.07 - 0.59	0.219	0.555	-	-	-	0.06 - 0.55	0.182	0.643	0.06 - 0.54	0.227	0.409
	80vs00	0.05 - 0.61	0.240	0.395	-	-	-	0.06 - 0.55	0.247	0.279	0.06 - 0.55	0.210	0.456
	90vs00	0.05 - 0.42	0.136	0.707	0.06 - 0.58	0.326	0.106	0.06 - 0.43	0.138	0.646	0.06 - 0.43	0.192	0.282
MatF	80vs90	0.09 - 0.73	0.388	0.153	-	-	-	0.09 - 0.61	0.183	0.836	0.08 - 0.68	0.181	0.849
	80vs00	0.07 - 0.55	0.182	0.690	-	-	-	0.06 - 0.51	0.182	0.619	0.07 - 0.52	0.244	0.292
	90vs00	0.07 - 0.54	0.260	0.241	0.08 - 0.67	0.242	0.579	0.06 - 0.52	0.221	0.389	0.07 - 0.56	0.276	0.171

Table 2C.2. Gini index quantifying the degree of aggregation for spiny dogfish life-history stages in the Northeast (US) shelf large marine ecosystem during spring (1968 – 2009) and autumn (1963 – 2009). Stages as defined in Table 2.1. DOM refers to which season exhibited a higher aggregation index (Aut = autumn, Spr = spring). DIFF quantifies the deviation between seasonal Gini indices. Note: spiny dogfish not sexed consistently until 1980.

Decade	Stage	Gini Index		Dom	Diff
		<u>SPRING</u>	<u>AUTUMN</u>		
1960s	Neo	0.985	0.990	Aut	0.005
1970s	Neo	0.990	0.995	Aut	0.005
1980s	Neo	0.985	0.996	Aut	0.011
	ImmM	0.977	0.986	Aut	0.010
	MatM	0.970	0.969	Spr	-0.001
	ImmF	0.955	0.974	Aut	0.019
	MatF	0.944	0.984	Aut	0.040
1990s	Neo	0.987	0.996	Aut	0.009
	ImmM	0.973	0.973	Spr	-0.001
	MatM	0.949	0.975	Aut	0.027
	ImmF	0.920	0.963	Aut	0.043
	MatF	0.926	0.983	Aut	0.057
2000s	Neo	0.986	0.991	Aut	0.005
	ImmM	0.986	0.986	Spr	-0.001
	MatM	0.941	0.949	Aut	0.008
	ImmF	0.917	0.944	Aut	0.027
	MatF	0.929	0.960	Aut	0.031

Figure 2C.1. Range of environmental conditions surveyed annually by the Northeast Fisheries Science Center (NEFSC) bottom trawl survey in the Northeast (US) shelf large marine ecosystem during spring (1968 – 2009) and autumn (1963 – 2009). The thick horizontal line reflects the median, the box represents the interquartile range and the 25th (bottom) and 75th (top) percentiles, the whiskers reflect either the maximum value or 1.5 times the interquartile range, and points reflect outliers. Notes: inshore strata were added in 1972 and 1973 for autumn and spring, respectively.

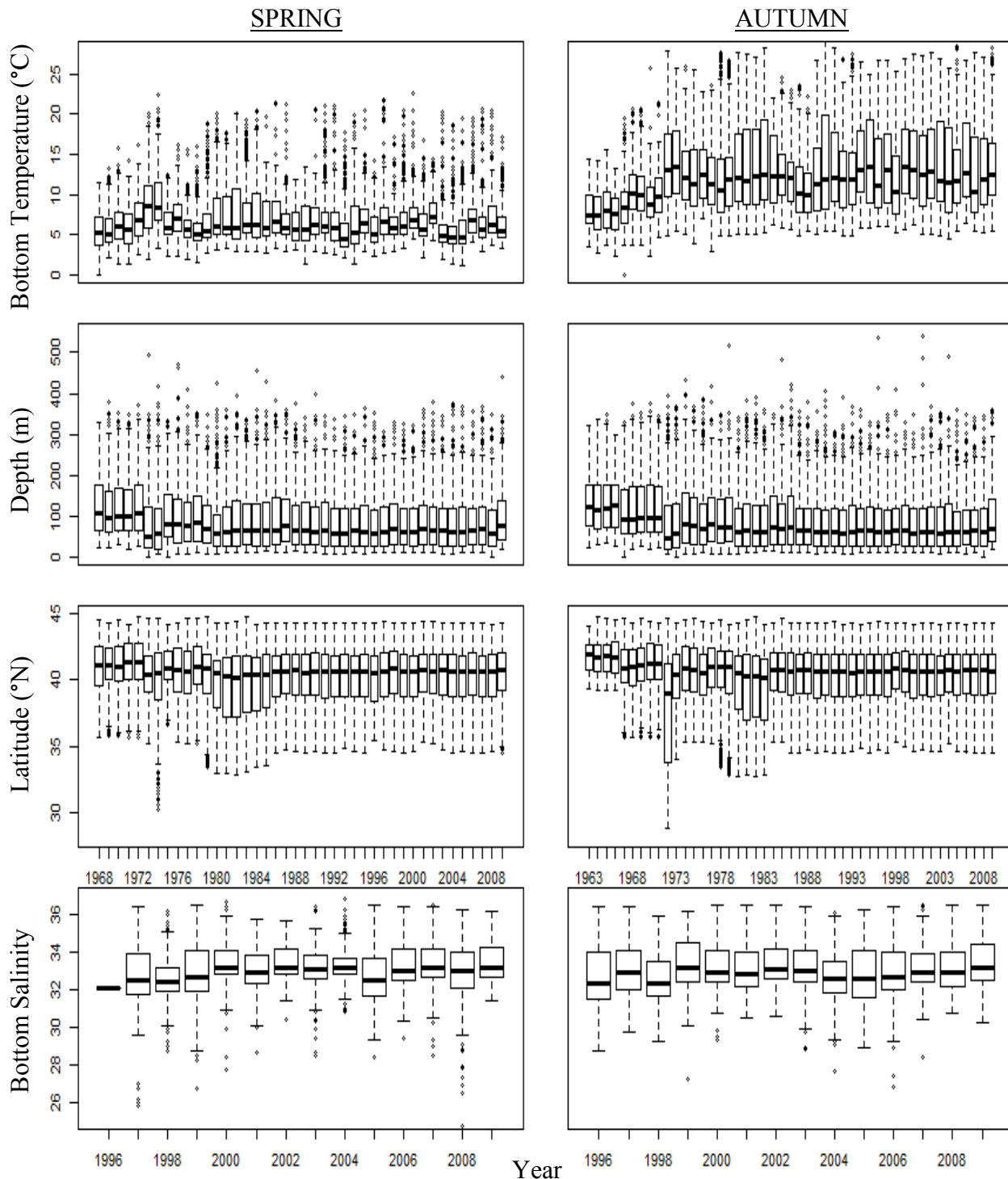


Figure 2C.2. Decadal cumulative distributions of available and occupied bottom temperature for spiny dogfish life-history stages in the Northeast (US) shelf large marine ecosystem during spring. CDFs shown include survey (thick black), neonate (orange), immature male (red), immature female (blue), mature male (green), and mature female (purple). Note: spiny dogfish not sexed consistently until 1980.

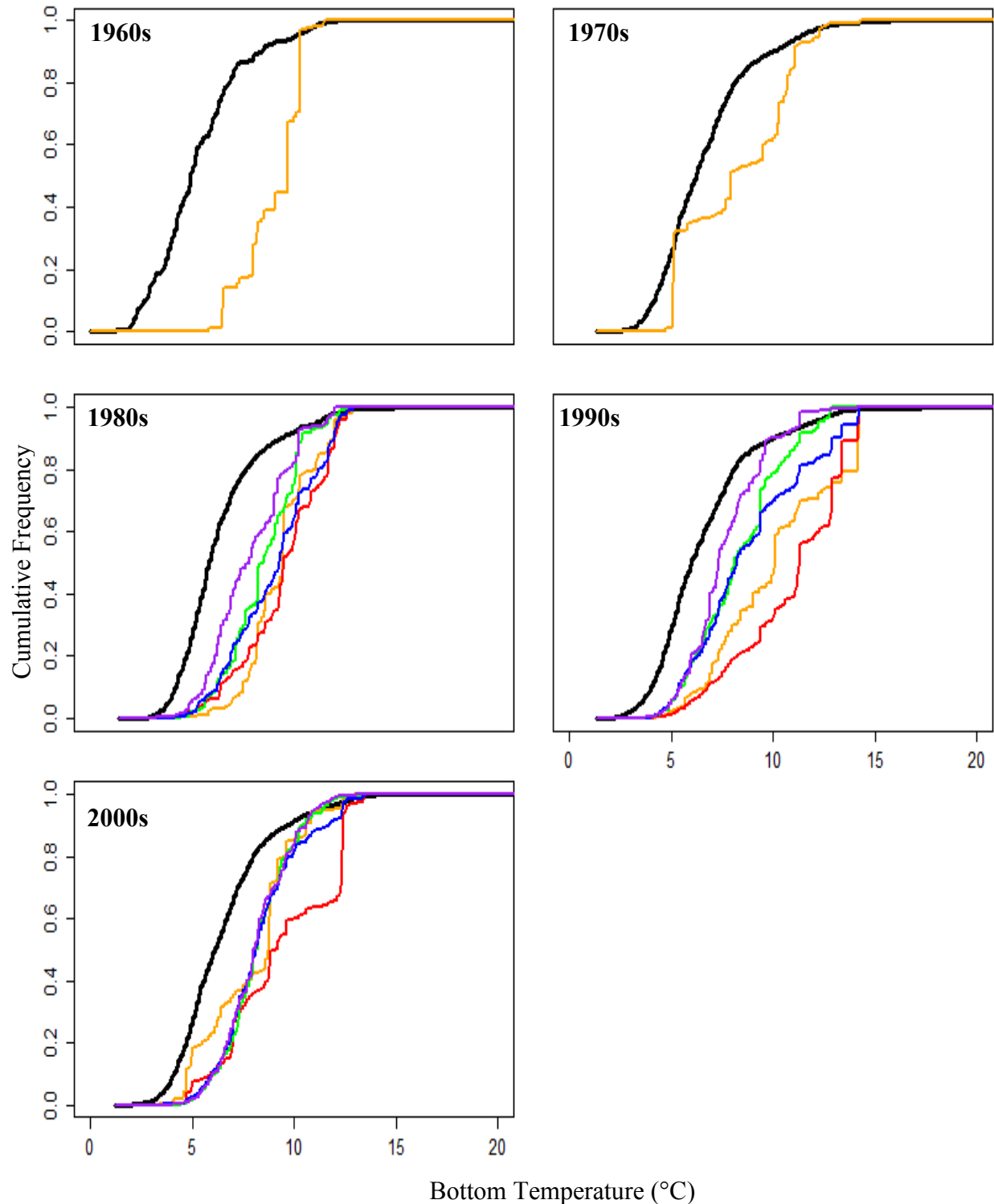


Figure 2C.3. Decadal cumulative distributions of available and occupied bottom temperature for spiny dogfish life-history stages in the Northeast (US) shelf large marine ecosystem during autumn. CDFs shown include survey (thick black), neonate (orange), immature male (red), immature female (blue), mature male (green), and mature female (purple). Note: spiny dogfish not sexed consistently until 1980.

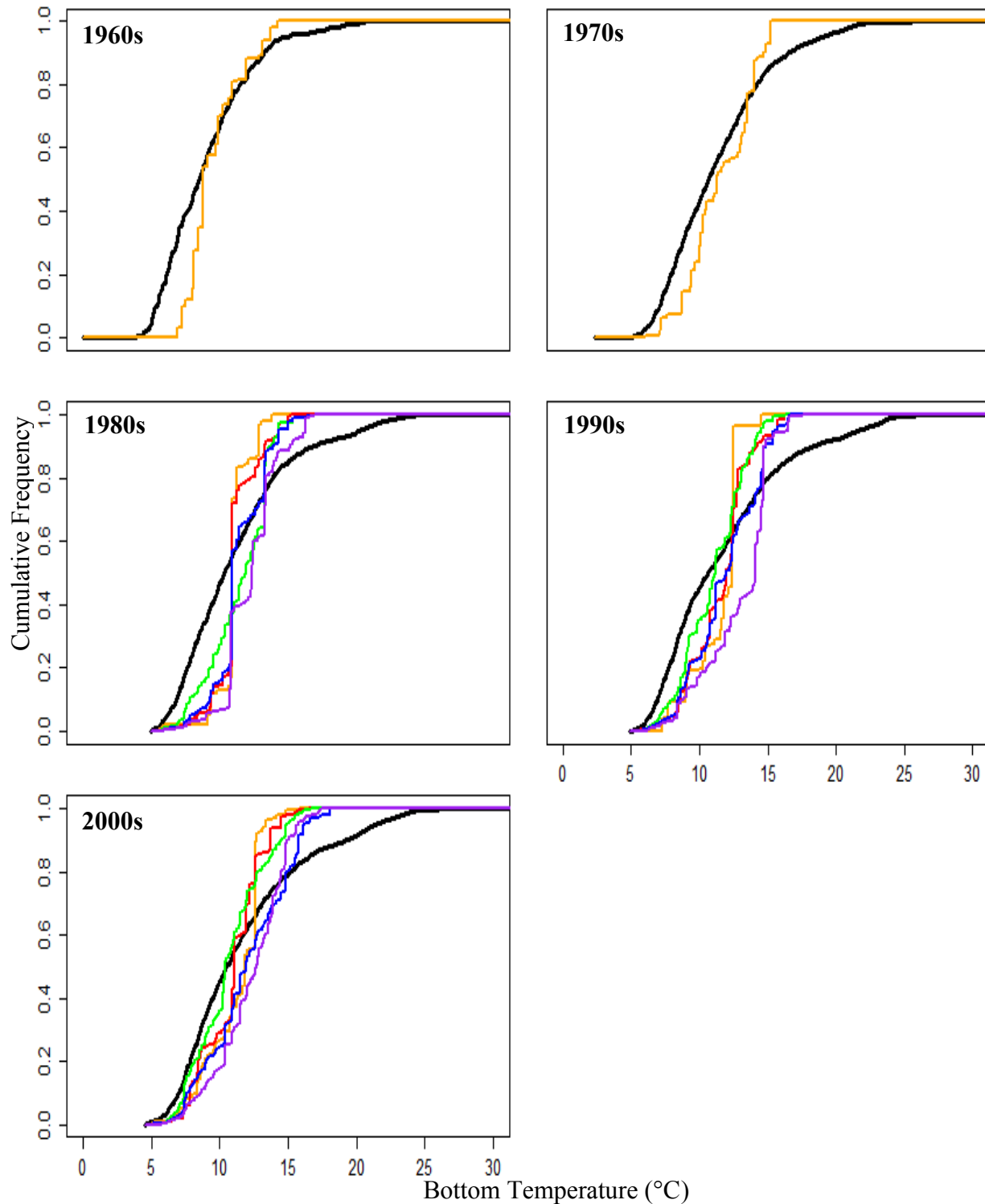


Figure 2C.4. Decadal cumulative distributions of available and occupied bottom salinity for spiny dogfish life-history stages in the Northeast (US) shelf large marine ecosystem during spring. CDFs shown include survey (thick black), neonate (orange), immature male (red), immature female (blue), mature male (green), and mature female (purple). Note: Salinity data has been collected consistently since 1996.

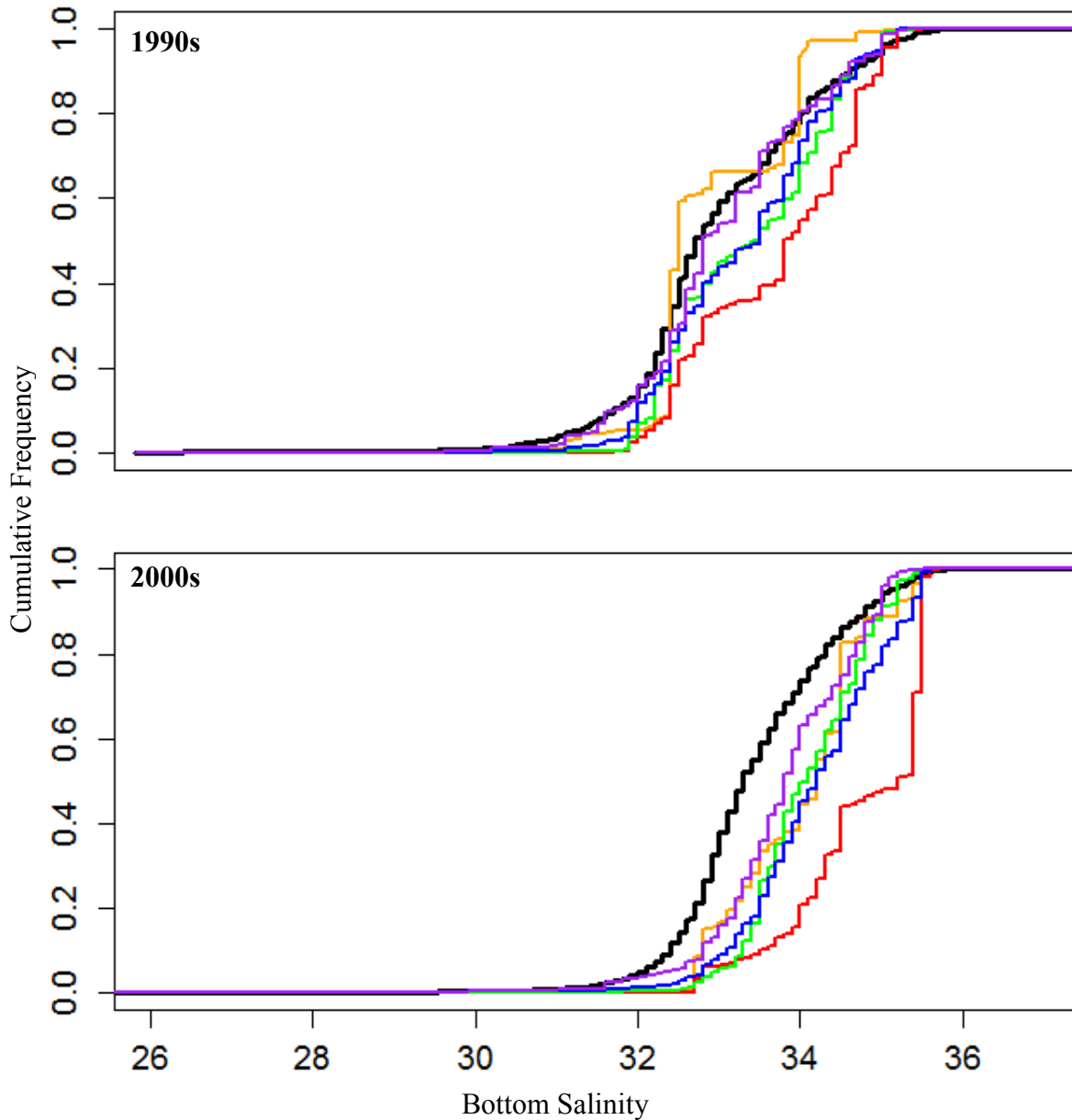


Figure 2C.5. Decadal cumulative distributions of available and occupied bottom salinity for spiny dogfish life-history stages in the Northeast (US) shelf large marine ecosystem during autumn. CDFs shown include survey (thick black), neonate (orange), immature male (red), immature female (blue), mature male (green), and mature female (purple). Note: Salinity data has been collected consistently since 1996.

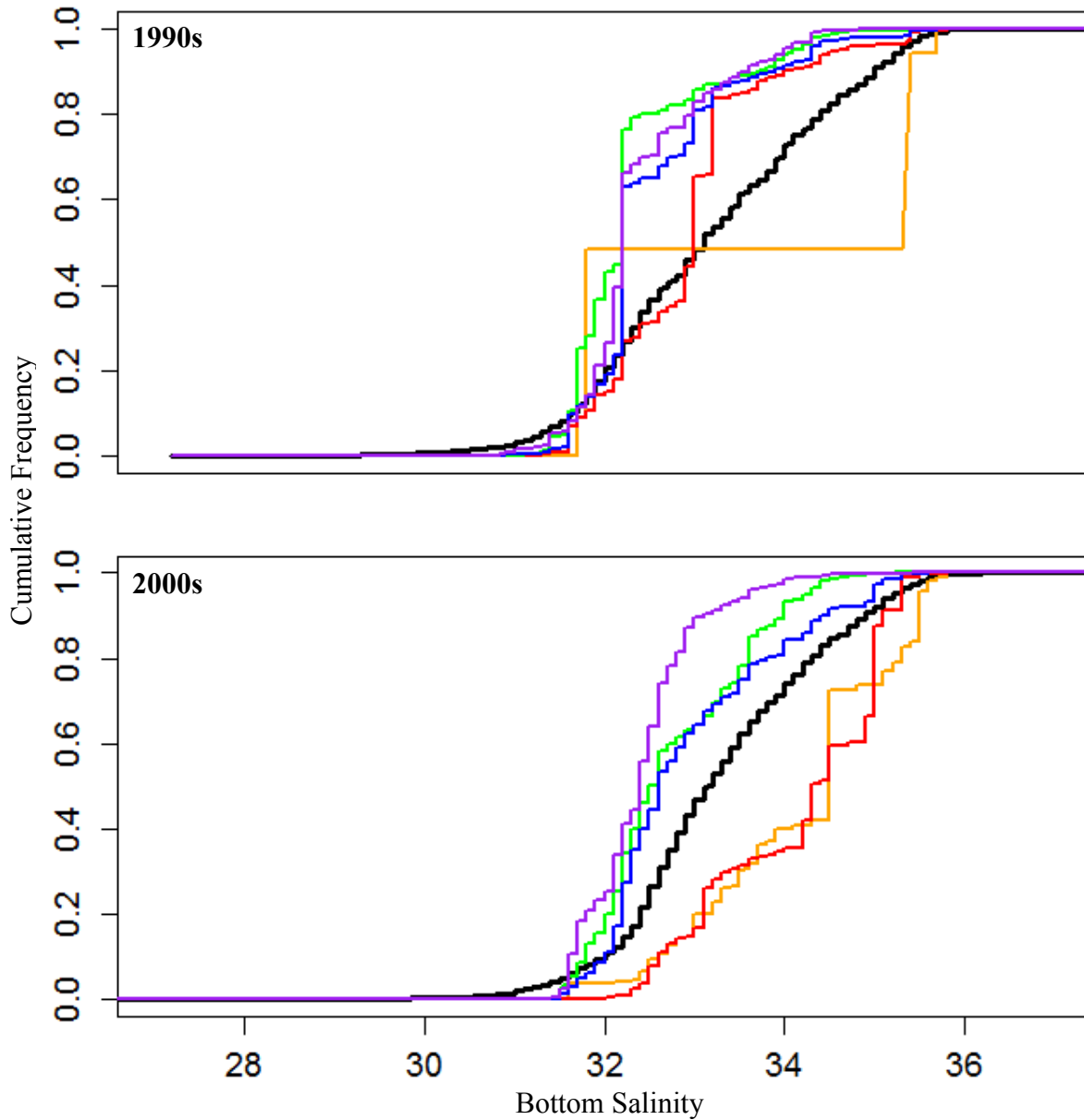


Figure 2C.6. Decadal cumulative distributions of available and occupied depth for spiny dogfish life-history stages in the Northeast (US) shelf large marine ecosystem spring. CDFs shown include survey (thick black), neonate (orange), immature male (red), immature female (blue), mature male (green), and mature female (purple). Note: spiny dogfish not sexed consistently until 1980.

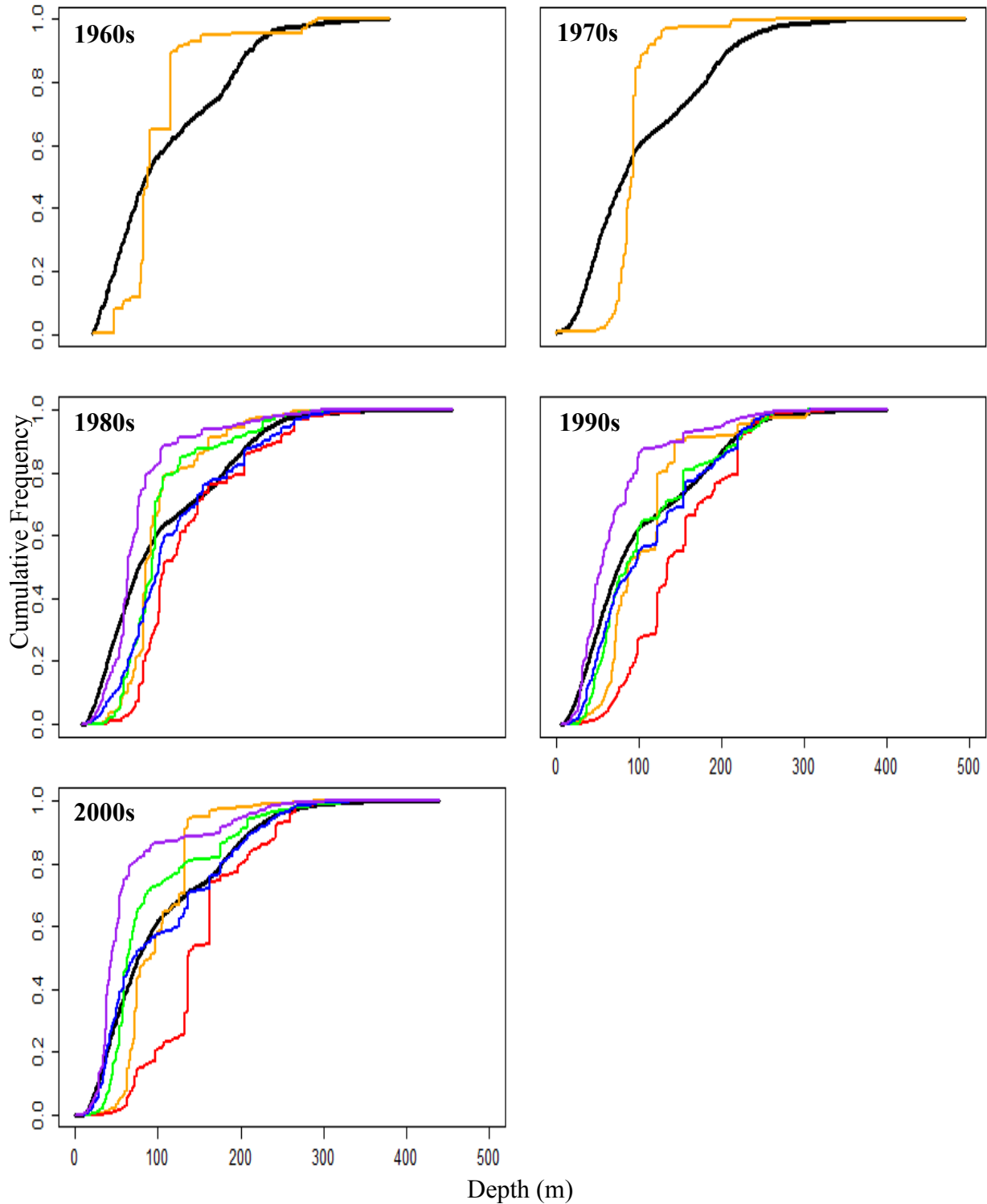


Figure 2C.7. Decadal cumulative distributions of available and occupied depth for spiny dogfish life-history stages in the Northeast (US) shelf large marine ecosystem during autumn. CDFs shown include survey (thick black), neonate (orange), immature male (red), immature female (blue), mature male (green), and mature female (purple). Note: spiny dogfish not sexed consistently until 1980.

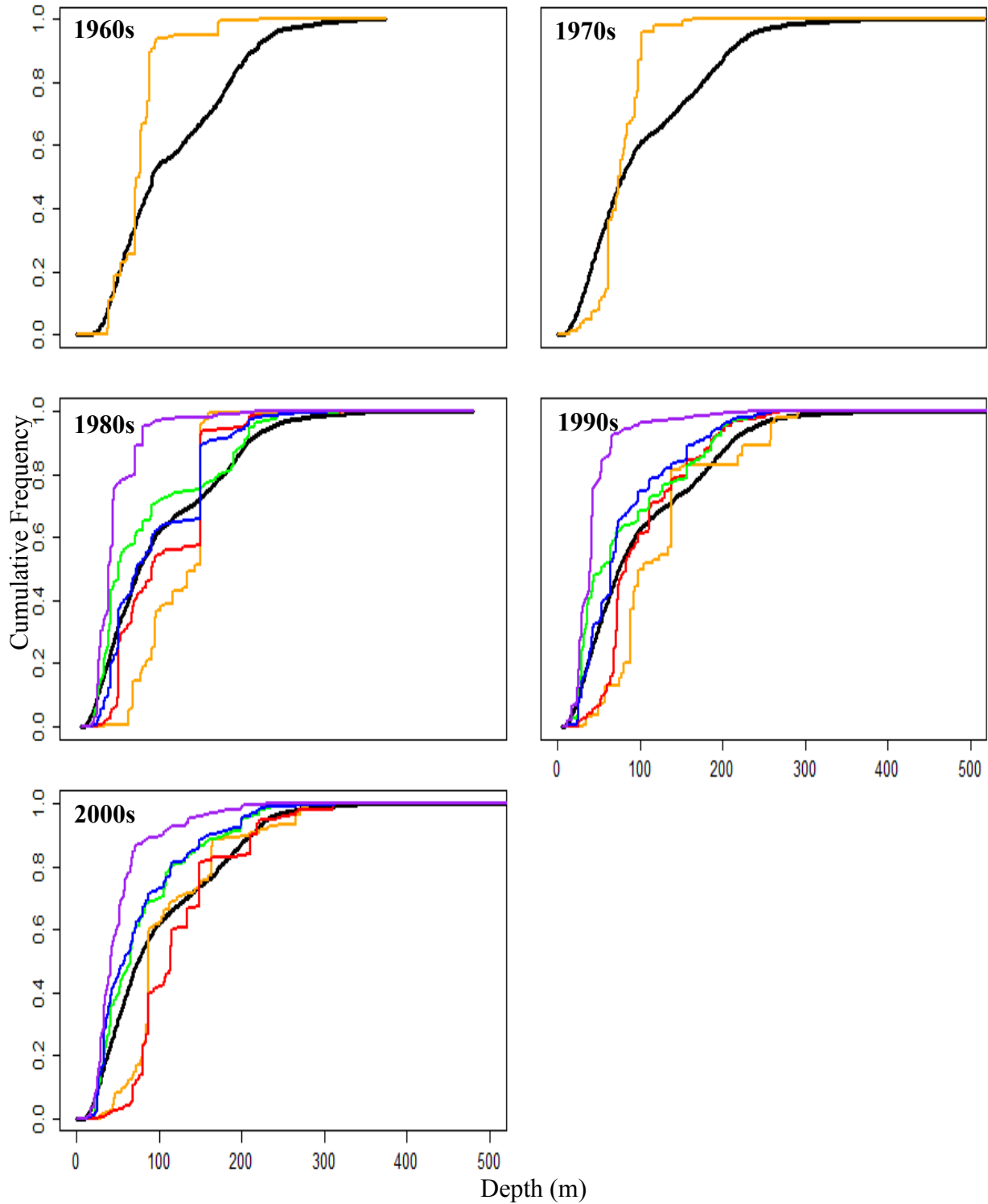


Figure 2C.8. Decadal cumulative distributions of available and occupied latitude for spiny dogfish life-history stages in the Northeast (US) shelf large marine ecosystem during spring. CDFs shown include survey (thick black), neonate (orange), immature male (red), immature female (blue), mature male (green), and mature female (purple). Note: spiny dogfish not sexed consistently until 1980.

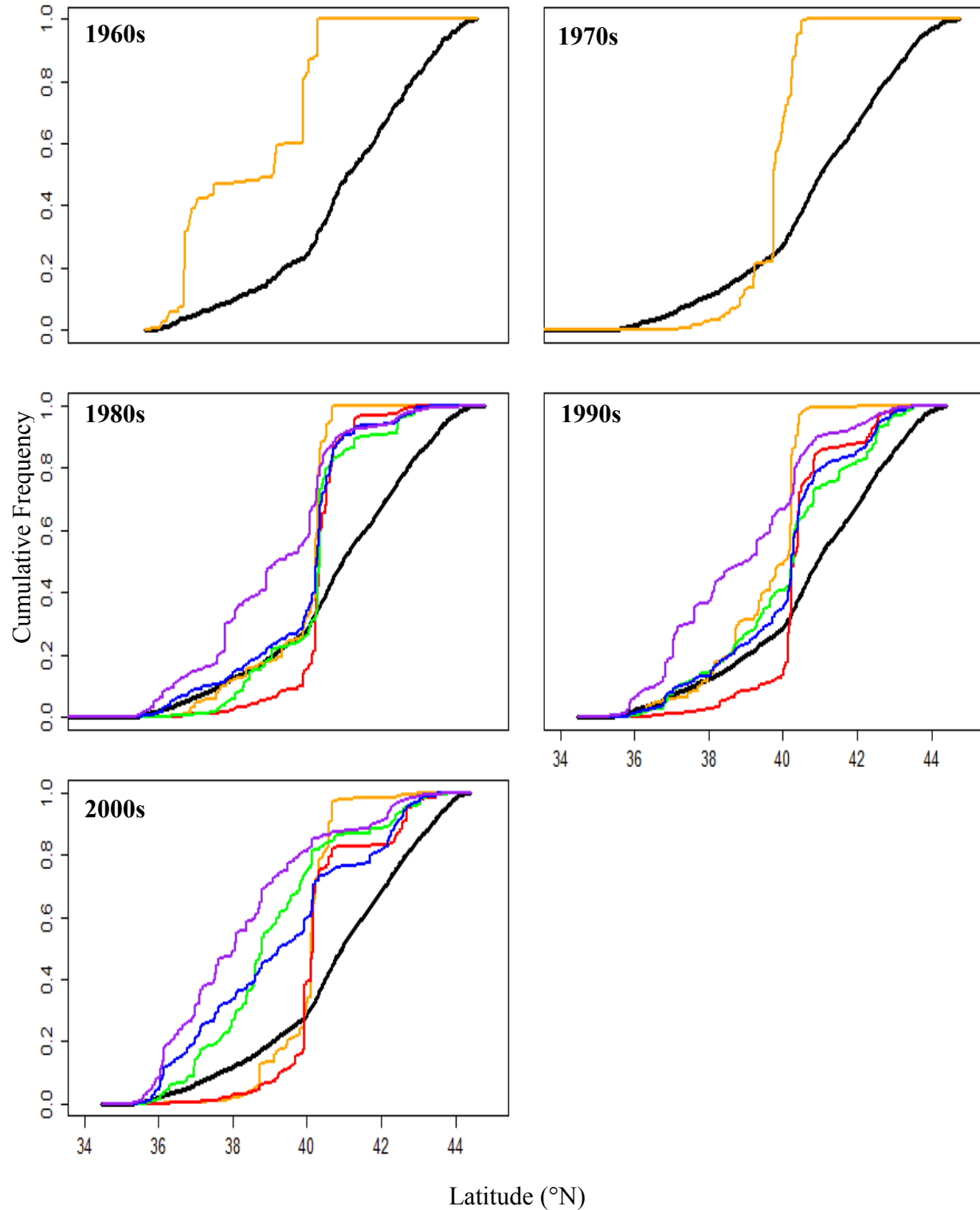


Figure 2C.9. Decadal cumulative distributions of available and occupied latitude for spiny dogfish life-history stages in the Northeast (US) shelf large marine ecosystem during autumn. CDFs shown include survey (thick black), neonate (orange), immature male (red), immature female (blue), mature male (green), and mature female (purple). Note: spiny dogfish not sexed consistently until 1980.

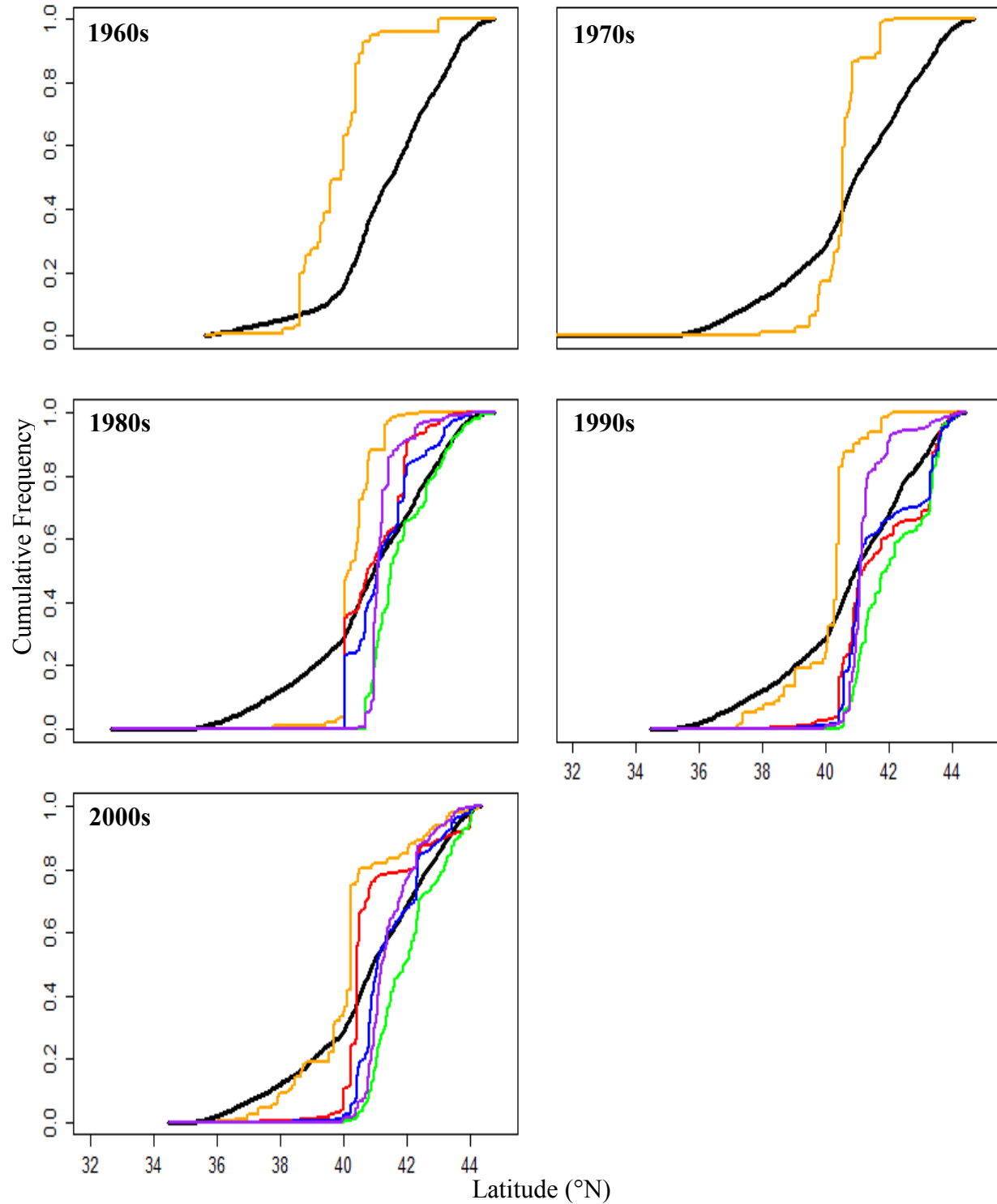


Figure 2C.10. Degree of aggregation as defined by the Lorenz curve for spiny dogfish life-history stages in the Northeast (US) shelf large marine ecosystem during spring (1968 – 2009) (dashed line) and autumn (1963 – 2009) (solid line) where Φ_i is the estimated percentage of the stock associated with each tow and A_i is the percentage of area associated with each tow. The more concave the curve, the more aggregated the distribution. Curves represent neonate (orange), immature male (red), mature male (green), immature female (blue), and mature female (purple). Notes: spiny dogfish not sexed consistently until 1980, x-axis begins at 80% and y-axis ends at 70%.

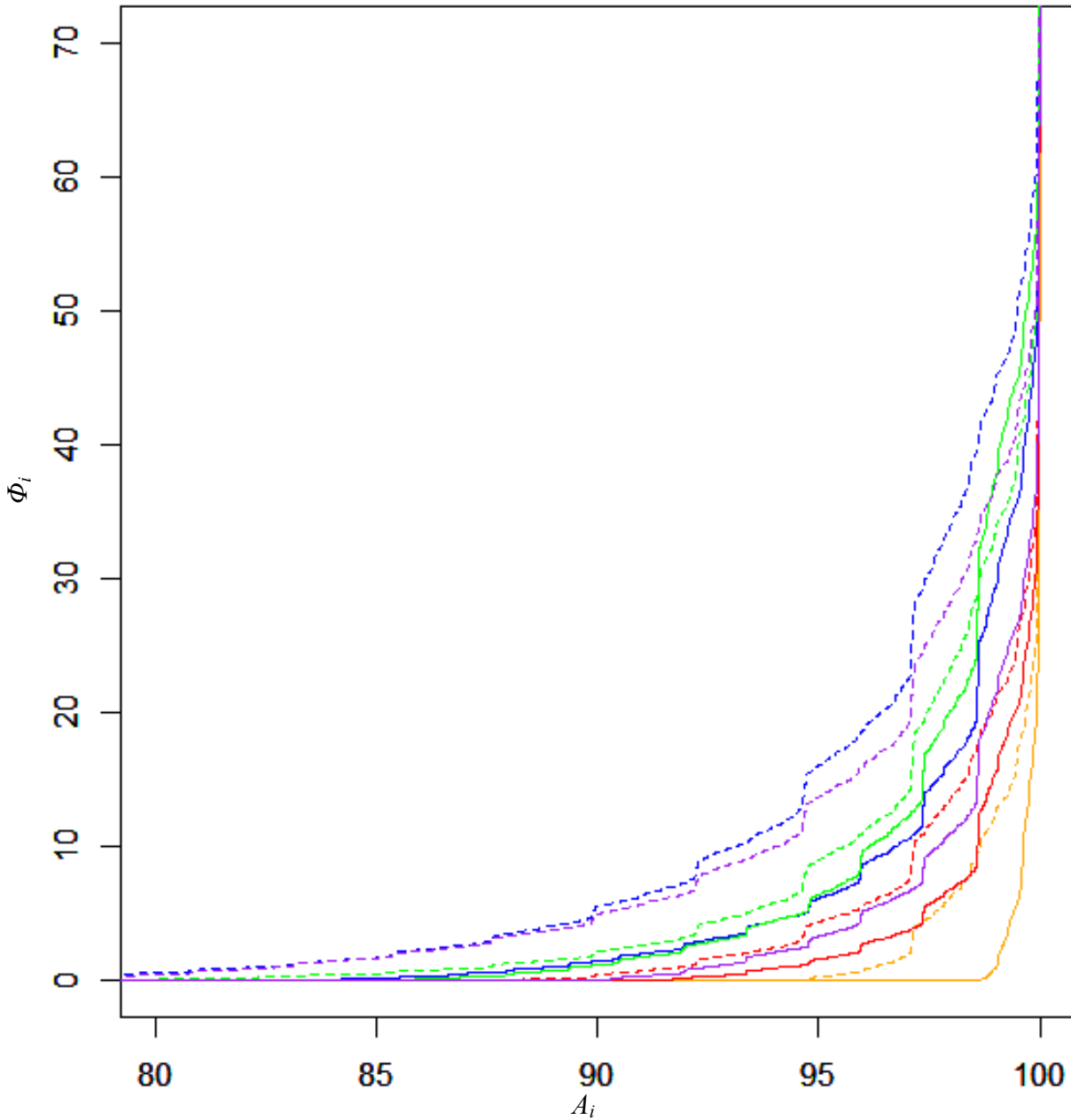


Figure 2C.11. Decadal degree of aggregation as defined by the Lorenz curve for spiny dogfish life-history stages in the Northeast (US) shelf large marine ecosystem during spring. Φ_i = estimated percentage of the stock associated with each tow, A_i = percentage of area associated with each tow. Curves represent neonate (orange), immature male (red), mature male (green), immature female (blue), and mature female (purple). Notes: spiny dogfish not sexed consistently until 1980, x-axes begin at 80% and y-axes end at 70%.

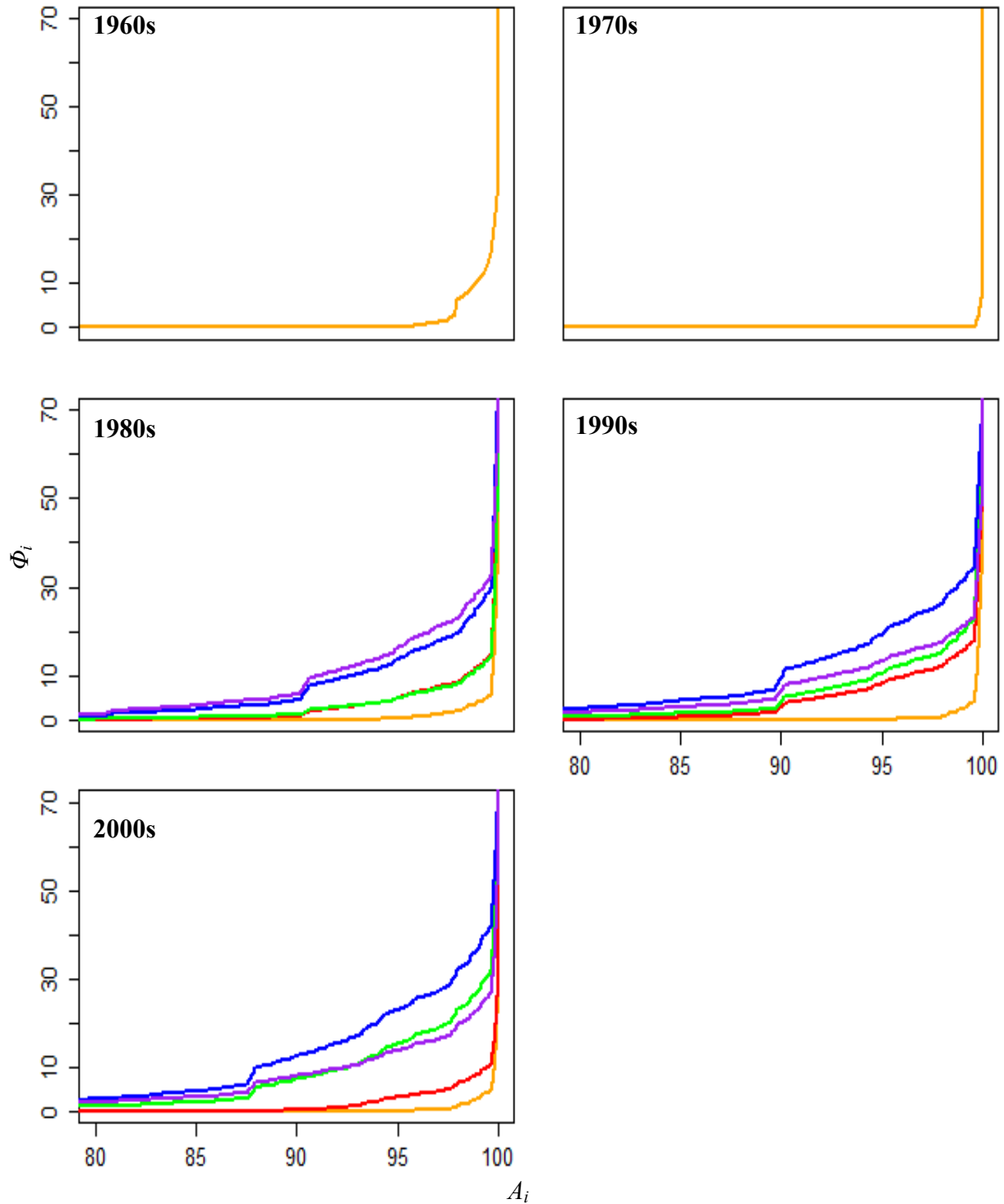
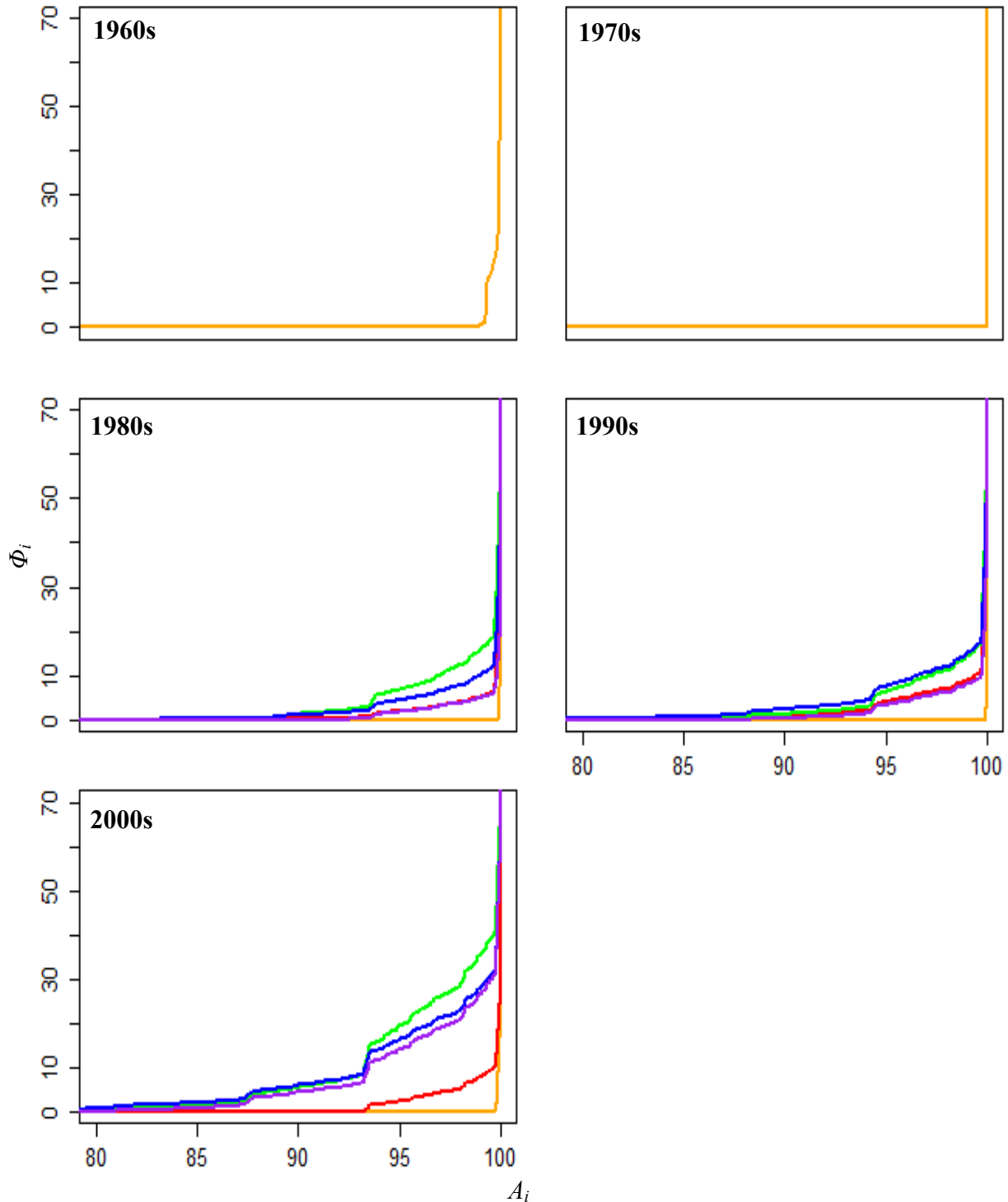


Figure 2C.12. Decadal degree of aggregation as defined by the Lorenz curve for spiny dogfish life-history stages in the Northeast (US) shelf large marine ecosystem during autumn. Φ_i = estimated percentage of the stock associated with each tow, A_i = percentage of area associated with each tow. Curves represent neonate (orange), immature male (red), mature male (green), immature female (blue), and mature female (purple). Notes: spiny dogfish not sexed consistently until 1980, x-axes begin at 80% and y-axes end at 70%.



Appendix 2D. Density-dependence

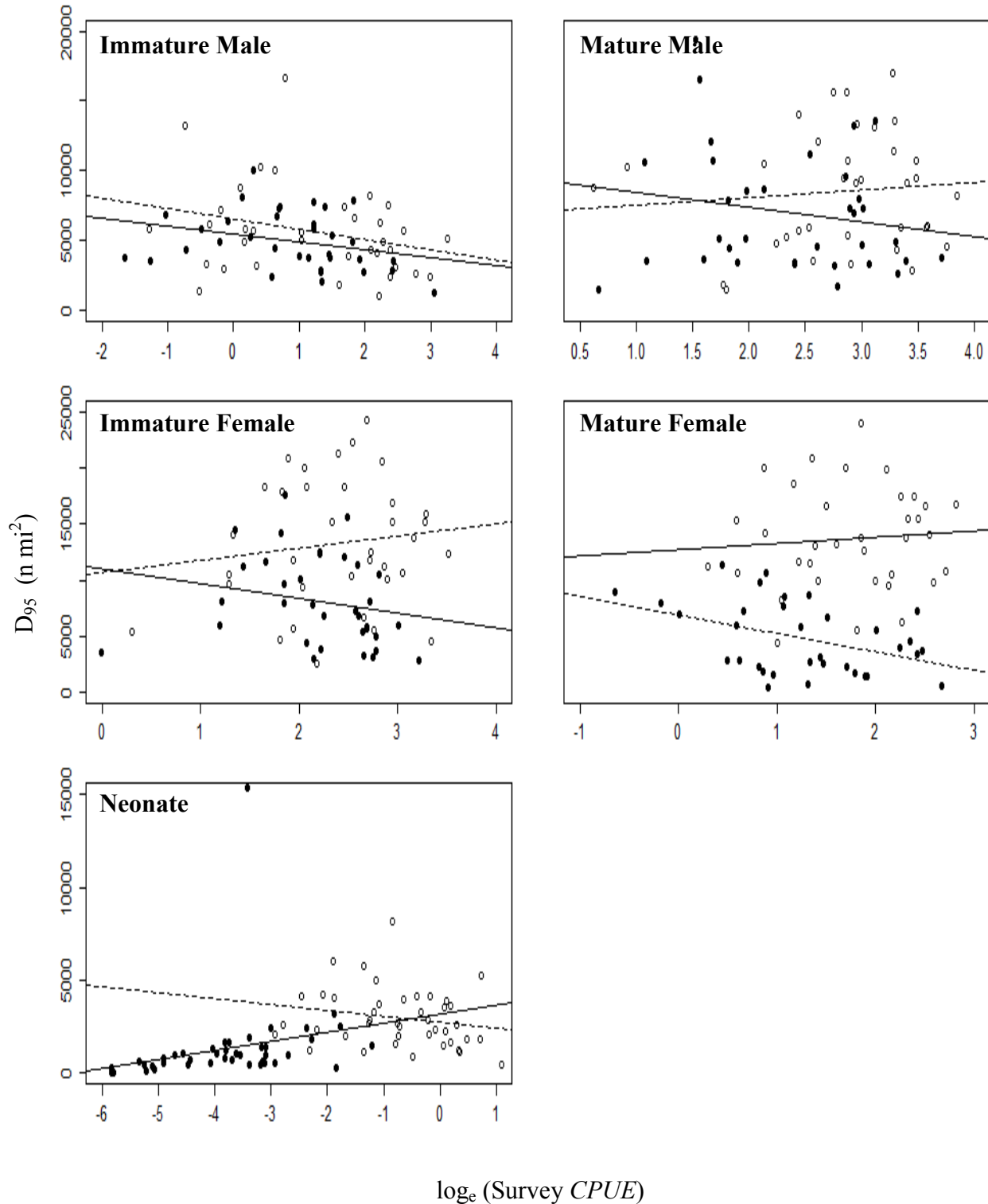
Table 2D.1. Linear regression between the annual distribution index D_{95} , or the minimum area over which 95% of the spiny dogfish population is spread, and \log_e transformed abundance (survey *CPUE*) for spiny dogfish life-history stages in the Northeast (US) shelf large marine ecosystem during spring (1968 – 2009) and autumn (1963 – 2009). Stages as defined in Table 2.1. N = number of years with data available, m = slope and b = y-intercept of the fitted regression line, R^2 = coefficient of determination, p = probability. Group-wide significance (bolded) based on an adjusted $\alpha = 0.0083$ (0.05 adjusted for 6 comparisons). Note: spiny dogfish not sexed consistently until 1980.

Stage	N	<u>SPRING</u>				<u>AUTUMN</u>				
		m	b	R^2	p	N	m	b	R^2	p
All	41	-1071.0	19540.0	0.01	0.5145	46	-3520.8	21433.8	0.22	0.0009
Neo	41	-312.7	2744.8	0.04	0.1993	41	489.5	3206.3	0.06	0.1182
ImmM	34	-746.8	6525.3	0.08	0.1010	33	-553.0	5439.8	0.08	0.0546
MatM	34	534.5	6986.5	0.01	0.5947	33	-1063.5	9468.5	0.03	0.2951
ImmF	34	1085.0	10670.0	0.02	0.4476	33	-1329.0	11072.0	0.04	0.0148
MatF	34	551.7	12744.4	0.01	0.6462	33	-1662.2	6858.1	0.17	0.0143

Table 2D.2. Correlations (r) between the annual distribution index D_{95} , or the minimum area over which 95% of the spiny dogfish population is spread, and \log_e transformed abundance (survey $CPUE$) for spiny dogfish life-history stages in the Northeast (US) shelf large marine ecosystem during spring (1968 – 2009) and autumn (1963 – 2009). Stages as defined in Table 2.1. N = number of years with data available, p = probability, β = power. Group-wide significance (bolded) based on an adjusted $\alpha = 0.0083$ (0.05 adjusted for 6 comparisons). Power (β) for correlation test estimated using the 'PWR' package in R. Note: spiny dogfish not sexed consistently until 1980.

Stage	N	<u>SPRING</u>			<u>AUTUMN</u>			
		r	p	β	N	r	p	β
All	42	-0.10	0.5145	0.09	47	-0.47	0.0009	0.92
Neo	42	-0.20	0.1993	0.24	42	0.24	0.1182	0.33
ImmM	35	-0.28	0.1010	0.37	34	-0.29	0.0979	0.38
MatM	35	0.09	0.5947	0.08	34	-0.18	0.2951	0.17
ImmF	35	0.13	0.4476	0.11	34	-0.21	0.2301	0.22
MatF	35	0.08	0.6462	0.07	34	-0.42	0.0143	0.70

Figure 2D.1. Relationship between the distribution index D_{95} , or the minimum area over which 95% of the spiny dogfish population is spread, and abundance (survey $CPUE$) for spiny dogfish life-history stages in the Northeast (US) shelf large marine ecosystem during spring (1968 – 2009) (empty circle) and autumn (1963 – 2009) (black circle). Dashed (spring) and solid (autumn) lines reflect fitted linear regressions. See Table 2D.1 for estimated parameters. Notes: spiny dogfish not sexed consistently until 1980, x- and y-axes differ between panels.



Appendix 3A. Boosted Regression Tree Analysis

Table 3A.1. Results summary from boosted regression tree (BRT) analyses modeling both the occurrence (PA) and abundance (PRES) of spiny dogfish life-history stages during autumn (1963 – 2009) and spring (1968 – 2009) in the Northeast (US) shelf large marine ecosystem. Results presented are based on optimum BRT models which minimized predictive deviance. # trees = estimated best number of trees, *lr* = learning rate, Dev = deviance explained. Stages and variables as defined in Tables 3.1 and 3.2, respectively. The three most influential variables are bolded for each model. Note: spiny dogfish not sexed consistently until 1980.

Stage	# trees	<i>lr</i>	Dev	Year	Depth	BT	Julian	Zenith	Region	BFN	LOLN	ILLN	HERN	MACN	Co
<u>AUTUMN</u>															
PA															
MatF	5400	0.0025	65.4	5.8	14.4	2.5	3.9	2.7	5.4	1.1	1.0	1.6	2.2	0.5	58.9
MatM	4600	0.005	71.0	5.5	4.2	3.3	12.3	2.0	7.5	1.0	0.6	0.7	0.9	0.3	61.8
ImmF	6050	0.0025	56.8	10.8	10.4	6.9	14.0	3.5	9.5	0.9	1.8	2.2	2.3	0.9	36.9
ImmM	5650	0.001	47.7	10.0	9.5	3.7	5.1	3.2	4.9	1.8	1.2	3.5	1.8	0.5	54.8
Neo	8200	0.0005	38.9	14.3	13.9	8.4	8.9	14.5	6.7	9.1	7.3	12.6	3.1	1.2	-
PRES															
MatF	16550	0.0005	79.6	10.7	20.3	10.2	11.4	14.9	6.4	3.6	20.4	0.5	0.4	0.4	0.9
MatM	12300	0.0005	67.3	2.5	22.8	15.0	2.8	28.5	0.8	10.3	8.5	4.2	0.8	2.7	1.0
ImmF	6100	0.0005	64.5	4.5	20.9	12.3	8.4	11.7	3.5	8.5	14.7	1.0	3.2	1.5	9.8
ImmM	10850	0.00005	23.3	1.6	1.3	2.1	1.0	2.7	1.1	0.6	1.3	86.3	0.3	1.5	0.0
Neo	24400	0.00005	29.3	1.3	24.6	0.7	1.4	2.8	3.6	1.8	1.7	62.0	0.0	0.0	-
<u>SPRING</u>															
PA															
MatF	7950	0.0025	44.5	7.1	10.1	16.8	3.9	2.8	7.4	1.0	1.0	0.2	0.5	3.6	45.7
MatM	5300	0.005	61.1	8.9	20.1	17.9	5.7	1.3	2.1	0.5	2.1	0.2	0.6	1.7	39.0
ImmF	5200	0.005	59.0	8.0	10.1	22.1	8.1	6.1	4.4	1.0	2.3	0.7	1.5	5.5	30.3

Stage	# trees	<i>lr</i>	Dev	Year	Depth	BT	Julian	Zenith	Region	BFN	LOLN	ILLN	HERN	MACN	Co
ImmM	6600	0.001	51.8	9.1	27.7	6.5	2.6	1.5	3.8	2.6	4.3	0.4	0.9	1.7	38.8
Neo	9550	0.001	41.7	8.1	20.1	10.7	4.8	3.3	3.4	6.9	28.8	3.7	1.1	9.0	-
PRES															
MatF	9850	0.001	73.7	16.6	8.9	13.0	25.2	13.4	1.1	6.1	8.2	0.4	2.3	2.1	2.8
MatM	6900	0.0025	86.3	4.6	7.2	12.6	7.2	5.9	9.6	4.4	10.6	2.1	23.9	11.5	0.5
ImmF	20000	0.0001	41.4	4.9	11.4	30.4	17.9	7.7	10.5	2.4	5.9	3.2	2.7	1.1	2.0
ImmM	5200	0.0005	82.4	7.5	9.7	16.8	18.1	9.6	9.0	5.5	11.7	11.3	0.2	0.5	0.0
Neo	5000	2.5E-05	14.3	17.9	6.4	12.0	18.8	13.9	1.9	15.8	5.5	6.6	0.7	0.4	-

Appendix 3B. Model selection

Table 3B.1. Model selection for occurrence (PA) of spiny dogfish life-history stages during autumn (1963 – 2009). A = optimal sub-model consisting of abiotic main effects, B = optimal sub-model consisting of biotic main effects, A & B = optimal sub-model combining abiotic and biotic terms, Overall = optimal final model combining important abiotic and biotic main effects with the five largest interactions identified from BRT analysis. Bolded text represents specified sub-model. Dev = % deviance explained, AIC = Akaike's Information Criterion. Note: spiny dogfish not sexed consistently until 1980.

Stage	Sub-Model	Optimal (Sub) Model	Dev (%)	AIC
MatF	A	PA ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region	37.9	3376
	B	PA ~ s(HERN) + s(ILLN) + s(LOLN) + s(MACN) + Co	37.7	3378
	A & B	PA ~ A + s(LOLN) + s(MACN) + Co	50.4	2709
	Overall	PA ~ A + s(HERN) + s(LOLN) + s(MACN) + Co + te(Zenith,Co) + te(Depth,Region) + te(Depth,Co) + te(Year,Co) + te(Julian,Depth)	52.1	2645
MatM	A	PA ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region	38.1	4145
	B	PA ~ s(BFN) + s(HERN) + s(ILLN) + s(LOLN) + Co	33.5	4436
	A & B	PA ~ A + B	48.5	3473
	Overall	PA ~ A + B + te(Julian,Depth) + te(Depth,Year) + te(Julian,Co) + te(Year,Region)	53.0	3206
ImmF	A	PA ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region	26.1	5206
	B	PA ~ s(BFN) + s(HERN) + s(LOLN) + s(MACN) + Co	21.9	5502
	A & B	PA ~ s(Year) + s(Depth) + s(BT) + s(Julian) + Region + s(HERN) + s(MACN) + Co	40.8	4186
	Overall	PA ~ s(Year) + s(Depth) + s(BT) + s(Julian) + Region + s(HERN) + s(MACN) + Co + te(Depth,Year) + te(BT,Year) + te(Julian,Depth) + te(Year,Region)	43.4	4045
ImmM	A	PA ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region	16.3	3898
	B	PA ~ s(ILLN) + s(LOLN) + Co	31.7	3167
	A & B	PA ~ A + s(LOLN) + Co	38.9	2854
	Overall	PA ~ A + s(LOLN) + Co + te(Year,Co) + te(Depth,Co) + te(Julian,Co) + te(BT,Co)	39.7	2835
Neo	A	PA ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region	15.2	1215
	B	PA ~ s(BFN) + s(LOLN) + s(ILLN) + s(HERN)	4.6	1348
	A & B	PA ~ A + s(BFN) + s(LOLN) + s(HERN)	16.8	1205
	Overall	PA ~ A + s(BFN) + s(LOLN) + s(HERN) + te(Year,Region) + te(Zenith,Year) + te(BFN,BT) + te(Depth,Year)	21.8	1152

Table 3B.2. Model selection for occurrence (PA) of spiny dogfish life-history stages during spring (1968 – 2009). A = optimal sub-model consisting of abiotic main effects, B = optimal sub-model consisting of biotic main effects, A & B = optimal sub-model combining abiotic and biotic terms, Overall = optimal final model combining important abiotic and biotic main effects with the five largest interactions identified from BRT analysis. Bolded text represents specified sub-model. Dev = % deviance explained, AIC = Akaike's Information Criterion. Note: spiny dogfish not sexed consistently until 1980.

Stage	Sub-Model	Optimal (Sub) Model	Dev (%)	AIC
MatF	A	PA ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region	18.4	6588
	B	PA ~ s(LOLN) + s(MACN) + Co	18.4	6563
	A & B	PA ~ A + B	28.2	5802
	Overall	PA ~ A + B + te(BT,Depth) + te(Depth,Region) + te(Julian,Depth) + te(BT,Region)	32.4	5520
MatM	A	PA ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region	26.3	5725
	B	PA ~ s(BFN) + s(LOLN) + s(MACN) + Co	19.3	6248
	A & B	PA ~ A + B	36.1	4981
	Overall	PA ~ A + s(BFN) + s(LOLN) + Co + te(Julian,Year) + te(BT,Depth) + te(Depth,Region) + te(Depth,Year)	43.0	4508
ImmF	A	PA ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region	23.8	6315
	B	PA ~ s(BFN) + s(MACN) + Co	19.3	6661
	A & B	PA ~ s(Year) + s(Depth) + s(BT) + s(Julian) + Region + s(MACN) + Co PA ~ s(Year) + s(Depth) + s(BT) + s(Julian) + Region + s(MACN) + Co +	33.4	5523
	Overall	te(Julian,Depth) + te(BT,Depth) + te(Depth,Co) + te(Depth,Region) + te(Depth,Year)	37.9	5222
ImmM	A	PA ~ s(Year) + s(Depth) + s(BT) + s(Zenith) + Region	27.9	4002
	B	PA ~ s(BFN) + s(ILLN) + s(LOLN) + Co	29.6	3901
	A & B	PA ~ A + s(BFN) + s(LOLN) + Co	44.2	3116
	Overall	PA ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region + s(BFN) + s(LOLN) + Co + te(Depth,Co) + te(Year,Co) + te(BT,Co) + te(Julian,BT)	46.1	3043
Neo	A	PA ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region	30.5	2825
	B	PA ~ s(BFN) + s(LOLN) + s(ILLN) + s(MACN)	12.7	3529
	A & B	PA ~ A + s(BFN) + s(LOLN) + s(MACN)	31.3	2807
	Overall	PA ~ A + s(BFN) + s(LOLN) + s(MACN) + te(LOLN,BT) + te(BT,Depth) + te(LOLN,Depth) + te(BT,Region)	34.3	2706

Table 3B.3. Model selection for abundance (PRES) of spiny dogfish life-history stages during autumn (1963 – 2009). A = optimal sub-model consisting of abiotic main effects, B = optimal sub-model consisting of biotic main effects, A & B = optimal sub-model combining abiotic and biotic terms, Overall = optimal final model combining important abiotic and biotic main effects with the five largest interactions identified from BRT analysis. Bolded text represents specified sub-model. Dev = % deviance explained, AIC = Akaike's Information Criterion. Note: spiny dogfish not sexed consistently until 1980.

Stage	Sub-Model	Optimal (Sub) Model	Dev (%)	AIC
MatF	A	PRES ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region	40.4	7406
	B	PRES ~ s(HERN) + s(ILLN) + s(LOLN) + Co	26.6	7835
	A & B	PRES ~ A + B	48.4	7167
	Overall	PRES ~ A + B + te(Zenith,Depth) + te(Zenith,Year) + te(Julian,Year) + te(LOLN,Region) + te(Depth,Co)	56.9	6946
MatM	A	PRES ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region	34.4	12965
	B	PRES ~ s(BFN) + s(HERN) + s(ILLN) + s(LOLN) + s(MACN) + Co	20.7	13720
	A & B	PRES ~ A + B	41.0	12627
	Overall	PRES ~ A + B + te(Zenith,Depth) + te(BT,Depth) + te(BFN,Depth) + te(Depth,Co) + te(Julian,Region)	45.6	12433
ImmF	A	PRES ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region	19.2	13802
	B	PRES ~ s(BFN) + s(HERN) + s(ILLN) + s(LOLN) + s(MACN) + Co	23.0	13606
	A & B	PRES ~ A + B	37.6	12877
	Overall	PRES ~ A + B + te(BT,Co) + te(Zenith,Depth) + te(BT,Region) + te(Julian,Depth) + te(Julian,Co)	45.4	12524
ImmM	A	PRES ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region	37.3	5826
	B	PRES ~ s(BFN) + s(HERN) + s(ILLN) + s(LOLN) + s(MACN) + Co	35.8	5866
	A & B	PRES ~ A + B	49.4	5497
	Overall	PRES ~ A + s(BFN) + s(ILLN) + s(LOLN) + s(MACN) + Co + te(ILLN,BT) + te(BT,Region) + te(MACN,ILLN) + te(BT,Year)	54.9	5377
Neo	A	PRES ~ s(Depth)	9.6	514
	B	PRES ~ s(ILLN) + s(MACN)	12.7	517
	A & B	PRES ~ A + s(MACN)	14.9	513
	Overall	PRES ~ s(Depth) + Region + B + te(ILLN,Region)	33.0	514

Table 3B.4. Model selection for abundance (PRES) of spiny dogfish life-history stages during spring (1968 – 2009). A = optimal sub-model consisting of abiotic main effects, B = optimal sub-model consisting of biotic main effects, A & B = optimal sub-model combining abiotic and biotic terms, Overall = optimal final model combining important abiotic and biotic main effects with the five largest interactions identified from BRT analysis. Bolded text represents specified sub-model. Dev = % deviance explained, AIC = Akaike's Information Criterion. Note: spiny dogfish not sexed consistently until 1980.

Stage	Sub-Model	Optimal (Sub) Model	Dev (%)	AIC
MatF	A	PRES ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region	37.7	15400
	B	PRES ~ s(BFN) + s(HERN) + s(ILLN) + s(LOLN) + s(MACN) + Co	21.3	16367
	A & B	PRES ~ A + B	46.2	14931
	Overall	PRES ~ A + B + te(LOLN,BT) + te(BT,Year) + te(BT,Depth)	48.8	14820
MatM	A	PRES ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region	25.4	18706
	B	PRES ~ s(BFN) + s(HERN) + s(ILLN) + s(LOLN) + s(MACN) + Co	15.2	19447
	A & B	PRES ~ A + s(HERN) + s(ILLN) + s(LOLN) + s(MACN) + Co	31.7	18270
	Overall	PRES ~ A + s(BFN) + s(HERN) + s(LOLN) + s(MACN) + Co + te(BT,Region) + te(HERN,BT) + te(Julian,Depth) + te(Zenith,BT) + te(Depth,Region)	39.4	17803
ImmF	A	PRES ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region	29.7	19787
	B	PRES ~ s(BFN) + s(HERN) + s(ILLN) + s(LOLN) + s(MACN) + Co	25.0	20142
	A & B	PRES ~ A + B	37.3	19270
	Overall	PRES ~ A + B + te(Julian,BT) + te(BT,Depth) + te(BT,Region) + te(BT,Year) + te(BT,Co)	43.7	18878
ImmM	A	PRES ~ s(Year) + s(Depth) + s(BT) + s(Zenith) + Region	45.8	7689
	B	PRES ~ s(BFN) + s(HERN) + s(ILLN) + s(LOLN) + s(MACN) + Co	26.9	8394
	A & B	PRES ~ A + B	51.9	7489
	Overall	PRES ~ s(Year) + s(Depth) + s(BT) + s(Zenith) + Region + s(Julian) + s(BFN) + s(HERN) + s(ILLN) + s(MACN) + Co + te(BT,Region) + te(BT,Year) + te(Julian,BT) + te(ILLN,Depth)	59.0	7294
Neo	A	PRES ~ s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region	30.9	3341
	B	PRES ~ s(BFN) + s(ILLN) + s(LOLN) + s(MACN) + s(HERN)	19.4	3480
	A & B	PRES ~ A + B	40.0	3261
	Overall	PRES ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region + B + te(BT,Region) + te(ILLN,BT) + te(BFN,Julian) + te(BT,Depth) + te(BT,Year)	50.4	3182

Appendix 3C. Full Generalized Additive Modeling results

Table 3C.1. GAM results describing the occurrence (PA) of spiny dogfish life-history stages during autumn (1963 – 2009). Range = y-axis range for each smoothed term with corresponding rank (). EDF = estimated degrees of freedom. NS = not significant, ↑ = increase, ↓ = decrease. ⁺ identifies trends for parametric term. - = not applicable. GB = Georges Bank, GM = Gulf of Maine, MA = Middle Atlantic Bight, SNE = Southern New England. Stages and variables as defined in Tables 3.1 and 3.2, respectively. Note: spiny dogfish not sexed consistently until 1980.

Stage	Variable	Range	EDF	Trend
MatF	Year	1.5 (7)	3.38	↓'87, ↑(peak '04), ↓
	Depth	0 (16)	0	NS
	BT	10 (2)	2.85	↑(peak 13.5°C), ↓
	Julian	1.7 (6)	2.18	↑(peak 308d), ↓
	Zenith	0.4 (12)	1	NS
	HERN	0.6 (10)	3.47	↑(peak 275), ↓
	LOLN	0.3 (14)	1.71	NS
	MACN	0.5 (11)	1	NS
	Zenith,CoA	0 (17)	0	NS
	Zenith,CoP	1.2 (8)	1	linear ↓
	Depth,GB	0.9 (9)	1	NS
	Depth,GM	2.1 (5)	2.81	NS
	Depth,MA	0 (18)	0	NS
	Depth,SNE	34 (1)	3.63	↑45m, ↓150m, ↑(peak 240m), ↓
	Depth,CoA	6.2 (3)	1	NS
	Depth,CoP	5 (4)	2.7	NS
	Year,CoA	0.25 (15)	0.49	NS
	Year,CoP	0.35 (13)	1.49	NS
	Julian,Depth	-	0.33	NS
	RegionGM ⁺	-	-	PA 1.93 higher than GB
RegionMA ⁺	-	-	PA NS diff from GB	
RegionSNE ⁺	-	-	PA NS diff from GB	
CoP ⁺	-	-	PA 2.87 higher than CoA	
MatM	Year	2.7(6)	3.87	↑(peak '89), ↓'95, ↑'02, ↓
	Depth	9 (3)	4	↑(peak 70m), ↓180m, ↑280m, ↓
	BT	11 (2)	2.92	↑(peak 13°C), ↓
	Julian	12 (1)	3.64	↑(peak 320d)
	Zenith	0.5 (11)	2.65	↑(peak 80°), ↓140°, ↑
	BFN	1 (9)	1.7	NS
	HERN	0.01 (13)	1.2	NS
	ILLN	0.3 (12)	1	NS
	LOLN	1.5 (8)	1	linear ↓
	Julian,CoA	0 (14)	0	NS

Stage	Variable	Range	EDF	Trend
MatM (cont'd)	Julian,CoP	3 (4)	3.27	(peak 245d), ↓305d, ↑
	Year,GB	2.8 (5)	2.56	(peak '80), ↓'96, ↑
	Year,GM	0.7 (10)	1	NS
	Year,MA	2.2 (7)	1	NS
	Year,SNE	0 (15)	0	NS
	Julian,Depth	-	5.61	complex
	Depth,Year	-	4.10	complex
	RegionGM ⁺	-	-	PA 1.54 higher than GB
	RegionMA ⁺	-	-	PA NS diff from GB
	RegionSNE ⁺	-	-	PA 0.55 lower than GB
	CoP ⁺	-	-	PA 2.94 higher than CoA
	ImmF	Year	5.1 (2)	4
Depth		0.65 (8)	2.15	NS
BT		14 (1)	3.01	↑(peak 13°C), ↓
Julian		1.2 (5)	2.2	NS
HERN		0.2 (10)	1	NS
MACN		0.4 (9)	2.61	NS
Year,GB		1.4 (4)	1.45	↓'96, ↑(peak '09)
Year,GM		1.6 (3)	3.76	↑'87, ↓'94, ↑(peak '03), ↓
Year,MA		0.8 (7)	1	NS
Year,SNE		1.1 (6)	1	linear ↑
Depth,Year		-	6.23	complex
Year,BT		-	0.35	NS
Julian,Depth		-	8.75	complex
RegionGM ⁺		-	-	PA 1.36 higher than GB
RegionMA ⁺		-	-	PA 0.85 lower than GB
RegionSNE ⁺		-	-	PA 0.45 higher than GB
CoP ⁺		-	-	PA 3.31 higher than CoA
ImmM	Year	0.7 (9)	2.31	NS
	Depth	3.4 (2)	3.67	↑(peak 380m)
	BT	9 (1)	2.83	↑(peak 13°C), ↓
	Julian	0 (12)	0	NS
	Zenith	0.65 (10)	1	linear ↓
	LOLN	1.4 (5)	1	NS
	Year,CoA	0 (13)	0	NS
	Year,CoP	1.4 (6)	3.69	(peak '80), ↓'87, ↑'94, ↓'03, ↑
	Depth,CoA	2.2 (4)	1.16	(peak 0m), ↓
	Depth,CoP	0.02 (11)	0.02	NS
	Julian,CoA	1.4(7)	1.61	NS
	Julian,CoP	1.2 (8)	3.34	NS
	BT,CoA	3.4 (3)	1	linear ↓

Stage	Variable	Range	EDF	Trend
ImmM (cont'd)	BT,CoP	0 (14)	0	NS
	RegionGM ⁺	-	-	PA 1.12 lower than GB
	RegionMA ⁺	-	-	PA NS diff from GB
	RegionSNE ⁺	-	-	PA NS diff from GB
	CoP ⁺	-	-	PA 3.57 higher than CoA
Neo	Year	1.3 (8)	2.04	NS
	Depth	2 (4)	3.11	NS
	BT	25 (1)	2.7	(peak 3°C), ↓
	Julian	1 (10)	1	NS
	Zenith	0.8 (11)	1.68	NS
	BFN	0.5 (12)	1	NS
	LOLN	5 (3)	1.78	NS
	HERN	1.5 (7)	1.91	↑(peak 850), ↓
	Year,GB	2 (5)	1.65	NS
	Year,GM	1.8 (6)	1	NS
	Year,MA	7 (2)	3.79	(peak '63), ↓'76, ↑'90, ↓'96, ↑
	Year,SNE	1.1 (9)	1	NS
	Zenith,Year	-	0.01	NS
	BFN,BT	-	2.96	complex
	Depth,Year	-	3.24	complex
	RegionGM ⁺	-	-	PA 1.18 lower than GB
	RegionMA ⁺	-	-	PA NS diff from GB
	RegionSNE ⁺	-	-	PA 0.68 higher than GB

Table 3C.2. GAM results describing the occurrence (PA) of spiny dogfish life-history stages during spring (1968 – 2009). Range = y-axis range for each smoothed term with corresponding rank (). EDF = estimated degrees of freedom. NS = not significant, ↑ = increase, ↓ = decrease. ⁺ identifies trends for parametric term. - = not applicable. GB = Georges Bank, GM = Gulf of Maine, MA = Middle Atlantic Bight, SNE = Southern New England. Stages and variables as defined in Tables 3.1 and 3.2, respectively. Note: spiny dogfish not sexed consistently until 1980.

Stage	Variable	Range (Rank)	EDF	Trend
MatF	Year	1.3 (11)	3.84	↑(peak '88), ↓'01, ↑
	Depth	6 (3)	3.19	↑(peak 85m), ↓290m, ↑
	BT	1.4 (10)	1.21	NS
	Julian	1.8 (9)	1	linear ↑
	Zenith	0.4 (13)	2.84	↓110°, ↑(peak 150°)
	LOLN	0.4 (14)	1	NS
	MACN	0.8 (12)	2.83	NS
	Depth,GB	0.01 (15)	0	NS
	Depth,GM	3.5 (5)	2.26	↓120m, ↑(peak 375m)
	Depth,MA	2 (8)	3.71	↑(peak 40m), ↓170m, ↑280m, ↓
	Depth,SNE	7 (2)	3.62	↑40m, ↓170m, ↑(peak 375m)
	BT,GB	4 (4)	1.14	NS
	BT,GM	14 (1)	1	linear ↑
	BT,MA	2.8 (6)	1	NS
	BT,SNE	2.6 (7)	2.64	NS
	BT,Depth	-	10.01	complex
	Julian,Depth	-	5.64	complex
	RegionGM ⁺	-	-	PA NS diff from GB
	RegionMA ⁺	-	-	PA 1.87 higher than GB
	RegionSNE ⁺	-	-	PA 0.41 lower than GB
	CoP ⁺	-	-	PA 1.99 higher than CoA
MatM	Year	4.4 (6)	1	linear ↑
	Depth	8 (3)	2.74	↑(peak 130m), ↓
	BT	6 (4)	2.58	↑(peak 9°C), ↓
	Julian	2.5 (8)	3.08	(peak 60d), ↓
	Zenith	0.32 (10)	1.03	linear ↓
	BFN	0.2 (11)	1	NS
	LOLN	0.6 (9)	2.8	NS
	Depth,GB	4 (7)	1	NS
	Depth,GM	9 (2)	1.93	NS
	Depth,MA	11 (1)	3.93	↑75m, ↓160m, ↑(peak 380m)
	Depth,SNE	6 (5)	2.86	↑85m, ↓160m, ↑(peak 300m), ↓
	Julian,Year	-	11.52	complex
	BT,Depth	-	6.42	complex
	Depth,Year	-	11.41	complex
	RegionGM ⁺	-	-	PA 1.43 lower than GB

Stage	Variable	Range (Rank)	EDF	Trend	
MatM (cont'd)	RegionMA ⁺	-	-	PA NS diff from GB	
	RegionSNE ⁺	-	-	PA 0.52 lower than GB	
	CoP ⁺	-	-	PA 1.99 higher than CoA	
ImmF	Year	1.6 (8)	1.57	↑(peak '09)	
	Depth	2.6 (6)	1	NS	
	BT	5 (2)	1.75	(peak 1-6°C), ↓	
	Julian	0.6 (10)	1.89	NS	
	MACN	1.1 (9)	3.62	↑(peak 200), ↓	
	Depth,CoA	4.5 (3)	2.86	↓100m, ↑(peak 290m), ↓	
	Depth,CoP	8 (1)	1	linear ↑	
	Depth,GB	0 (11)	0	NS	
	Depth,GM	3.3 (5)	1	linear ↑	
	Depth,MA	4 (4)	3.98	↑70m, ↓170m, ↑(peak 380m)	
	Depth,SNE	2.5 (7)	3.94	↑70m, ↓170m, ↑(peak 280m), ↓	
	Julian,Depth	-	6.17	complex	
	BT,Depth	-	9.26	complex	
	Depth,Year	-	10.95	complex	
	RegionGM ⁺	-	-	PA 0.74 lower than GB	
	RegionMA ⁺	-	-	PA 1.00 higher than GB	
	RegionSNE ⁺	-	-	PA NS diff from GB	
	CoP ⁺	-	-	PA 2.22 higher than CoA	
	ImmM	Year	0.42 (10)	1.88	NS
		Depth	3.6 (2)	3.86	↑(peak 90m), ↓165m, ↑290m, ↓
BT		6 (1)	3.51	↑(peak 13.5°C), ↓	
Julian		3.4 (3)	1	linear ↓	
Zenith		0.6 (8)	1.58	(peak 20°), ↓	
BFN		0.6 (9)	2.87	NS	
LOLN		0.85 (7)	2.89	↓850, ↑(peak 3500)	
Depth,CoA		0 (11)	0	NS	
Depth,CoP		2.7 (5)	2.6	↑(peak 160m), ↓	
Year,CoA		0 (12)	0	NS	
Year,CoP		1.3 (6)	3.58	(peak '80), ↓'03, ↑	
BT,CoA		3.25 (4)	1.89	NS	
BT,CoP		0 (13)	0	NS	
Julian,BT		-	8.07	complex	
RegionGM ⁺		-	-	PA 0.69 lower than GB	
RegionMA ⁺		-	-	PA NS diff from GB	
RegionSNE ⁺		-	-	PA NS diff from GB	
CoP ⁺		-	-	PA 2.54 higher than CoA	
Neo		Year	0.95 (6)	3.89	↑'87, ↓'99, ↑(peak '09)
		Depth	6 (3)	3.88	↑115m, ↓165m, ↑(peak 240m), ↓
	BT	7 (2)	1.01	NS	

Stage	Variable	Range (Rank)	EDF	Trend
Neo (cont'd)	Julian	3.8 (4)	2.57	(peak 57d), ↓
	Zenith	0.6 (8)	2.84	↑(peak 60°), ↓125°, ↑
	BFN	0.8 (7)	3.56	↑(peak 350), ↓
	LOLN	0.1 (11)	1	NS
	MACN	0.5 (10)	3.64	↑200, ↓300, ↑(peak 1500)
	BT,GB	12 (1)	1	linear ↑
	BT,GM	0 (12)	0	NS
	BT,MA	0.6 (9)	1	NS
	BT,SNE	1.4 (5)	1	NS
	LOLN,BT	-	3.42	NS
	BT,Depth	-	4.09	complex
	LOLN,Depth	-	0.22	NS
	RegionGM ⁺	-	-	PA NS diff from GB
	RegionMA ⁺	-	-	PA 3.03 higher than GB
	RegionSNE ⁺	-	-	PA 2.78 higher than GB

Table 3C.3. GAM results describing the abundance (PRES) of spiny dogfish life-history stages during autumn (1963 – 2009). Range = y-axis range for each smoothed term with corresponding rank (). EDF = estimated degrees of freedom. NS = not significant, ↑ = increase, ↓ = decrease. ⁺ identifies trends for parametric term. - = not applicable. GB = Georges Bank, GM = Gulf of Maine, MA = Middle Atlantic Bight, SNE = Southern New England. Stages and variables as defined in Tables 3.1 and 3.2, respectively. Note: spiny dogfish not sexed consistently until 1980.

Stage	Variable	Range (Rank)	EDF	Trend
MatF	Year	3.2 (1)	3.24	↓'95, ↑(peak'09)
	Depth	0.014 (11)	1	NS
	BT	2.1 (5)	3.86	↑(peak 14.5°C), ↓
	Julian	2.1 (6)	3.4	(peak 254d), ↓305d, ↑
	Zenith	2.8 (3)	2.81	↓100°, ↑(peak 150°)
	HERN	0.13 (10)	2.54	↓125, ↑(peak 400)
	ILLN	0.32 (8)	1.2	(peak 0), ↓
	LOLN	0.17 (9)	1	NS
	LOLN,GB	3 (2)	3.85	(peak 0), ↓200, ↑400, ↓
	LOLN,GM	0.002 (12)	0	NS
	LOLN,MA	0 (13)	0	NS
	LOLN,SNE	1.7 (7)	3.05	(peak 0), ↓
	Depth,CoA	0 (14)	0	NS
	Depth,CoP	2.5 (4)	1	linear ↓
	Zenith,Depth	-	8.35	complex
	Zenith,Year	-	10.24	complex
	Julian,Year	-	4.41	complex
	RegionGM ⁺	-	-	PRES 1.22 higher than GB
	RegionMA ⁺	-	-	PRES NS diff from GB
	RegionSNE ⁺	-	-	PRES 1.47 higher than GB
	CoP ⁺	-	-	PRES 1.15 higher than CoA
	MatM	Year	1.3 (8)	2.79
Depth		3.9 (4)	1	linear ↓
BT		3.5 (5)	3.3	↑(peak 12°C), ↓
Julian		1.5 (7)	1.02	NS
Zenith		4.3 (2)	4	(peak 37°), ↓67°, ↑102°, ↓
BFN		0.68 (13)	2.99	(peak 0), ↓
HERN		0.7 (12)	2.86	↑(peak 200)
ILLN		0.85 (11)	3.92	↑(peak 15), ↓55, ↑
LOLN		1.2 (9)	2.93	↑(peak 250), ↓
MACN		0.4 (15)	3.88	(peak 0), ↓
Depth,CoA		0.6 (14)	1	NS
Depth,CoP		1.05 (10)	2.34	↑(peak 85m), ↓225m, ↑
Julian,GB		14 (1)	3.83	↑278d, ↓284d, ↑(peak 296d), ↓
Julian,GM		4.1 (3)	2.24	(peak 256d), ↓
Julian,SNE		3.2 (6)	2.84	↑276d, ↓284d, ↑(peak 302d), ↓

Stage	Variable	Range (Rank)	EDF	Trend
MatM (cont'd)	Zenith,Depth	-	14.93	complex
	BT,Depth	-	3.57	NS
	BFN,Depth	-	0	NS
	RegionGM ⁺	-	-	PRES 1.18 higher than GB
	RegionSNE ⁺	-	-	PRES 1.01 higher than GB
	CoP ⁺	-	-	PRES 1.01 higher than CoA
ImmF	Year	1.1 (10)	3.94	↑'87, ↓'94, ↑(peak '05), ↓
	Depth	2.1 (6)	1	linear ↓
	BT	4 (2)	4	const (4-10°C), ↑(peak 14°C), ↓
	Julian	2.2 (5)	3.26	↓(265d), ↑(peak 320d)
	Zenith	0.9 (11)	2.25	(peak 40°), ↓120°, ↑
	BFN	0.2 (17)	1.57	NS
	HERN	0.3 (15)	2.83	↑(peak ~1000)
	ILLN	0.35 (14)	2.49	↑(peak 40), ↓
	LOLN	1.4 (9)	3.85	↑(peak 250), ↓
	MACN	0.1 (18)	1	linear ↓
	BT,CoA	0.25 (16)	1.27	NS
	BT,CoP	1.6 (8)	1.31	NS
	BT,GB	4 (3)	3.94	↓8°C, ↑11°C, ↓15°C, ↑(peak 18°C)
	BT,GM	2.7 (4)	1	NS
	BT,MA	6.8 (1)	2.63	(peak 4°C), ↓10°C, ↑11.5°C, ↓14°C, ↑
	BT,SNE	0.6 (13)	1.48	NS
	Julian,CoA	0.9 (12)	1	NS
	Julian,CoP	1.9 (7)	2.21	↑(peak 290d), ↓
	Julian,Depth	-	11.91	complex
	Zenith,Depth	-	5.16	NS
	RegionGM ⁺	-	-	PRES 0.79 higher than GB
	RegionMA ⁺	-	-	PRES 1.52 lower than GB
	RegionSNE ⁺	-	-	PRES NS diff from GB
CoP ⁺	-	-	PRES 1.80 higher than CoA	
ImmM	Year	2.1 (4)	3.44	↑'88, ↓'97, ↑(peak '09)
	Depth	1.05 (9)	1.88	↑(peak ~300m)
	BT	5.2 (3)	4	(peak 5°C), ↓7°C, ↑9.5°C, ↓
	Julian	1.7 (6)	3.01	↑(peak 286d), ↓
	Zenith	1.25 (8)	2.05	(peak 40°), ↓
	BFN	0.21 (12)	1	linear ↓
	ILLN	0.3 (11)	1	NS
	LOLN	1.6 (7)	1.88	(peak 0), ↓
	MACN	0.2 (13)	3.06	NS
	BT,GB	0.6 (10)	1.11	NS
	BT,GM	7 (2)	3.56	↑8.5°C, ↓10°C, ↑(peak ~13°C)
	BT,MA	1.7 (5)	1	NS

Stage	Variable	Range (Rank)	EDF	Trend
ImmM (cont'd)	BT,SNE	11.5 (1)	2.96	↑(peak 7.5°C), ↓9.5°C, ↑11°C, ↓
	ILLN,BT	-	7.67	complex
	MACN,ILLN	-	3.89	complex
	BT,Year	-	7.56	complex
	RegionGM ⁺	-	-	PRES 0.68 lower than GB
	RegionMA ⁺	-	-	PRES NS diff from GB
	RegionSNE ⁺	-	-	PRES NS diff from GB
	CoP ⁺	-	-	PRES 1.99 higher than CoA
Neo	Depth	0.7 (5)	1	linear ↑
	ILLN	1.2 (2)	1	NS
	MACN	0.1 (6)	1	NS
	ILLN,GB	3.2 (1)	1	linear ↑
	ILLN,GM	0 (7)	0	NS
	ILLN,MA	1 (3)	1	NS
	ILLN,SNE	1 (4)	1	NS
	RegionGM ⁺	-	-	PRES 3.01 lower than GB
	RegionMA ⁺	-	-	PRES 2.38 lower than GB
	RegionSNE ⁺	-	-	PRES 1.97 lower than GB

Table 3C.4. GAM results describing the abundance (PRES) of spiny dogfish life-history stages during spring (1968 – 2009). Range = y-axis range for each smoothed term with corresponding rank (). EDF = estimated degrees of freedom. NS = not significant, ↑ = increase, ↓ = decrease. ⁺identifies trends for parametric term. - = not applicable. GB = Georges Bank, GM = Gulf of Maine, MA = Middle Atlantic Bight, SNE = Southern New England. Stages and variables as defined in Tables 3.1 and 3.2, respectively. Note: spiny dogfish not sexed consistently until 1980.

Stage	Variable	Range (Rank)	EDF	Trend	
MatF	Year	0.85 (5)	1	linear ↓	
	Depth	1.6 (2)	2.99	↑(peak 100m), ↓	
	BT	0.45 (8)	1.08	NS	
	Julian	1.3 (3)	3.77	(peak 57d), ↓115d, ↑	
	Zenith	0.24 (10)	1.49	(peak 25°), ↓	
	BFN	0.37 (9)	2.8	(peak 0), ↓	
	HERN	0.5 (7)	3.91	↓70, ↑(peak 400)	
	ILLN	1 (4)	2.93	(peak 0), ↓	
	LOLN	5 (1)	2.62	(peak 0), ↓	
	MACN	0.8 (6)	3.03	↑(peak 225), ↓	
	BT,Depth	-	6.8	complex	
	LOLN,BT	-	12.76	complex	
	BT,Year	-	7.07	complex	
	RegionGM ⁺	-	-	PRES NS diff from GB	
	RegionMA ⁺	-	-	PRES 0.67 higher than GB	
	RegionSNE ⁺	-	-	PRES 0.34 higher than GB	
	CoP ⁺	-	-	PRES 1.09 higher than CoA	
	MatM	Year	0.51 (15)	3.02	↑(peak '98), ↓
		Depth	3.3 (7)	2.42	↑(peak 135m), ↓
		BT	75 (3)	1	linear ↓
Julian		1.3 (10)	3.11	↑(peak 88d), ↓118d, ↑	
Zenith		0.29 (16)	1	NS	
BFN		0.26 (17)	3.85	↑(peak 185), ↓370, ↑	
HERN		0.75 (12)	1.88	NS	
LOLN		0.55 (14)	3.07	(peak 0), ↓575, ↑2000, ↓	
MACN		0.57 (13)	2.96	↑(peak 250), ↓	
BT,GB		84 (1)	2.33	↑(peak 14°C)	
BT,GM		56 (5)	2.95	↑(peak 11.5°C), ↓	
BT,MA		82 (2)	1.34	↑(peak 14°C)	
BT,SNE		75 (4)	3.88	↑(peak 14°C)	
Depth,GB		1.9 (9)	2.34	↑(peak 130m), ↓290m, ↑	
Depth,GM		1.3 (11)	1	NS	
Depth,MA		3.5 (6)	2.57	↑(peak 170m), ↓	
Depth,SNE		2.9 (8)	3.98	↑130m, ↓260m, ↑(peak ~400)	
HERN,BT		-	7.54	complex	
Julian,Depth		-	14.63	complex	

Stage	Variable	Range (Rank)	EDF	Trend	
MatM (cont'd)	Zenith,BT	-	6.08	complex	
	RegionGM ⁺	-	-	PRES 1.67 lower than GB	
	RegionMA ⁺	-	-	PRES 0.87 higher than GB	
	RegionSNE ⁺	-	-	PRES NS diff from GB	
	CoP ⁺	-	-	PRES 0.96 higher than CoA	
ImmF	Year	0.32 (15)	1.77	↑(peak '88), ↓	
	Depth	2 (4)	1	linear ↓	
	BT	1 (8)	1	NS	
	Julian	3.6 (2)	3.77	↓85d, ↑(peak 122d), ↓	
	Zenith	0.65 (11)	3.51	↑(peak 65°), ↓	
	BFN	0.48 (13)	1.88	(peak 0), ↓	
	HERN	0.7 (10)	2.82	↓120, ↑(peak ~1300)	
	ILLN	0.26 (16)	1.26	(peak 0), ↓	
	LOLN	0.38 (14)	1.96	↑(peak 2400), ↓	
	MACN	0.58 (12)	3.7	↑(peak 300), ↓	
	BT,GB	1.2 (7)	2.1	NS	
	BT,GM	34 (1)	3.86	(peak 3°C), ↓7.5°C, ↑9.5°C, ↓	
	BT,MA	1.7 (5)	1	NS	
	BT,SNE	1 (9)	1	NS	
	BT,CoA	3.2 (3)	2.86	↑(peak 11.5°C), ↓	
	BT,CoP	1.3 (6)	1	NS	
	Julian,BT	-	14.44	complex	
	BT,Depth	-	10.44	complex	
	BT,Year	-	7.3	complex	
	RegionGM ⁺	-	-	PRES 1.65 lower than GB	
	RegionMA ⁺	-	-	PRES 0.27 lower than GB	
	RegionSNE ⁺	-	-	PRES 0.53 lower than GB	
	CoP ⁺	-	-	PRES 1.18 higher than CoA	
	ImmM	Year	1.2 (7)	4	↓'84, ↑(peak '94), ↓'02, ↑
		Depth	4.7 (6)	4	(peak 0m), ↓75m, ↑190m, ↓
		BT	55 (3)	2	(peak 3°C), ↓
		Julian	0.75 (8)	2.12	NS
Zenith		0.65 (9)	2.37	↑(peak 75°), ↓	
BFN		0.4 (11)	2.83	↑(peak 250), ↓	
HERN		0.64 (10)	2.91	NS	
ILLN		0.32 (12)	1	linear ↓	
MACN		0.18 (13)	1	NS	
BT,GB		60 (1)	2.92	↑(peak 14°C)	
BT,GM		41 (5)	2.84	↑(peak 11.5°C), ↓	
BT,MA		58 (2)	1	linear ↑	
BT,SNE		54 (4)	3.86	↑(peak 14°C)	
BT,Year		-	12.91	complex	
Julian,BT		-	2.38	complex	

Stage	Variable	Range (Rank)	EDF	Trend
ImmM (cont'd)	ILLN,Depth	-	11.99	complex
	RegionGM ⁺	-	-	PRES 2.60 lower than GB
	RegionMA ⁺	-	-	PRES 0.44 lower than GB
	RegionSNE ⁺	-	-	PRES NS diff from GB
	CoP ⁺	-	-	PRES 1.92 higher than CoA
Neo	Year	1.5 (6)	3.61	↑(peak '83), ↓
	Depth	1.6 (5)	2.28	↑(peak 175m), ↓
	BT	0.5 (10)	1	NS
	Julian	0.7 (8)	1.73	NS
	Zenith	2.1 (4)	4	(peak 34°), ↓55°, ↑78°, ↓114°, ↑
	BFN	1.3 (7)	2.51	(peak 0), ↓
	LOLN	0.5 (11)	3.01	↓270, ↑(peak 2000)
	ILLN	0.06 (13)	1	NS
	MACN	0.6 (9)	2.75	↑(peak 250)
	HERN	0.07 (12)	1.19	NS
	BT,GB	4.7 (1)	1	NS
	BT,GM	0 (14)	0	NS
	BT,MA	2.2 (3)	3.01	↑(peak 10.5°C), ↓
	BT,SNE	4.5 (2)	1	NS
	ILLN,BT	-	6.68	complex
	BFN,Julian	-	7.65	complex
	BT,Depth	-	3.02	NS
	BT,Year	-	7.08	complex
	RegionGM ⁺	-	-	PRES 2.88 lower than GB
	RegionMA ⁺	-	-	PRES NS diff from GB
	RegionSNE ⁺	-	-	PRES 0.63 higher than GB

Appendix 3D. Occurrence (PA) Models for Autumn

Figure 3D.1. Partial GAM plots identifying the additive effect of each variable on the probability of occurrence of mature female spiny dogfish during autumn. Variables as defined in Table 3.2. The y-axis represents the degree of smoothing (variable, estimated degrees of freedom) 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'. Range estimates exclude extreme values where rugs are sparse. Some smoothes have been graphically abbreviated due to a lack of data at the endpoints. The gray region reflects the 95% confidence intervals around the response curves. NS = not significant.

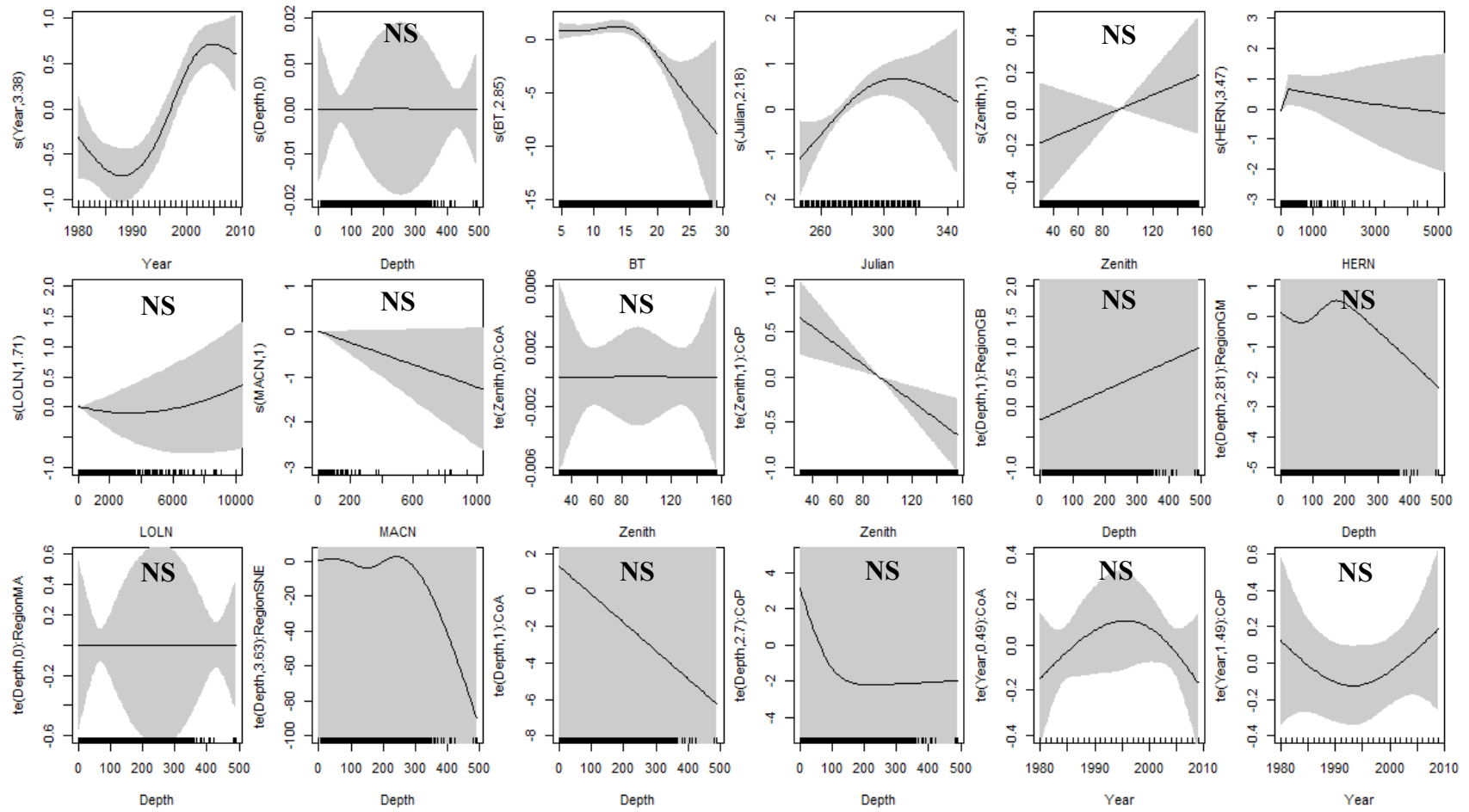


Figure 3D.2. Partial GAM derived effects of important interactions on the occurrence of mature female spiny dogfish during autumn. Interaction effects shown as perspective plots without error bounds. The response on the z-axis reflects the tensor smooth (variable 1, variable 2, estimated degrees of freedom). NS = not significant.

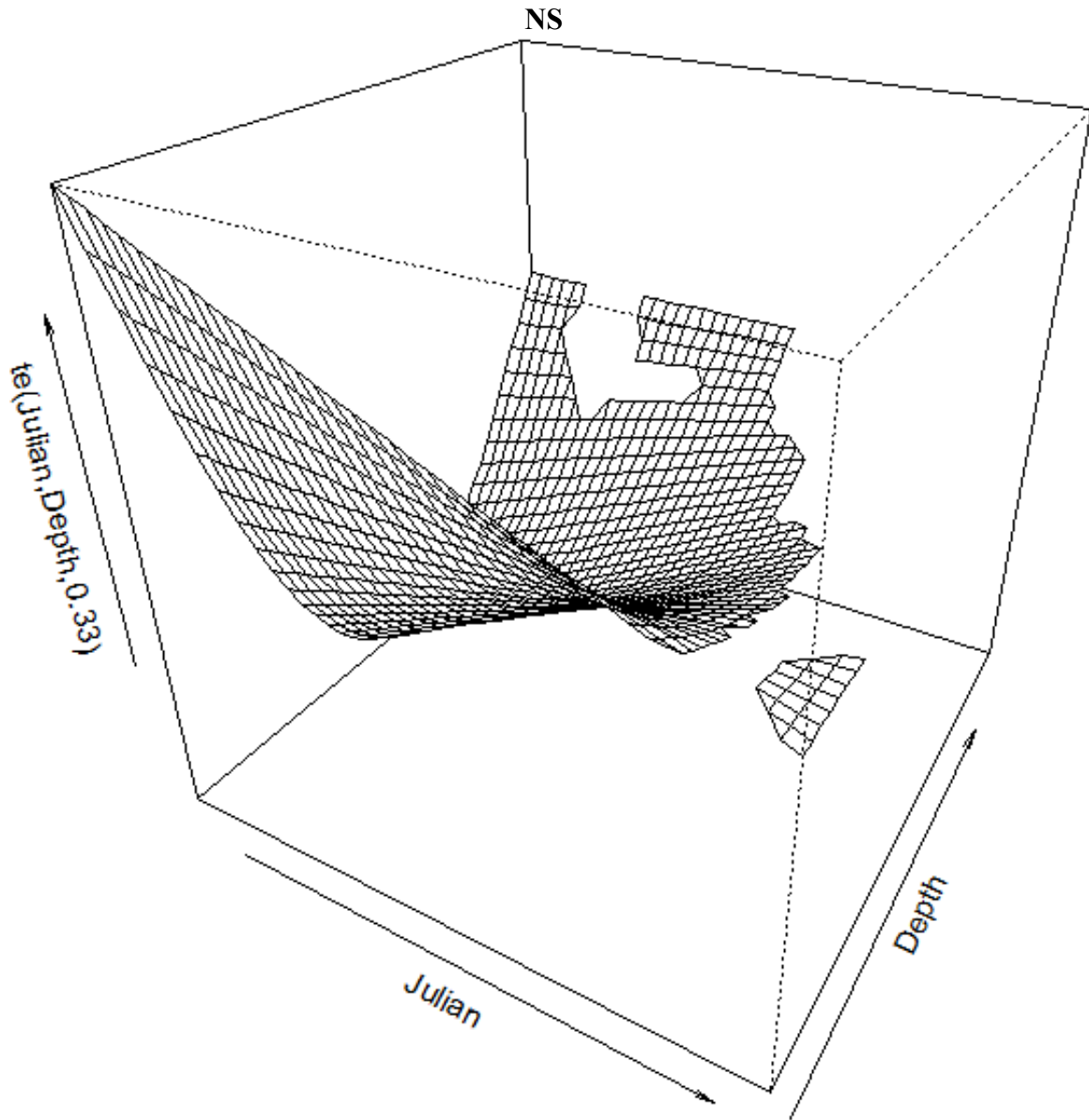


Figure 3D.3. Partial GAM plots identifying the additive effect of each variable on the probability of occurrence of immature female spiny dogfish during autumn. Variables as defined in Table 3.2. The y-axis represents the degree of smoothing (variable, estimated degrees of freedom) with its range indicative of the relative importance of each covariate. The x-axis reflects the relative density of data points as shown by the 'rug'. Range estimates exclude extreme values where rugs are sparse. Some smoothes have been graphically abbreviated due to a lack of data at the endpoints. The gray region reflects the 95% confidence intervals around the response curves. NS = not significant.

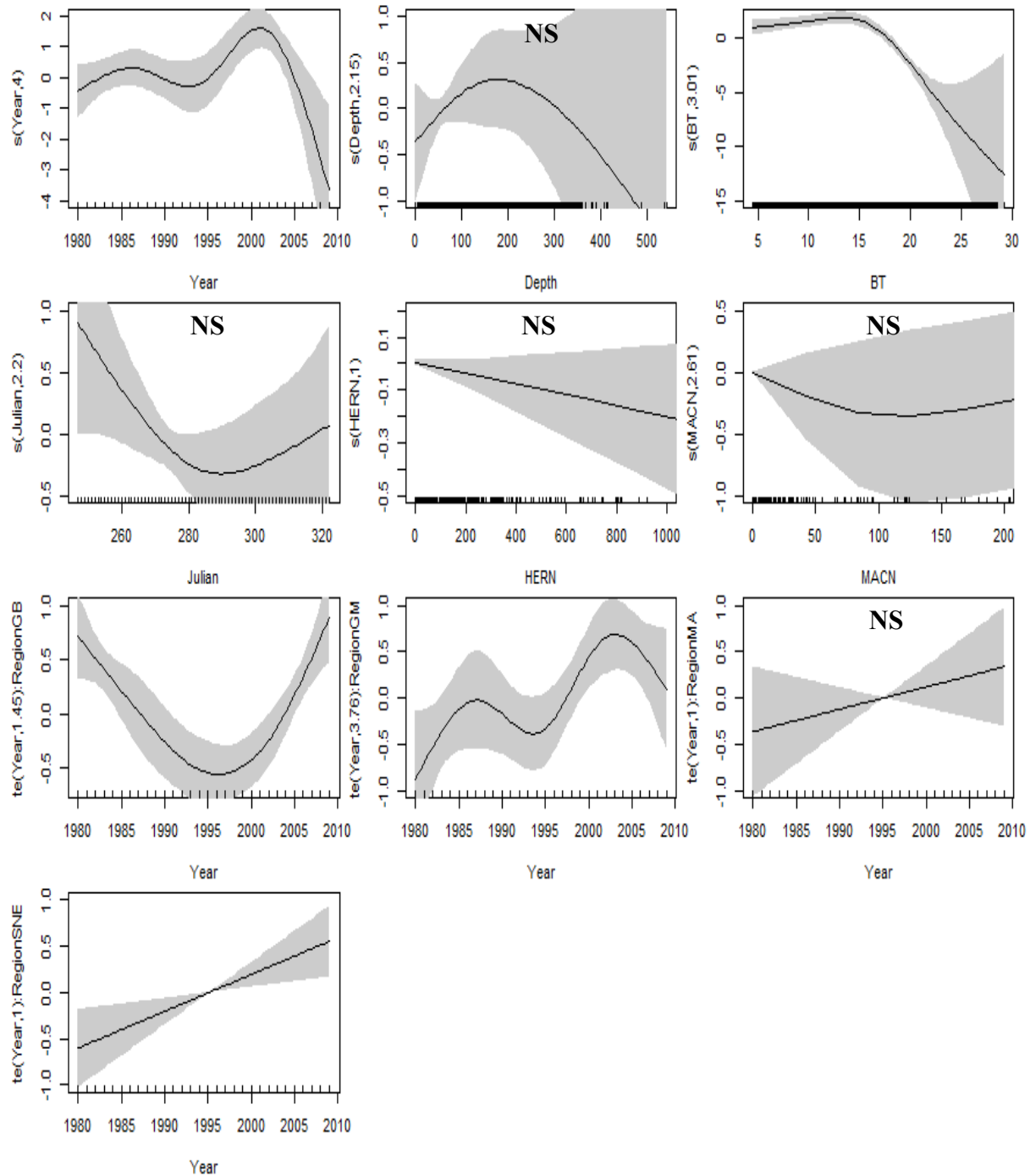


Figure 3D.4. Partial GAM derived effects of important interactions on the occurrence of immature female spiny dogfish during autumn. Interaction effects shown as perspective plots without error bounds. The response on the z-axis reflects the tensor smooth (variable 1, variable 2, estimated degrees of freedom). NS = not significant.

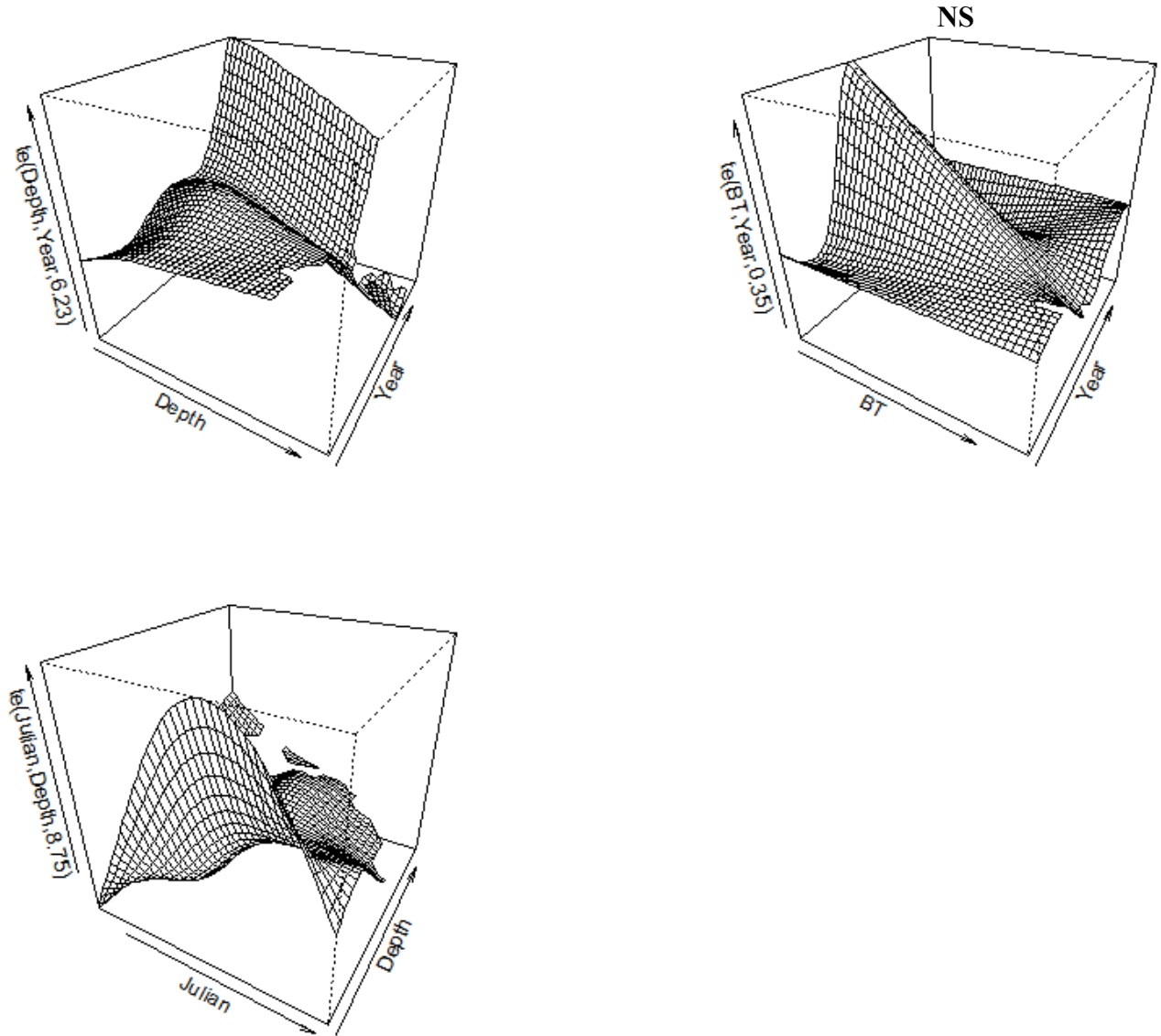


Figure 3D.5. Partial GAM plots identifying the additive effect of each variable on the probability of occurrence of immature male spiny dogfish during autumn. Variables as defined in Table 3.2. The y-axis represents the degree of smoothing (variable, estimated degrees of freedom) with its range indicative of the relative importance of each covariate. The x-axis reflects the relative density of data points as shown by the 'rug'. Range estimates exclude extreme values where rugs are sparse. Some smoothes have been graphically abbreviated due to a lack of data at the endpoints. The gray region reflects the 95% confidence intervals around the response curves. NS = not significant.

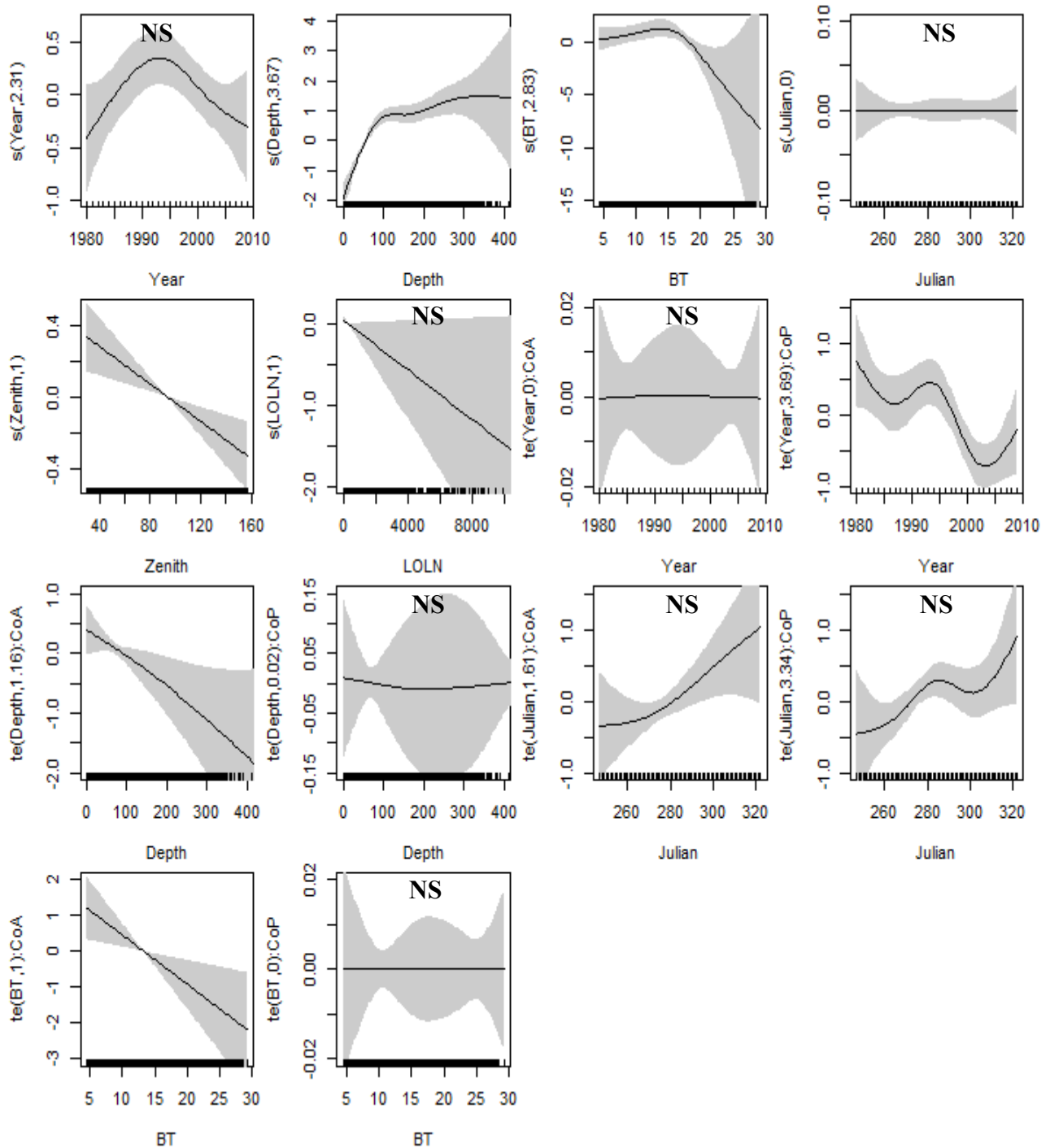


Figure 3D.6. Partial GAM plots identifying the additive effect of each variable on the probability of occurrence of neonate spiny dogfish during autumn. Variables as defined in Table 3.2. The y-axis represents the degree of smoothing (variable, estimated degrees of freedom) with its range indicative of the relative importance of each covariate. The x-axis reflects the relative density of data points as shown by the 'rug'. Range estimates exclude extreme values where rugs are sparse. Some smoothes have been graphically abbreviated due to a lack of data at the endpoints. The gray region reflects the 95% confidence intervals around the response curves. NS = not significant.

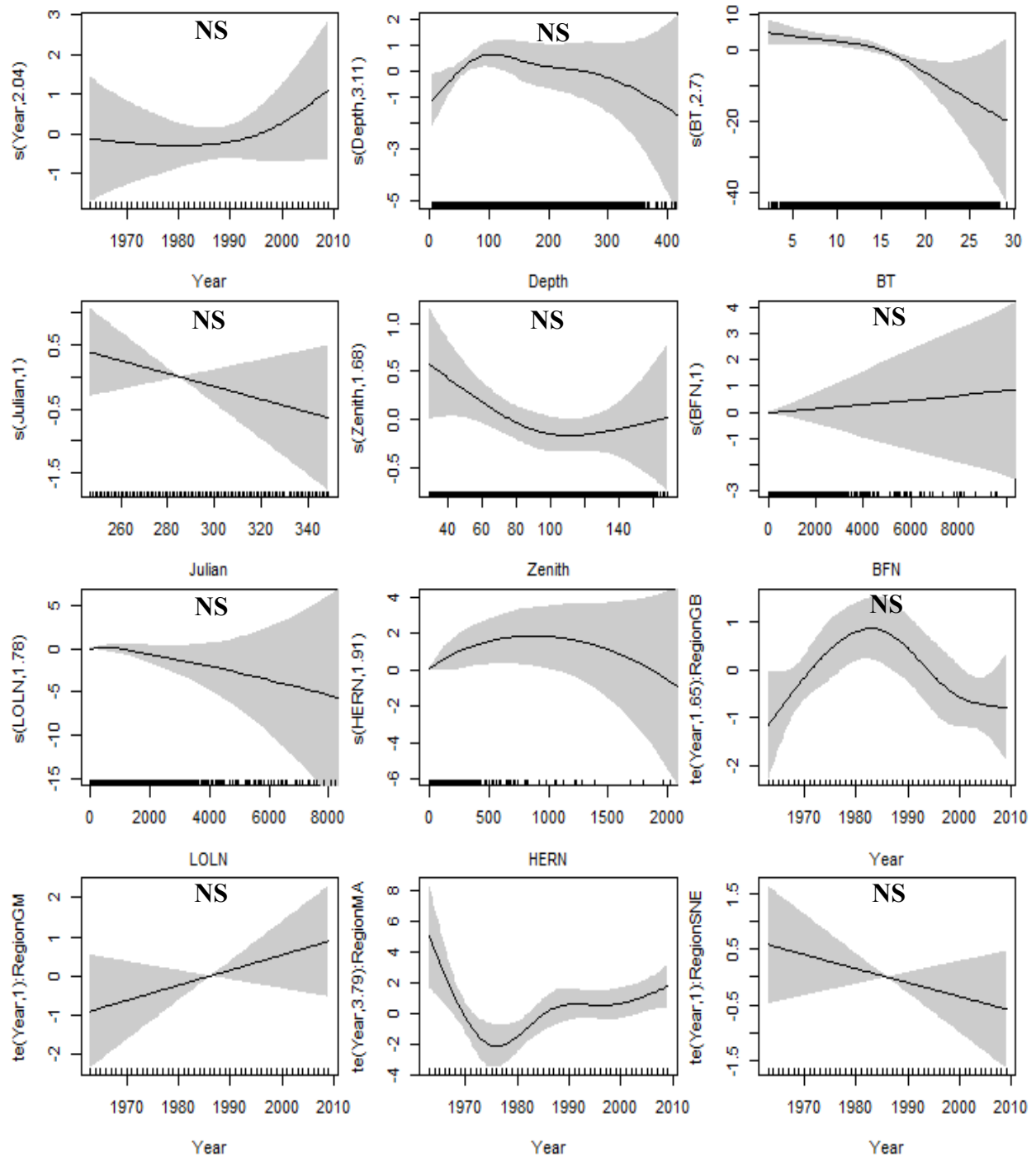


Figure 3D.7. Partial GAM derived effects of important interactions on the occurrence of neonate spiny dogfish during autumn. Interaction effects shown as perspective plots without error bounds. The response on the z-axis reflects the tensor smooth (variable 1, variable 2, estimated degrees of freedom). NS = not significant.

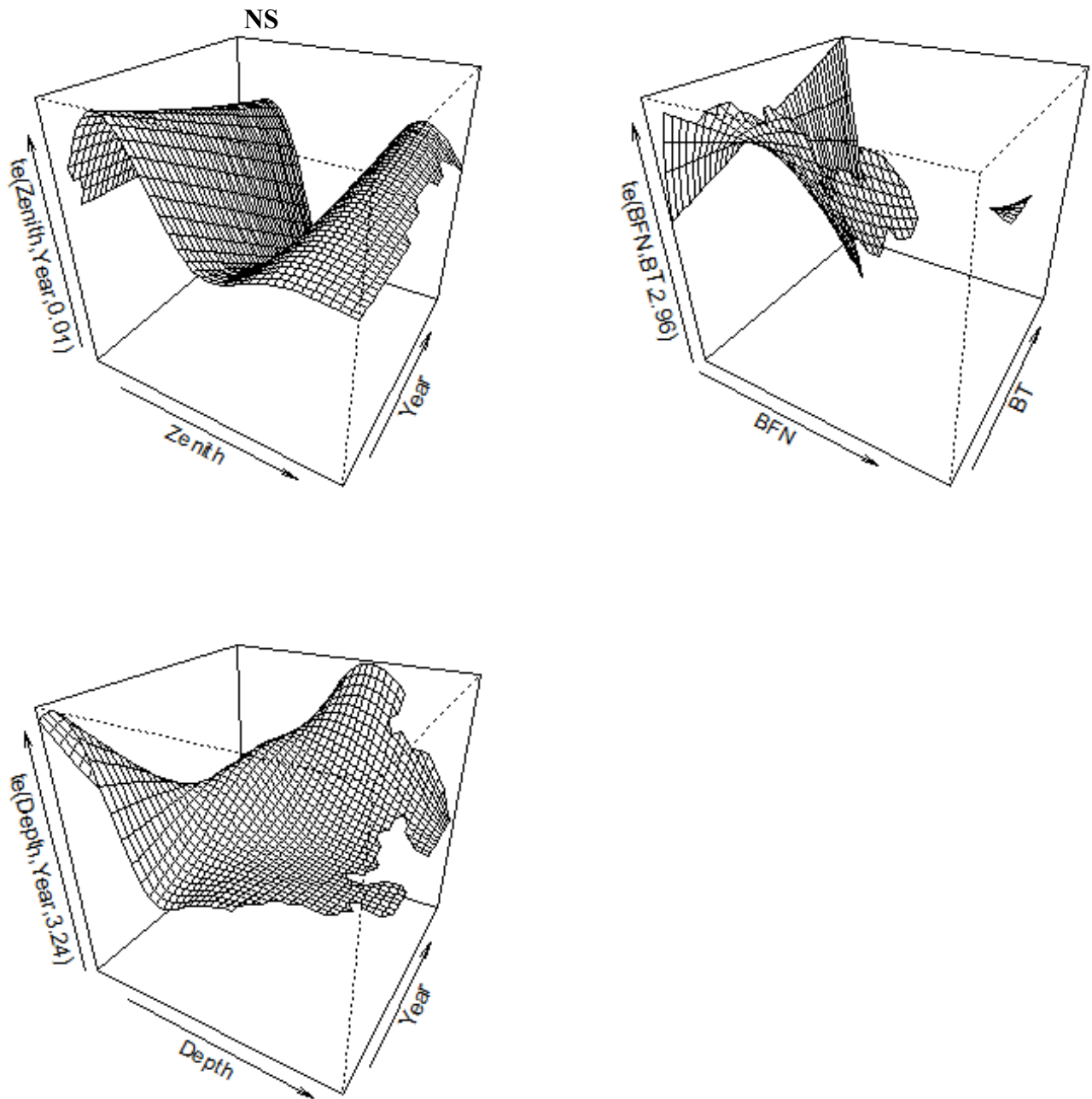


Figure 3D.8. Relationships between the Pearson residuals and all potential explanatory variables based on the optimal mature female spiny dogfish occurrence model during autumn. Note: Mature Male PA (bottom right) represents co-occurrence.

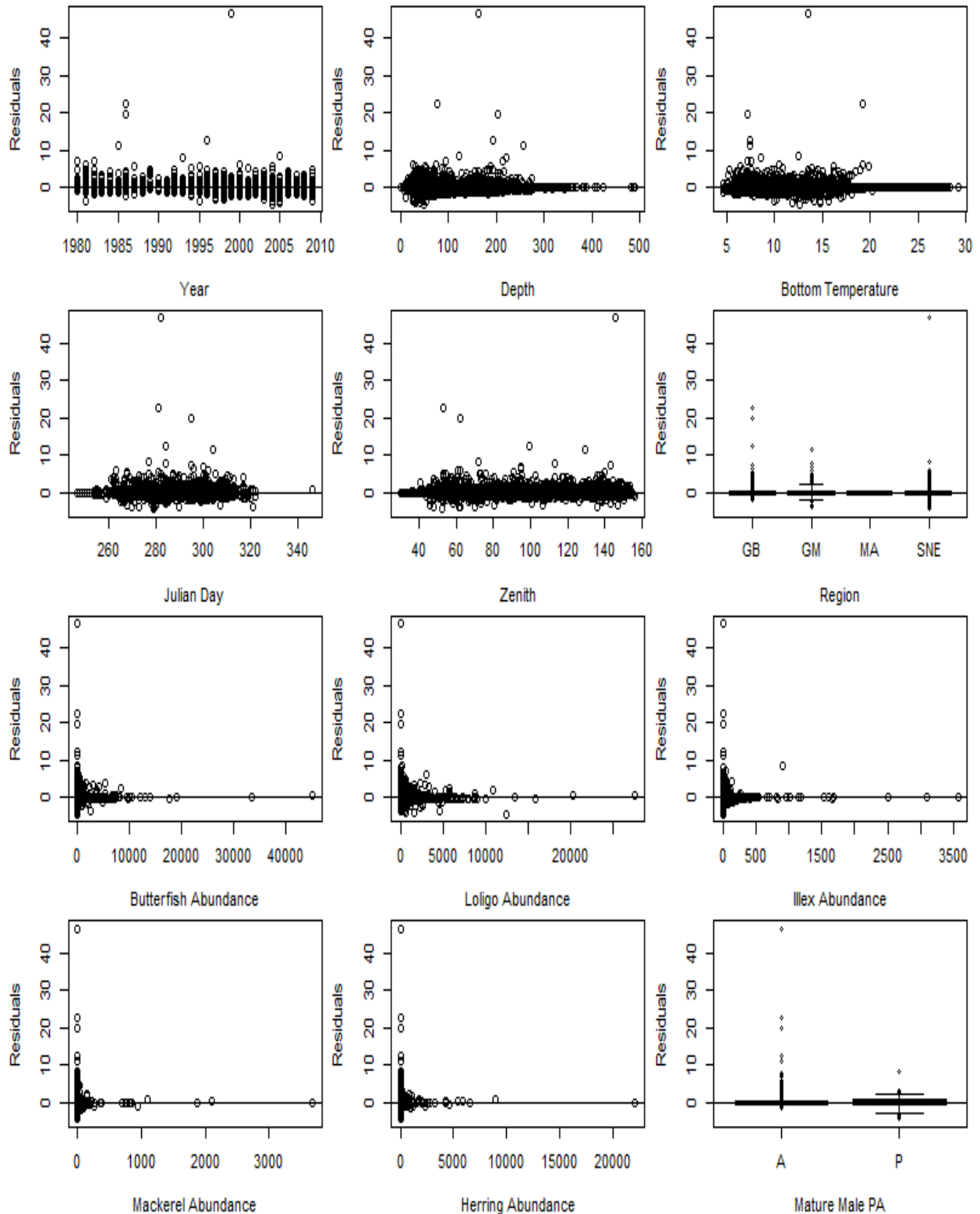


Figure 3D.9. Relationships between the Pearson residuals and all potential explanatory variables based on the optimal mature male spiny dogfish occurrence model during autumn. Note: Mature Female PA (bottom right) represents co-occurrence.

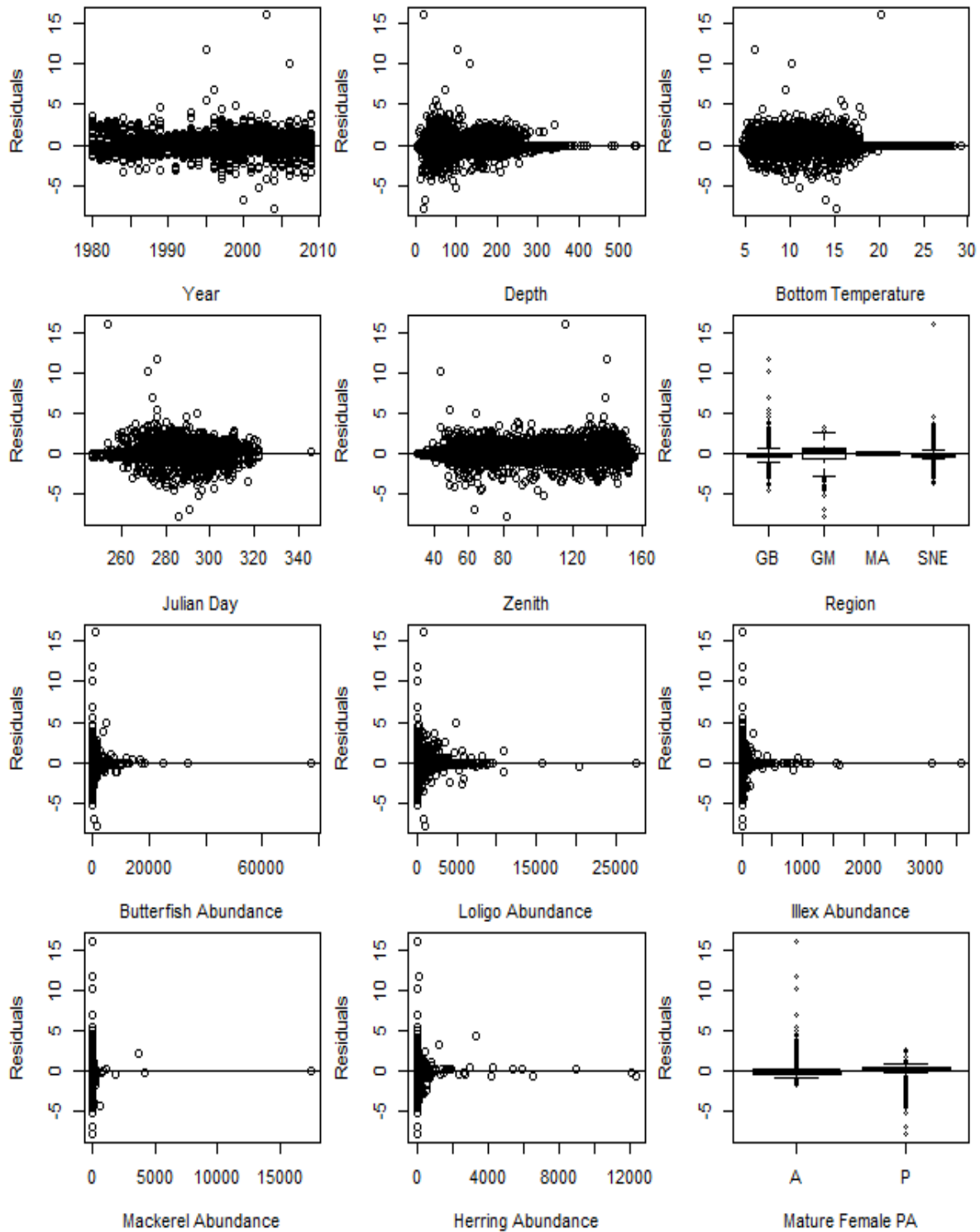


Figure 3D.10. Relationships between the Pearson residuals and all potential explanatory variables based on the optimal immature female spiny dogfish occurrence model during autumn. Note: Immature Male PA (bottom right) represents co-occurrence.

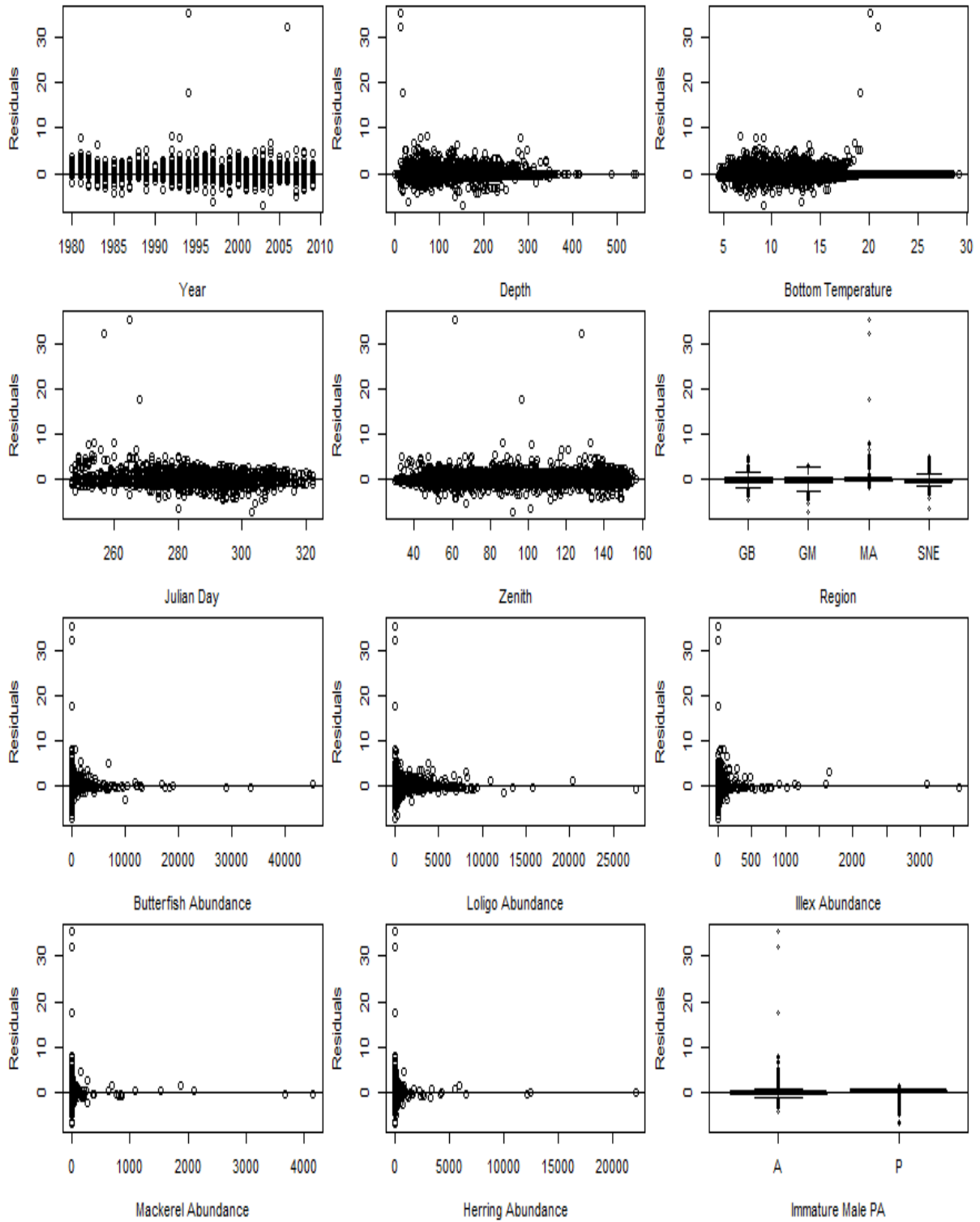


Figure 3D.11. Relationships between the Pearson residuals and all potential explanatory variables based on the optimal immature male spiny dogfish occurrence model during autumn. Note: Immature Female PA (bottom right) represents co-occurrence.

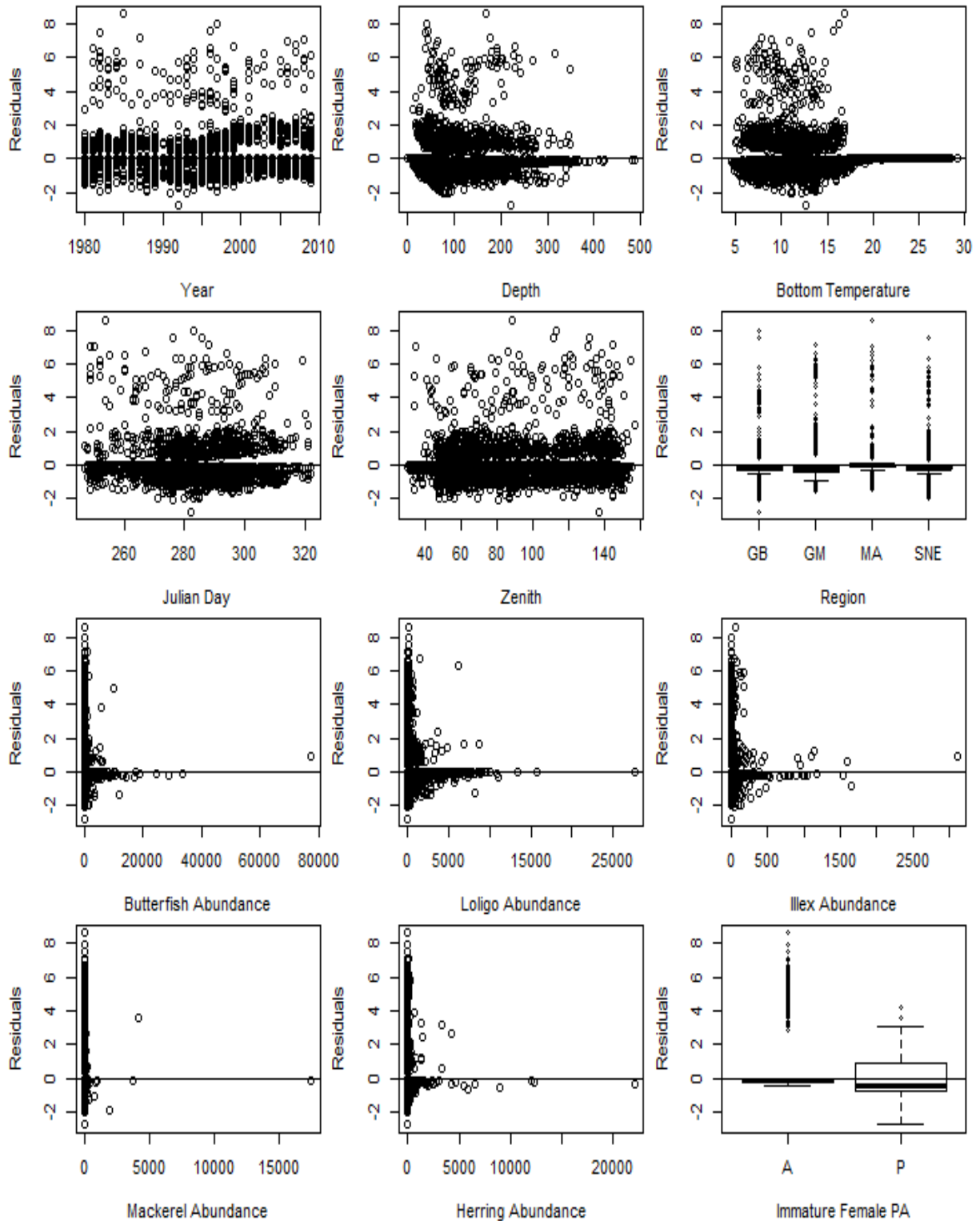


Figure 3D.12. Relationships between the Pearson residuals and all potential explanatory variables based on the optimal neonate spiny dogfish occurrence model during autumn.

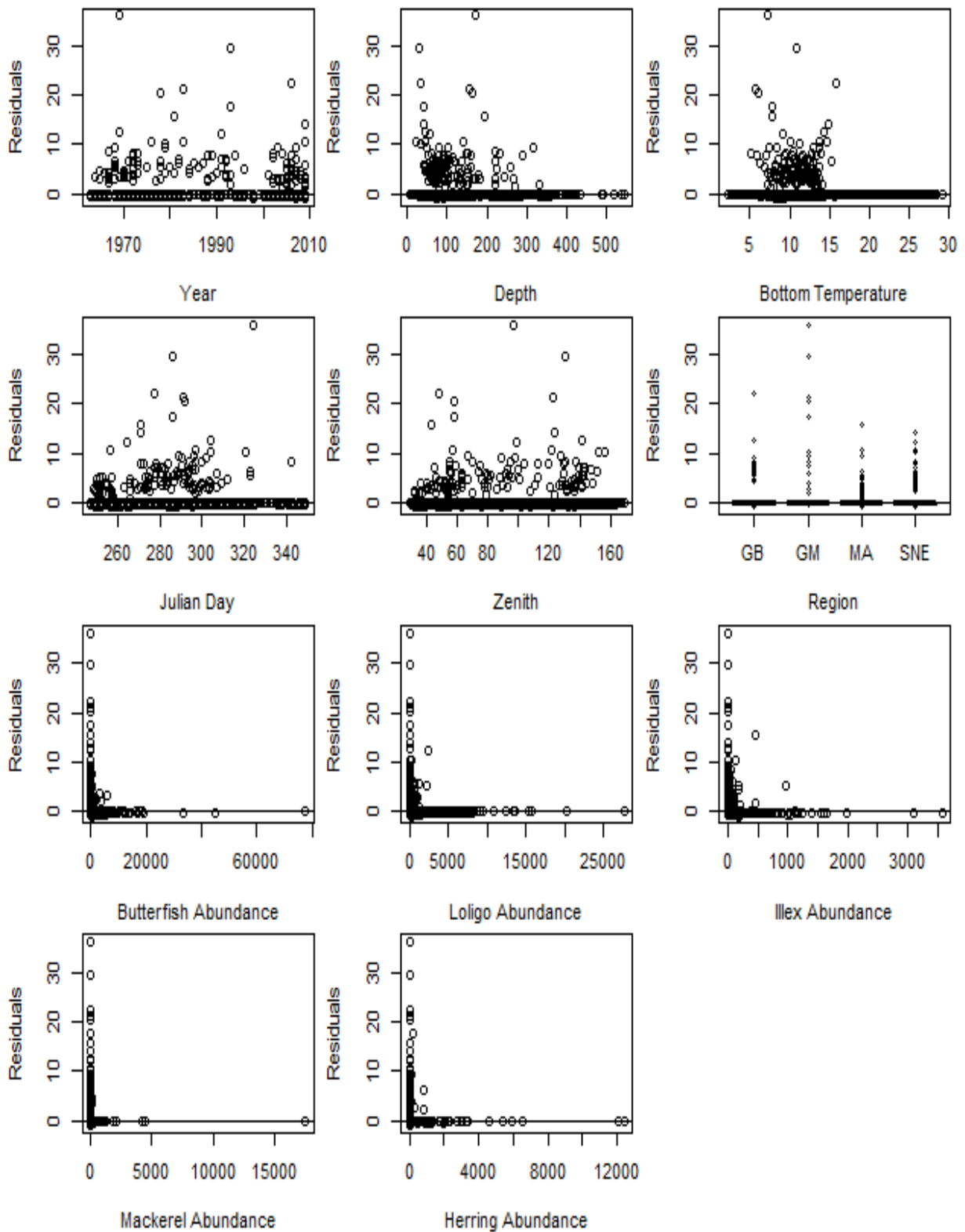


Figure 3D.13. Comparison of the predicted probability of occurrence (filled contours) as determined by inverse distance weighted interpolation versus observed occurrence (points) in the Northeast (US) shelf large marine ecosystem for mature female spiny dogfish during autumn. MA = Middle Atlantic Bight, SNE = Southern New England, GB = Georges Bank, and GM = Gulf of Maine. Solid gray indicates land masses. Note: interpolation carried out in ArcGIS using spatial analyst.

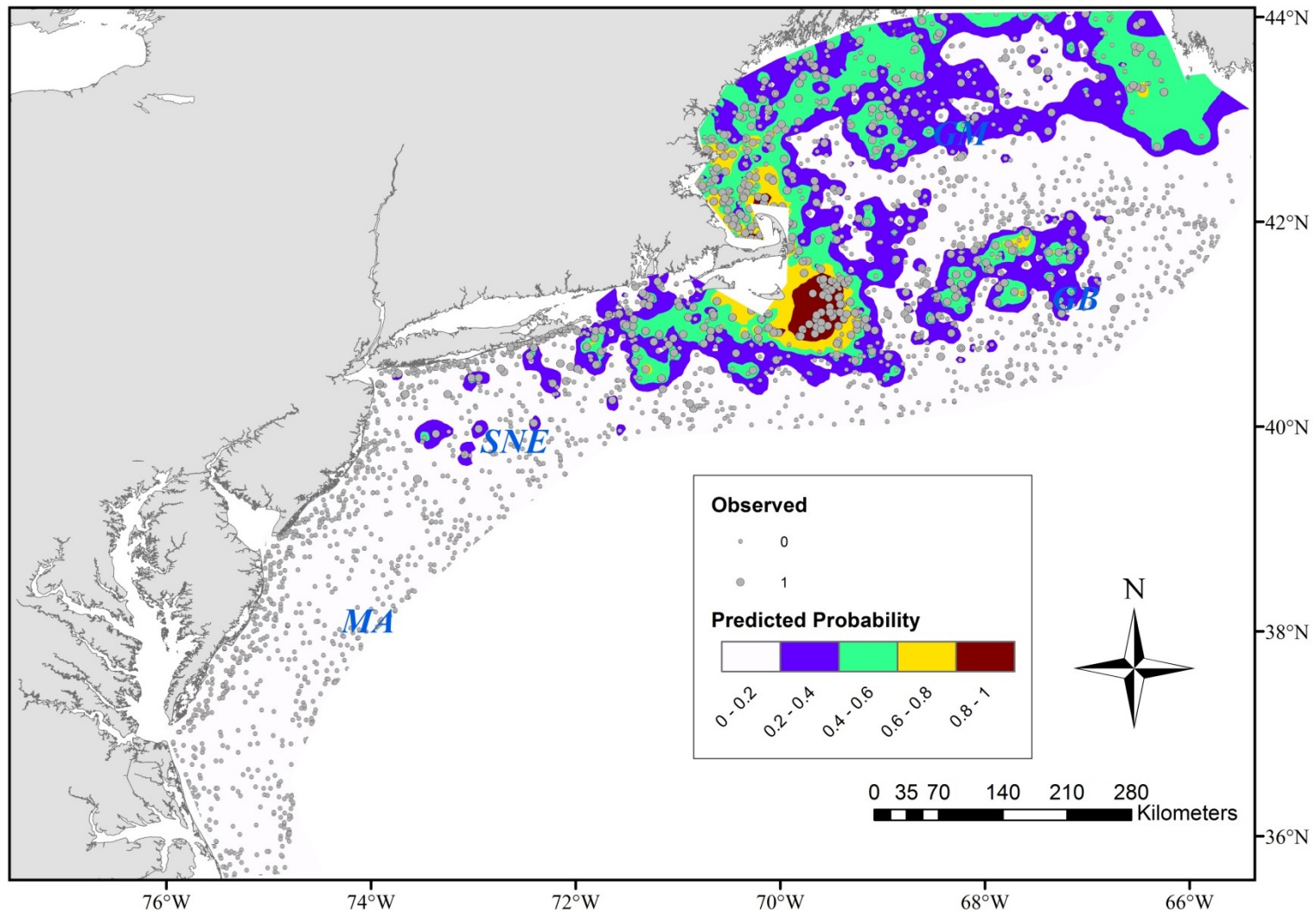


Figure 3D.14. Comparison of the predicted probability of occurrence (filled contours) as determined by inverse distance weighted interpolation versus observed occurrence (points) in the Northeast (US) shelf large marine ecosystem for mature male spiny dogfish during autumn. MA = Middle Atlantic Bight, SNE = Southern New England, GB = Georges Bank, and GM = Gulf of Maine. Solid gray indicates land masses. Note: interpolation carried out in ArcGIS using spatial analyst.

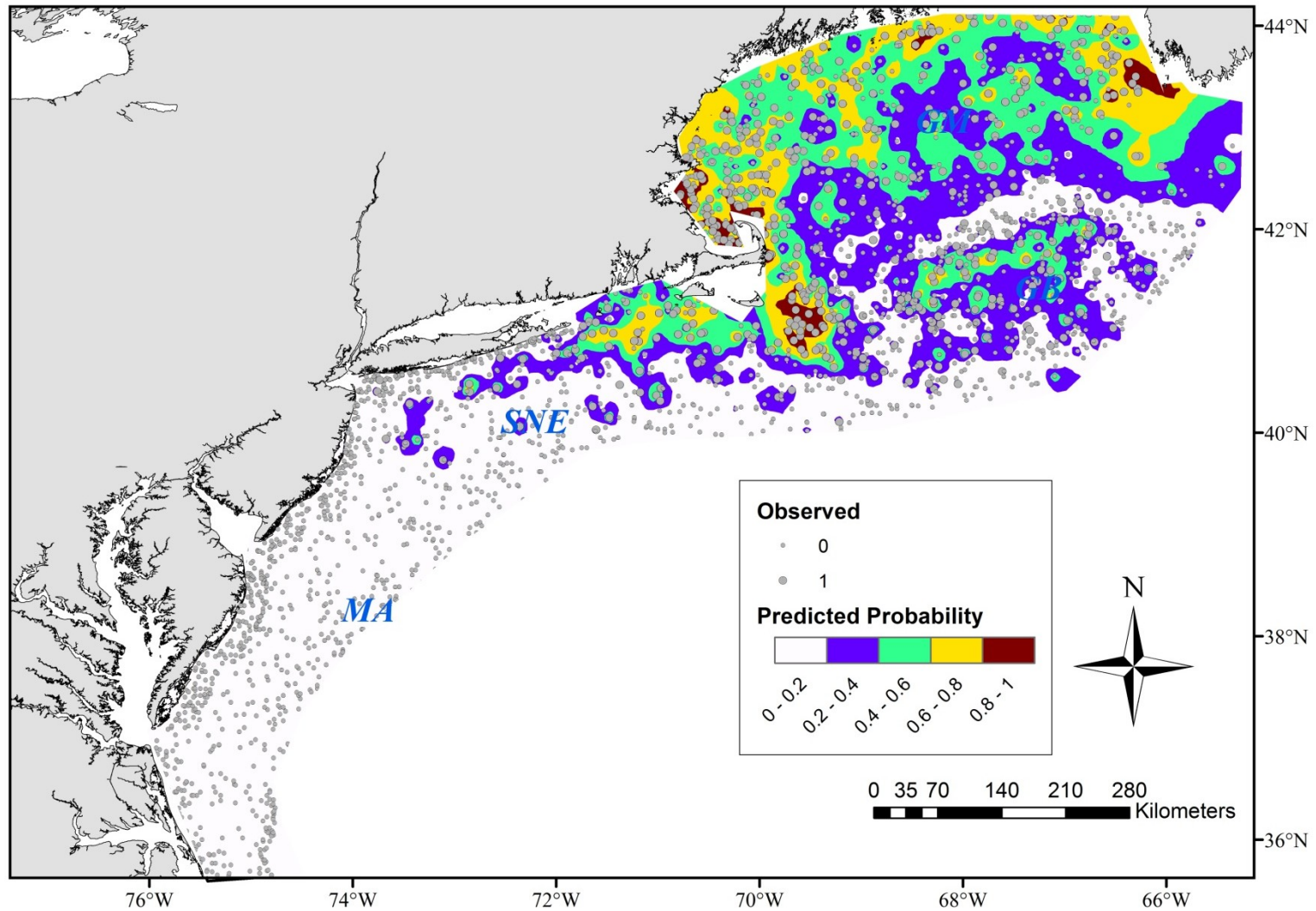


Figure 3D.15. Comparison of the predicted probability of occurrence (filled contours) as determined by inverse distance weighted interpolation versus observed occurrence (points) in the Northeast (US) shelf large marine ecosystem for immature female spiny dogfish during autumn. MA = Middle Atlantic Bight, SNE = Southern New England, GB = Georges Bank, and GM = Gulf of Maine. Solid gray indicates land masses. Note: interpolation carried out in ArcGIS using spatial analyst.

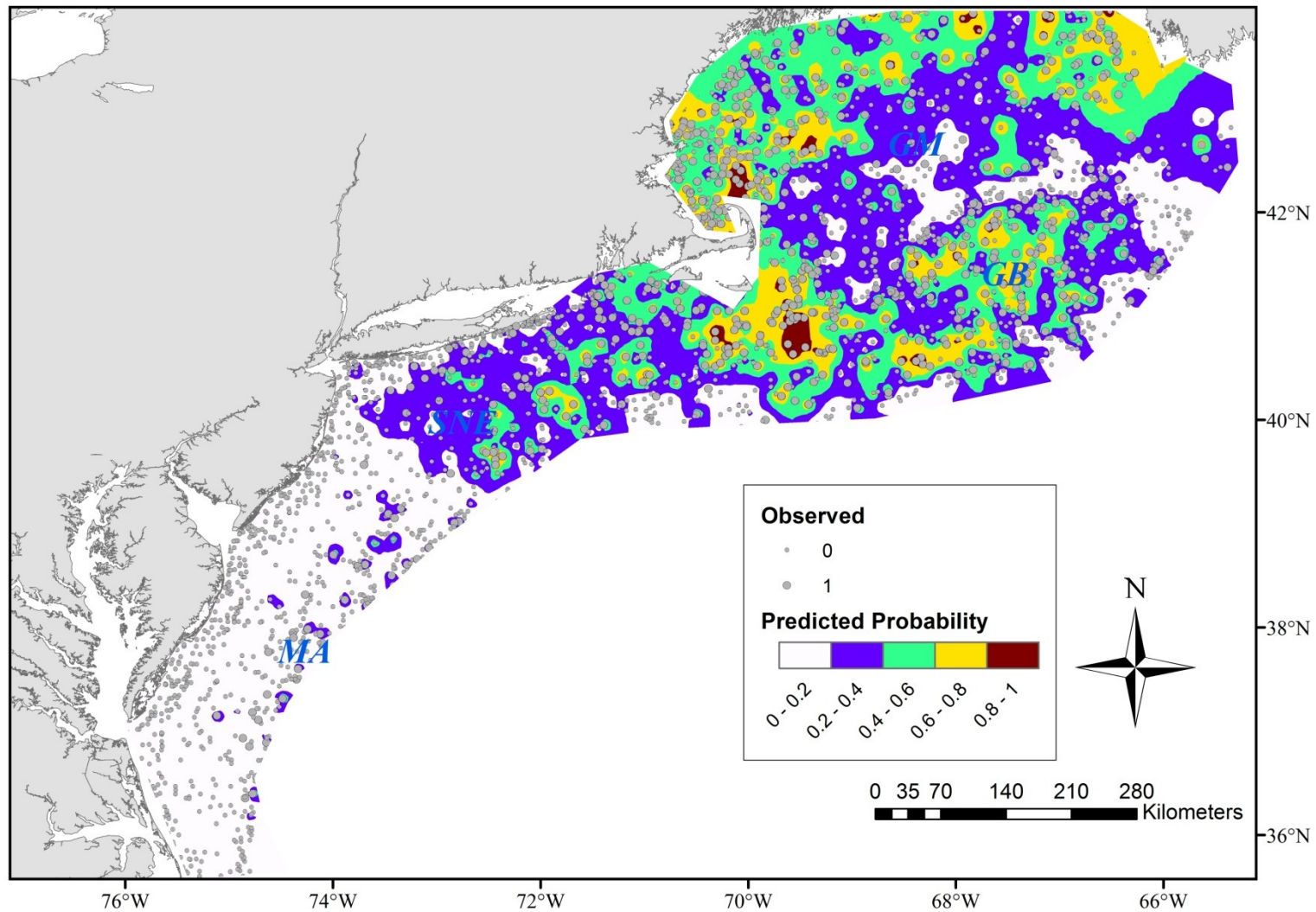


Figure 3D.16. Comparison of the predicted probability of occurrence (filled contours) as determined by inverse distance weighted interpolation versus observed occurrence (points) in the Northeast (US) shelf large marine ecosystem for immature male spiny dogfish during autumn. MA = Middle Atlantic Bight, SNE = Southern New England, GB = Georges Bank, and GM = Gulf of Maine. Solid gray indicates land masses. Note: interpolation carried out in ArcGIS using spatial analyst.

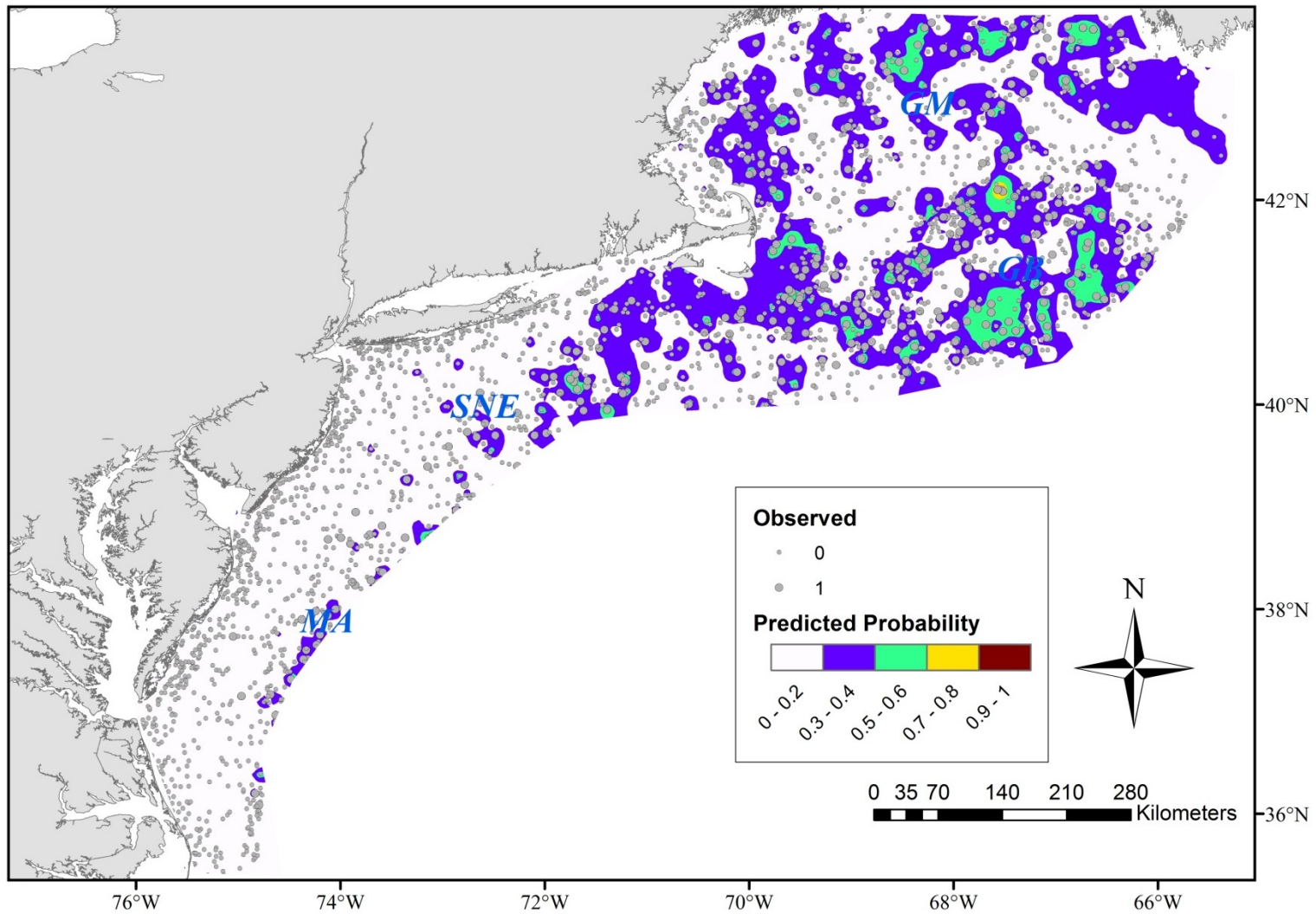
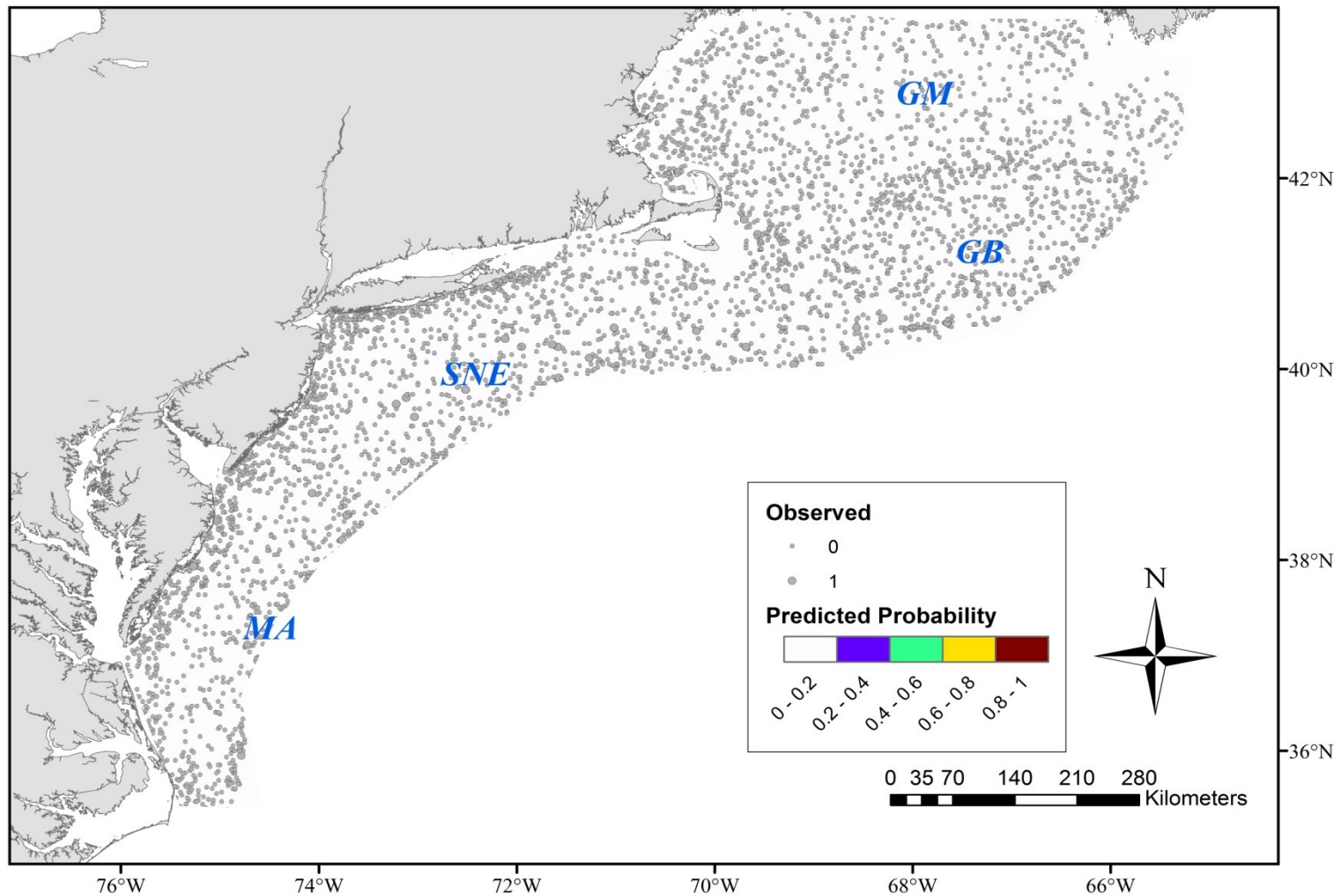


Figure 3D.17. Comparison of the predicted probability of occurrence (filled contours) as determined by inverse distance weighted interpolation versus observed occurrence (points) in the Northeast (US) shelf large marine ecosystem for neonate spiny dogfish during autumn. MA = Middle Atlantic Bight, SNE = Southern New England, GB = Georges Bank, and GM = Gulf of Maine. Solid gray indicates land masses. Note: interpolation carried out in ArcGIS using spatial analyst.



Appendix 3E. Occurrence (PA) Models for Spring

Figure 3E.1. Partial GAM plots identifying the additive effect of each variable on the probability of occurrence of mature female spiny dogfish during spring. Variables as defined in Table 3.2. The y-axis represents the degree of smoothing (variable, estimated degrees of freedom) 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'. Range estimates exclude extreme values where rugs are sparse. Some smoothes have been graphically abbreviated due to a lack of data at the endpoints. The gray region reflects the 95% confidence intervals around the response curves. NS = not significant.

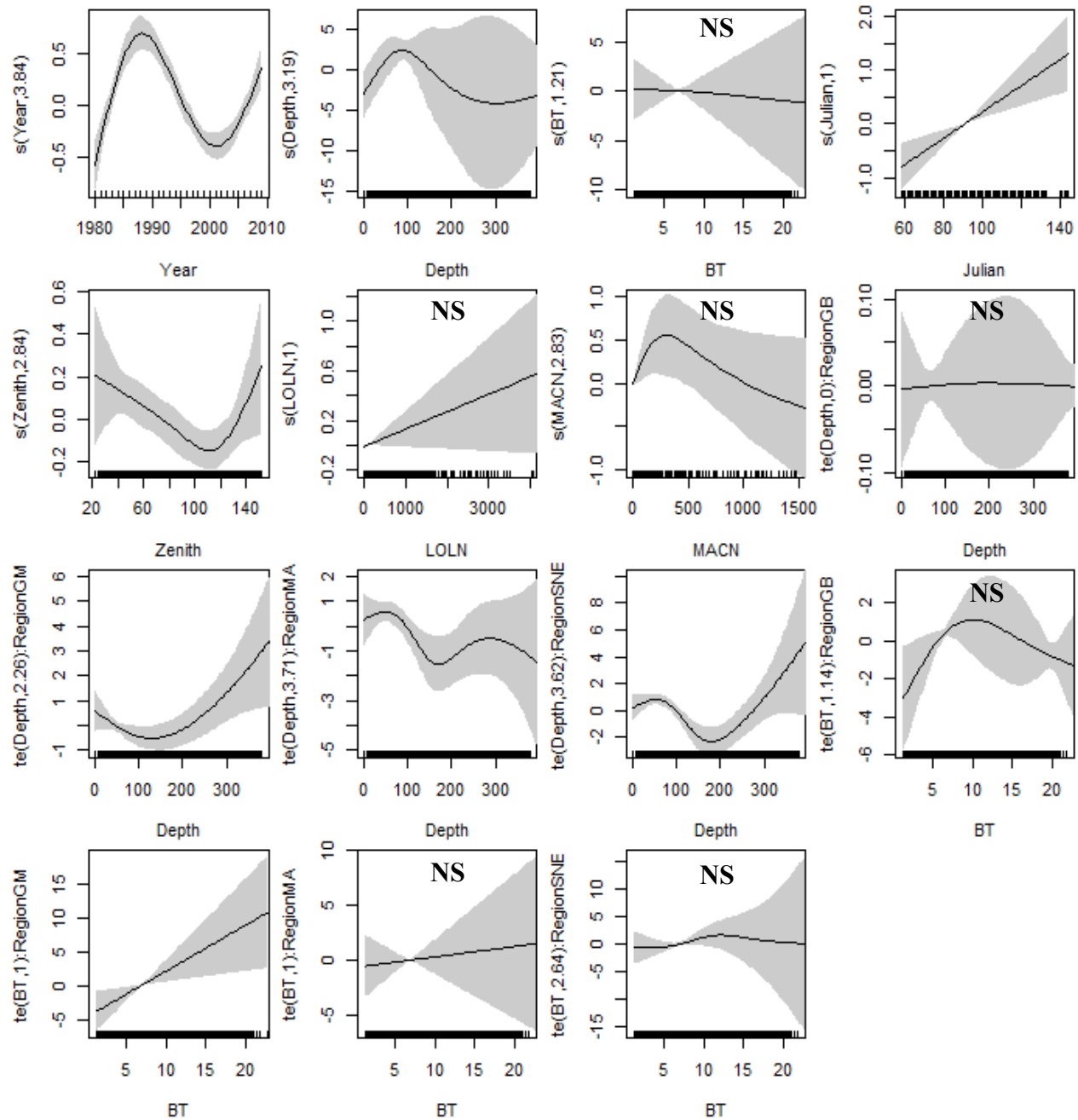


Figure 3E.2. Partial GAM derived effects of important interactions on the occurrence of mature female spiny dogfish during spring. Interaction effects shown as perspective plots without error bounds. The response on the z-axis reflects the tensor smooth (variable 1, variable 2, estimated degrees of freedom).

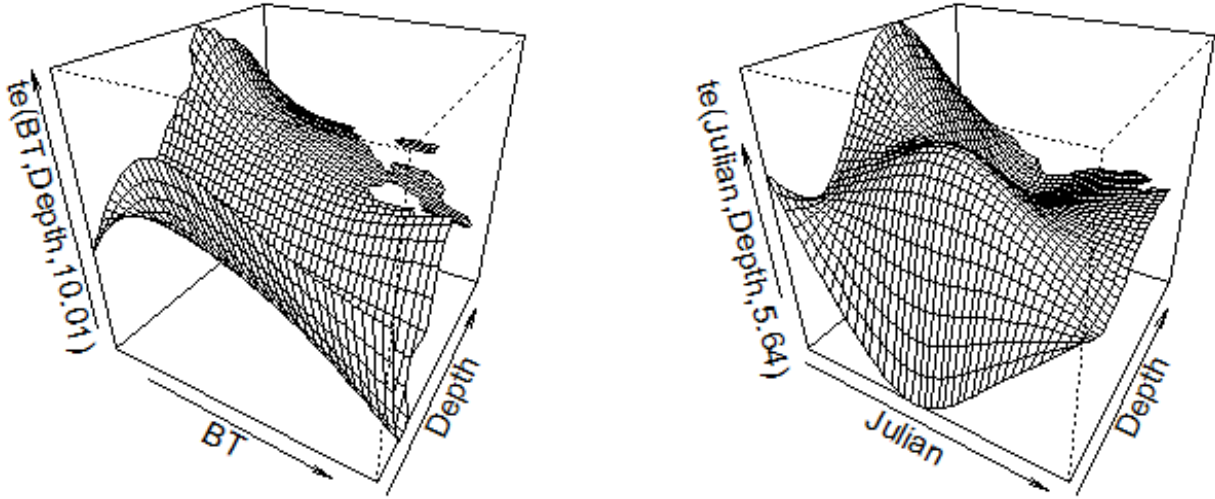


Figure 3E.3. Partial GAM plots identifying the additive effect of each variable on the probability of occurrence of mature male spiny dogfish during spring. Variables as defined in Table 3.2. The y-axis represents the degree of smoothing (variable, estimated degrees of freedom) with its range indicative of the relative importance of each covariate. The x-axis reflects the relative density of data points as shown by the 'rug'. Range estimates exclude extreme values where rugs are sparse. Some smoothes have been graphically abbreviated due to a lack of data at the endpoints. The gray region reflects the 95% confidence intervals around the response curves. NS = not significant.

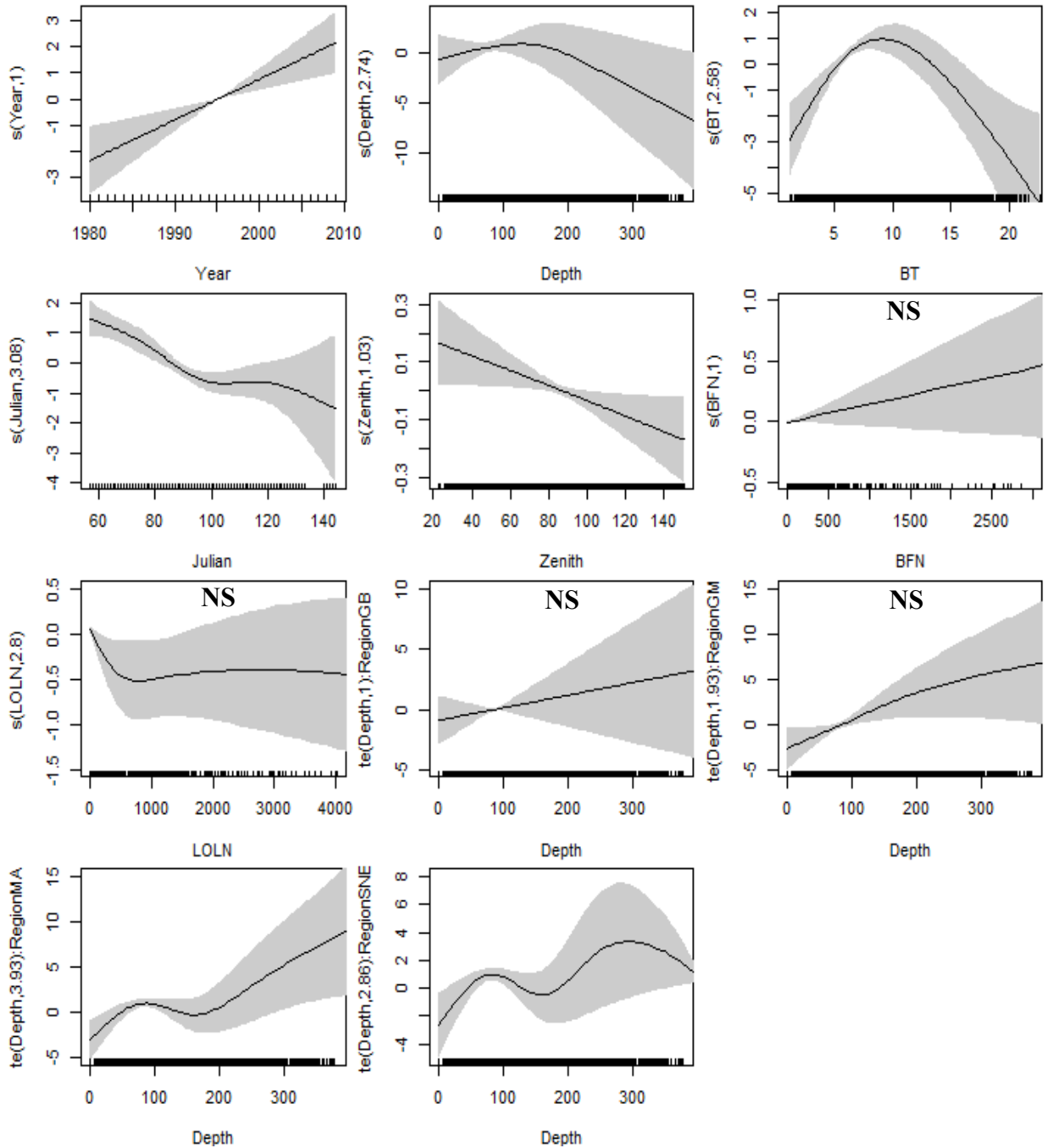


Figure 3E.4. Partial GAM derived effects of important interactions on the occurrence of mature male spiny dogfish during spring. Interaction effects shown as perspective plots without error bounds. The response on the z-axis reflects the tensor smooth (variable 1, variable 2, estimated degrees of freedom).

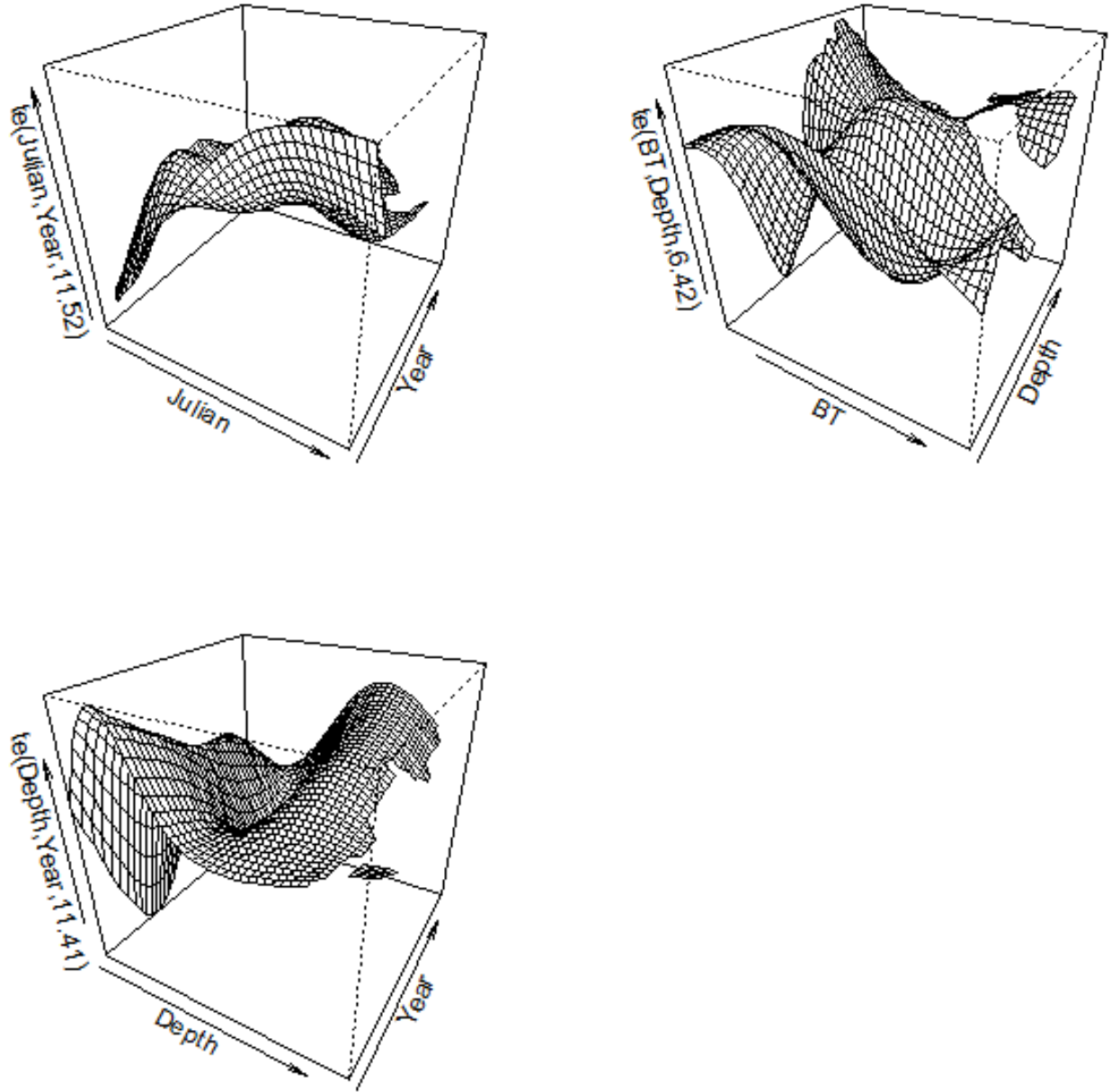


Figure 3E.5. Partial GAM plots identifying the additive effect of each variable on the probability of occurrence of immature female spiny dogfish during spring. Variables as defined in Table 3.2. The y-axis represents the degree of smoothing (variable, estimated degrees of freedom) with its range indicative of the relative importance of each covariate. The x-axis reflects the relative density of data points as shown by the 'rug'. Range estimates exclude extreme values where rugs are sparse. Some smoothes have been graphically abbreviated due to a lack of data at the endpoints. The gray region reflects the 95% confidence intervals around the response curves. NS = not significant.

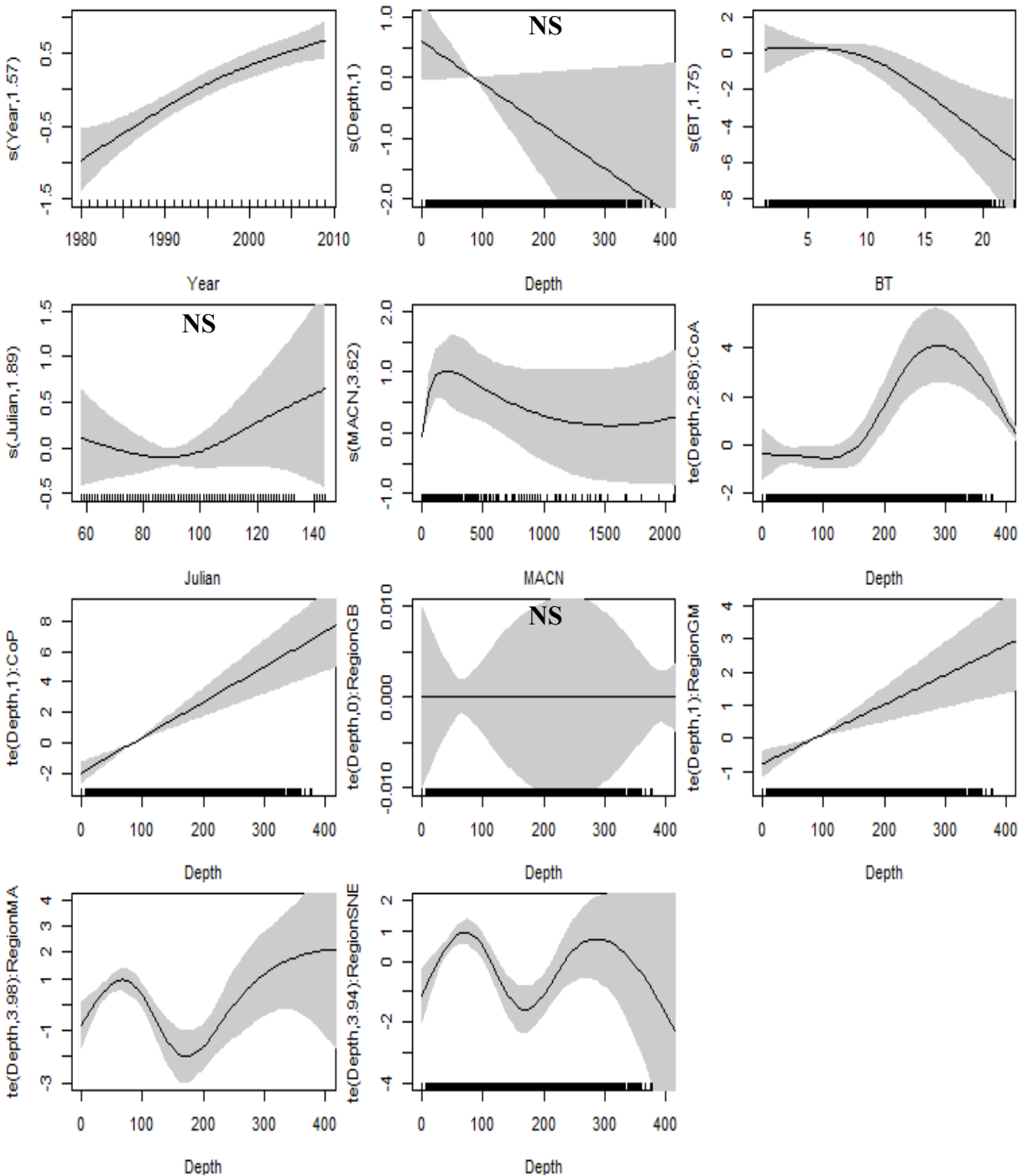


Figure 3E.6. Partial GAM derived effects of important interactions on the occurrence of immature female spiny dogfish during spring. Interaction effects shown as perspective plots without error bounds. The response on the z-axis reflects the tensor smooth (variable 1, variable 2, estimated degrees of freedom).

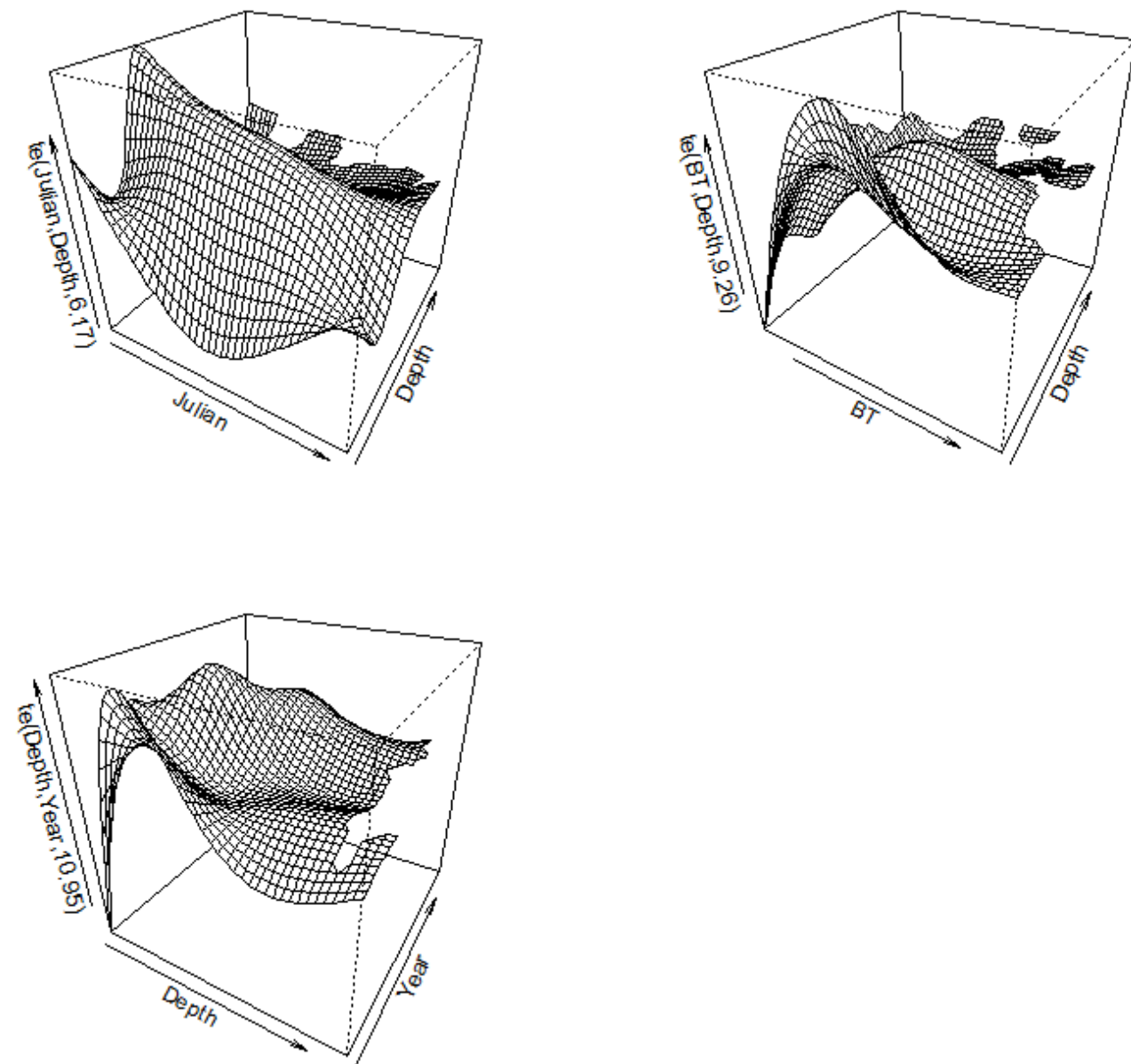


Figure 3E.7. Partial GAM plots identifying the additive effect of each variable on the probability of occurrence of neonate spiny dogfish during spring. Variables as defined in Table 3.2. The y-axis represents the degree of smoothing (variable, estimated degrees of freedom) with its range indicative of the relative importance of each covariate. The x-axis reflects the relative density of data points as shown by the 'rug'. Range estimates exclude extreme values where rugs are sparse. Some smoothes have been graphically abbreviated due to a lack of data at the endpoints. The gray region reflects the 95% confidence intervals around the response curves. NS = not significant.

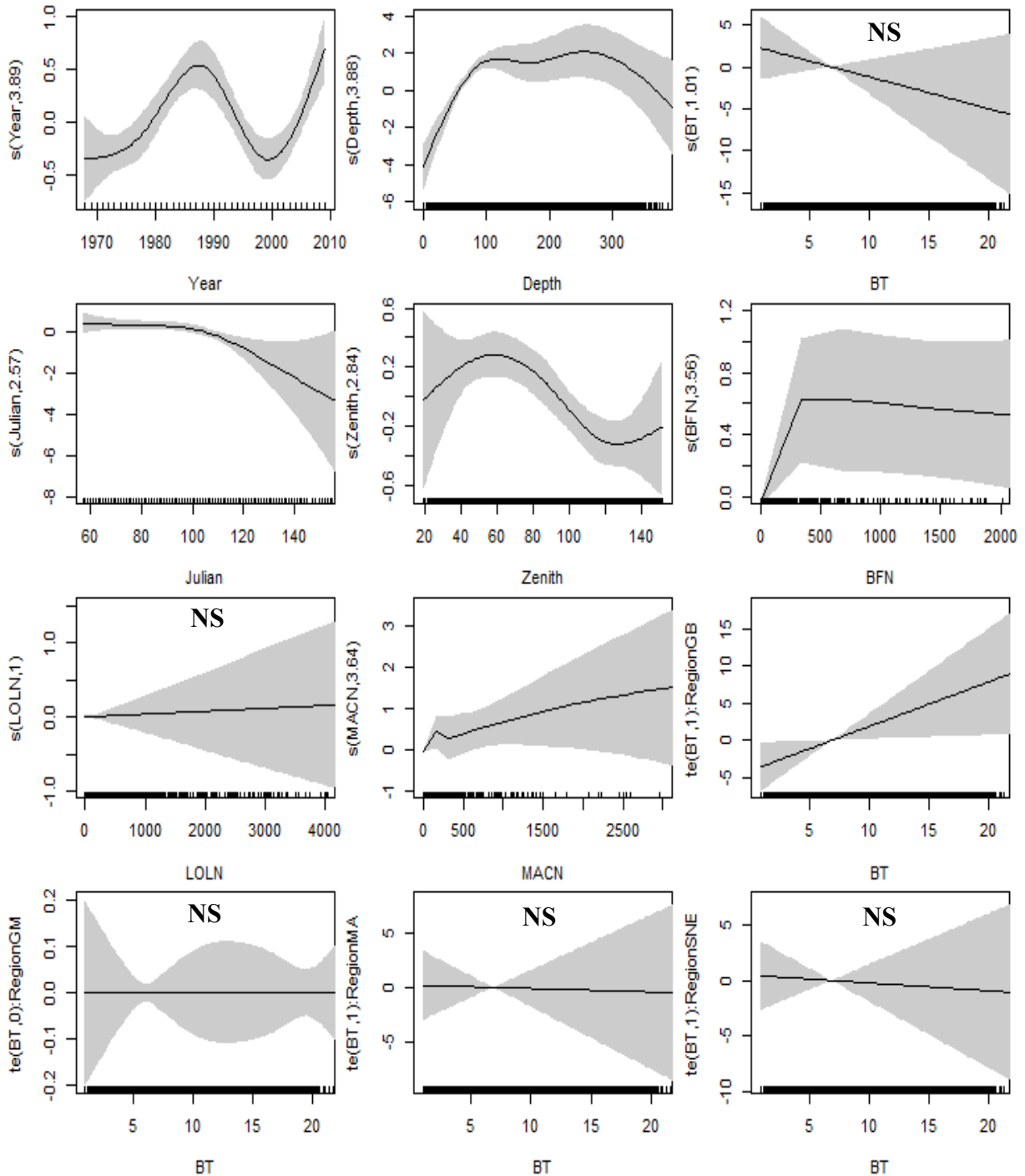


Figure 3E.8. Partial GAM derived effects of important interactions on the occurrence of neonate spiny dogfish during spring. Interactions effects shown as perspective plots without error bounds. The response on the z-axis reflects the tensor smooth (variable 1, variable 2, estimated degrees of freedom). NS = not significant.

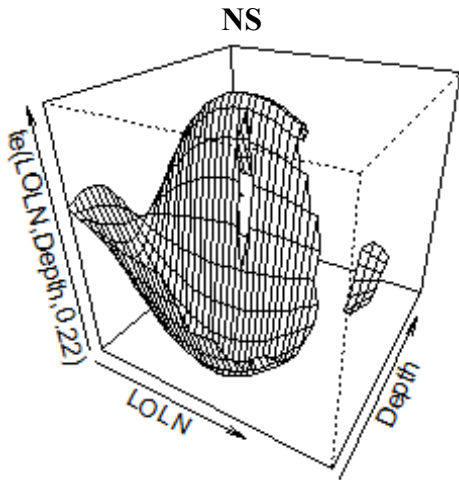
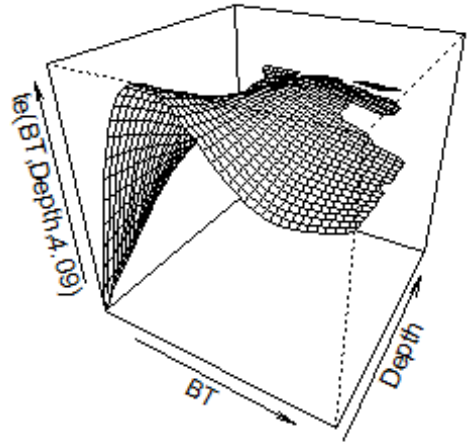
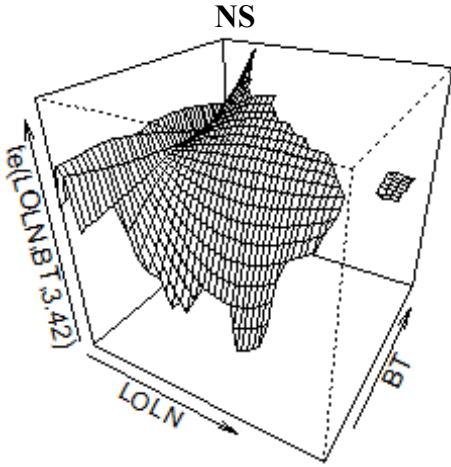


Figure 3E.9. Relationships between the Pearson residuals and all potential explanatory variables based on the optimal mature female spiny dogfish occurrence model during spring. Note: Mature Male PA (bottom right) represents co-occurrence.

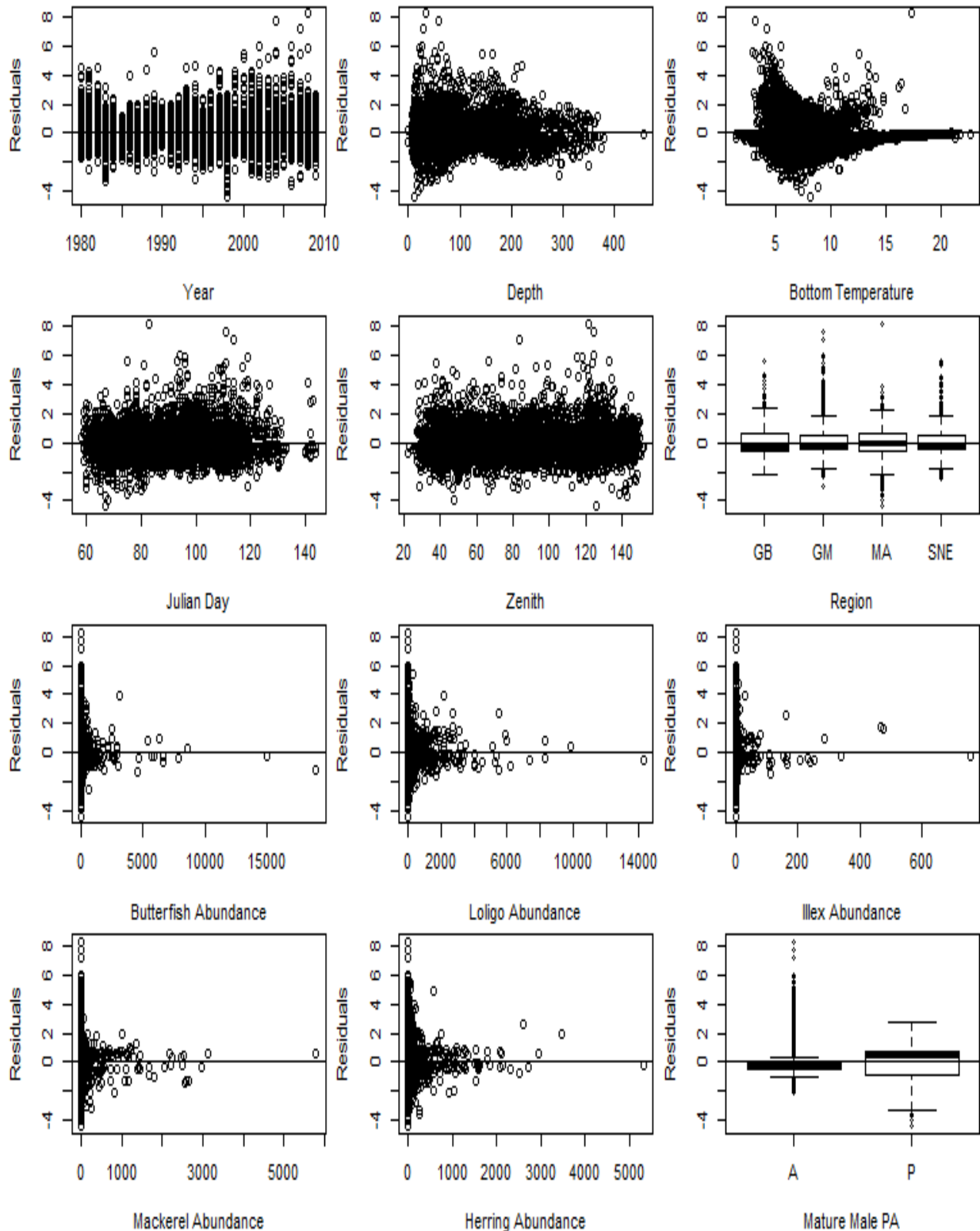


Figure 3E.10. Relationships between the Pearson residuals and all potential explanatory variables based on the optimal mature male spiny dogfish occurrence model during spring. Note: Mature Female PA (bottom right) represents co-occurrence.

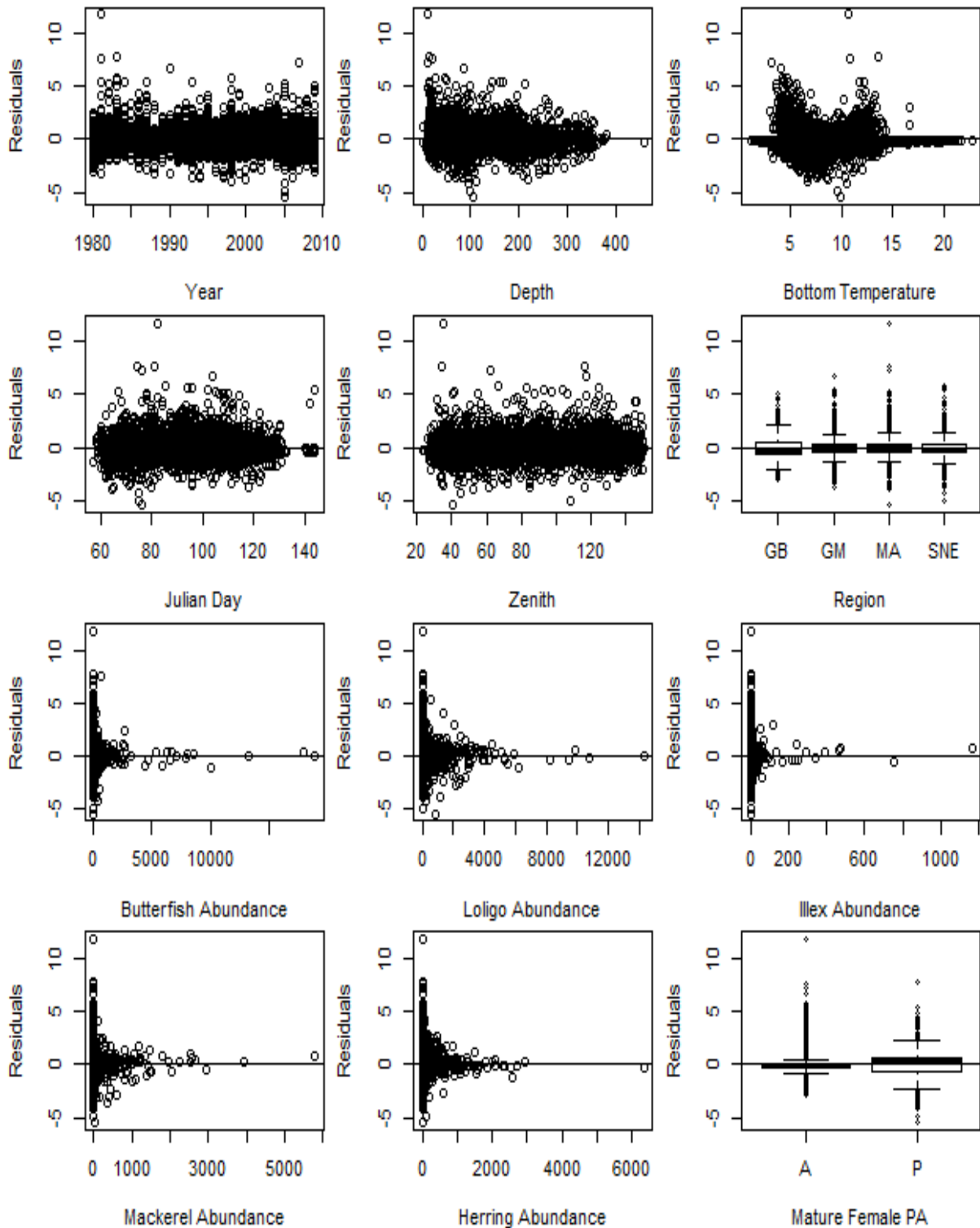


Figure 3E.11. Relationships between the Pearson residuals and all potential explanatory variables based on the optimal immature female spiny dogfish occurrence model during spring. Note: Immature Male PA (bottom right) represents co-occurrence.

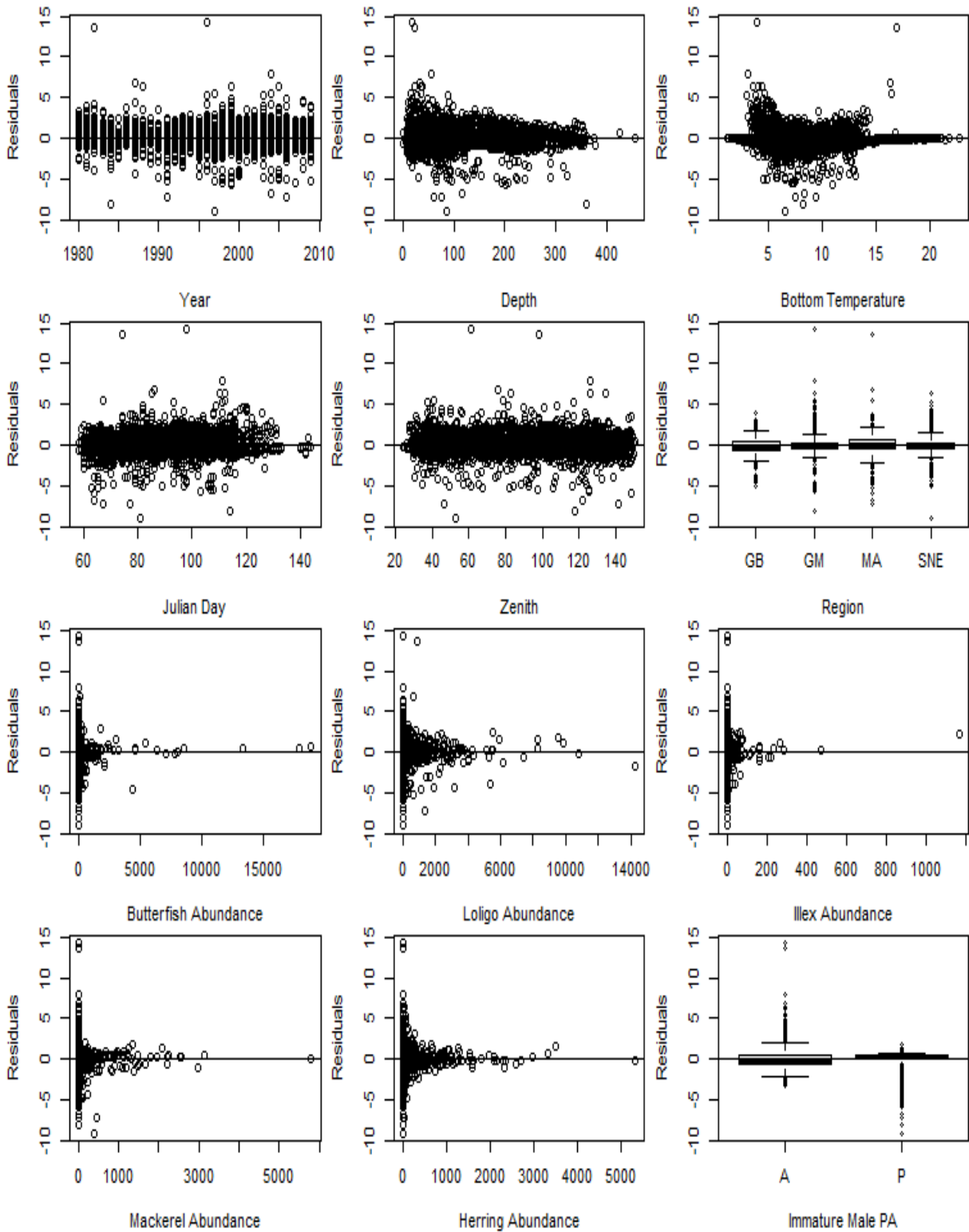


Figure 3E.12. Relationships between the Pearson residuals and all potential explanatory variables based on the optimal immature male spiny dogfish occurrence model during spring. Note: Immature Female PA (bottom right) represents co-occurrence.

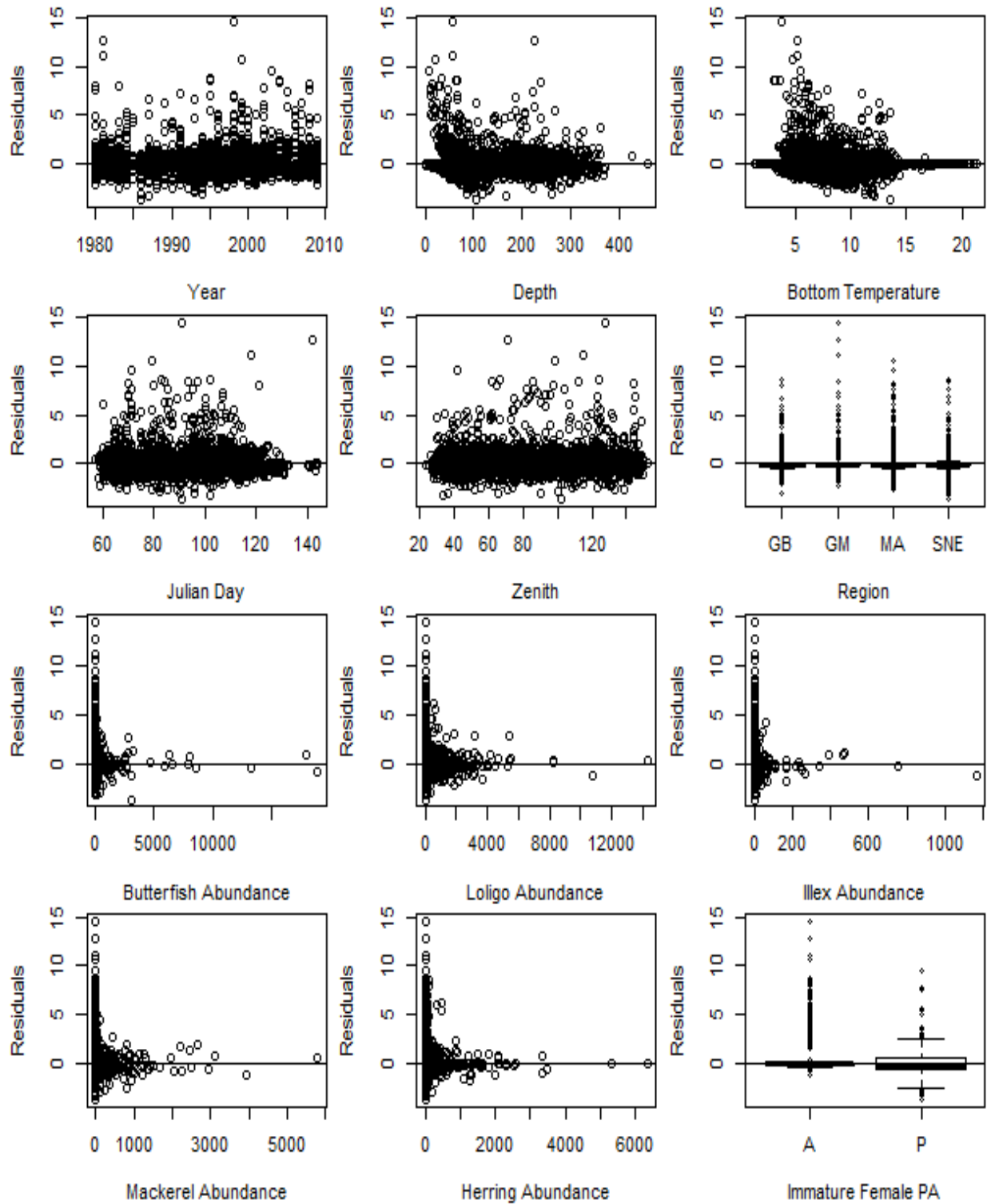
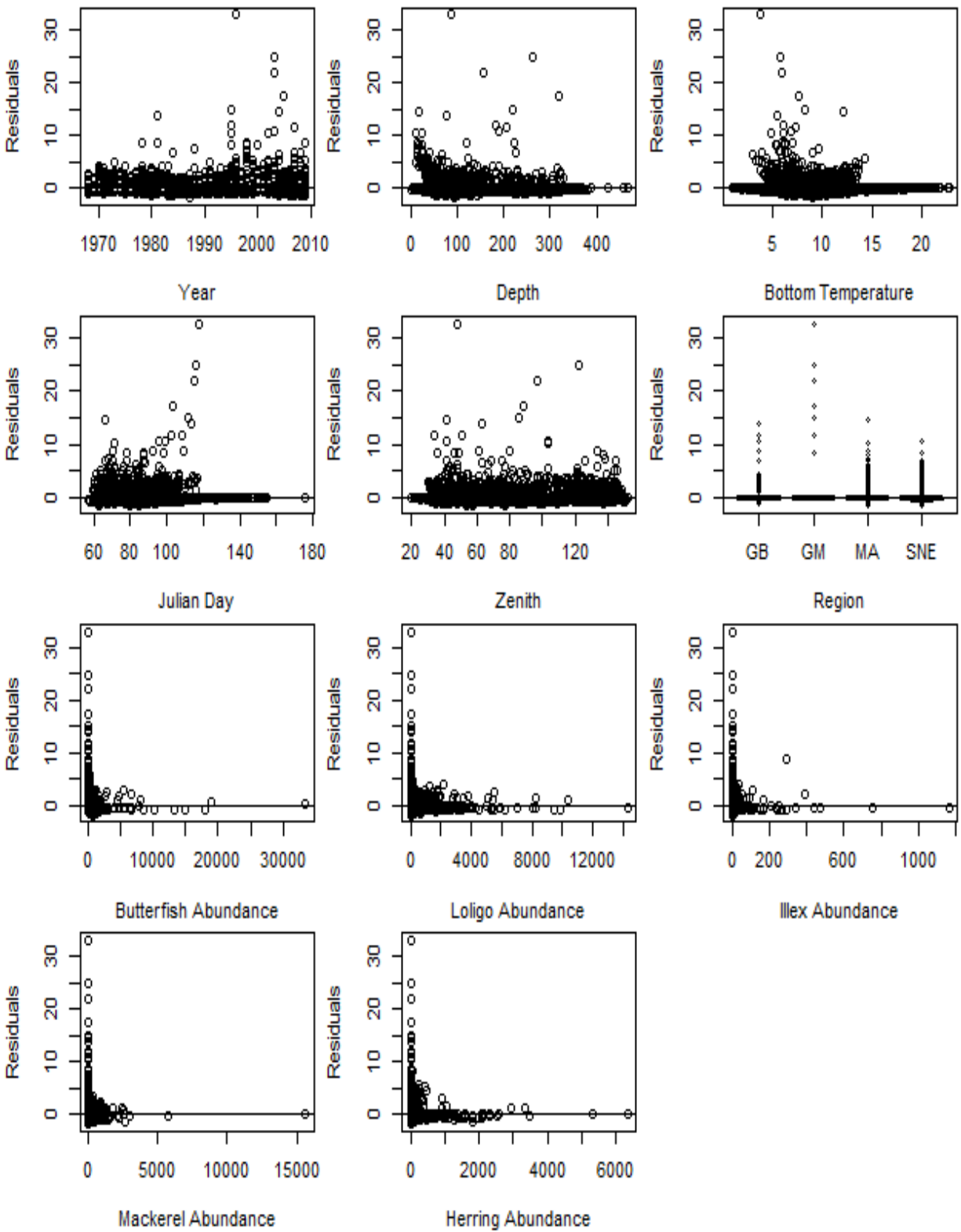


Figure 3E.13. Relationships between the Pearson residuals and all potential explanatory variables based on the optimal neonate spiny dogfish occurrence model during spring.



Appendix 3F. Abundance (PRES) Models for Autumn

Figure 3F.1. Partial GAM plots identifying the additive effect of each variable on the probability of increasing abundance of mature male spiny dogfish during autumn. Variables as defined in Table 3.2. The y-axis represents the degree of smoothing (variable, estimated degrees of freedom) 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'. Range estimates exclude extreme values where rugs are sparse. Some smoothes have been graphically abbreviated due to a lack of data at the endpoints. The gray region reflects the 95% confidence intervals around the response curves. NS = not significant.

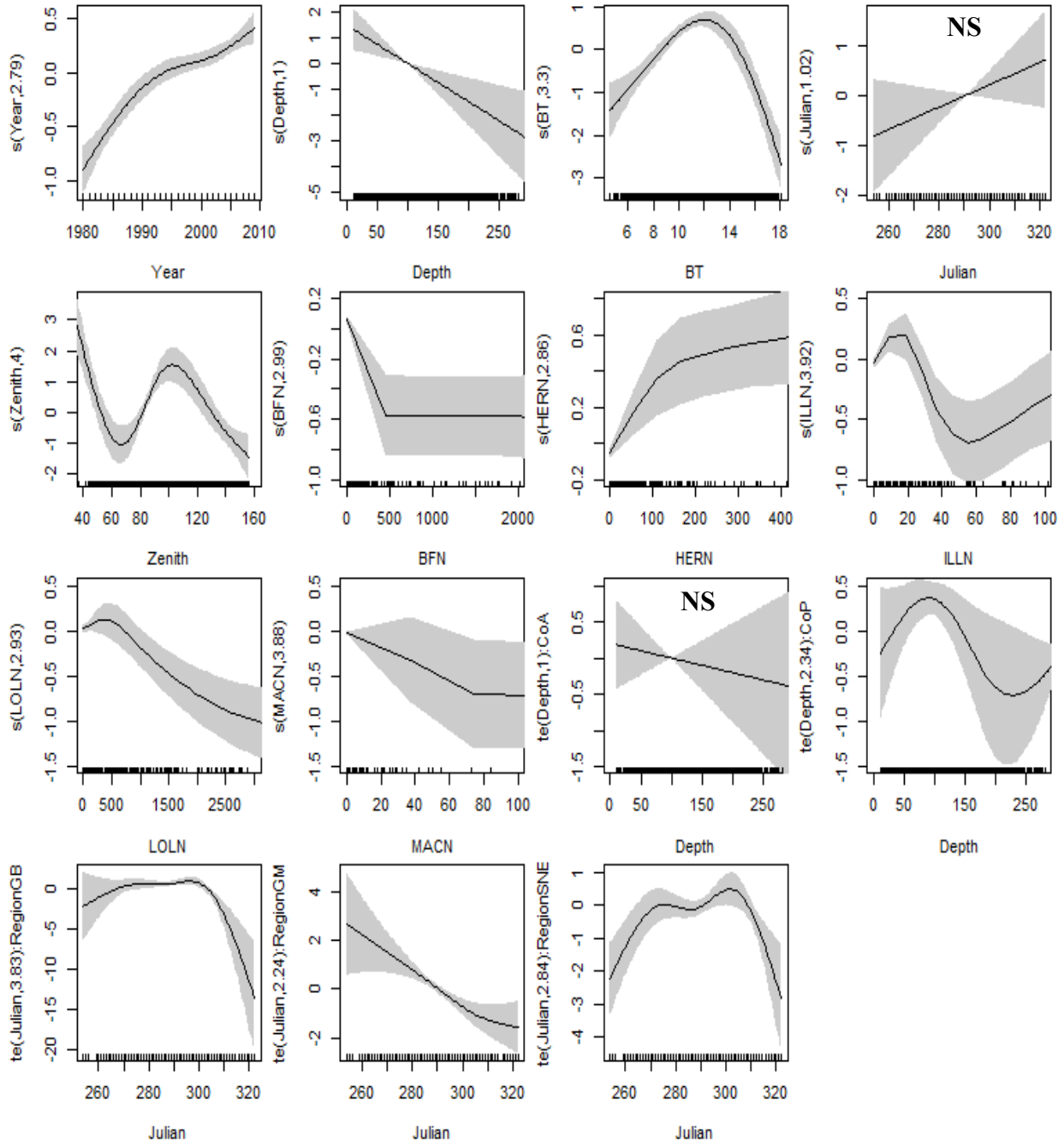


Figure 3F.2. Partial GAM derived effects of important interactions on the abundance of mature male spiny dogfish during autumn. Interaction effects shown as perspective plots without error bounds. The response on the z-axis reflects the tensor smooth (variable 1, variable 2, estimated degrees of freedom). NS = not significant.

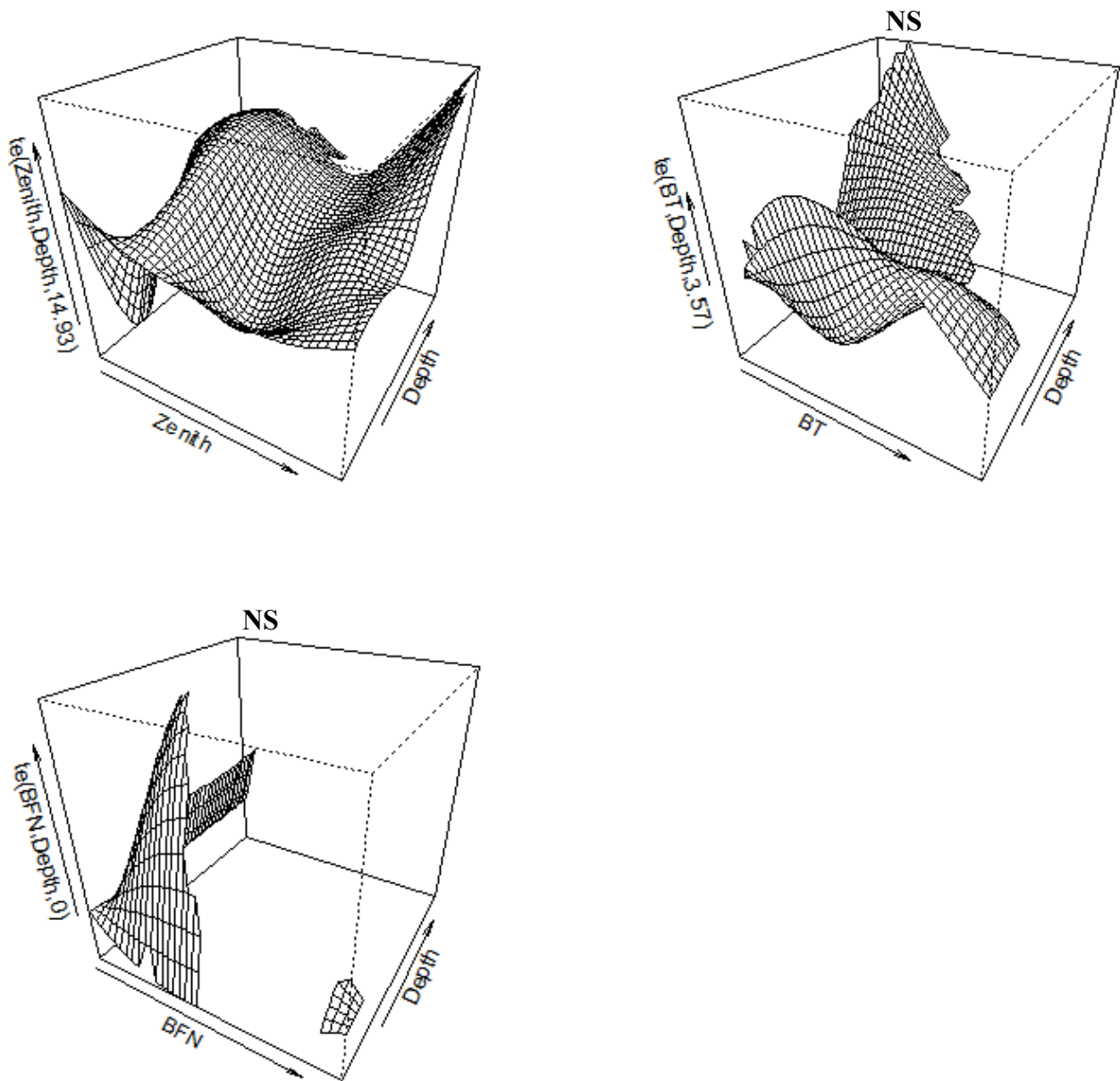


Figure 3F.3. Partial GAM plots identifying the additive effect of each variable on the probability of increasing abundance of immature female spiny dogfish during autumn. Variables as defined in Table 3.2. The y-axis represents the degree of smoothing (variable, estimated degrees of freedom) with its range indicative of the relative importance of each covariate. The x-axis reflects the relative density of data points as shown by the 'rug'. Range estimates exclude extreme values where rugs are sparse. Some smoothes have been graphically abbreviated due to a lack of data at the endpoints. The gray region reflects the 95% confidence intervals around the response curves. NS = not significant.

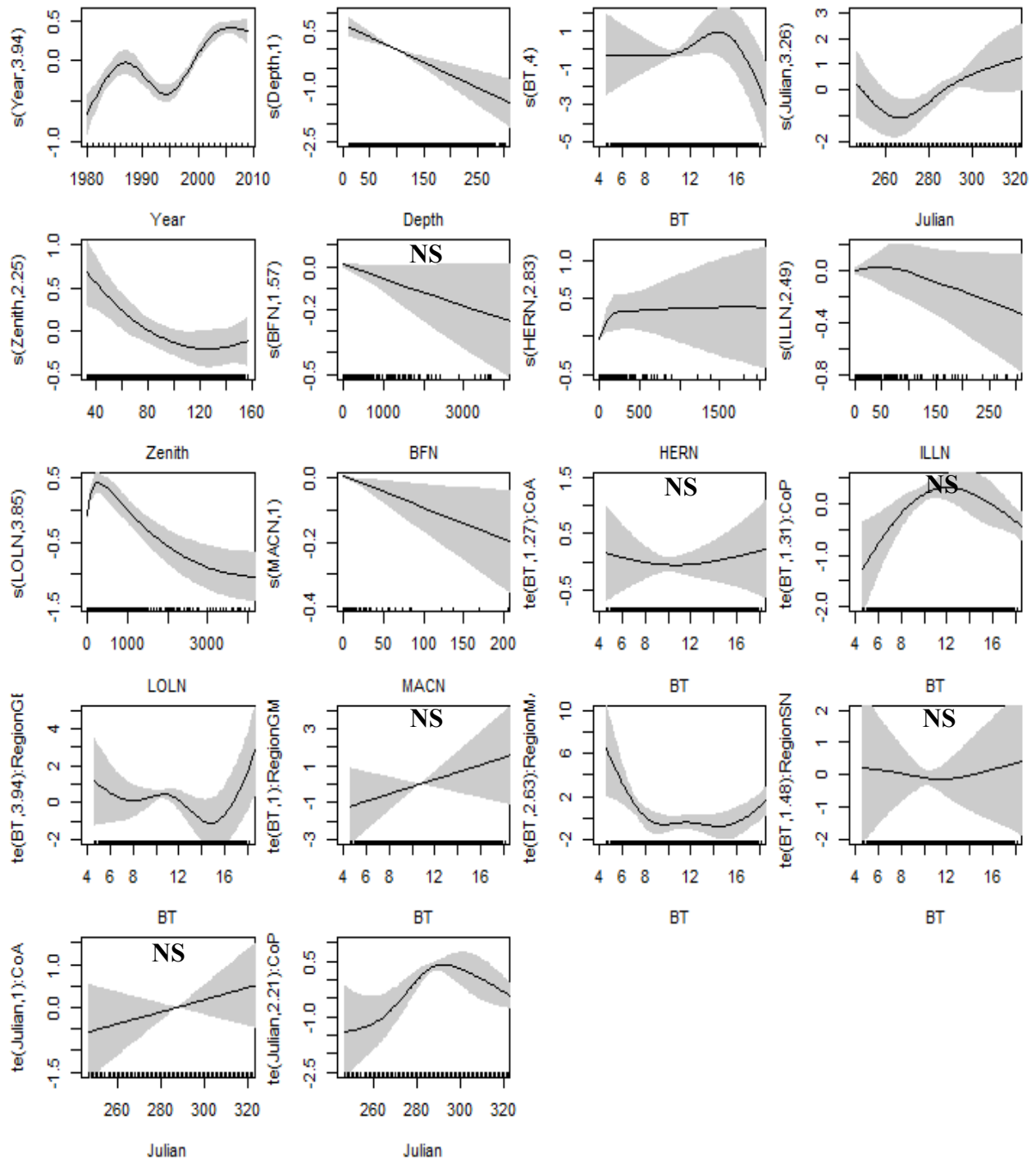


Figure 3F.4. Partial GAM derived effects of important interactions on the abundance of immature female spiny dogfish during autumn. Interaction effects shown as perspective plots without error bounds. The response on the z-axis reflects the tensor smooth (variable 1, variable 2, estimated degrees of freedom). NS = not significant.

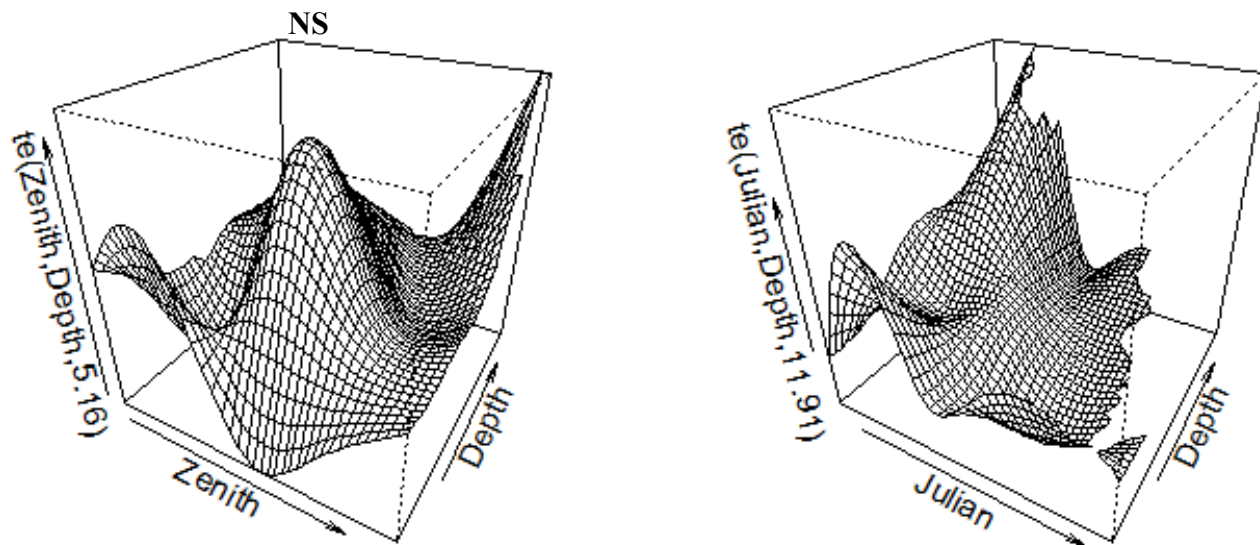


Figure 3F.5. Partial GAM plots identifying the additive effect of each variable on the probability of increasing abundance of immature male spiny dogfish during autumn. Variables as defined in Table 3.2. The y-axis represents the degree of smoothing (variable, estimated degrees of freedom) with its range indicative of the relative importance of each covariate. The x-axis reflects the relative density of data points as shown by the 'rug'. Range estimates exclude extreme values where rugs are sparse. Some smoothes have been graphically abbreviated due to a lack of data at the endpoints. The gray region reflects the 95% confidence intervals around the response curves. NS = not significant.

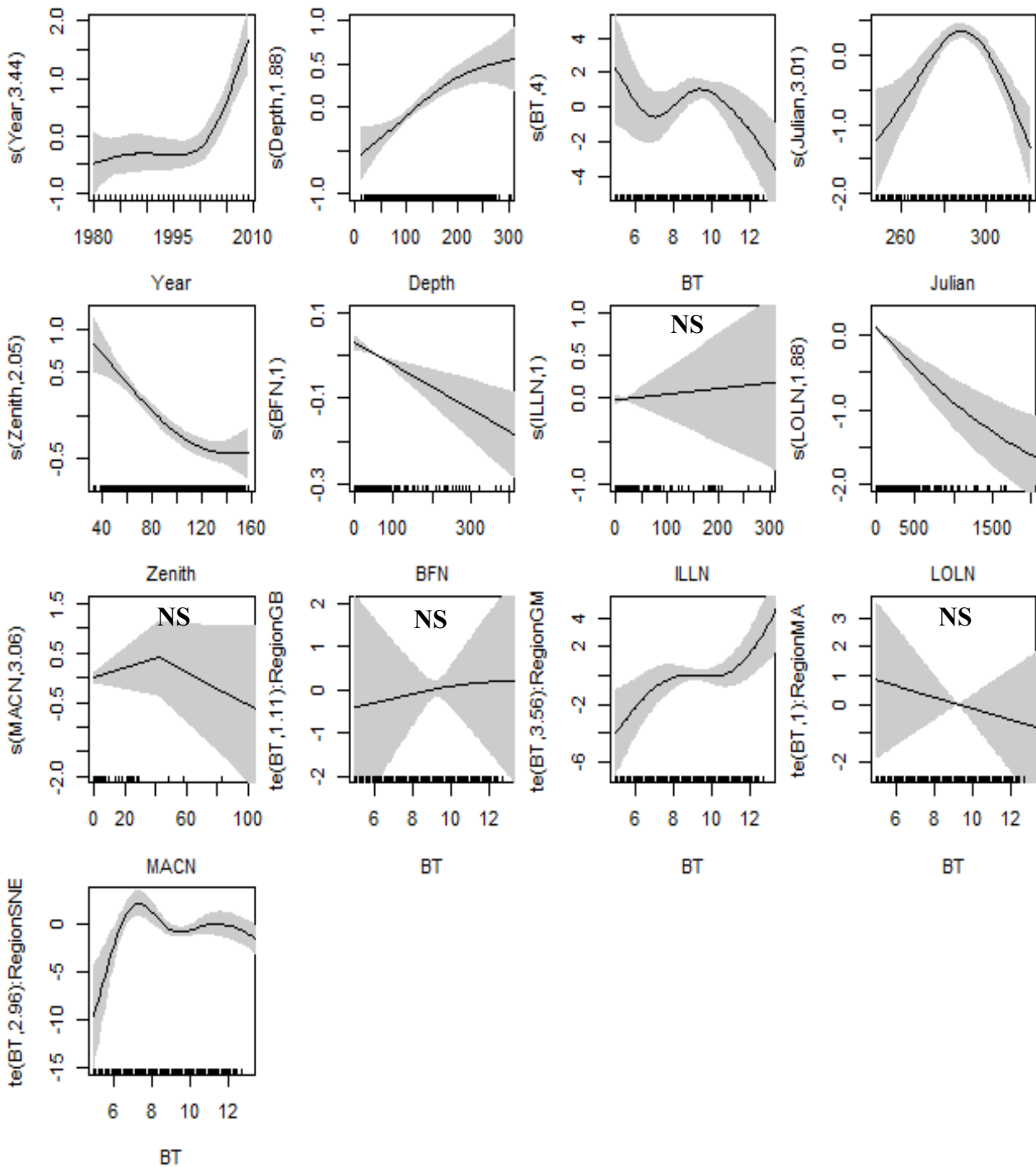


Figure 3F.6. Partial GAM derived effects of important interactions on the abundance of immature male spiny dogfish during autumn. Interaction effects shown as perspective plots without error bounds. The response on the z-axis reflects the tensor smooth (variable 1, variable 2, estimated degrees of freedom).

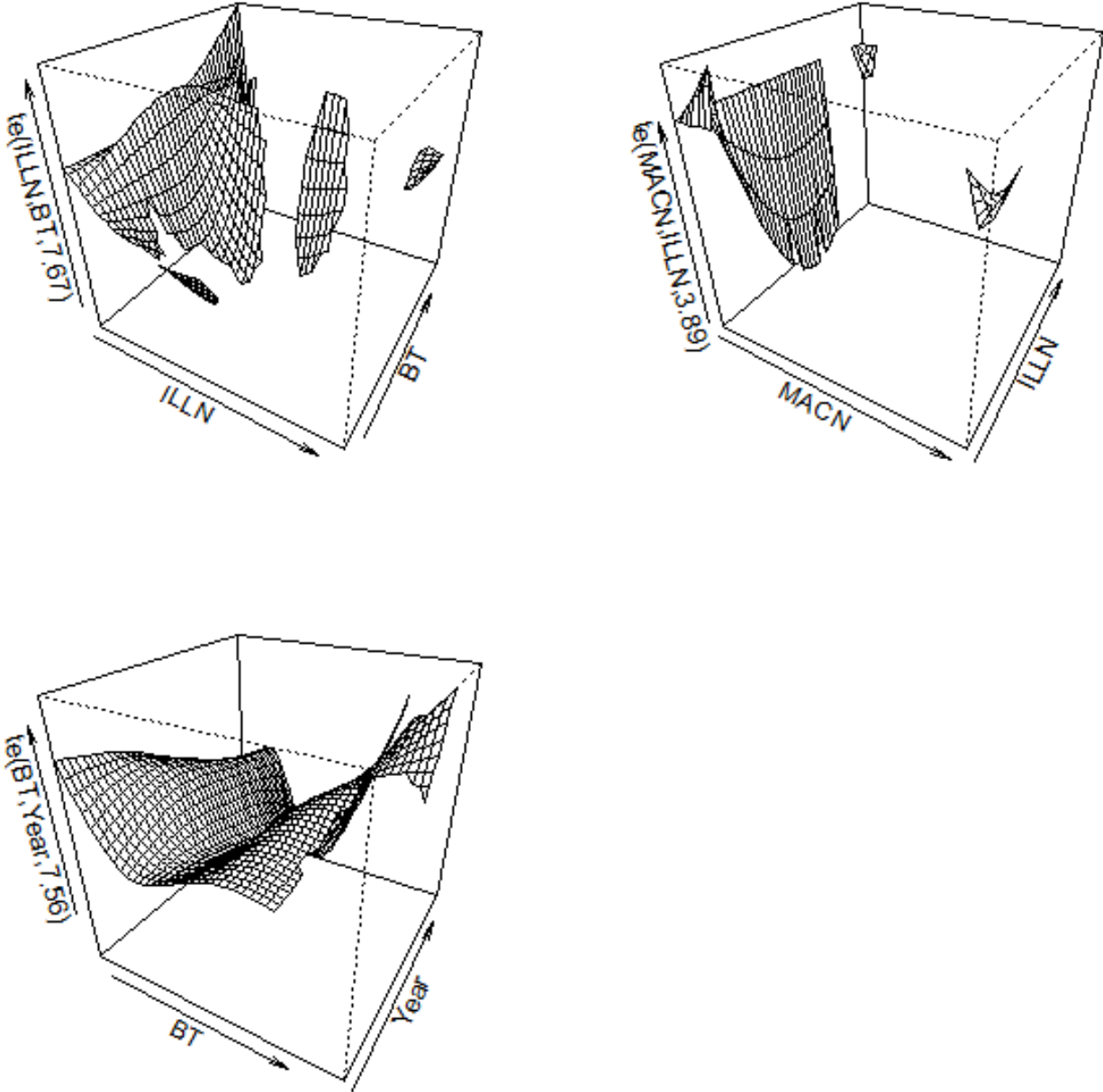


Figure 3F.7. Partial GAM plots identifying the additive effect of each variable on the probability of increasing abundance of neonate spiny dogfish during autumn. Variables as defined in Table 3.2. The y-axis represents the degree of smoothing (variable, estimated degrees of freedom) with its range indicative of the relative importance of each covariate. The x-axis reflects the relative density of data points as shown by the 'rug'. Range estimates exclude extreme values where rugs are sparse. Some smoothes have been graphically abbreviated due to a lack of data at the endpoints. The gray region reflects the 95% confidence intervals around the response curves. NS = not significant.

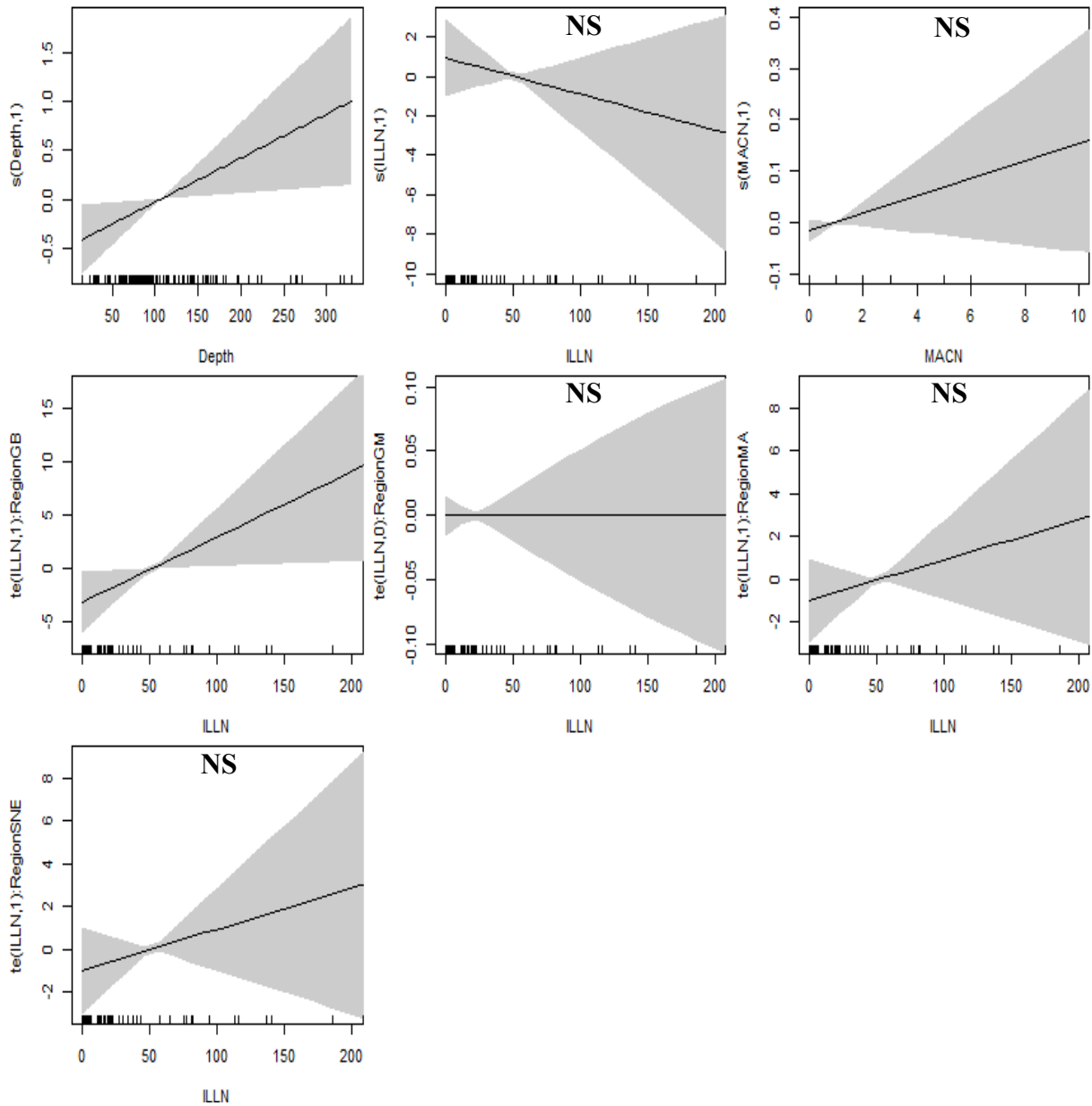


Figure 3F.8. Relationships between the Pearson residuals and all potential explanatory variables based on the optimal mature female spiny dogfish abundance model during autumn. Note: Mature Male PA (bottom right) represents co-occurrence.

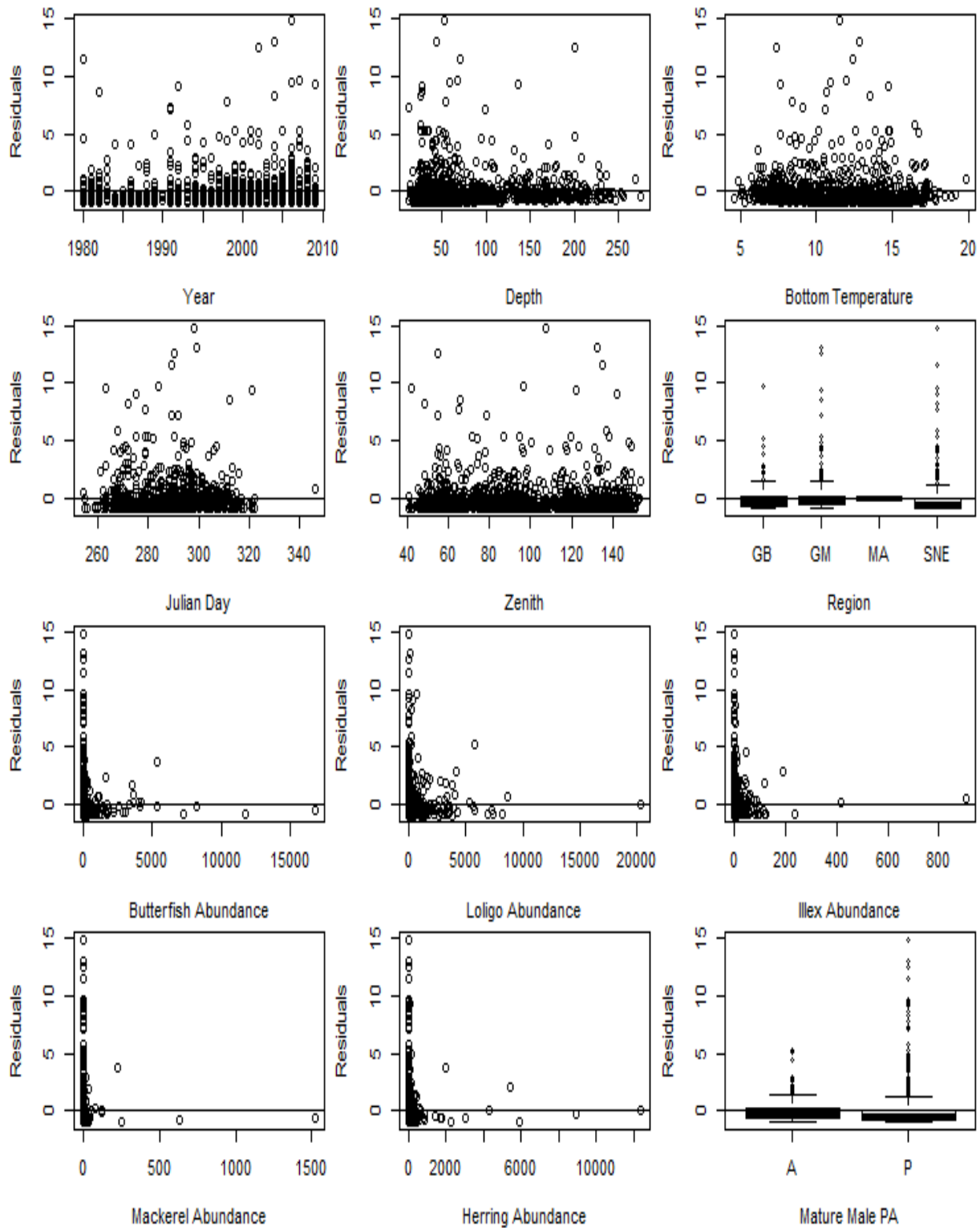


Figure 3F.9. Relationships between the Pearson residuals and all potential explanatory variables based on the optimal mature male spiny dogfish abundance model during autumn. Note: Mature Female PA (bottom right) represents co-occurrence.

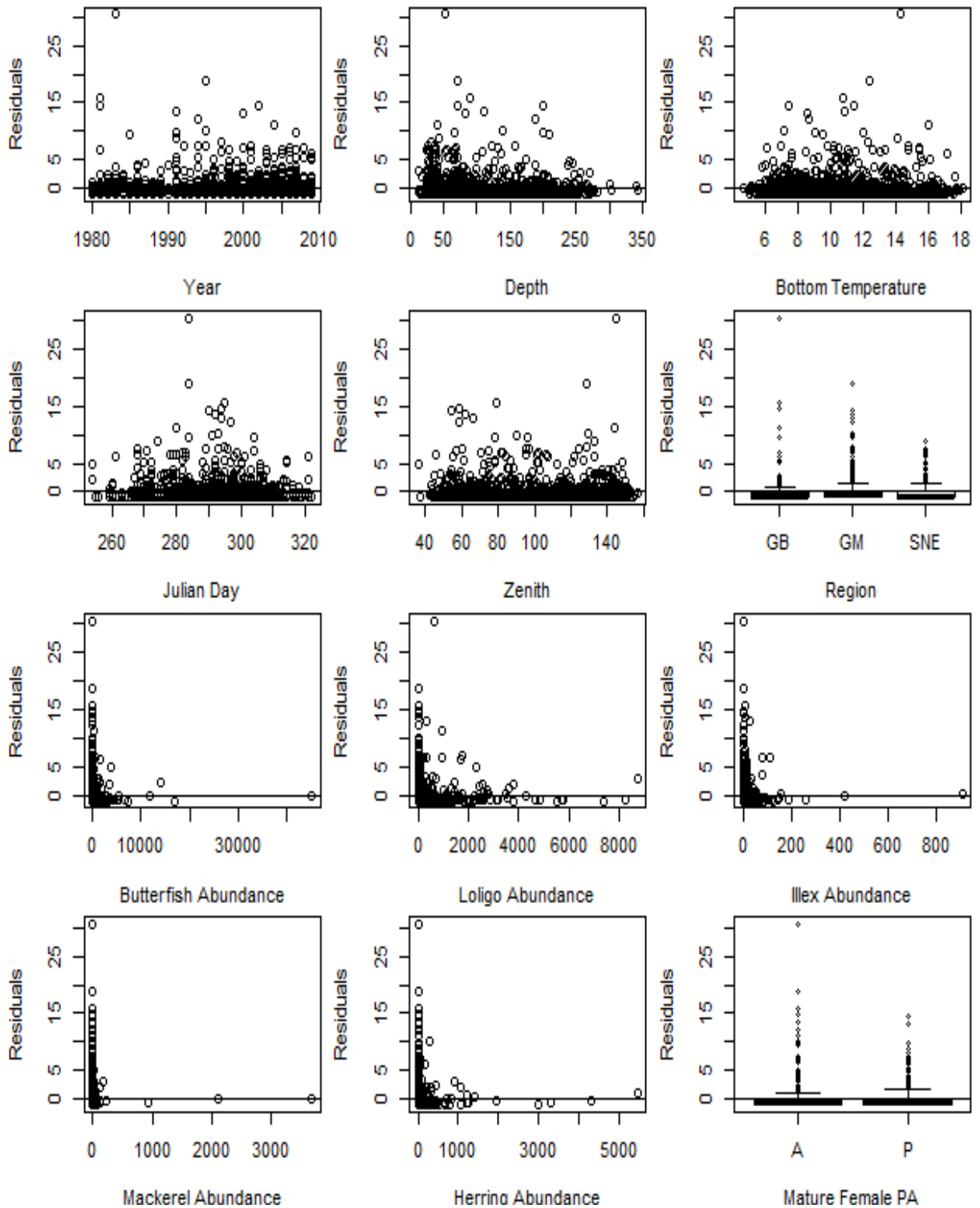


Figure 3F.10. Relationships between the Pearson residuals and all potential explanatory variables based on the optimal immature female spiny dogfish abundance model during autumn. Note: Immature Male PA (bottom right) represents co-occurrence.

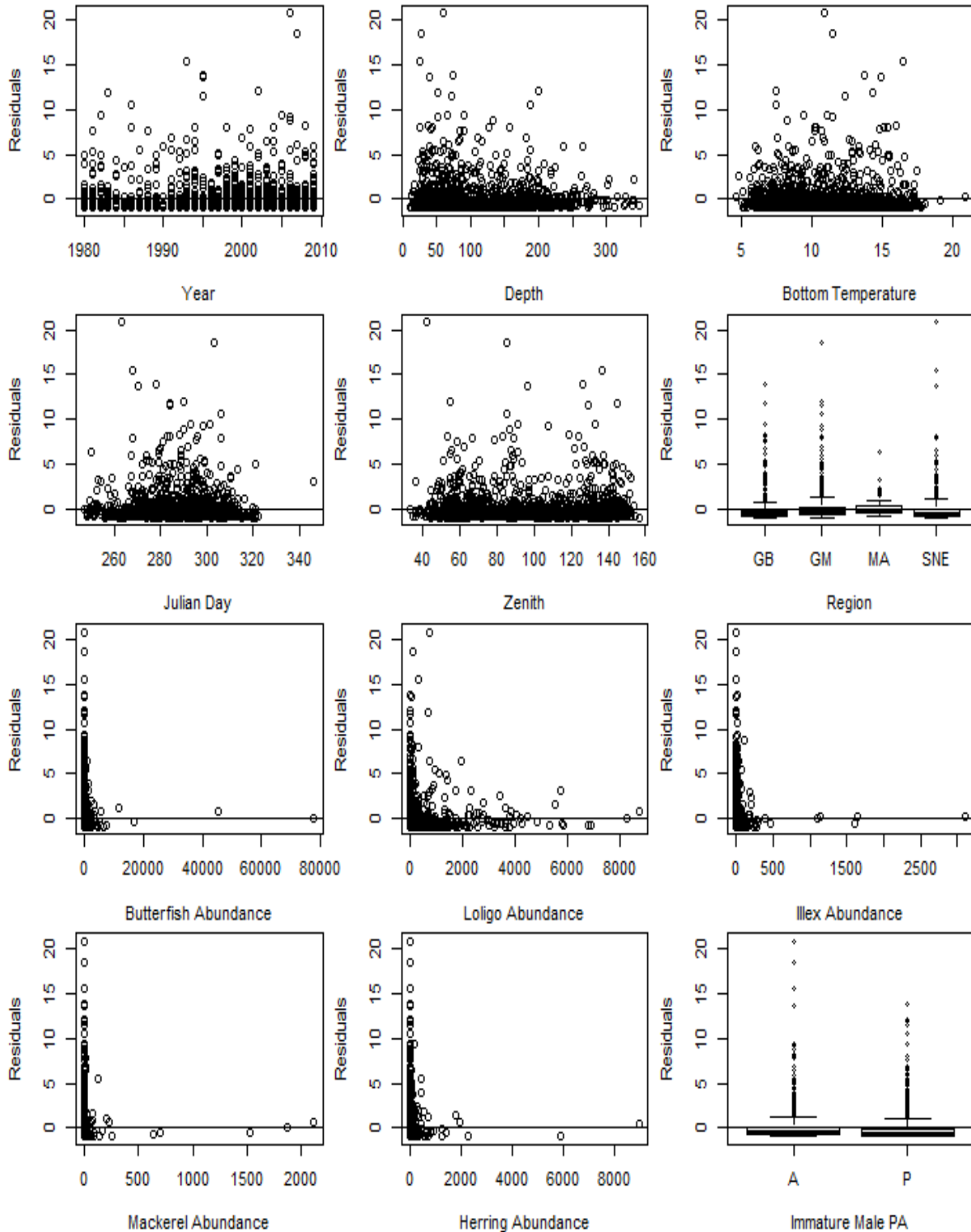


Figure 3F.11. Relationships between the Pearson residuals and all potential explanatory variables based on the optimal immature male spiny dogfish abundance model during autumn. Note: Immature Female PA (bottom right) represents co-occurrence.

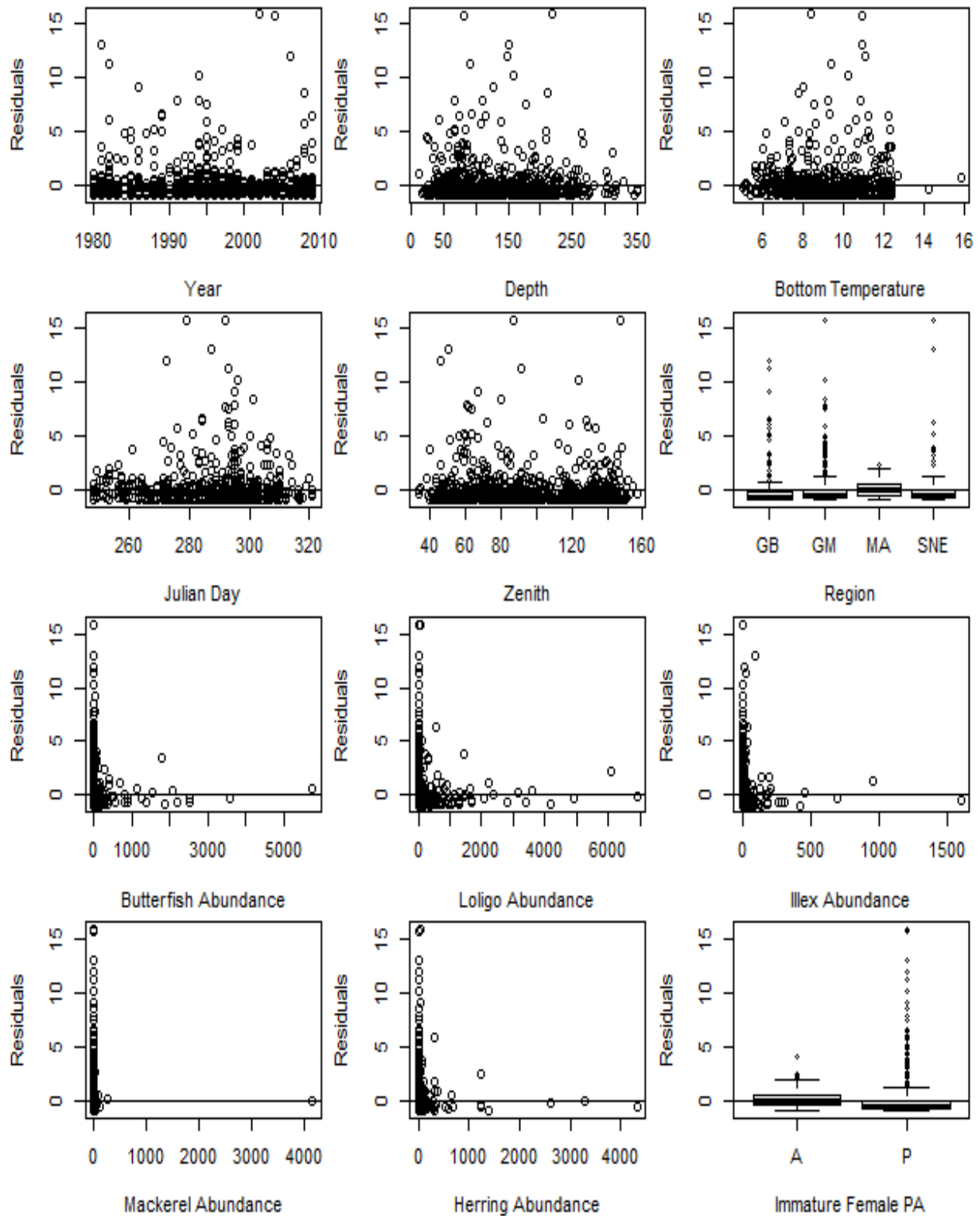


Figure 3F.12. Relationships between the Pearson residuals and all potential explanatory variables based on the optimal neonate spiny dogfish abundance model during autumn.

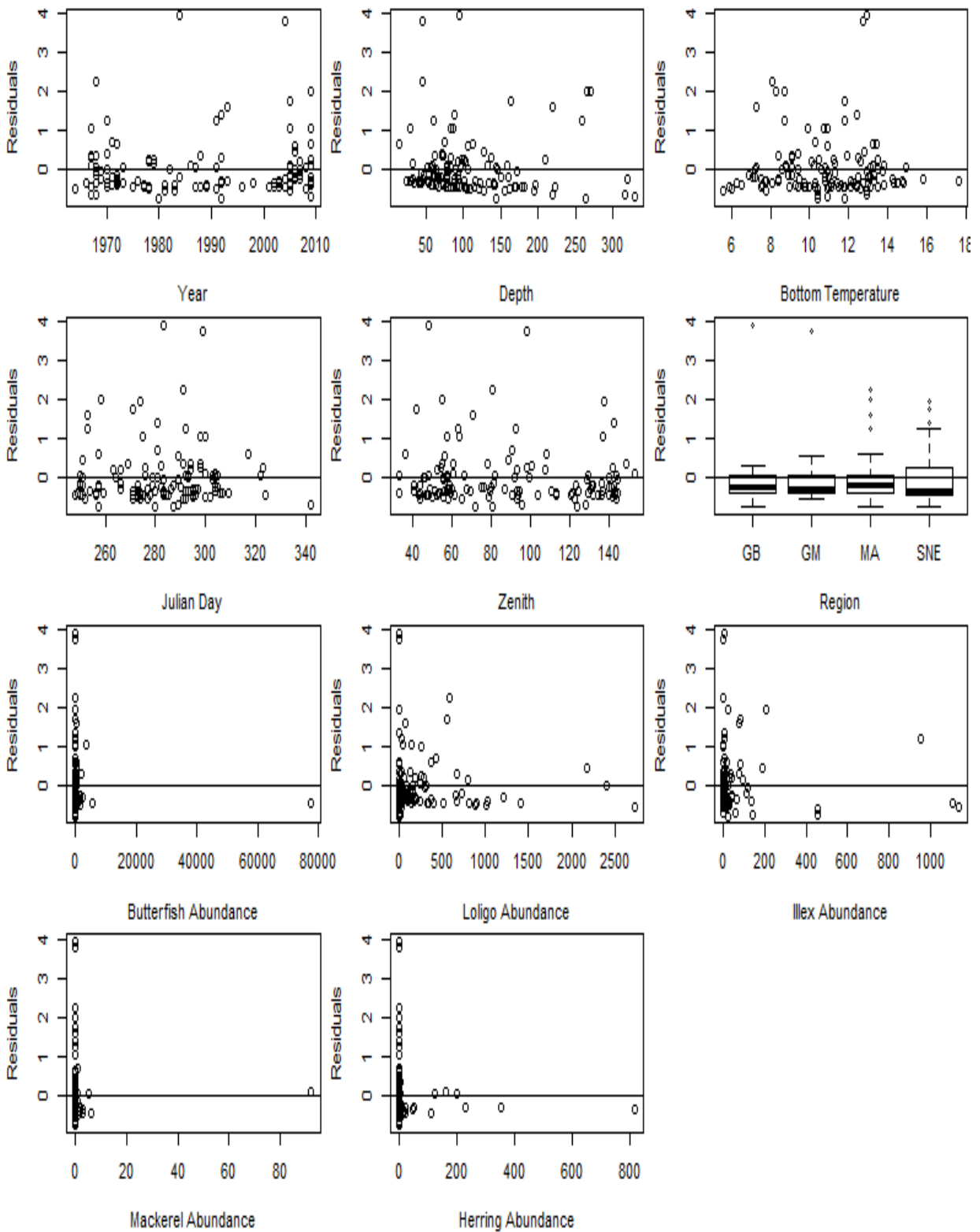


Figure 3F.13. Comparison of the predicted abundance (filled contours) as determined by inverse distance weighted interpolation versus observed abundance (points) in the Northeast (US) shelf large marine ecosystem for mature female spiny dogfish during autumn. MA = Middle Atlantic Bight, SNE = Southern New England, GB = Georges Bank, and GM = Gulf of Maine. Solid gray indicates land masses. Note: interpolation carried out in ArcGIS using spatial analyst.

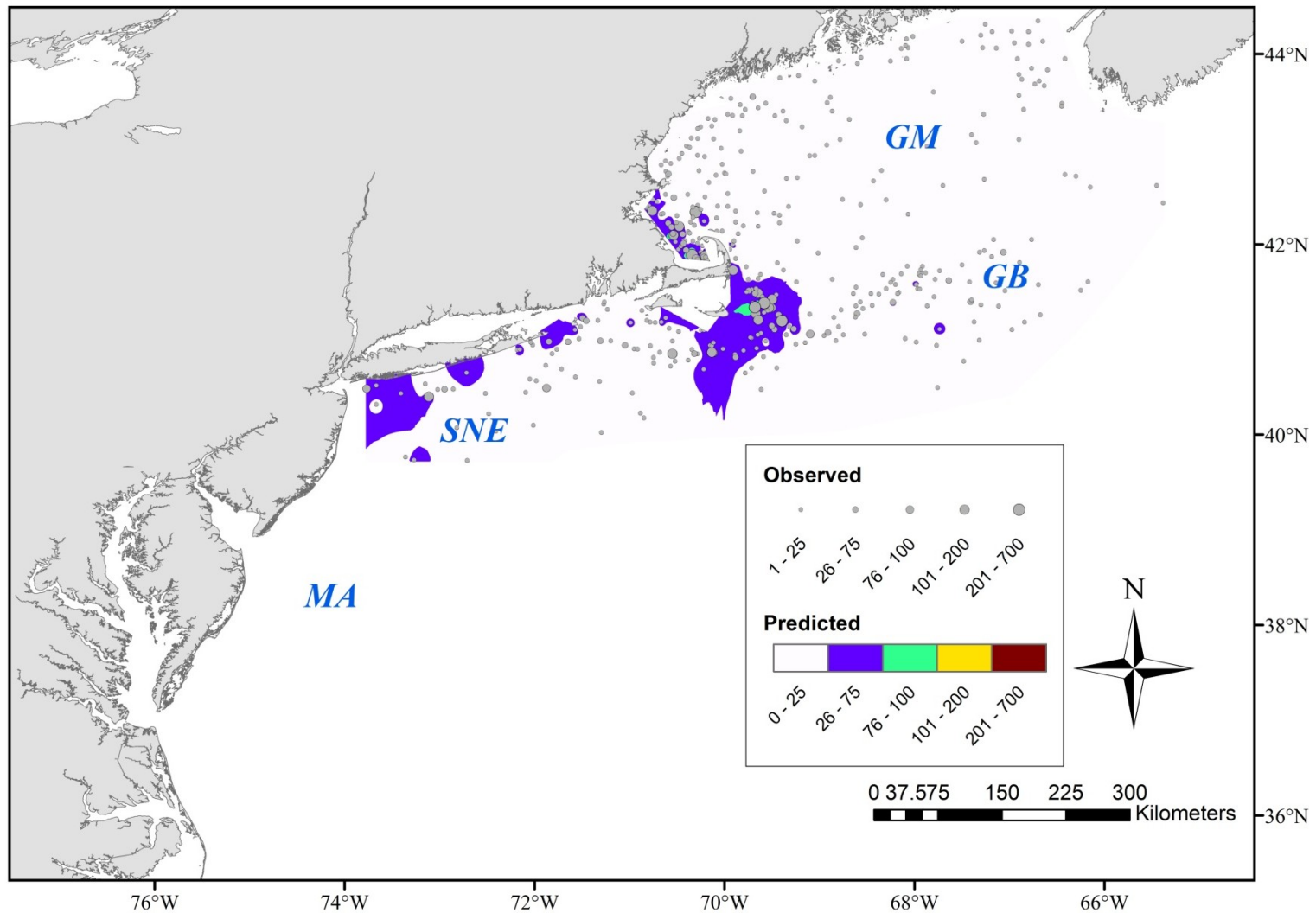


Figure 3F.14. Comparison of the predicted abundance (filled contours) as determined by inverse distance weighted interpolation versus observed abundance (points) in the Northeast (US) shelf large marine ecosystem for mature male spiny dogfish during autumn. MA = Middle Atlantic Bight, SNE = Southern New England, GB = Georges Bank, and GM = Gulf of Maine. Solid gray indicates land masses. Note: interpolation carried out in ArcGIS using spatial analyst.

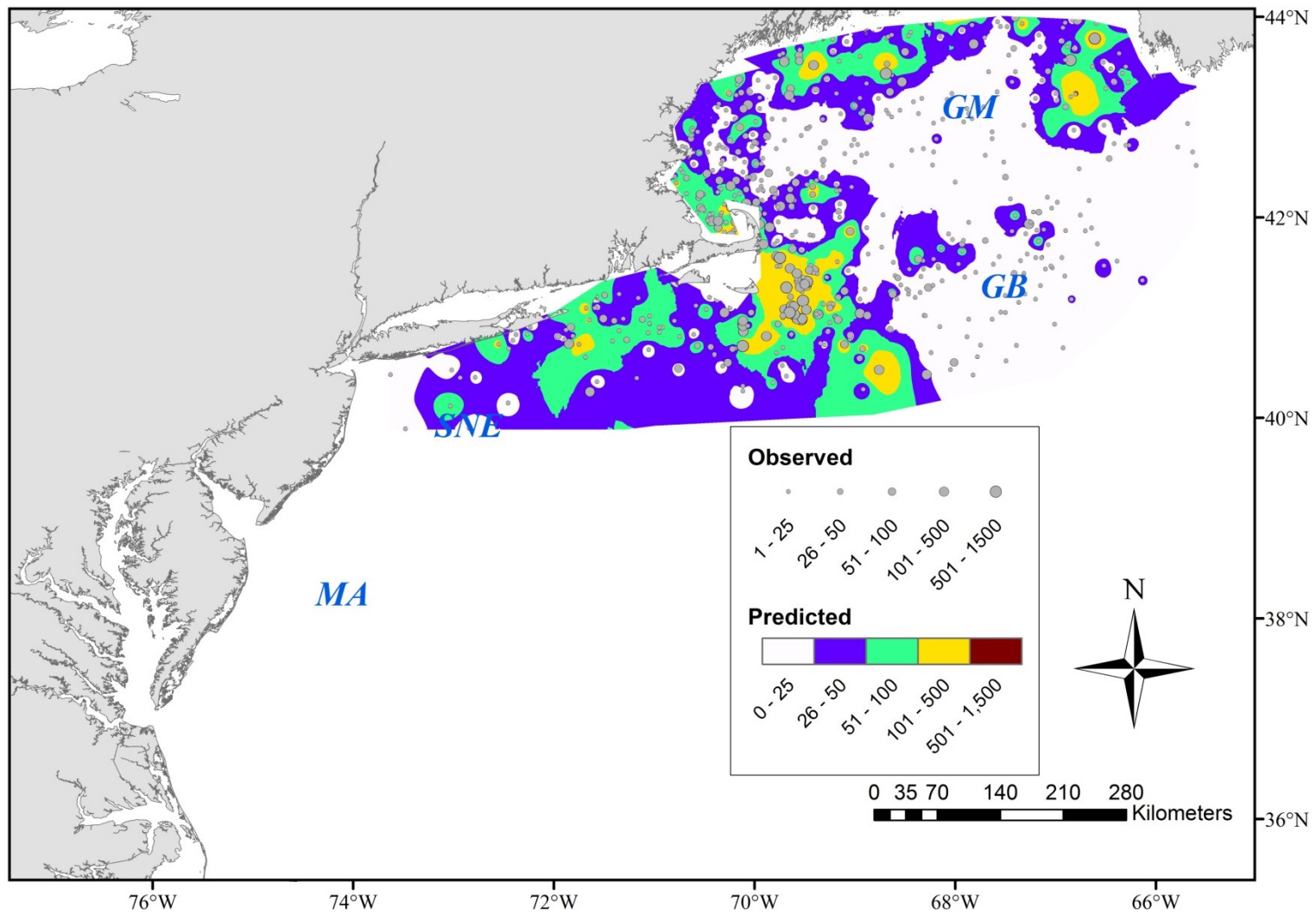


Figure 3F.15. Comparison of the predicted abundance (filled contours) as determined by inverse distance weighted interpolation versus observed abundance (points) in the Northeast (US) shelf large marine ecosystem for immature female spiny dogfish during autumn. MA = Middle Atlantic Bight, SNE = Southern New England, GB = Georges Bank, and GM = Gulf of Maine. Solid gray indicates land masses. Note: interpolation carried out in ArcGIS using spatial analyst.

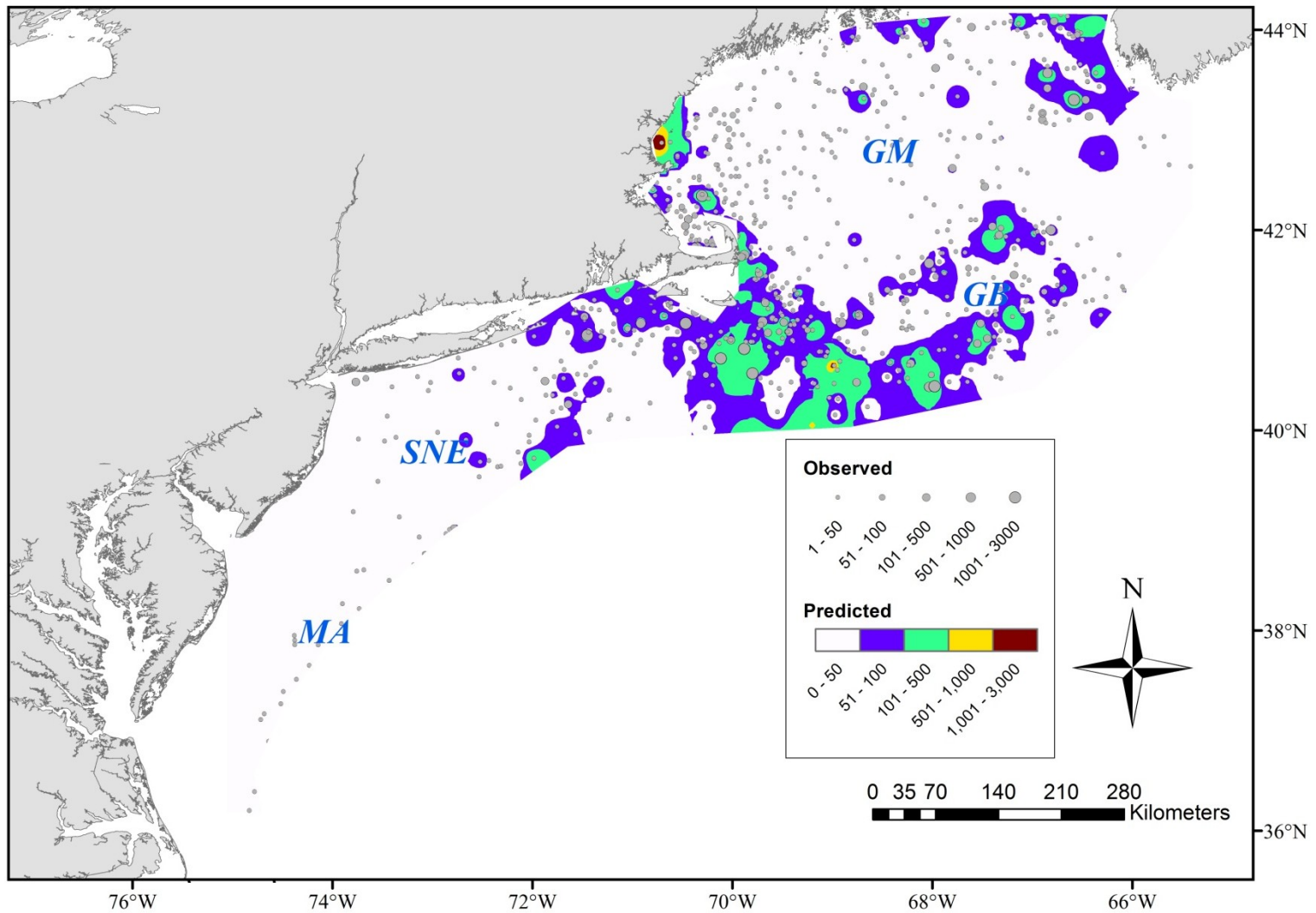


Figure 3F.16. Comparison of the predicted abundance (filled contours) as determined by inverse distance weighted interpolation versus observed abundance (points) in the Northeast (US) shelf large marine ecosystem for immature male spiny dogfish during autumn. MA = Middle Atlantic Bight, SNE = Southern New England, GB = Georges Bank, and GM = Gulf of Maine. Solid gray indicates land masses. Note: interpolation carried out in ArcGIS using spatial analyst.

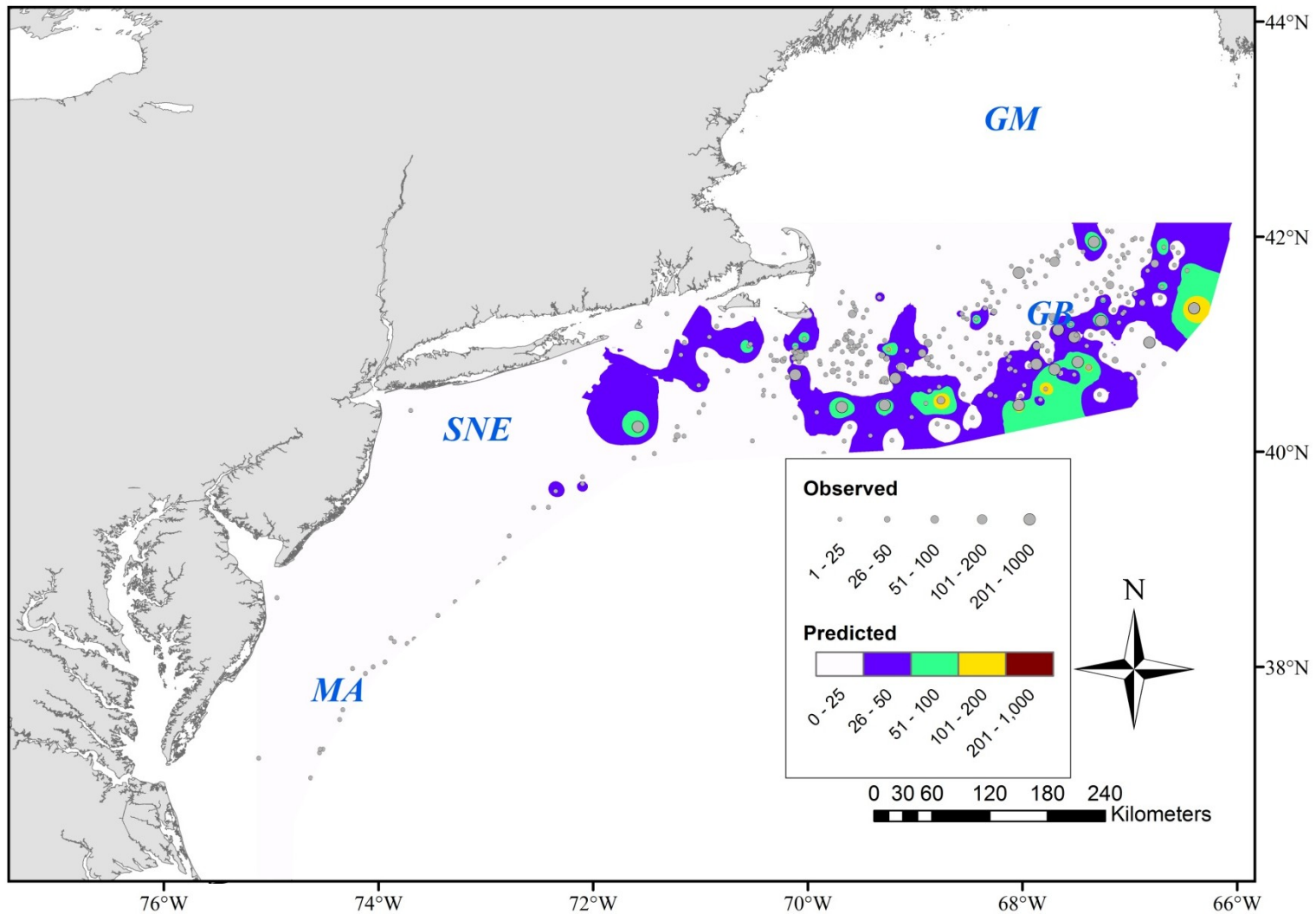
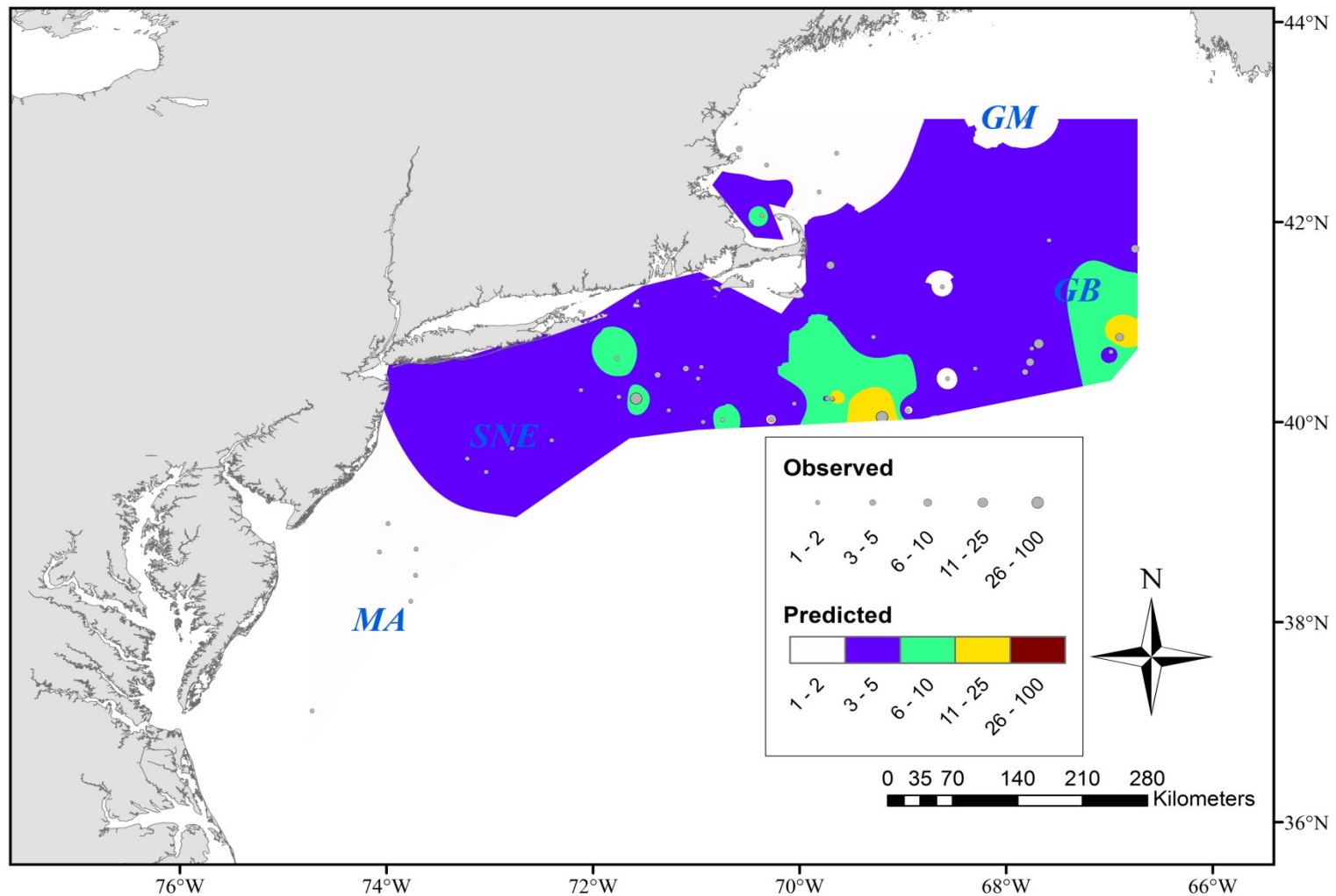


Figure 3F.17. Comparison of the predicted abundance (filled contours) as determined by inverse distance weighted interpolation versus observed abundance (points) in the Northeast (US) shelf large marine ecosystem for neonate spiny dogfish during autumn. MA = Middle Atlantic Bight, SNE = Southern New England, GB = Georges Bank, and GM = Gulf of Maine. Solid gray indicates land masses. Note: interpolation carried out in ArcGIS using spatial analyst.



Appendix 3G. Abundance (PRES) Models for Spring

Figure 3G.1. Partial GAM plots identifying the additive effect of each variable on the probability of increasing abundance of mature female spiny dogfish during spring. Variables as defined in Table 3.2. The y-axis represents the degree of smoothing (variable, estimated degrees of freedom) 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'. Range estimates exclude extreme values where rugs are sparse. Some smoothes have been graphically abbreviated due to a lack of data at the endpoints. The gray region reflects the 95% confidence intervals around the response curves. NS = not significant.

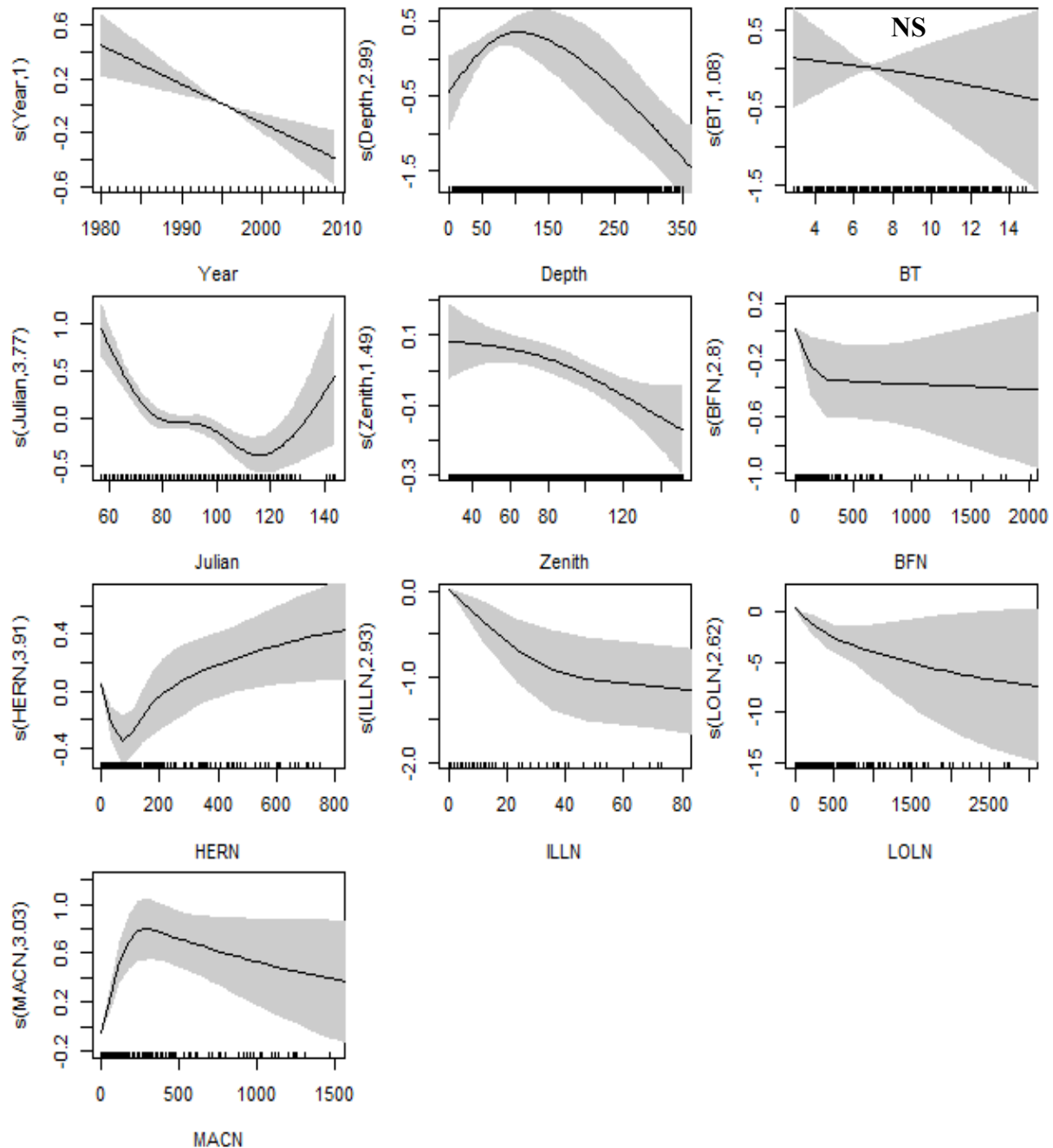


Figure 3G.2. Partial GAM derived effects of important interactions on the abundance of mature female spiny dogfish during spring. Interaction effects shown as perspective plots without error bounds. The response on the z-axis reflects the tensor smooth (variable 1, variable 2, estimated degrees of freedom).

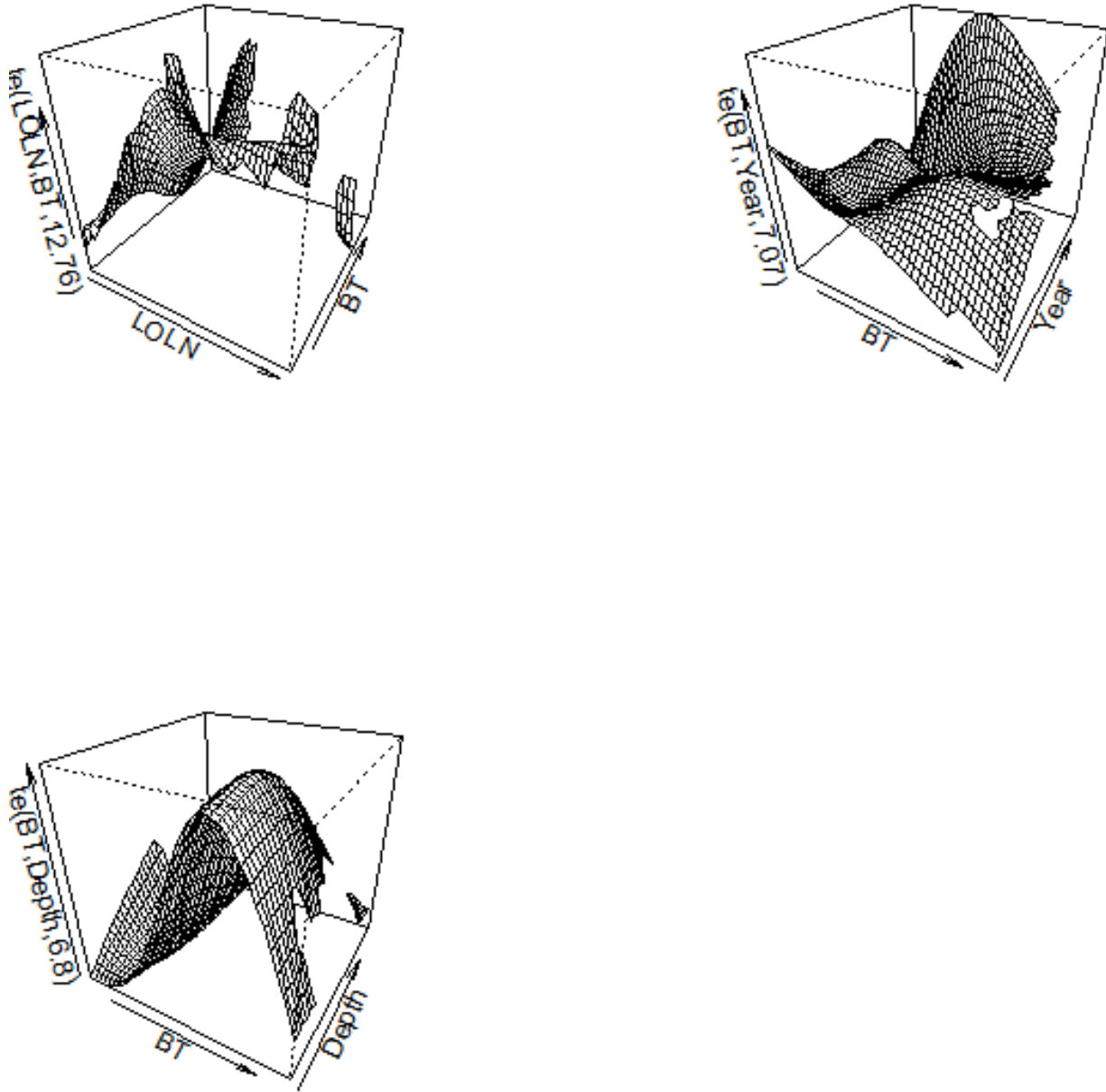


Figure 3G.3. Partial GAM plots identifying the additive effect of each variable on the probability of increasing abundance of mature male spiny dogfish during spring. Variables as defined in Table 3.2. The y-axis represents the degree of smoothing (variable, estimated degrees of freedom) with its range indicative of the relative importance of each covariate. The x-axis reflects the relative density of data points as shown by the 'rug'. Range estimates exclude extreme values where rugs are sparse. Some smooths have been graphically abbreviated due to a lack of data at the endpoints. The gray region reflects the 95% confidence intervals around the response curves. NS = not significant.

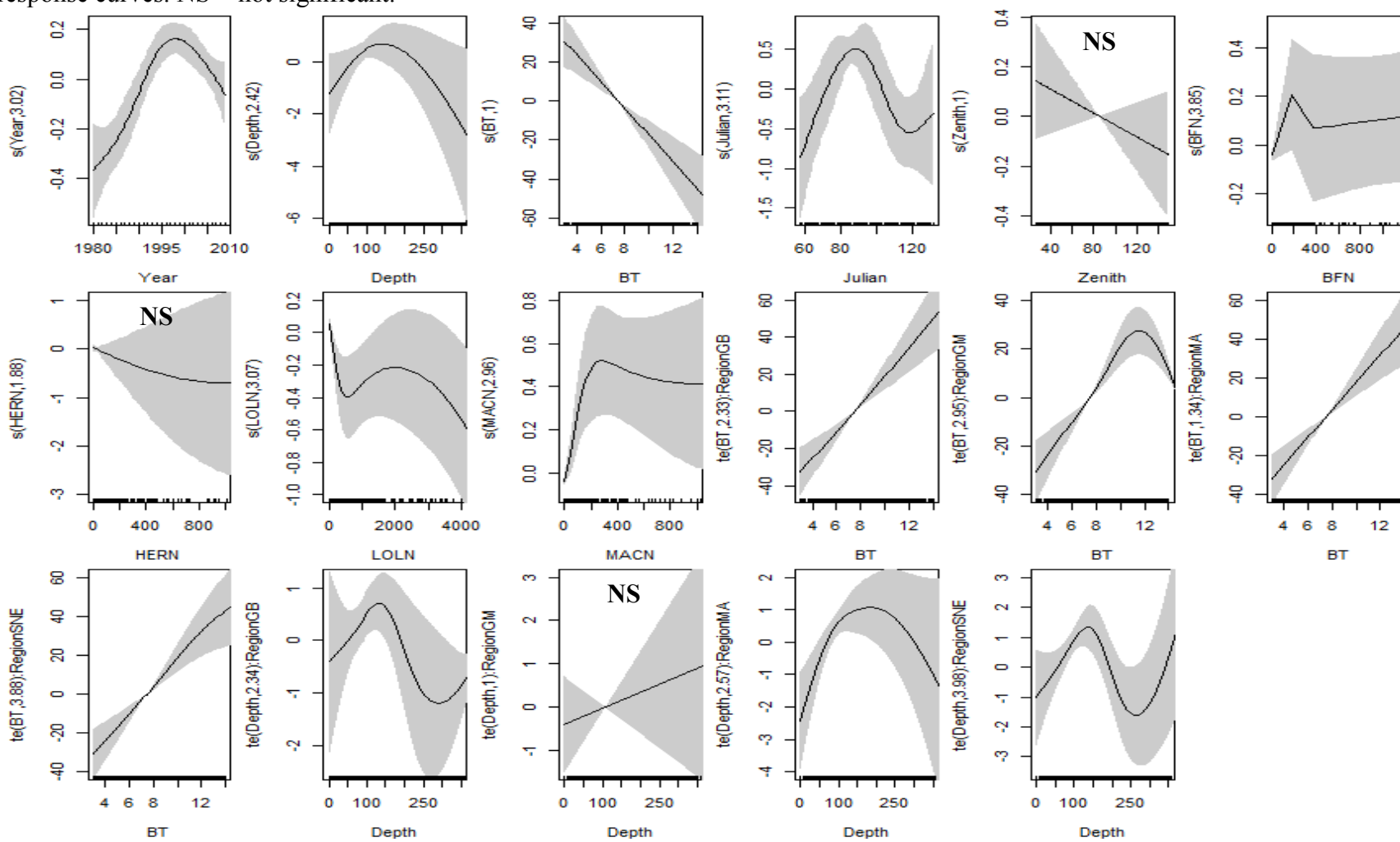


Figure 3G.4. Partial GAM derived effects of important interactions on the abundance of mature male spiny dogfish during spring. Interaction effects shown as perspective plots without error bounds. The response on the z-axis reflects the tensor smooth (variable 1, variable 2, estimated degrees of freedom).

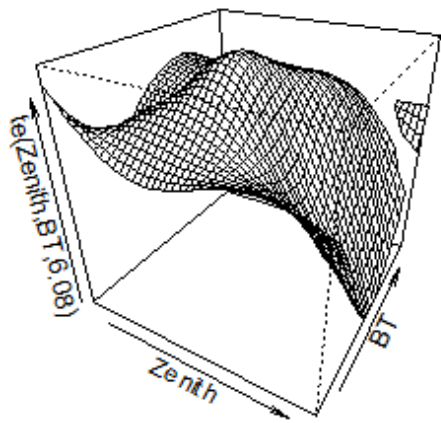
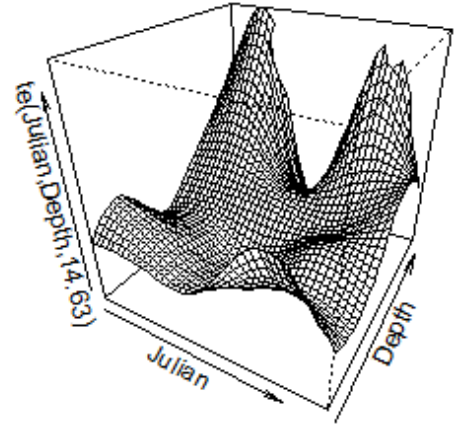
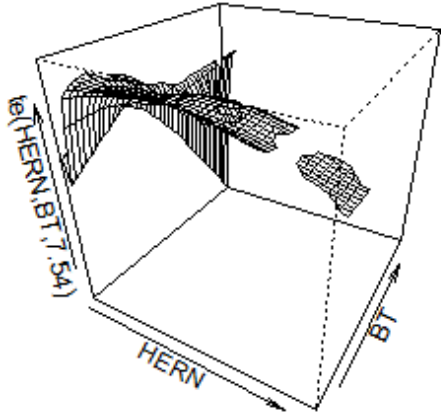


Figure 3G.5. Partial GAM plots identifying the additive effect of each variable on the probability of increasing abundance of immature female spiny dogfish during spring. Variables as defined in Table 3.2. The y-axis represents the degree of smoothing (variable, estimated degrees of freedom) with its range indicative of the relative importance of each covariate. The x-axis reflects the relative density of data points as shown by the 'rug'. Range estimates exclude extreme values where rugs are sparse. Some smoothes have been graphically abbreviated due to a lack of data at the endpoints. The gray region reflects the 95% confidence intervals around the response curves. NS = not significant.

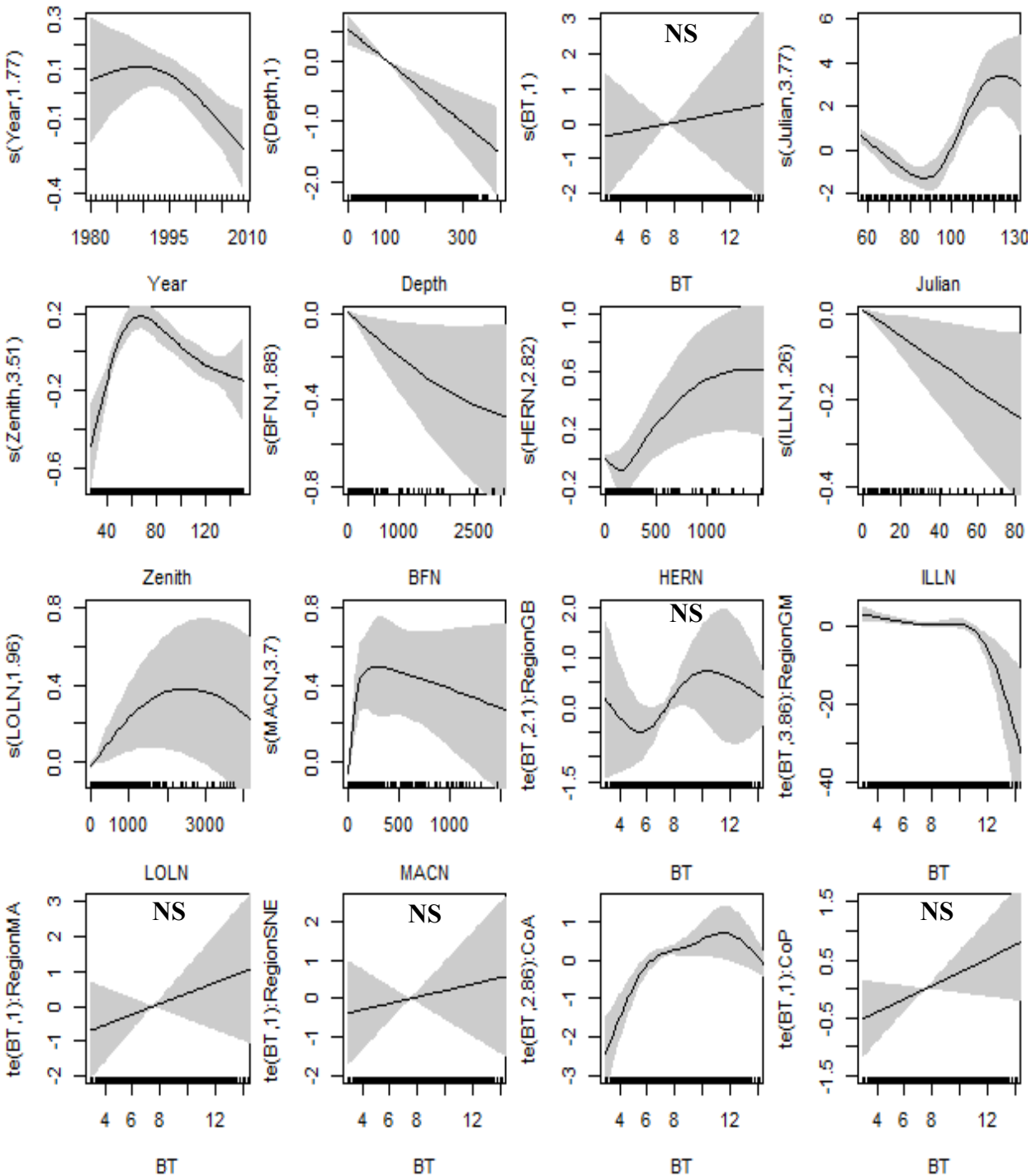


Figure 3G.6. Partial GAM derived effects of important interactions on the abundance of immature female spiny dogfish during spring. Interaction effects shown as perspective plots without error bounds. The response on the z-axis reflects the tensor smooth (variable 1, variable 2, estimated degrees of freedom).

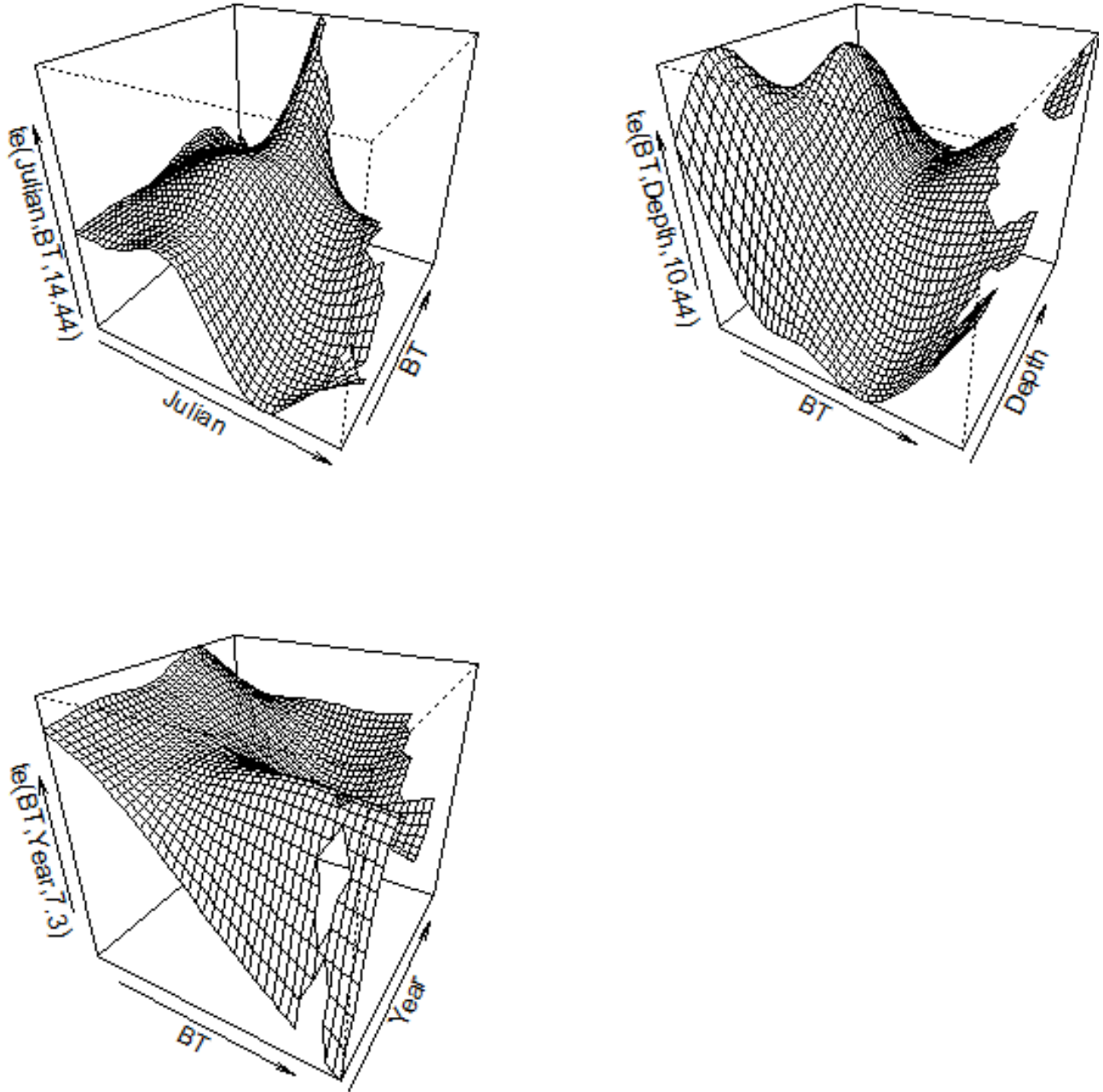


Figure 3G.7. Partial GAM plots identifying the additive effect of each variable on the probability of increasing abundance of neonate spiny dogfish during spring. Variables as defined in Table 3.2. The y-axis represents the degree of smoothing (variable, estimated degrees of freedom) with its range indicative of the relative importance of each covariate. The x-axis reflects the relative density of data points as shown by the 'rug'. Range estimates exclude extreme values where rugs are sparse. Some smoothes have been graphically abbreviated due to a lack of data at the endpoints. The gray region reflects the 95% confidence intervals around the response curves. NS = not significant.

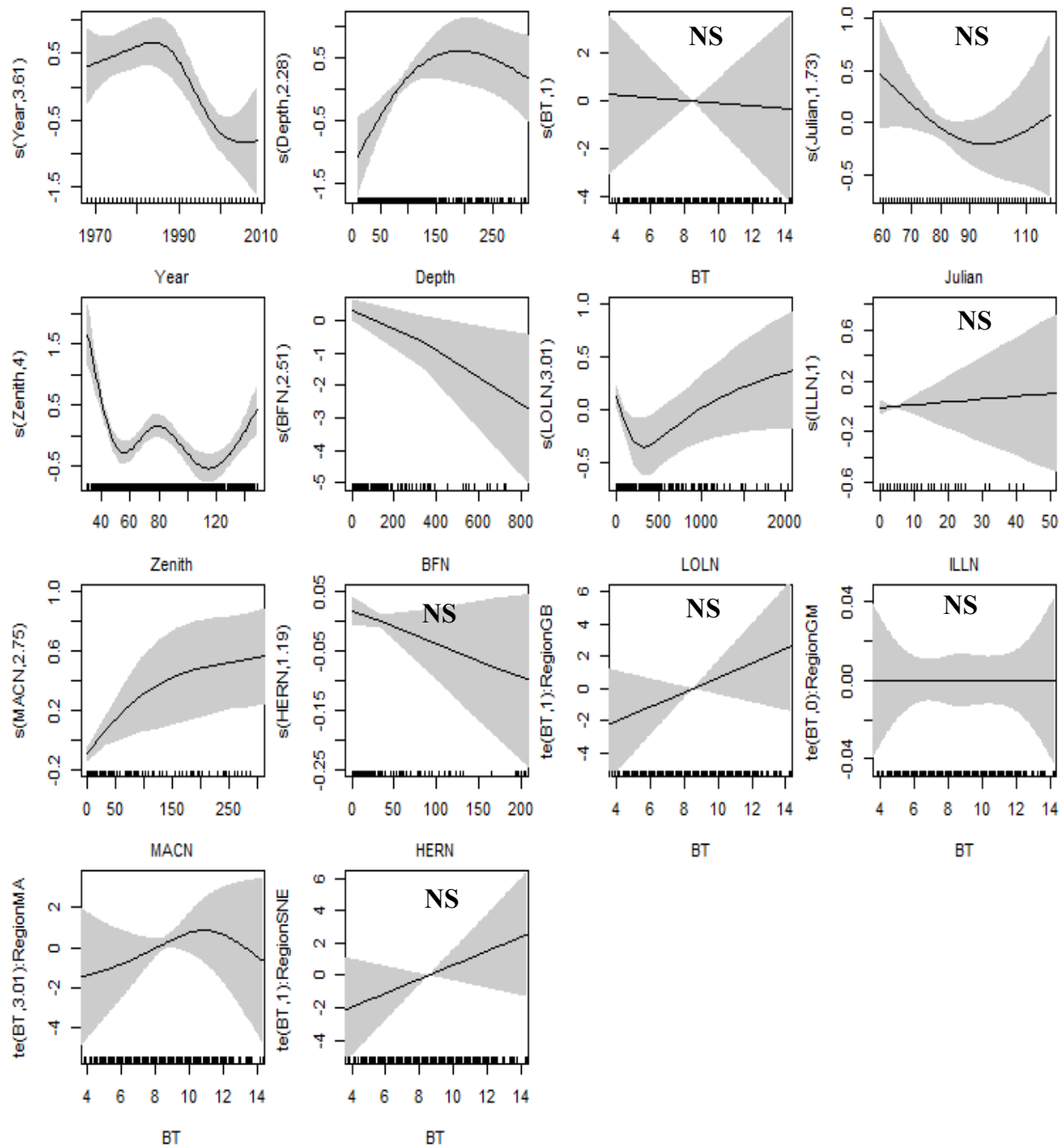


Figure 3G.8. Partial GAM derived effects of important interactions on the abundance of neonate spiny dogfish during spring. Interaction effects shown as perspective plots without error bounds. The response on the z-axis reflects the tensor smooth (variable 1, variable 2, estimated degrees of freedom). NS = not significant.

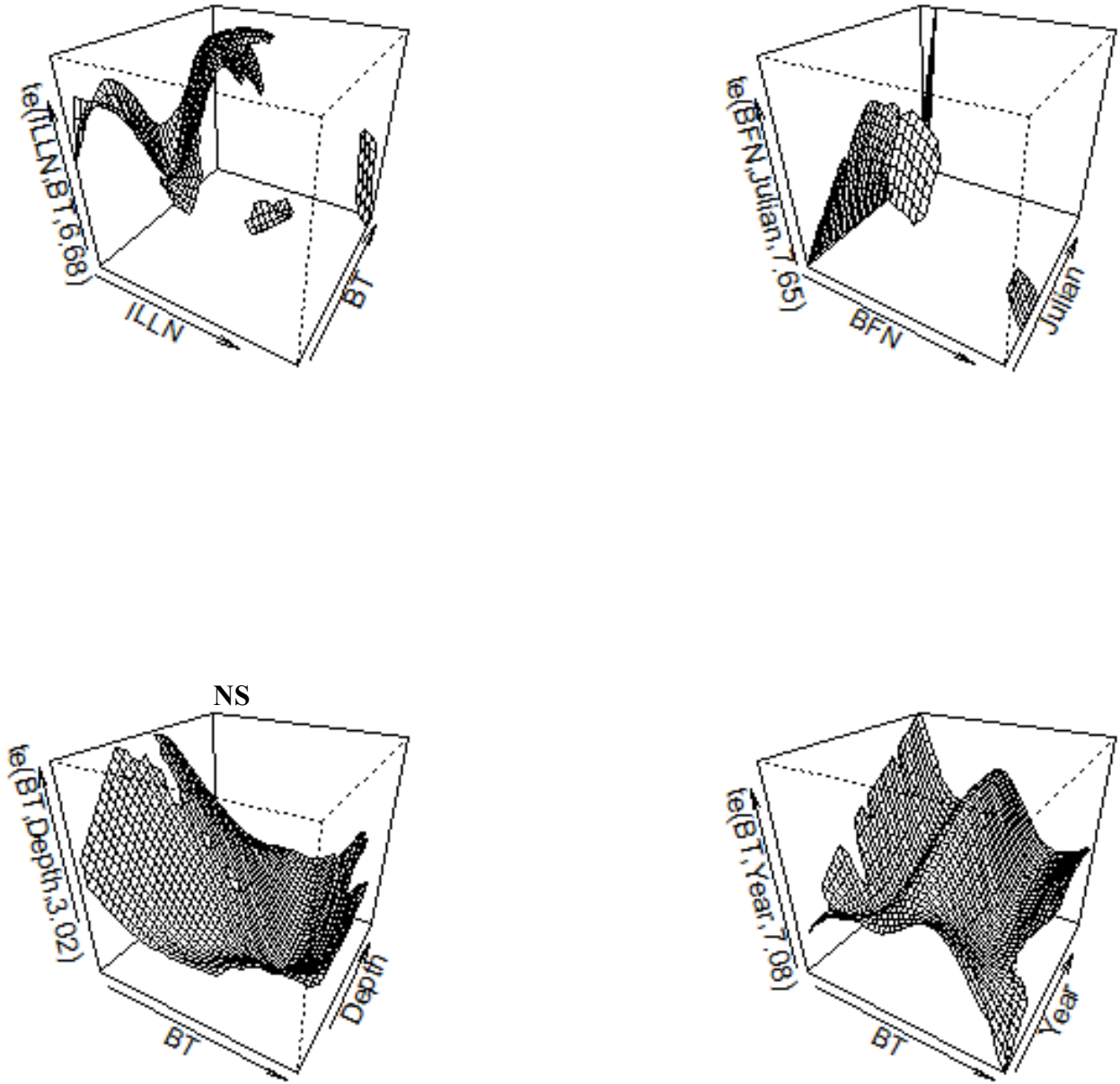


Figure 3G.9. Relationships between the Pearson residuals and all potential explanatory variables based on the optimal mature female spiny dogfish abundance model during spring. Note: Mature Male PA (bottom right) represents co-occurrence.

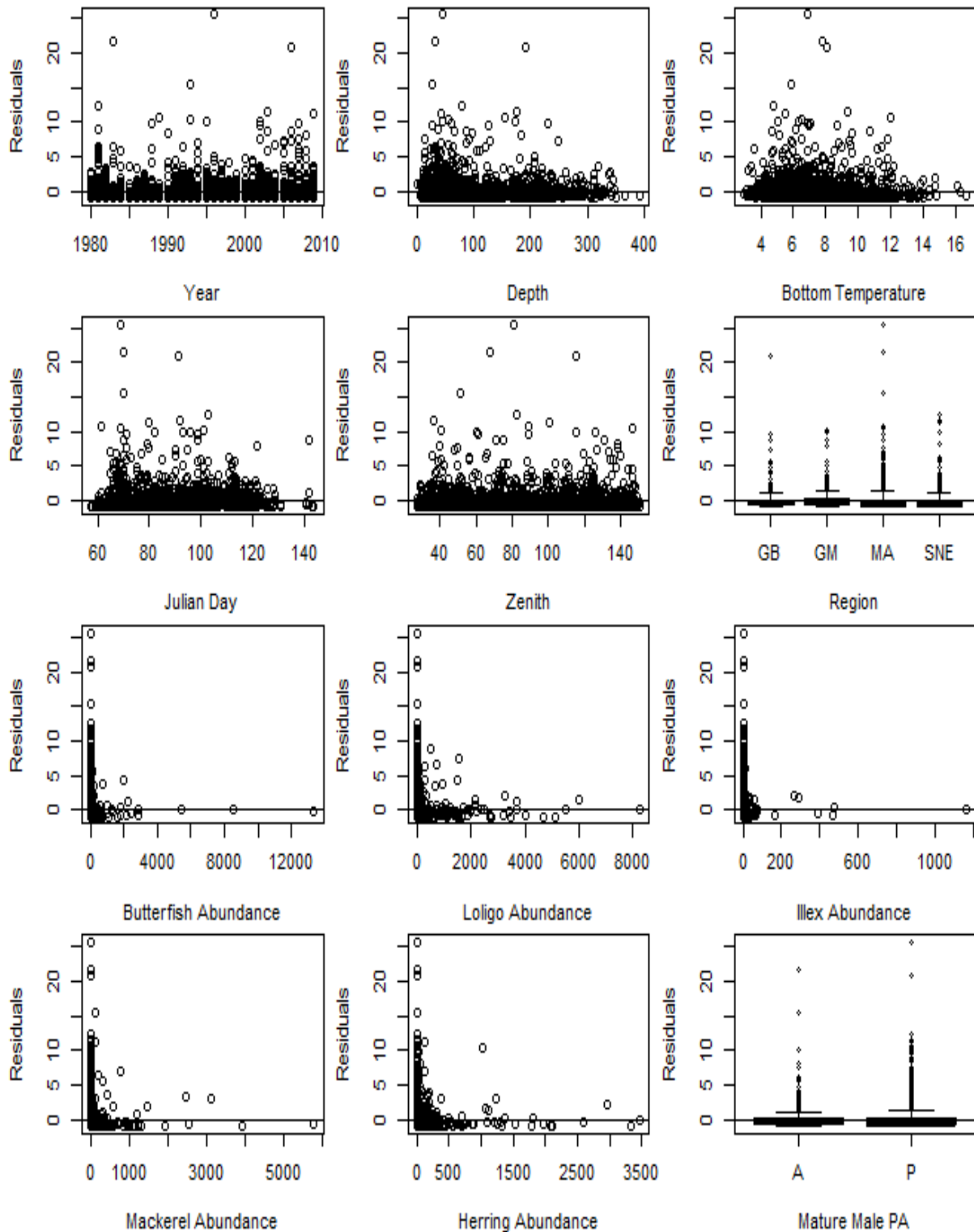


Figure 3G.10. Relationships between the Pearson residuals and all potential explanatory variables based on the optimal mature male spiny dogfish abundance model during spring. Note: Mature Female PA (bottom right) represents co-occurrence.

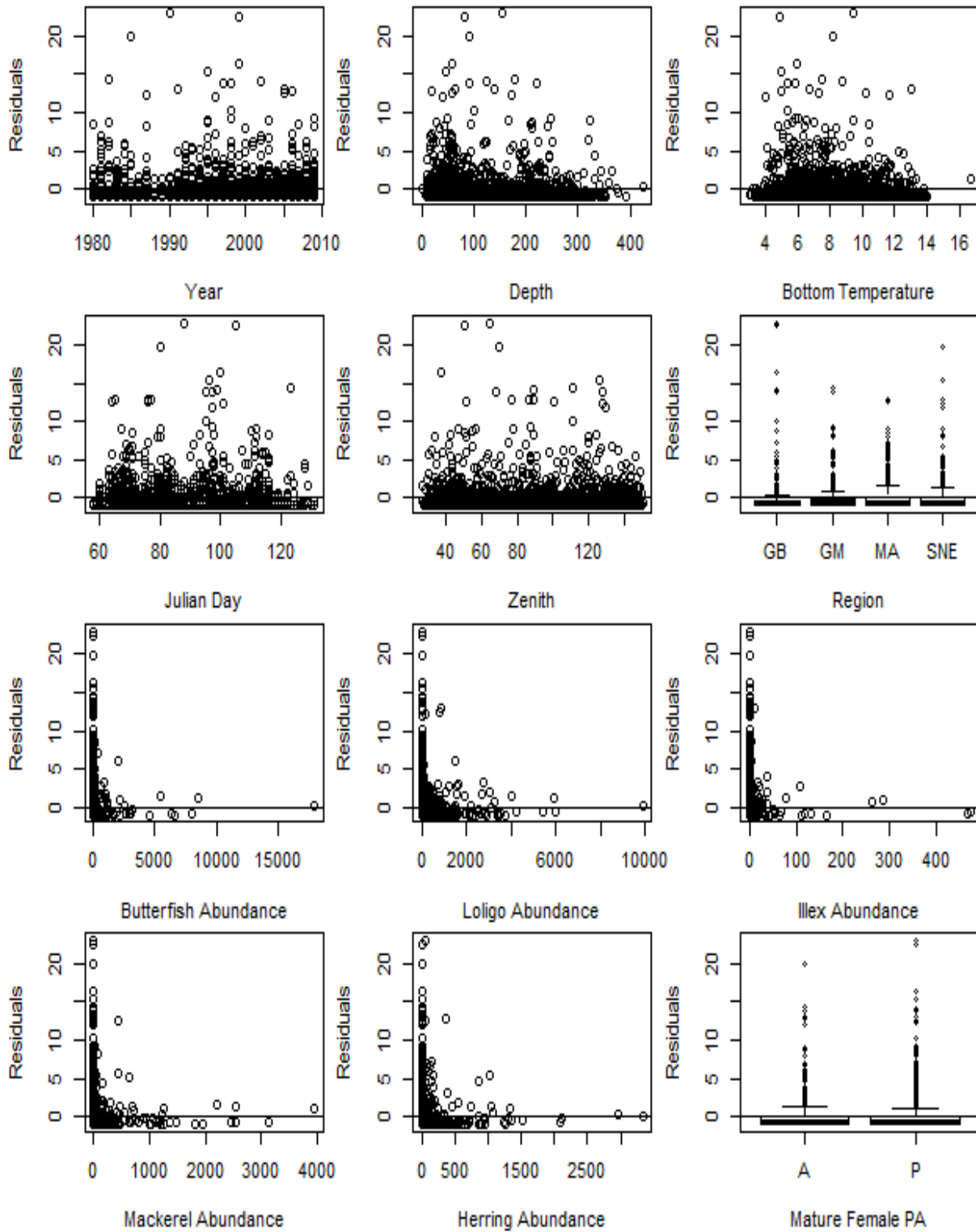


Figure 3G.11. Relationships between the Pearson residuals and all potential explanatory variables based on the optimal immature female spiny dogfish abundance model during spring. Note: Immature Male PA (bottom right) represents co-occurrence.

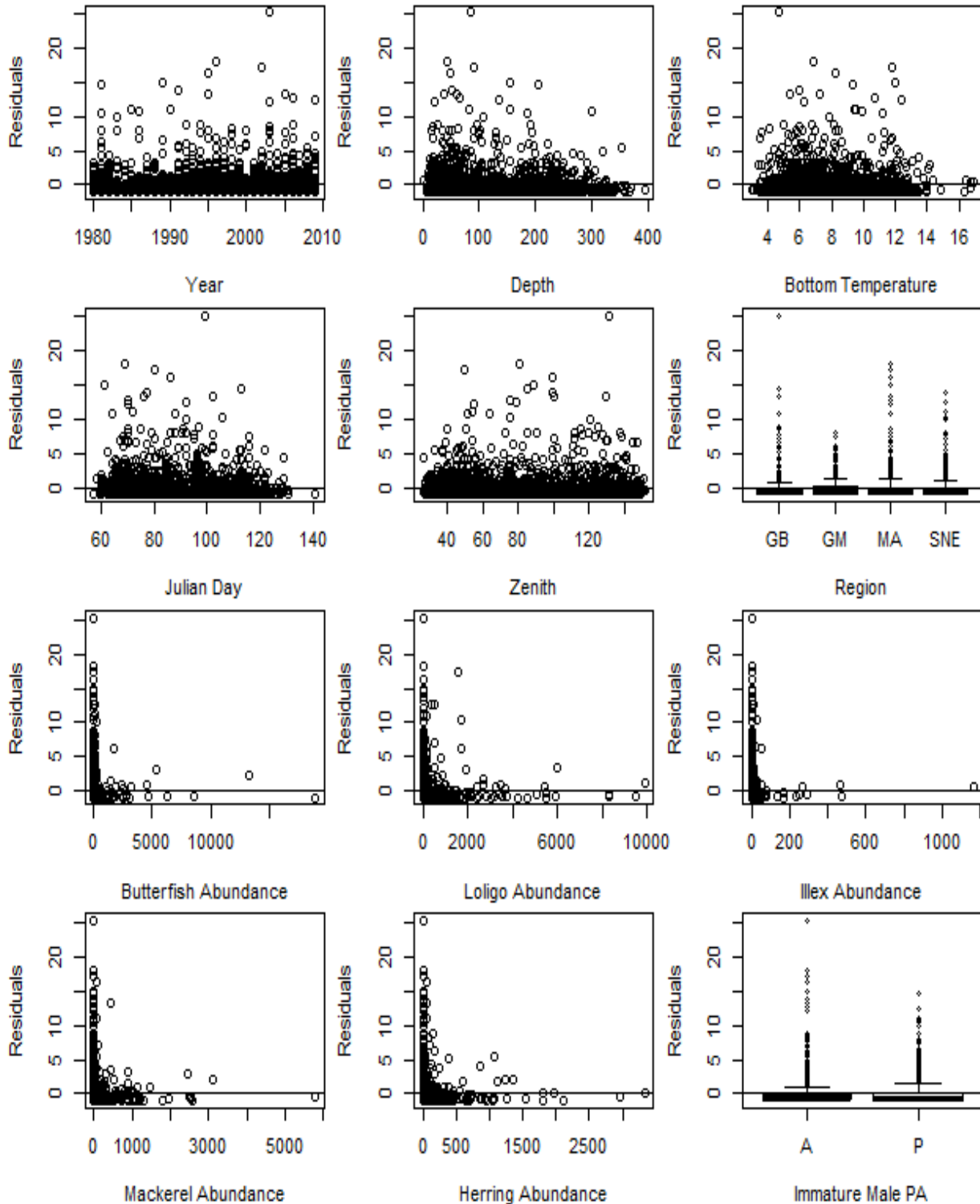


Figure 3G.12. Relationships between the Pearson residuals and all potential explanatory variables based on the optimal immature male spiny dogfish abundance model during spring. Note: Immature Female PA (bottom right) represents co-occurrence.

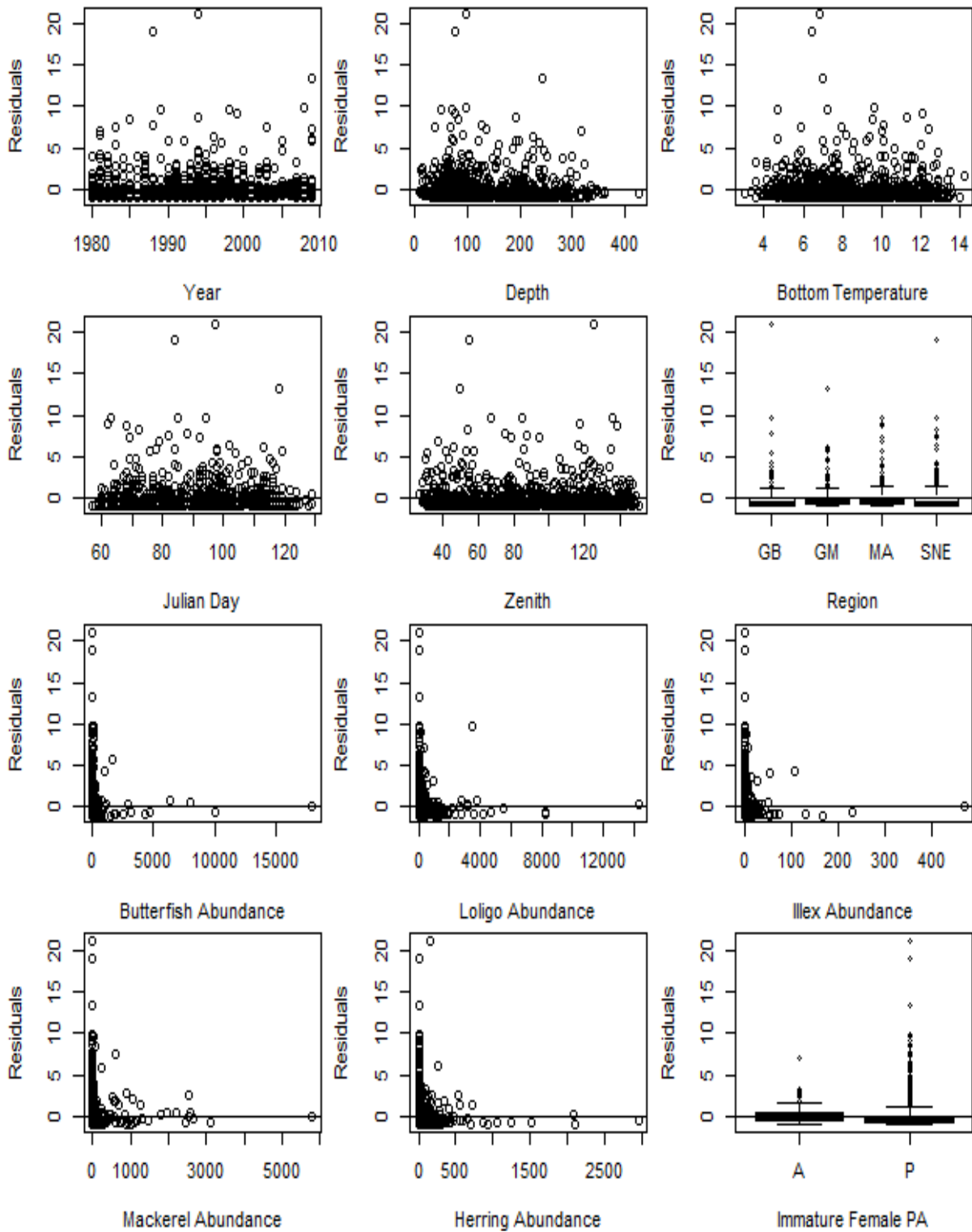


Figure 3G.13. Relationships between the Pearson residuals and all potential explanatory variables based on the optimal neonate spiny dogfish abundance model during spring.

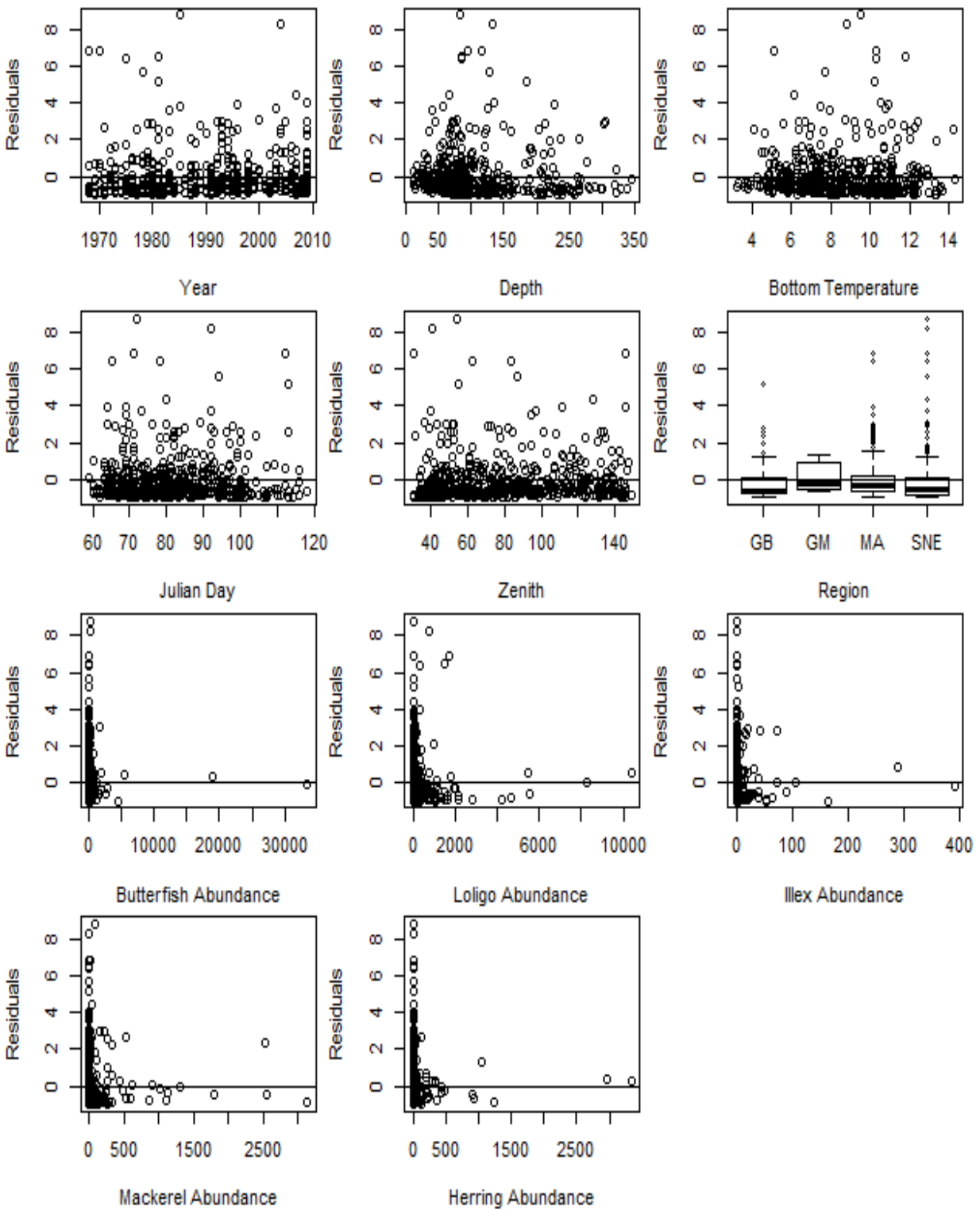


Figure 3G.14. Comparison of the predicted abundance (filled contours) as determined by inverse distance weighted interpolation versus observed abundance (points) in the Northeast (US) shelf large marine ecosystem for mature female spiny dogfish during spring. MA = Middle Atlantic Bight, SNE = Southern New England, GB = Georges Bank, and GM = Gulf of Maine. Solid gray indicates land masses. Note: interpolation carried out in ArcGIS using spatial analyst.

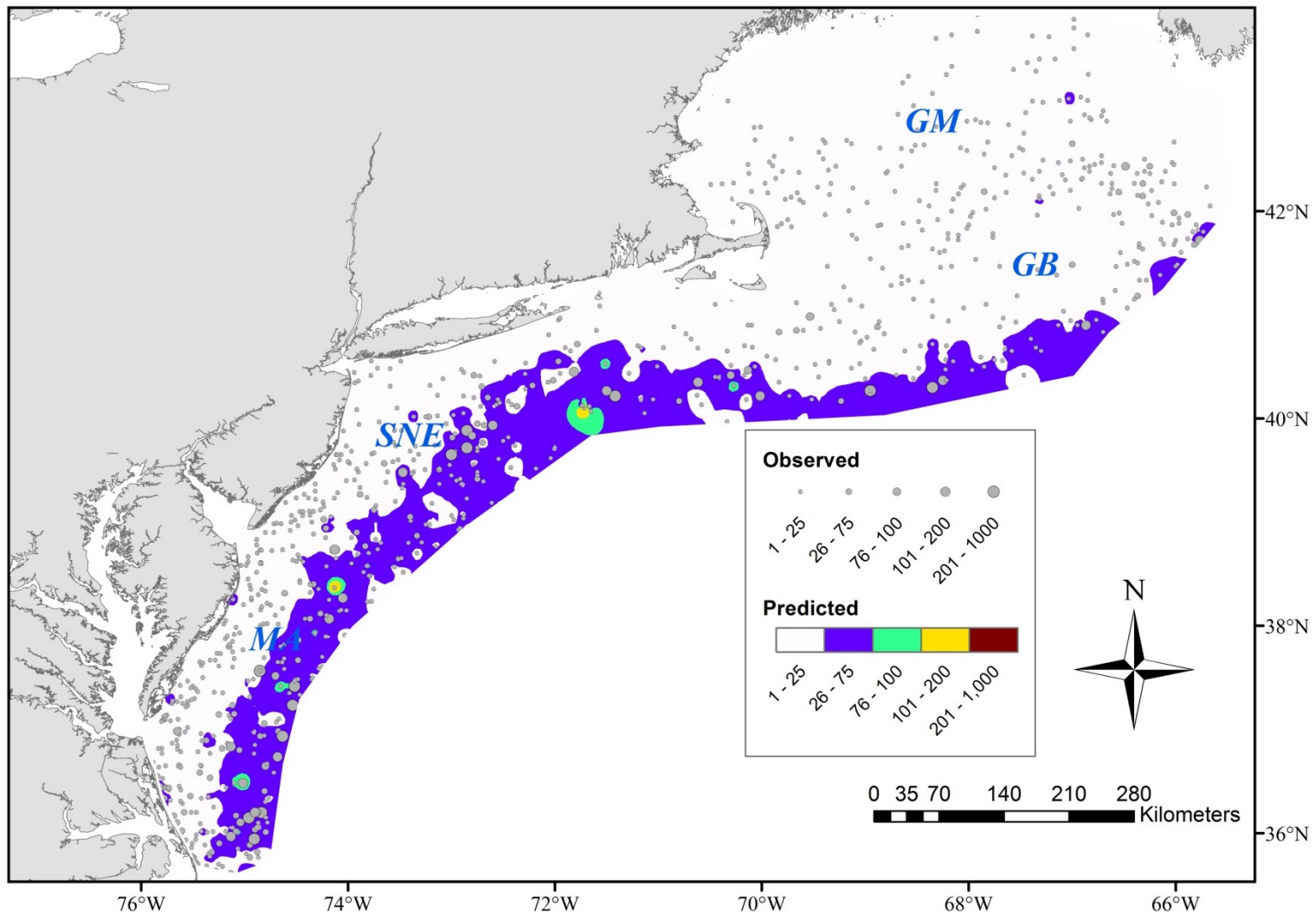


Figure 3G.15. Comparison of the predicted abundance (filled contours) as determined by inverse distance weighted interpolation versus observed abundance (points) in the Northeast (US) shelf large marine ecosystem for mature male spiny dogfish during spring. MA = Middle Atlantic Bight, SNE = Southern New England, GB = Georges Bank, and GM = Gulf of Maine. Solid gray indicates land masses. Note: interpolation carried out in ArcGIS using spatial analyst.

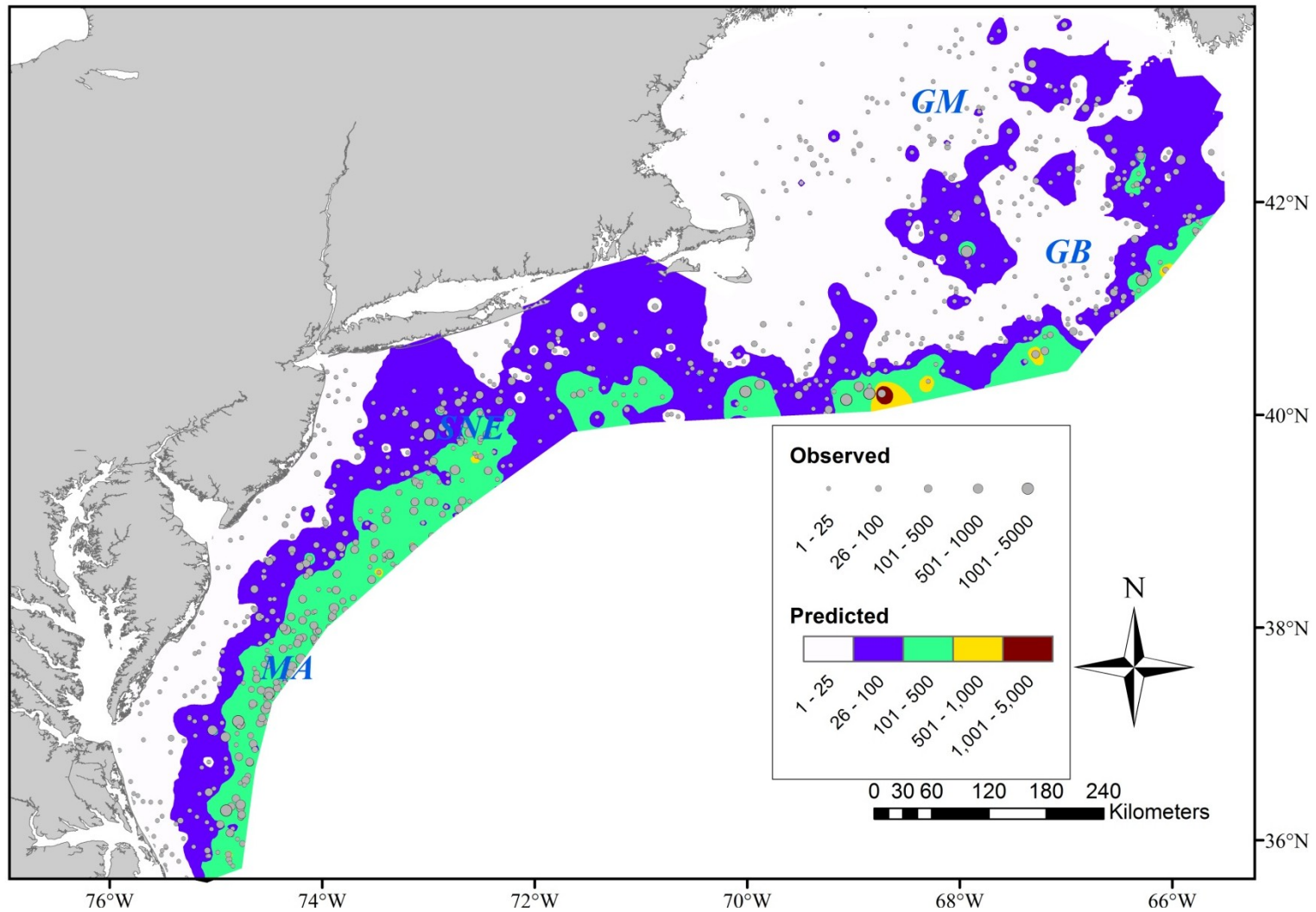


Figure 3G.16. Comparison of the predicted abundance (filled contours) as determined by inverse distance weighted interpolation versus observed abundance (points) in the Northeast (US) shelf large marine ecosystem for immature female spiny dogfish during spring. MA = Middle Atlantic Bight, SNE = Southern New England, GB = Georges Bank, and GM = Gulf of Maine. Solid gray indicates land masses. Note: interpolation carried out in ArcGIS using spatial analyst.

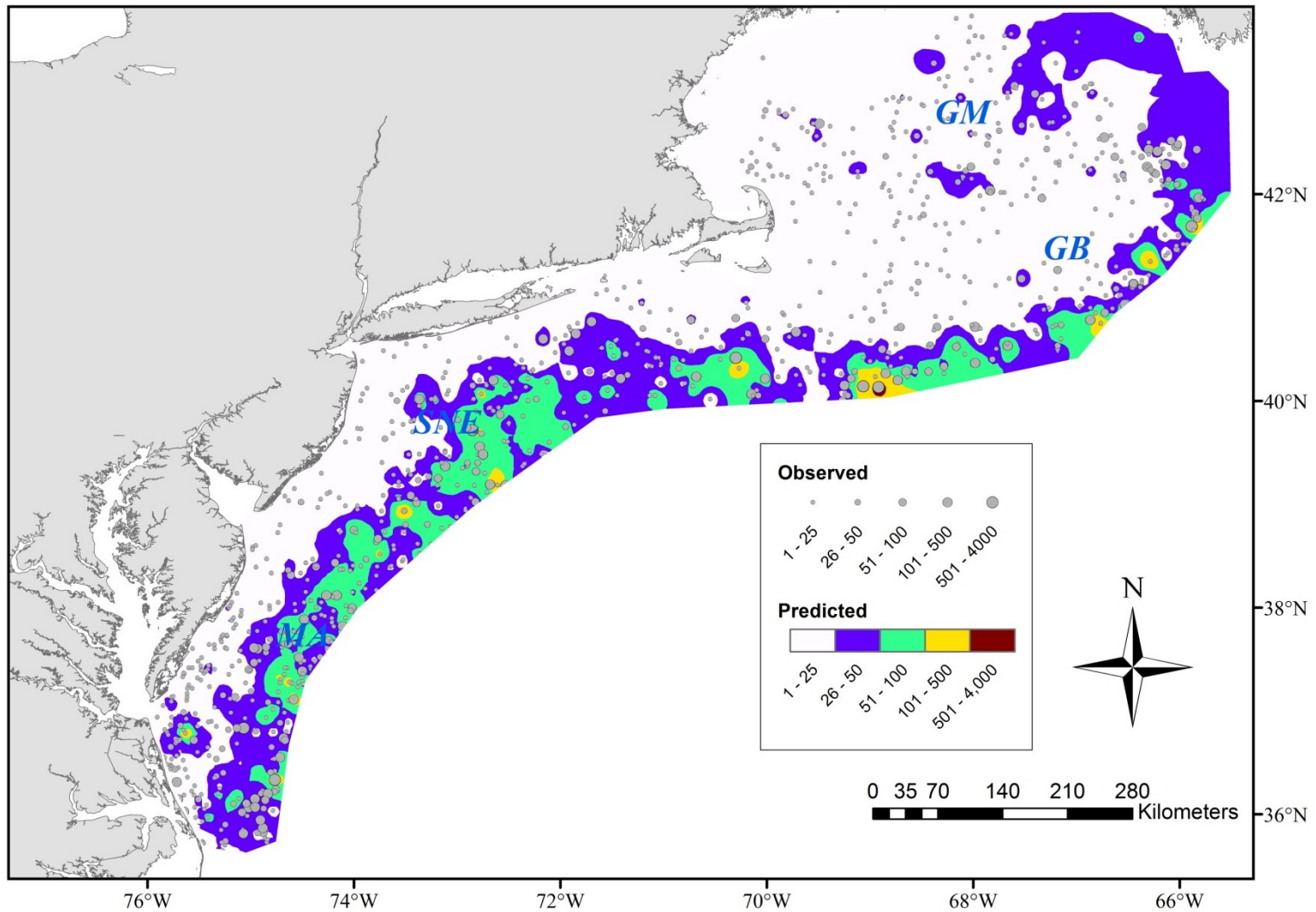


Figure 3G.17. Comparison of the predicted abundance (filled contours) as determined by inverse distance weighted interpolation versus observed abundance (points) in the Northeast (US) shelf large marine ecosystem for immature male spiny dogfish during spring. MA = Middle Atlantic Bight, SNE = Southern New England, GB = Georges Bank, and GM = Gulf of Maine. Solid gray indicates land masses. Note: interpolation carried out in ArcGIS using spatial analyst.

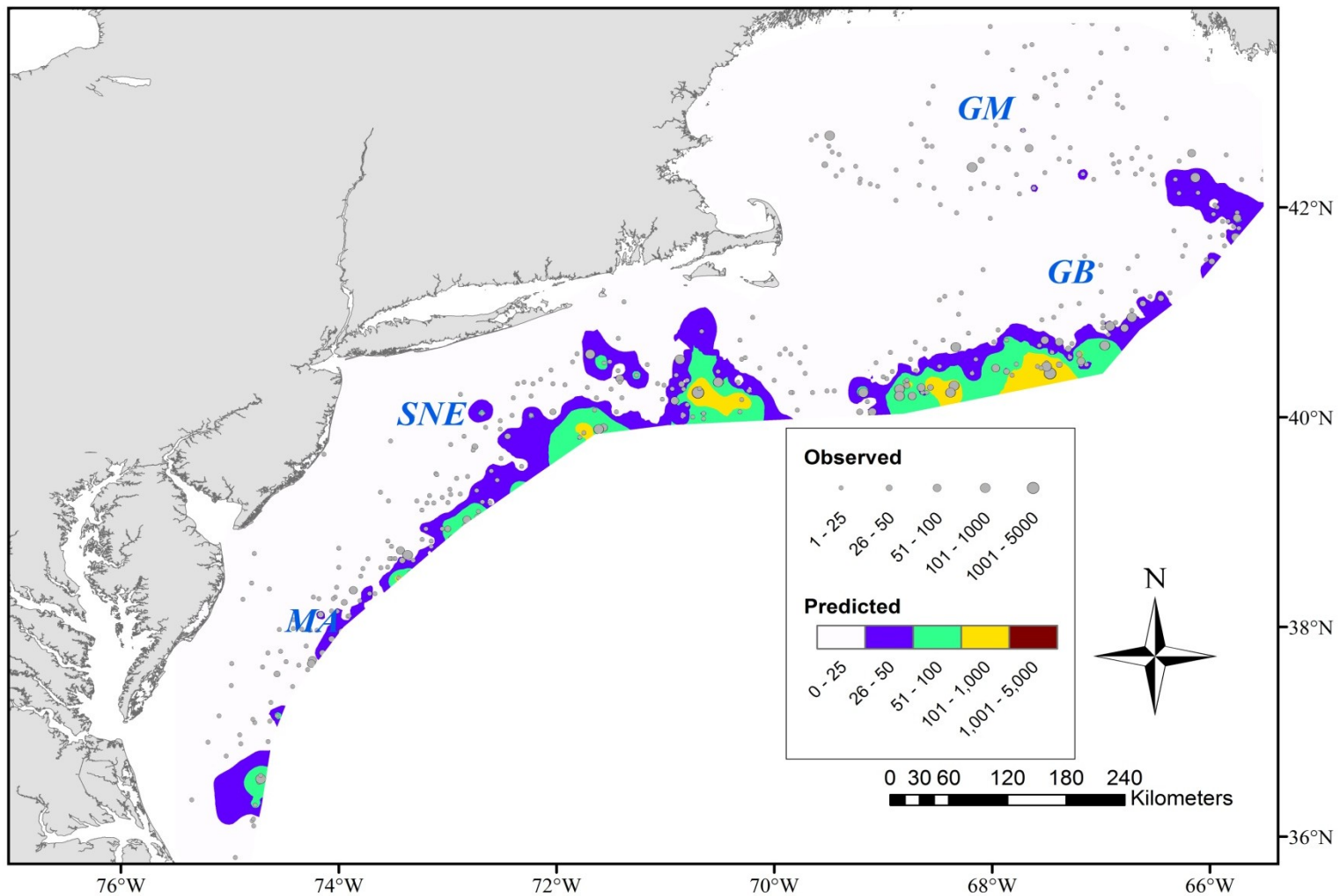
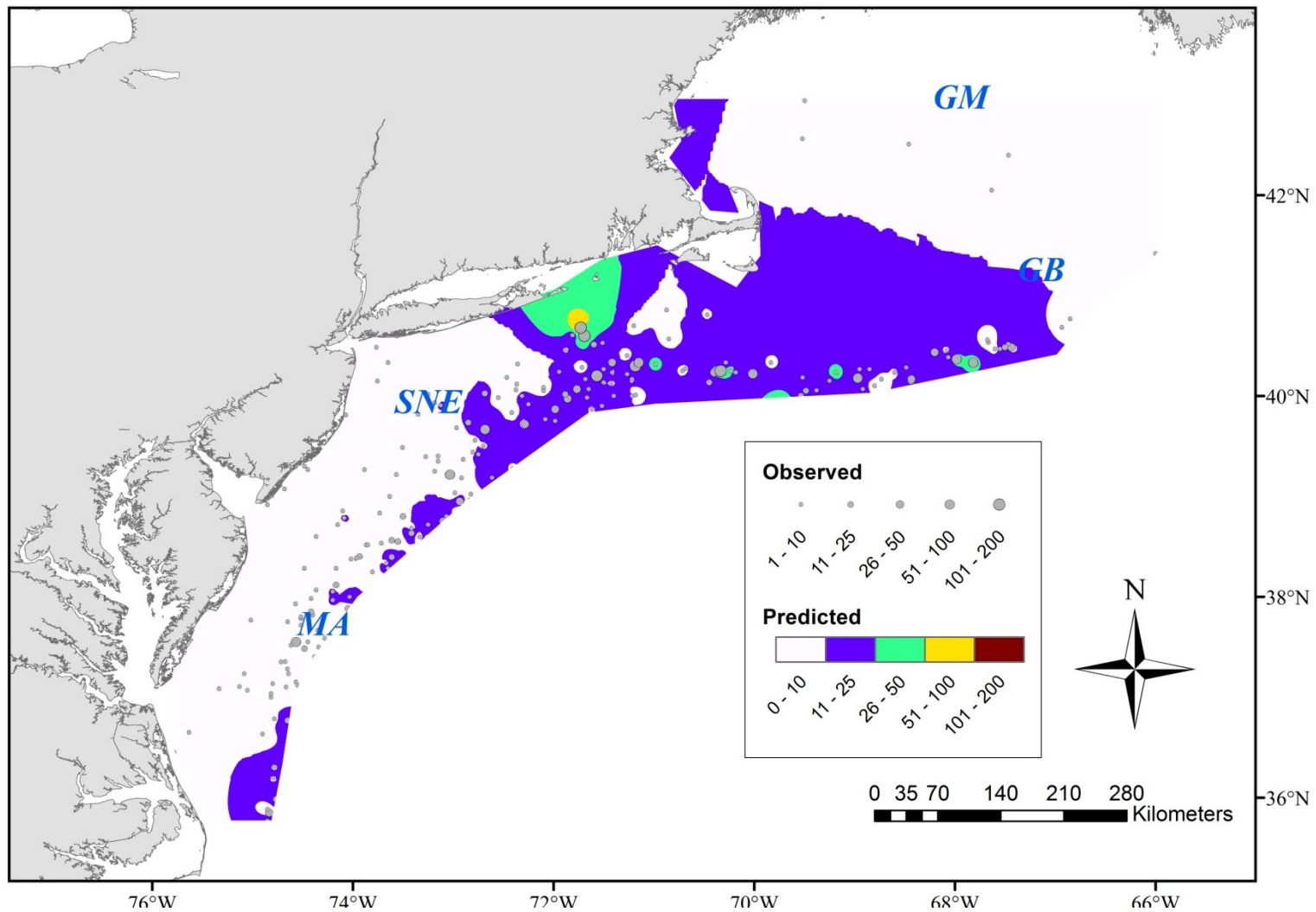


Figure 3G.18. Comparison of the predicted abundance (filled contours) as determined by inverse distance weighted interpolation versus observed abundance (points) in the Northeast (US) shelf large marine ecosystem for neonate spiny dogfish during spring. MA = Middle Atlantic Bight, SNE = Southern New England, GB = Georges Bank, and GM = Gulf of Maine. Solid gray indicates land masses. Note: interpolation carried out in ArcGIS using spatial analyst.



Appendix 3H. Projected Distributions Under Different Temperature Scenarios

Figure 3H.1. Hypothetical predicted probability of mature female spiny dogfish occurrence during autumn in the Northeast (US) shelf large marine ecosystem for a year exhibiting average (BT_{avg}), warmer ($BT_{avg} + 1^{\circ}C$), and cooler ($BT_{avg} - 1^{\circ}C$) bottom temperatures. Probabilities include < 0.5 (red), $0.5 - 0.6$ (orange), $0.6 - 0.7$ (yellow), $0.7 - 0.8$ (green), $0.8 - 0.9$ (light blue), and $0.9 - 1.0$ (dark blue). Note: only the abiotic sub-model was used for prediction due to uncertainty regarding how prey species would respond to temperature changes. MA = Middle Atlantic Bight, SNE = Southern New England, GB = Georges Bank, and GM = Gulf of Maine. Solid gray indicates land masses.

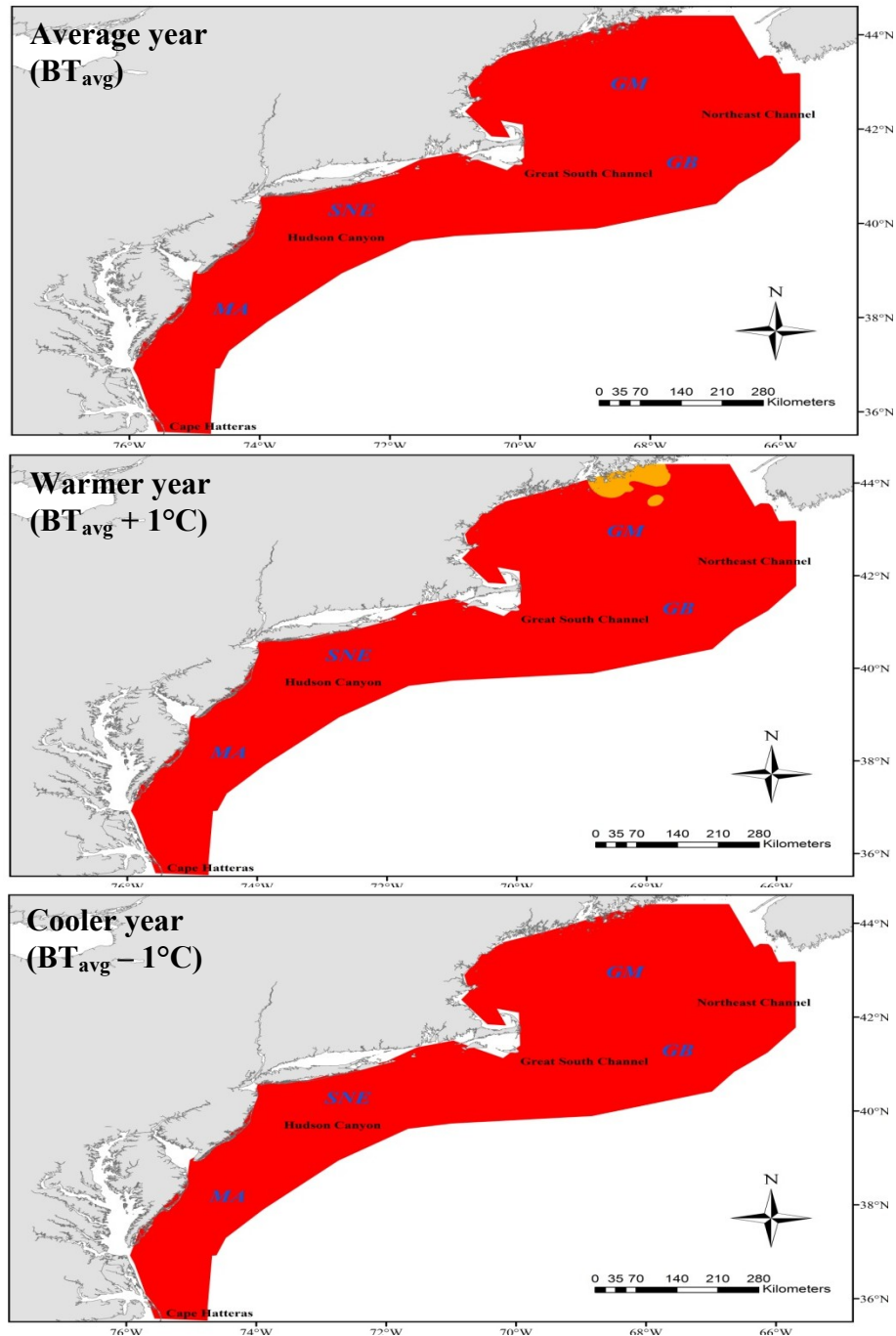


Figure 3H.2. Hypothetical predicted probability of mature male spiny dogfish occurrence during autumn in the Northeast (US) shelf large marine ecosystem for a year exhibiting average (BT_{avg}), warmer ($BT_{avg} + 1^{\circ}C$), and cooler ($BT_{avg} - 1^{\circ}C$) bottom temperatures. Probabilities include < 0.5 (red), $0.5 - 0.6$ (orange), $0.6 - 0.7$ (yellow), $0.7 - 0.8$ (green), $0.8 - 0.9$ (light blue), and $0.9 - 1.0$ (dark blue). Note: only the abiotic sub-model was used for prediction due to uncertainty regarding how prey species would respond to temperature changes. MA = Middle Atlantic Bight, SNE = Southern New England, GB = Georges Bank, and GM = Gulf of Maine. Solid gray indicates land masses.

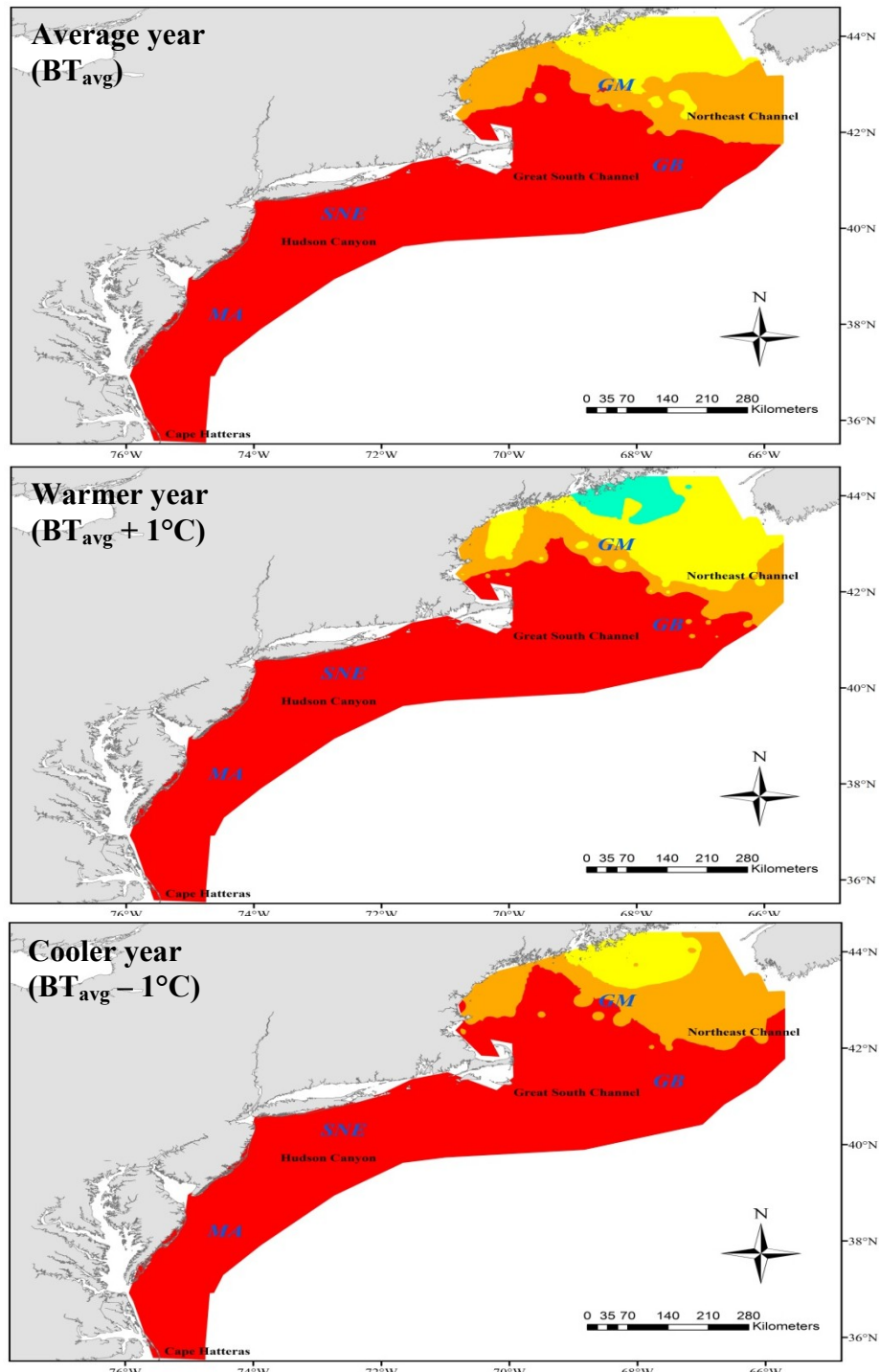


Figure 3H.3. Hypothetical predicted probability of immature female spiny dogfish occurrence during autumn in the Northeast (US) shelf large marine ecosystem for a year exhibiting average (BT_{avg}), warmer ($BT_{avg} + 1^{\circ}C$), and cooler ($BT_{avg} - 1^{\circ}C$) bottom temperatures. Probabilities include < 0.5 (red), $0.5 - 0.6$ (orange), $0.6 - 0.7$ (yellow), $0.7 - 0.8$ (green), $0.8 - 0.9$ (light blue), and $0.9 - 1.0$ (dark blue). Note: only the abiotic sub-model was used for prediction due to uncertainty regarding how prey species would respond to temperature changes. MA = Middle Atlantic Bight, SNE = Southern New England, GB = Georges Bank, and GM = Gulf of Maine. Solid gray indicates land masses.

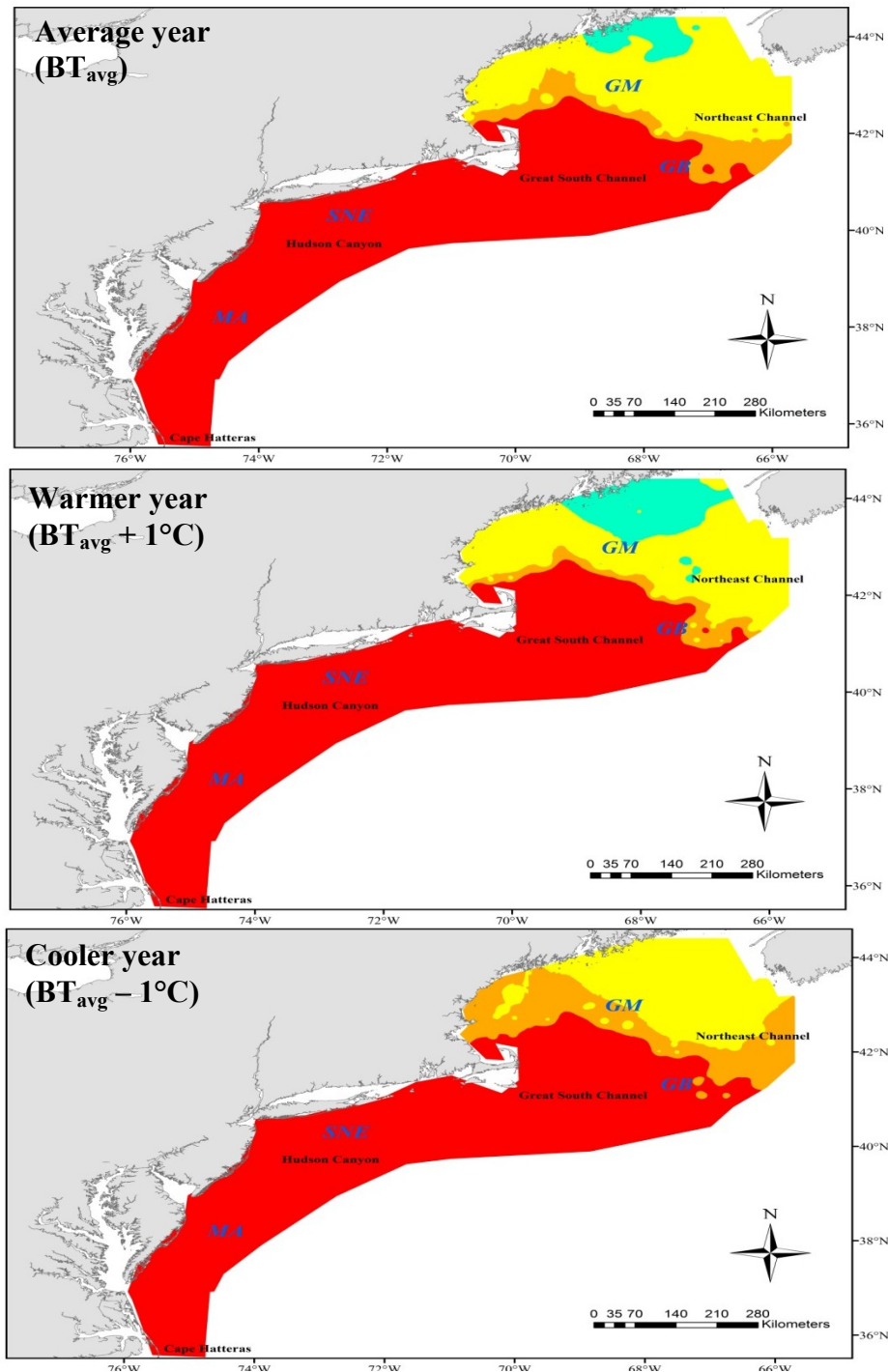


Figure 3H.4. Hypothetical predicted probability of immature male spiny dogfish occurrence during autumn in the Northeast (US) shelf large marine ecosystem for a year exhibiting average (BT_{avg}), warmer ($BT_{avg} + 1^{\circ}C$), and cooler ($BT_{avg} - 1^{\circ}C$) bottom temperatures. Probabilities include < 0.5 (red), $0.5 - 0.6$ (orange), $0.6 - 0.7$ (yellow), $0.7 - 0.8$ (green), $0.8 - 0.9$ (light blue), and $0.9 - 1.0$ (dark blue). Note: only the abiotic sub-model was used for prediction due to uncertainty regarding how prey species would respond to temperature changes. MA = Middle Atlantic Bight, SNE = Southern New England, GB = Georges Bank, and GM = Gulf of Maine. Solid gray indicates land masses.

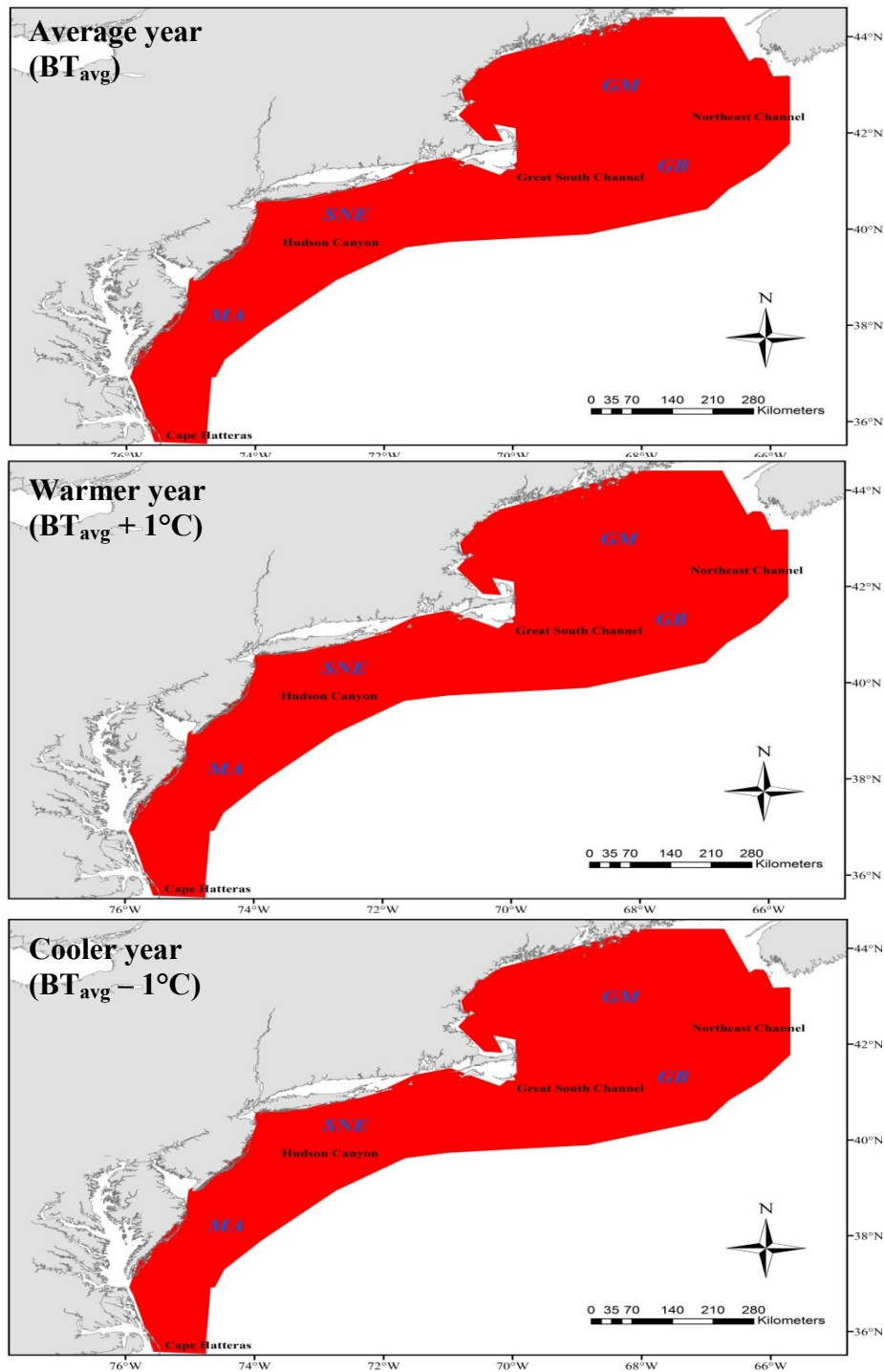


Figure 3H.5. Hypothetical predicted probability of neonate spiny dogfish occurrence during autumn in the Northeast (US) shelf large marine ecosystem for a year exhibiting average (BT_{avg}), warmer ($BT_{avg} + 1^{\circ}C$), and cooler ($BT_{avg} - 1^{\circ}C$) bottom temperatures. Probabilities include < 0.5 (red), $0.5 - 0.6$ (orange), $0.6 - 0.7$ (yellow), $0.7 - 0.8$ (green), $0.8 - 0.9$ (light blue), and $0.9 - 1.0$ (dark blue). Note: only the abiotic sub-model was used for prediction due to uncertainty regarding how prey species would respond to temperature changes. MA = Middle Atlantic Bight, SNE = Southern New England, GB = Georges Bank, and GM = Gulf of Maine. Solid gray indicates land masses.

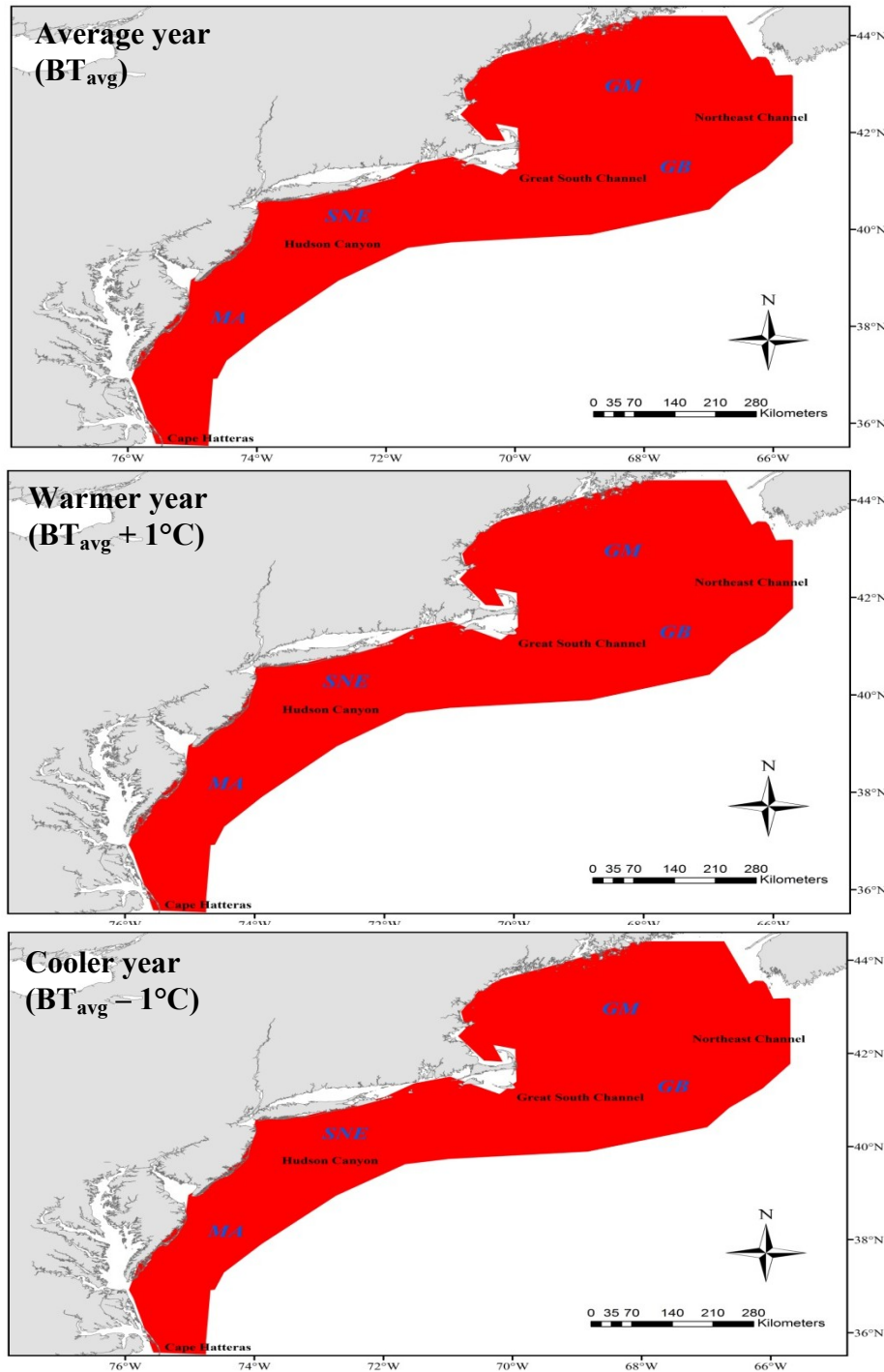


Figure 3H.6. Hypothetical predicted probability of mature male spiny dogfish occurrence during spring in the Northeast (US) shelf large marine ecosystem for a year exhibiting average (BT_{avg}), warmer ($BT_{avg} + 1^{\circ}C$), and cooler ($BT_{avg} - 1^{\circ}C$) bottom temperatures. Probabilities include < 0.5 (red), $0.5 - 0.6$ (orange), $0.6 - 0.7$ (yellow), $0.7 - 0.8$ (green), $0.8 - 0.9$ (light blue), and $0.9 - 1.0$ (dark blue). Note: only the abiotic sub-model was used for prediction due to uncertainty regarding how prey species would respond to temperature changes. MA = Middle Atlantic Bight, SNE = Southern New England, GB = Georges Bank, and GM = Gulf of Maine. Solid gray indicates land masses.

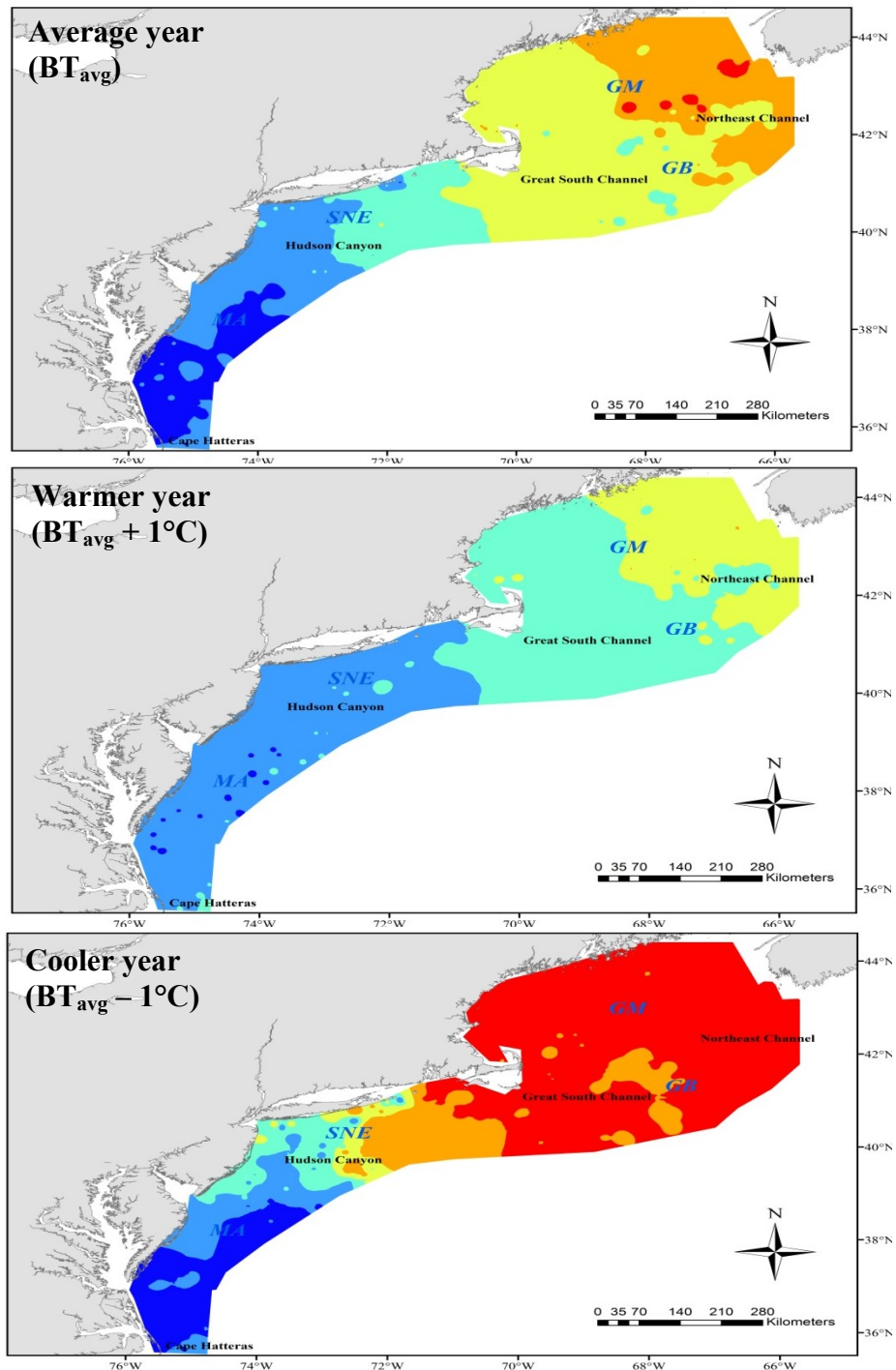


Figure 3H.7. Hypothetical predicted probability of immature female spiny dogfish occurrence during spring in the Northeast (US) shelf large marine ecosystem for a year exhibiting average (BT_{avg}), warmer ($BT_{avg} + 1^{\circ}C$), and cooler ($BT_{avg} - 1^{\circ}C$) bottom temperatures. Probabilities include < 0.5 (red), $0.5 - 0.6$ (orange), $0.6 - 0.7$ (yellow), $0.7 - 0.8$ (green), $0.8 - 0.9$ (light blue), and $0.9 - 1.0$ (dark blue). Note: only the abiotic sub-model was used for prediction due to uncertainty regarding how prey species would respond to temperature changes. MA = Middle Atlantic Bight, SNE = Southern New England, GB = Georges Bank, and GM = Gulf of Maine. Solid gray indicates land masses.

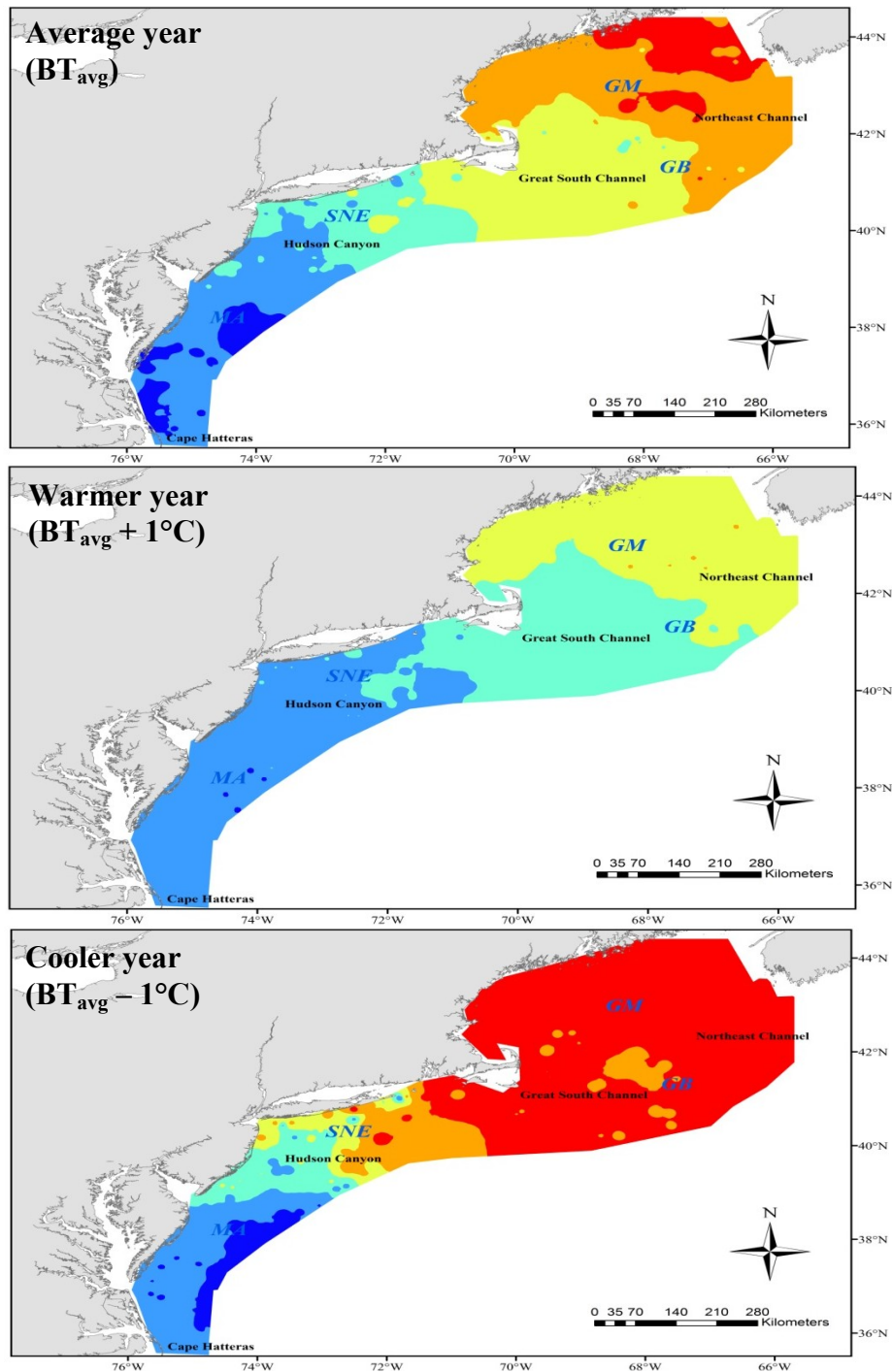
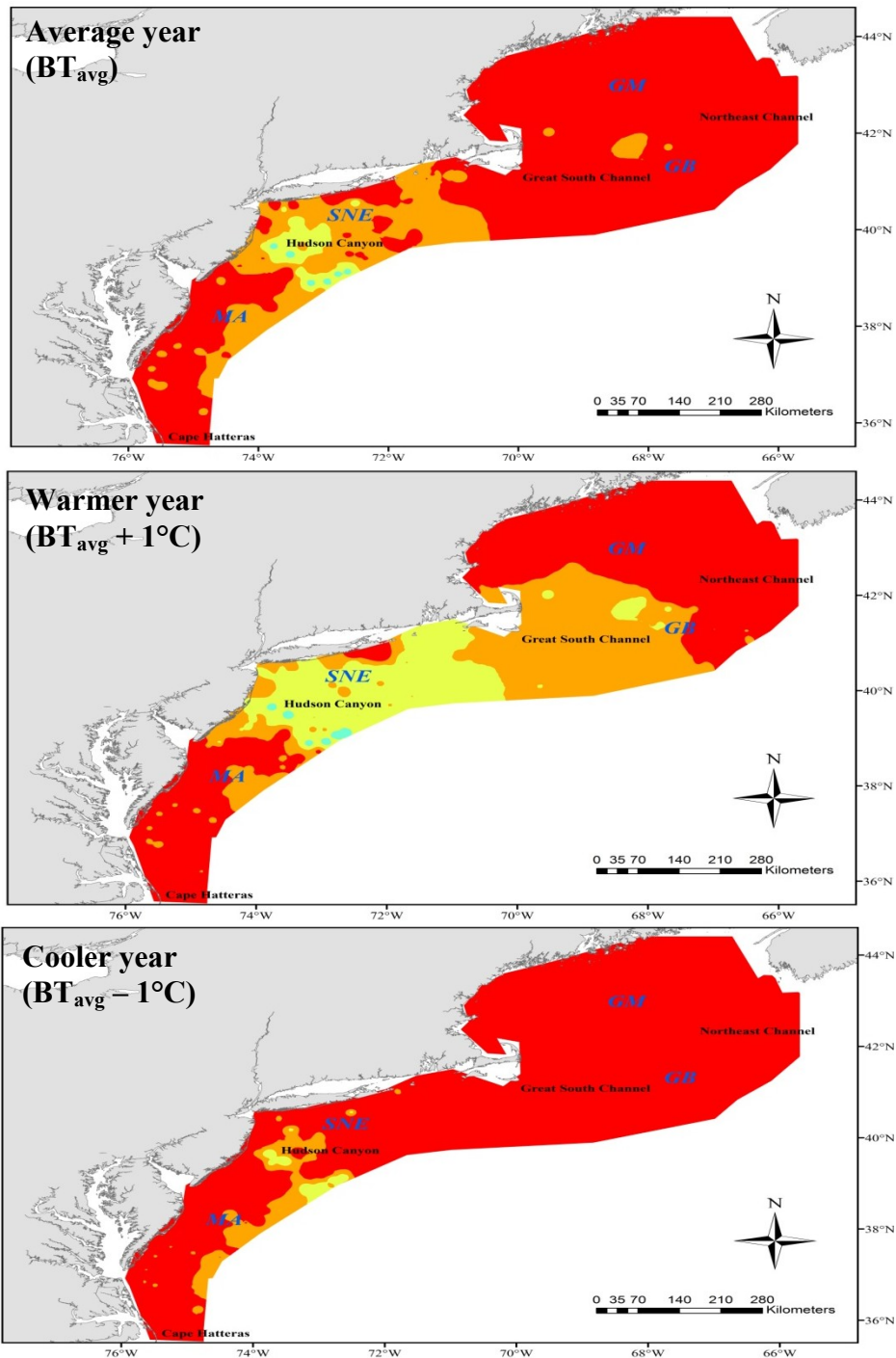


Figure 3H.8. Hypothetical predicted probability of immature male spiny dogfish occurrence during spring in the Northeast (US) shelf large marine ecosystem for a year exhibiting average (BT_{avg}), warmer ($BT_{avg} + 1^{\circ}C$), and cooler ($BT_{avg} - 1^{\circ}C$) bottom temperatures. Probabilities include < 0.5 (red), $0.5 - 0.6$ (orange), $0.6 - 0.7$ (yellow), $0.7 - 0.8$ (green), $0.8 - 0.9$ (light blue), and $0.9 - 1.0$ (dark blue). Note: only the abiotic sub-model was used for prediction due to uncertainty regarding how prey species would respond to temperature changes. MA = Middle Atlantic Bight, SNE = Southern New England, GB = Georges Bank, and GM = Gulf of Maine. Solid gray indicates land masses.



Appendix 4A. Factors Considered Influential on Survey Catchability

Table 4A.1. Summary of factors suggested to influence survey catchability of marine fishes throughout the literature.

Factor	References
vessel type	Fréon et al. 1993; Casey and Myers 1998; Benoît and Swain 2003; Salthaug and Aanes 2003
crew	Pennington and Godø 1995
gear type	Pennington and Godø 1995; Korsbrekke and Nakken 1999; Benoît and Swain 2003; Trenkel et al. 2004; Ward and Myers 2005; Fraser et al. 2007
time of year	Beamish 1965; Godø and Walsh 1992; Casey and Myers 1998; Aglen et al. 1999; Benoît and Swain 2003; Trenkel et al. 2004; Fraser et al. 2007
time of day	Casey and Myers 1998; Korsbrekke and Nakken 1999; Petrakis et al. 2001; Adlerstein and Ehrich 2002; Benoît and Swain 2003; Trenkel et al. 2004; Fraser et al. 2007
depth	Pitt 1967; Casey and Myers 1998; Petrakis et al. 2001
current speed	Michalsen et al. 1996
current direction	Michalsen et al. 1996; Aglen et al. 1999
bottom topography	Casey and Myers 1998
fish size	Engås and Soldal 1992; Francis and Williams 1995; Michalsen et al. 1996; Casey and Myers 1998; Somarakis et al. 1998; Korsbrekke and Nakken 1999; Petrakis et al. 2001; Rivoirard and Wieland 2001; Benoît and Swain 2003; Trenkel et al. 2004; Fraser et al. 2007
spatial structure of stock	Pennington and Godø 1995; Godø et al. 1999
endogenous rhythms	Fréon et al. 1993
environmental conditions	Francis and Williams 1995; Pennington and Godø 1995
temperature	Godø and Walsh 1992; Vance and Staples 1992; Aglen et al. 1999; Swain et al. 2000
light intensity	Walsh 1988; Michalsen et al. 1996; Casey and Myers 1998
tides	Michalsen et al. 1996
fish behavior	Godø and Walsh 1992; Francis and Williams 1995; Casey and Myers 1998; Somarakis et al. 1998; Aglen et al. 1999; Petrakis et al. 2001; Fraser et al. 2007
vertical fish distribution	Beamish 1965; Stoner 1991; Godø and Walsh 1992; Fréon et al. 1993; Pennington and Godø 1995; Casey and Myers 1998; Aglen et al. 1999; Petrakis et al. 2001; Benoît and Swain 2003

horizontal fish distribution	Stoner 1991; Benoît and Swain 2003
herding	Francis and Williams 1995; Michalsen et al. 1996; Aglen et al. 1999; Korsbrekke and Nakken 1999; Benoît and Swain 2003; Fraser et al. 2007
hiding	Benoît and Swain 2003
learning	Fréon et al. 1993
density-dependence	Fréon et al. 1993; Somarakis et al. 1998; Aglen et al. 1999; Godø et al. 1999; Korsbrekke and Nakken 1999; Swain et al. 2000; Francis et al. 2003; Trenkel et al. 2004; Gauthier and Rose 2005; Ellis and Wang 2007

Appendix 4B. Tow Classification of NEFSC Survey Stations

Table 4B.1. Classification of NEFSC bottom trawl tows used in *CPUE* analyses for spiny dogfish and prey species based on time of day (N = night [zenith $\geq 108^\circ$], D = day [zenith $< 108^\circ$]) and depth (SH = shallow [depth < 75 m], DE = deep [depth ≥ 75 m]) during spring (1968 – 2009) and autumn (1963 – 2009) in the Northeast (US) shelf large marine ecosystem.

Year	SPRING				AUTUMN				Year	SPRING				AUTUMN			
	N	D	SH	DE	N	D	SH	DE		N	D	SH	DE	N	D	SH	DE
1963	-	-	-	-	92	91	46	137	1987	117	217	167	167	123	193	182	134
1964	-	-	-	-	82	102	55	129	1988	105	209	186	128	122	185	169	138
1965	-	-	-	-	82	110	51	141	1989	106	185	163	128	129	192	192	129
1966	-	-	-	-	88	102	50	140	1990	114	197	180	131	130	202	194	138
1967	-	-	-	-	122	150	99	173	1991	125	199	183	141	128	200	196	132
1968	92	171	90	173	118	157	105	170	1992	111	196	189	118	132	192	201	123
1969	97	170	95	172	123	142	94	171	1993	108	211	194	125	113	212	188	137
1970	105	183	90	198	129	172	106	195	1994	117	209	189	137	135	196	200	131
1971	101	210	101	210	131	179	112	198	1995	124	201	191	134	127	199	184	142
1972	93	213	97	209	283	361	397	247	1996	112	223	202	133	120	200	188	132
1973	136	355	299	192	190	253	254	189	1997	117	210	187	140	120	207	198	129
1974	122	284	232	174	165	214	175	204	1998	135	225	202	158	133	199	187	145
1975	85	184	128	141	175	231	197	209	1999	112	210	191	131	142	196	195	143
1976	128	256	185	199	141	199	179	161	2000	104	220	192	132	114	215	198	131
1977	105	250	172	183	180	239	199	220	2001	105	212	174	143	121	209	203	127
1978	117	280	184	213	237	319	286	270	2002	114	203	184	133	120	201	192	129
1979	146	331	253	224	266	322	304	284	2003	112	209	194	127	128	194	190	132
1980	151	317	277	191	180	240	249	171	2004	116	210	196	130	120	191	188	123
1981	124	271	233	162	164	252	234	182	2005	121	208	189	140	129	193	195	127
1982	141	279	233	187	170	241	241	170	2006	124	215	191	148	141	216	208	149
1983	141	260	235	166	156	251	237	170	2007	123	232	199	156	138	204	197	145
1984	134	257	221	170	130	207	177	160	2008	103	232	196	139	130	211	198	143
1985	140	231	214	157	142	198	182	158	2009	119	254	186	187	136	198	177	157
1986	126	235	203	158	138	214	180	172									

Appendix 4C. Spiny Dogfish and Prey Species Aggregations

Table 4C.1. Night (N) and day (D) distributions of spiny dogfish life-history stages and prey species aggregations during spring (1968 – 2009) and autumn (1963 – 2009) in the Northeast (US) shelf large marine ecosystem. Stages and species as defined in Table 4.1.

Aggregations defined by the 95th percentile of catch distribution (C_{95th}). TS = Kolmogorov-Smirnov (KS) test statistic, p = probability, C = mean catch for specified period (N or D) for Mann-Whitney U (MWU) test. Significance (bolded) based on an adjusted α of 0.0045 ($\alpha = 0.05$ corrected for 11 comparisons between stages/species). Note: spiny dogfish not sexed consistently until 1980.

Stage/ Species	C_{95th}	Number of Aggregations		KS		MWU		
		N	D	TS	p	C_N	C_D	p
<u>SPRING</u>								
All	366	96	272	0.17	0.0289	843.58	1220.57	0.0120
Neo	54	10	32	0.20	0.9207	123.50	140.59	0.7788
ImmM	140	23	68	0.22	0.3590	424.22	645.76	0.4163
MatM	336	29	138	0.13	0.7984	668.00	906.93	0.8376
ImmF	140	51	151	0.13	0.5636	405.75	504.90	0.8365
MatF	78	60	136	0.14	0.3487	215.18	281.35	0.7585
BF	651	37	95	0.18	0.3460	3324.22	2794.88	0.7040
HER	263	70	213	0.18	0.0763	690.19	813.47	0.0920
ILL	57	0	60	-	-	-	-	-
LOL	1494	24	176	0.14	0.8143	2967.25	3148.55	0.9700
MAC	420	18	101	0.24	0.3193	1449.11	1170.82	0.1142
<u>AUTUMN</u>								
All	353	86	200	0.19	0.0247	857.76	1132.62	0.0361
Neo	11	2	8	0.75	0.3291	26.00	19.75	0.2357
ImmM	102	20	58	0.14	0.9398	281.30	472.66	0.9044
MatM	256	37	96	0.21	0.2042	638.43	799.30	0.0457
ImmF	161	39	111	0.14	0.6426	491.28	552.34	0.6012
MatF	110	35	55	0.13	0.8471	365.91	414.09	0.8199
BF	1292	35	372	0.16	0.3772	2798.97	4094.01	0.1946
HER	311	36	93	0.30	0.0214	772.67	1815.47	0.0091
ILL	92	56	270	0.27	0.0022	210.11	357.87	0.0015
LOL	1825	19	441	0.31	0.0545	2832.11	3846.08	0.0102
MAC	86	1	56	-	-	-	-	-

Appendix 4D. Diel- and Depth-dependent Catch Rates of Spiny Dogfish and Prey Species

Figure 4D.1. Annual mean catch rates and ratios for all spiny dogfish combined in the Northeast (US) shelf large marine ecosystem during spring (1968 – 2009) (left panel) and autumn (1963 – 2009) (right panel). Top row displays day (gray line) and night (black line) catch rates and N/D ratios (dotted). Bottom row displays shallow (gray line) and deep (black line) catch rates and SH/DE ratios (dotted). Notes: spiny dogfish not sexed consistently until 1980 and both y-axes differ between panels.

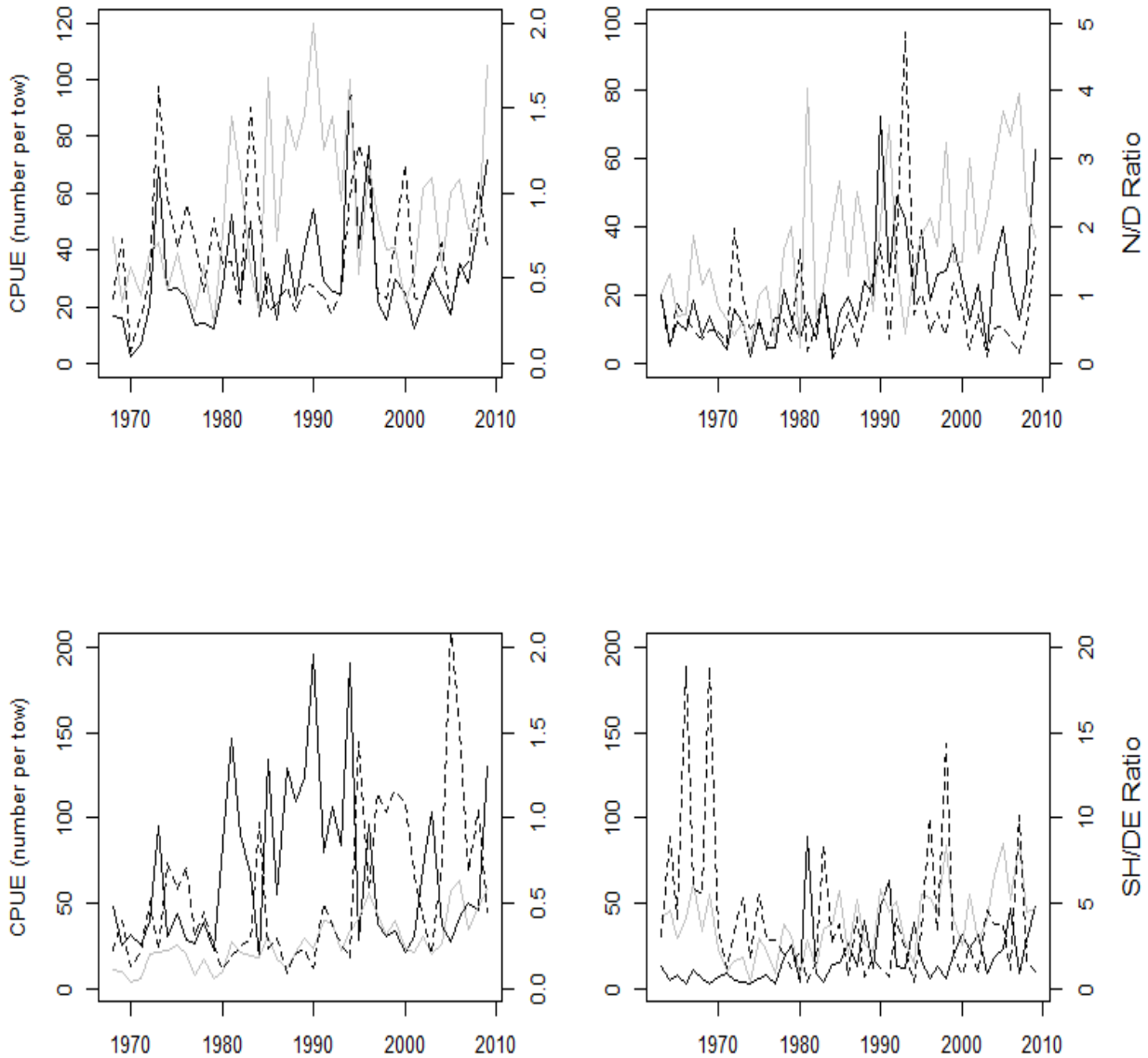


Figure 4D.2. Annual mean catch rates and ratios for neonate ($TL \leq 26$ cm) spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring (1968 – 2009) (left panel) and autumn (1963 – 2009) (right panel). Top row displays day (gray line) and night (black line) catch rates and N/D ratios (dotted). Bottom row displays shallow (gray line) and deep (black line) catch rates and SH/DE ratios (dotted). Notes: spiny dogfish not sexed consistently until 1980 and both y-axes differ between panels.

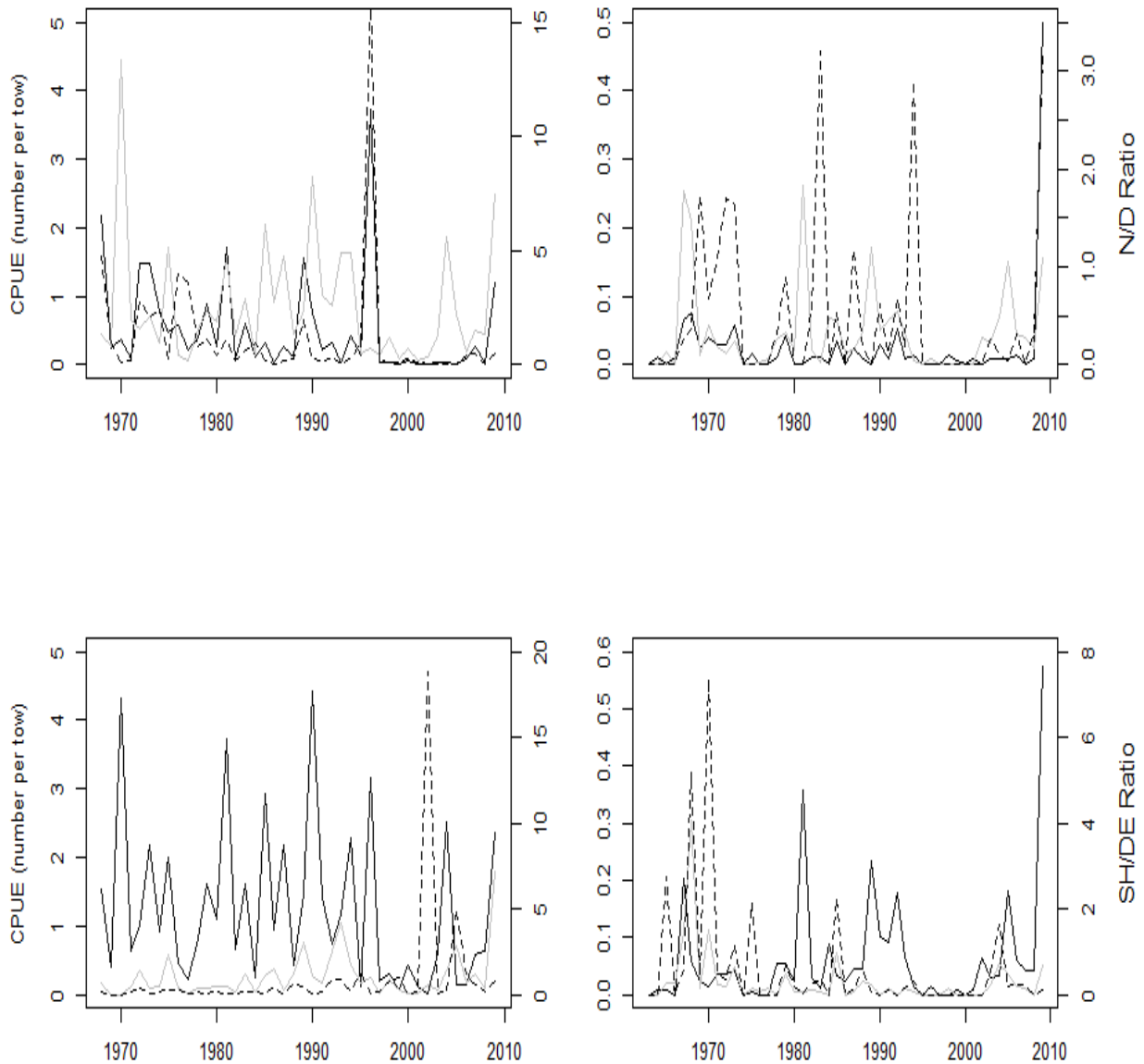


Figure 4D.3. Annual mean catch rates and ratios for immature male ($26 < TL < 60$ cm) spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring (1968 – 2009) (left panel) and autumn (1963 – 2009) (right panel). Top row displays day (gray line) and night (black line) catch rates and N/D ratios (dotted). Bottom row displays shallow (gray line) and deep (black line) catch rates and SH/DE ratios (dotted). Notes: spiny dogfish not sexed consistently until 1980 and both y-axes differ between panels.

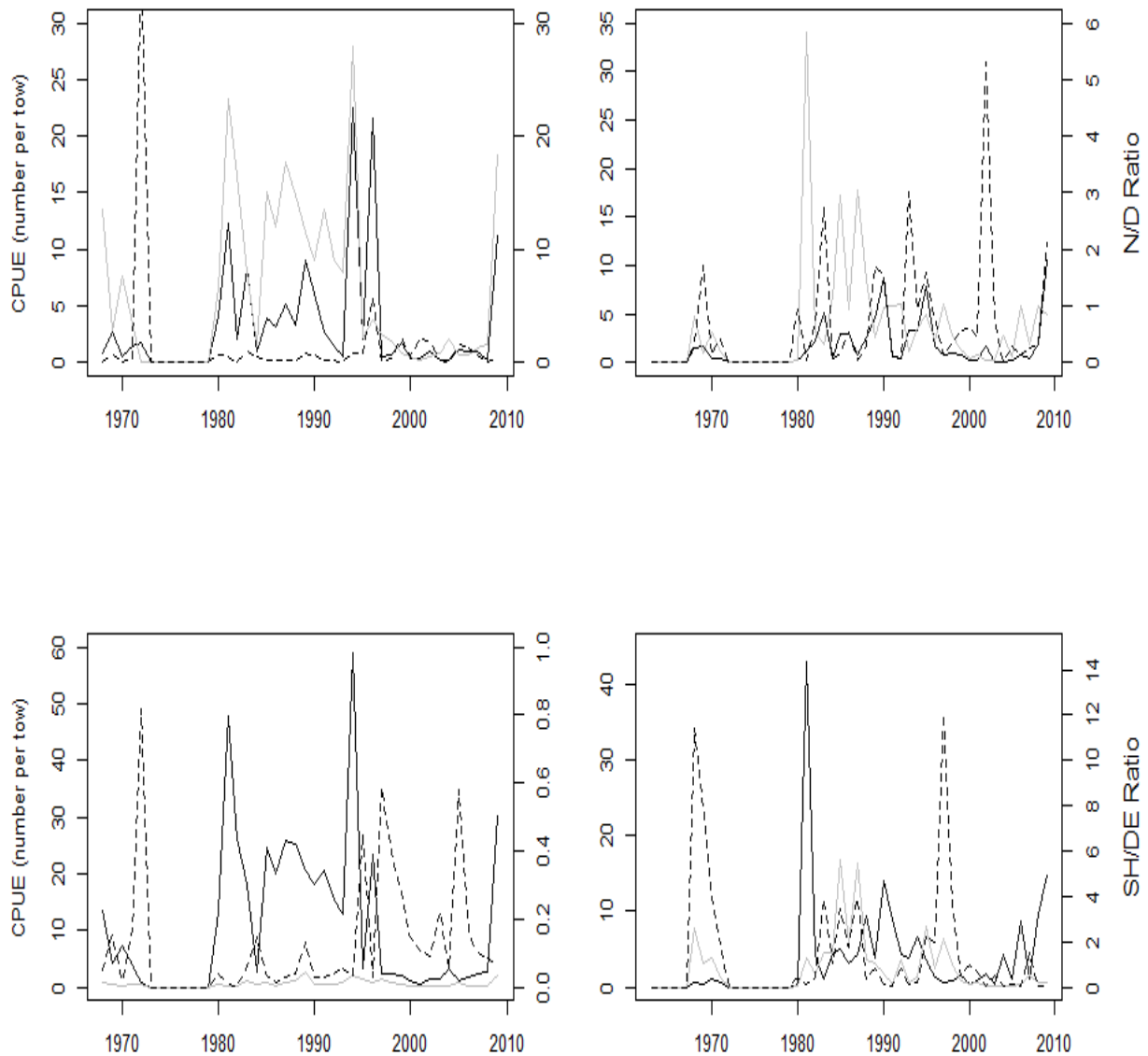


Figure 4D.4. Annual mean catch rates and ratios for mature male (TL \geq 60 cm) spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring (1968 – 2009) (left panel) and autumn (1963 – 2009) (right panel). Top row displays day (gray line) and night (black line) catch rates and N/D ratios (dotted). Bottom row displays shallow (gray line) and deep (black line) catch rates and SH/DE ratios (dotted). Notes: spiny dogfish not sexed consistently until 1980 and both y-axes differ between panels.

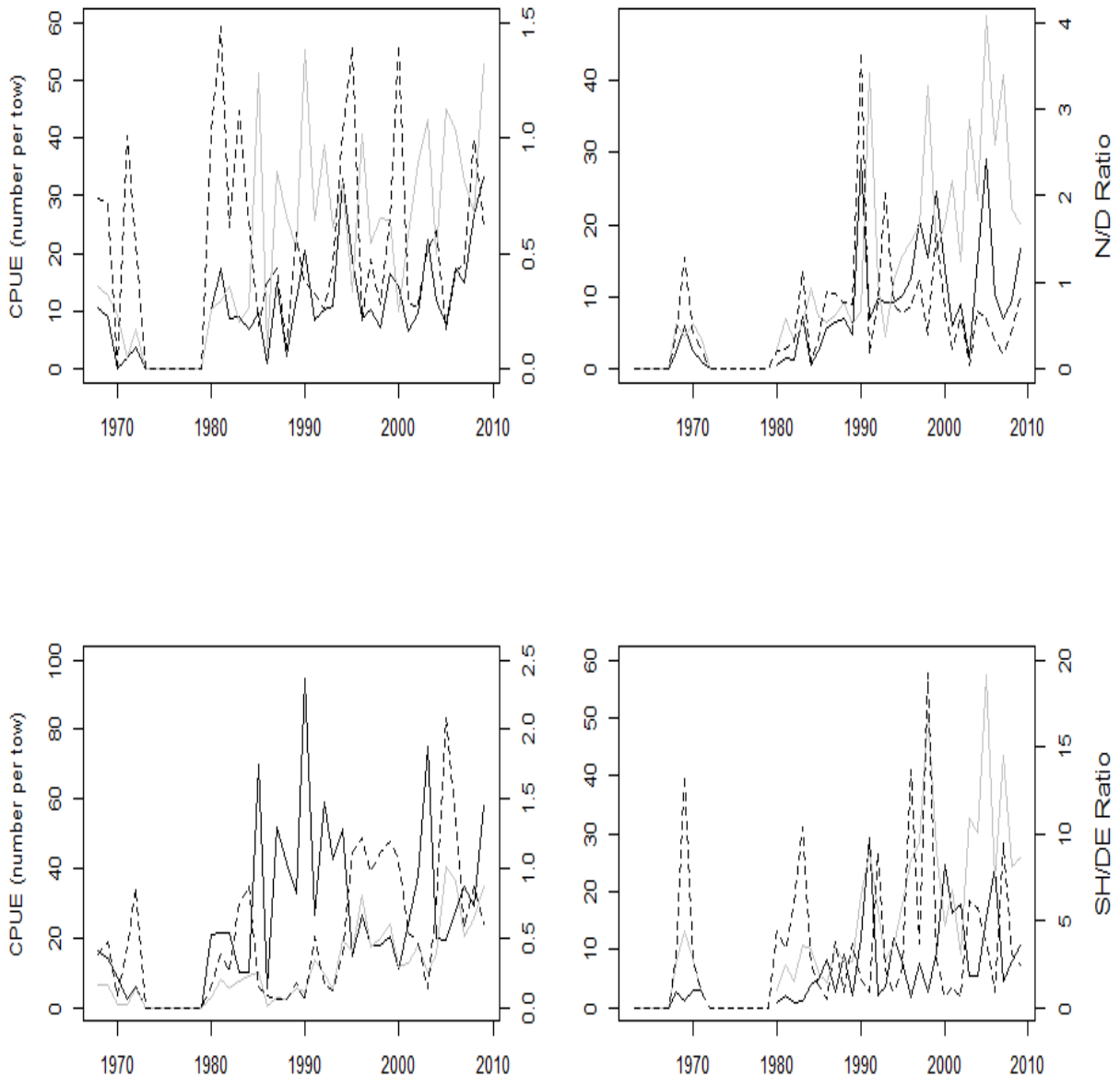


Figure 4D.5. Annual mean catch rates and ratios for immature female ($26 < TL < 80$) spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring (1968 – 2009) (left panel) and autumn (1963 – 2009) (right panel). Top row displays day (gray line) and night (black line) catch rates and N/D ratios (dotted). Bottom row displays shallow (gray line) and deep (black line) catch rates and SH/DE ratios (dotted). Notes: spiny dogfish not sexed consistently until 1980 and both y-axes differ between panels.

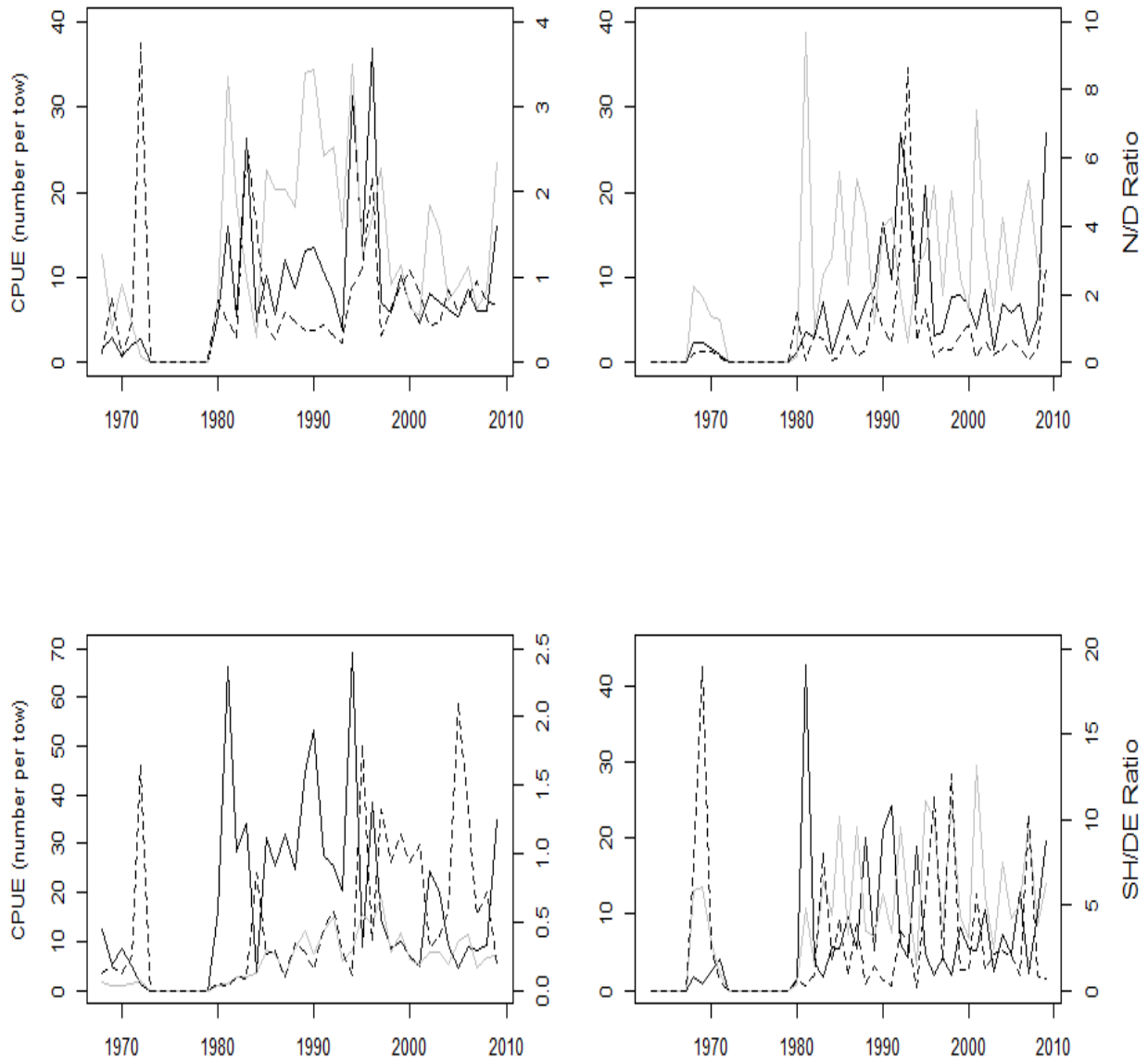


Figure 4D.6. Annual mean catch rates and ratios for mature female (TL \geq 80 cm) spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring (1968 – 2009) (left panel) and autumn (1963 – 2009) (right panel). Top row displays day (gray line) and night (black line) catch rates and N/D ratios (dotted). Bottom row displays shallow (gray line) and deep (black line) catch rates and SH/DE ratios (dotted). Notes: spiny dogfish not sexed consistently until 1980 and both y-axes differ between panels.

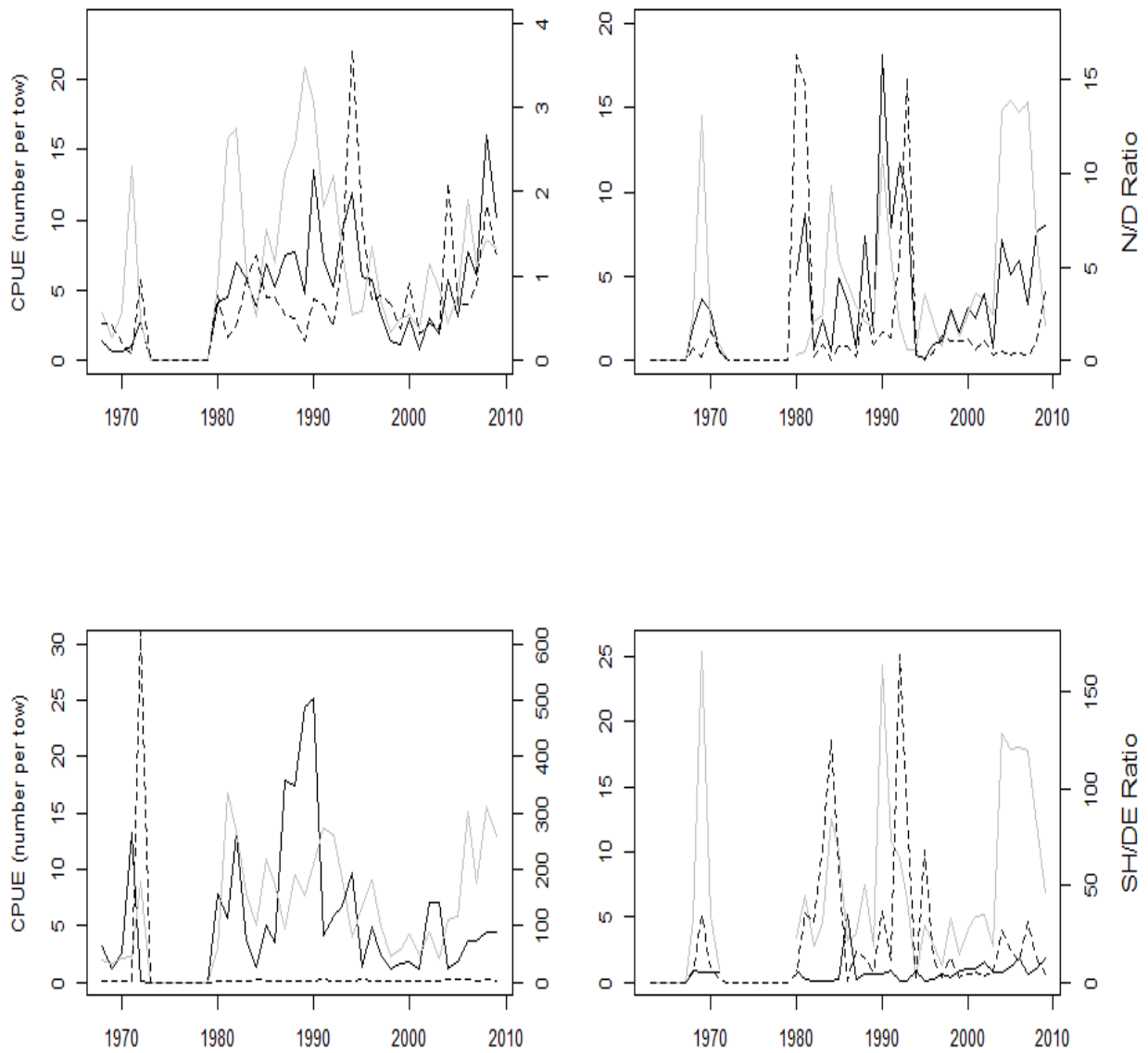


Figure 4D.7. Annual mean catch rates and ratios for butterfish in the Northeast (US) shelf large marine ecosystem during spring (1968 – 2009) (left panel) and autumn (1963 – 2009) (right panel). Top row displays day (gray line) and night (black line) catch rates and N/D ratios (dotted). Bottom row displays shallow (gray line) and deep (black line) catch rates and SH/DE ratios (dotted). Note: both y-axes differ in scales.

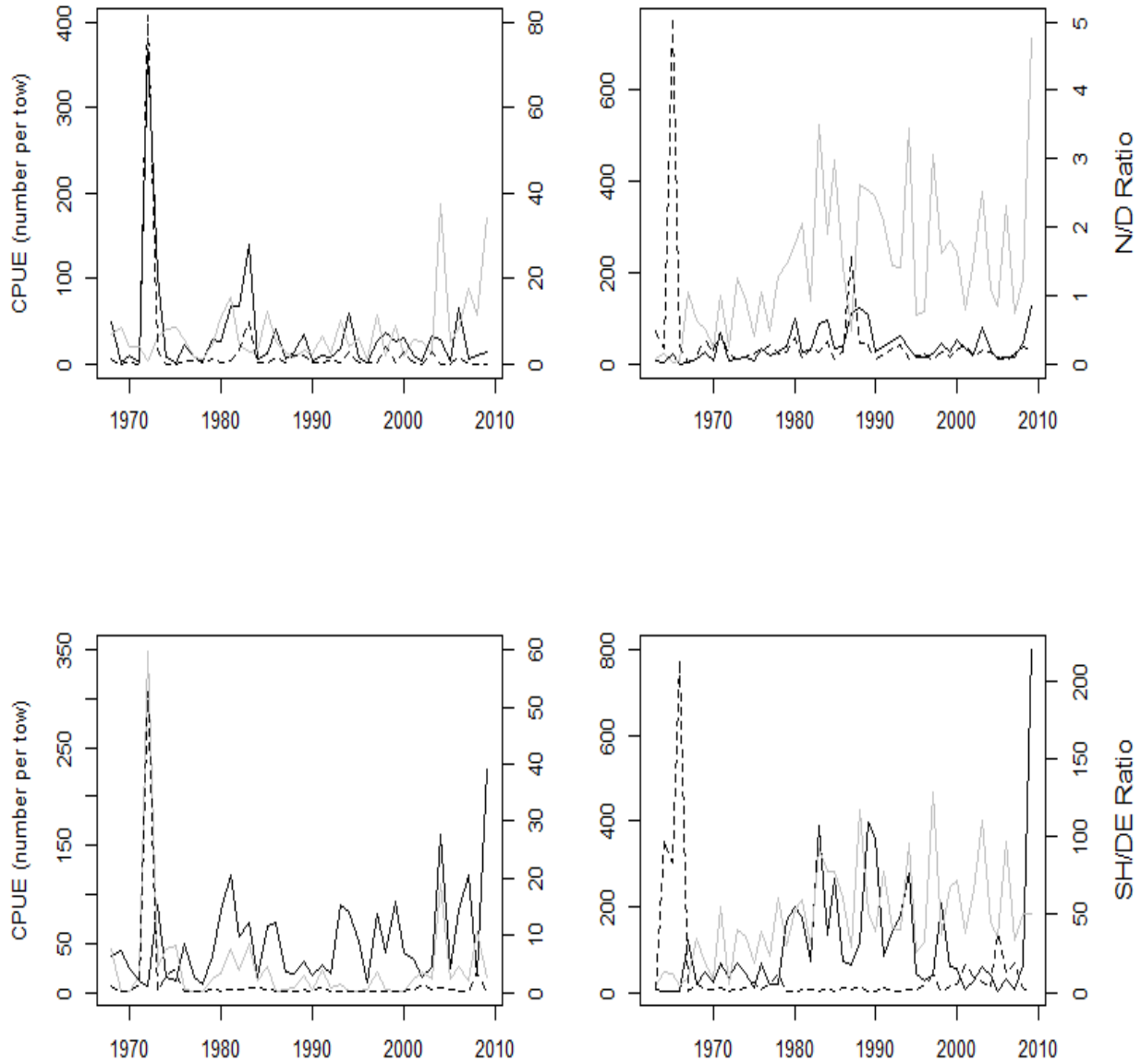


Figure 4D.8. Annual mean catch rates and ratios for Atlantic herring in the Northeast (US) shelf large marine ecosystem during spring (1968 – 2009) (left panel) and autumn (1963 – 2009) (right panel). Top row displays day (gray line) and night (black line) catch rates and N/D ratios (dotted). Bottom row displays shallow (gray line) and deep (black line) catch rates and SH/DE ratios (dotted). Note: both y-axes differ in scales.

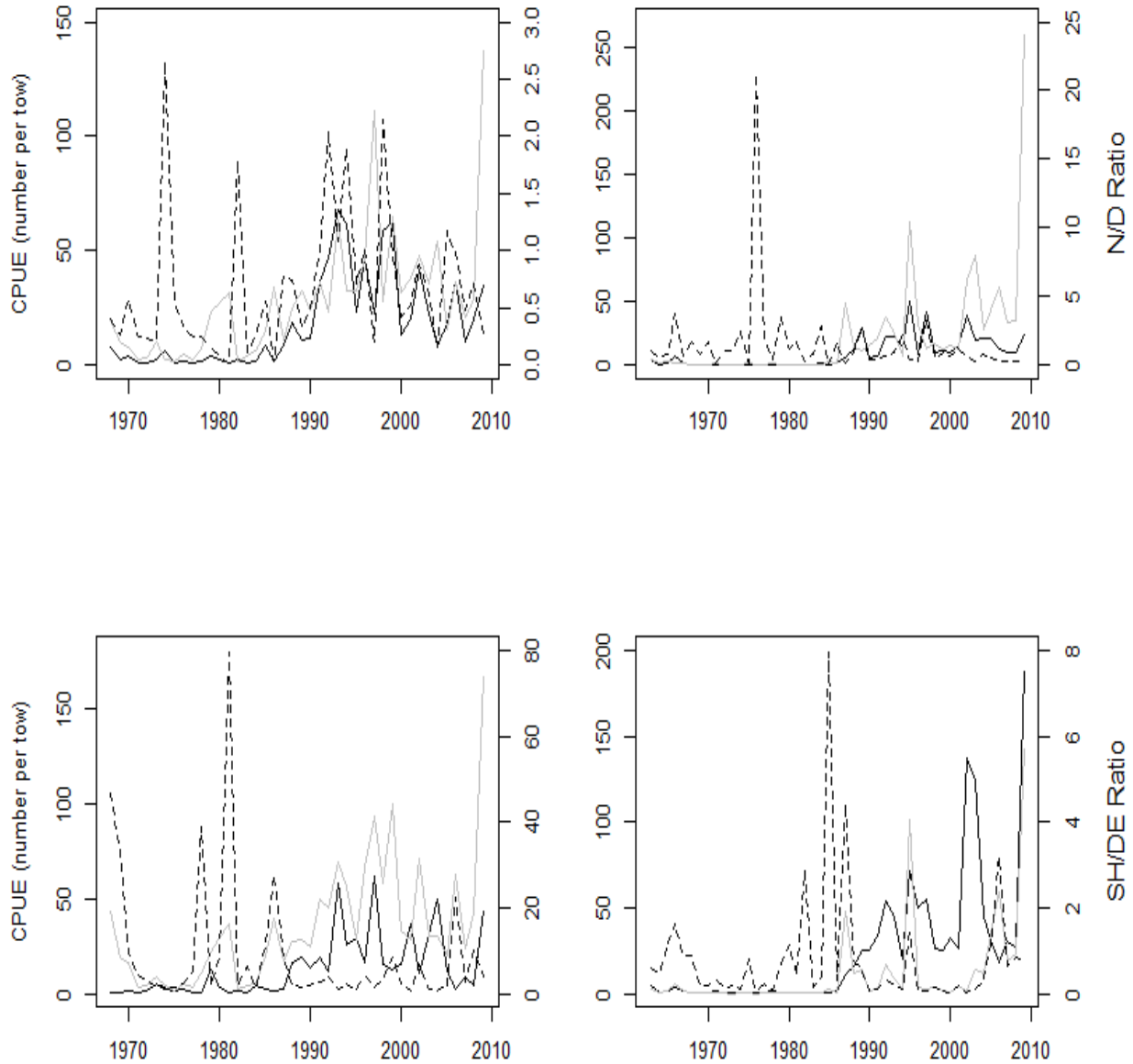


Figure 4D.9. Annual mean catch rates and ratios for *Illex* sp. in the Northeast (US) shelf large marine ecosystem during spring (1968 – 2009) (left panel) and autumn (1963 – 2009) (right panel). Top row displays day (gray line) and night (black line) catch rates and N/D ratios (dotted). Bottom row displays shallow (gray line) and deep (black line) catch rates and SH/DE ratios (dotted). Note: both y-axes differ in scales.

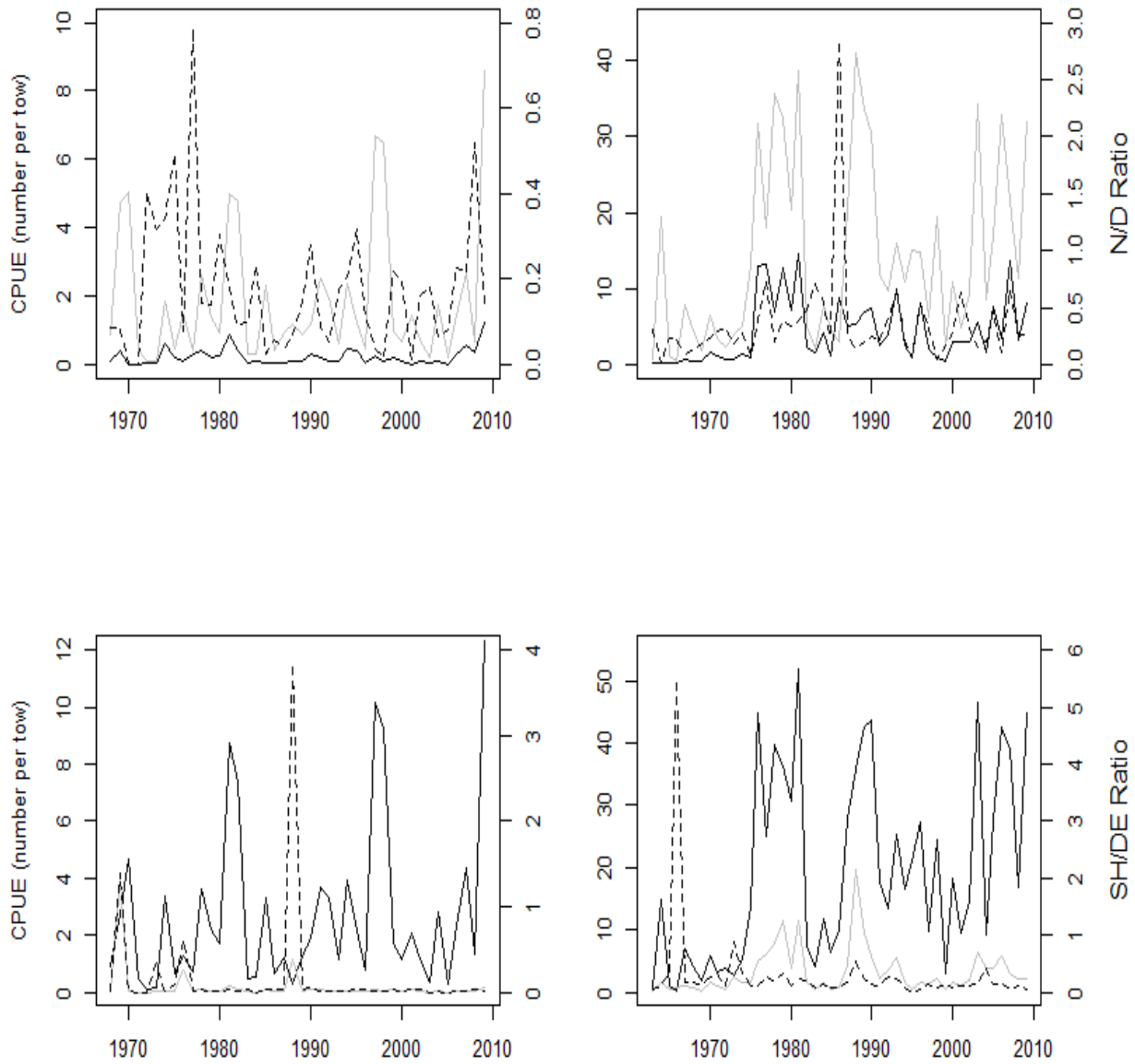


Figure 4D.10. Annual mean catch rates and ratios for *Loligo* sp. in the Northeast (US) shelf large marine ecosystem during spring (1968 – 2009) (left panel) and autumn (1963 – 2009) (right panel). Top row displays day (gray line) and night (black line) catch rates and N/D ratios (dotted). Bottom row displays shallow (gray line) and deep (black line) catch rates and SH/DE ratios (dotted). Note: both y-axes differ in scales.

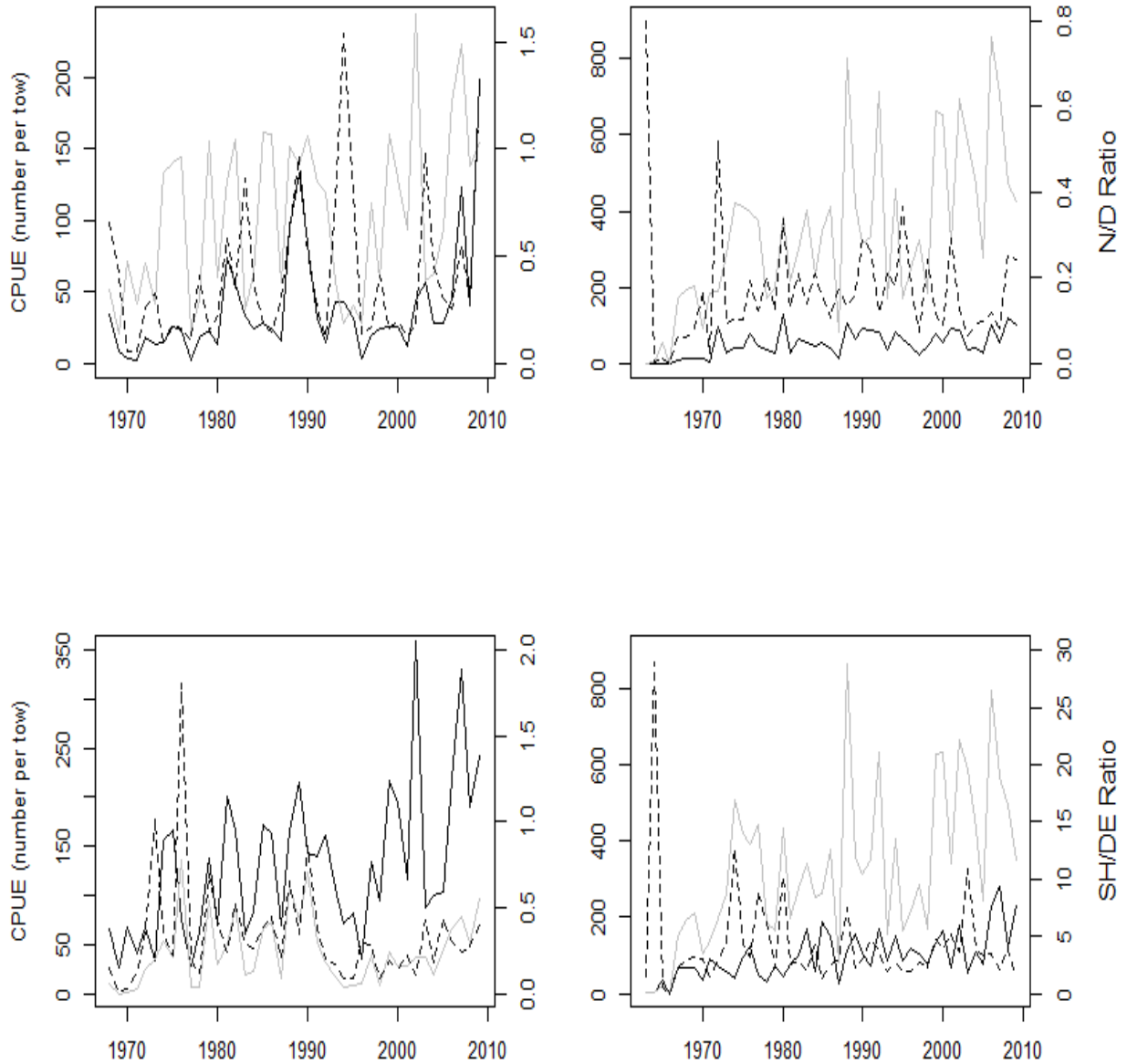
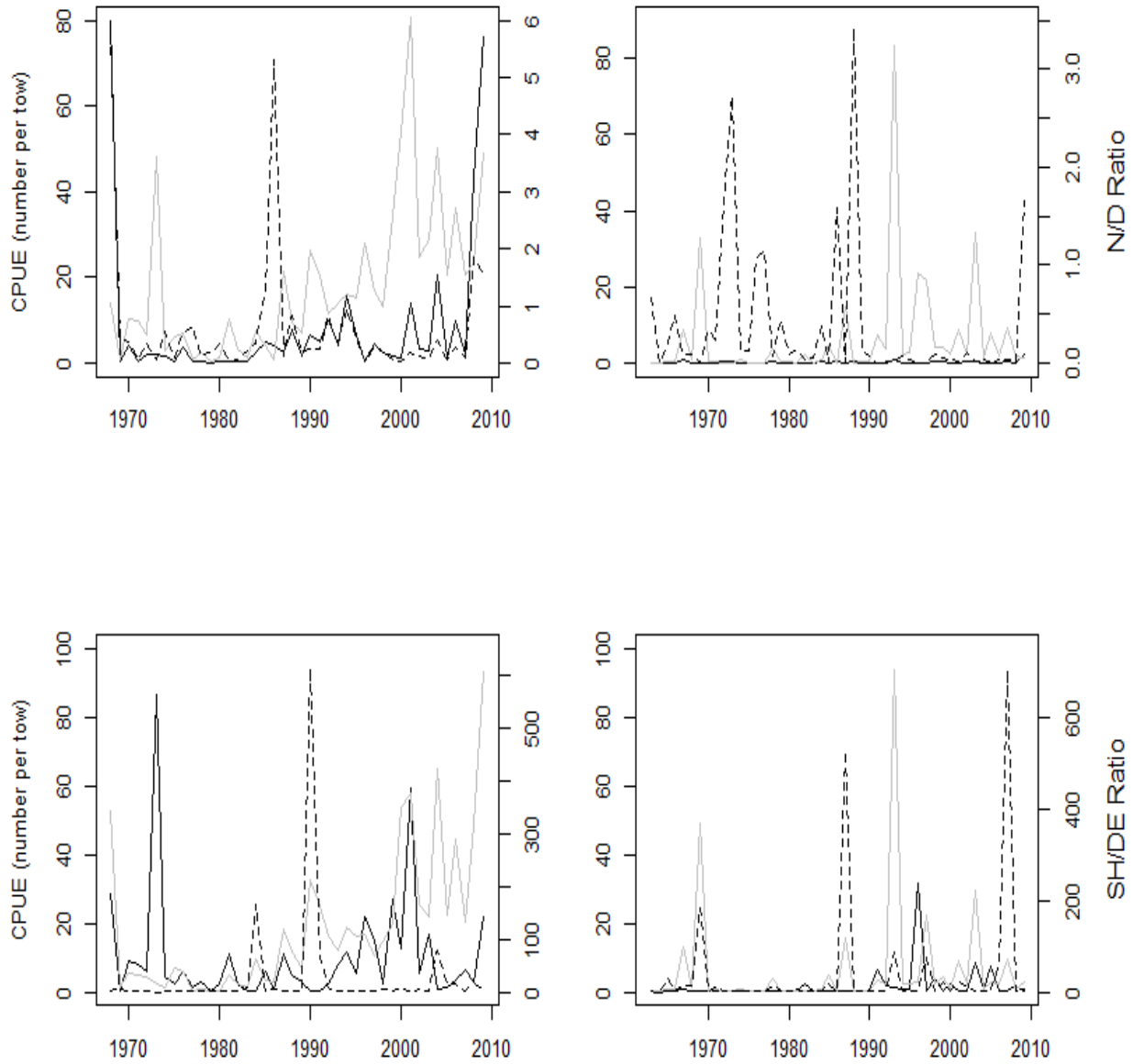


Figure 4D.11. Annual mean catch rates and ratios for Atlantic mackerel in the Northeast (US) shelf large marine ecosystem during spring (1968 – 2009) (left panel) and autumn (1963 – 2009) (right panel). Top row displays day (gray line) and night (black line) catch rates and N/D ratios (dotted). Bottom row displays shallow (gray line) and deep (black line) catch rates and SH/DE ratios (dotted). Note: both y-axes differ in scales.



Appendix 4E. Diel Habitat Preference for Spiny Dogfish and Prey Species

Methods. Habitat preference during both day and night was estimated for all spiny dogfish stages and prey species following the nonparametric method described in Perry and Smith (1994). Thereafter, habitat preferences were compared within each spiny dogfish stage and prey species to test whether they occupied statistically different habitat during day and night. The null hypothesis of no difference in habitat distribution (i.e., due to chance alone) was tested for each spiny dogfish stage and prey species by randomizing and comparing the CDFs occupied during day and night. The strength of association was determined using a Kolmogorov-Smirnov type test statistic (*TS*) for the maximum difference between CDFs. This *TS* was compared to a pseudo-population of 10,000 randomized test statistics (*PPTS*) obtained by randomization with significance estimated as $p = \frac{\# PPTS > TS}{Total PPTS}$.

Results. Day (Table 4E.1; Figures 4E.1-4) and night (Table 4E.2; Figures 4E.1-4) habitat preference revealed very few significant differences between time periods for any species (Table 4E.3, Figures 4E.5-10). Significantly ($p < 0.05$) colder waters were inhabited during the day by herring during spring (Figure 4E.8) and by mature male spiny dogfish (Figure 4E.5) and *Loligo* sp. (Figure 4E.8) during autumn. During autumn, significantly ($p < 0.05$) deeper day-time depths were preferred by both neonates (Figure 4E.7) and *Loligo* sp. (Figure 4E.10). *Loligo* sp. also occupied more saline environments during autumn (Fig 4E.9).

Table 4E.1. Day-time habitat associations for spiny dogfish life-history stages and prey species in the Northeast (US) shelf large marine ecosystem for bottom temperature (BT), bottom salinity (BS), and depth during spring (1968 – 2009) and autumn (1963 – 2009). Habitat percentiles (5th, 50th [median], 95th), *D* = range of absolute vertical distances between distributions, *TS* = test statistic, and *p* = probability. Significance (bolded) based on an *a priori* $\alpha = 0.05$. Stages and species as defined in Table 4.1. Note: spiny dogfish not sexed consistently until 1980.

Variable	Stage/ Species	5 th	50 th	95 th	SPRING			-	AUTUMN			<i>TS</i>	<i>p</i>
					<i>D</i>	<i>TS</i>	<i>p</i>		5 th	50 th	95 th		
BT (°C)	Survey	3.6	6.0	11.1	-	-	-	5.9	10.3	20.3	-	-	-
	Neo	4.9	8.9	12.3	0.04 - 0.36	0.4465	0.0000	7.3	10.9	13.7	0.05 - 0.48	0.2005	0.2983
	ImmM	5.1	10.0	13.3	0.05 - 0.34	0.5930	0.0000	7.8	10.9	14.4	0.05 - 0.55	0.2818	0.1745
	MatM	5.3	8.2	11.8	0.03 - 0.38	0.4259	0.0000	6.9	10.4	14.8	0.04 - 0.28	0.1426	0.0949
	ImmF	5.0	8.5	12.9	0.03 - 0.28	0.4291	0.0000	7.4	11.1	15.8	0.03 - 0.33	0.2304	0.0102
	MatF	5.0	7.6	11.3	0.03 - 0.33	0.3634	0.0000	7.5	13.1	15.5	0.05 - 0.33	0.3113	0.0006
	BF	7.2	10.1	13.2	0.04 - 0.42	0.6875	0.0000	8.2	13.2	21.7	0.02 - 0.18	0.3794	0.0000
	HER	2.5	5.1	7.9	0.02 - 0.23	0.2409	0.0000	5.3	8.0	11.3	0.05 - 0.43	0.3936	0.0003
	ILL	5.6	11.9	14.0	0.04 - 0.44	0.6562	0.0000	5.7	11.1	14.3	0.03 - 0.18	0.1616	0.0011
	LOL	7.7	11.2	13.7	0.02 - 0.17	0.7356	0.0000	9.0	13.4	20.5	0.01 - 0.09	0.3739	0.0000
MAC	4.8	6.6	13.6	0.04 - 0.50	0.1955	0.0483	7.2	10.8	15.4	0.07 - 0.71	0.1966	0.7985	
BS	Survey	31.8	33.2	35.0	-	-	-	31.4	33.1	35.3	-	-	-
	Neo	32.6	34.2	35.4	0.06 - 0.54	0.3488	0.0621	31.6	33.9	35.6	0.07 - 0.70	0.3321	0.1837
	ImmM	32.6	34.5	35.6	0.07 - 0.54	0.4711	0.0018	32.0	33.2	35.1	0.06 - 0.70	0.2120	0.5782
	MatM	32.3	34.0	35.2	0.04 - 0.39	0.3642	0.0004	31.6	32.4	34.2	0.05 - 0.40	0.2792	0.0231
	ImmF	32.1	34.0	35.5	0.04 - 0.40	0.3173	0.0014	31.6	32.5	35.0	0.04 - 0.54	0.2496	0.1231
	MatF	31.9	33.8	35.0	0.04 - 0.39	0.2740	0.0172	31.5	32.4	33.6	0.06 - 0.50	0.4337	0.0034
	BF	33.2	34.7	35.7	0.05 - 0.49	0.4798	0.0001	31.0	32.6	35.7	0.03 - 0.30	0.1934	0.0351
	HER	31.3	32.8	33.9	0.04 - 0.32	0.2742	0.0002	31.8	32.9	34.2	0.07 - 0.64	0.2159	0.5765
	ILL	33.6	35.3	35.7	0.06 - 0.50	0.7577	0.0000	32.4	34.9	35.7	0.03 - 0.30	0.4329	0.0000
	LOL	33.6	35.0	35.7	0.03 - 0.27	0.6449	0.0000	31.6	32.8	35.4	0.02 - 0.15	0.1603	0.0000

	MAC	32.6	33.3	34.3	0.05 - 0.53	0.1732	0.3880	31.9	33.2	34.2	0.09 - 0.86	0.2622	0.7336
Depth (m)	Survey	20.4	81.0	237.1	-	-	-	20.0	77.4	230.9	-	-	-
	Neo	55.1	85.7	189.2	0.04 - 0.40	0.2859	0.0043	45.0	95.3	164.4	0.05 - 0.46	0.2974	0.0284
	ImmM	63.7	132.0	251.3	0.05 - 0.35	0.3652	0.0000	44.0	95.2	207.6	0.05 - 0.51	0.2308	0.2970
	MatM	40.2	78.2	234.8	0.03 - 0.30	0.1608	0.0122	22.9	64.5	206.9	0.03 - 0.25	0.1292	0.1195
	ImmF	29.6	93.9	239.2	0.03 - 0.24	0.0839	0.4431	26.3	69.1	202.0	0.04 - 0.33	0.1287	0.2766
	MatF	26.6	59.2	205.0	0.03 - 0.31	0.2706	0.0002	19.2	41.7	131.9	0.05 - 0.35	0.4111	0.0000
	BF	32.2	91.3	151.1	0.04 - 0.37	0.2537	0.0037	15.1	60.1	123.1	0.02 - 0.18	0.2833	0.0000
	HER	20.9	57.1	116.8	0.02 - 0.19	0.3479	0.0000	40.8	94.8	197.3	0.05 - 0.40	0.2433	0.0757
	ILL	70.4	138.3	246.7	0.04 - 0.31	0.4102	0.0000	50.3	111.0	219.6	0.02 - 0.19	0.2832	0.0000
	LOL	35.2	92.2	157.3	0.02 - 0.16	0.2321	0.0000	21.3	45.8	120.0	0.01 - 0.08	0.3076	0.0000
MAC	28.6	56.3	159.8	0.03 - 0.30	0.3218	0.0000	24.6	56.3	102.1	0.08 - 0.64	0.3528	0.2150	

Table 4E.2. Night-time habitat associations for spiny dogfish life-history stages and prey species in the Northeast (US) shelf large marine ecosystem for bottom temperature (BT), bottom salinity (BS), and depth during spring (1968 – 2009) and autumn (1963 – 2009). Habitat percentiles (5th, 50th [median], 95th), *D* = range of absolute vertical distances between distributions, *TS* = test statistic, and *p* = probability. Significance (bolded) based on an *a priori* $\alpha = 0.05$. Stages and species as defined in Table 4.1. Note: spiny dogfish not sexed consistently until 1980.

Variable	Stage/ Species	5 th	50 th	95 th	SPRING			-	AUTUMN			<i>TS</i>	<i>p</i>
					<i>D</i>	<i>TS</i>	<i>p</i>		5 th	50 th	95 th		
BT (°C)	Survey	3.4	5.9	11.2	-	-	-	5.9	10.0	19.7	-	-	-
	Neo	6.1	9.0	14.3	0.06 - 0.67	0.6301	0.0001	7.2	12.5	14.0	0.06 - 0.58	0.3339	0.1231
	ImmM	5.3	10.1	14.3	0.05 - 0.58	0.5817	0.0001	8.0	12.0	14.4	0.06 - 0.42	0.3166	0.0043
	MatM	5.2	8.1	11.7	0.03 - 0.30	0.4384	0.0000	7.1	11.9	14.8	0.04 - 0.36	0.3028	0.0017
	ImmF	5.1	8.2	14.2	0.03 - 0.43	0.3950	0.0002	7.7	12.5	15.5	0.05 - 0.37	0.3699	0.0001
	MatF	5.0	7.9	11.0	0.03 - 0.28	0.3775	0.0000	8.4	12.5	16.3	0.05 - 0.38	0.4173	0.0000
	BF	7.8	10.1	12.9	0.05 - 0.67	0.7692	0.0000	9.9	12.9	20.7	0.03 - 0.24	0.4288	0.0000
	HER	3.3	5.6	8.4	0.03 - 0.29	0.1391	0.0860	5.1	6.9	9.8	0.04 - 0.32	0.5543	0.0000
	ILL	6.2	11.1	13.1	0.04 - 0.29	0.6885	0.0000	6.9	11.0	14.3	0.02 - 0.24	0.1690	0.0062
	LOL	7.8	11.1	13.9	0.03 - 0.27	0.7607	0.0000	11.1	16.3	21.9	0.02 - 0.15	0.6000	0.0000
MAC	5.3	6.2	9.2	0.07 - 0.53	0.3403	0.0310	6.6	11.1	15.3	0.05 - 0.42	0.1980	0.2476	
BS	Survey	31.6	33.2	35.1	-	-	-	31.5	33.2	35.1	-	-	-
	Neo	33.0	33.7	35.1	0.07 - 0.74	0.4175	0.1146	32.3	34.5	35.2	0.09 - 0.81	0.6191	0.0242
	ImmM	32.8	34.7	35.6	0.06 - 0.74	0.4994	0.0166	31.9	34.4	35.1	0.08 - 0.61	0.4752	0.0094
	MatM	32.5	33.8	34.9	0.05 - 0.40	0.3519	0.0010	31.5	32.2	34.1	0.06 - 0.61	0.3947	0.0225
	ImmF	32.3	33.9	35.2	0.04 - 0.47	0.2950	0.0701	31.7	32.6	34.6	0.06 - 0.57	0.2322	0.3036
	MatF	32.2	33.5	35.1	0.05 - 0.42	0.2741	0.0443	31.6	32.4	33.6	0.06 - 0.60	0.4421	0.0218
	BF	33.6	35.0	35.5	0.08 - 0.76	0.7011	0.0006	31.2	33.1	35.7	0.04 - 0.40	0.1189	0.6500
	HER	31.9	32.8	33.8	0.04 - 0.38	0.2666	0.0255	32.4	33.5	34.7	0.05 - 0.55	0.3225	0.0512
	ILL	33.7	35.2	35.7	0.06 - 0.45	0.7197	0.0000	32.2	34.9	35.6	0.03 - 0.39	0.4304	0.0000
	LOL	33.7	35.1	35.6	0.05 - 0.41	0.7200	0.0000	31.3	32.4	34.4	0.03 - 0.25	0.3849	0.0000

	MAC	32.7	33.3	33.9	0.08 - 0.70	0.3567	0.2591	31.9	32.5	33.6	0.06 - 0.70	0.4860	0.0196
Depth (m)	Survey	19.8	70.2	228.0	-	-	-	21.3	78.2	231.6	-	-	-
	Neo	51.2	94.7	122.5	0.06 - 0.49	0.3762	0.0066	38.9	86.6	243.2	0.06 - 0.60	0.2616	0.2916
	ImmM	64.5	113.4	240.5	0.04 - 0.45	0.4302	0.0002	36.4	75.7	217.9	0.05 - 0.38	0.2019	0.1391
	MatM	35.2	75.3	200.0	0.03 - 0.23	0.1391	0.0588	24.8	42.9	192.0	0.04 - 0.36	0.3089	0.0004
	ImmF	32.2	90.9	235.2	0.03 - 0.35	0.1655	0.1040	25.9	49.3	184.1	0.04 - 0.32	0.2666	0.0011
	MatF	22.1	55.6	187.7	0.04 - 0.27	0.2192	0.0025	24.9	42.1	78.6	0.05 - 0.37	0.4905	0.0000
	BF	37.7	86.2	173.1	0.05 - 0.56	0.3781	0.0212	18.3	70.6	120.5	0.03 - 0.21	0.3153	0.0000
	HER	25.1	60.4	103.0	0.03 - 0.23	0.2971	0.0000	65.1	153.8	226.8	0.03 - 0.30	0.4080	0.0000
	ILL	52.2	123.9	246.0	0.03 - 0.29	0.4803	0.0000	47.8	96.1	268.8	0.02 - 0.23	0.2285	0.0001
	LOL	29.4	87.1	163.2	0.03 - 0.26	0.1643	0.0280	18.1	35.2	73.2	0.02 - 0.14	0.5232	0.0000
MAC	24.1	58.0	109.0	0.06 - 0.49	0.3126	0.0427	34.1	68.3	190.8	0.04 - 0.42	0.2080	0.1788	

Table 4E.3. Temporal comparisons of habitat associations for spiny dogfish life-history stages and prey species in the Northeast (US) shelf large marine ecosystem for bottom temperature (BT), bottom salinity (BS), and depth during spring (1968 – 2009) and autumn (1963 – 2009). D = range of absolute vertical distance between distributions, TS = test statistic, and p = probability. Significance (bolded) based on an *a priori* $\alpha = 0.05$. Stages and species as defined in Table 4.1. Note: spiny dogfish not sexed consistently until 1980.

Variable	Stage/ Species	SPRING			AUTUMN		
		D	TS	p	D	TS	p
BT (°C)	Neo	0.05 - 0.58	0.1930	0.6135	0.08 - 0.62	0.3379	0.2184
	ImmM	0.06 - 0.58	0.2010	0.5478	0.06 - 0.67	0.3390	0.2890
	MatM	0.04 - 0.42	0.0772	0.9391	0.05 - 0.42	0.2545	0.0474
	ImmF	0.04 - 0.40	0.1095	0.7286	0.05 - 0.46	0.2560	0.1040
	MatF	0.04 - 0.44	0.0858	0.9103	0.06 - 0.48	0.1241	0.8758
	BF	0.06 - 0.55	0.2904	0.1528	0.04 - 0.33	0.1146	0.4912
	HER	0.04 - 0.36	0.2108	0.0162	0.07 - 0.62	0.3429	0.1429
	ILL	0.06 - 0.54	0.2243	0.4338	0.04 - 0.32	0.0794	0.8475
	LOL	0.03 - 0.31	0.1054	0.4065	0.02 - 0.19	0.3266	0.0000
	MAC	0.05 - 0.69	0.1619	0.6347	0.13 - 0.91	0.1229	1.0000
BS	Neo	0.07 - 0.80	0.3073	0.4739	0.08 - 0.88	0.3485	0.5312
	ImmM	0.06 - 0.76	0.1589	0.9482	0.06 - 0.88	0.3430	0.4584
	MatM	0.05 - 0.57	0.0878	0.9809	0.07 - 0.61	0.1428	0.9008
	ImmF	0.04 - 0.58	0.0686	0.9969	0.06 - 0.66	0.1395	0.9020
	MatF	0.05 - 0.61	0.1802	0.6031	0.07 - 0.69	0.0858	0.9993
	BF	0.07 - 0.76	0.2412	0.6589	0.04 - 0.54	0.1536	0.5765
	HER	0.04 - 0.46	0.0685	0.9902	0.07 - 0.80	0.4012	0.2849
	ILL	0.05 - 0.77	0.1462	0.9664	0.05 - 0.49	0.1630	0.5326
	LOL	0.03 - 0.46	0.1178	0.7261	0.02 - 0.25	0.3017	0.0000
	MAC	0.07 - 0.77	0.2388	0.5599	0.07 - 0.97	0.4538	0.6206
Depth (m)	Neo	0.07 - 0.58	0.1951	0.6415	0.08 - 0.68	0.4251	0.0472
	ImmM	0.07 - 0.56	0.2865	0.2137	0.07 - 0.66	0.2933	0.4179
	MatM	0.05 - 0.39	0.1167	0.7384	0.05 - 0.41	0.2256	0.0850
	ImmF	0.04 - 0.39	0.1821	0.3062	0.05 - 0.45	0.2390	0.1217
	MatF	0.05 - 0.41	0.0832	0.9584	0.06 - 0.50	0.1862	0.4458
	BF	0.07 - 0.56	0.2443	0.3494	0.03 - 0.32	0.1565	0.1488
	HER	0.04 - 0.33	0.1606	0.2510	0.08 - 0.60	0.3793	0.0615
	ILL	0.07 - 0.58	0.2512	0.3583	0.04 - 0.30	0.1661	0.0978
	LOL	0.04 - 0.31	0.1314	0.3962	0.02 - 0.16	0.2468	0.0000
	MAC	0.06 - 0.49	0.1054	0.9599	0.11 - 0.86	0.3632	0.6951

Figure 4E.1. Cumulative distributions of available and occupied bottom temperature ($^{\circ}\text{C}$), bottom salinity, and depth (m) for spiny dogfish life-history stages during both day (left panel) and night (right panel) in the Northeast (US) shelf large marine ecosystem during spring (1968-2009). CDFs shown include survey (thick black), neonate (orange), immature male (red), mature male (green), immature female (blue), and mature female (purple). Notes: spiny dogfish not sexed consistently until 1980 and salinity data has been collected consistently since 1996.

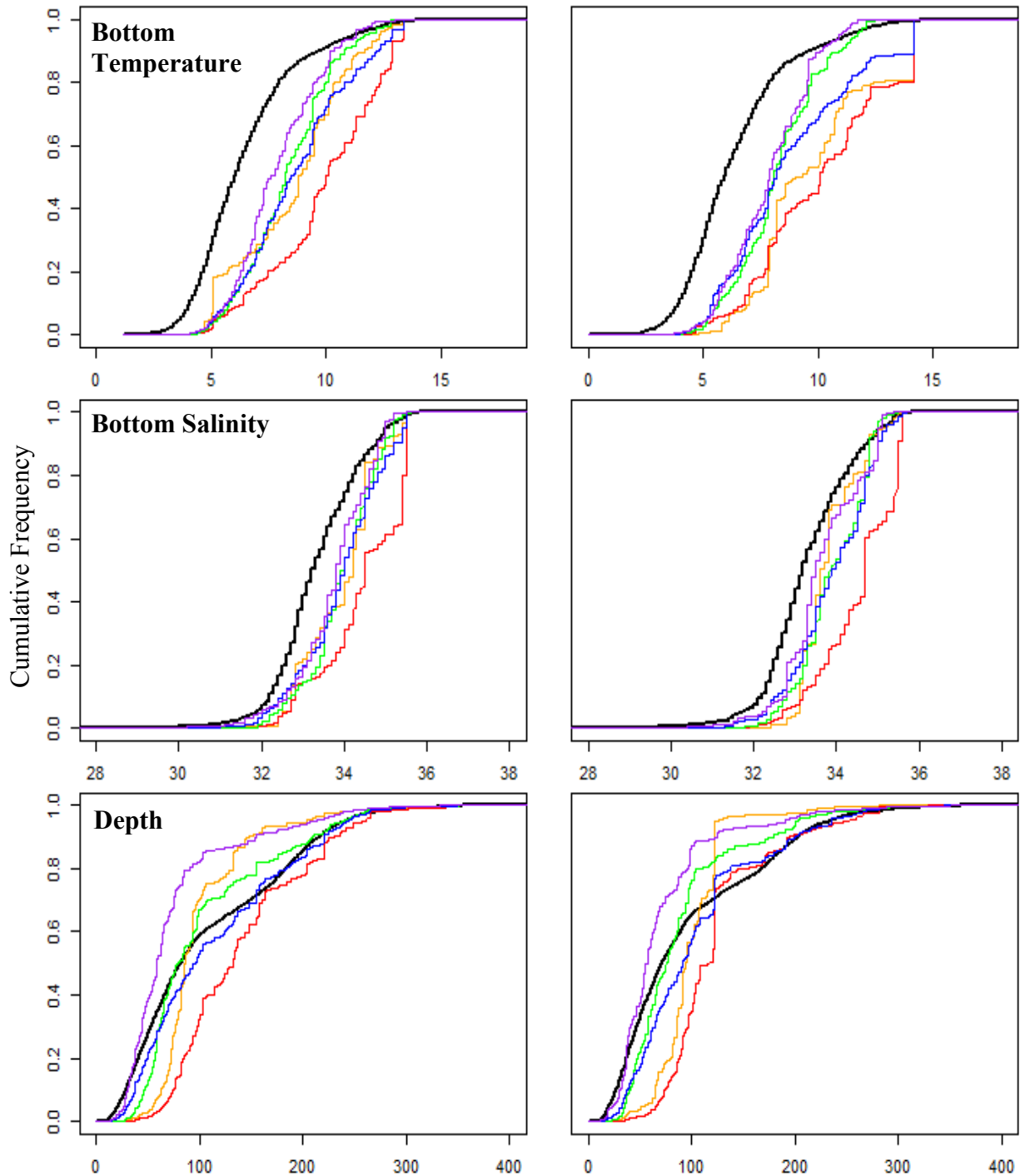


Figure 4E.2. Cumulative distributions of available and occupied bottom temperature ($^{\circ}\text{C}$), bottom salinity, and depth (m) for prey species during both day (left panel) and night (right panel) in the Northeast (US) shelf large marine ecosystem during spring (1968-2009). CDFs shown include survey (thick black), butterfish (orange), Atlantic herring (red), *Illex* sp. (green), *Loligo* sp. (blue), and Atlantic mackerel (purple). Note: salinity data has been collected consistently since 1996.

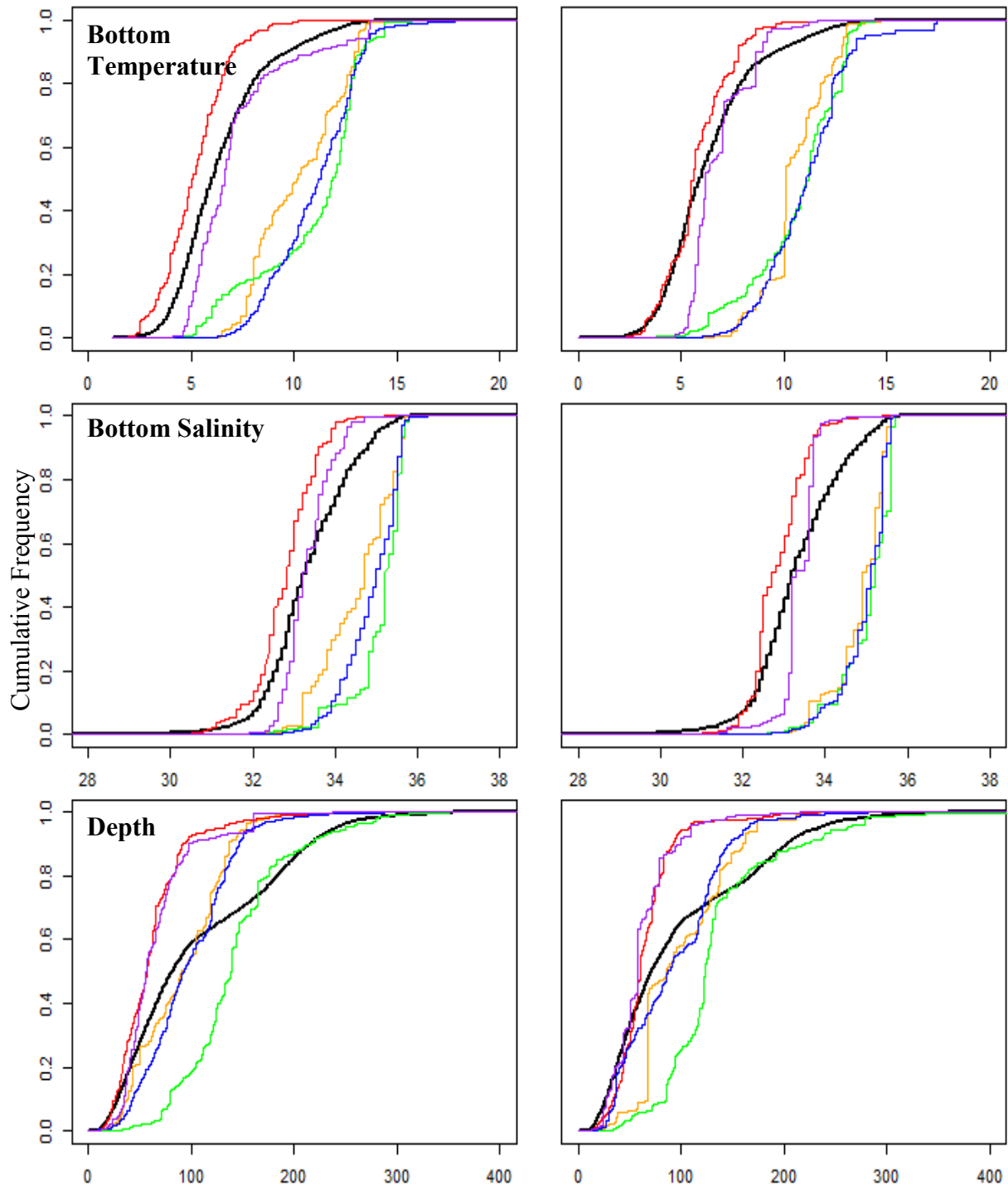


Figure 4E.3. Cumulative distributions of available and occupied bottom temperature ($^{\circ}\text{C}$), bottom salinity, and depth (m) for spiny dogfish life-history stages during both day (left panel) and night (right panel) in the Northeast (US) shelf large marine ecosystem during autumn (1963-2009). CDFs shown include survey (thick black), neonate (orange), immature male (red), mature male (green), immature female (blue), and mature female (purple). Notes: spiny dogfish not sexed consistently until 1980 and salinity data has been collected consistently since 1996.

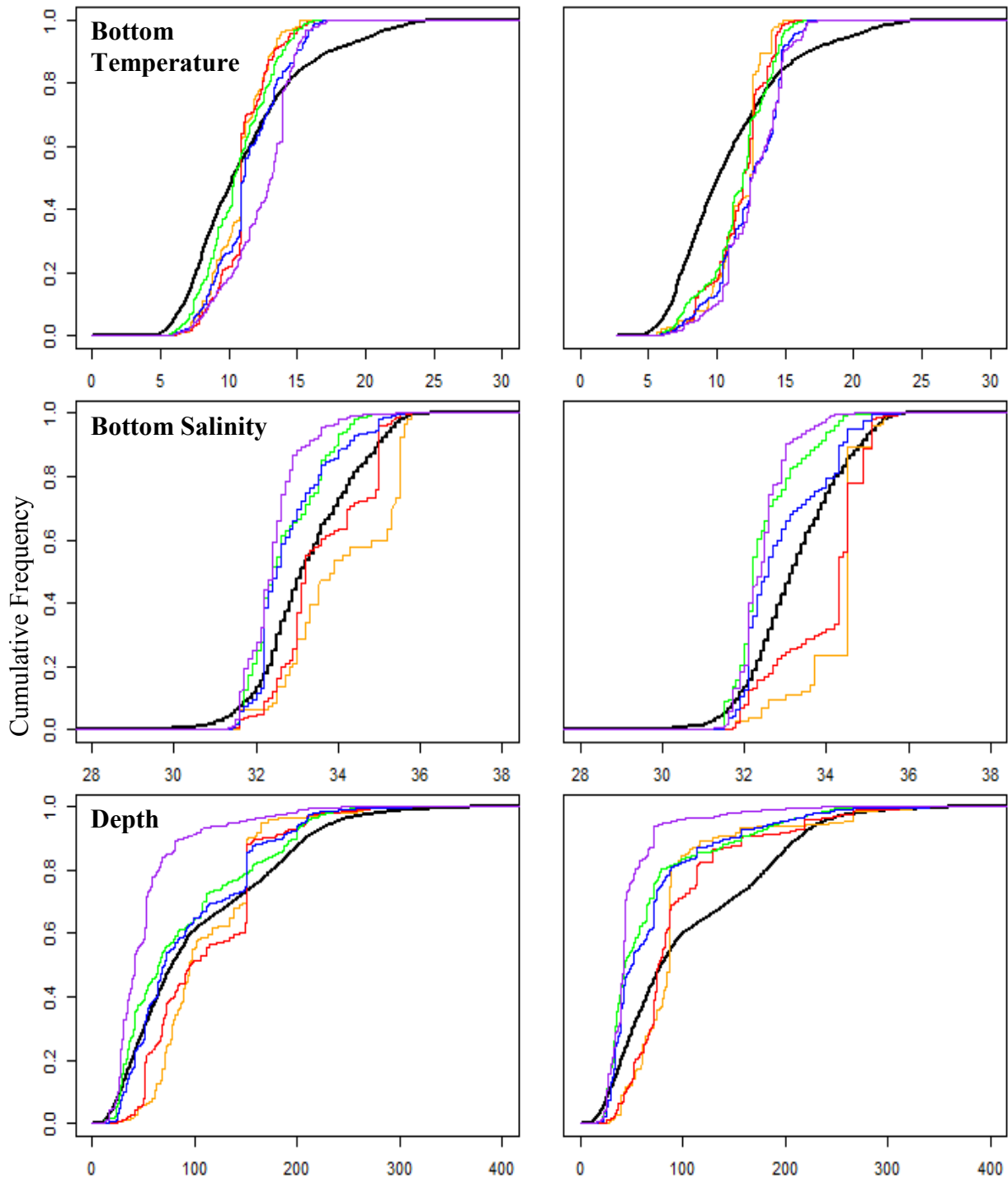


Figure 4E.4. Cumulative distributions of available and occupied bottom temperature ($^{\circ}\text{C}$), bottom salinity, and depth (m) for prey species during both day (left panel) and night (right panel) in the Northeast (US) shelf large marine ecosystem during autumn (1963-2009). CDFs shown include survey (thick black), butterfish (orange), Atlantic herring (red), *Illex* sp. (green), *Loligo* sp. (blue), and Atlantic mackerel (purple). Note: salinity data has been collected consistently since 1996.

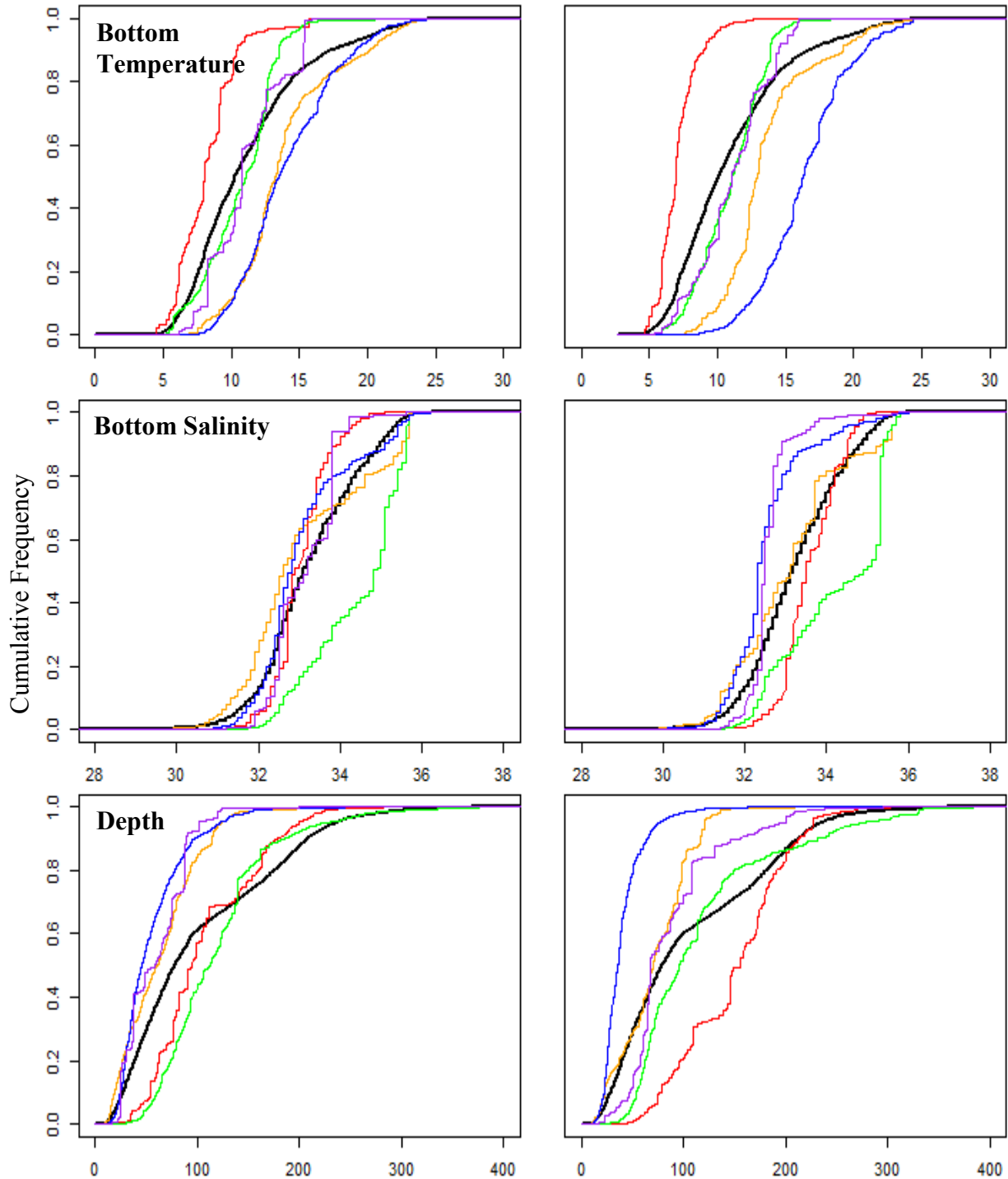


Figure 4E.5. Comparison of day (gray line) and night (black line) bottom temperature preference for spiny dogfish life-history stages during spring (1968 – 2009) (left panel) and autumn (1963 – 2009) (right panel) in the Northeast (US) shelf large marine ecosystem. *Sig indicates significant difference ($p < 0.05$) between night and day. Notes: spiny dogfish not sexed consistently until 1980 and x-axis ranges differ between panels.

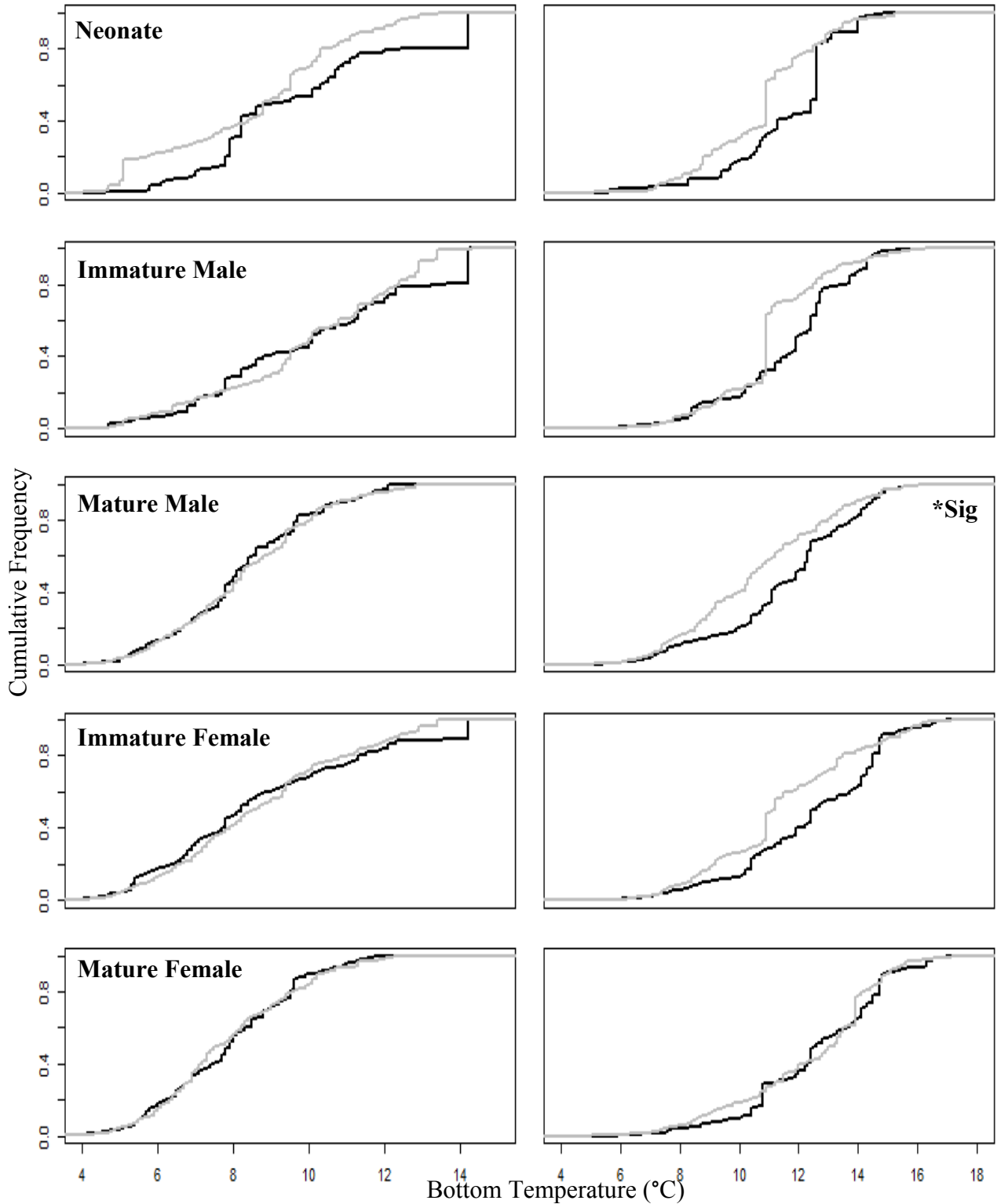


Figure 4E.6. Comparison of day (gray line) and night (black line) bottom salinity preference for spiny dogfish life-history stages during spring (1968 – 2009) (left panel) and autumn (1963 – 2009) (right panel) in the Northeast (US) shelf large marine ecosystem. Notes: spiny dogfish not sexed consistently until 1980 and salinity data has been collected consistently since 1996.

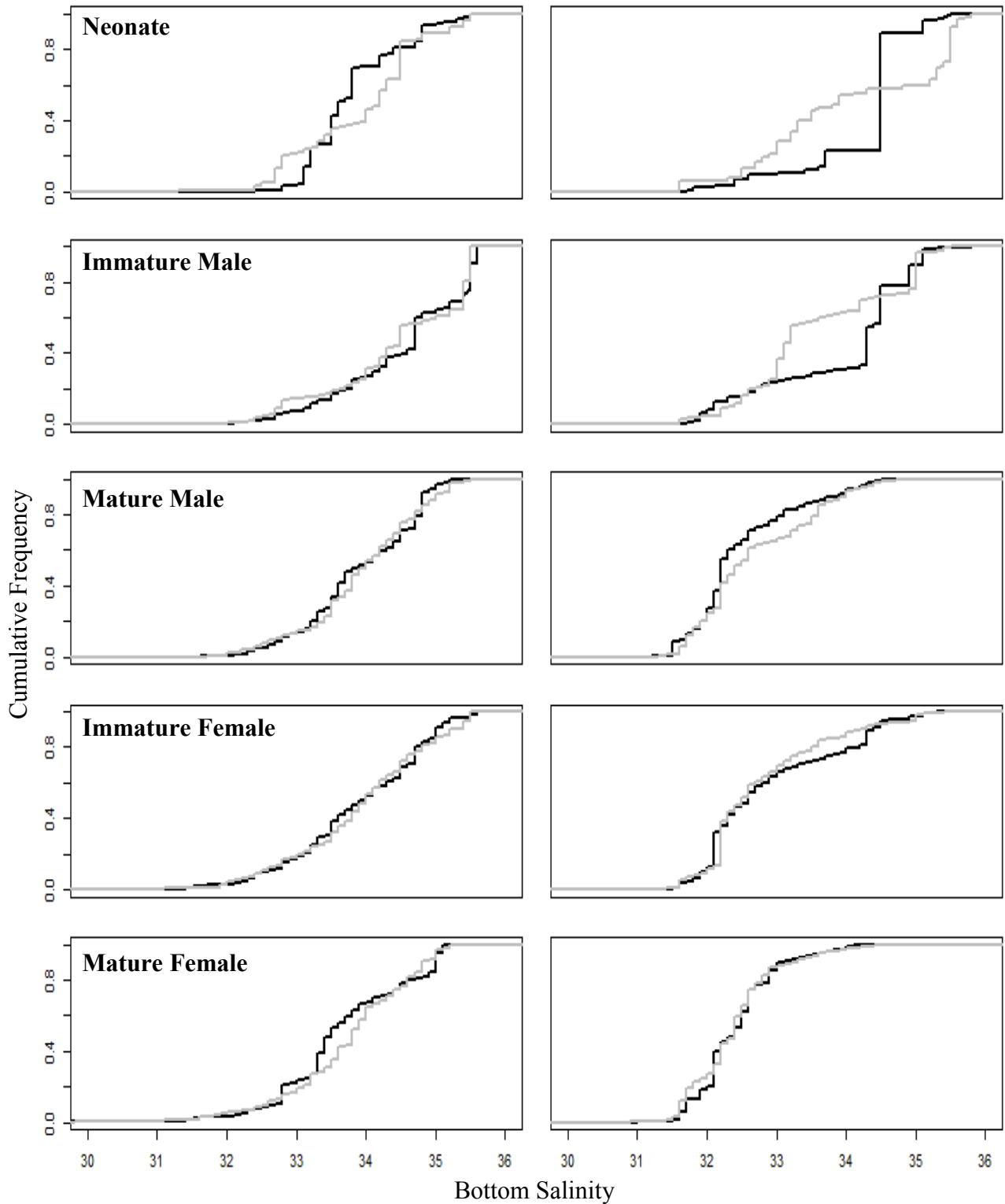


Figure 4E.7. Comparison of day (gray line) and night (black line) depth preference for spiny dogfish life-history stages during spring (1968 – 2009) (left panel) and autumn (1963 – 2009) (right panel) in the Northeast (US) shelf large marine ecosystem. *Sig indicates significant difference ($p < 0.05$) between night and day. Note: spiny dogfish not sexed consistently until 1980.

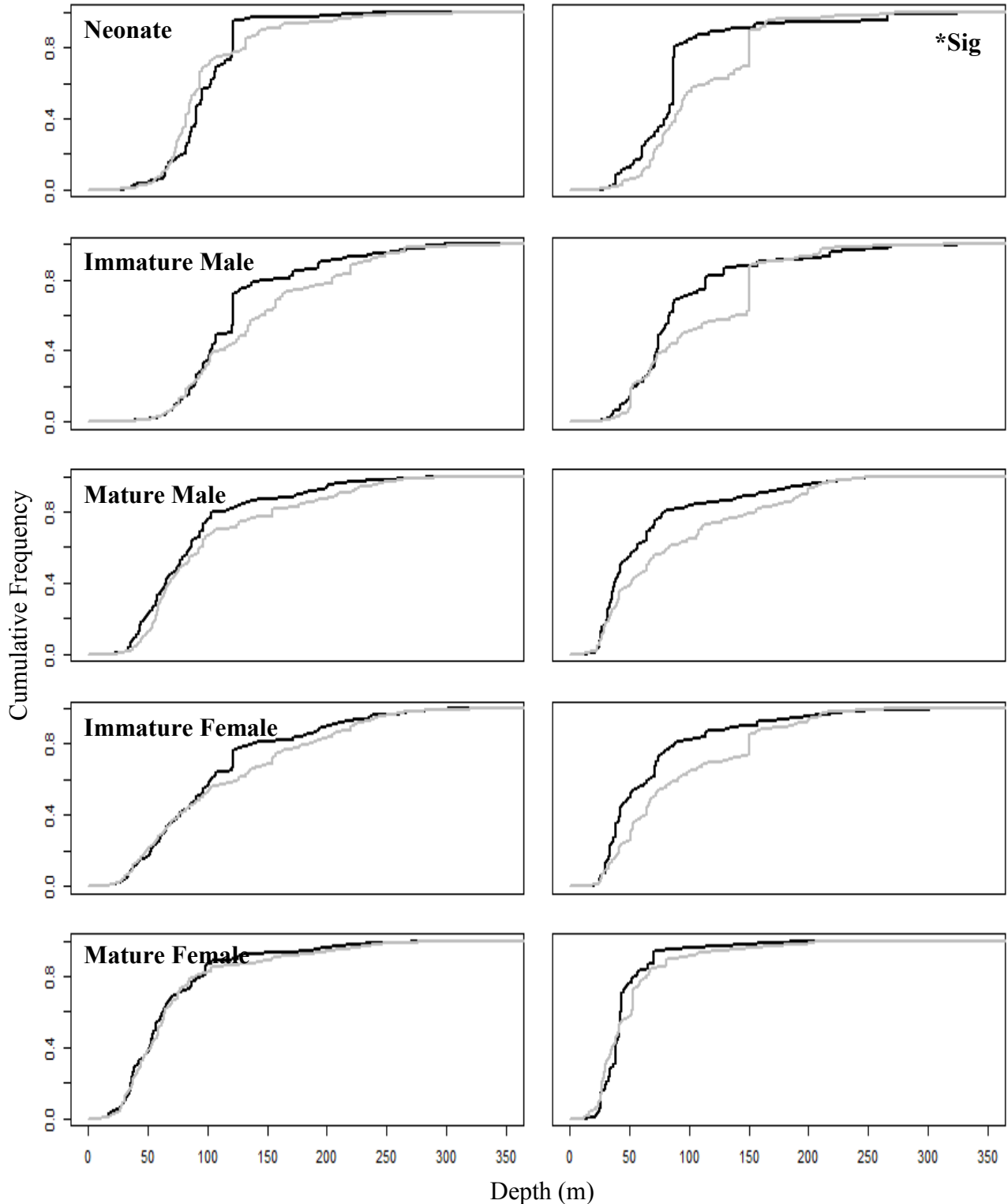


Figure 4E.8. Comparison of day (gray line) and night (black line) bottom temperature preference for prey species during spring (1968 – 2009) (left panel) and autumn (1963 – 2009) (right panel) in the Northeast (US) shelf large marine ecosystem. *Sig indicates significant difference ($p < 0.05$) between night and day. Notes: x-axis ranges differ between panels.

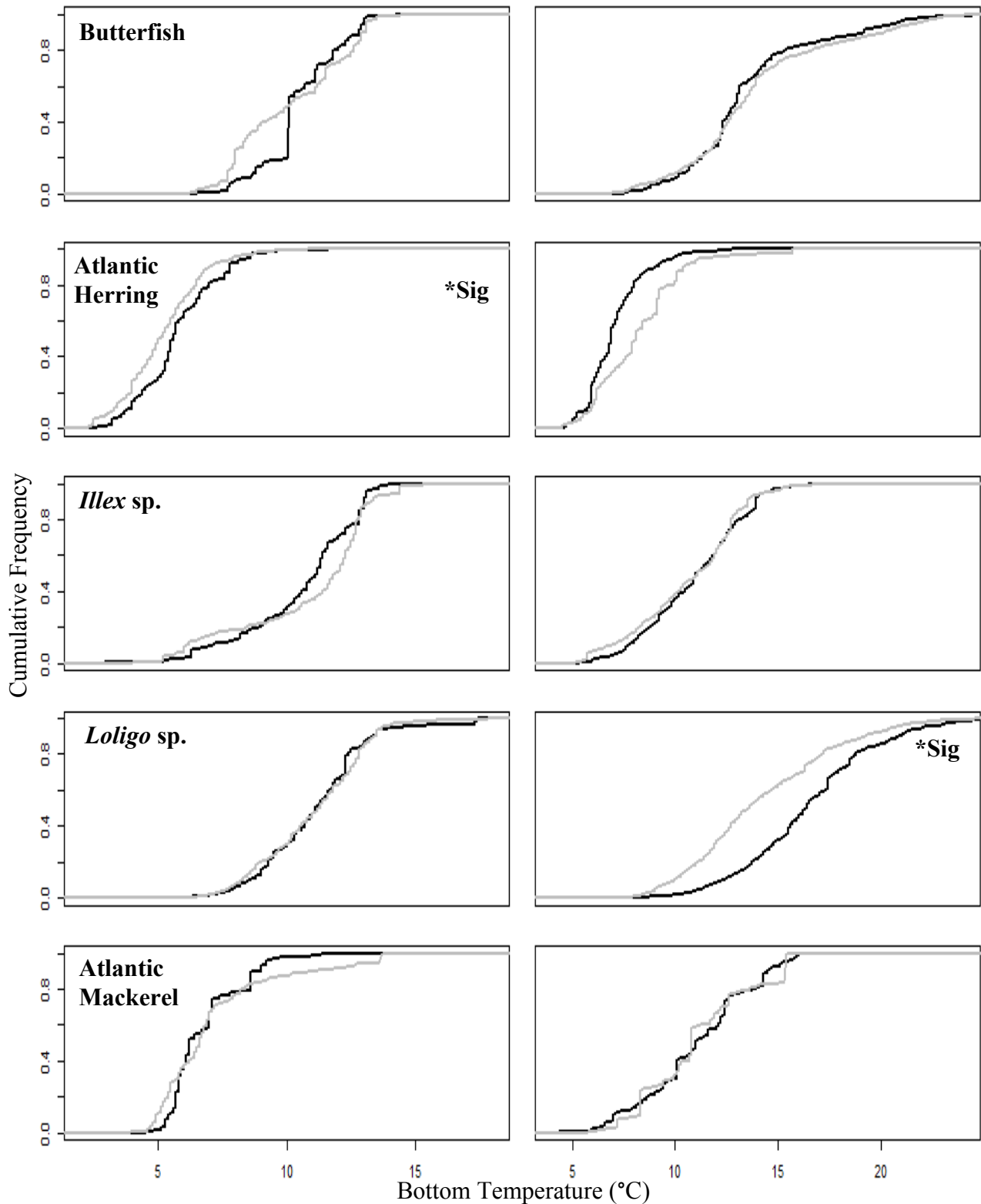


Figure 4E.9. Comparison of day (gray line) and night (black line) bottom salinity preference for prey species during spring (1968 – 2009) (left panel) and autumn (1963 – 2009) (right panel) in the Northeast (US) shelf large marine ecosystem. *Sig indicates significant difference ($p < 0.05$) between night and day. Note: salinity data has been collected consistently since 1996.

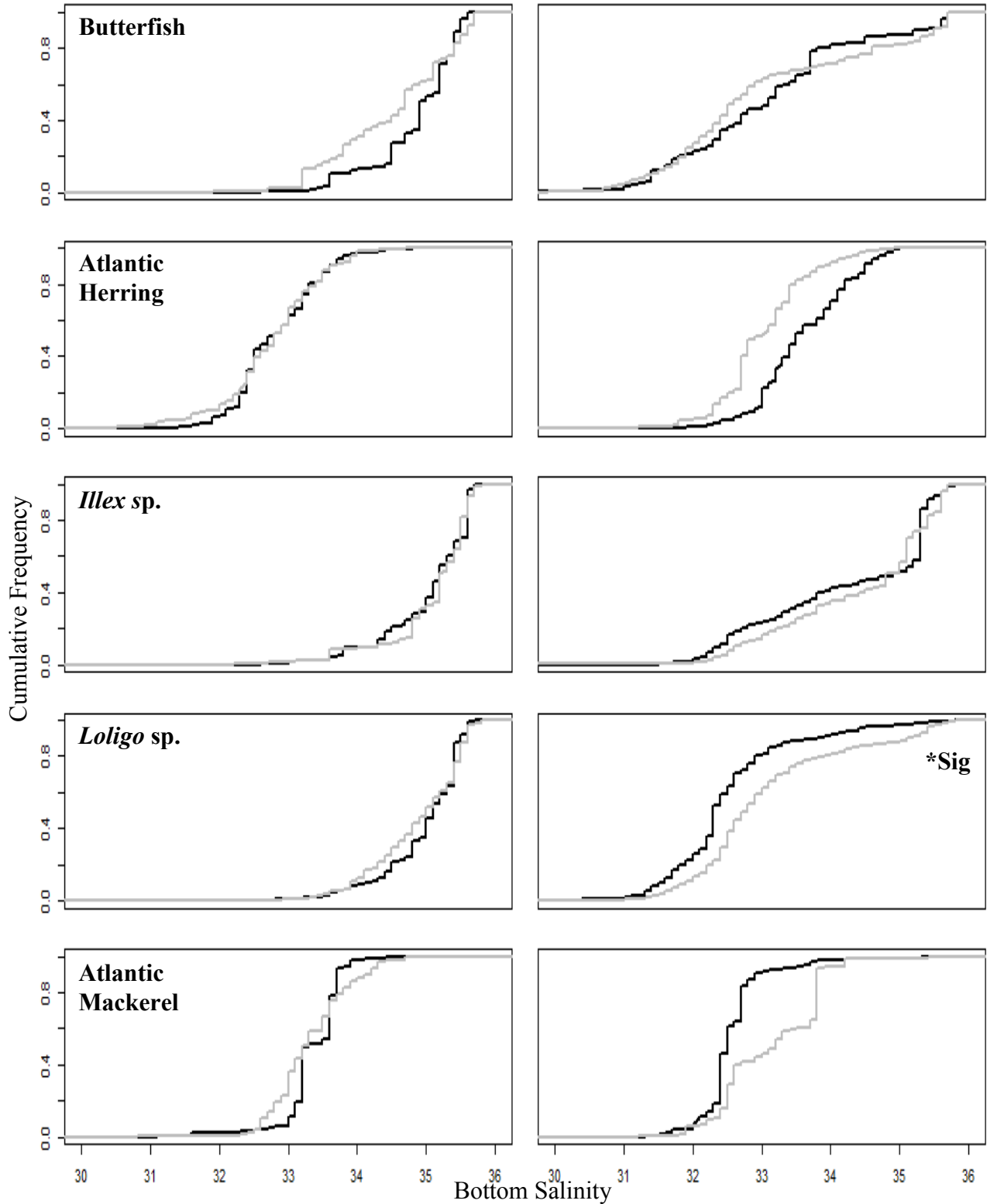
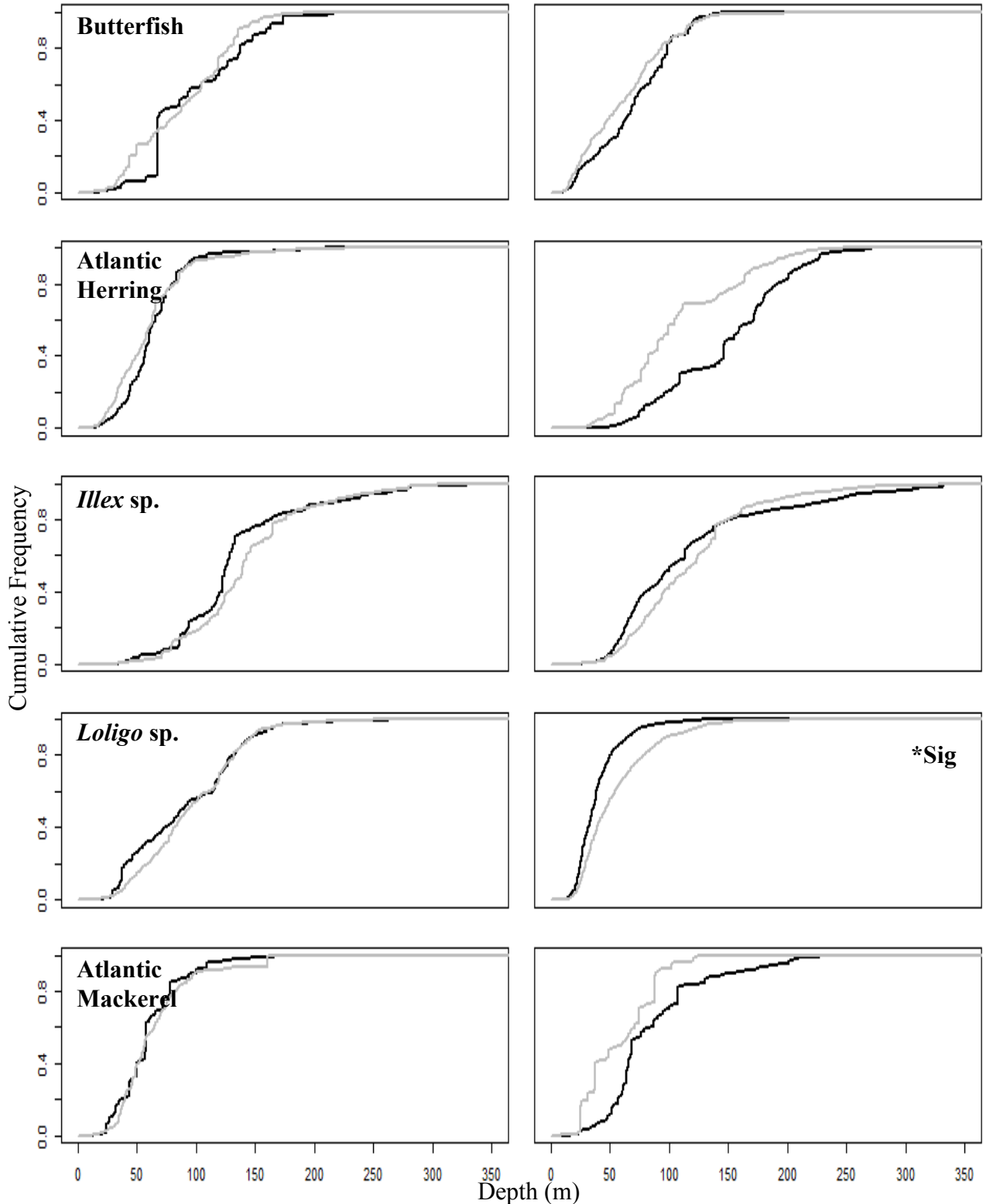


Figure 4E.10. Comparison of day (gray line) and night (black line) depth preference for prey species during spring (1968 – 2009) (left panel) and autumn (1963 – 2009) (right panel) in the Northeast (US) shelf large marine ecosystem. *Sig indicates significant difference ($p < 0.05$) between night and day.



Appendix 4F. Regional CPUE for Spiny Dogfish and Prey Species Adjusted for Diel Variation

Figure 4F.1. Unadjusted CPUE (solid) and day-night adjusted CPUE (dotted) when appropriate for All Regions (Gulf of Maine, Georges Bank, Southern New England, Middle Atlantic Bight) derived from the NEFSC bottom trawl survey during spring (1968 – 2009). Notes: spiny dogfish not sexed consistently until 1980 and y-axes differ between panels.

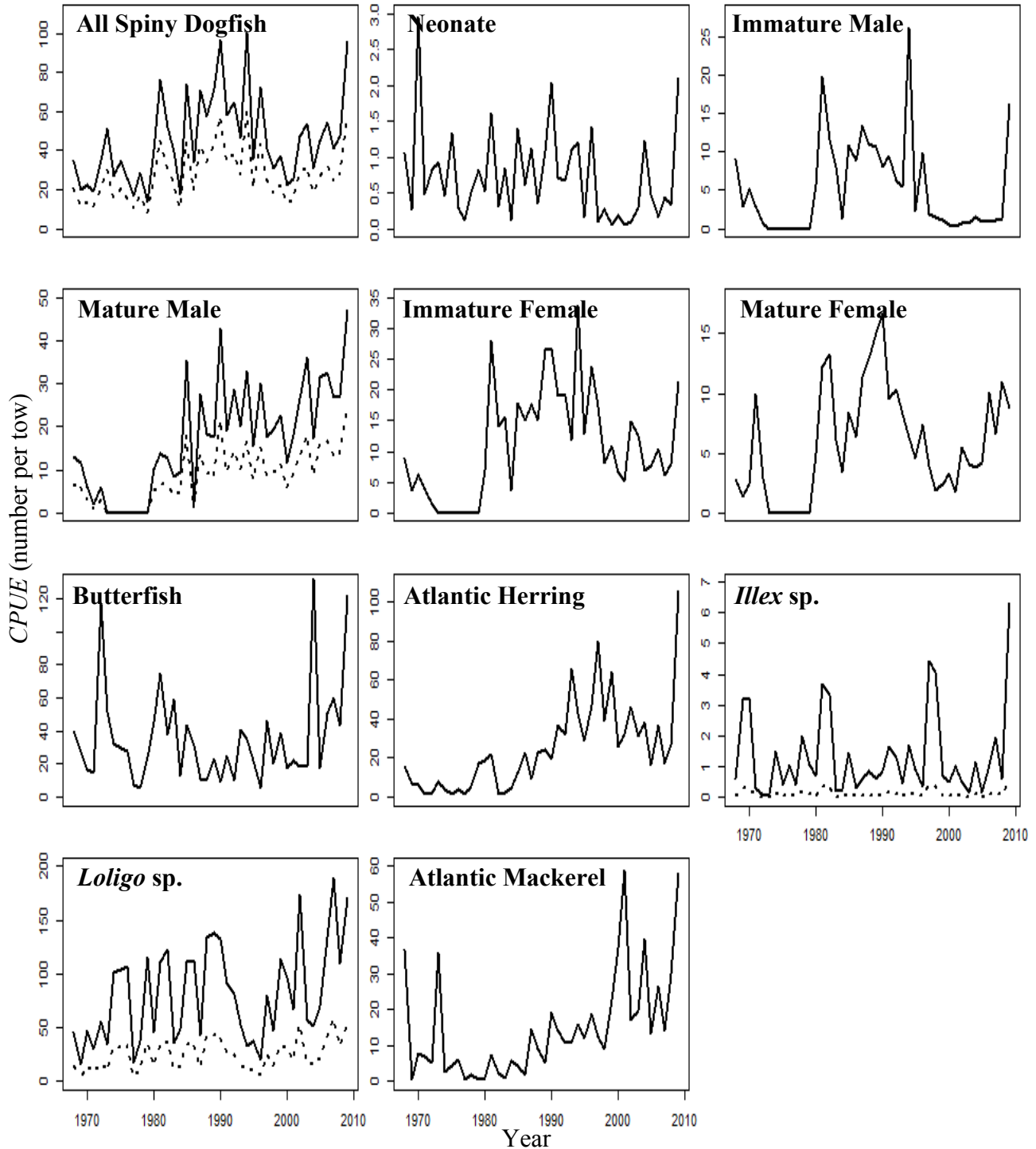


Figure 4F.2. Unadjusted *CPUE* (solid) and day-night adjusted *CPUE* (dotted) when appropriate for Georges Bank derived from the NEFSC bottom trawl survey during spring (1968 – 2009). Notes: spiny dogfish not sexed consistently until 1980 and y-axes differ between panels.

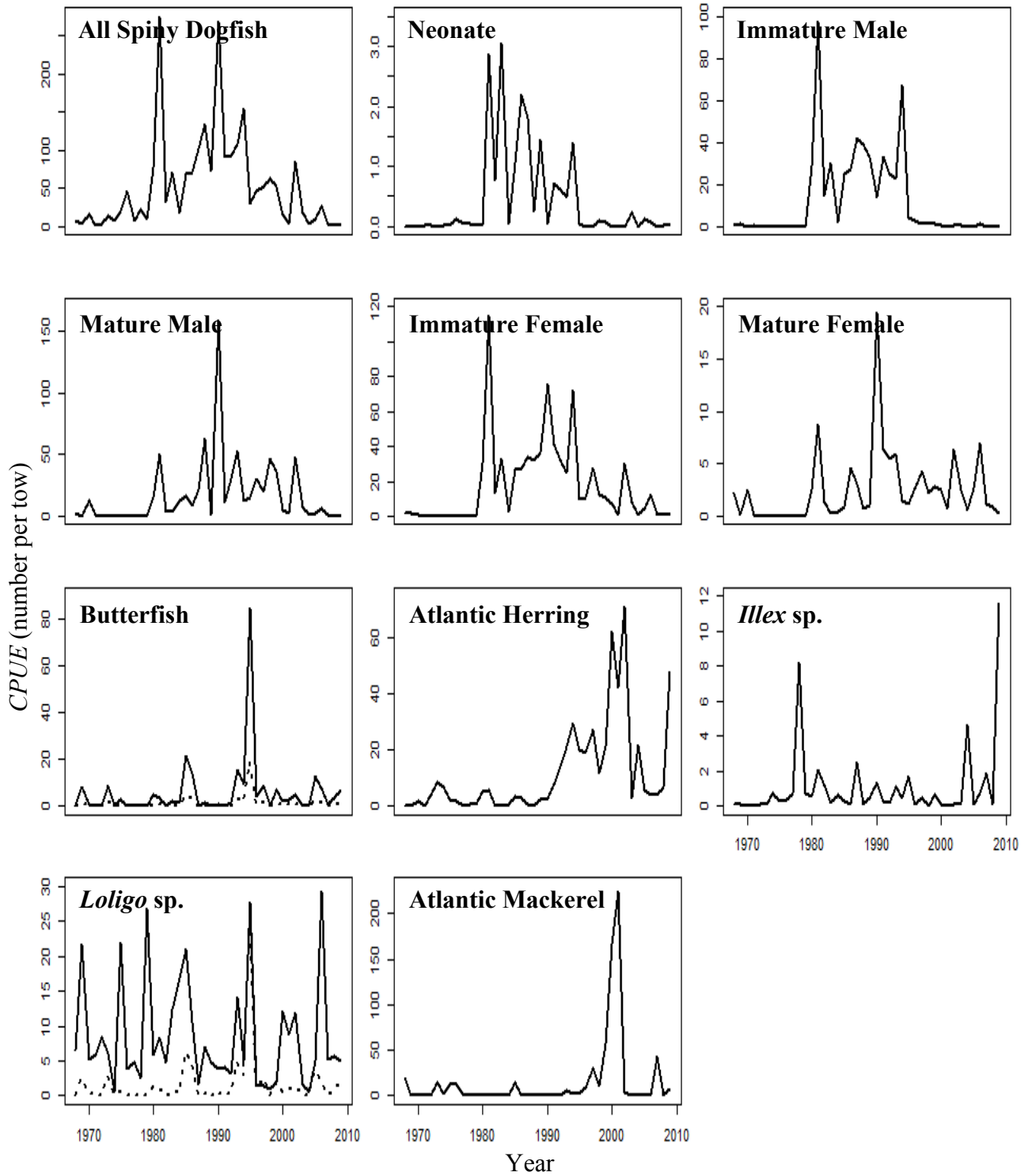


Figure 4F.3. Unadjusted *CPUE* (solid) and day-night adjusted *CPUE* (dotted) when appropriate for the Gulf of Maine derived from the NEFSC bottom trawl survey during spring (1968 – 2009). Notes: spiny dogfish not sexed consistently until 1980 and y-axes differ between panels.

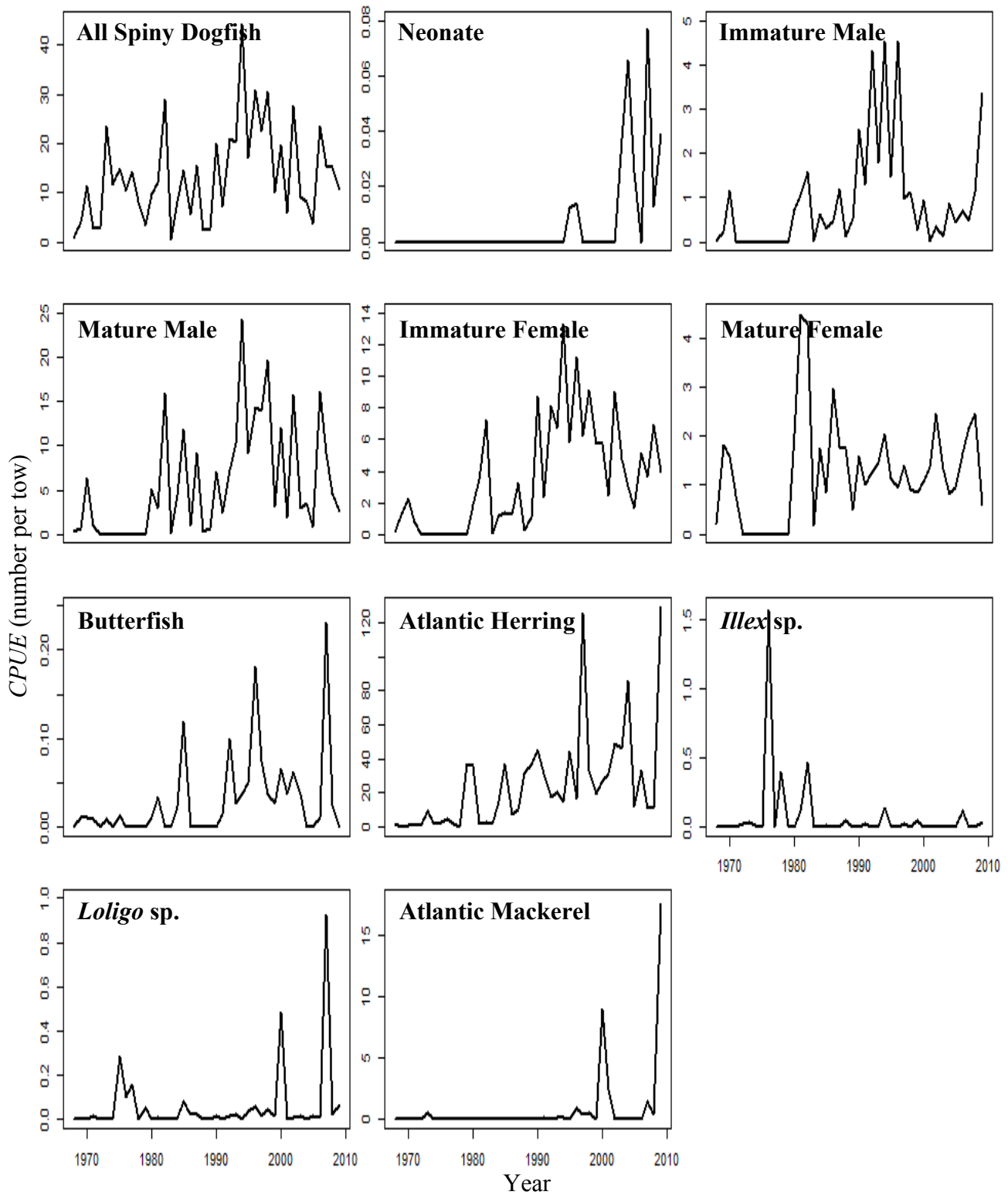


Figure 4F.4. Unadjusted *CPUE* (solid) and day-night adjusted *CPUE* (dotted) when appropriate for the Middle Atlantic Bight derived from the NEFSC bottom trawl survey during spring (1968 – 2009). Notes: spiny dogfish not sexed consistently until 1980 and y-axes differ between panels.

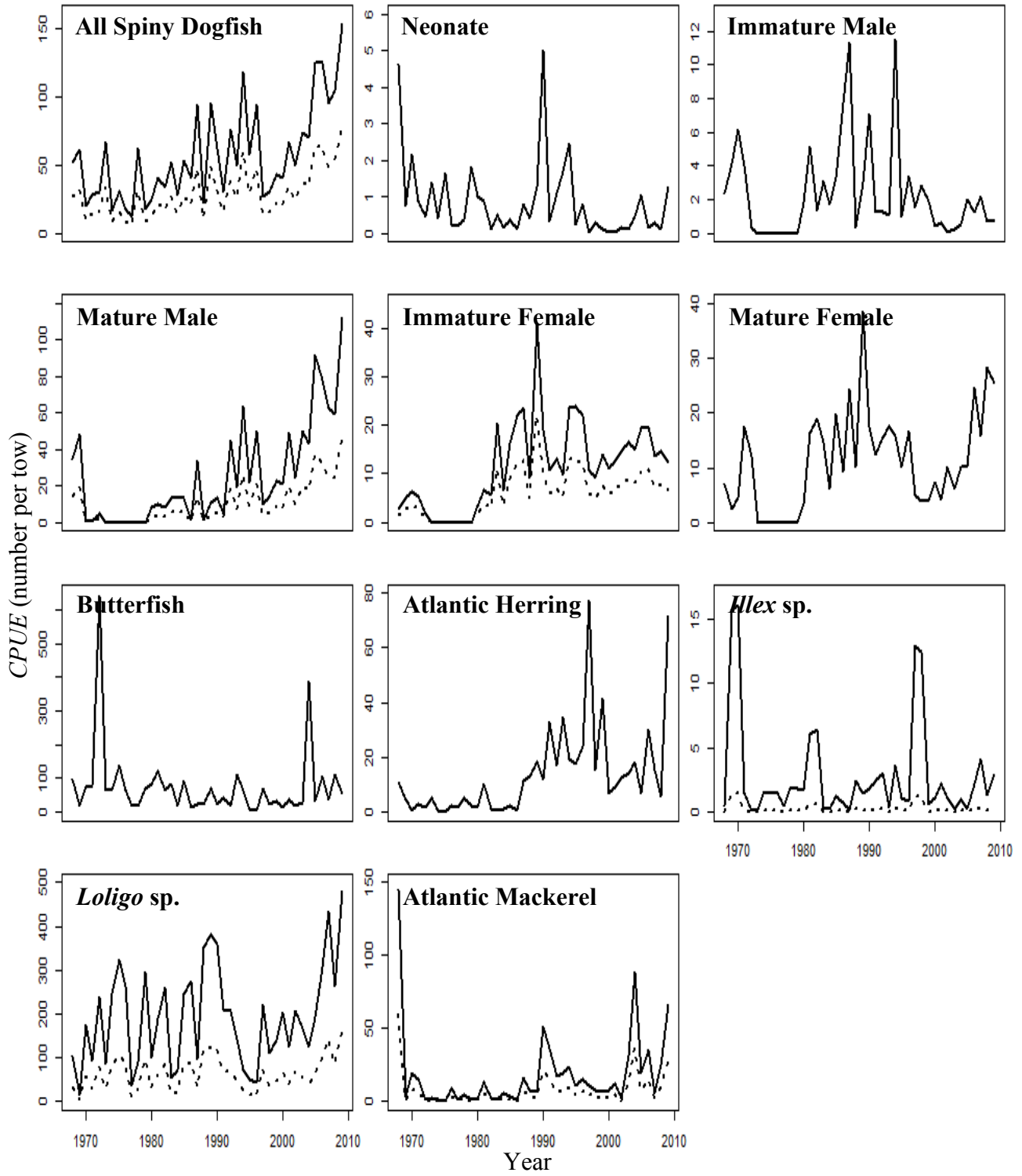


Figure 4F.5. Unadjusted *CPUE* (solid) and day-night adjusted *CPUE* (dotted) when appropriate for the Southern New England derived from the NEFSC bottom trawl survey during spring (1968 – 2009). Notes: spiny dogfish not sexed consistently until 1980 and y-axes differ between panels.

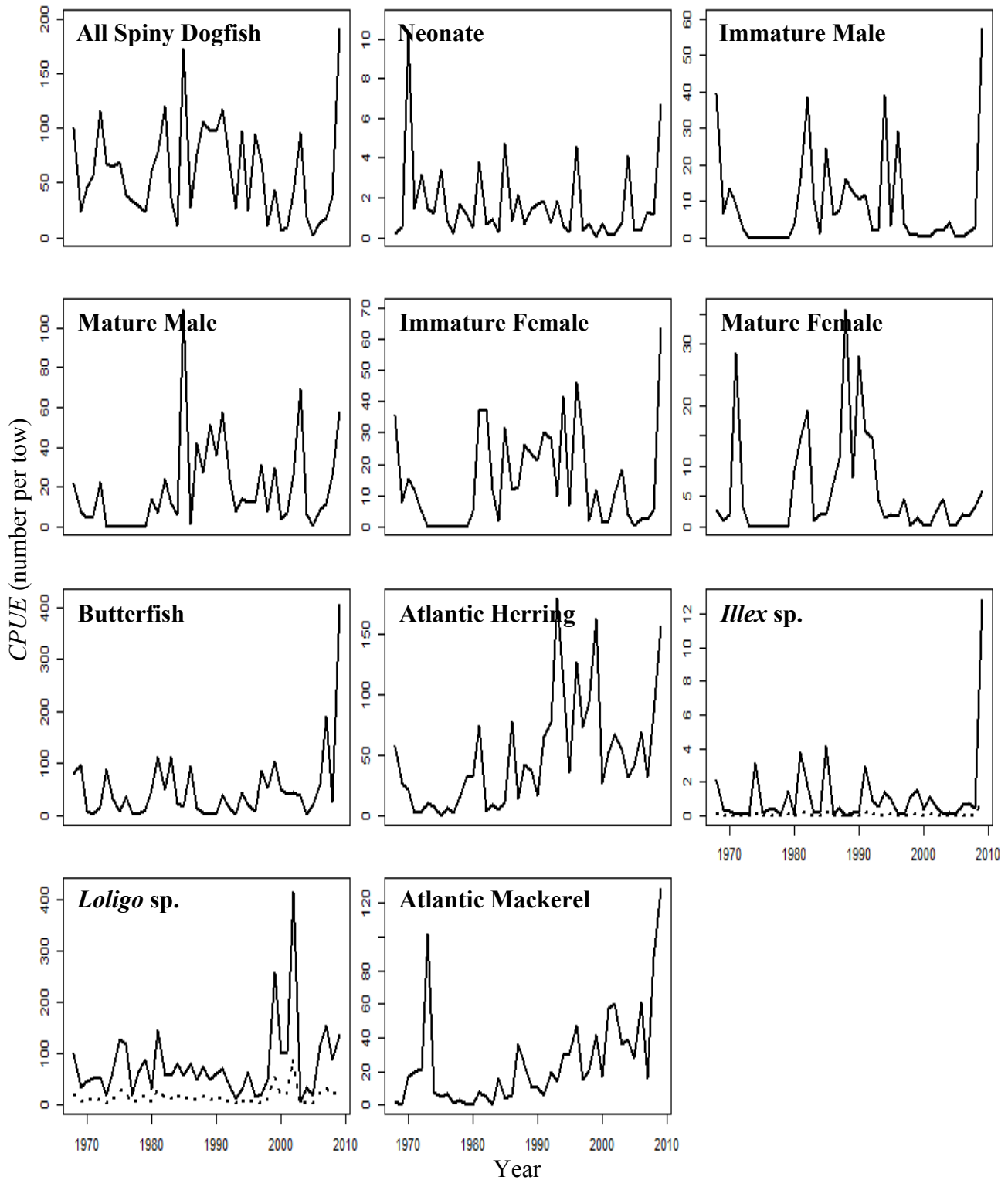


Figure 4F.6. Unadjusted *CPUE* (solid) and day-night adjusted *CPUE* (dotted) when appropriate for Georges Bank derived from the NEFSC bottom trawl survey during autumn (1963 – 2009). Notes: spiny dogfish not sexed consistently until 1980 and y-axes differ between panels.

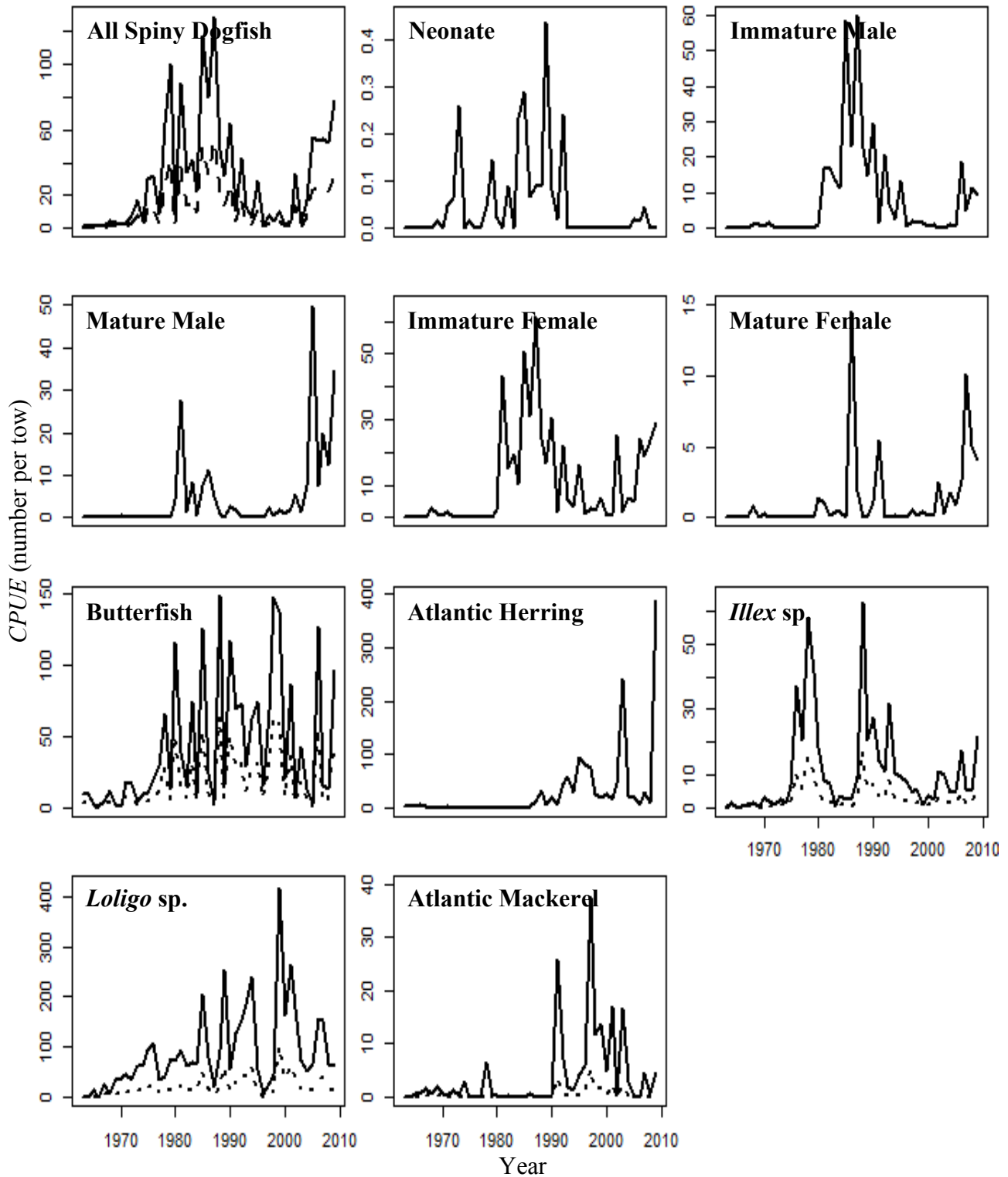


Figure 4F.7. Unadjusted *CPUE* (solid) and day-night adjusted *CPUE* (dotted) when appropriate for the Gulf of Maine derived from the NEFSC bottom trawl survey during autumn (1963 – 2009). Notes: spiny dogfish not sexed consistently until 1980 and y-axes differ between panels.

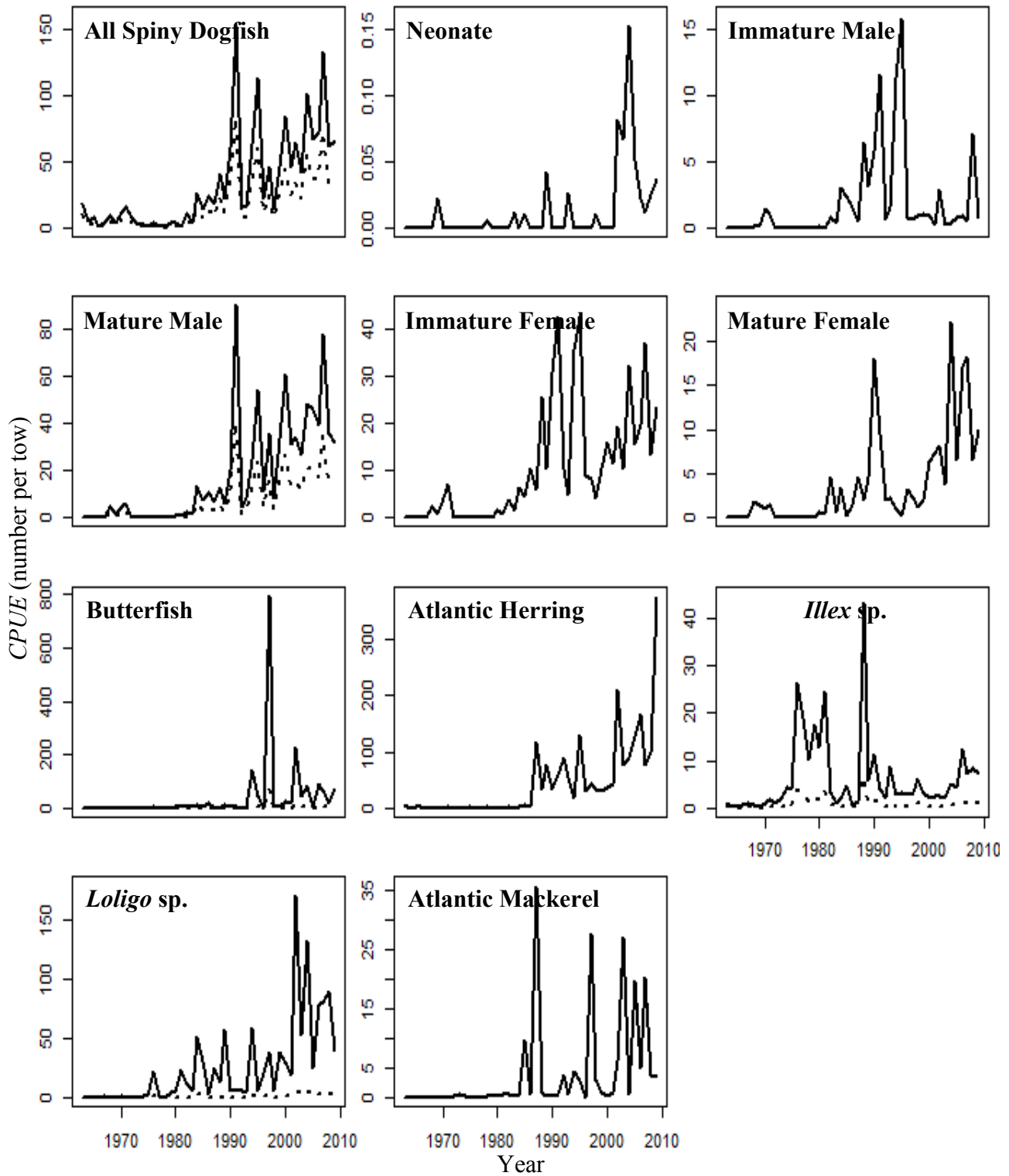


Figure 4F.8. Unadjusted *CPUE* (solid) and day-night adjusted *CPUE* (dotted) when appropriate for the Middle Atlantic Bight derived from the NEFSC bottom trawl survey during autumn (1963 – 2009). Notes: spiny dogfish not sexed consistently until 1980 and y-axes differ between panels.

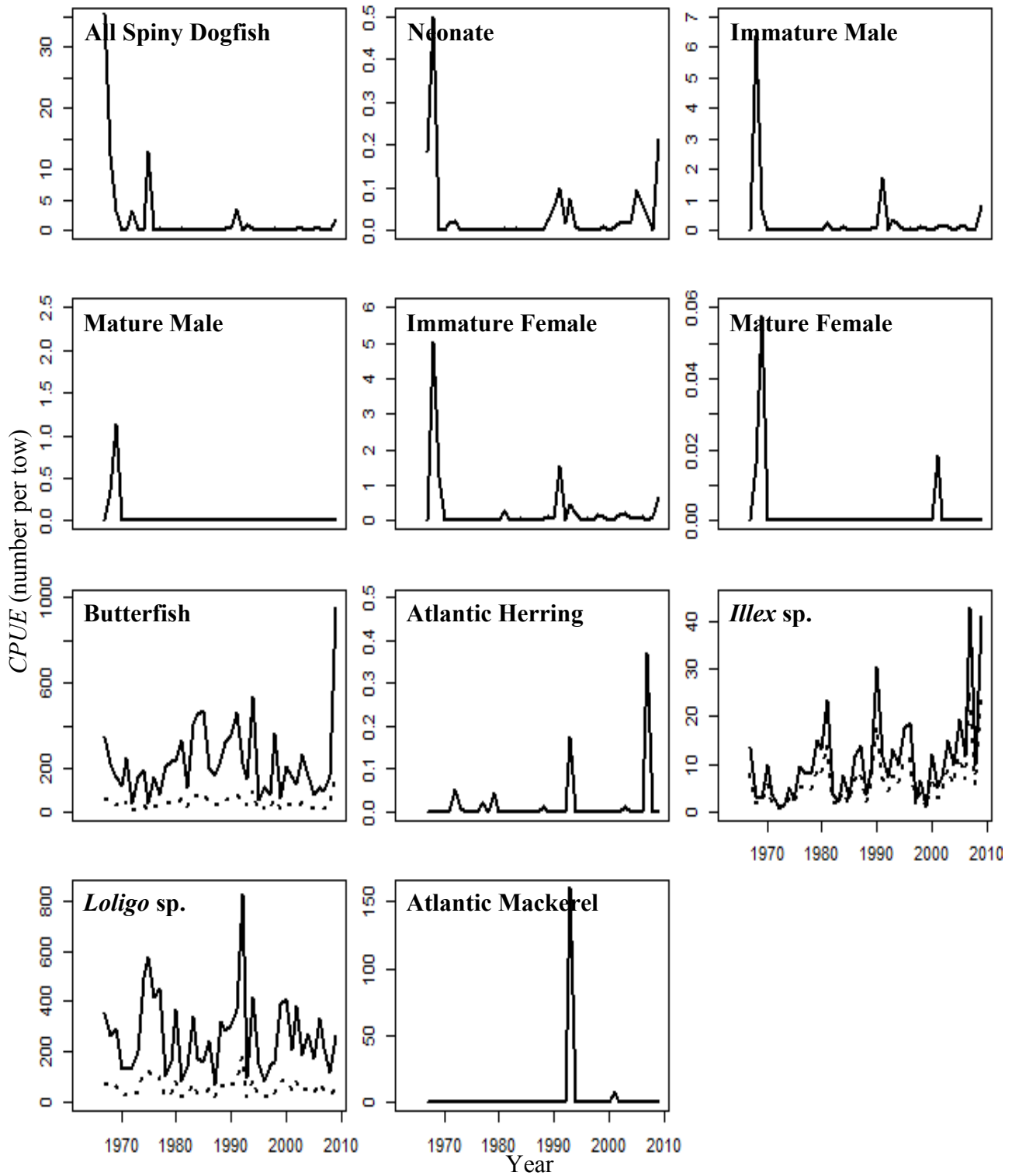
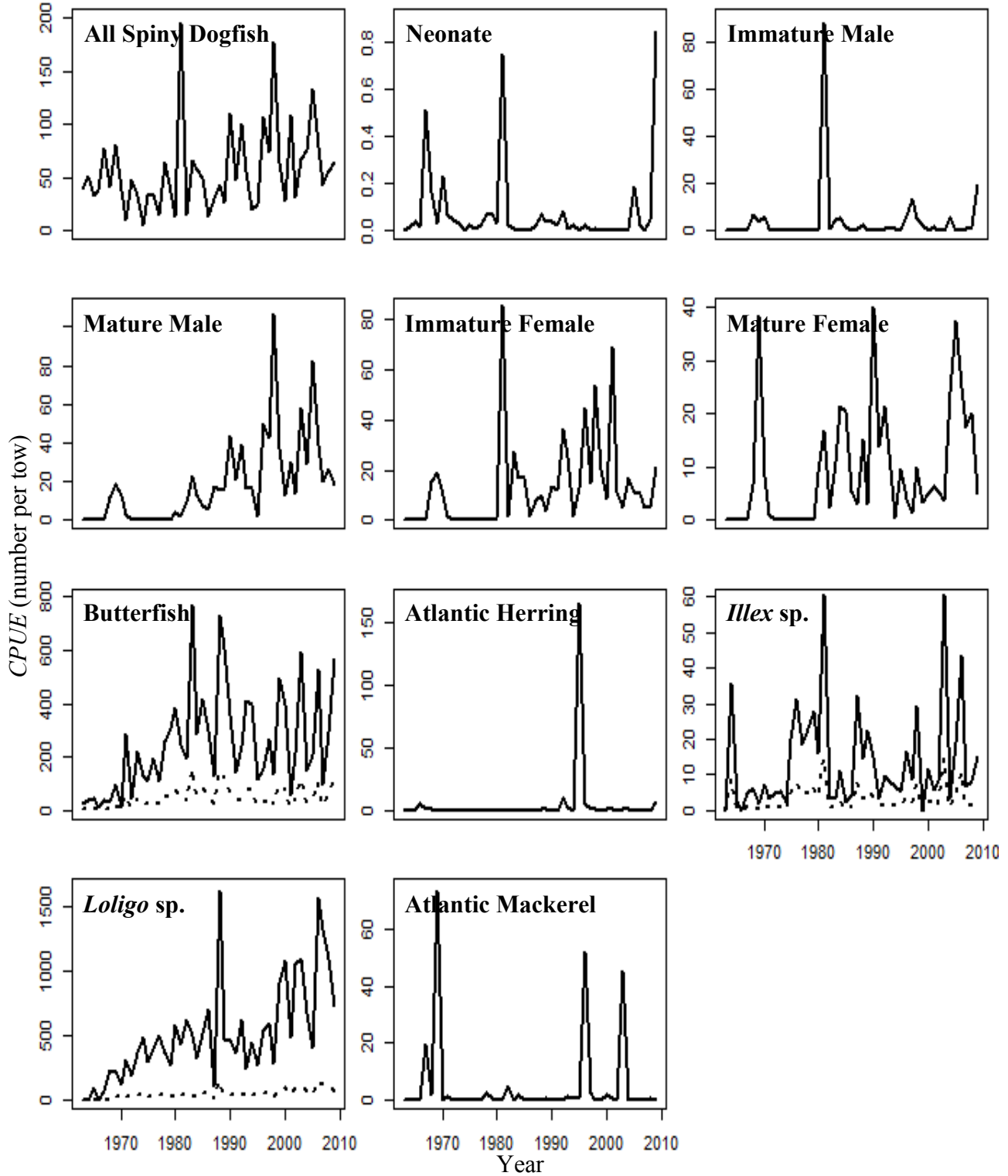


Figure 4F.9. Unadjusted *CPUE* (solid) and day-night adjusted *CPUE* (dotted) when appropriate for the Southern New England derived from the NEFSC bottom trawl survey during autumn (1963 – 2009). Notes: spiny dogfish not sexed consistently until 1980 and y-axes differ between panels.



Appendix 4G. Full GAM Concerning the Probability of Day-time Catch During Spring

Figure 4G.1. Partial GAM plots identifying the additive effect of each variable on the probability of day-time catch for all spiny dogfish combined during spring. The y-axis represents the degree of smoothing (variable, estimated degrees of freedom) 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 gray region reflects the 95% confidence intervals around the response curves. Absence of term within the optimum model represented by empty box. NS = not significant.

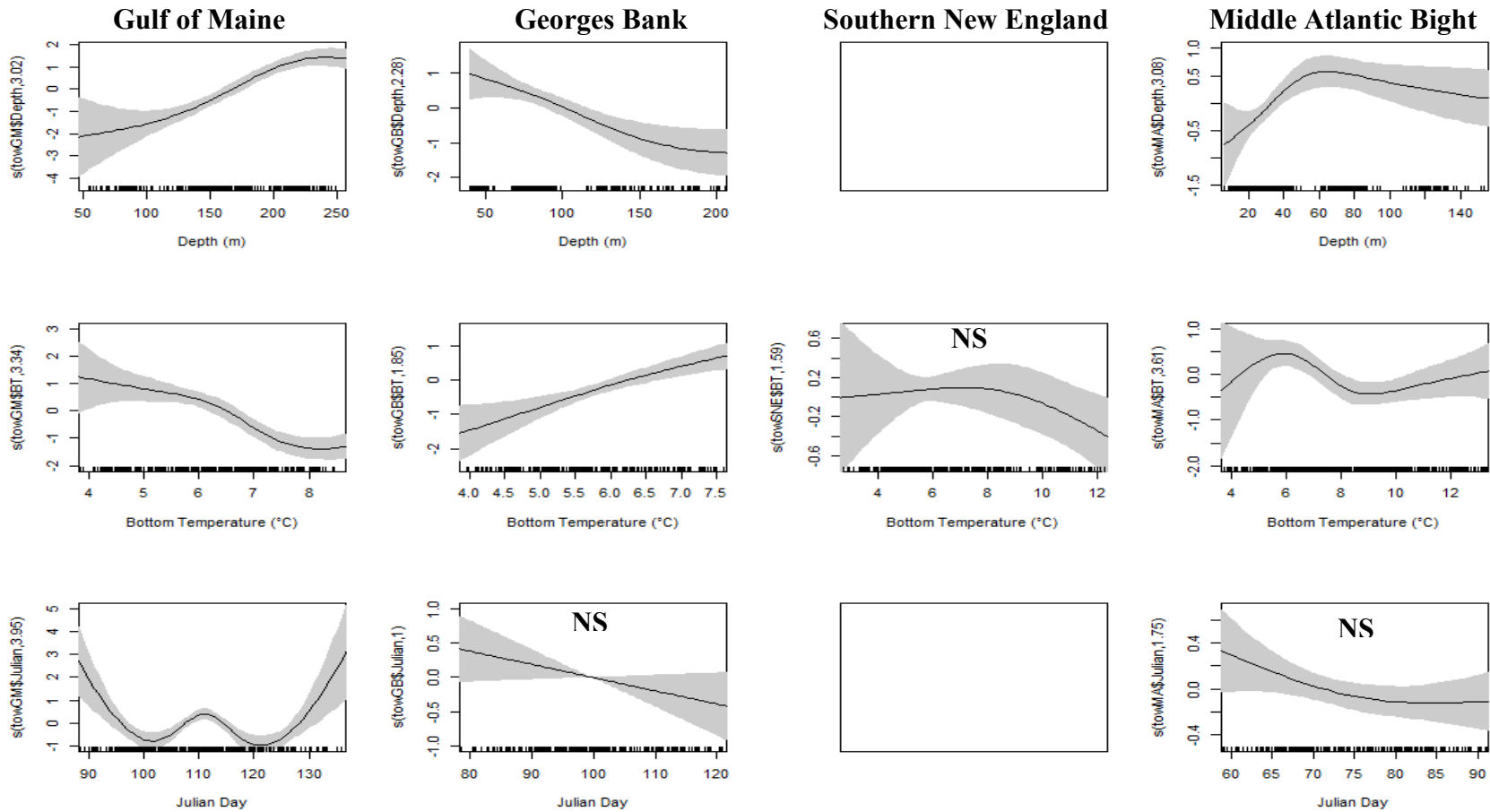


Figure 4G.2. Partial GAM plots identifying the additive effect of each variable on the probability of day-time catch for butterfish during spring. The y-axis represents the degree of smoothing (variable, estimated degrees of freedom) with its range indicative of the relative importance of each covariate. 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 gray region reflects the 95% confidence intervals around the response curves. Absence of term within the optimum model represented by empty box. NS = not significant.

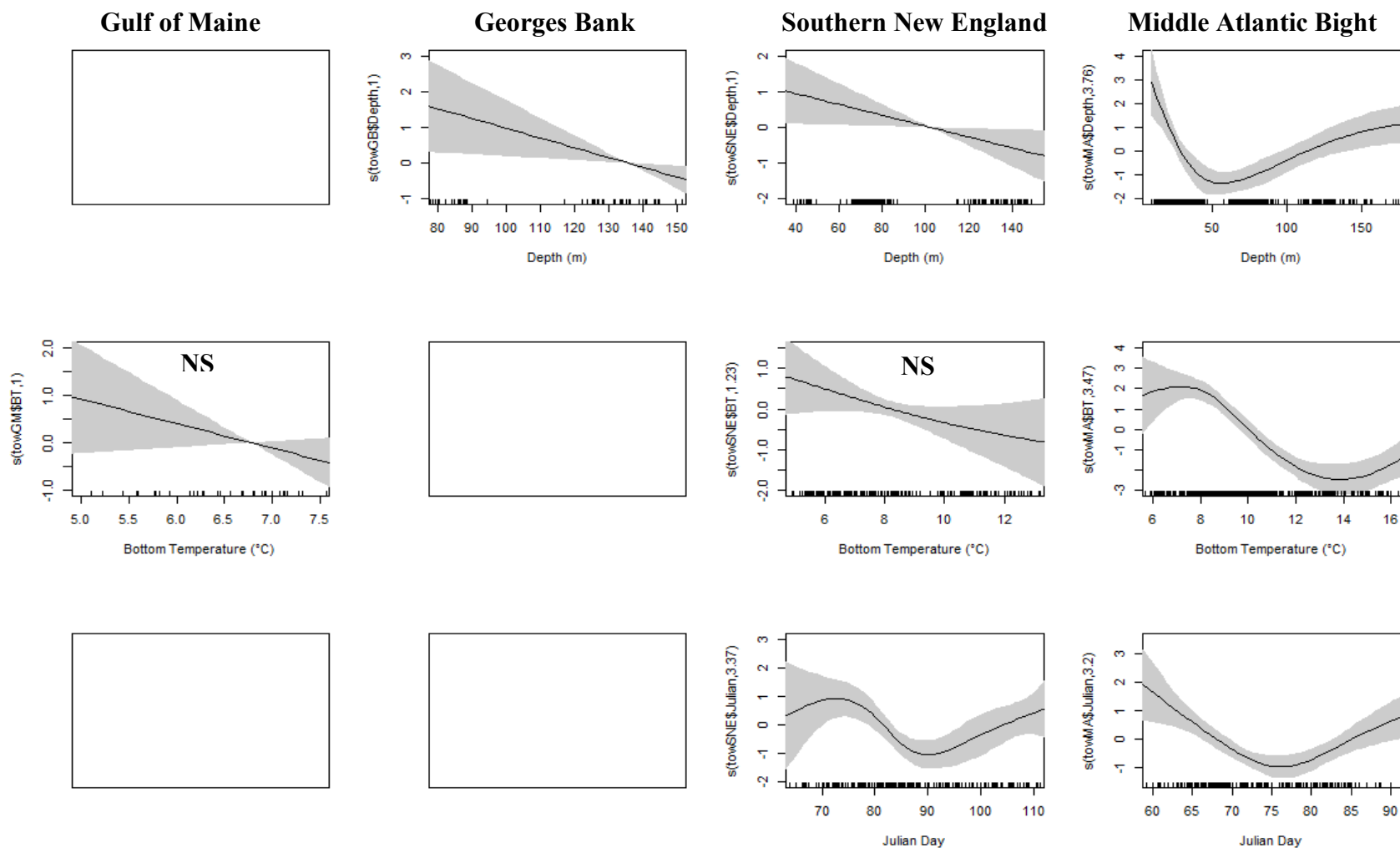


Figure 4G.3. Partial GAM plots identifying the additive effect of each variable on the probability of day-time catch for Atlantic herring during spring. The y-axis represents the degree of smoothing (variable, estimated degrees of freedom) with its range indicative of the relative importance of each 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 gray region reflects the 95% confidence intervals around the response curves. Absence of term within the optimum model represented by empty box. NS = not significant.

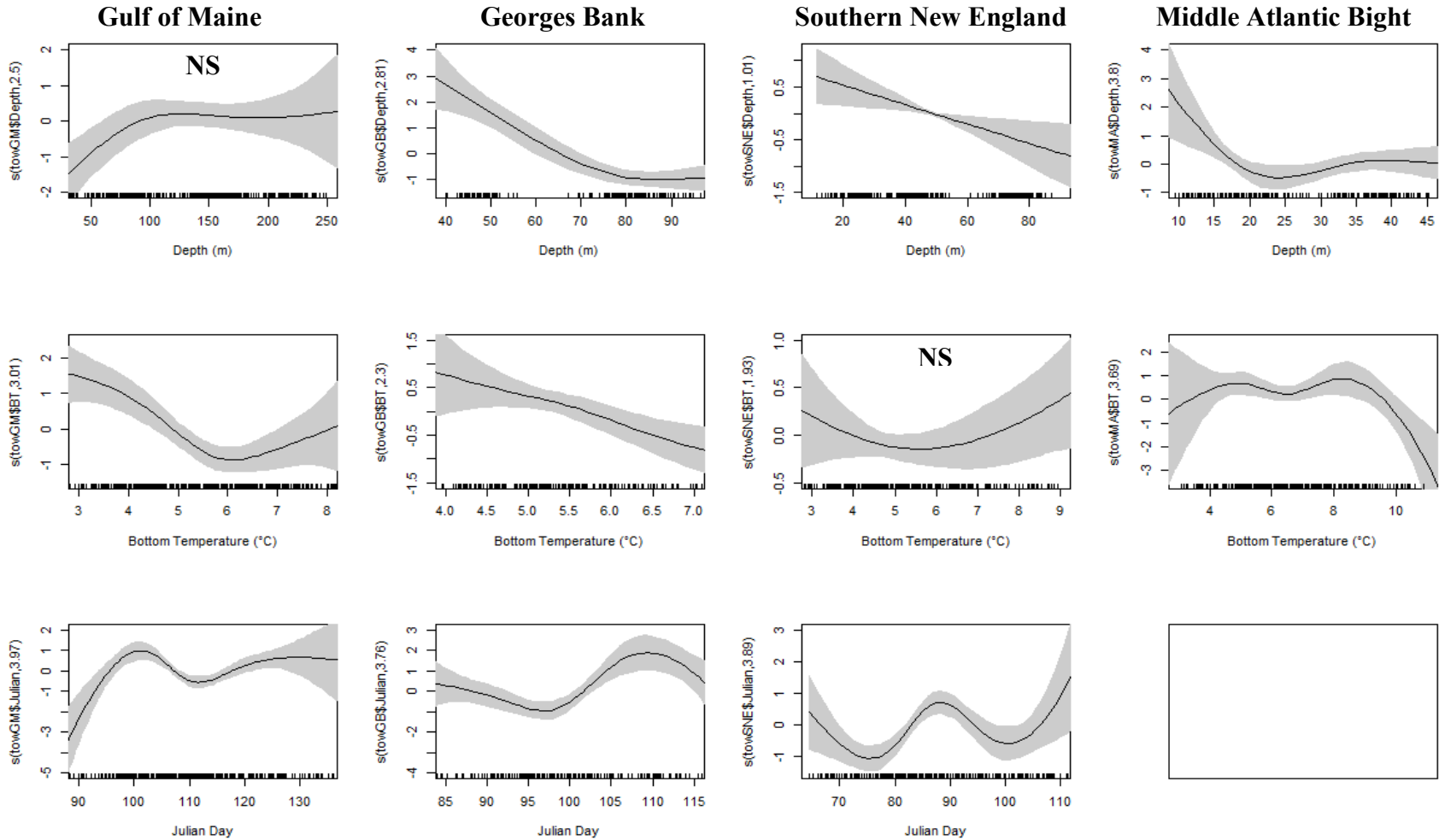


Figure 4G.4. Partial GAM plots identifying the additive effect of each variable on the probability of day-time catch for *Illex* sp. during spring. The y-axis represents the degree of smoothing (variable, estimated degrees of freedom) with its range indicative of the relative importance of each covariate. 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 gray region reflects the 95% confidence intervals around the response curves. Absence of term within the optimum model represented by empty box. NS = not significant.

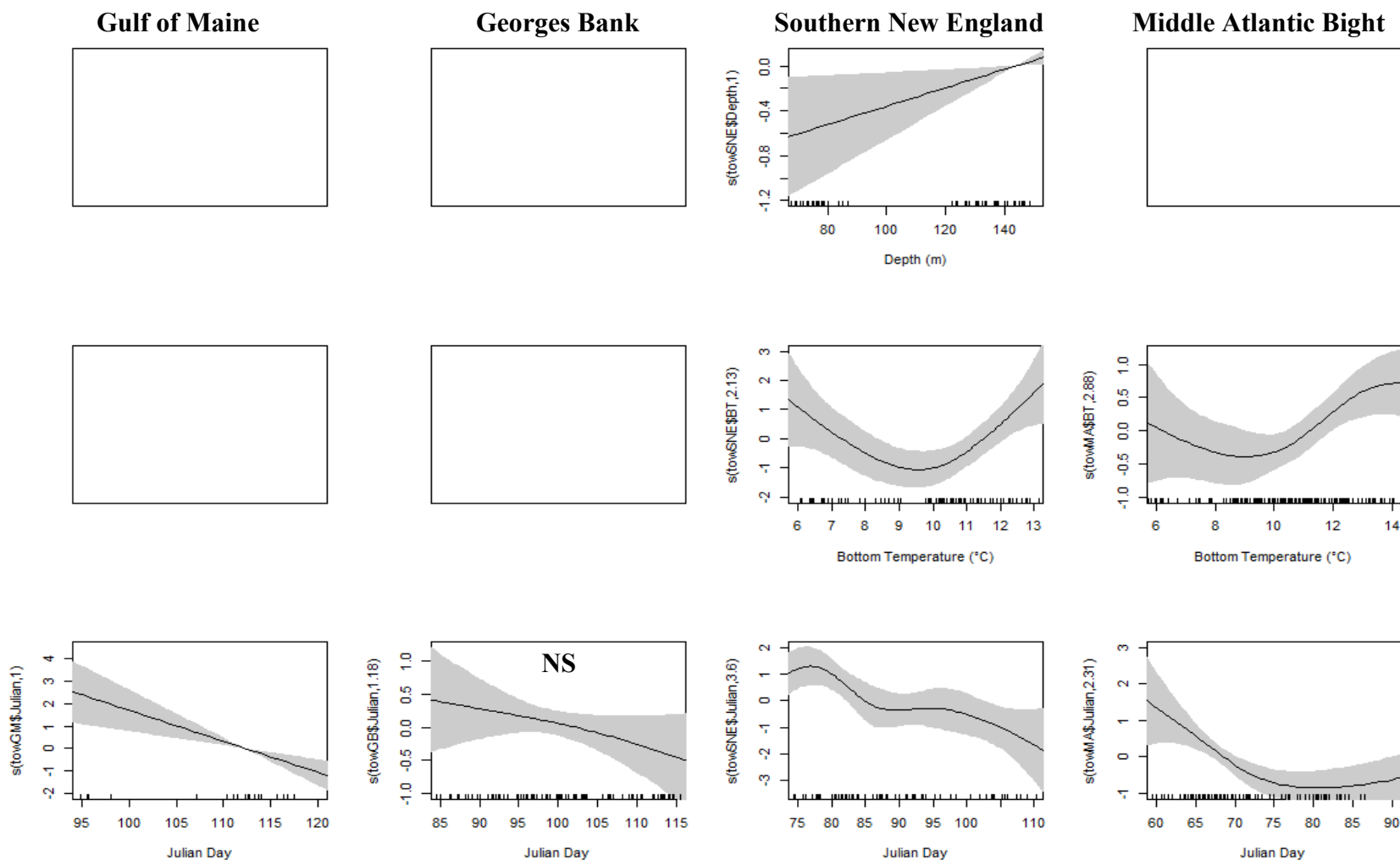


Figure 4G.5. Partial GAM plots identifying the additive effect of each variable on the probability of day-time catch for *Loligo* sp. during spring. The y-axis represents the degree of smoothing (variable, estimated degrees of freedom) with its range indicative of the relative importance of each covariate. 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 gray region reflects the 95% confidence intervals around the response curves. Absence of term within the optimum model represented by empty box. NS = not significant.

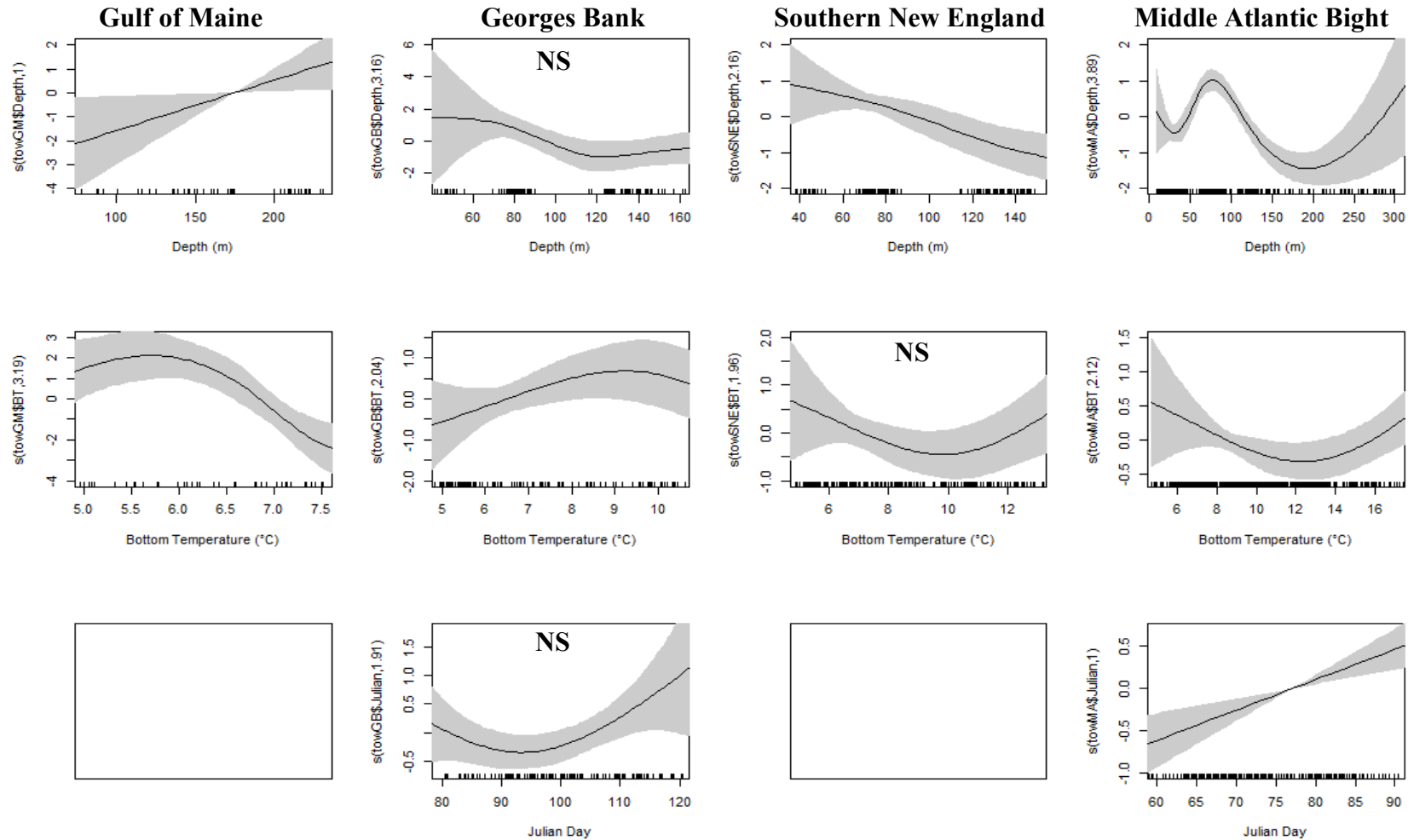


Figure 4G.6. Partial GAM plots identifying the additive effect of each variable on the probability of day-time catch for Atlantic mackerel during spring. The y-axis represents the degree of smoothing (variable, estimated degrees of freedom) with its range indicative of the relative importance of each 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 gray region reflects the 95% confidence intervals around the response curves. Absence of term within the optimum model represented by empty box. NS = not significant.

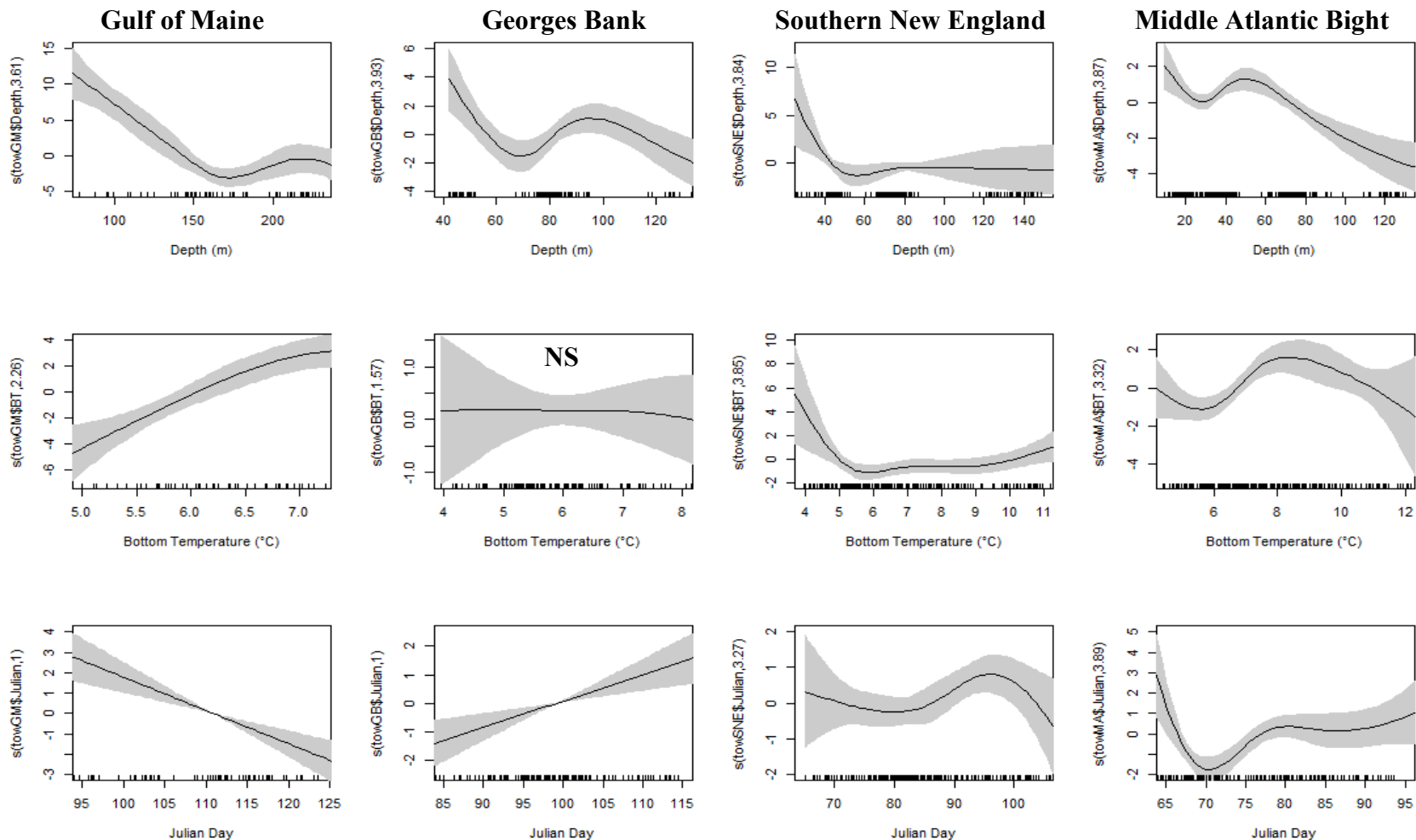


Figure 4G.7. Relationships between the Pearson residuals and explanatory variables (depth, bottom temperature, and Julian day) based on the optimal spiny dogfish GAM during spring.

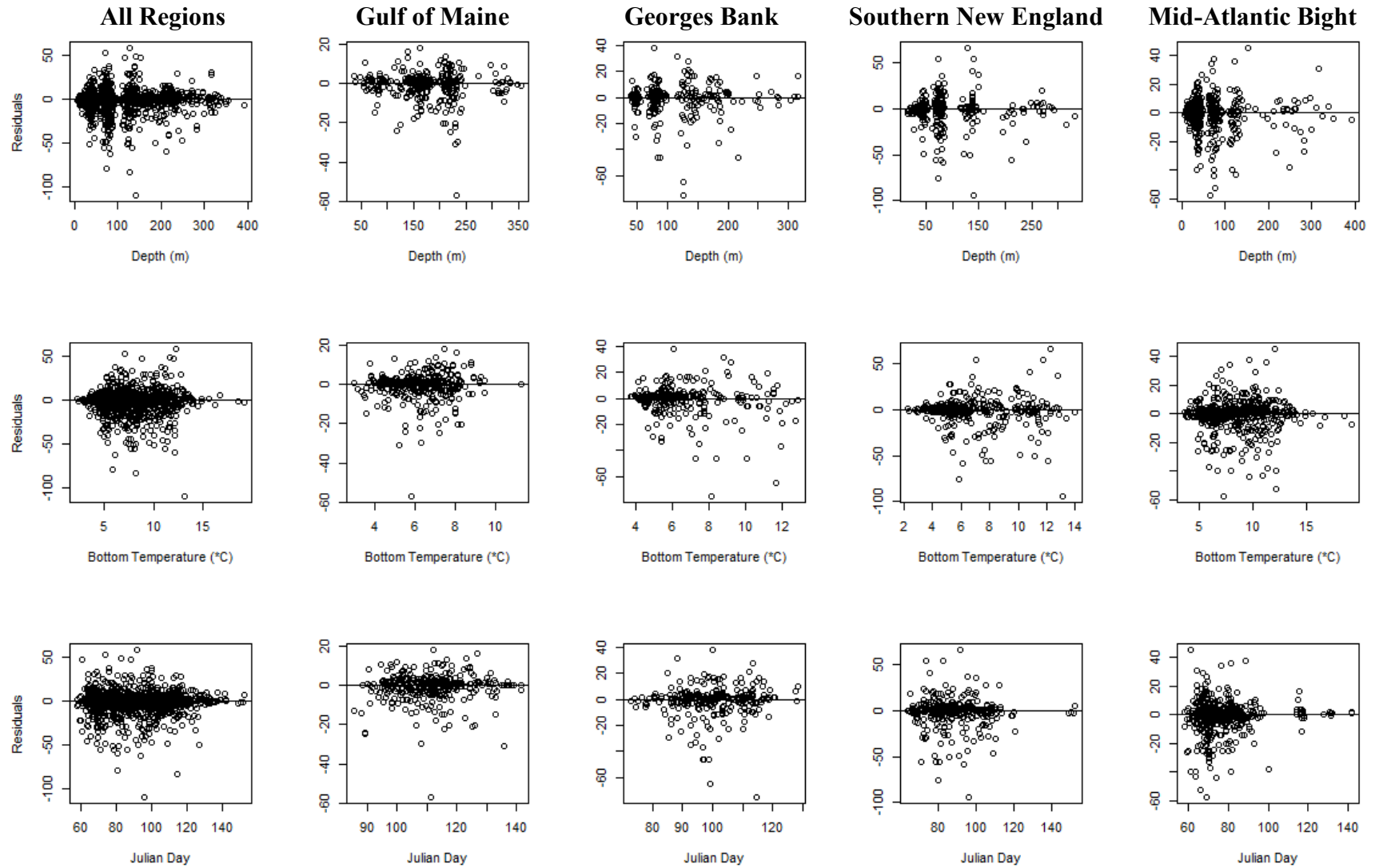


Figure 4G.8. Relationships between the Pearson residuals and explanatory variables (depth, bottom temperature, and Julian day) based on the optimal butterfish GAM during spring.

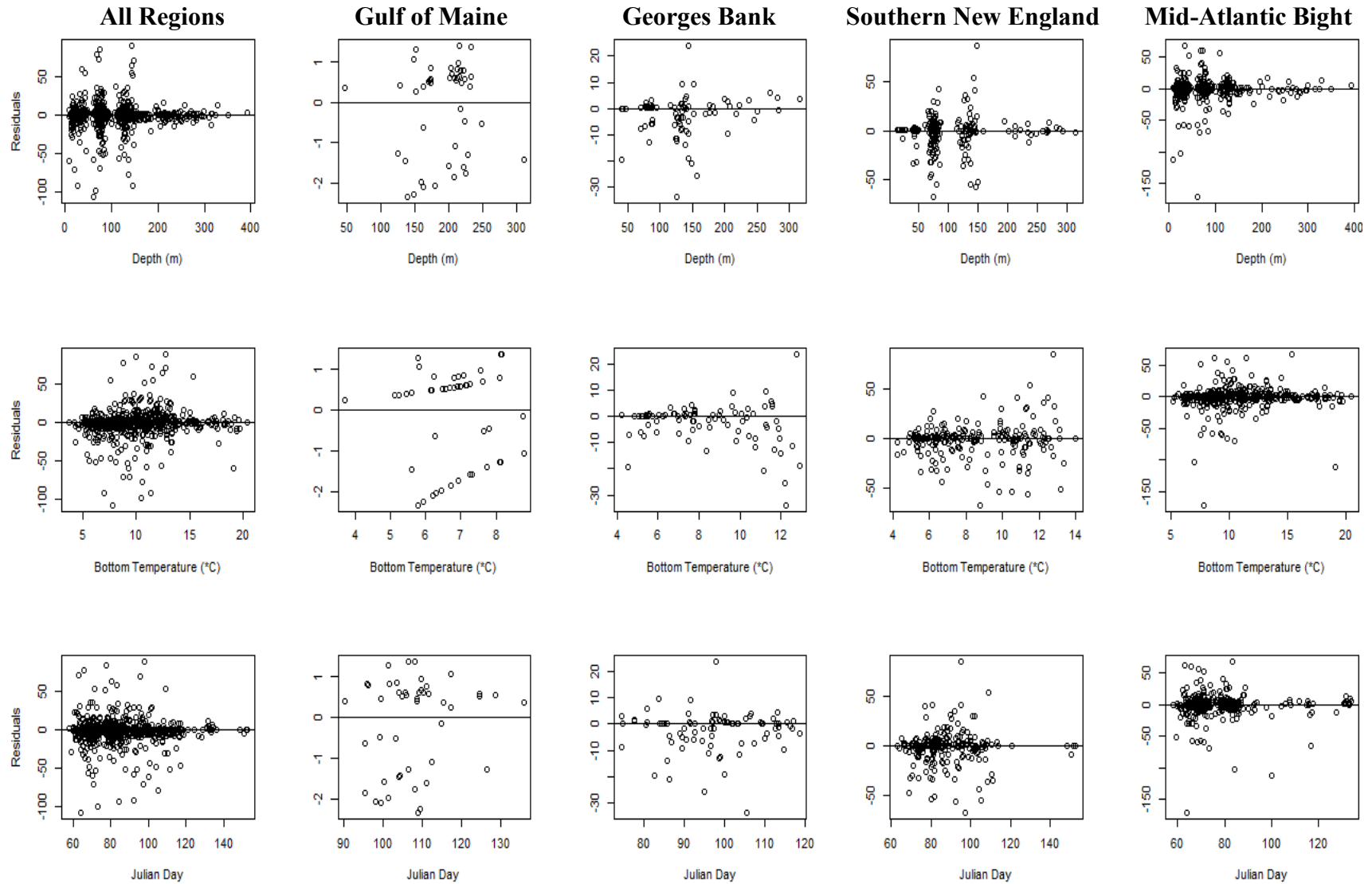


Figure 4G.9. Relationships between the Pearson residuals and explanatory variables (depth, bottom temperature, and Julian day) based on the optimal Atlantic herring GAM during spring.

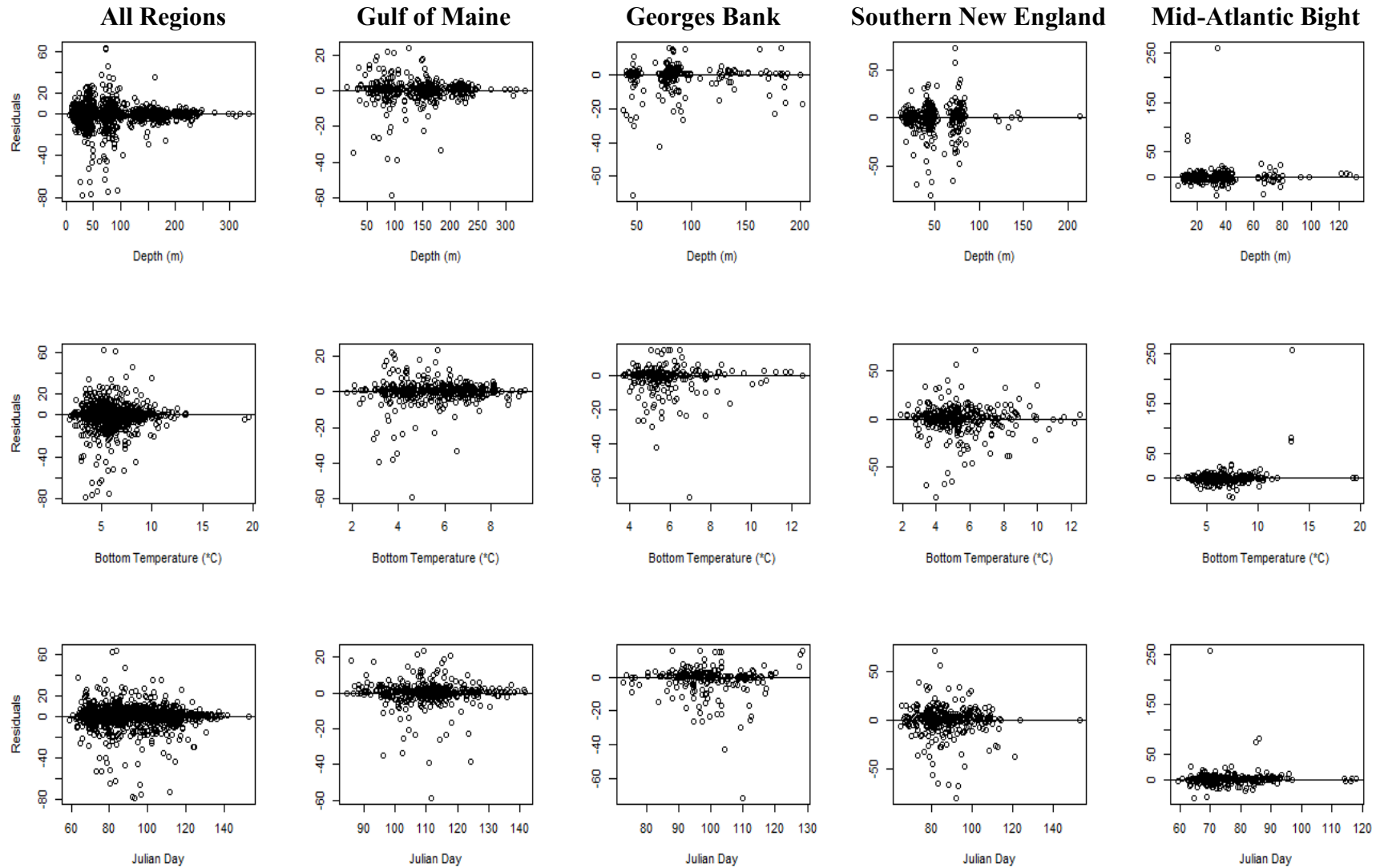


Figure 4G.10. Relationships between the Pearson residuals and explanatory variables (depth, bottom temperature, and Julian day) based on the optimal *Illex* sp. GAM during spring.

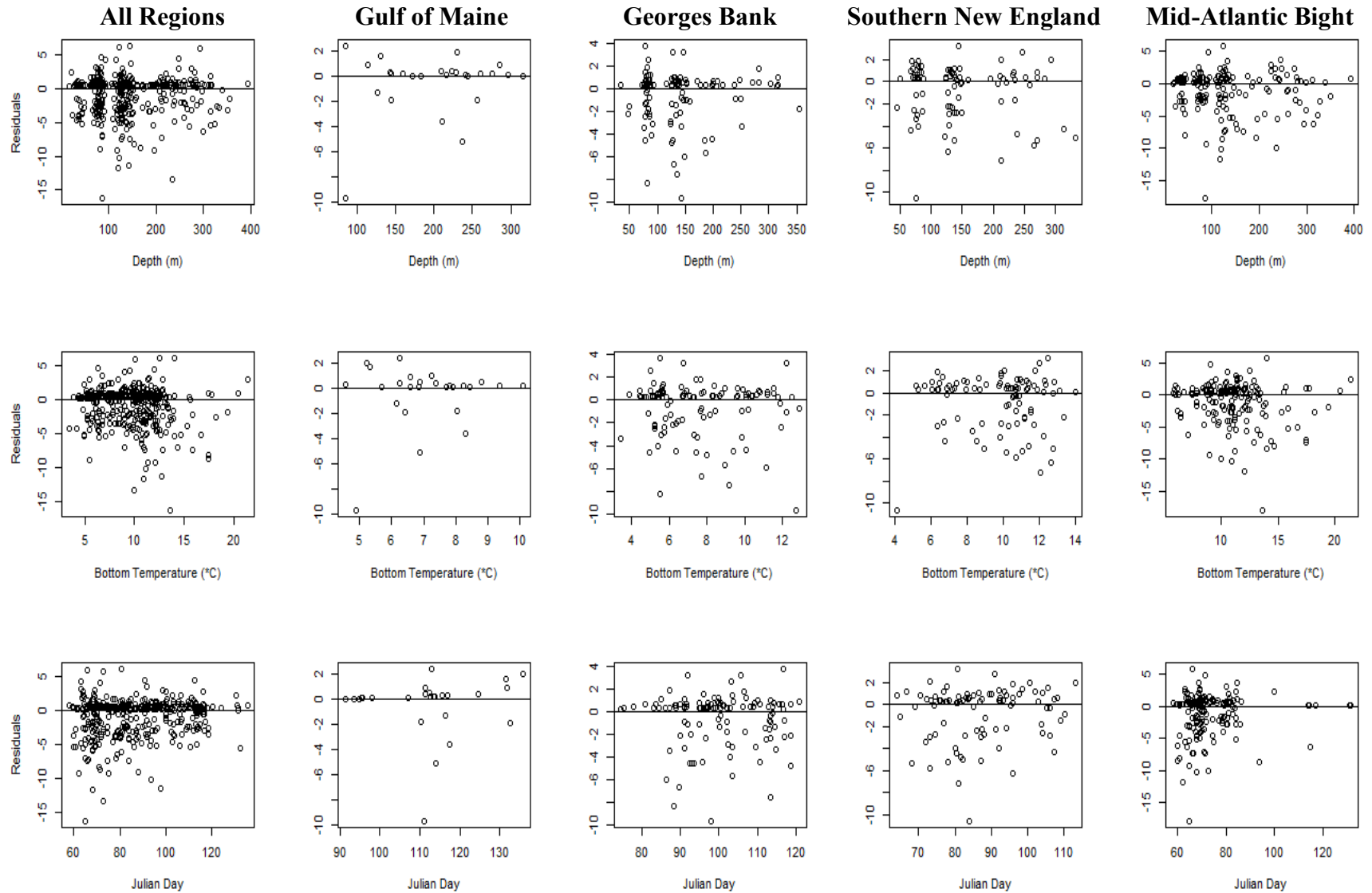


Figure 4G.11. Relationships between the Pearson residuals and explanatory variables (depth, bottom temperature, and Julian day) based on the optimal *Loligo* sp. GAM during spring.

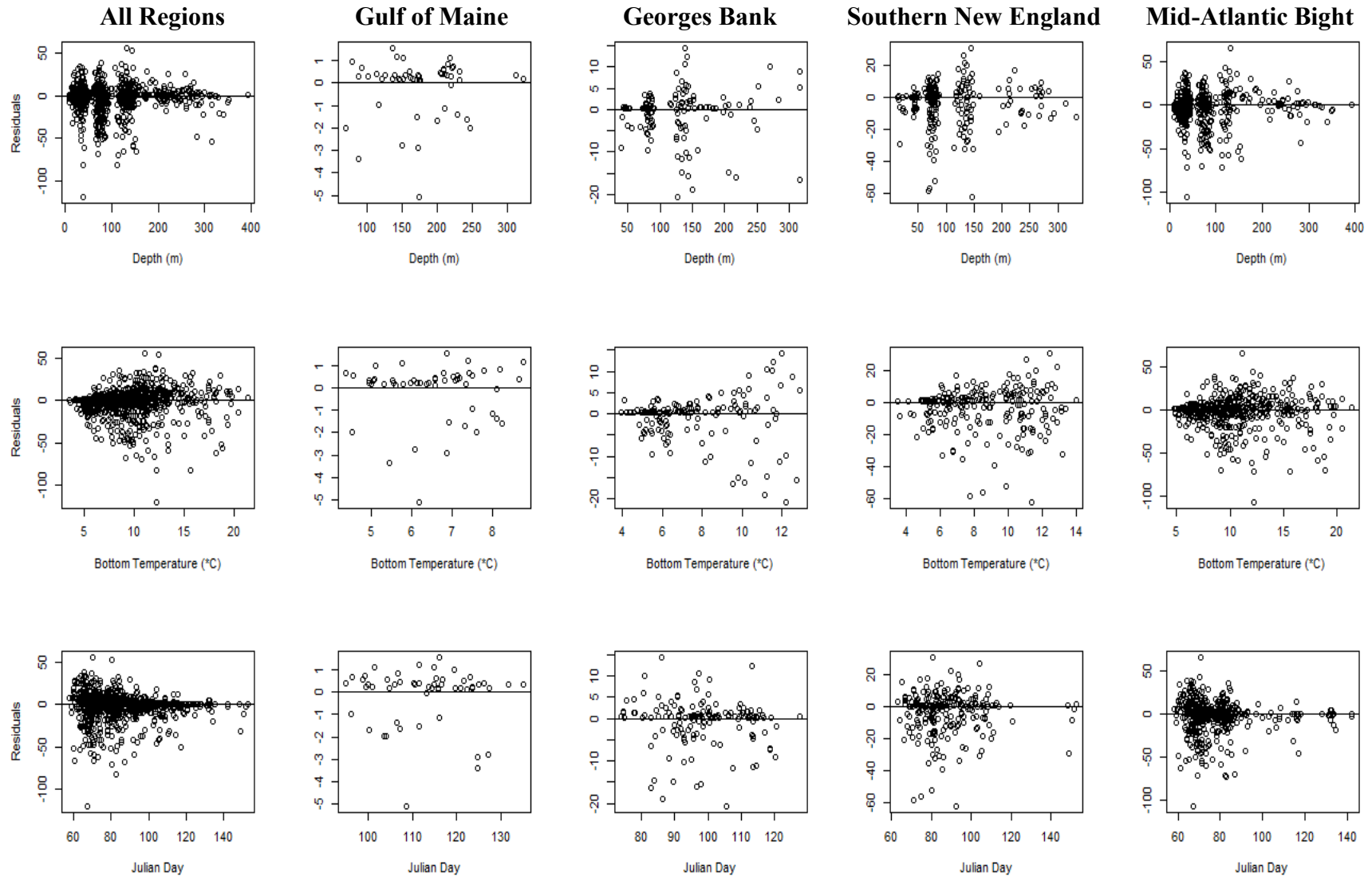
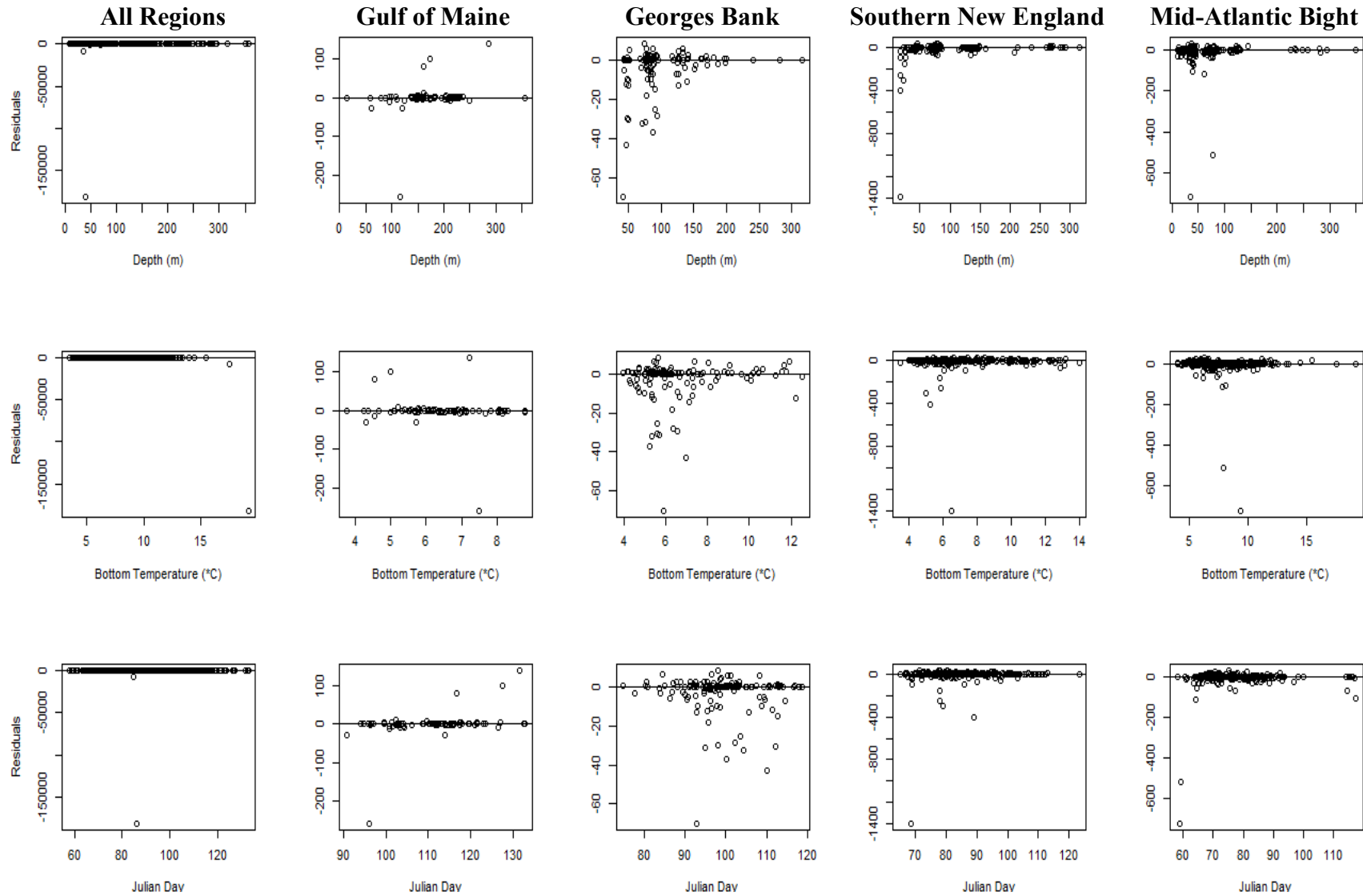


Figure 4G.12. Relationships between the Pearson residuals and explanatory variables (depth, bottom temperature, and Julian day) based on the optimal Atlantic mackerel GAM during spring.



Appendix 4H. Full GAM Results Concerning the Probability of Day-time Catch During Autumn

Figure 4H.1. Partial GAM plots identifying the additive effect of each variable on the probability of day-time catch for all spiny dogfish combined during autumn. The y-axis represents the degree of smoothing (variable, estimated degrees of freedom) 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 gray region reflects the 95% confidence intervals around the response curves. Absence of term within the optimum model represented by empty box.

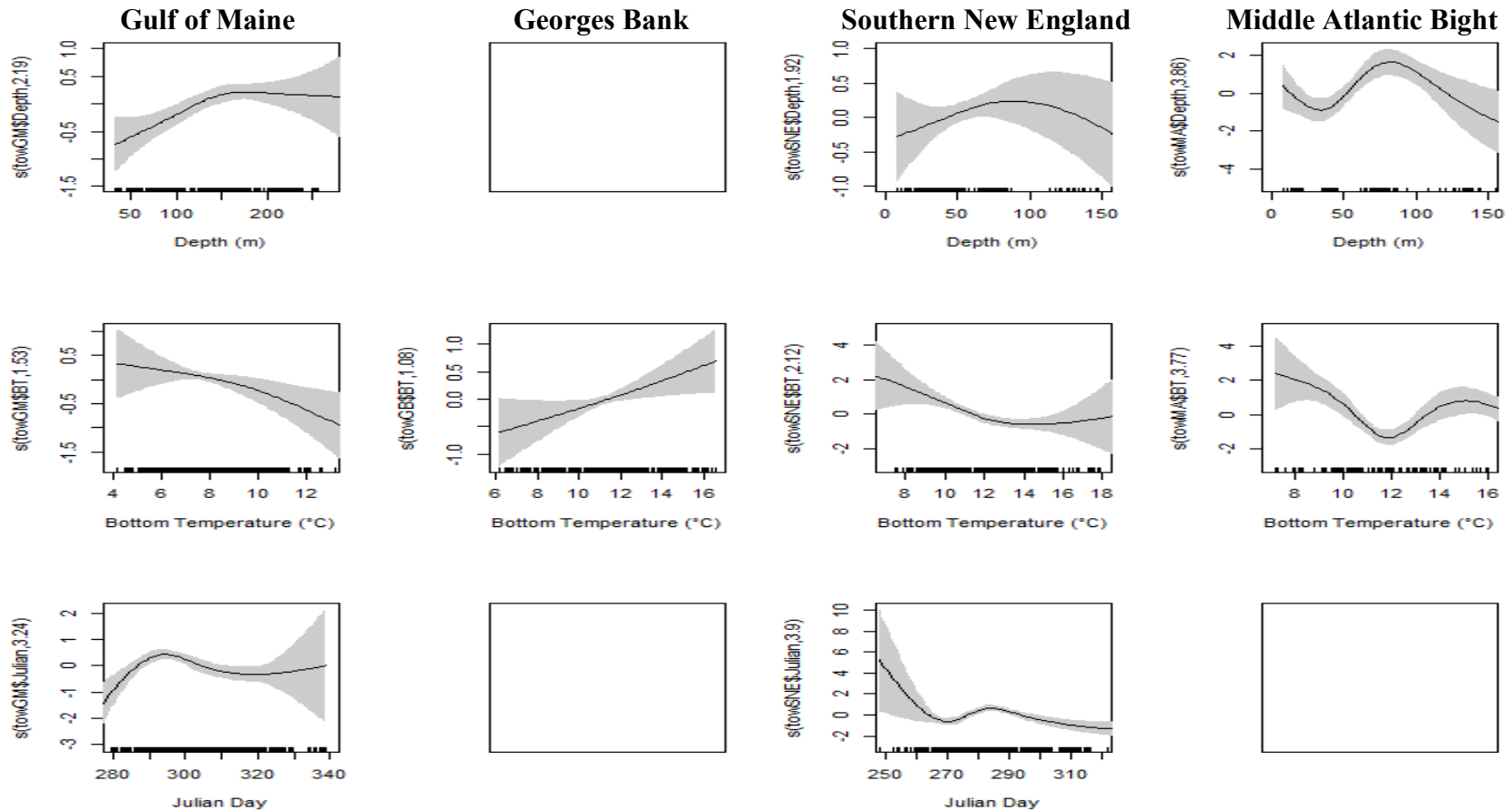


Figure 4H.2. Partial GAM plots identifying the additive effect of each variable on the probability of day-time catch for butterfish during autumn. The y-axis represents the degree of smoothing (variable, estimated degrees of freedom) with its range indicative of the relative importance of each covariate. 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 gray region reflects the 95% confidence intervals around the response curves. Absence of term within the optimum model represented by empty box. NS = not significant.

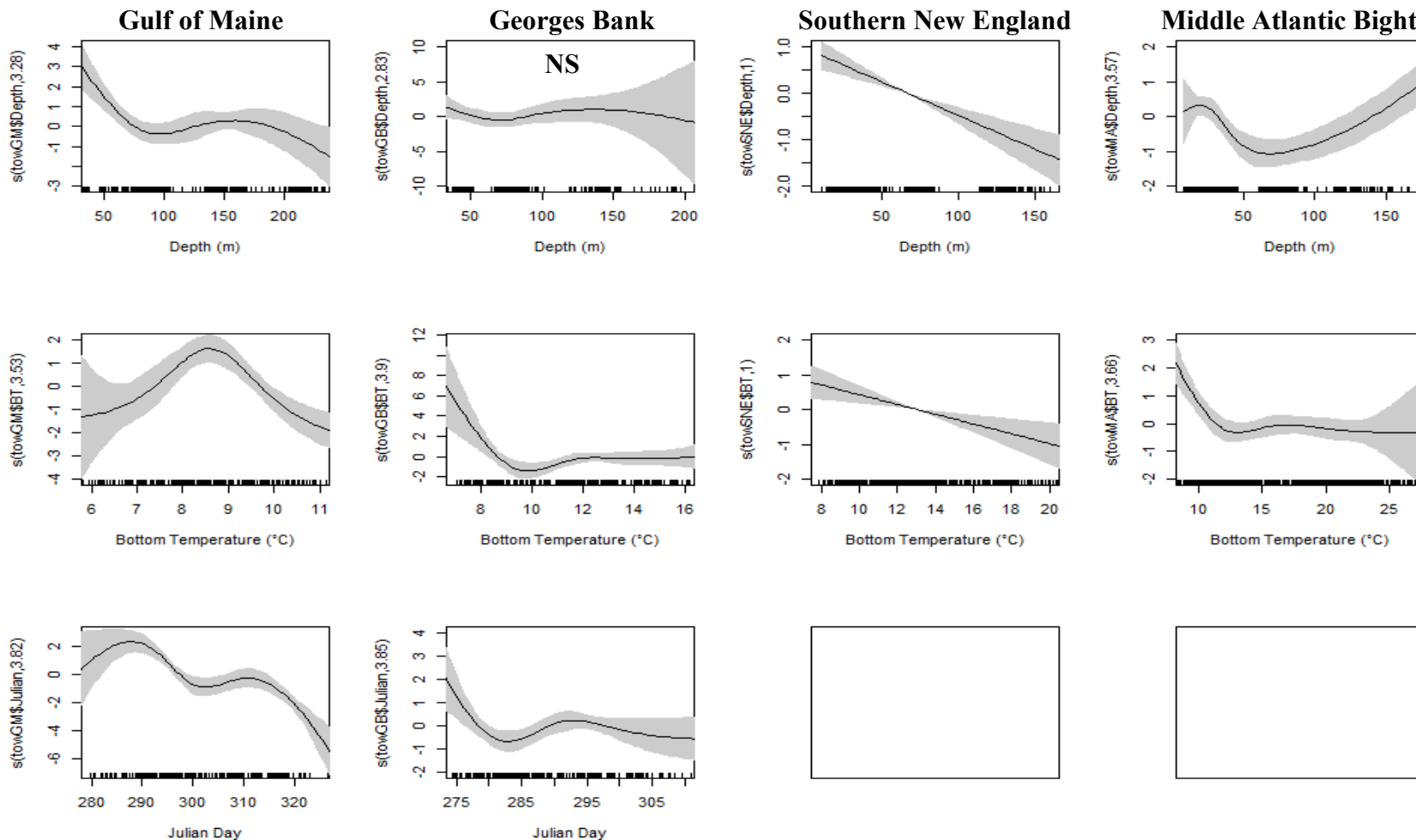


Figure 4H.3. Partial GAM plots identifying the additive effect of each variable on the probability of day-time catch for Atlantic herring during autumn. The y-axis represents the degree of smoothing (variable, estimated degrees of freedom) with its range indicative of the relative importance of each 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 gray region reflects the 95% confidence intervals around the response curves. Absence of term within the optimum model represented by empty box.

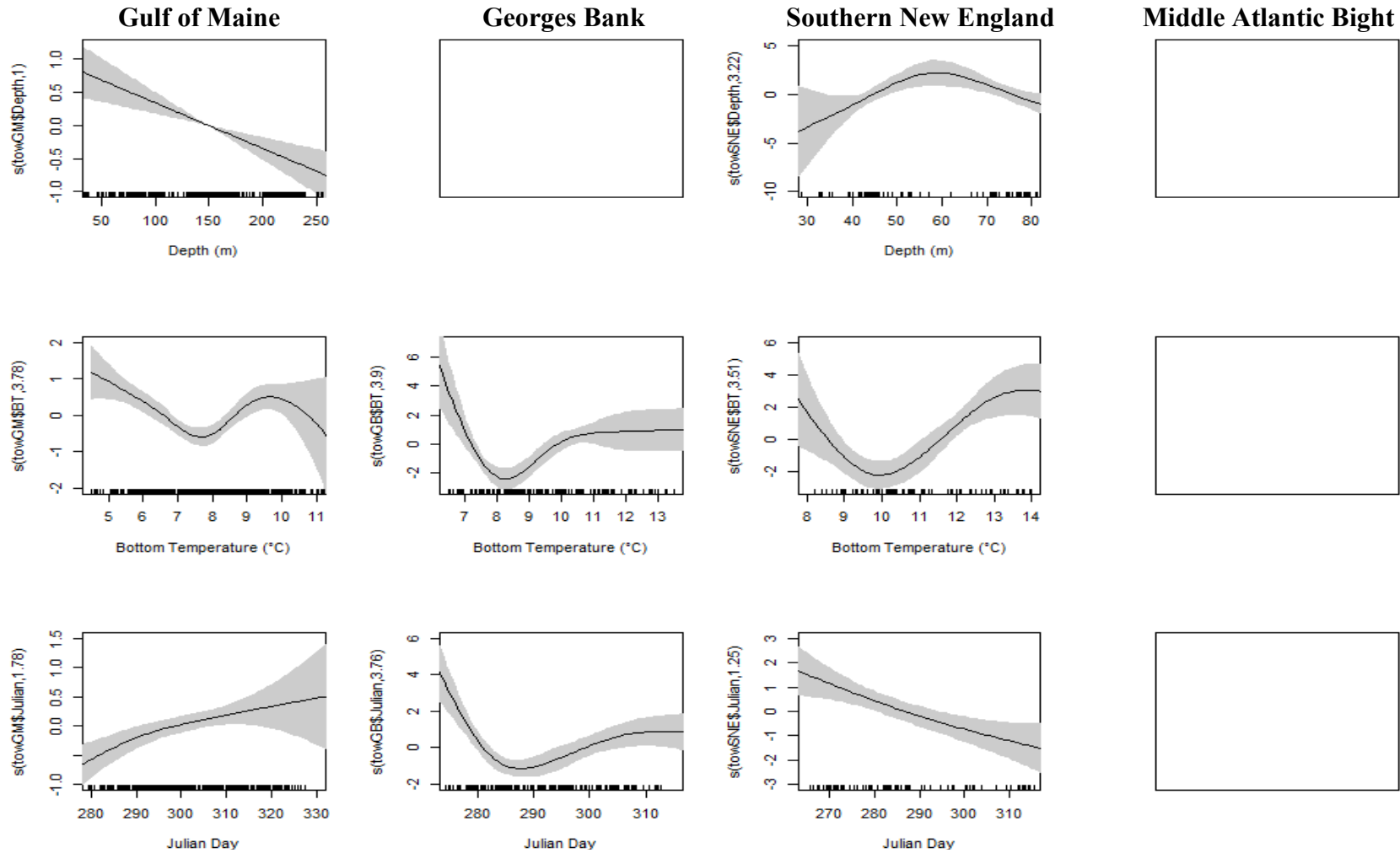


Figure 4H.4. Partial GAM plots identifying the additive effect of each variable on the probability of day-time catch for *Illex* sp. during autumn. The y-axis represents the degree of smoothing (variable, estimated degrees of freedom) with its range indicative of the relative importance of each covariate. 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 gray region reflects the 95% confidence intervals around the response curves. Absence of term within the optimum model represented by empty box.

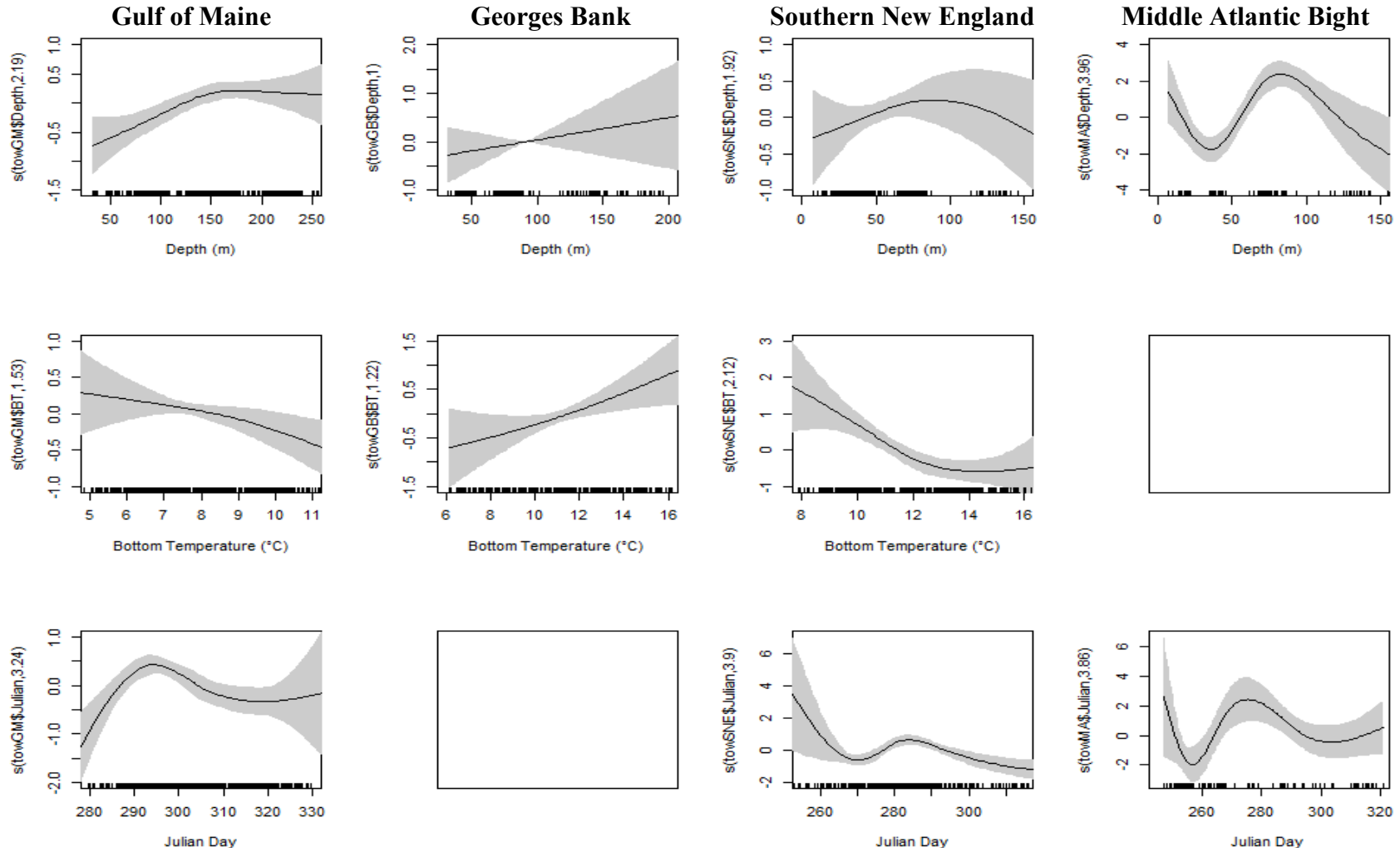


Figure 4H.5. Partial GAM plots identifying the additive effect of each variable on the probability of day-time catch for *Loligo* sp. during autumn. The y-axis represents the degree of smoothing (variable, estimated degrees of freedom) with its range indicative of the relative importance of each covariate. 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 gray region reflects the 95% confidence intervals around the response curves. Absence of term within the optimum model represented by empty box. NS = not significant.

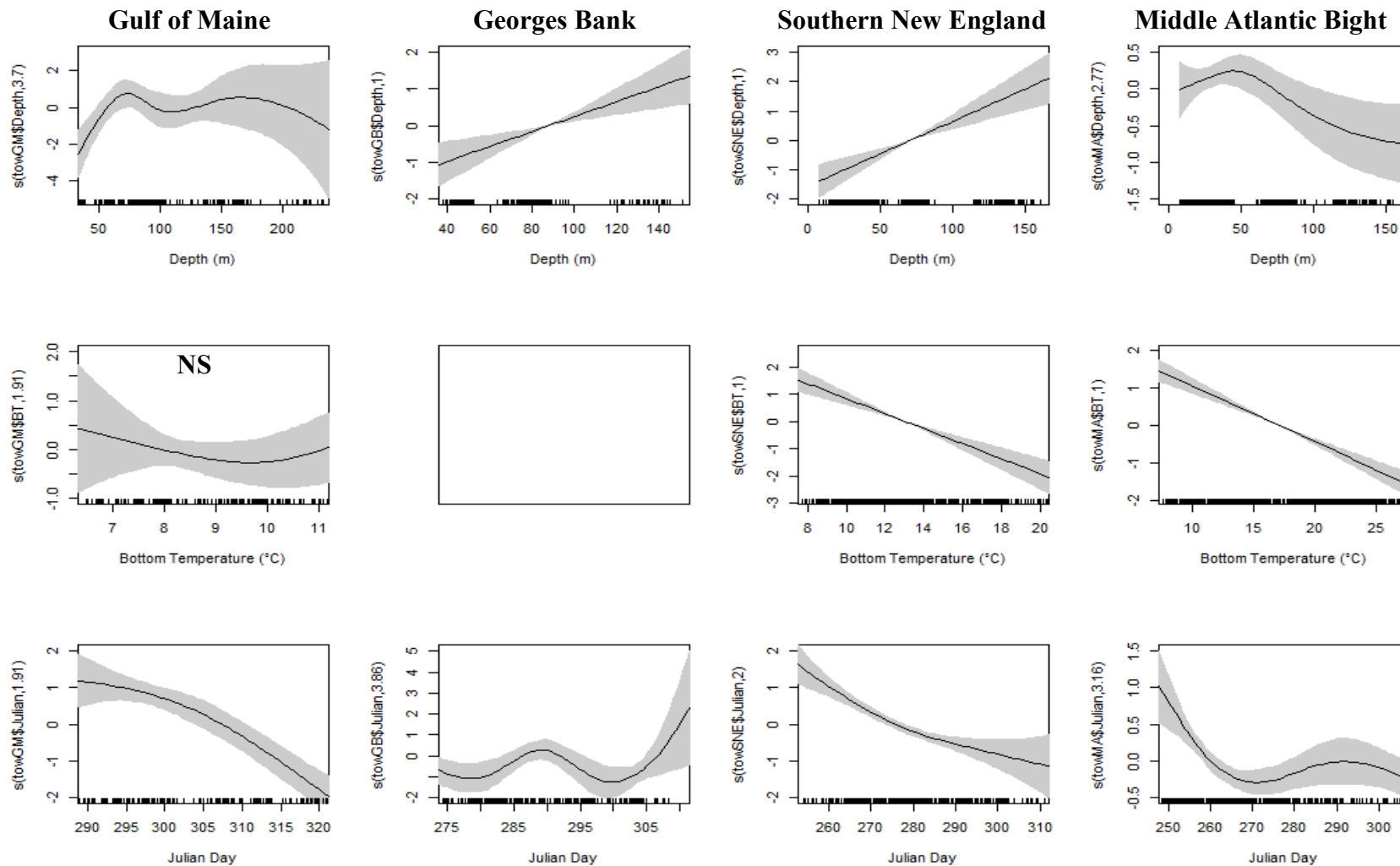


Figure 4H.6. Partial GAM plots identifying the additive effect of each variable on the probability of day-time catch for Atlantic mackerel during autumn. The y-axis represents the degree of smoothing (variable, estimated degrees of freedom) with its range indicative of the relative importance of each 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 gray region reflects the 95% confidence intervals around the response curves. Absence of term within the optimum model represented by empty box.

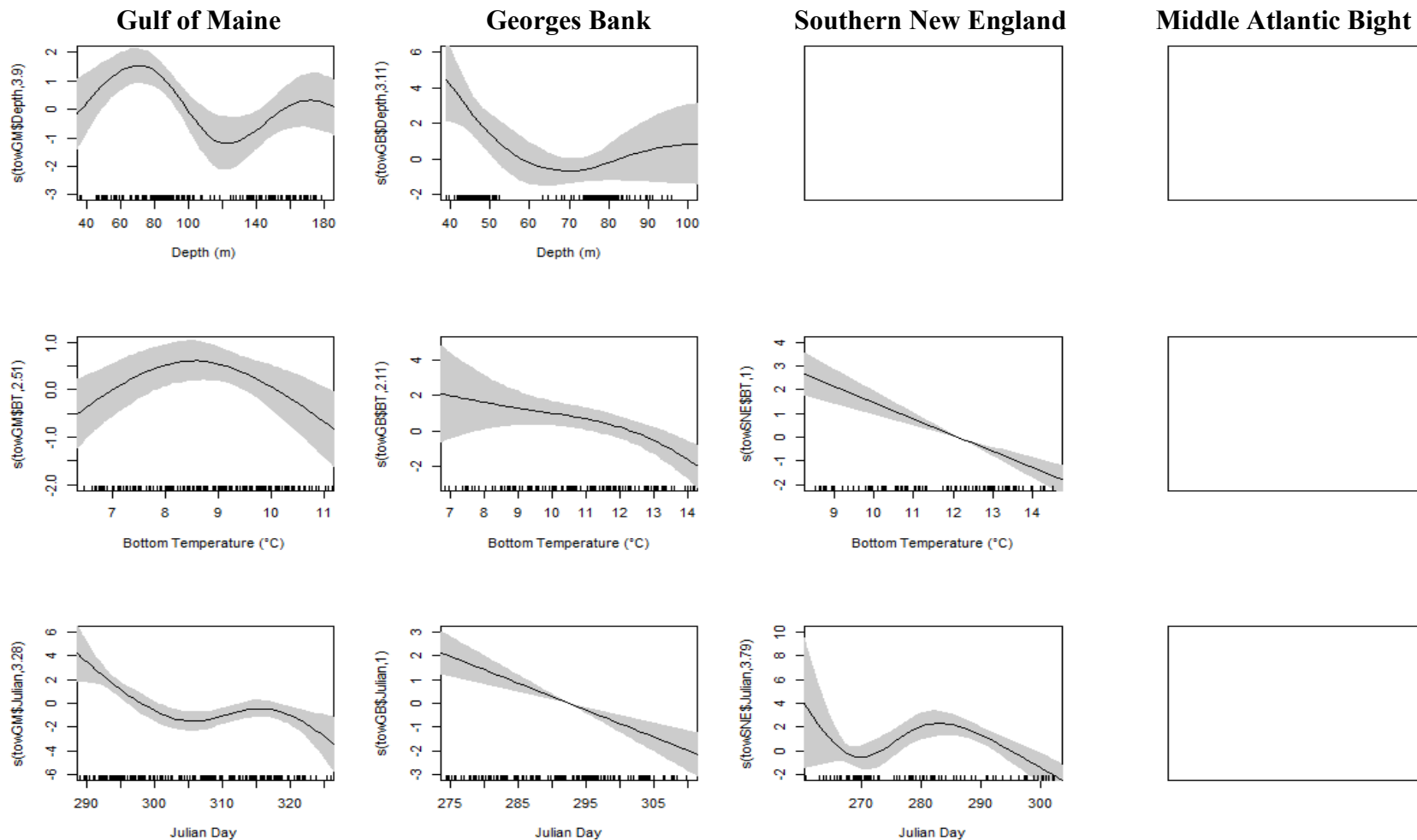


Figure 4H.7. Relationships between the Pearson residuals and explanatory variables (depth, bottom temperature, and Julian day) based on the optimal spiny dogfish GAM during autumn.

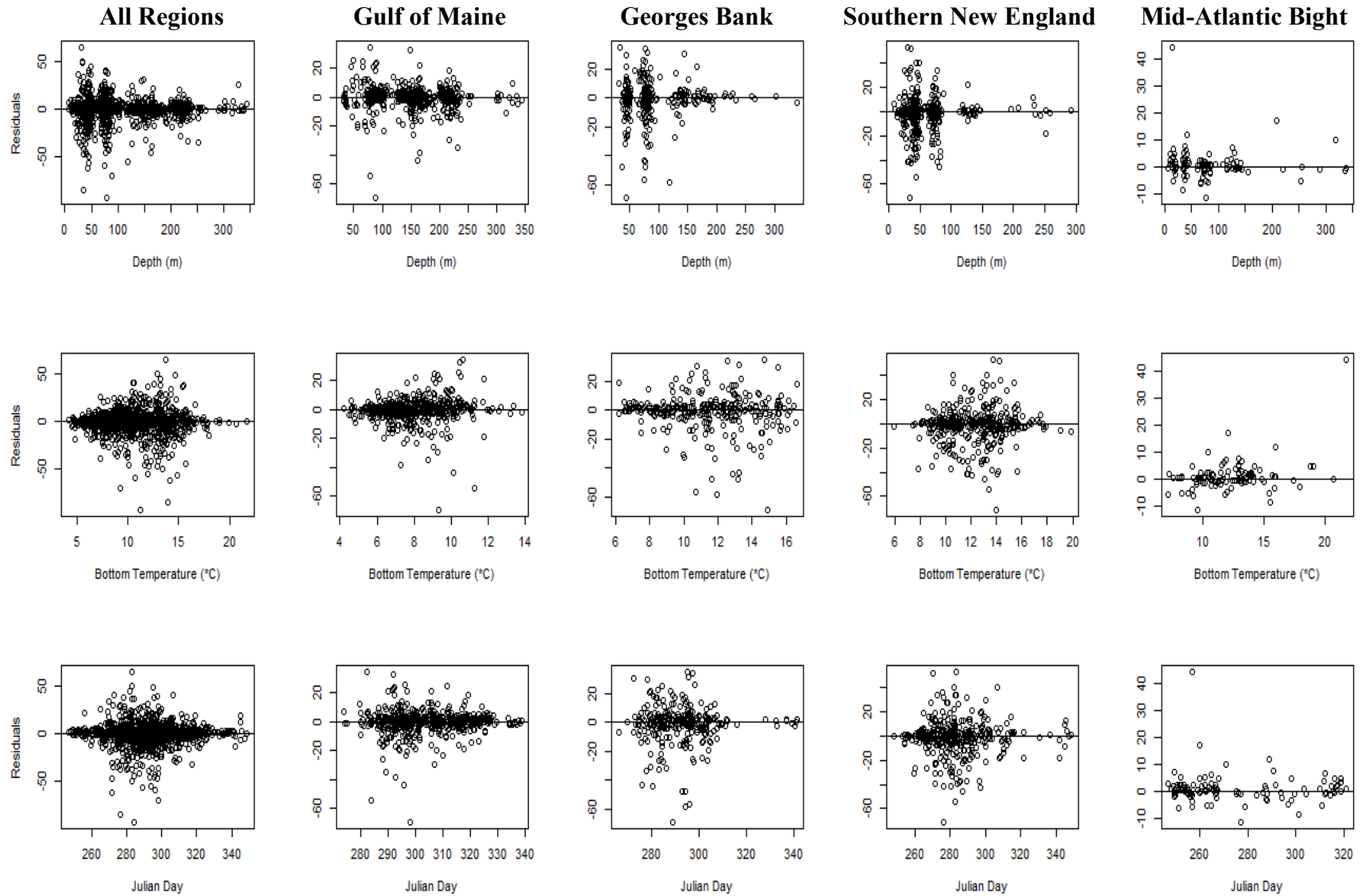


Figure 4H.8. Relationships between the Pearson residuals and explanatory variables (depth, bottom temperature, and Julian day) based on the optimal butterfish GAM during autumn.

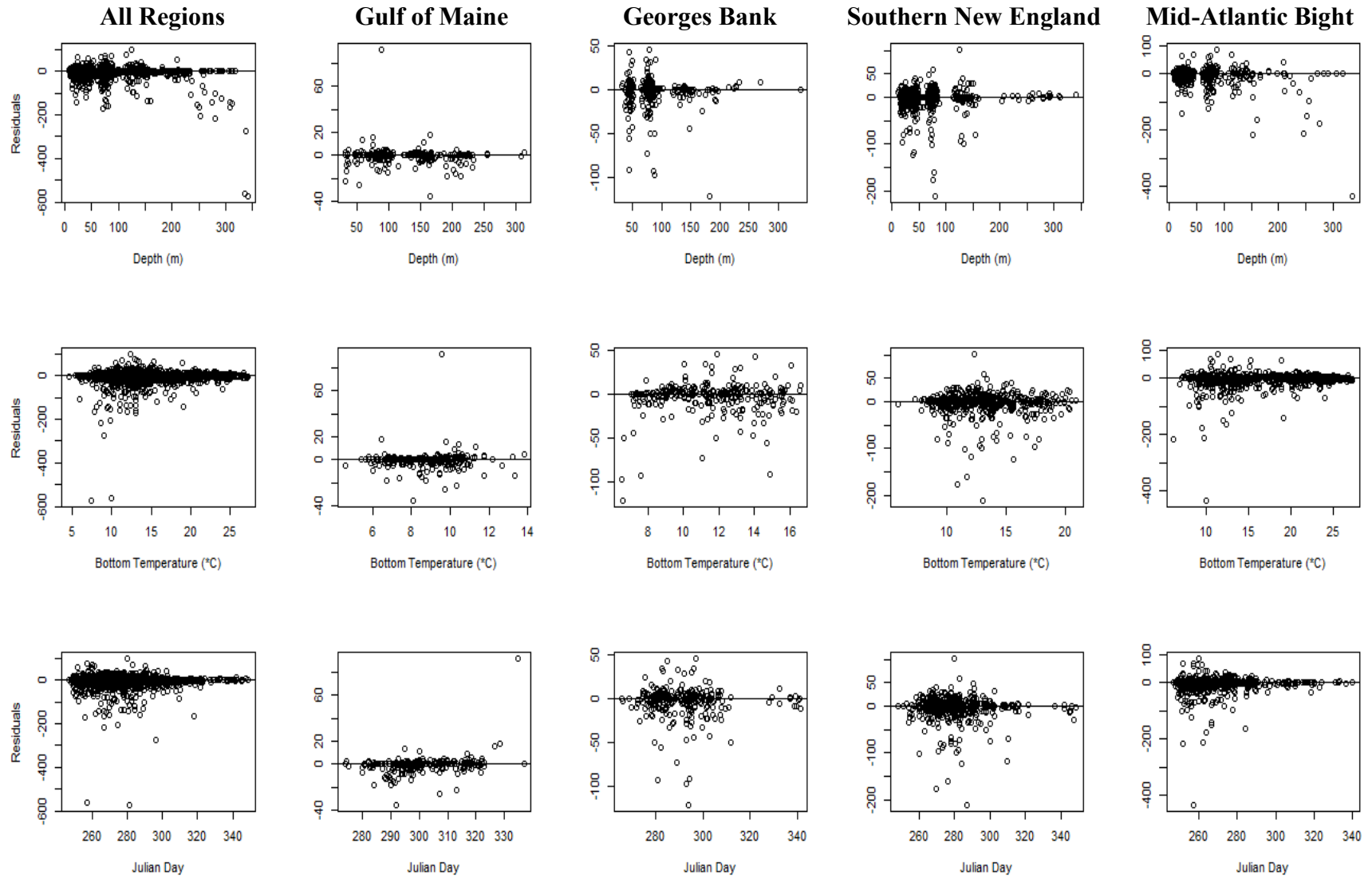


Figure 4H.9. Relationships between the Pearson residuals and explanatory variables (depth, bottom temperature, and Julian day) based on the optimal Atlantic herring GAM during autumn.

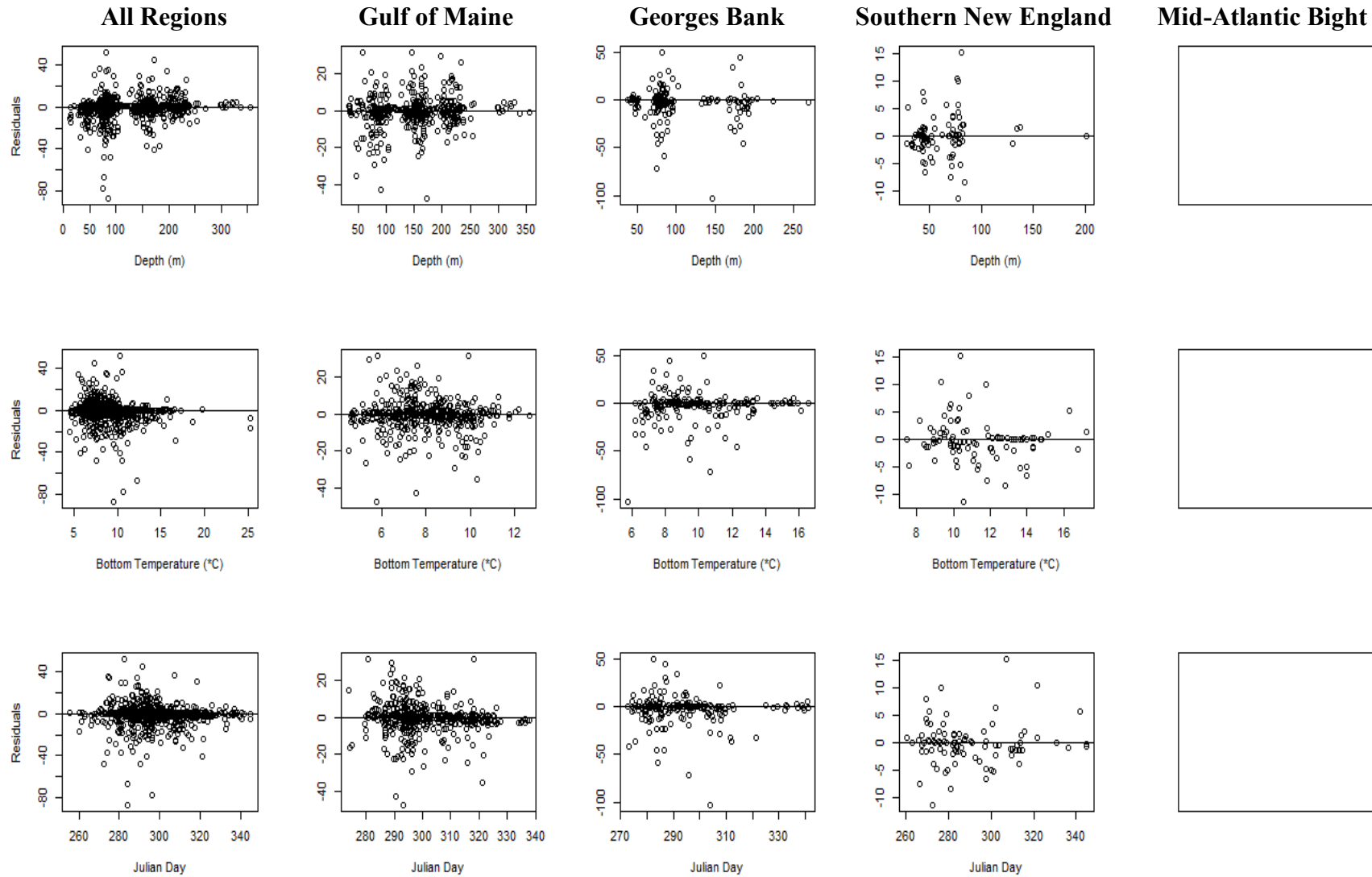


Figure 4H.10. Relationships between the Pearson residuals and explanatory variables (depth, bottom temperature, and Julian day) based on the optimal *Illex* sp. GAM during autumn.

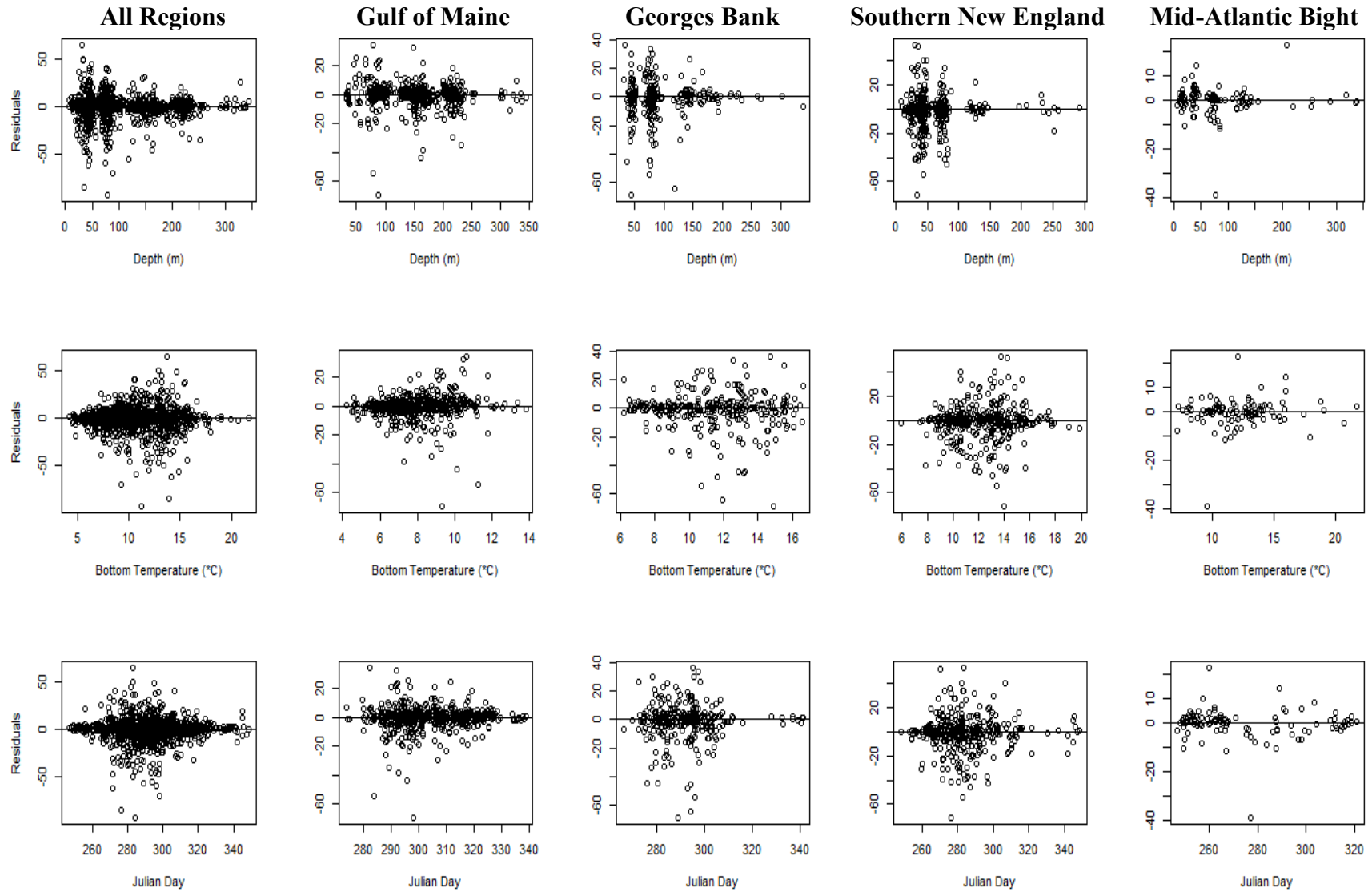


Figure 4H.11 Relationships between the Pearson residuals and explanatory variables (depth, bottom temperature, and Julian day) based on the optimal *Loligo* sp. GAM during autumn.

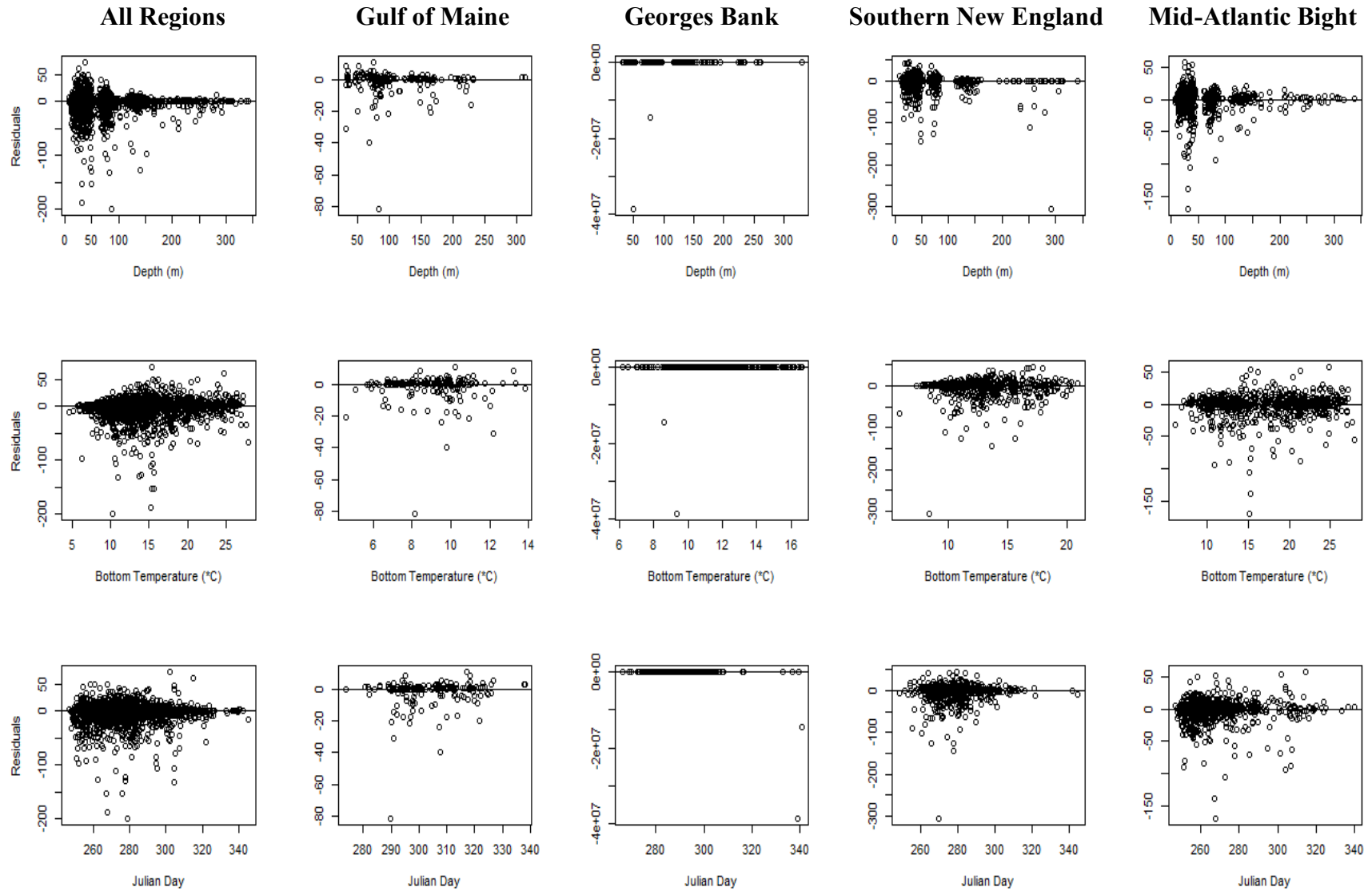
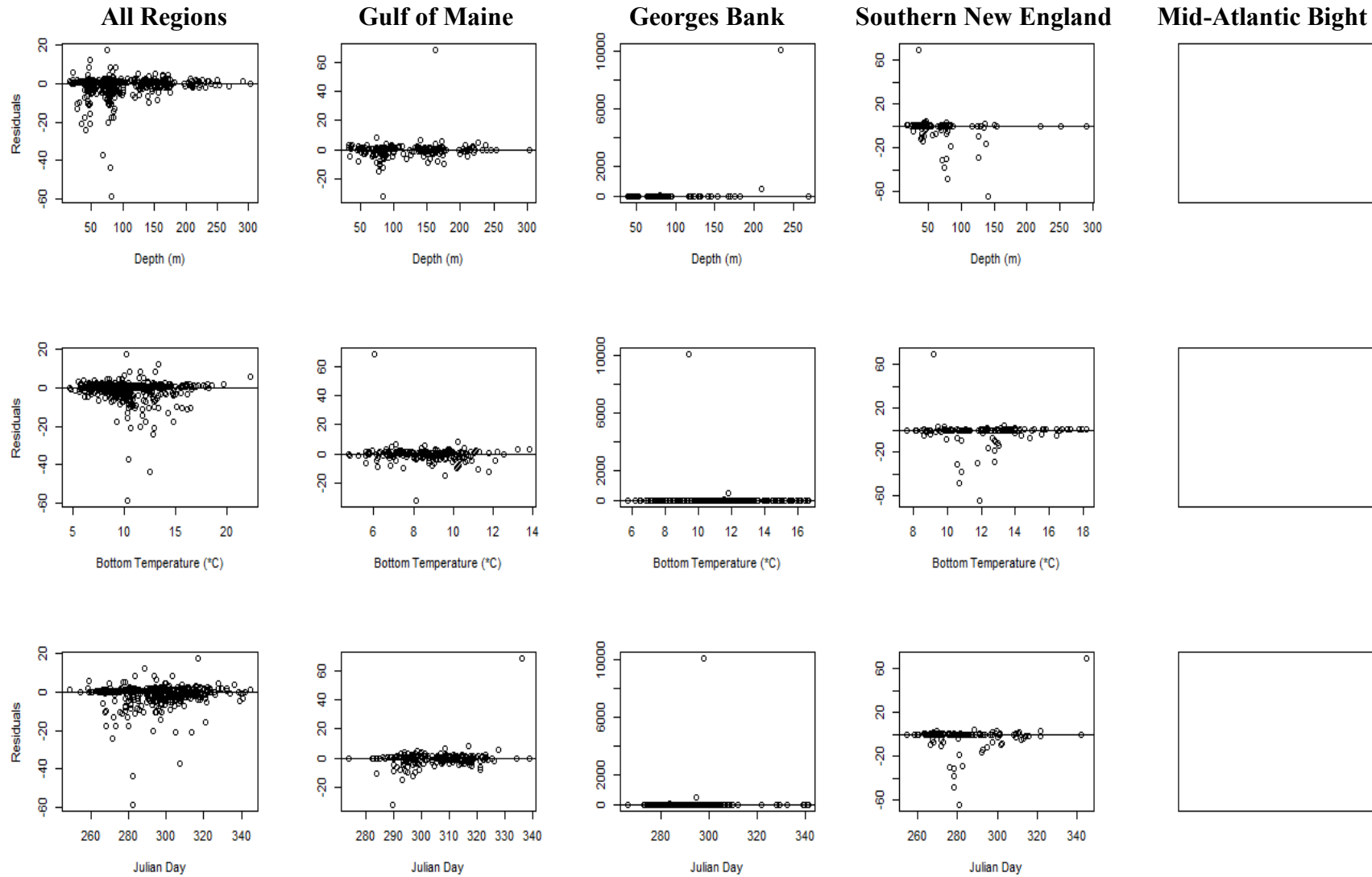
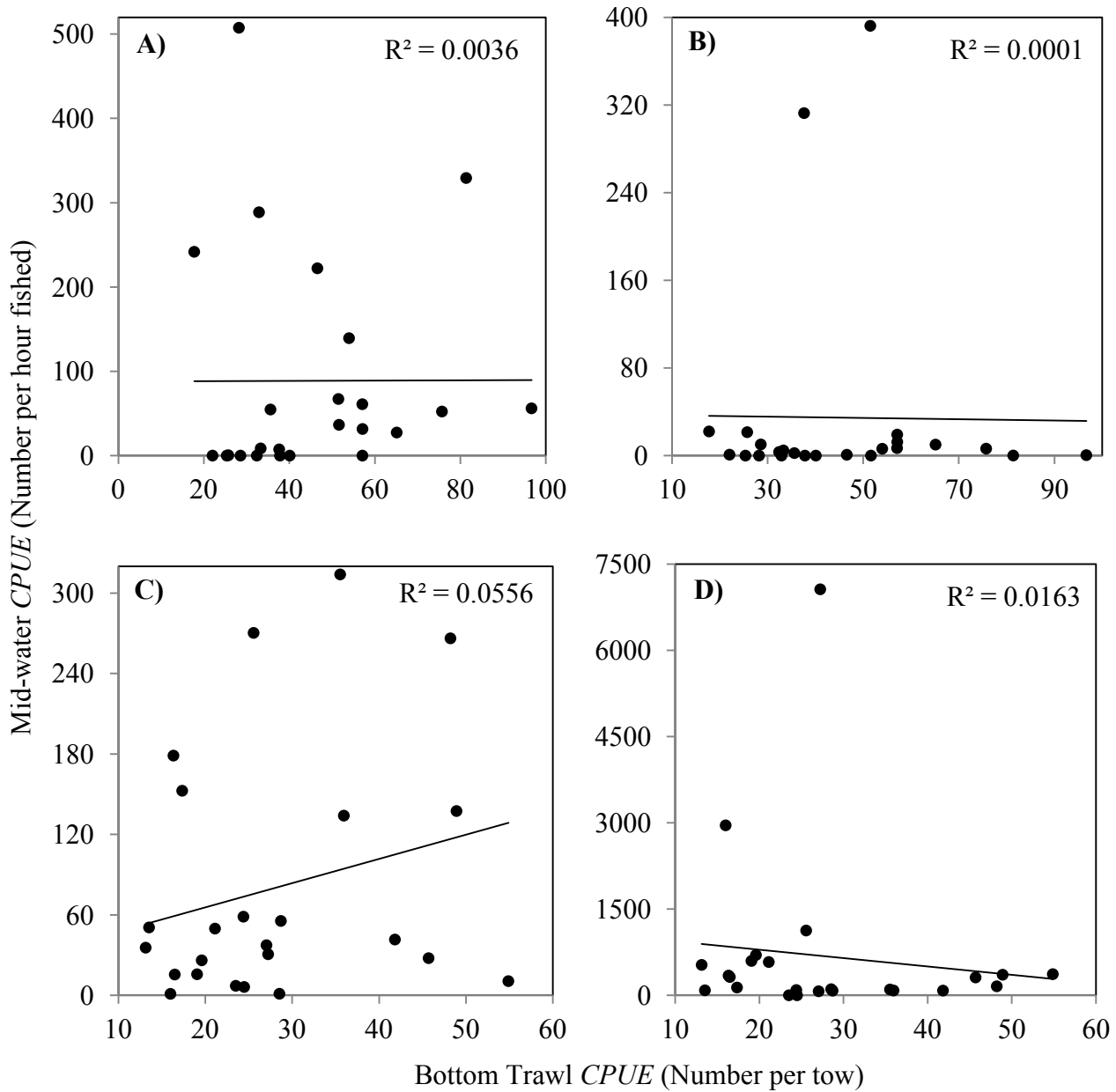


Figure 4H.12. Relationships between the Pearson residuals and explanatory variables (depth, bottom temperature, and Julian day) based on the optimal Atlantic mackerel GAM during autumn.



Appendix 4I. Comparison of *CPUE* from NEFSC Bottom Trawl Surveys and Fishery-Dependent Mid-Water Trawl Surveys

Figure 4I.1. Comparison of annual mean *CPUE* from fisheries-independent bottom trawl (BT) surveys and fisheries-dependent mid-water (MW) trawl surveys for spiny dogfish. Bottom trawl *CPUE* reflects numbers caught per tow. Midwater *CPUE* reflects the number caught per hour fished. A) Spring BT vs MW pair trawl, B) Spring BT vs MW trawl, C) Autumn BT vs MW pair trawl, D) Autumn BT vs MW trawl.



Appendix 5A. Summary of Commercial Fishery Statistics

Table 5A.1. Effort, catch, and fishing location of spiny dogfish commercial fisheries by gear according to NEFSC fisheries observer data during autumn and spring since 1989 in the Northeast (US) shelf large marine ecosystem. #Obs = number of fishing events, Effort = number of hours fished, Catch = number caught, % Kept = amount of catch landed relative to total catch, Lat = latitude, Lon = longitude [min = minimum, mean = average, max = maximum]. - indicates no data available.

Fishery	Year Range	# Obs	Effort	Catch	% Kept	Lat (°N)			Lon (°W)		
						min	mean	max	min	mean	max
<u>AUTUMN</u>											
Drift gillnet	98 - 10	4235	27573	207741	41	33.84	38.66 ± 2.78	43.40	-78.50	-73.87 ± 2.24	-67.47
Longline	91, 02 - 10	2320	61232	667349	12	38.89	41.34 ± 0.36	44.08	-72.90	-69.18 ± 0.54	-67.71
Otter trawl	89 - 10	37614	999293	2896848	8	35.31	41.26 ± 1.34	44.34	-75.94	-69.80 ± 2.12	-63.78
Scallop dredge	92 - 10	74326	556852	37470	0	35.74	39.94 ± 1.21	42.86	-75.84	-71.45 ± 2.56	-65.64
Sink gill net	89 - 10	28184	2170685	5753870	61	33.13	40.98 ± 2.59	44.35	-78.57	-71.55 ± 2.56	-66.21
Other trawls	91 - 95, 99 - 00, 02 - 10	3548	189161	595608	1	33.84	40.57 ± 1.66	44.50	-78.53	-70.79 ± 2.40	-66.45
Haddock separator	09 - 10	820	24705	38526	0	41.01	41.68 ± 0.40	42.78	-71.50	-67.98 ± 1.07	-66.45
Midwater pair	92 - 95, 99, 03 - 10	1758	146288	416490	2	36.83	40.81 ± 1.49	44.41	-74.43	-70.81 ± 1.53	-67.19
Midwater	91, 00, 03 - 10	164	5349	126894	0	36.51	41.85 ± 1.78	44.50	-74.74	-70.15 ± 1.75	-67.24
Pair	-	-	-	-	-	-	-	-	-	-	-
Ruhle	-	-	-	-	-	-	-	-	-	-	-
Scallop	04 - 08, 10	707	10021	13683	1	37.10	38.62 ± 0.97	40.79	-74.89	-73.91 ± 0.77	-71.92
Shrimp	02, 04, 10	21	495	0	-	33.84	39.85 ± 2.13	41.62	-78.53	-71.45 ± 2.39	-70.35
Twin	04, 06 - 07, 10	78	2303	15	0	37.18	38.51 ± 1.12	40.76	-75.11	-72.82 ± 2.68	-66.92

SPRING

Drift gillnet	94 - 10	1751	8501	75384	4	34.66	37.78 ± 2.76	43.93	-76.81	-74.06 ± 2.60	-67.49
Longline	91 - 93, 95, 99, 03 - 10	923	26471	36512	10	33.08	42.01 ± 0.76	44.10	-78.53	-68.62 ± 1.34	-67.28
Otter trawl	89 - 10	37075	1056873	1969274	6	34.93	41.27 ± 1.11	44.26	-76.01	-69.06 ± 1.87	-65.63
Scallop dredge	92 - 10	67292	501951	82277	0	36.59	39.30 ± 0.97	42.83	-75.07	-72.98 ± 1.72	-66.44
Sink gill net	90 - 10	25030	2653280	2076738	82	33.80	40.36 ± 2.63	44.12	-78.56	-72.08 ± 2.55	-67.34
Other trawls	89 - 97, 00 - 10	1770	37709	151355	7	37.31	41.50 ± 1.78	44.42	-74.78	-70.28 ± 2.19	-66.47
Haddock separator	10	199	7035	8328	0	40.62	41.61 ± 0.56	42.71	-69.37	-67.84 ± 0.54	-67.25
Midwater pair	00, 02 - 05, 07 - 10	286	8123	107841	10	37.79	41.20 ± 1.48	43.53	-74.41	-70.63 ± 1.97	-67.18
Midwater	94, 00, 04 - 10	102	3595	8820	0	38.27	40.91 ± 1.30	43.24	-74.27	-70.79 ± 1.79	-67.95
Pair	92 - 93	84	1787	11679	1	40.66	41.46 ± 0.44	42.13	-68.45	-67.44 ± 0.51	-66.47
Ruhle	09 - 10	118	3974	3	0	40.60	41.08 ± 0.30	42.03	-68.51	-67.70 ± 0.34	-67.01
Scallop	01 - 02, 04 - 05, 07 - 10	315	3027	14250	1	37.31	38.74 ± 0.77	40.61	-74.78	-73.74 ± 0.54	-72.17
Shrimp	89 - 97, 04 - 08, 10	628	8719	182	0	39.27	43.16 ± 0.70	44.42	-72.30	-70.04 ± 0.59	-68.11
Twin	06 - 07	38	1449	252	0	40.12	41.23 ± 0.84	42.11	-69.20	-68.69 ± 0.46	-67.67

Appendix 5B. Statistics for Moran's *I*

Table 5B.1. Moran's *I* and spatial correlation of *CPUE* for the sink gill net fishery, the otter trawl fishery, and the NEFSC bottom trawl survey during autumn and spring from 1989 through 2009. Locations were provided by station latitude and longitude. *I* = Moran's statistic with values = +1 indicative of clustering of spiny dogfish *CPUE*, values = -1 indicative of dispersion, and values = 0 random. $E(I)$ = expectation and $Var(I)$ = variance under the assumption that fish are captured at random during the Moran test, *dev* = statistic standard deviate, *p* = probability. Significance (bolded) based on an $\alpha = 0.05$. - indicates no data available.

Year	Sink Gill Net					Otter Trawl					Survey				
	<i>I</i>	$E(I)$	$Var(I)$	<i>dev</i>	<i>p</i>	<i>I</i>	$E(I)$	$Var(I)$	<i>dev</i>	<i>p</i>	<i>I</i>	$E(I)$	$Var(I)$	<i>dev</i>	<i>p</i>
<u>AUTUMN</u>															
1989	0.25	-0.003	0.001	9.26	0.000	0.02	-0.002	0.000	1.21	0.226	0.26	-0.003	0.001	8.61	0.000
1990	0.33	-0.007	0.002	7.62	0.000	0.11	-0.003	0.001	4.92	0.000	0.16	-0.003	0.001	6.00	0.000
1991	0.34	-0.001	0.000	24.36	0.000	0.17	-0.001	0.000	12.03	0.000	0.14	-0.003	0.001	5.25	0.000
1992	0.14	-0.001	0.000	10.32	0.000	0.04	-0.002	0.000	1.79	0.074	0.17	-0.003	0.001	6.04	0.000
1993	0.62	-0.001	0.000	37.66	0.000	0.07	-0.002	0.001	3.04	0.002	0.25	-0.003	0.001	10.16	0.000
1994	0.07	0.000	0.000	7.07	0.000	0.02	-0.005	0.000	1.67	0.095	0.24	-0.003	0.001	7.98	0.000
1995	0.31	-0.001	0.000	21.03	0.000	0.43	-0.002	0.000	20.51	0.000	0.01	-0.003	0.001	0.71	0.478
1996	0.38	-0.001	0.000	30.27	0.000	0.29	-0.002	0.000	13.91	0.000	0.12	-0.003	0.000	6.90	0.000
1997	0.61	-0.001	0.000	35.01	0.000	0.13	-0.005	0.001	4.26	0.000	0.11	-0.003	0.001	3.93	0.000
1998	0.42	-0.001	0.000	30.38	0.000	0.27	-0.007	0.002	6.47	0.000	0.21	-0.003	0.001	8.23	0.000
1999	0.42	-0.001	0.000	28.69	0.000	0.40	-0.003	0.000	24.09	0.000	0.28	-0.003	0.001	10.80	0.000
2000	0.34	-0.001	0.000	26.92	0.000	0.05	-0.002	0.000	2.55	0.011	0.13	-0.003	0.001	4.74	0.000
2001	0.24	-0.001	0.000	13.02	0.000	0.04	-0.001	0.000	4.65	0.000	0.30	-0.003	0.001	10.13	0.000
2002	0.45	-0.001	0.000	28.87	0.000	0.04	-0.001	0.000	5.46	0.000	0.11	-0.003	0.001	4.36	0.000
2003	0.17	-0.001	0.000	10.92	0.000	0.18	-0.001	0.000	13.86	0.000	0.16	-0.003	0.000	8.47	0.000
2004	0.26	-0.001	0.000	19.19	0.000	0.11	0.000	0.000	13.46	0.000	0.46	-0.003	0.001	14.18	0.000
2005	0.19	-0.001	0.000	13.94	0.000	0.09	0.000	0.000	12.23	0.000	0.49	-0.003	0.001	16.48	0.000
2006	0.37	-0.001	0.000	22.46	0.000	0.23	0.000	0.000	23.16	0.000	0.04	-0.003	0.001	1.86	0.063
2007	0.11	-0.001	0.000	11.21	0.000	0.01	0.000	0.000	4.09	0.000	0.19	-0.003	0.001	7.17	0.000

Year	Sink Gill Net					Otter Trawl					Survey				
	<i>I</i>	<i>E(I)</i>	<i>Var(I)</i>	<i>dev</i>	<i>p</i>	<i>I</i>	<i>E(I)</i>	<i>Var(I)</i>	<i>dev</i>	<i>p</i>	<i>I</i>	<i>E(I)</i>	<i>Var(I)</i>	<i>dev</i>	<i>p</i>
2008	0.39	-0.001	0.000	22.02	0.000	0.10	0.000	0.000	13.64	0.000	0.14	-0.003	0.001	5.00	0.000
2009	0.38	-0.001	0.000	25.28	0.000	0.14	0.000	0.000	16.10	0.000	0.18	-0.003	0.001	6.30	0.000
<u>SPRING</u>															
1989	-	-	-	-	-	0.09	-0.001	0.000	4.82	0.000	0.05	-0.003	0.001	1.93	0.054
1990	0.13	-0.004	0.001	5.00	0.000	0.57	-0.002	0.001	24.37	0.000	0.00	-0.003	0.000	0.67	0.506
1991	0.26	-0.005	0.001	7.40	0.000	0.07	-0.002	0.001	3.32	0.001	0.11	-0.003	0.001	3.86	0.000
1992	0.37	-0.001	0.000	25.29	0.000	0.21	-0.001	0.000	14.72	0.000	0.15	-0.003	0.001	5.00	0.000
1993	0.45	0.000	0.000	30.80	0.000	0.14	-0.003	0.001	5.93	0.000	0.05	-0.003	0.000	3.31	0.001
1994	0.62	-0.001	0.000	39.36	0.000	0.04	-0.002	0.000	1.71	0.088	0.09	-0.003	0.001	3.26	0.001
1995	0.23	-0.001	0.000	23.41	0.000	0.20	-0.001	0.000	11.72	0.000	0.16	-0.003	0.001	5.07	0.000
1996	0.49	-0.001	0.000	35.03	0.000	0.04	-0.002	0.000	2.63	0.009	0.11	-0.003	0.001	4.72	0.000
1997	0.47	0.000	0.000	40.02	0.000	0.49	-0.003	0.001	16.59	0.000	0.16	-0.003	0.001	5.23	0.000
1998	0.35	-0.001	0.000	28.60	0.000	0.00	-0.004	0.000	0.22	0.827	0.09	-0.003	0.001	3.68	0.000
1999	0.30	-0.001	0.000	20.33	0.000	0.06	-0.003	0.000	3.41	0.001	0.32	-0.003	0.001	10.60	0.000
2000	0.04	-0.001	0.000	7.36	0.000	0.24	-0.002	0.000	14.28	0.000	0.20	-0.003	0.001	7.10	0.000
2001	0.35	-0.001	0.000	27.80	0.000	0.02	-0.002	0.000	1.22	0.223	0.24	-0.003	0.001	8.14	0.000
2002	0.59	-0.001	0.000	33.13	0.000	0.06	-0.002	0.000	4.26	0.000	0.04	-0.003	0.000	2.64	0.008
2003	0.10	-0.002	0.000	6.56	0.000	0.00	0.000	0.000	0.33	0.741	0.04	-0.003	0.000	2.99	0.003
2004	0.41	-0.001	0.000	27.86	0.000	0.28	-0.001	0.000	22.92	0.000	0.19	-0.003	0.001	6.77	0.000
2005	0.52	-0.001	0.000	29.52	0.000	0.02	0.000	0.000	2.69	0.007	0.13	-0.003	0.000	6.26	0.000
2006	0.11	-0.001	0.000	6.85	0.000	0.03	0.000	0.000	3.49	0.000	0.19	-0.003	0.001	6.69	0.000
2007	0.33	-0.001	0.000	27.69	0.000	0.04	0.000	0.000	10.37	0.000	0.65	-0.003	0.001	21.38	0.000
2008	0.03	-0.001	0.000	4.46	0.000	0.41	0.000	0.000	46.54	0.000	0.44	-0.003	0.001	13.98	0.000
2009	0.04	-0.001	0.000	3.10	0.002	0.34	0.000	0.000	38.14	0.000	0.08	-0.003	0.001	3.07	0.002

Appendix 5C. Statistics for Center of Spiny Dogfish Abundance

Table 5C.1. Bivariate spiny dogfish sample statistics collected from the otter trawl and sink gill net fisheries during autumn and spring between 1989 and 2009 in the Northeast (US) shelf large marine ecosystem. *N* = sample size, Lat = latitude, Lon = longitude, SD = standard deviation, COV = covariance, *r* = Pearson's correlation coefficient. - indicates no data available.

Year	<i>N</i>	Sink Gill Net						Otter Trawl						
		Mean Lat (°N)	Mean Lon (°W)	Lat SD	Lon SD	COV	<i>r</i>	<i>N</i>	Mean Lat (°N)	Mean Lon (°W)	Lat SD	Lon SD	COV	<i>r</i>
AUTUMN														
1989	216	42.726	-69.918	0.07	0.11	-0.008	-0.999	227	41.556	-70.241	0.07	0.12	-0.009	-0.994
1990	111	42.772	-69.807	0.15	0.24	-0.034	-0.998	171	40.829	-71.185	0.11	0.20	-0.023	-0.991
1991	1069	42.791	-69.721	0.02	0.02	0.000	-0.998	553	40.679	-71.471	0.03	0.06	-0.002	-0.984
1992	826	42.796	-69.874	0.02	0.03	-0.001	-0.997	275	41.199	-70.968	0.07	0.12	-0.008	-0.994
1993	559	42.121	-70.423	0.03	0.05	-0.001	-0.987	204	41.619	-70.312	0.08	0.14	-0.011	-0.993
1994	761	42.510	-70.479	0.02	0.03	-0.001	-0.996	47	40.816	-71.409	0.45	0.78	-0.349	-0.999
1995	450	42.236	-70.420	0.03	0.05	-0.002	-0.997	147	41.218	-71.702	0.12	0.23	-0.028	-0.995
1996	527	41.511	-71.057	0.03	0.05	-0.001	-0.982	176	39.781	-73.324	0.15	0.28	-0.042	-0.996
1997	395	42.094	-70.390	0.04	0.07	-0.003	-0.998	43	39.895	-72.681	0.44	0.81	-0.356	-0.994
1998	873	41.906	-70.654	0.01	0.02	0.000	-0.991	60	40.525	-72.596	0.26	0.47	-0.124	-0.999
1999	464	42.087	-70.314	0.03	0.04	-0.001	-0.997	102	41.581	-69.989	0.18	0.29	-0.053	-0.998
2000	117	42.081	-70.317	0.17	0.27	-0.046	-0.997	86	41.547	-70.073	0.18	0.31	-0.055	-0.992
2001	65	42.119	-70.560	0.26	0.42	-0.111	-0.997	196	41.700	-70.654	0.07	0.12	-0.008	-0.986
2002	168	42.232	-70.456	0.10	0.17	-0.017	-0.999	595	41.715	-70.029	0.03	0.05	-0.001	-0.996
2003	410	41.974	-70.464	0.04	0.07	-0.003	-0.998	522	41.656	-70.000	0.04	0.06	-0.002	-0.991
2004	1214	42.344	-70.462	0.01	0.02	0.000	-0.999	1110	41.526	-70.657	0.02	0.03	0.000	-0.992
2005	994	42.261	-70.306	0.02	0.03	0.000	-0.998	1641	41.651	-69.918	0.01	0.02	0.000	-0.997
2006	257	42.253	-70.111	0.06	0.10	-0.006	-0.998	906	41.513	-69.481	0.02	0.03	-0.001	-0.995
2007	335	41.911	-70.044	0.05	0.08	-0.004	-0.999	1536	41.569	-69.434	0.01	0.02	0.000	-0.997

Year	Sink Gill Net							Otter Trawl						
	<i>N</i>	Mean Lat (°N)	Mean Lon (°W)	Lat SD	Lon SD	COV	<i>r</i>	<i>N</i>	Mean Lat (°N)	Mean Lon (°W)	Lat SD	Lon SD	COV	<i>r</i>
2008	335	41.255	-71.074	0.04	0.07	-0.003	-0.979	1068	41.471	-69.440	0.02	0.03	0.000	-0.993
2009	391	41.403	-71.129	0.04	0.06	-0.002	-0.972	1264	41.239	-70.082	0.01	0.02	0.000	-0.991
<u>SPRING</u>														
1989	0	-	-	-	-	-	-	241	40.563	-70.378	0.07	0.13	-0.009	-0.989
1990	23	42.095	-69.673	0.96	1.61	-1.549	-0.999	238	40.109	-71.447	0.06	0.12	-0.007	-0.988
1991	36	42.587	-69.137	0.51	0.81	-0.408	-0.995	192	40.576	-70.750	0.09	0.17	-0.016	-0.994
1992	459	41.913	-70.143	0.03	0.06	-0.002	-0.995	279	40.923	-69.555	0.07	0.11	-0.008	-0.987
1993	271	42.396	-69.588	0.06	0.11	-0.007	-0.995	88	41.531	-68.496	0.18	0.32	-0.058	-0.989
1994	209	37.784	-74.082	0.07	0.14	-0.009	-0.953	157	41.571	-67.958	0.12	0.19	-0.022	-0.995
1995	366	38.788	-73.233	0.04	0.08	-0.003	-0.952	257	40.221	-70.616	0.07	0.14	-0.009	-0.979
1996	282	38.508	-73.518	0.06	0.12	-0.007	-0.983	139	39.968	-70.893	0.14	0.28	-0.038	-0.984
1997	550	39.955	-72.414	0.03	0.05	-0.001	-0.970	90	40.509	-71.119	0.25	0.35	-0.112	-0.995
1998	554	39.128	-73.194	0.03	0.06	-0.002	-0.973	56	40.303	-70.795	0.37	0.70	-0.260	-0.985
1999	429	39.735	-72.271	0.03	0.06	-0.002	-0.956	50	41.002	-69.427	0.32	0.55	-0.177	-0.989
2000	274	39.344	-72.404	0.05	0.10	-0.004	-0.943	173	40.970	-69.519	0.08	0.15	-0.012	-0.978
2001	93	38.910	-73.413	0.14	0.25	-0.033	-0.950	166	40.939	-70.012	0.09	0.17	-0.015	-0.983
2002	62	41.236	-71.044	0.28	0.45	-0.125	-0.994	196	41.588	-68.955	0.07	0.11	-0.008	-0.990
2003	54	41.863	-70.076	0.26	0.43	-0.112	-1.000	687	41.398	-69.223	0.02	0.04	-0.001	-0.982
2004	235	41.686	-70.254	0.07	0.12	-0.008	-0.997	646	40.955	-69.885	0.03	0.04	-0.001	-0.981
2005	113	41.040	-70.958	0.19	0.30	-0.056	-0.995	1805	41.532	-68.456	0.01	0.02	0.000	-0.993
2006	94	41.291	-70.713	0.16	0.26	-0.041	-0.996	698	41.343	-68.955	0.02	0.04	-0.001	-0.994
2007	164	40.573	-71.187	0.11	0.19	-0.020	-0.973	1119	40.886	-70.130	0.01	0.03	0.000	-0.984
2008	152	39.964	-71.581	0.10	0.19	-0.018	-0.952	1171	41.072	-69.383	0.01	0.03	0.000	-0.989
2009	155	41.183	-70.506	0.11	0.18	-0.019	-0.980	1045	40.460	-70.547	0.02	0.03	-0.001	-0.979

Table 5C.2. Bivariate spiny dogfish sample statistics collected from the NEFSC bottom trawl survey during autumn and spring between 1989 and 2009 in the Northeast (US) shelf large marine ecosystem. N = sample size, Lat = latitude, Lon = longitude, SD = standard deviation, COV = covariance, r = Pearson's correlation coefficient.

Year	AUTUMN							SPRING						
	N	Mean Lat (°N)	Mean Lon (°W)	Lat SD	Lon SD	COV	r	N	Mean Lat (°N)	Mean Lon (°W)	Lat SD	Lon SD	COV	r
1989	102	41.939	-68.710	0.31	0.51	-0.156	-0.997	149	39.133	-72.160	0.16	0.30	-0.047	-0.987
1990	107	41.863	-68.299	0.33	0.53	-0.175	-0.998	167	39.614	-71.605	0.14	0.26	-0.036	-0.986
1991	78	42.182	-68.686	0.43	0.70	-0.298	-0.996	178	39.817	-71.503	0.13	0.23	-0.029	-0.987
1992	97	41.792	-69.129	0.34	0.58	-0.197	-0.998	152	39.414	-71.885	0.17	0.31	-0.052	-0.986
1993	84	41.874	-69.424	0.42	0.71	-0.299	-0.997	151	39.584	-71.369	0.15	0.28	-0.042	-0.981
1994	98	42.260	-68.560	0.35	0.55	-0.194	-0.997	149	39.512	-71.067	0.17	0.31	-0.053	-0.982
1995	91	42.366	-68.710	0.34	0.55	-0.184	-0.998	186	39.813	-71.327	0.12	0.23	-0.028	-0.979
1996	121	41.557	-69.761	0.27	0.43	-0.121	-0.998	172	39.737	-70.941	0.16	0.30	-0.049	-0.984
1997	134	41.987	-69.030	0.21	0.35	-0.073	-0.996	191	40.115	-70.951	0.14	0.24	-0.032	-0.987
1998	146	41.602	-70.032	0.21	0.36	-0.076	-0.997	205	39.888	-71.174	0.15	0.26	-0.038	-0.983
1999	158	41.879	-69.693	0.17	0.29	-0.050	-0.997	186	40.130	-71.125	0.16	0.29	-0.046	-0.989
2000	111	42.244	-69.527	0.26	0.42	-0.108	-0.997	176	39.826	-71.519	0.16	0.29	-0.047	-0.982
2001	122	41.993	-69.546	0.24	0.40	-0.095	-0.997	156	39.456	-71.981	0.17	0.34	-0.059	-0.988
2002	126	42.006	-69.349	0.19	0.31	-0.059	-0.996	212	39.788	-72.158	0.10	0.18	-0.017	-0.980
2003	114	41.866	-69.921	0.29	0.48	-0.140	-0.997	162	39.304	-71.738	0.17	0.33	-0.055	-0.985
2004	109	41.517	-70.068	0.25	0.42	-0.106	-0.998	144	38.846	-72.631	0.19	0.37	-0.070	-0.986
2005	128	41.650	-69.849	0.23	0.38	-0.089	-0.998	141	38.527	-72.714	0.21	0.42	-0.087	-0.989
2006	171	41.870	-69.521	0.15	0.24	-0.036	-0.997	200	39.367	-72.483	0.14	0.26	-0.035	-0.987
2007	124	41.771	-69.515	0.23	0.39	-0.089	-0.999	191	38.992	-72.739	0.13	0.25	-0.032	-0.989
2008	139	41.720	-69.077	0.20	0.33	-0.065	-0.998	198	39.094	-72.887	0.12	0.23	-0.027	-0.988
2009	156	41.212	-69.714	0.16	0.27	-0.044	-0.996	203	39.287	-72.420	0.13	0.25	-0.033	-0.992

Appendix 5D. Semivariogram Modeling

Table 5D.1. Best-fit semivariogram models and parameters for the spatial distribution of spiny dogfish derived from the sink gill net fishery between 1989 and 2009 during both autumn and spring in the Northeast (US) shelf large marine ecosystem. Semivariogram parameters include the sill (C_s), the nugget (C_0), and the range (a). Anisotropy parameters include the ratio of the minor to major lengths (Ratio) and the angle for the principal direction of continuity (Angle). Models include exponential (Exp), gaussian (Gau), and spherical (Sph) with the numbers in parentheses reflective of initial parameters (C_s, C_0, a). - = not applicable.

Year	Model*	AUTUMN					SPRING					
		C_s	C_0	a (km)	Ratio	Angle (°)	Model*	C_s	C_0	a (km)	Ratio	Angle (°)
1989	I	3.07	3.75	0.25	0.84	39.33	-	-	-	-	-	-
1990	I	1.61	3.00	0.22	0.69	47.97	I	0.82	0.01	0.50	0.91	169.72
1991	I	2.22	3.95	0.72	0.80	73.87	II	2.08	0.00	0.10	0.86	95.19
1992	I	1.48	4.24	1.71	0.72	49.64	III	5.83	1.01	1.32	0.71	58.88
1993	IV	2.35	4.85	2.03	0.83	63.66	III	3.42	0.91	2.18	0.76	41.62
1994	II	5.02	0.00	0.12	0.76	32.91	III	2.67	0.60	1.69	0.81	36.50
1995	I	4.47	3.07	2.03	0.54	48.39	III	5.17	1.17	3.19	0.65	45.61
1996	IV	6.05	3.06	1.36	0.61	46.28	III	5.77	0.57	2.95	0.62	35.58
1997	I	4.49	3.75	0.74	0.83	51.81	III	6.09	1.38	2.11	0.65	32.72
1998	II	7.90	3.54	1.07	0.61	45.51	III	3.51	2.68	1.46	0.84	36.59
1999	I	6.45	2.76	0.90	0.72	44.25	II	5.93	0.00	0.16	0.73	41.35
2000	I	1.16	0.41	0.72	0.52	32.13	III	8.80	2.69	3.45	0.83	47.53
2001	I	1.95	0.42	0.62	0.48	37.03	II	1.26	0.00	0.33	0.48	48.88
2002	II	6.55	0.00	0.43	0.40	47.11	VI	4.75	0.53	0.34	0.84	170.16
2003	IV	4.66	3.89	0.61	0.77	44.52	0	-	1.38	0.00	-	-
2004	III	3.28	3.19	1.23	0.75	69.82	0	-	2.58	0.00	-	-
2005	III	1.39	4.01	1.26	0.90	70.16	II	1.74	0.00	0.28	0.83	74.23
2006	I	1.40	2.03	0.87	0.61	57.23	0	-	1.16	0.00	-	-
2007	II	5.07	0.00	0.12	0.62	42.73	II	0.86	1.08	1.73	0.87	162.58
2008	II	5.69	0.00	0.15	0.61	52.20	III	1.88	0.00	0.21	0.79	28.33
2009	V	8.52	0.00	0.24	0.65	57.19	I	2.28	0.00	1.71	0.57	55.86

*0 = Nugget model, I = Sph (3, 5, 1), II = Exp (3, 5, 1), III = Gau (3, 5, 1), IV = Sph (5, 10, 1), V = Exp (5, 10, 1), VI = Gau (5, 10, 1).

Table 5D.2. Best-fit semivariogram models and parameters for the spatial distribution of spiny dogfish derived from the otter trawl fishery between 1989 and 2009 during both autumn and spring in the Northeast (US) shelf large marine ecosystem. Semivariogram parameters include the sill (C_s), the nugget (C_0), and the range (a). Anisotropy parameters include the ratio of the minor to major lengths (Ratio) and the angle for the principal direction of continuity (Angle). Models include exponential (Exp), gaussian (Gau), and spherical (Sph) with the numbers in parentheses reflective of initial parameters (C_s, C_0, a). - = not applicable.

Year	Model*	AUTUMN					SPRING					
		C_s	C_0	a (km)	Ratio	Angle (°)	Model*	C_s	C_0	a (km)	Ratio	Angle (°)
1989	I	1.70	7.92	0.90	0.83	33	II	3.48	5.92	0.32	0.56	50
1990	I	1.70	11.49	0.82	0.82	40	VIII	11.17	3.99	0.31	0.68	71
1991	I	3.67	7.55	1.24	0.77	56	VII	2.73	6.48	1.63	0.80	71
1992	II	10.94	0.00	0.07	0.80	39	III	2.13	7.34	1.10	0.79	53
1993	VIII	11.30	0.00	0.08	0.73	65	VIII	6.13	2.53	0.24	0.63	48
1994	II	10.13	3.79	3.10	0.63	45	0	-	7.36	0.00	-	-
1995	I	547.39	3.56	420.36	0.80	38	II	2.79	3.63	0.56	0.81	47
1996	III	5.31	4.81	1.09	0.78	62	III	4.37	2.40	1.26	0.74	61
1997	III	3.94	3.53	6.18	0.27	50	I	2.82	2.93	1.97	0.86	71
1998	III	11.28	1.41	0.27	0.61	42	0	-	4.49	0.00	-	-
1999	VII	6.33	3.21	1.06	0.66	42	0	-	3.03	0.00	-	-
2000	III	3.79	1.76	1.21	0.72	48	IV	2.54	4.35	0.97	0.65	46
2001	III	9.53	3.73	2.09	0.77	35	VI	3.52	4.28	0.59	0.77	41
2002	II	4.43	3.01	0.73	0.70	54	IV	5.26	3.31	0.68	0.82	47
2003	IV	511.63	4.45	570.53	0.69	56	II	1.49	3.57	0.24	0.82	69
2004	III	10.02	4.62	1.96	0.76	48	I	1.99	4.11	0.87	0.69	49
2005	II	25.68	3.07	8.06	0.88	57	I	0.67	3.89	0.70	0.81	52
2006	II	4.44	5.19	0.43	0.85	81	I	2.02	3.57	0.86	0.93	109
2007	III	8.95	8.22	4.02	0.73	58	IV	225.25	3.89	487.13	0.79	53
2008	I	16.71	3.54	11.75	0.92	43	I	1.07	4.37	0.52	0.88	48
2009	III	12.43	6.57	3.86	0.92	90	I	1.38	3.46	0.80	0.82	52

*0 = Nugget model, I = Sph (3, 5, 1), II = Exp (3, 5, 1), III = Gau (3, 5, 1), IV = Sph (5, 10, 1), VI = Gau (5, 10, 1), VII = Sph (10, 20, 1), VIII = Exp (10, 20, 1).

Table 5D.3. Best-fit semivariogram models and parameters for the spatial distribution of spiny dogfish derived from the NEFSC bottom trawl survey between 1989 and 2009 during both autumn and spring in the Northeast (US) shelf large marine ecosystem.. Semivariogram parameters include the sill (C_s), the nugget (C_0), and the range (a). Anisotropy parameters include the ratio of the minor to major lengths (Ratio) and the angle for the principal direction of continuity (Angle). Models include exponential (Exp), gaussian (Gau), and spherical (Sph) with the numbers in parentheses reflective of initial parameters (C_s, C_0, a).

Year	Model*	AUTUMN					SPRING					
		C_s	C_0	a (km)	Ratio	Angle (°)	Model*	C_s	C_0	a (km)	Ratio	Angle (°)
1989	I	5.05	1.20	1.85	0.79	125	I	8.79	1.10	2.66	0.46	68
1990	II	4.71	2.39	0.61	0.86	130	I	10.40	0.02	1.94	0.63	65
1991	I	5.67	1.72	2.14	0.91	165	I	10.49	0.00	1.89	0.64	79
1992	I	6.93	0.51	2.17	0.63	38	I	10.25	0.22	1.52	0.66	59
1993	I	5.15	1.17	1.72	0.92	9	I	10.70	0.00	2.21	0.64	74
1994	II	5.99	0.71	0.84	0.82	89	I	11.69	0.00	2.13	0.51	51
1995	II	6.13	1.07	1.02	0.76	69	II	9.91	0.00	0.61	0.52	55
1996	II	12.22	1.60	3.67	0.98	126	I	10.08	0.00	1.52	0.63	54
1997	II	6.76	0.92	1.09	0.79	121	I	8.23	1.46	1.54	0.62	55
1998	II	8.21	1.33	1.21	0.82	66	I	6.79	0.96	1.08	0.57	43
1999	II	9.91	0.97	2.27	0.67	59	II	7.29	1.82	0.62	0.64	40
2000	II	10.19	0.26	2.12	0.65	47	I	6.37	1.61	1.27	0.71	48
2001	II	11.47	1.54	2.95	0.75	67	I	7.16	0.77	1.50	0.63	48
2002	II	8.17	1.83	2.02	0.72	67	II	7.21	0.99	0.72	0.71	52
2003	II	6.79	3.05	2.84	0.76	56	I	7.90	1.11	1.68	0.62	55
2004	II	13.34	1.47	2.50	0.81	71	I	7.20	0.61	1.70	0.65	54
2005	II	10.42	0.60	1.20	0.87	86	I	4.71	2.35	1.78	0.66	57
2006	II	19.21	2.08	5.92	0.90	106	II	7.90	0.58	0.80	0.56	49
2007	II	16.67	0.96	3.85	0.88	117	I	7.86	0.90	1.82	0.67	51
2008	II	9.20	1.80	1.92	0.78	79	II	8.59	0.00	0.71	0.59	53
2009	II	7.71	2.24	0.81	0.87	131	II	9.39	1.35	1.46	0.48	57

*I = Sph (3, 5, 1), II = Exp (3, 5, 1).

Figure 5D.1. Sample (points) and fitted (line) variograms of spiny dogfish *CPUE* during 1989 in the Northeast (US) shelf large marine ecosystem for the sink gill net and otter trawl fisheries and the NEFSC bottom trawl survey during autumn (left panel) and spring (right panel). Notes: ranges on x- and y-axes differ between panels.

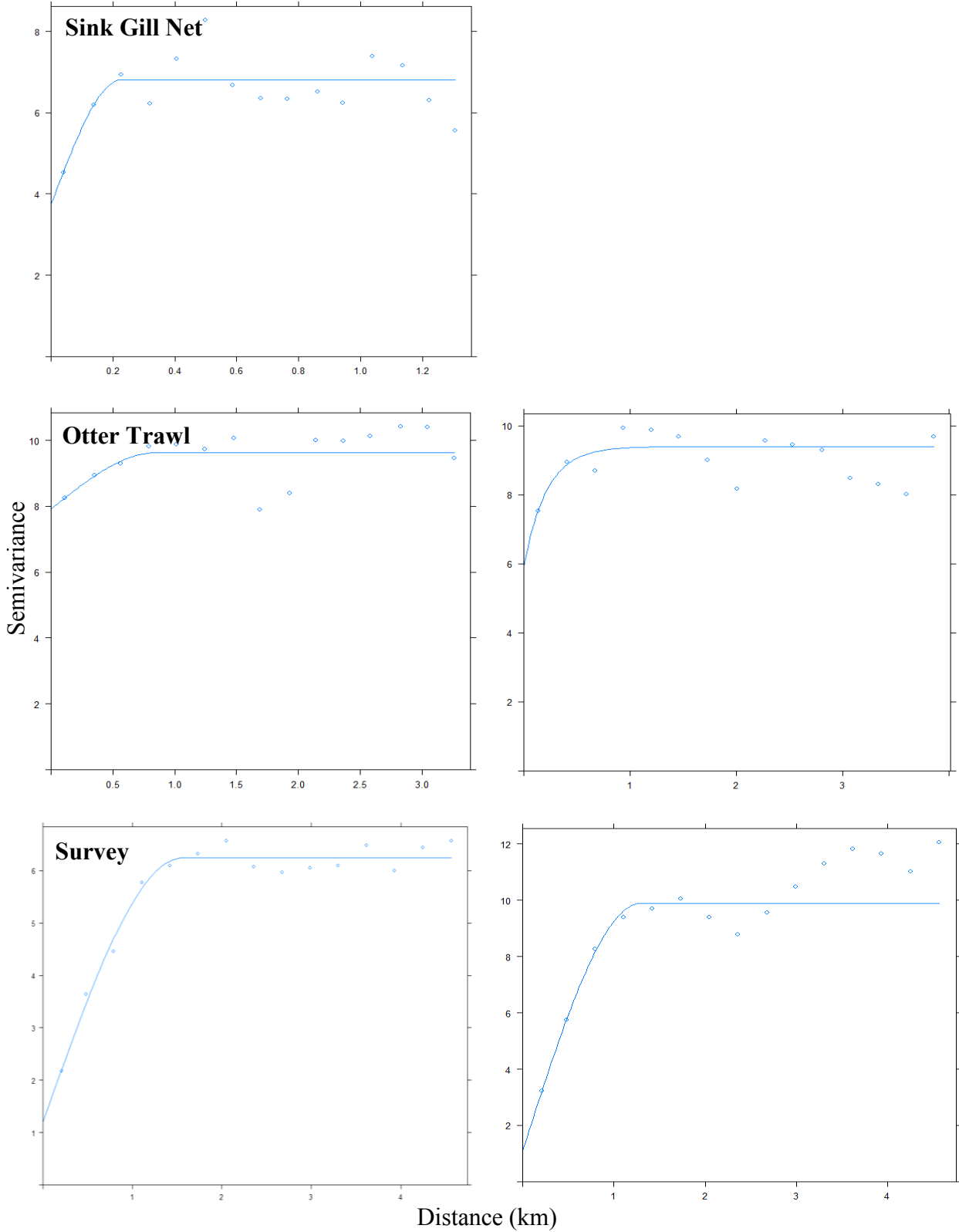


Figure 5D.2. Sample (points) and fitted (line) variograms of spiny dogfish *CPUE* during 1990 in the Northeast (US) shelf large marine ecosystem for the sink gill net and otter trawl fisheries and the NEFSC bottom trawl survey during autumn (left panel) and spring (right panel). Notes: ranges on x- and y-axes differ between panels.

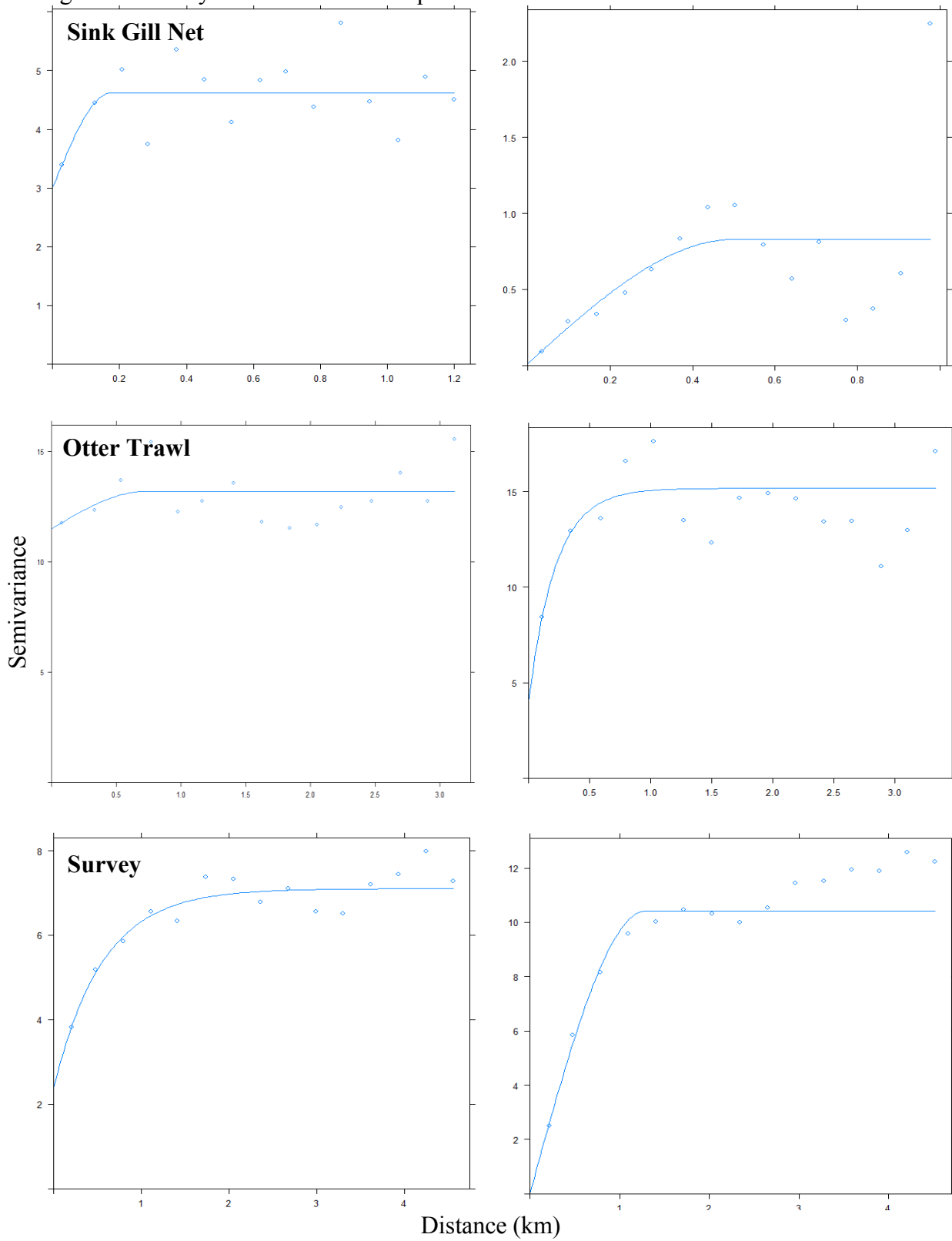


Figure 5D.3. Sample (points) and fitted (line) variograms of spiny dogfish *CPUE* during 1991 in the Northeast (US) shelf large marine ecosystem for the sink gill net and otter trawl fisheries and the NEFSC bottom trawl survey during autumn (left panel) and spring (right panel). Notes: ranges on x- and y-axes differ between panels.

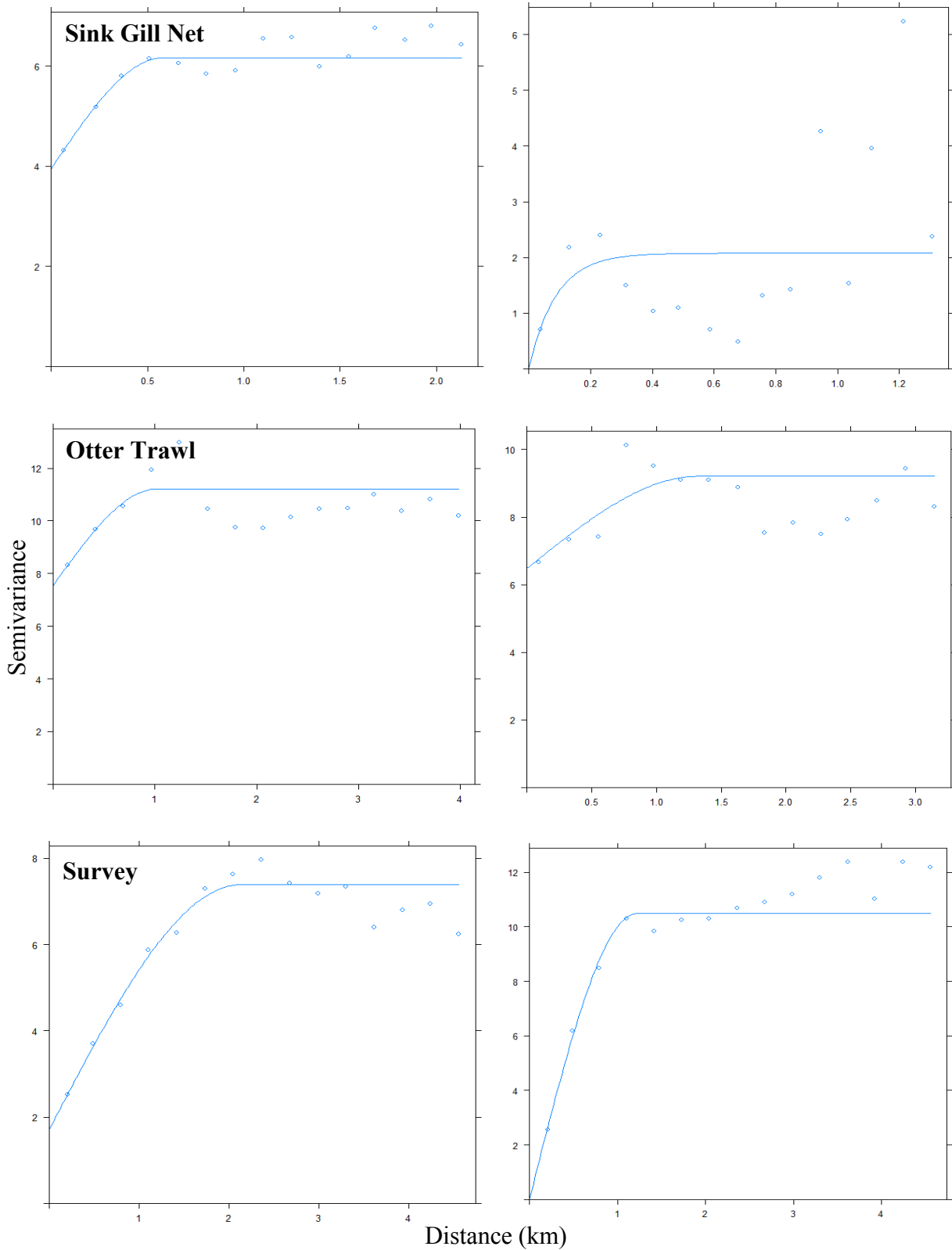


Figure 5D.4. Sample (points) and fitted (line) variograms of spiny dogfish *CPUE* during 1992 in the Northeast (US) shelf large marine ecosystem for the sink gill net and otter trawl fisheries and the NEFSC bottom trawl survey during autumn (left panel) and spring (right panel). Notes: ranges on x- and y-axes differ between panels.

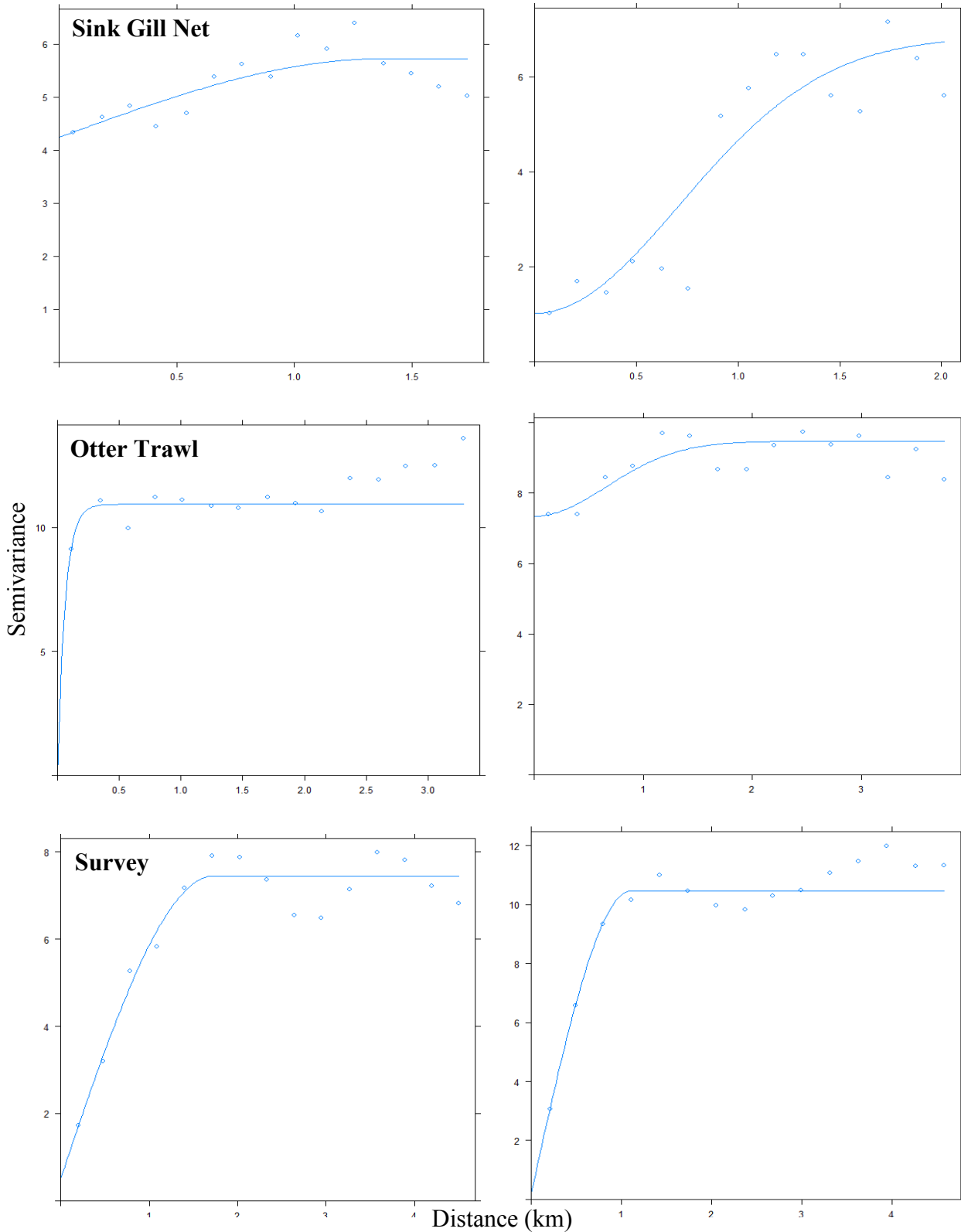


Figure 5D.5. Sample (points) and fitted (line) variograms of spiny dogfish *CPUE* during 1993 in the Northeast (US) shelf large marine ecosystem for the sink gill net and otter trawl fisheries and the NEFSC bottom trawl survey during autumn (left panel) and spring (right panel). Notes: ranges on x- and y-axes differ between panels.

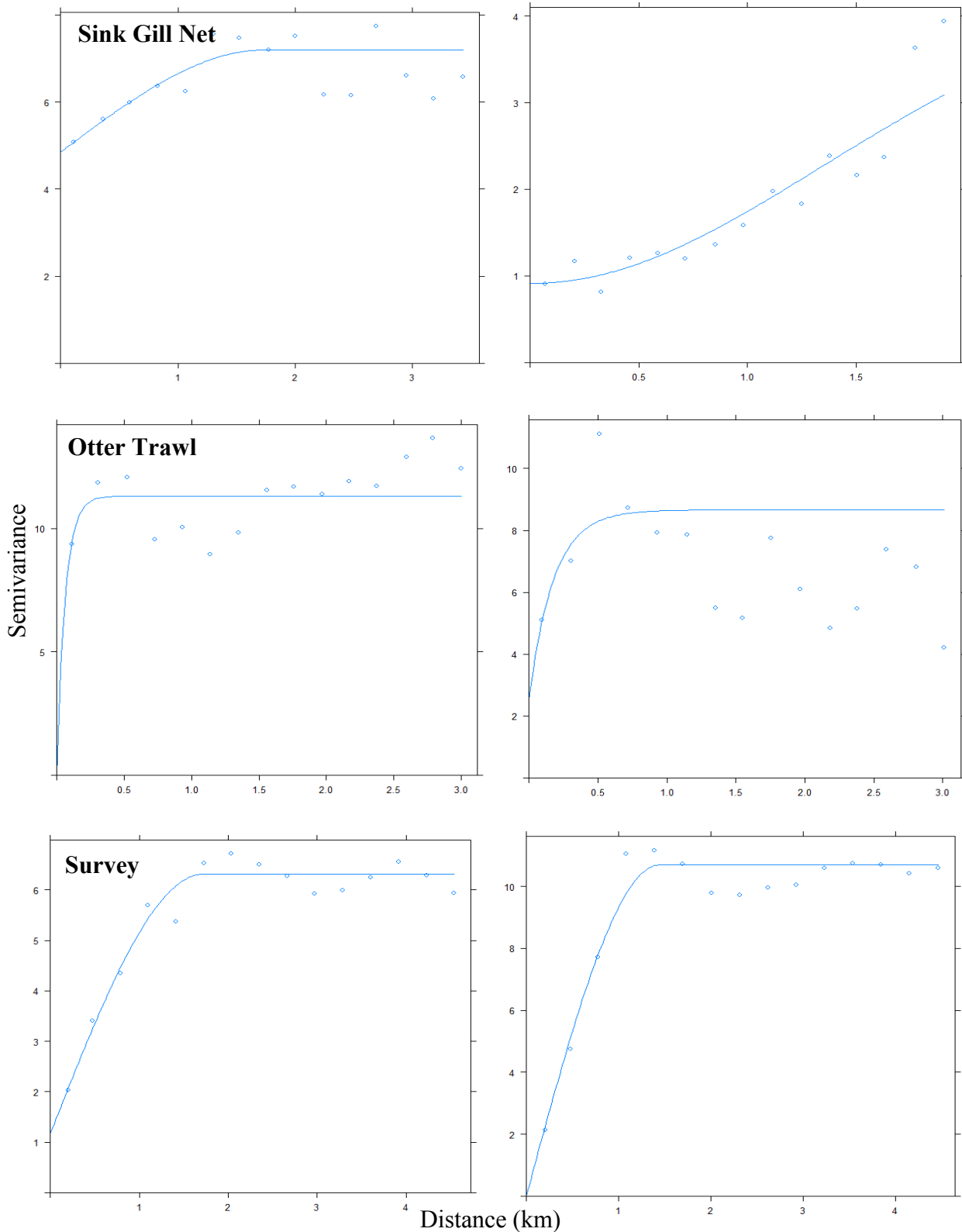


Figure 5D.6. Sample (points) and fitted (line) variograms of spiny dogfish *CPUE* during 1994 in the Northeast (US) shelf large marine ecosystem for the sink gill net and otter trawl fisheries and the NEFSC bottom trawl survey during autumn (left panel) and spring (right panel). Notes: ranges on x- and y-axes differ between panels.

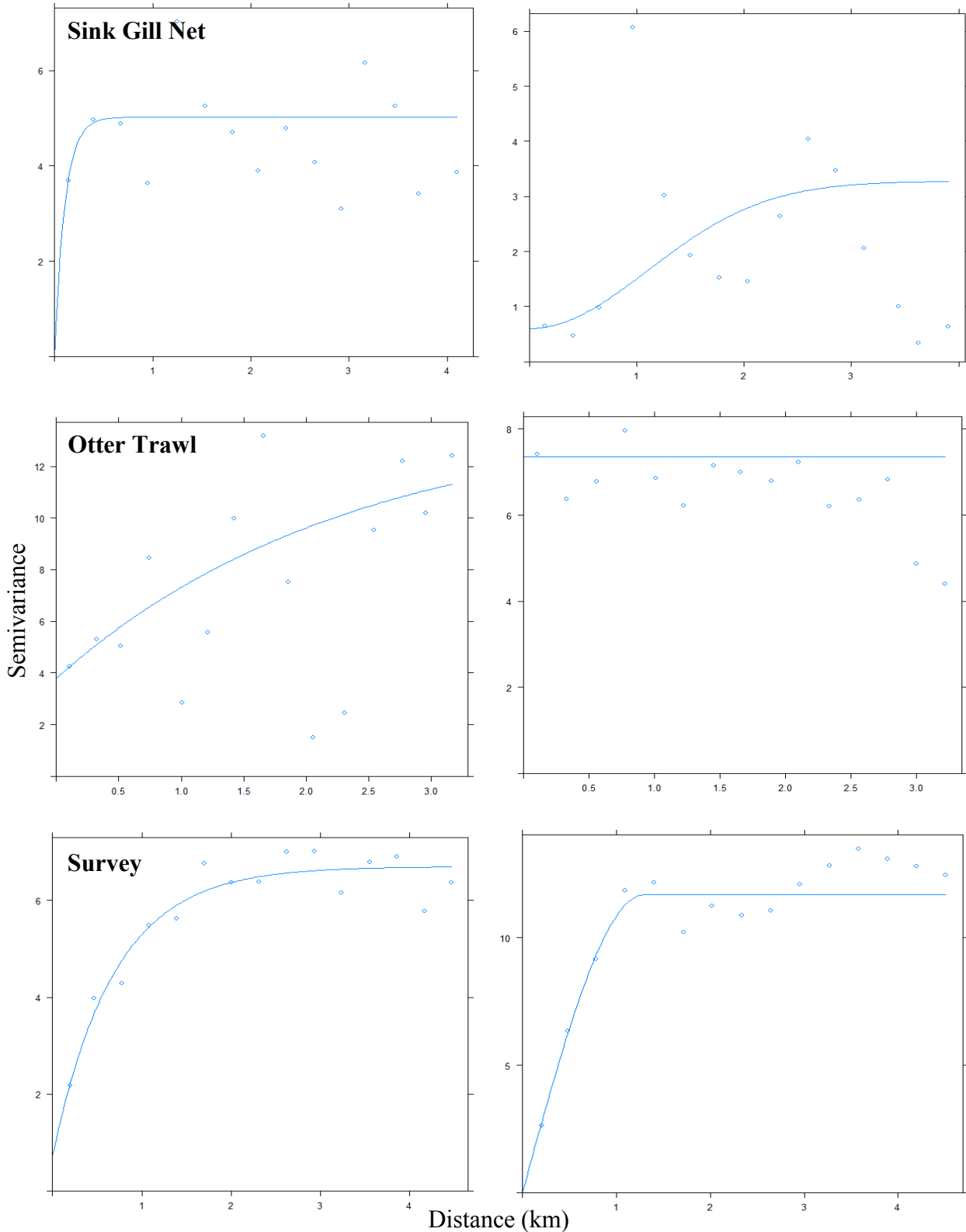


Figure 5D.7. Sample (points) and fitted (line) variograms of spiny dogfish *CPUE* during 1995 in the Northeast (US) shelf large marine ecosystem for the sink gill net and otter trawl fisheries and the NEFSC bottom trawl survey during autumn (left panel) and spring (right panel). Notes: ranges on x- and y-axes differ between panels.

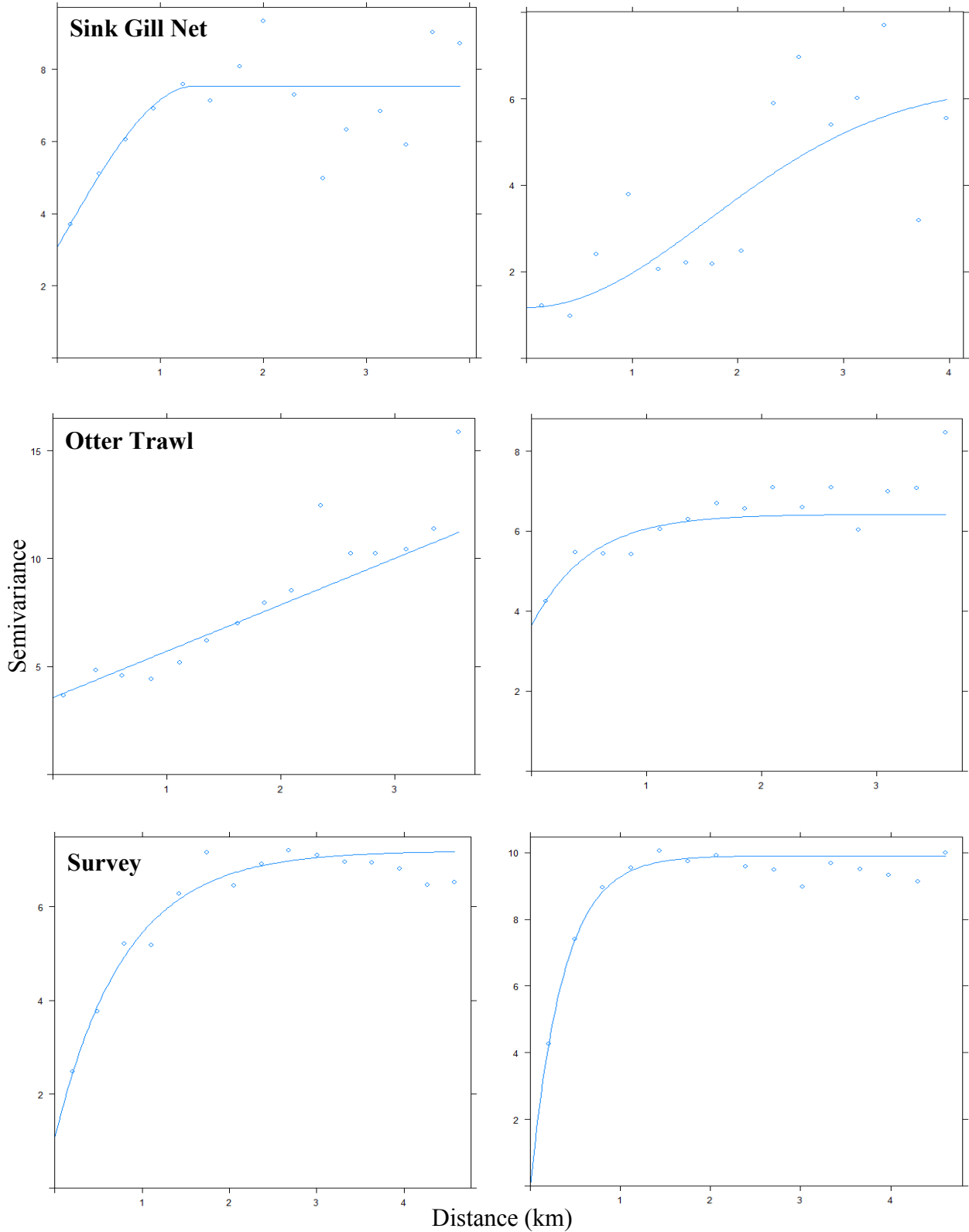


Figure 5D.8. Sample (points) and fitted (line) variograms of spiny dogfish *CPUE* during 1996 in the Northeast (US) shelf large marine ecosystem for the sink gill net and otter trawl fisheries and the NEFSC bottom trawl survey during autumn (left panel) and spring (right panel). Notes: ranges on x- and y-axes differ between panels.

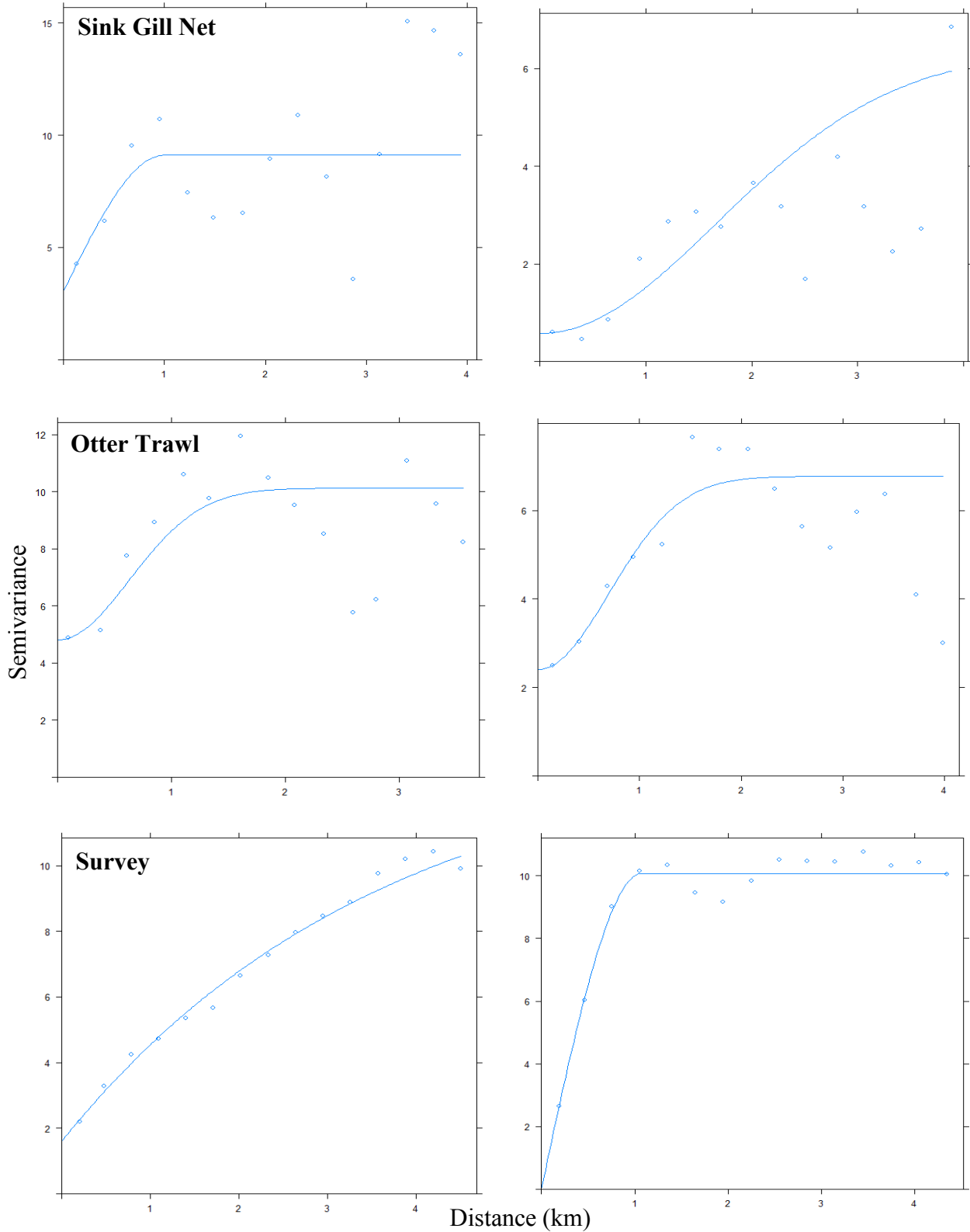


Figure 5D.9. Sample (points) and fitted (line) variograms of spiny dogfish *CPUE* during 1997 in the Northeast (US) shelf large marine ecosystem for the sink gill net and otter trawl fisheries and the NEFSC bottom trawl survey during autumn (left panel) and spring (right panel). Notes: ranges on x- and y-axes differ between panels.

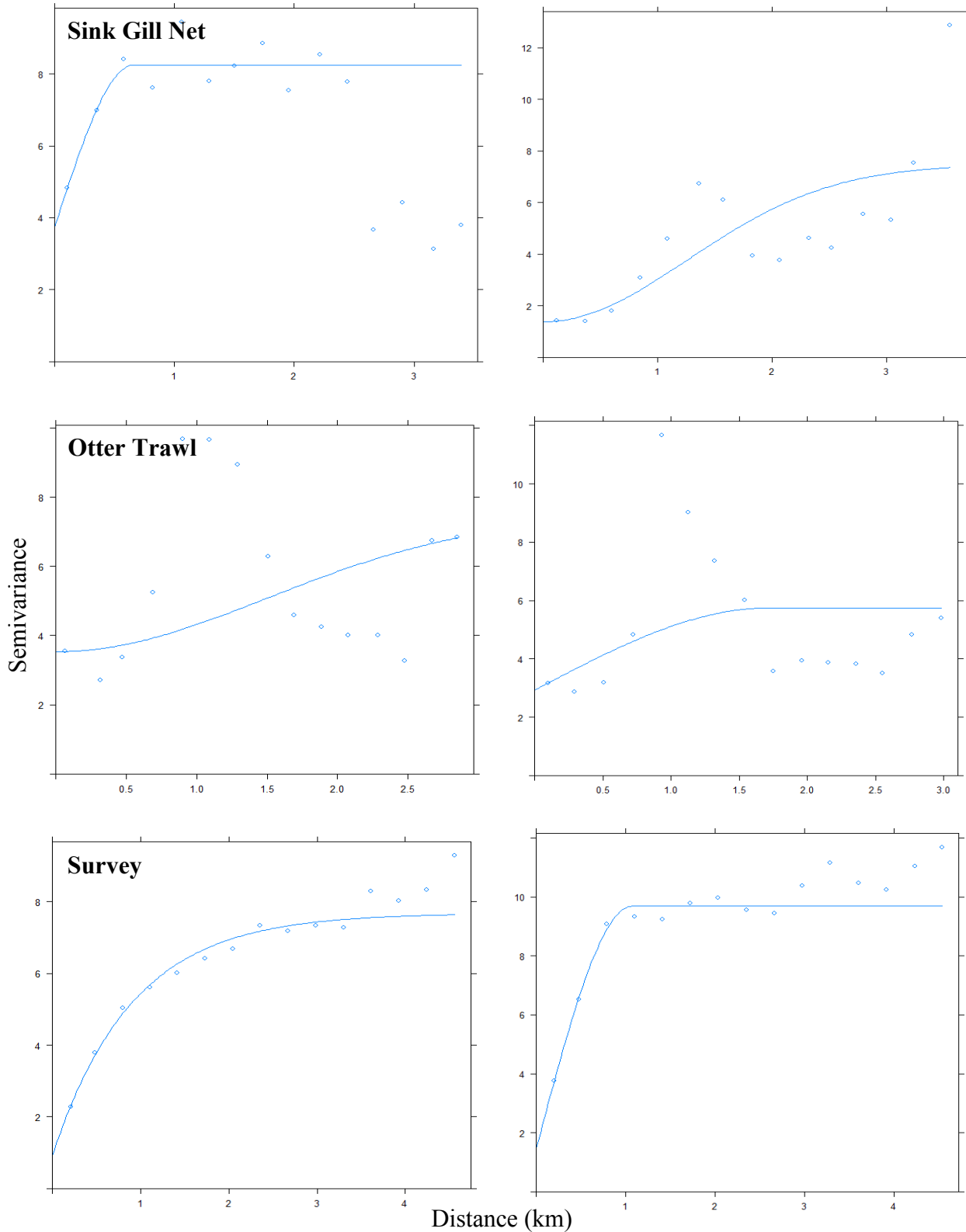


Figure 5D.10. Sample (points) and fitted (line) variograms of spiny dogfish *CPUE* during 1998 in the Northeast (US) shelf large marine ecosystem for the sink gill net and otter trawl fisheries and the NEFSC bottom trawl survey during autumn (left panel) and spring (right panel). Notes: ranges on x- and y-axes differ between panels.

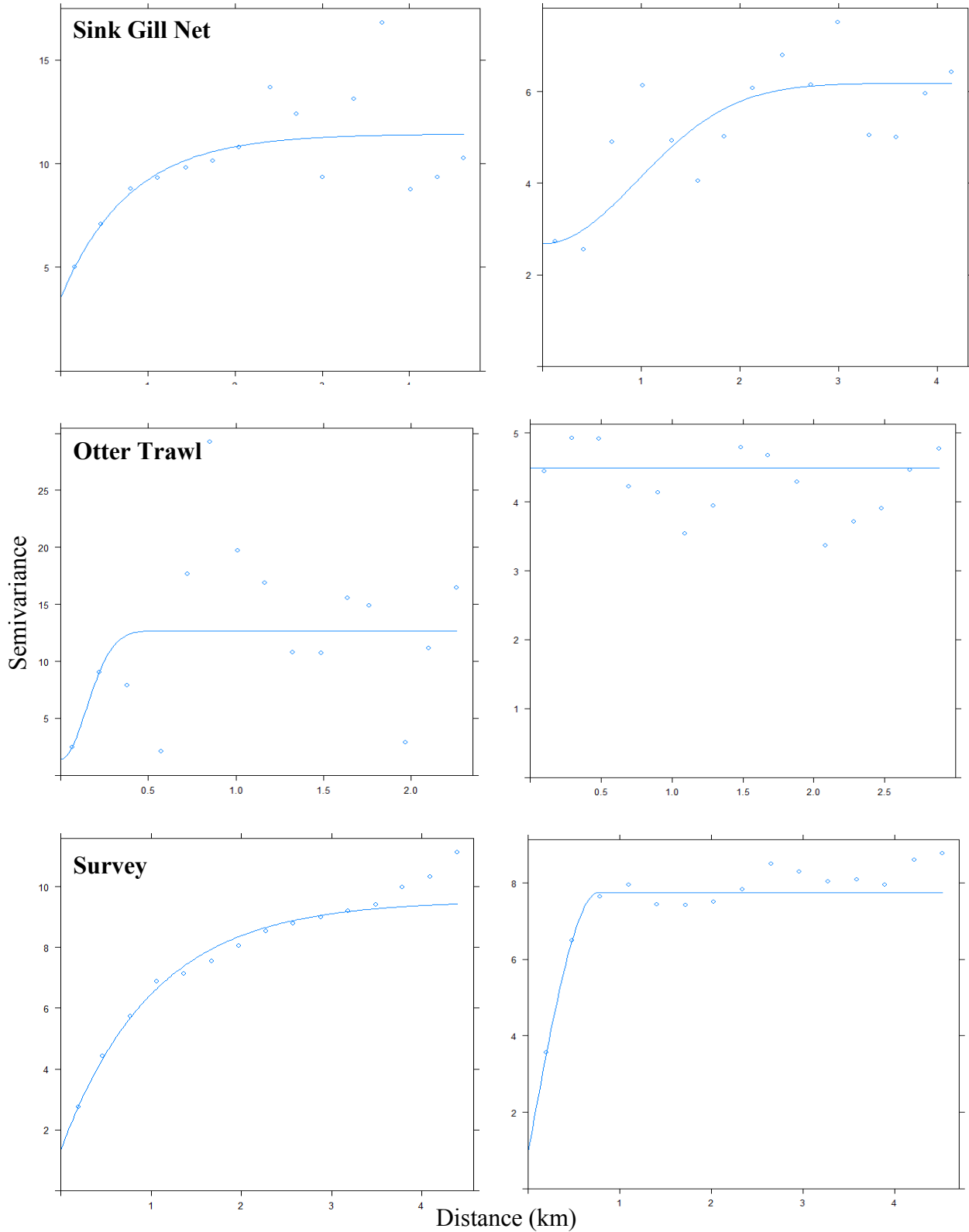


Figure 5D.11. Sample (points) and fitted (line) variograms of spiny dogfish *CPUE* during 1999 in the Northeast (US) shelf large marine ecosystem for the sink gill net and otter trawl fisheries and the NEFSC bottom trawl survey during autumn (left panel) and spring (right panel). Notes: ranges on x- and y-axes differ between panels.

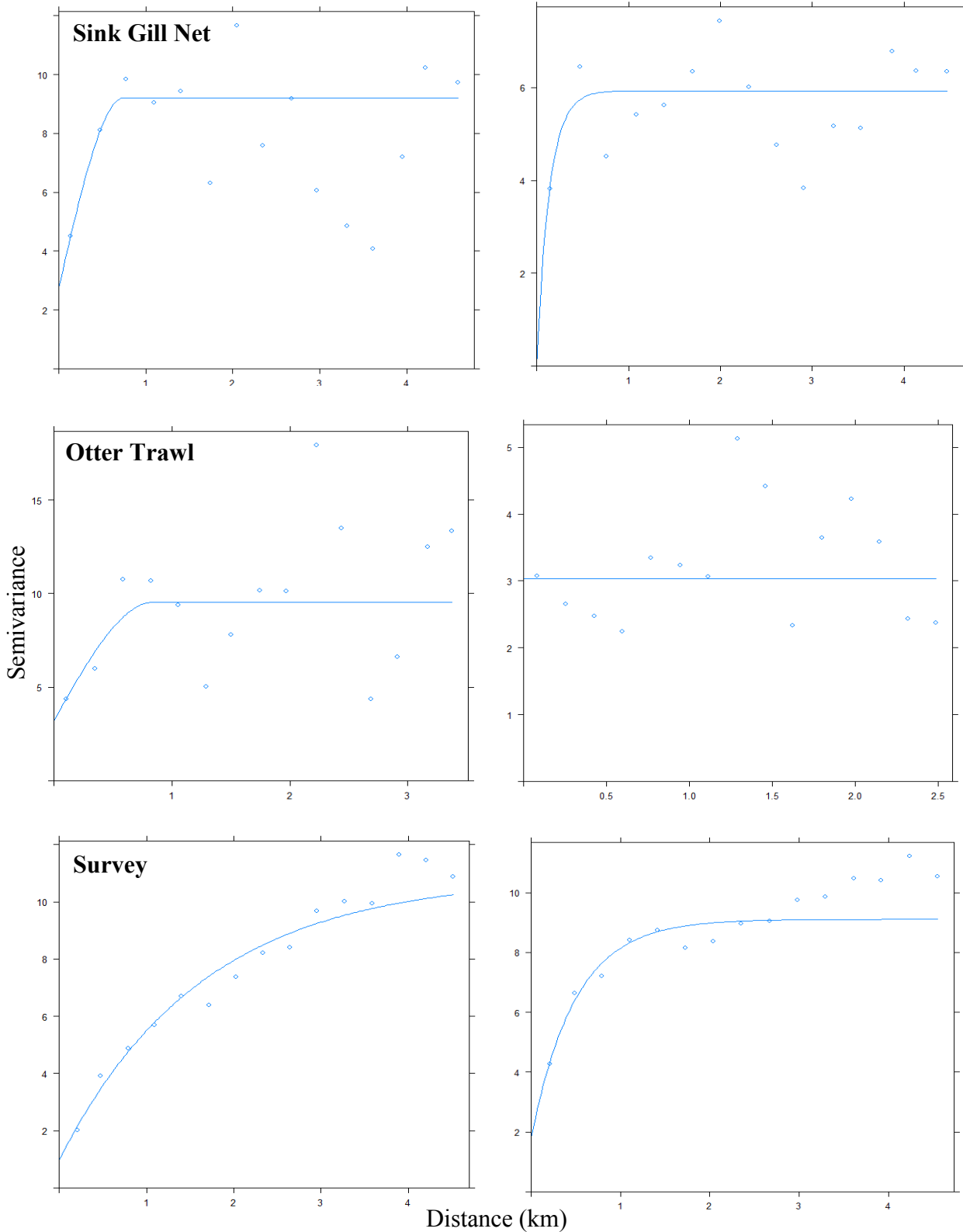


Figure 5D.12. Sample (points) and fitted (line) variograms of spiny dogfish *CPUE* during 2000 in the Northeast (US) shelf large marine ecosystem for the sink gill net and otter trawl fisheries and the NEFSC bottom trawl survey during autumn (left panel) and spring (right panel). Notes: ranges on x- and y-axes differ between panels.

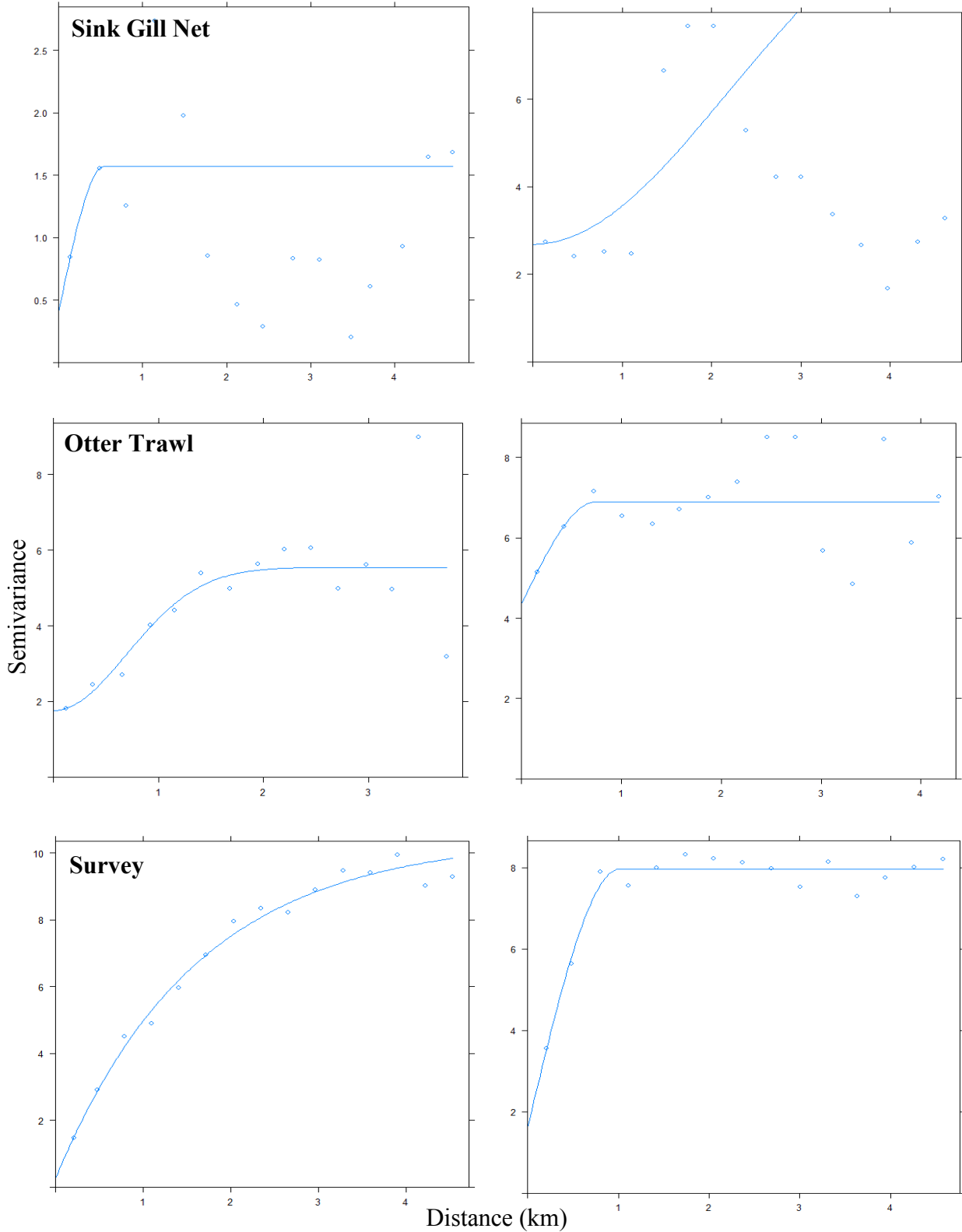


Figure 5D.13. Sample (points) and fitted (line) variograms of spiny dogfish *CPUE* during 2001 in the Northeast (US) shelf large marine ecosystem for the sink gill net and otter trawl fisheries and the NEFSC bottom trawl survey during autumn (left panel) and spring (right panel). Notes: ranges on x- and y-axes differ between panels.

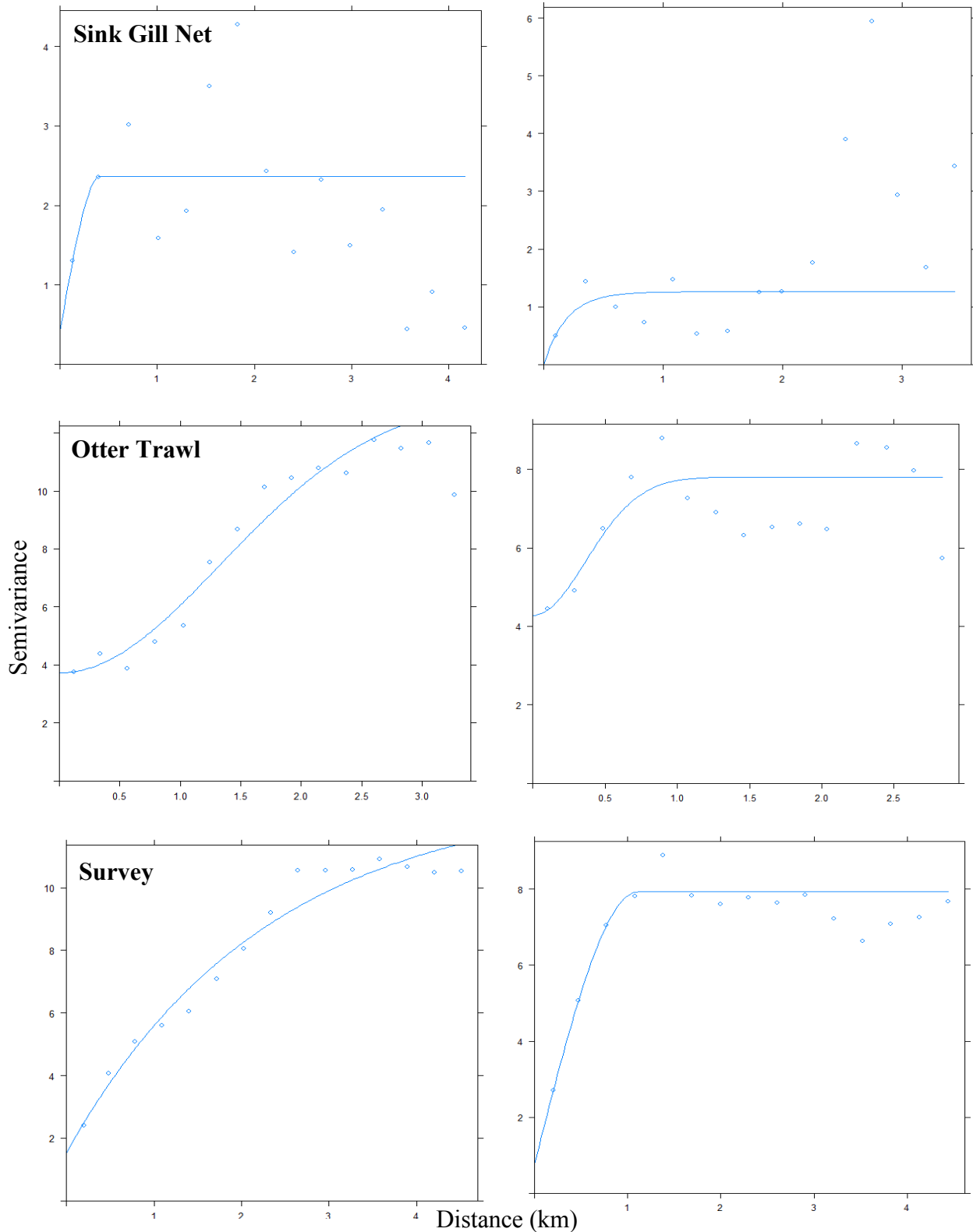


Figure 5D.14. Sample (points) and fitted (line) variograms of spiny dogfish *CPUE* during 2002 in the Northeast (US) shelf large marine ecosystem for the sink gill net and otter trawl fisheries and the NEFSC bottom trawl survey during autumn (left panel) and spring (right panel). Notes: ranges on x- and y-axes differ between panels.

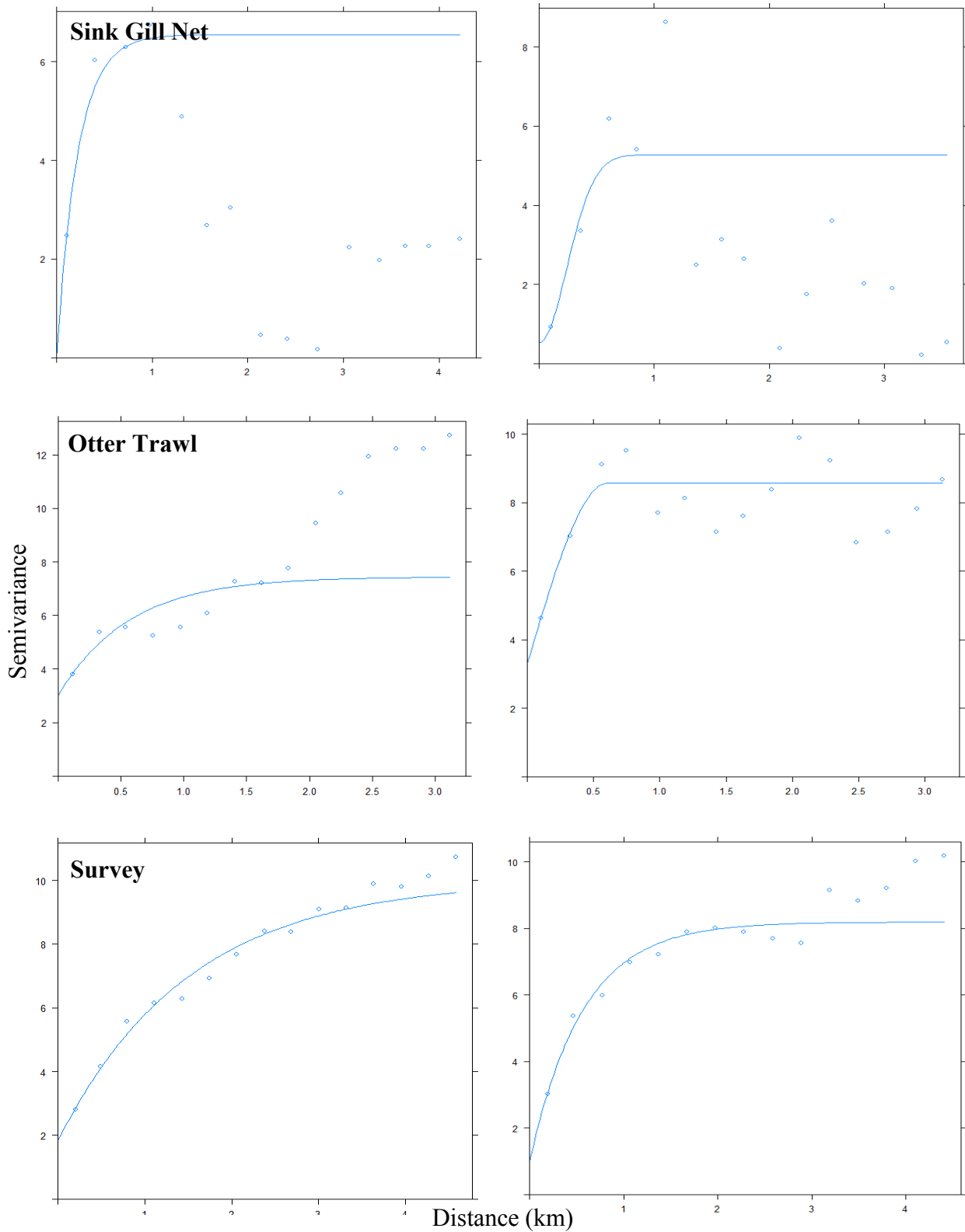


Figure 5D.15. Sample (points) and fitted (line) variograms of spiny dogfish *CPUE* during 2003 in the Northeast (US) shelf large marine ecosystem for the sink gill net and otter trawl fisheries and the NEFSC bottom trawl survey during autumn (left panel) and spring (right panel). Notes: ranges on x- and y-axes differ between panels.

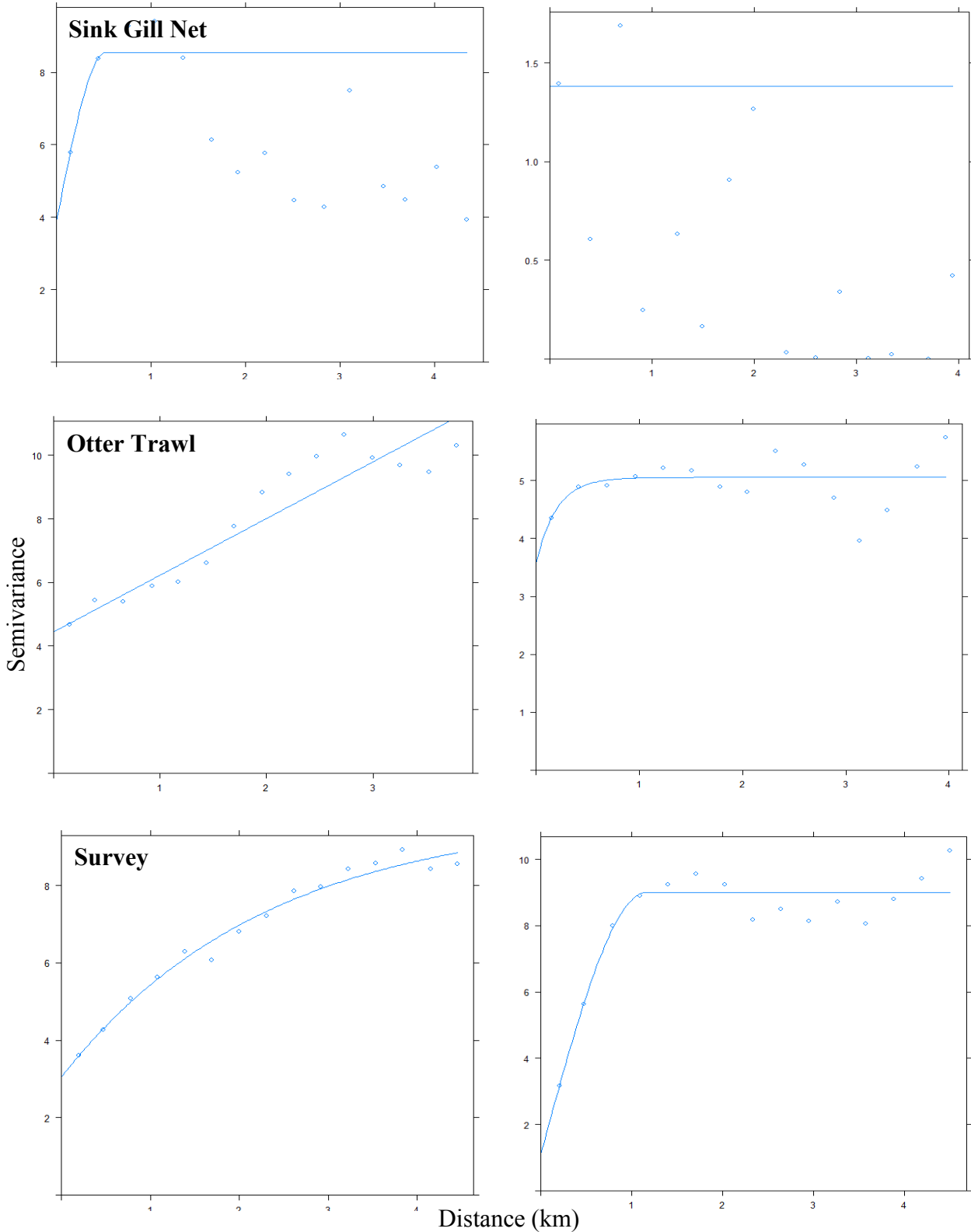


Figure 5D.16. Sample (points) and fitted (line) variograms of spiny dogfish *CPUE* during 2004 in the Northeast (US) shelf large marine ecosystem for the sink gill net and otter trawl fisheries and the NEFSC bottom trawl survey during autumn (left panel) and spring (right panel). Notes: ranges on x- and y-axes differ between panels.

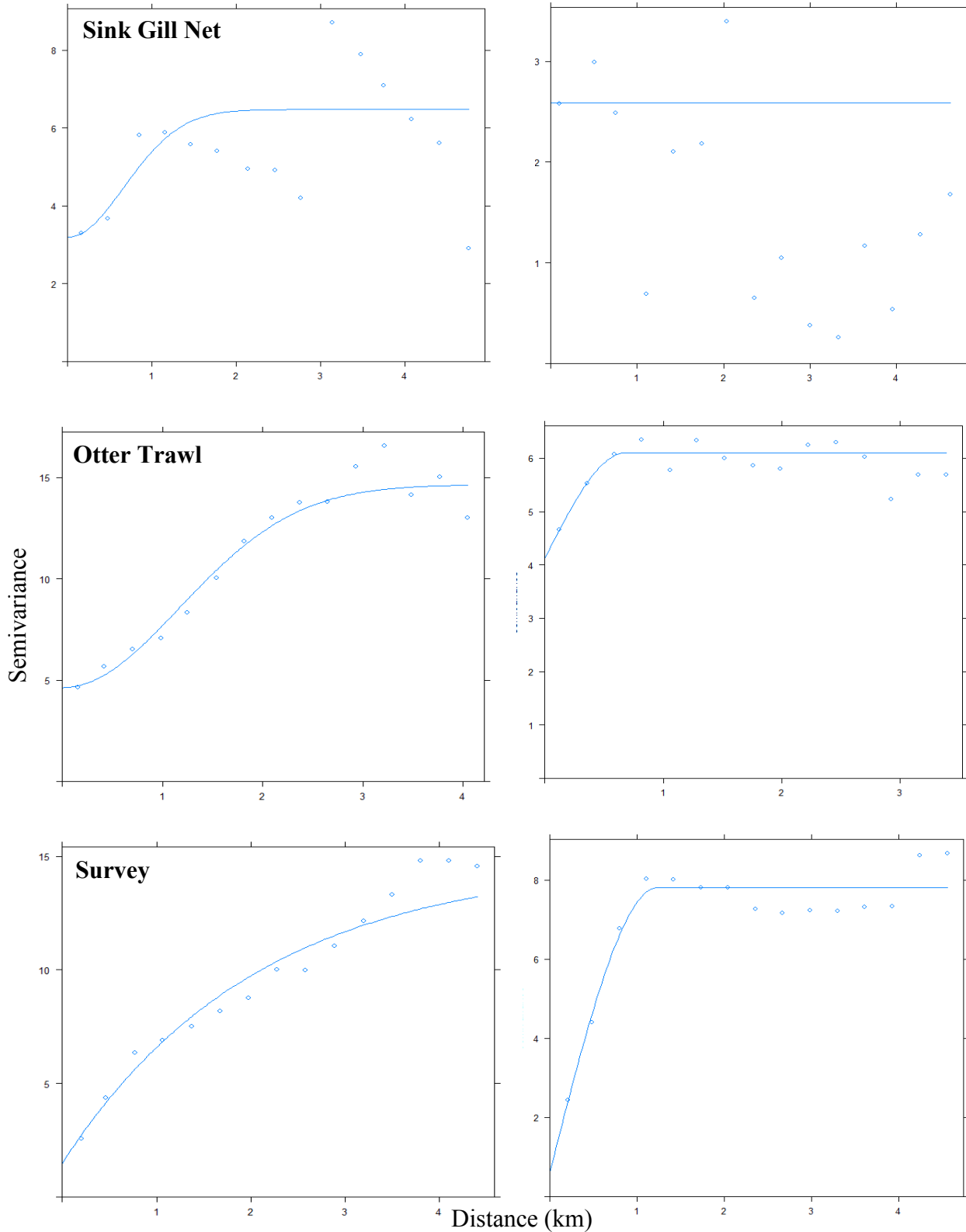


Figure 5D.17. Sample (points) and fitted (line) variograms of spiny dogfish *CPUE* during 2005 in the Northeast (US) shelf large marine ecosystem for the sink gill net and otter trawl fisheries and the NEFSC bottom trawl survey during autumn (left panel) and spring (right panel). Notes: ranges on x- and y-axes differ between panels.

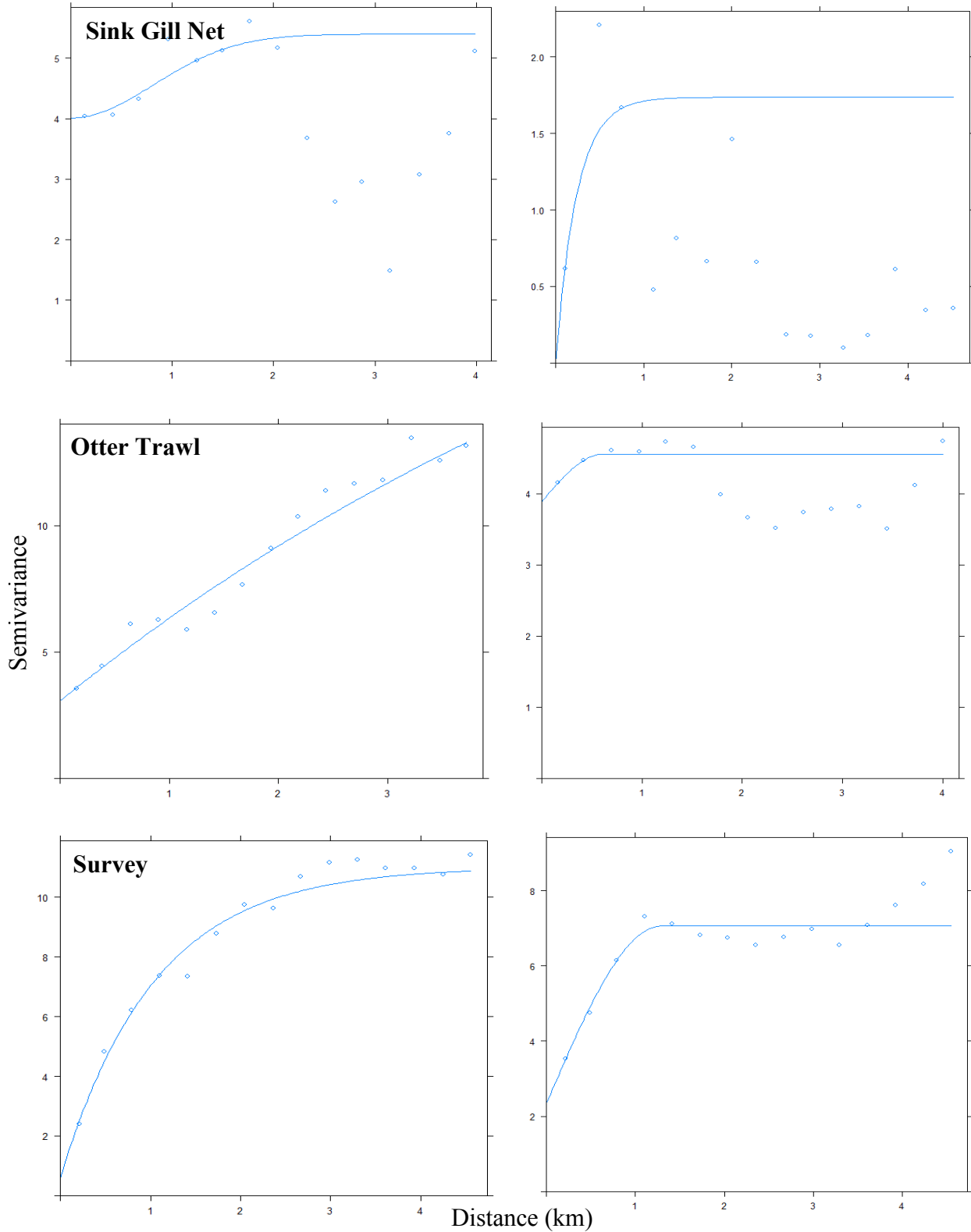


Figure 5D.18. Sample (points) and fitted (line) variograms of spiny dogfish *CPUE* during 2006 in the Northeast (US) shelf large marine ecosystem for the sink gill net and otter trawl fisheries and the NEFSC bottom trawl survey during autumn (left panel) and spring (right panel). Notes: ranges on x- and y-axes differ between panels.

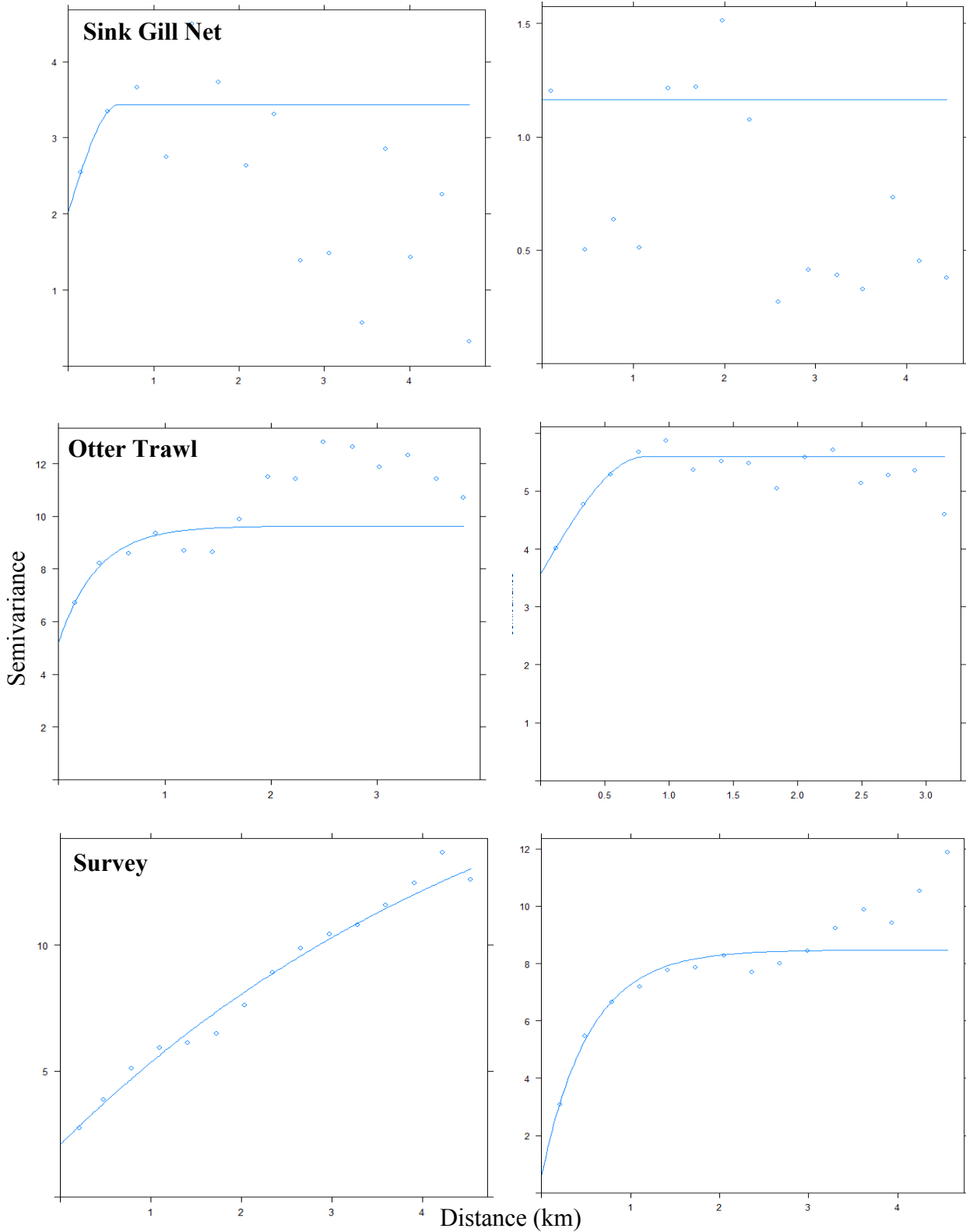


Figure 5D.19. Sample (points) and fitted (line) variograms of spiny dogfish *CPUE* during 2007 in the Northeast (US) shelf large marine ecosystem for the sink gill net and otter trawl fisheries and the NEFSC bottom trawl survey during autumn (left panel) and spring (right panel). Notes: ranges on x- and y-axes differ between panels.

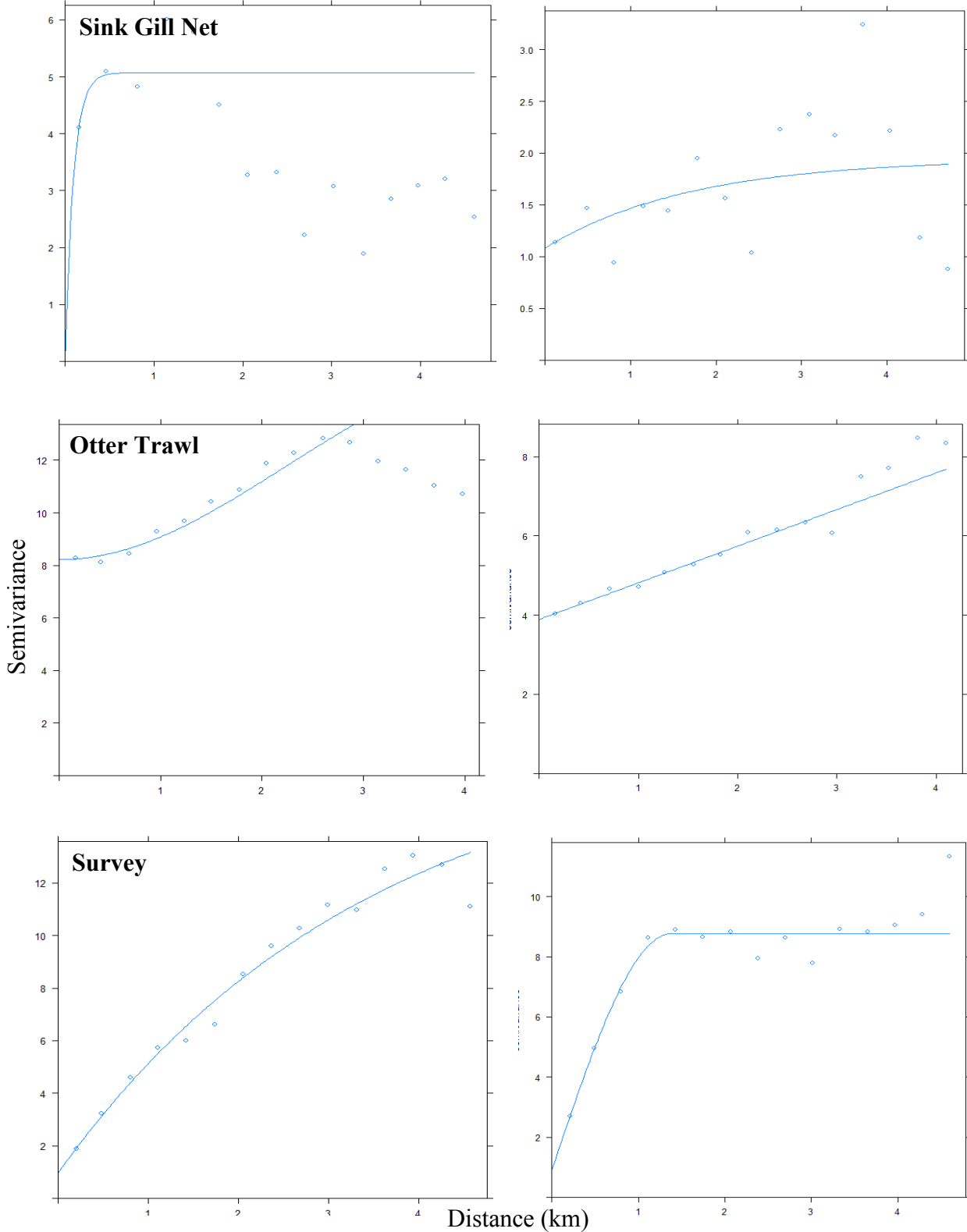


Figure 5D.20. Sample (points) and fitted (line) variograms of spiny dogfish *CPUE* during 2008 in the Northeast (US) shelf large marine ecosystem for the sink gill net and otter trawl fisheries and the NEFSC bottom trawl survey during autumn (left panel) and spring (right panel). Notes: ranges on x- and y-axes differ between panels.

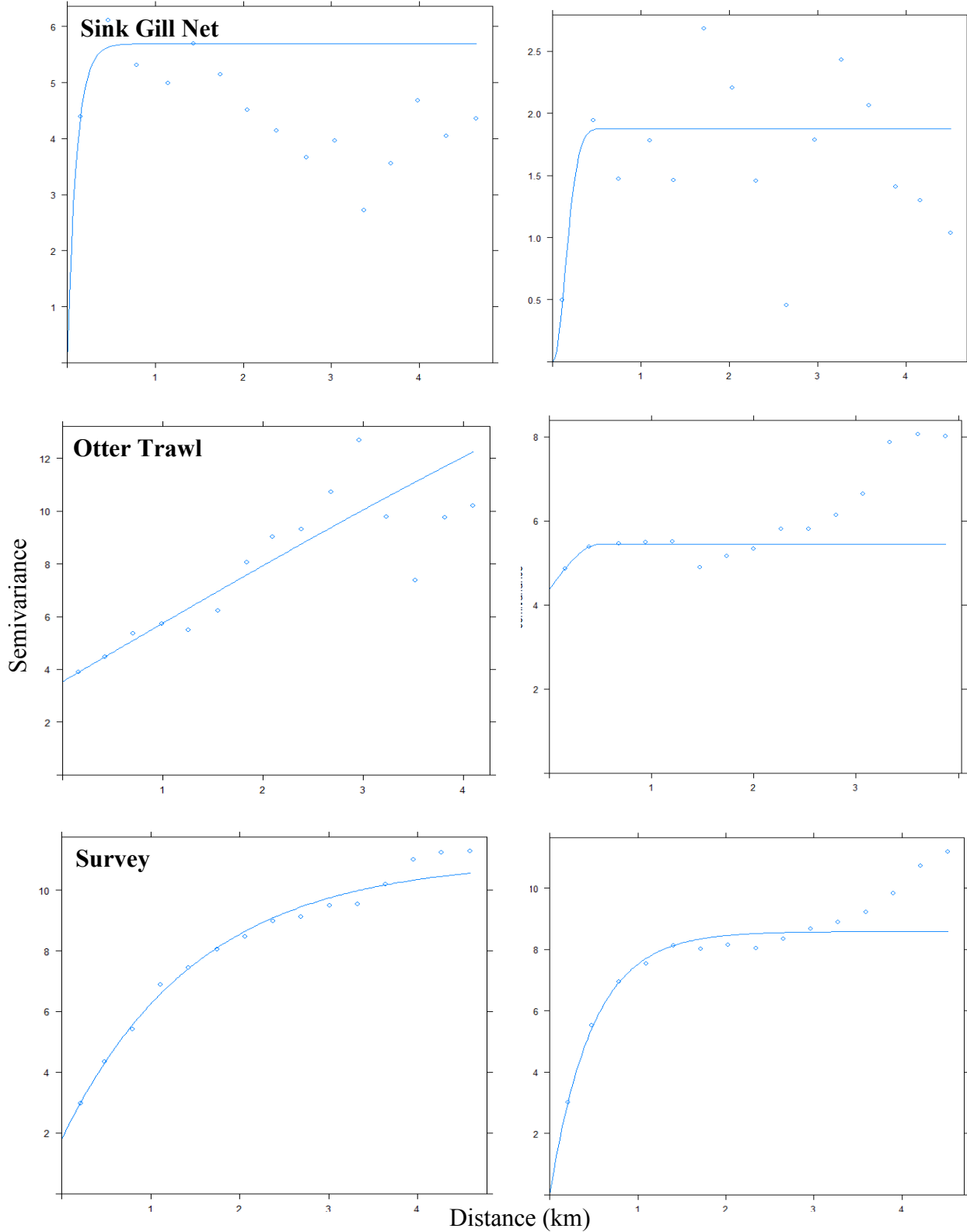
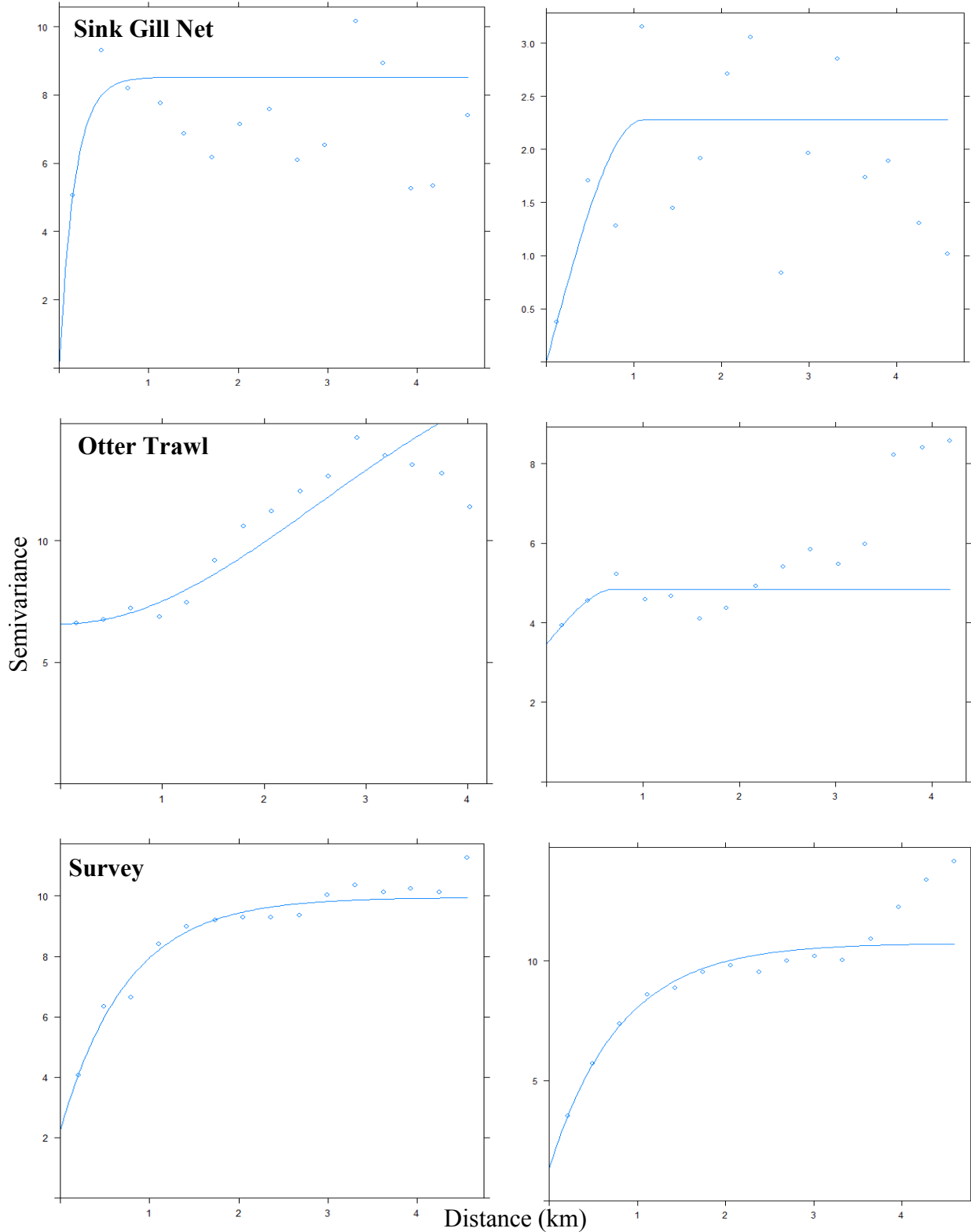


Figure 5D.21. Sample (points) and fitted (line) variograms of spiny dogfish *CPUE* during 2009 in the Northeast (US) shelf large marine ecosystem for the sink gill net and otter trawl fisheries and the NEFSC bottom trawl survey during autumn (left panel) and spring (right panel). Notes: ranges on x- and y-axes differ between panels.



Appendix 5E. Spatial Distribution of Fishery Effort

Figure 5E.1. Spatial distribution of fishing effort in the Northeast (US) shelf large marine ecosystem during autumn (left panel) and spring (right panel) of 1989 for the domestic A) sink gill net and B) otter trawl fisheries. Cell size $\sim 560 \text{ km}^2$ where values reflect the average effort (number of hours fished) obtained through rasterization of the original fisheries observer data.

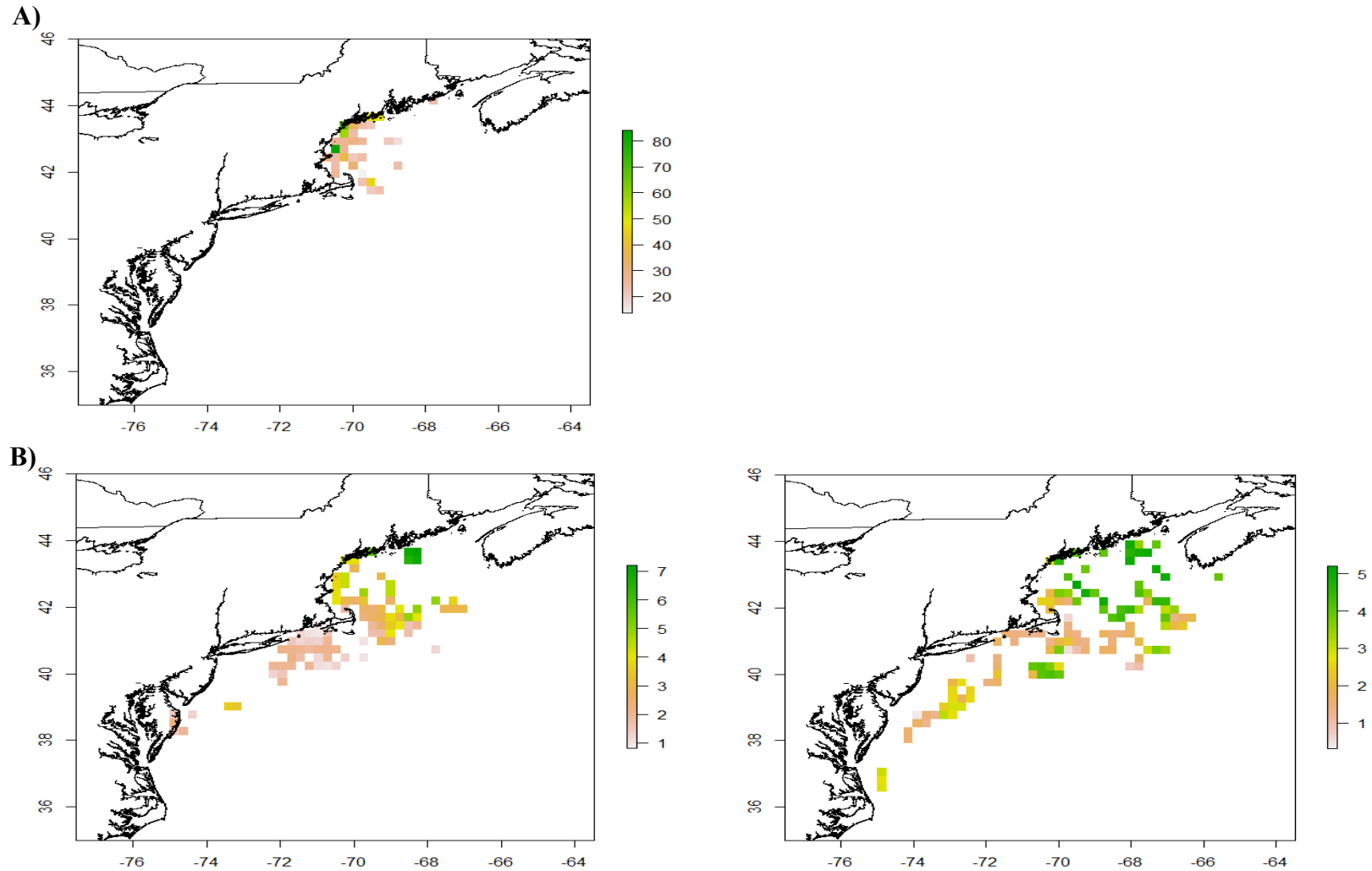


Figure 5E.2. Spatial distribution of fishing effort in the Northeast (US) shelf large marine ecosystem during autumn (left panel) and spring (right panel) of 1990 for the domestic A) sink gill net and B) otter trawl fisheries. Cell size $\sim 560 \text{ km}^2$ where values reflect the average effort (number of hours fished) obtained through rasterization of the original fisheries observer data.

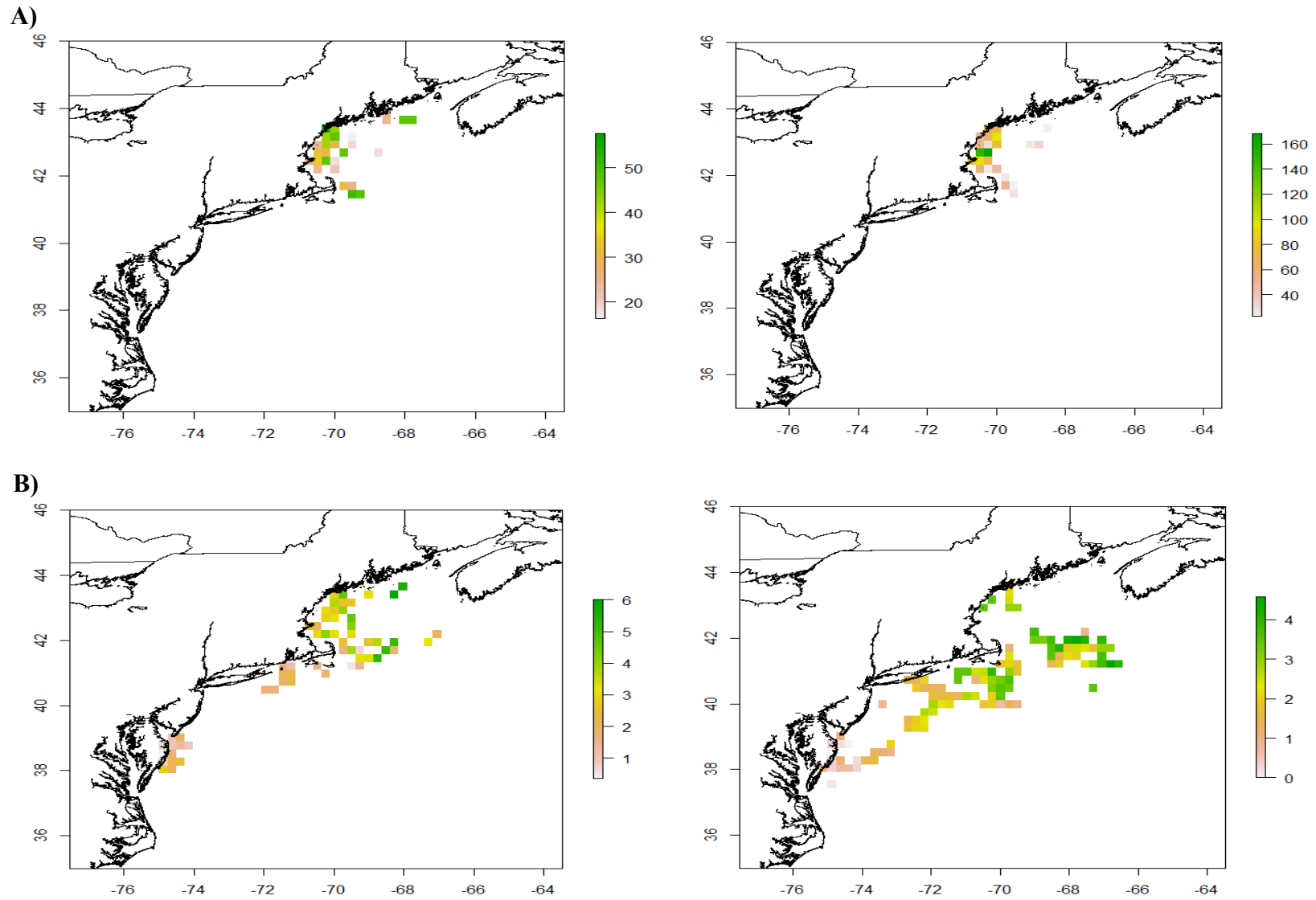


Figure 5E.3. Spatial distribution of fishing effort in the Northeast (US) shelf large marine ecosystem during autumn (left panel) and spring (right panel) of 1991 for the domestic A) sink gill net and B) otter trawl fisheries. Cell size $\sim 560 \text{ km}^2$ where values reflect the average effort (number of hours fished) obtained through rasterization of the original fisheries observer data.

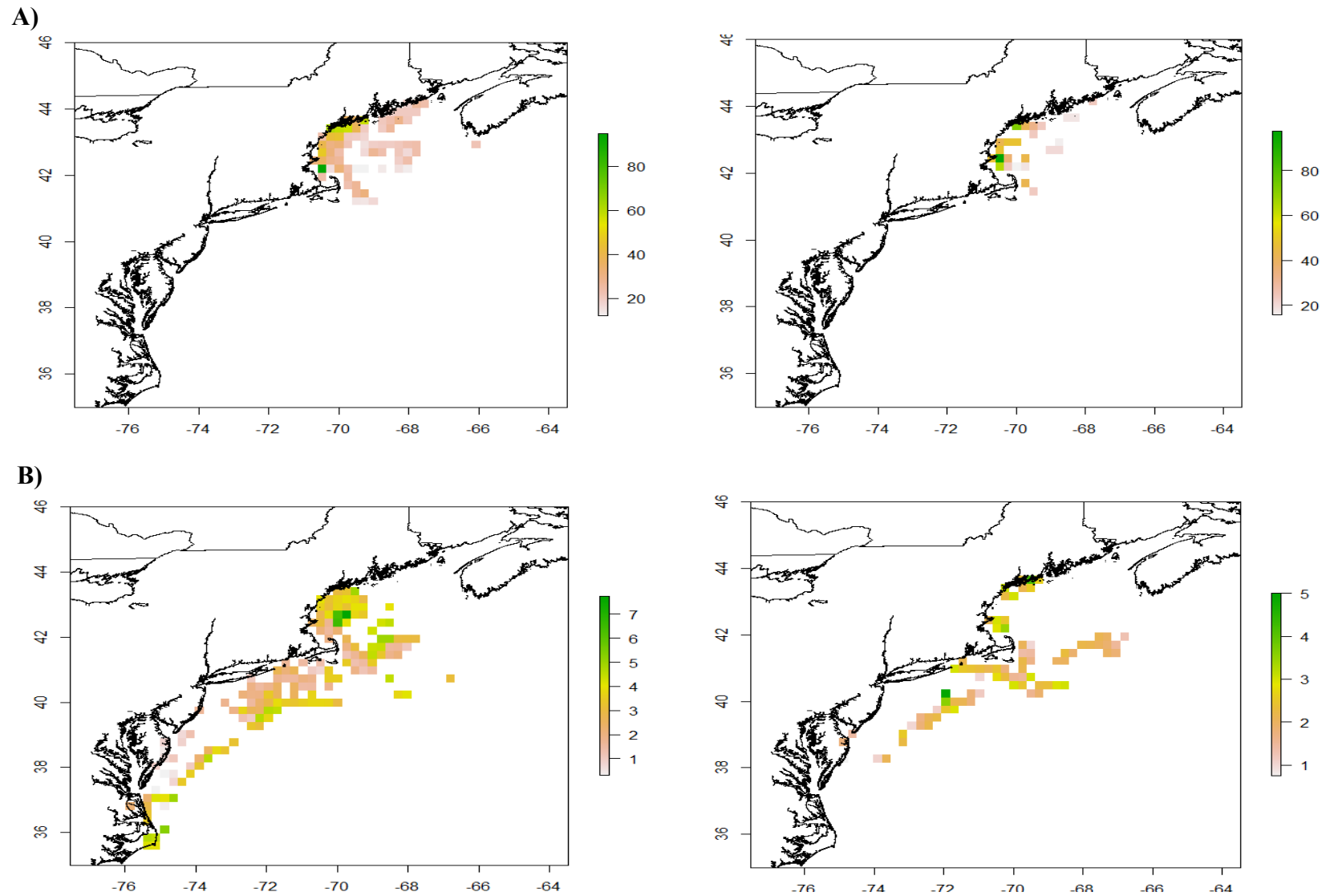


Figure 5E.4. Spatial distribution of fishing effort in the Northeast (US) shelf large marine ecosystem during autumn (left panel) and spring (right panel) of 1992 for the domestic A) sink gill net and B) otter trawl fisheries. Cell size $\sim 560 \text{ km}^2$ where values reflect the average effort (number of hours fished) obtained through rasterization of the original fisheries observer data.

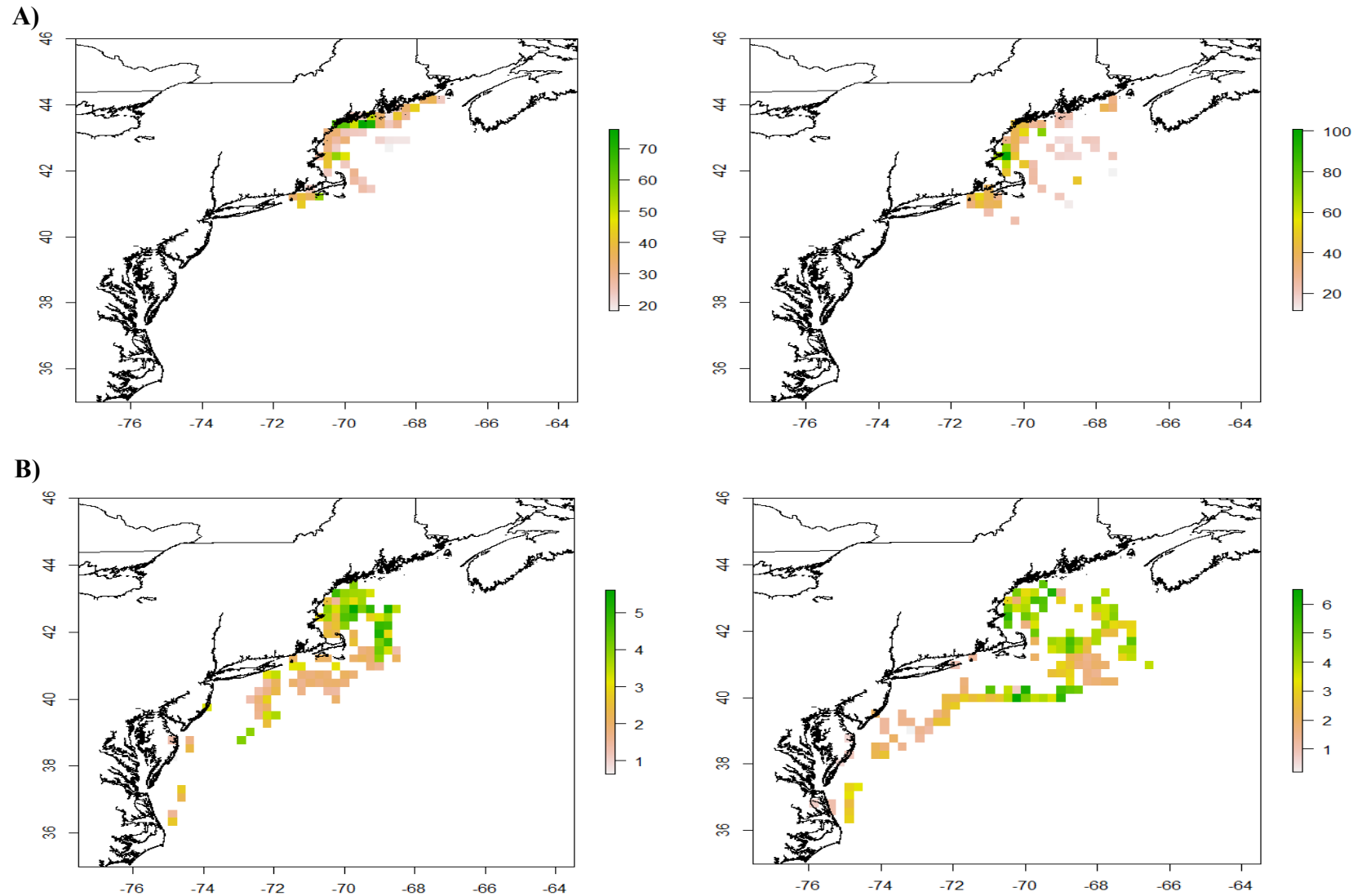


Figure 5E.5. Spatial distribution of fishing effort in the Northeast (US) shelf large marine ecosystem during autumn (left panel) and spring (right panel) of 1993 for the domestic A) sink gill net and B) otter trawl fisheries. Cell size $\sim 560 \text{ km}^2$ where values reflect the average effort (number of hours fished) obtained through rasterization of the original fisheries observer data.

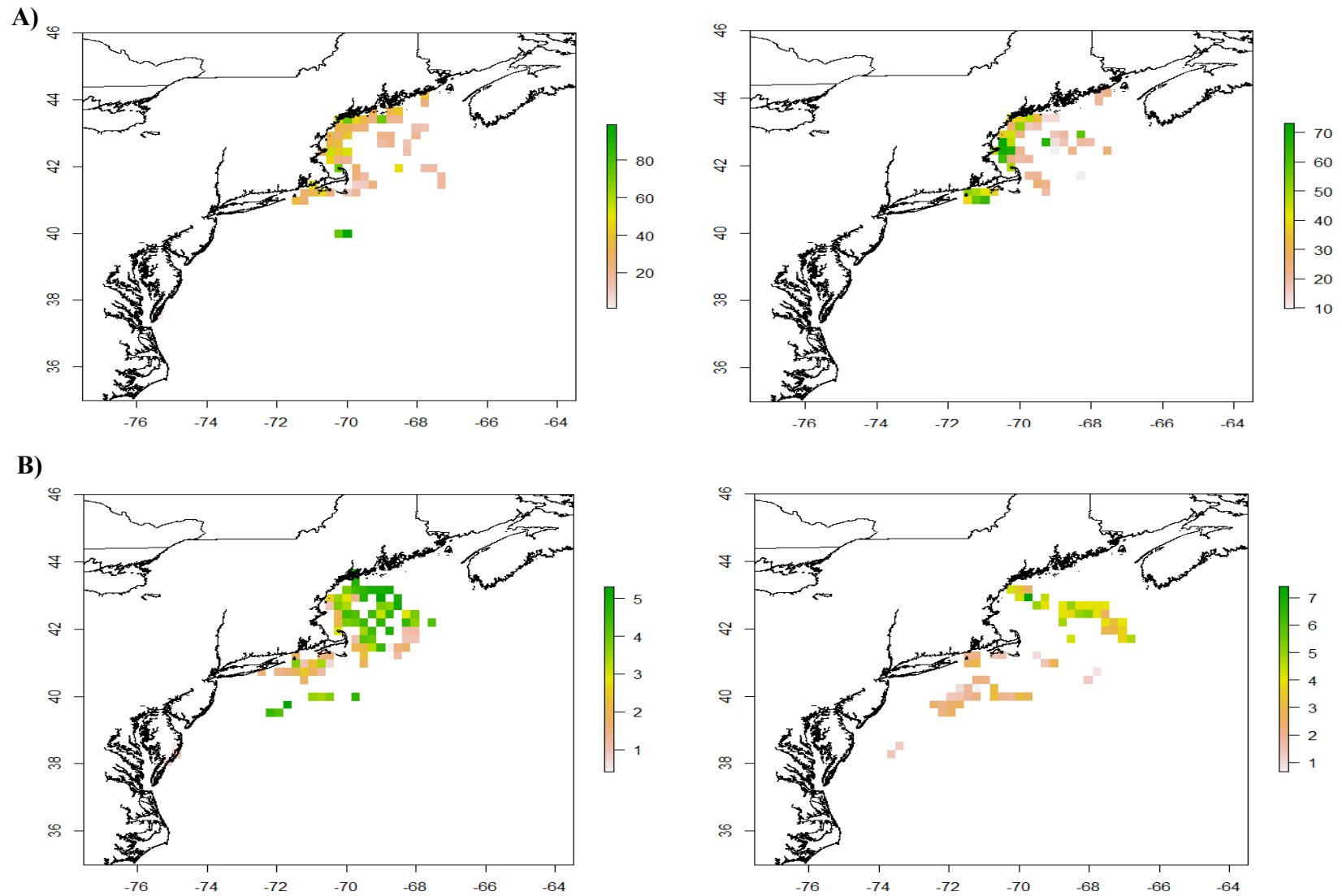


Figure 5E.6. Spatial distribution of fishing effort in the Northeast (US) shelf large marine ecosystem during autumn (left panel) and spring (right panel) of 1994 for the domestic A) sink gill net and B) otter trawl fisheries. Cell size $\sim 560 \text{ km}^2$ where values reflect the average effort (number of hours fished) obtained through rasterization of the original fisheries observer data.

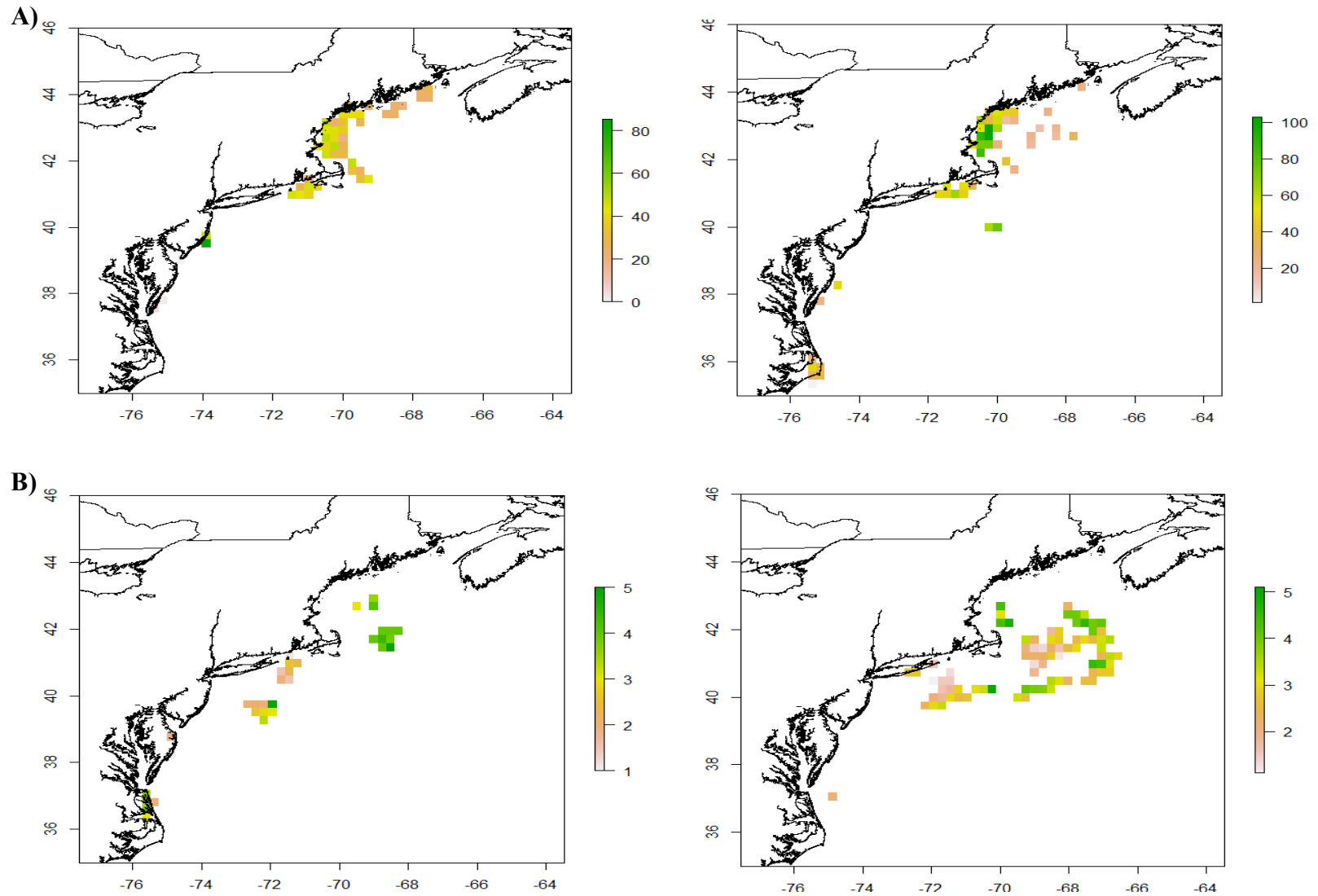


Figure 5E.7. Spatial distribution of fishing effort in the Northeast (US) shelf large marine ecosystem during autumn (left panel) and spring (right panel) of 1995 for the domestic A) sink gill net and B) otter trawl fisheries. Cell size $\sim 560 \text{ km}^2$ where values reflect the average effort (number of hours fished) obtained through rasterization of the original fisheries observer data.

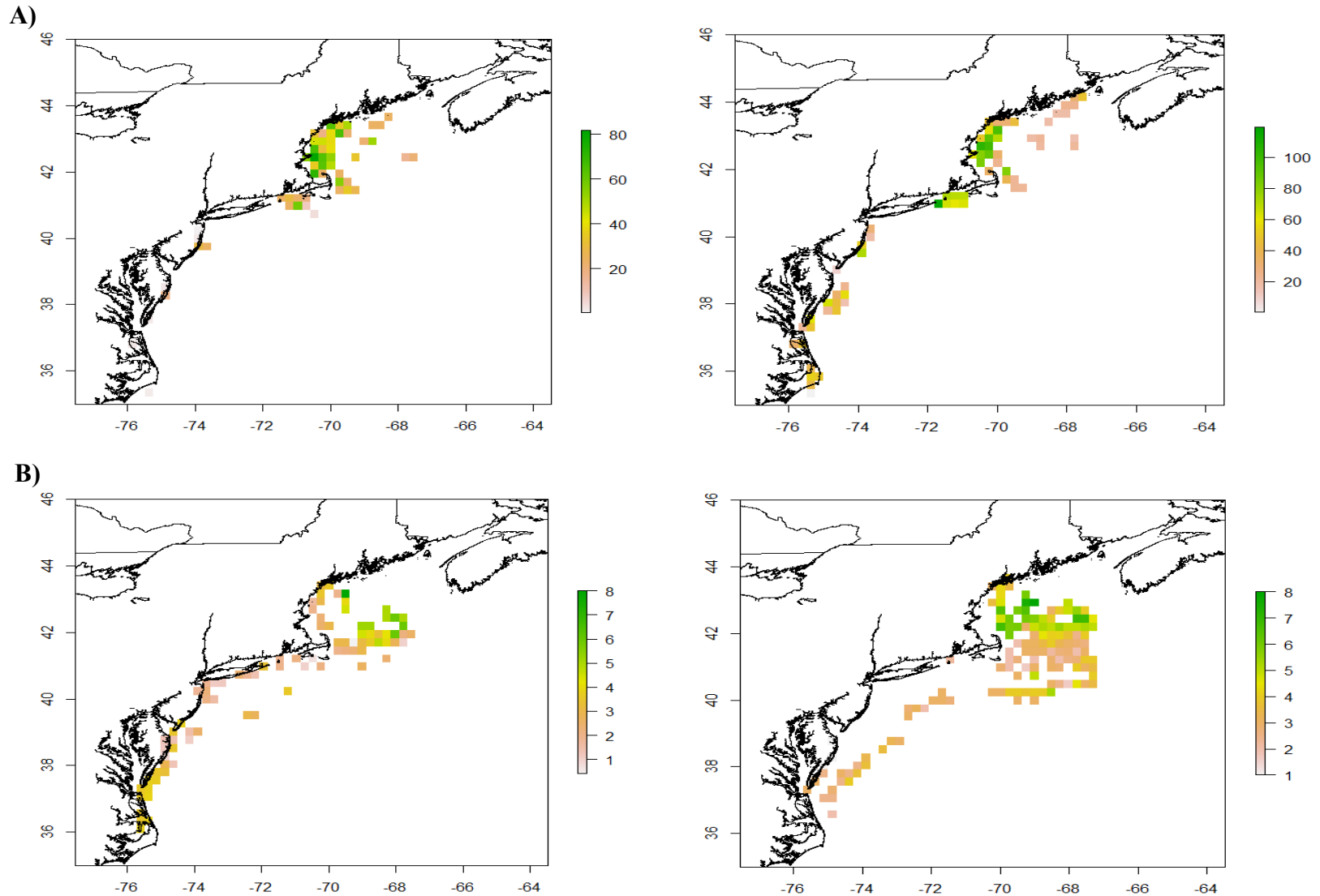


Figure 5E.8. Spatial distribution of fishing effort in the Northeast (US) shelf large marine ecosystem during autumn (left panel) and spring (right panel) of 1996 for the domestic A) sink gill net and B) otter trawl fisheries. Cell size $\sim 560 \text{ km}^2$ where values reflect the average effort (number of hours fished) obtained through rasterization of the original fisheries observer data.

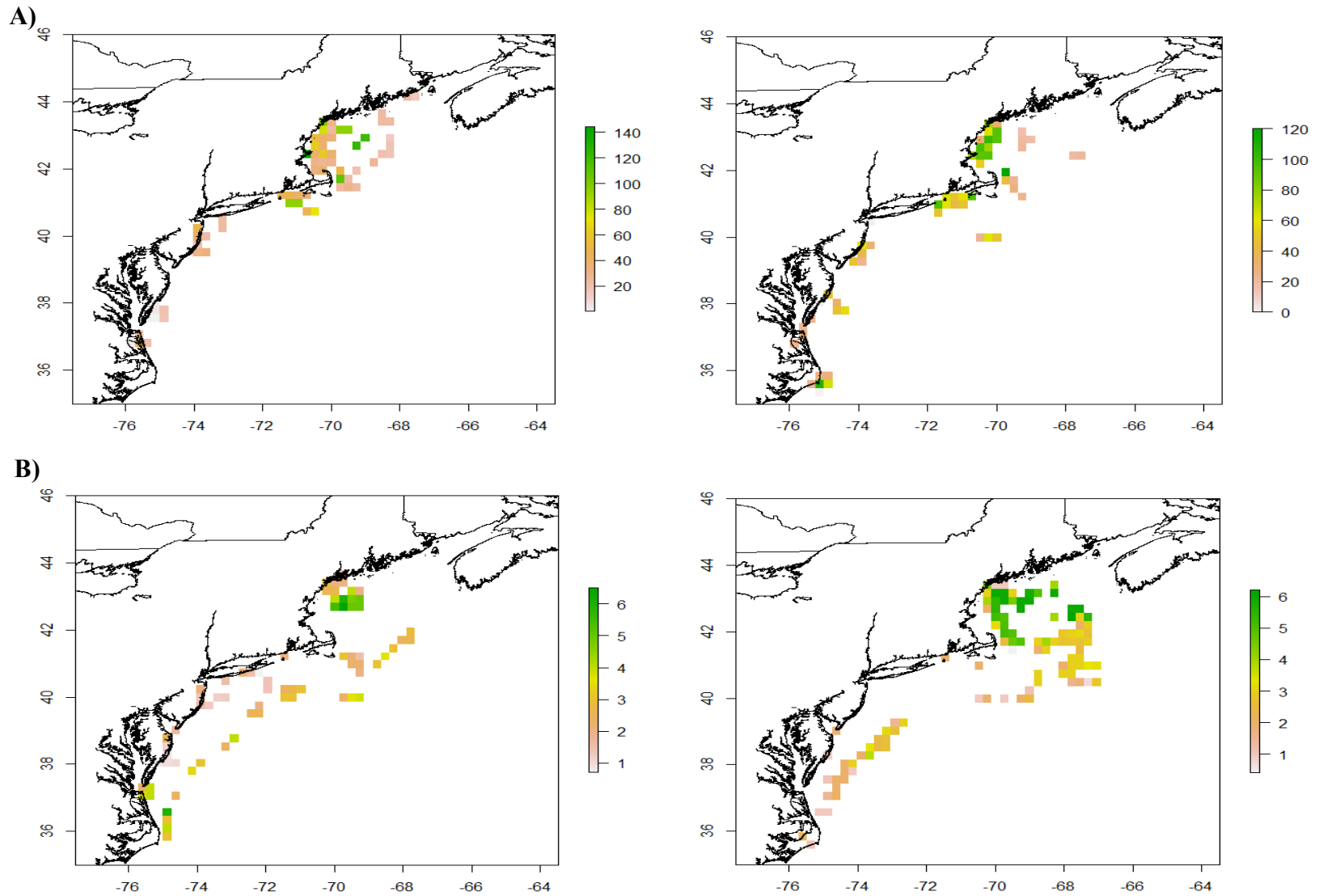


Figure 5E.9. Spatial distribution of fishing effort in the Northeast (US) shelf large marine ecosystem during autumn (left panel) and spring (right panel) of 1997 for the domestic A) sink gill net and B) otter trawl fisheries. Cell size $\sim 560 \text{ km}^2$ where values reflect the average effort (number of hours fished) obtained through rasterization of the original fisheries observer data.

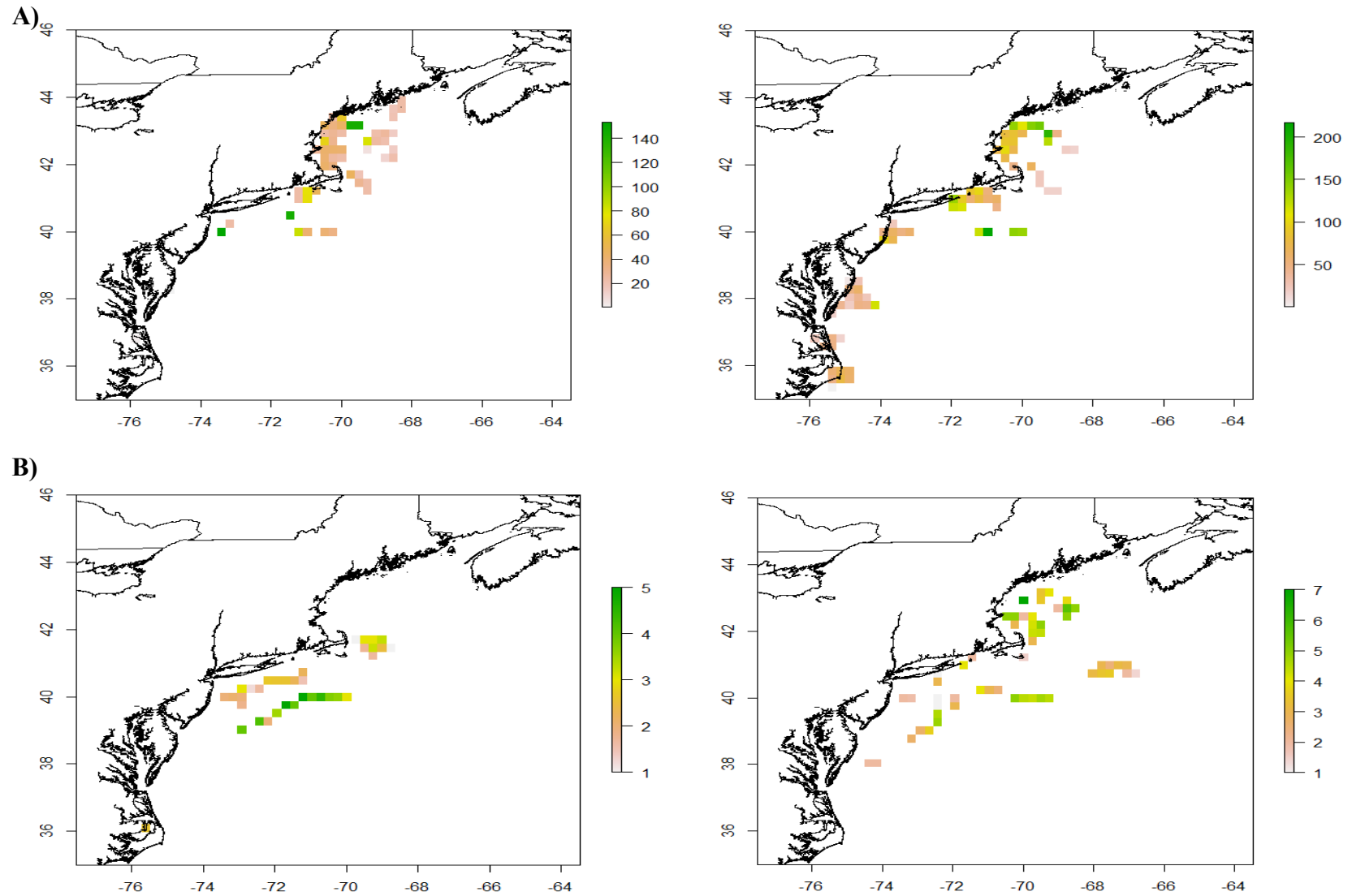


Figure 5E.10. Spatial distribution of fishing effort in the Northeast (US) shelf large marine ecosystem during autumn (left panel) and spring (right panel) of 1998 for the domestic A) sink gill net and B) otter trawl fisheries. Cell size $\sim 560 \text{ km}^2$ where values reflect the average effort (number of hours fished) obtained through rasterization of the original fisheries observer data.

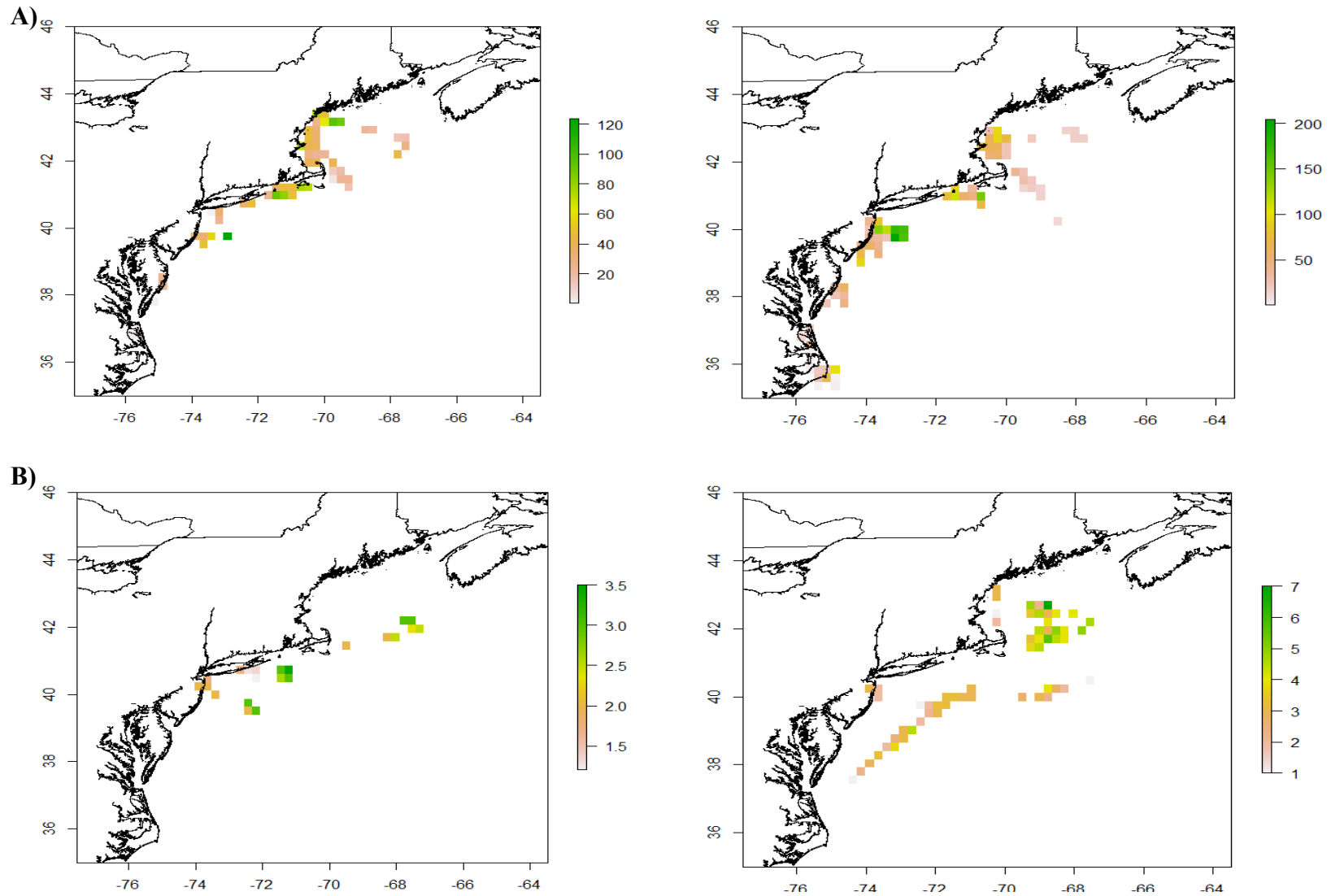


Figure 5E.11. Spatial distribution of fishing effort in the Northeast (US) shelf large marine ecosystem during autumn (left panel) and spring (right panel) of 1999 for the domestic A) sink gill net and B) otter trawl fisheries. Cell size $\sim 560 \text{ km}^2$ where values reflect the average effort (number of hours fished) obtained through rasterization of the original fisheries observer data.

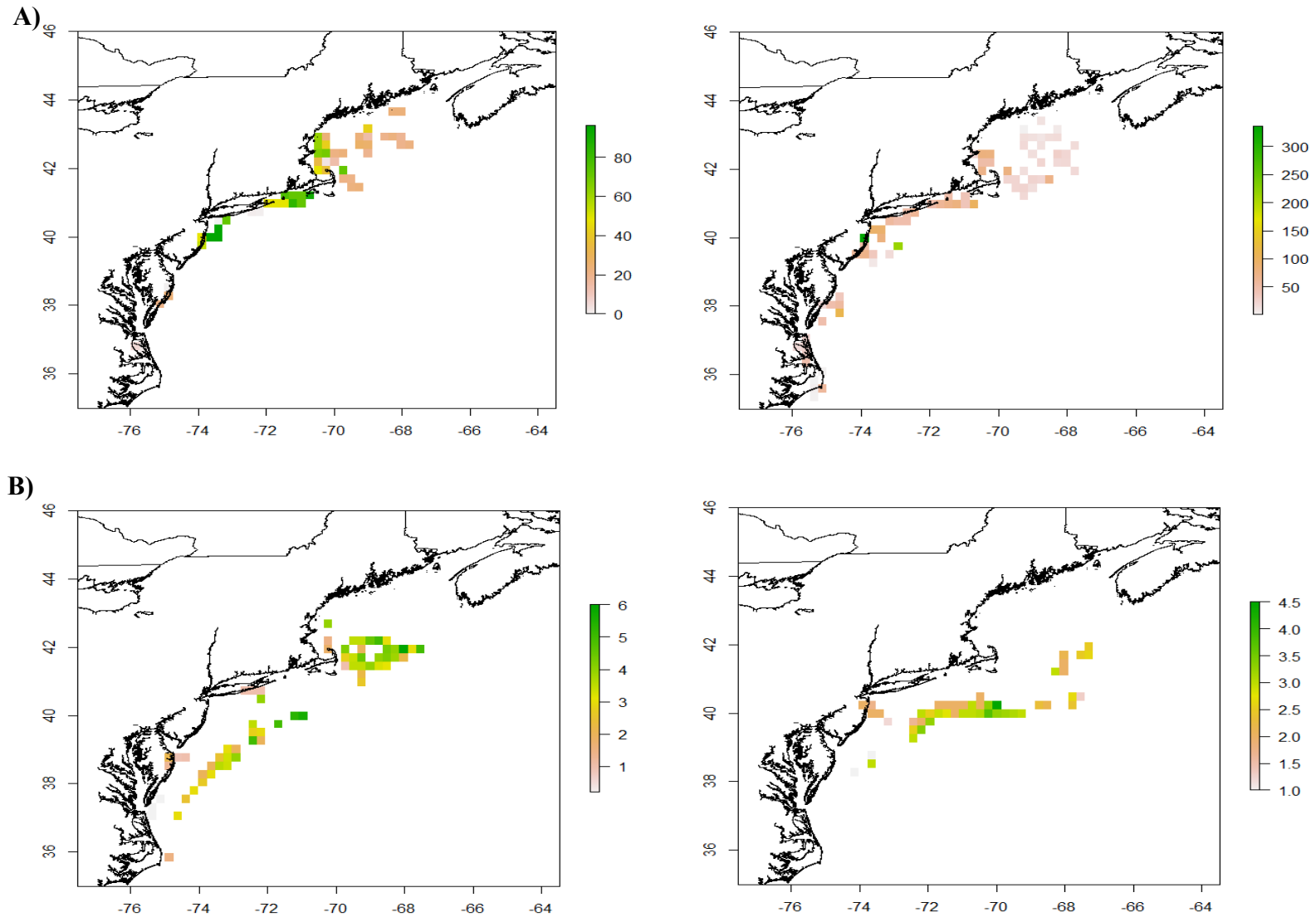


Figure 5E.12. Spatial distribution of fishing effort in the Northeast (US) shelf large marine ecosystem during autumn (left panel) and spring (right panel) of 2000 for the domestic A) sink gill net and B) otter trawl fisheries. Cell size $\sim 560 \text{ km}^2$ where values reflect the average effort (number of hours fished) obtained through rasterization of the original fisheries observer data.

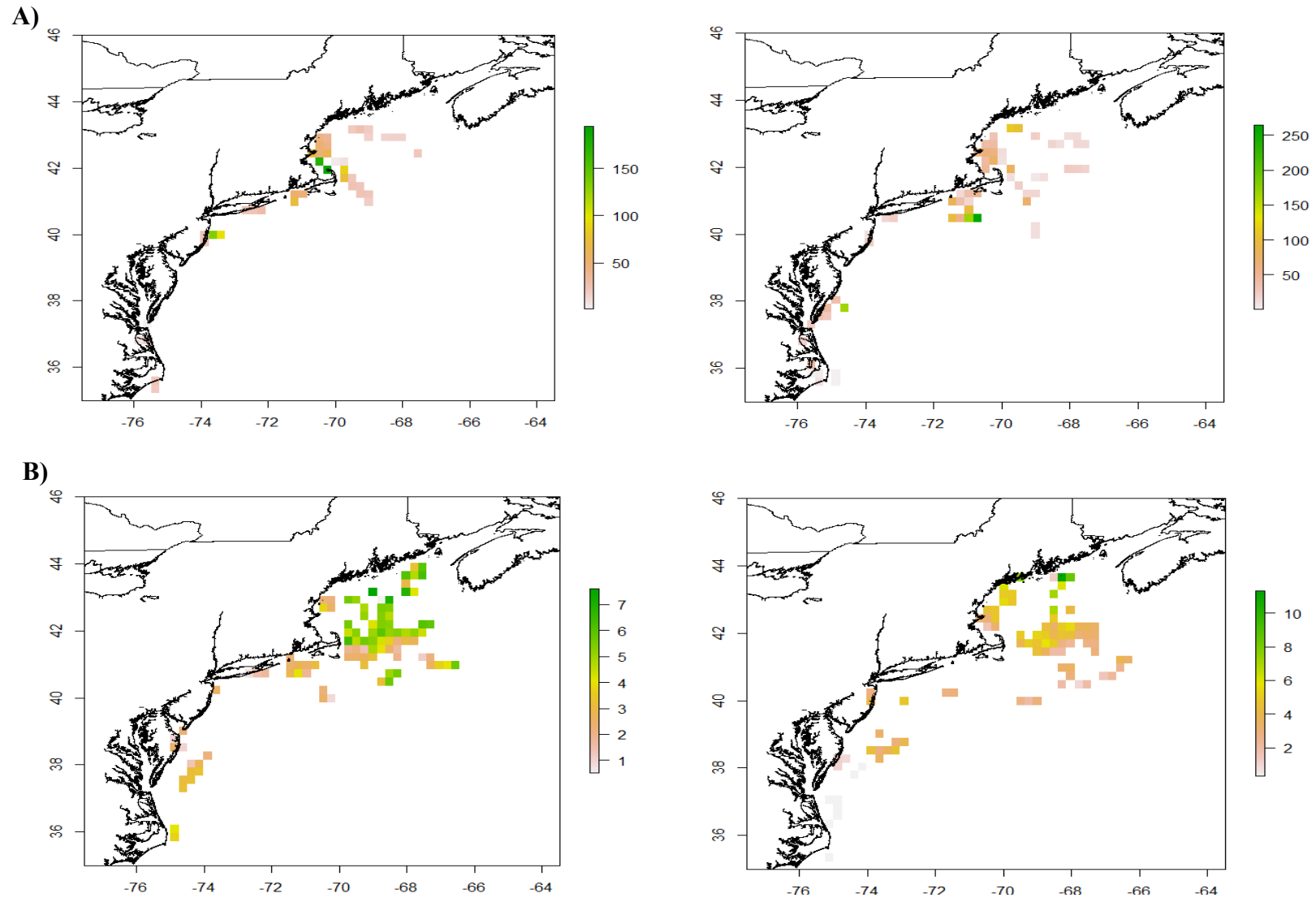


Figure 5E.13. Spatial distribution of fishing effort in the Northeast (US) shelf large marine ecosystem during autumn (left panel) and spring (right panel) of 2001 for the domestic A) sink gill net and B) otter trawl fisheries. Cell size $\sim 560 \text{ km}^2$ where values reflect the average effort (number of hours fished) obtained through rasterization of the original fisheries observer data.

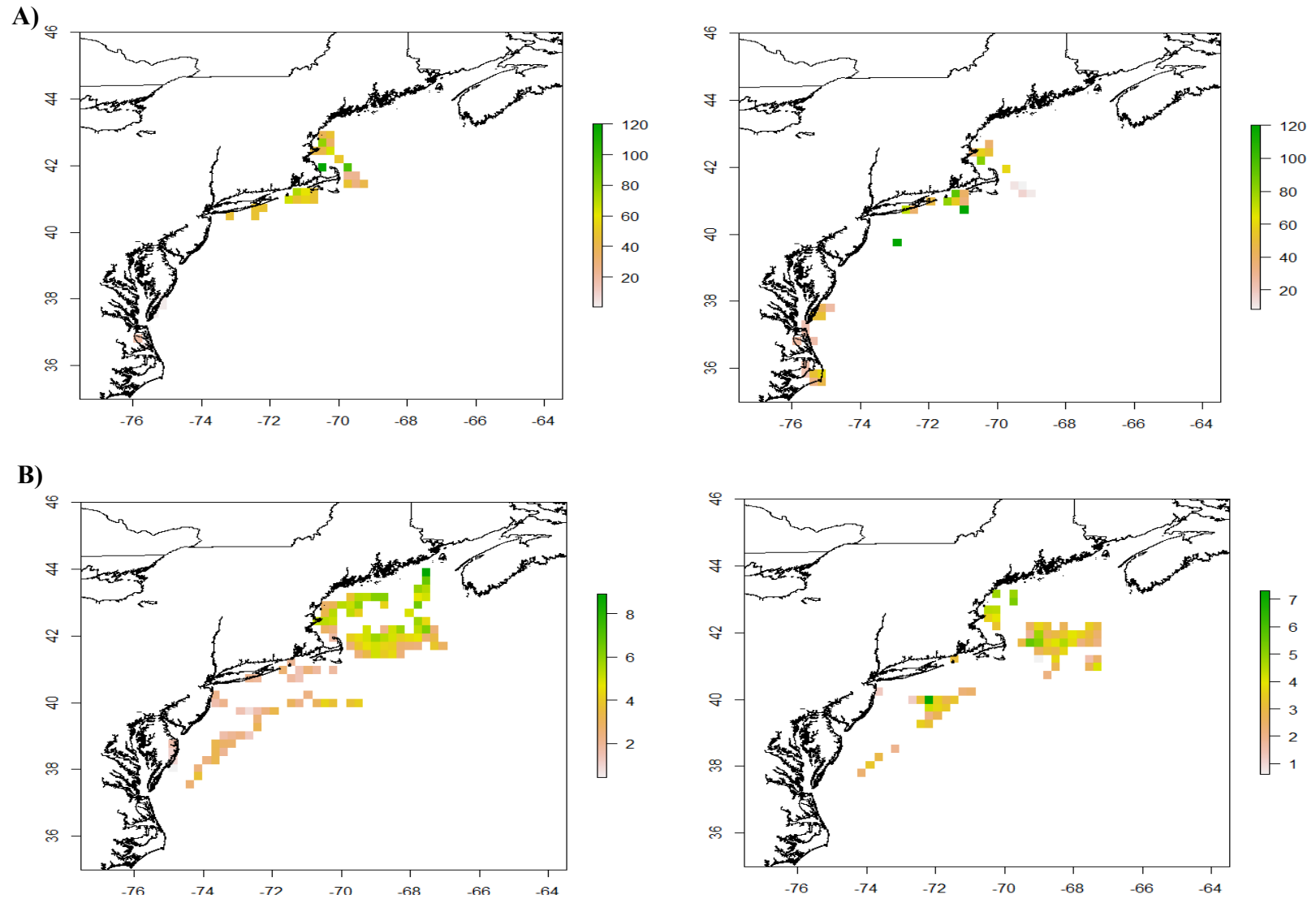


Figure 5E.14. Spatial distribution of fishing effort in the Northeast (US) shelf large marine ecosystem during autumn (left panel) and spring (right panel) of 2002 for the domestic A) sink gill net and B) otter trawl fisheries. Cell size $\sim 560 \text{ km}^2$ where values reflect the average effort (number of hours fished) obtained through rasterization of the original fisheries observer data.

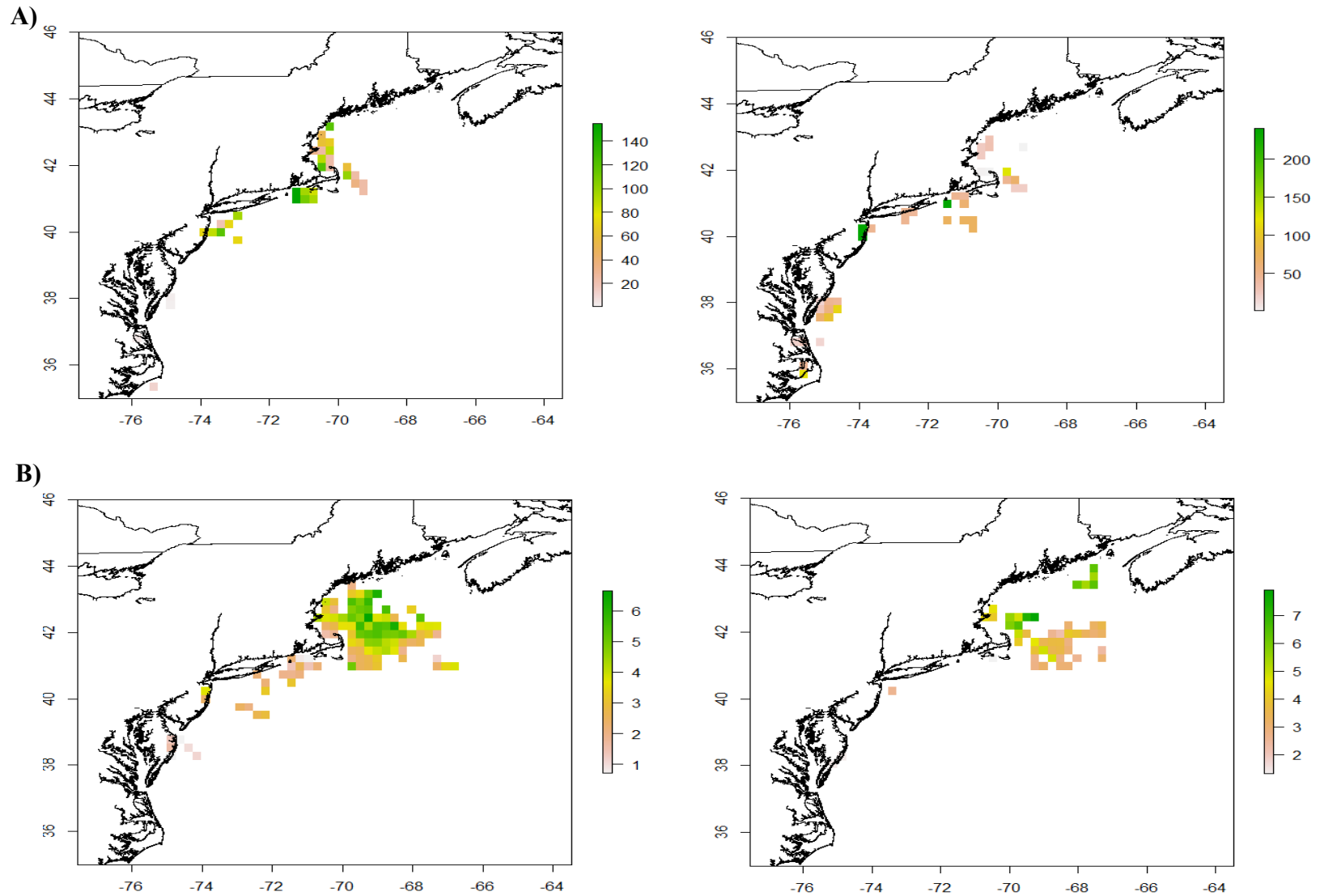


Figure 5E.15. Spatial distribution of fishing effort in the Northeast (US) shelf large marine ecosystem during autumn (left panel) and spring (right panel) of 2003 for the domestic A) sink gill net and B) otter trawl fisheries. Cell size $\sim 560 \text{ km}^2$ where values reflect the average effort (number of hours fished) obtained through rasterization of the original fisheries observer data.

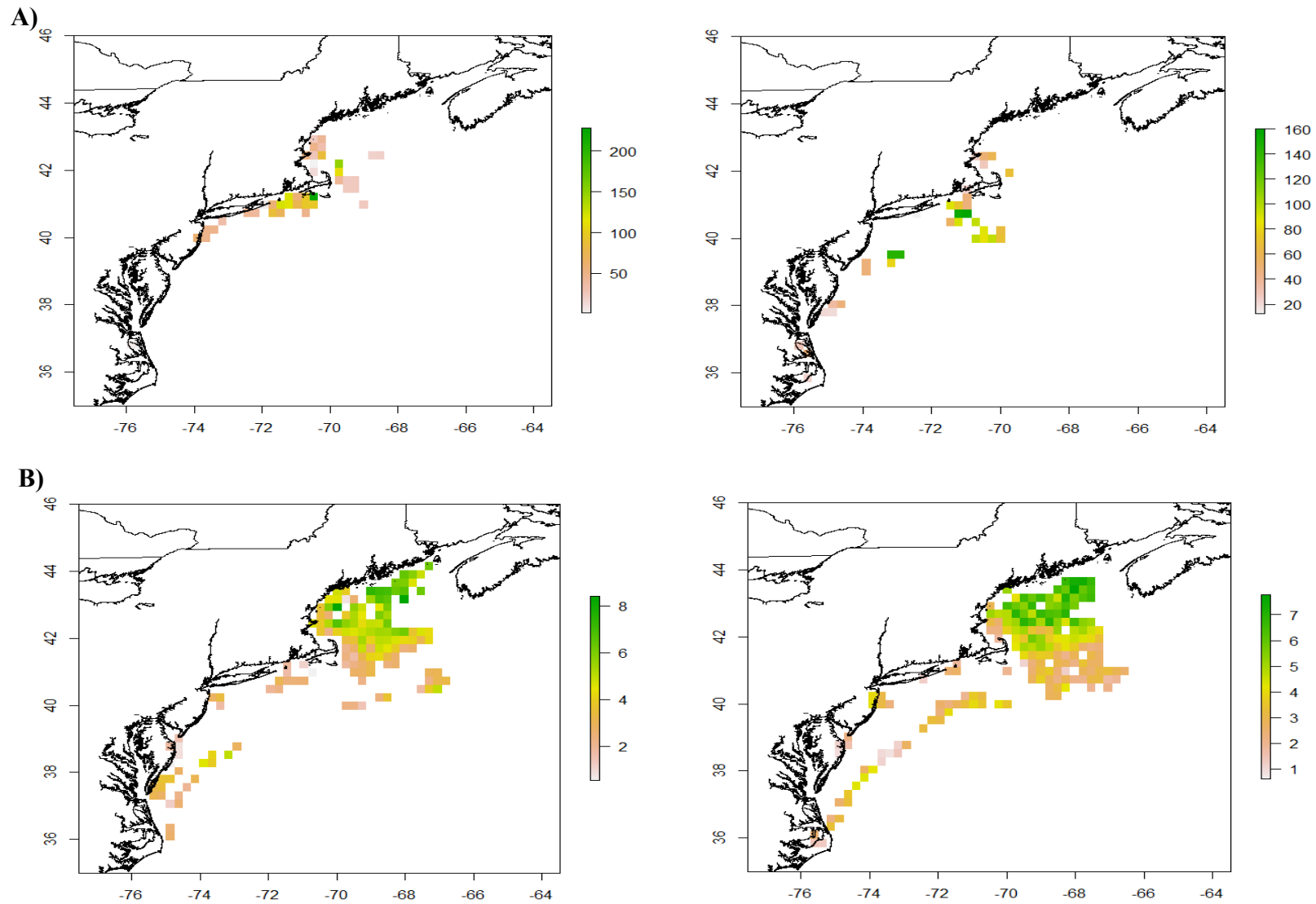


Figure 5E.16. Spatial distribution of fishing effort in the Northeast (US) shelf large marine ecosystem during autumn (left panel) and spring (right panel) of 2004 for the domestic A) sink gill net and B) otter trawl fisheries. Cell size $\sim 560 \text{ km}^2$ where values reflect the average effort (number of hours fished) obtained through rasterization of the original fisheries observer data.

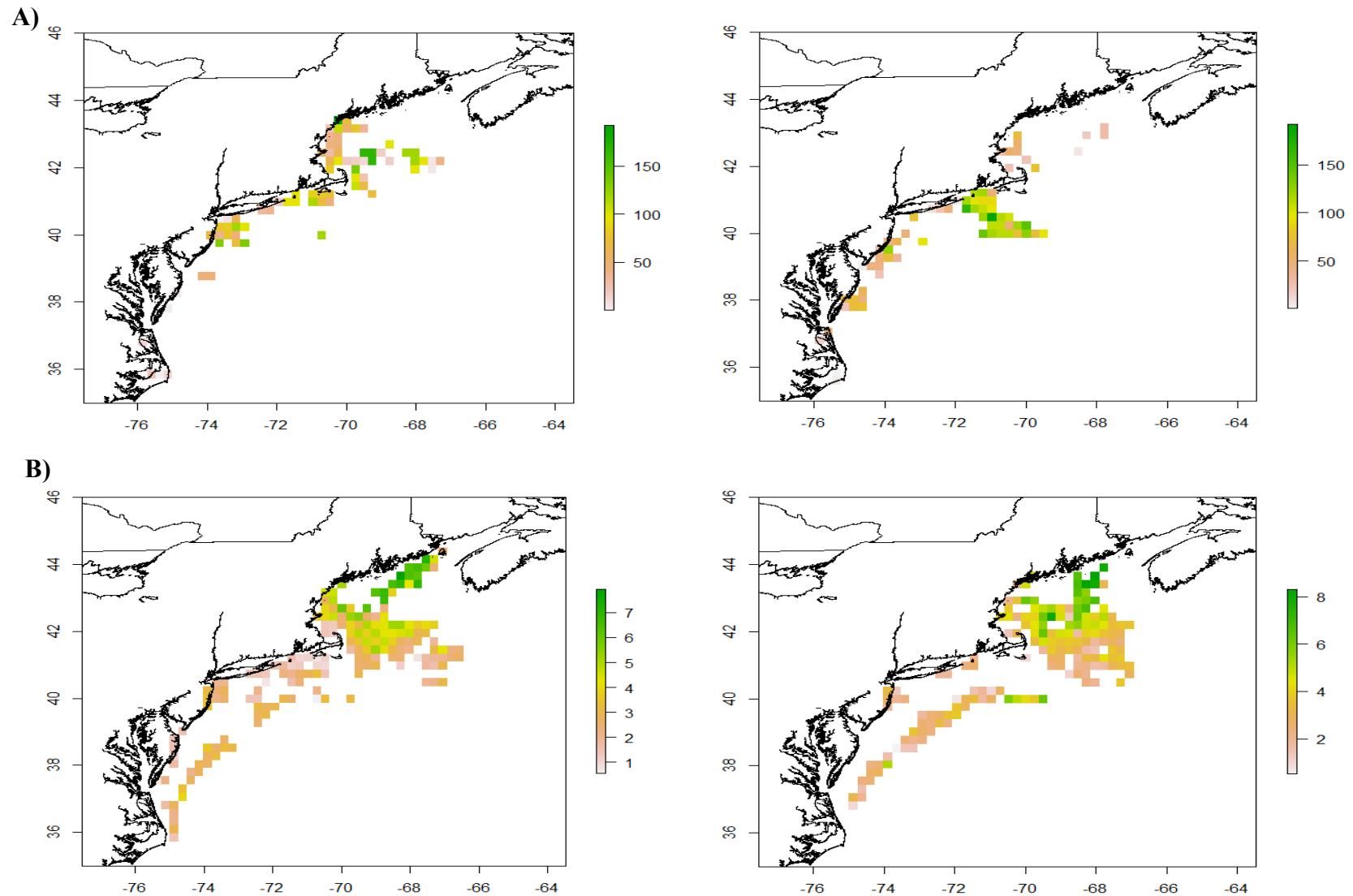


Figure 5E.17. Spatial distribution of fishing effort in the Northeast (US) shelf large marine ecosystem during autumn (left panel) and spring (right panel) of 2005 for the domestic A) sink gill net and B) otter trawl fisheries. Cell size $\sim 560 \text{ km}^2$ where values reflect the average effort (number of hours fished) obtained through rasterization of the original fisheries observer data.

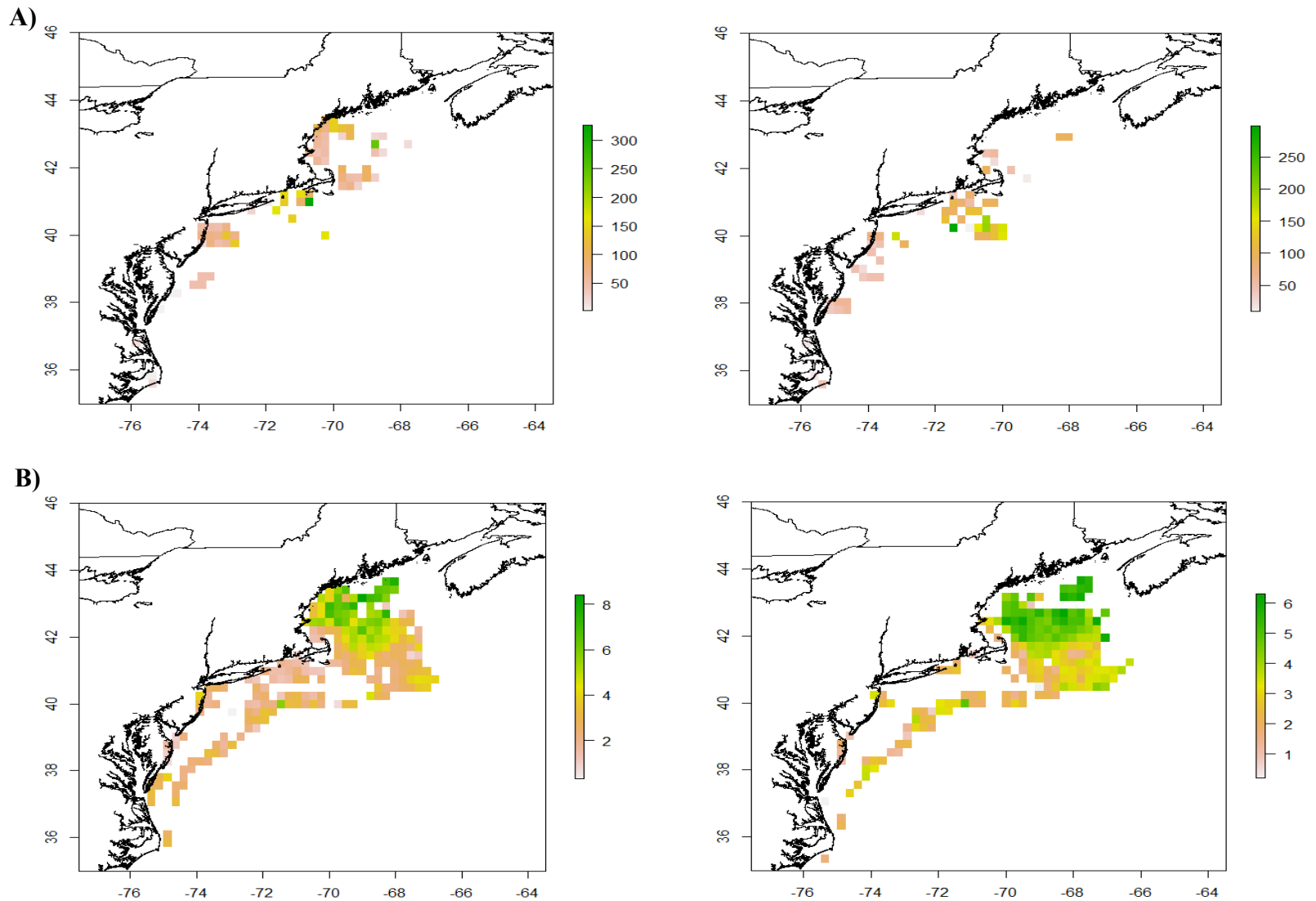


Figure 5E.18. Spatial distribution of fishing effort in the Northeast (US) shelf large marine ecosystem during autumn (left panel) and spring (right panel) of 2006 for the domestic A) sink gill net and B) otter trawl fisheries. Cell size $\sim 560 \text{ km}^2$ where values reflect the average effort (number of hours fished) obtained through rasterization of the original fisheries observer data.

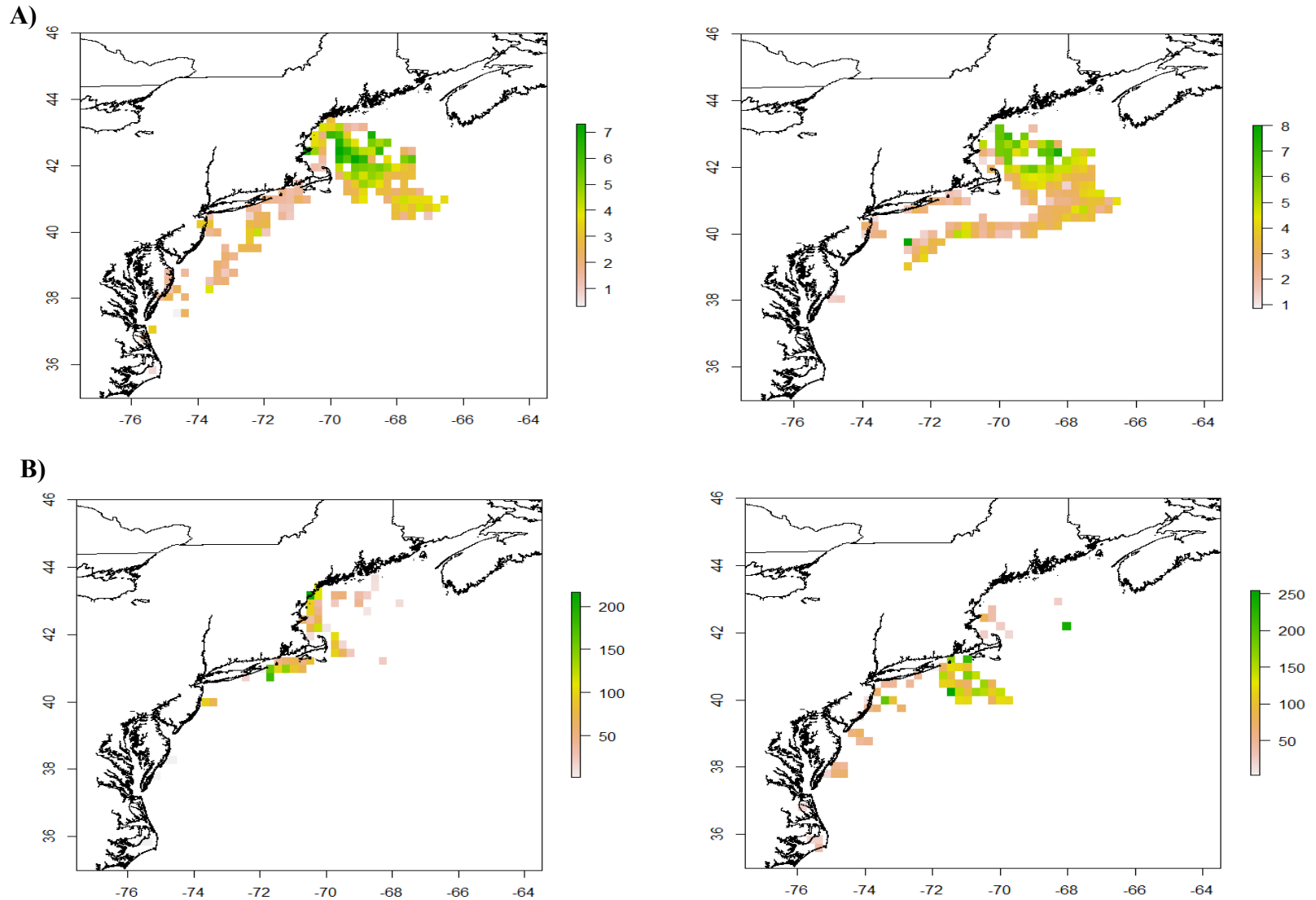


Figure 5E.19. Spatial distribution of fishing effort in the Northeast (US) shelf large marine ecosystem during autumn (left panel) and spring (right panel) of 2007 for the domestic A) sink gill net and B) otter trawl fisheries. Cell size $\sim 560 \text{ km}^2$ where values reflect the average effort (number of hours fished) obtained through rasterization of the original fisheries observer data.

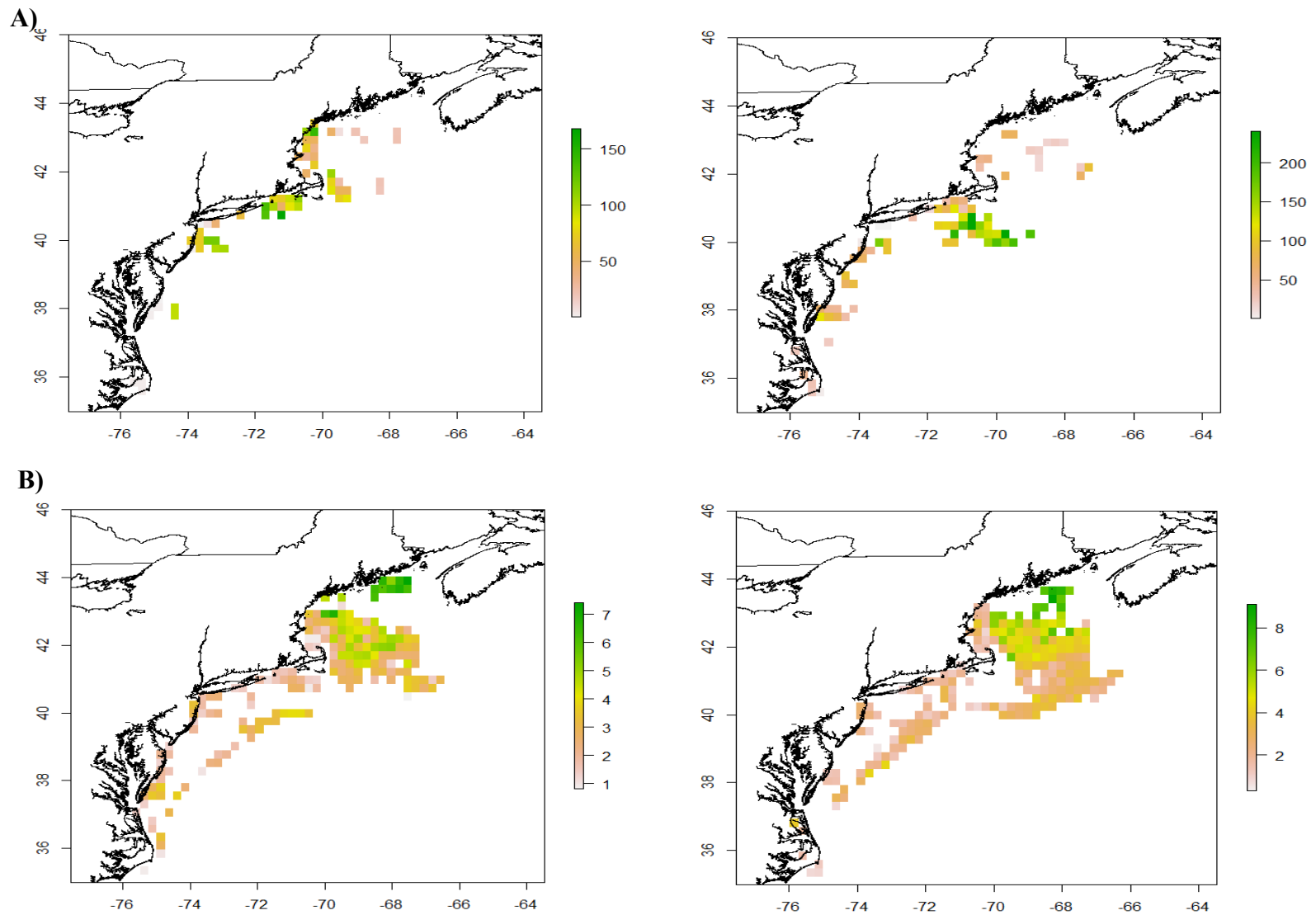


Figure 5E.20. Spatial distribution of fishing effort in the Northeast (US) shelf large marine ecosystem during autumn (left panel) and spring (right panel) of 2008 for the domestic A) sink gill net and B) otter trawl fisheries. Cell size $\sim 560 \text{ km}^2$ where values reflect the average effort (number of hours fished) obtained through rasterization of the original fisheries observer data.

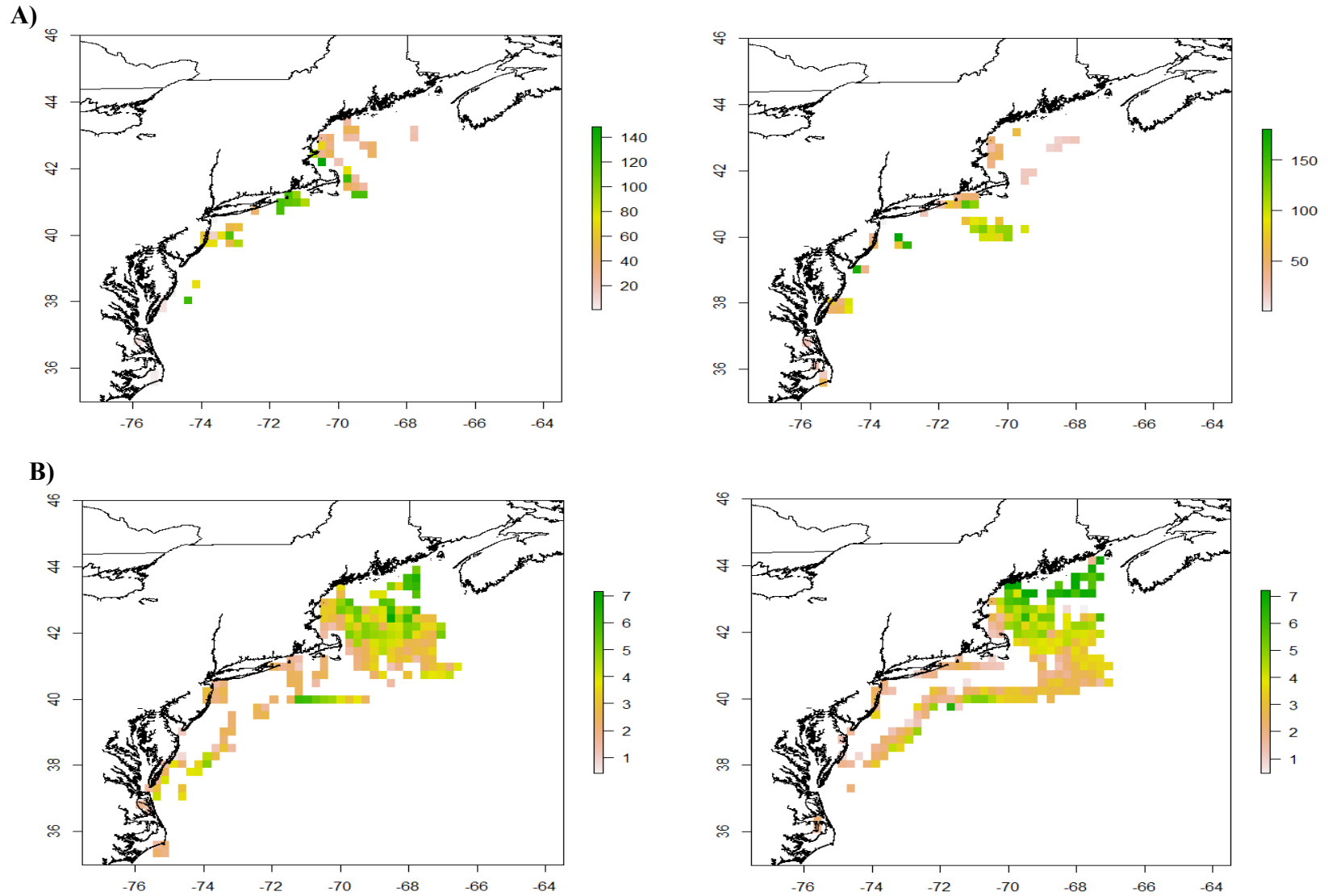
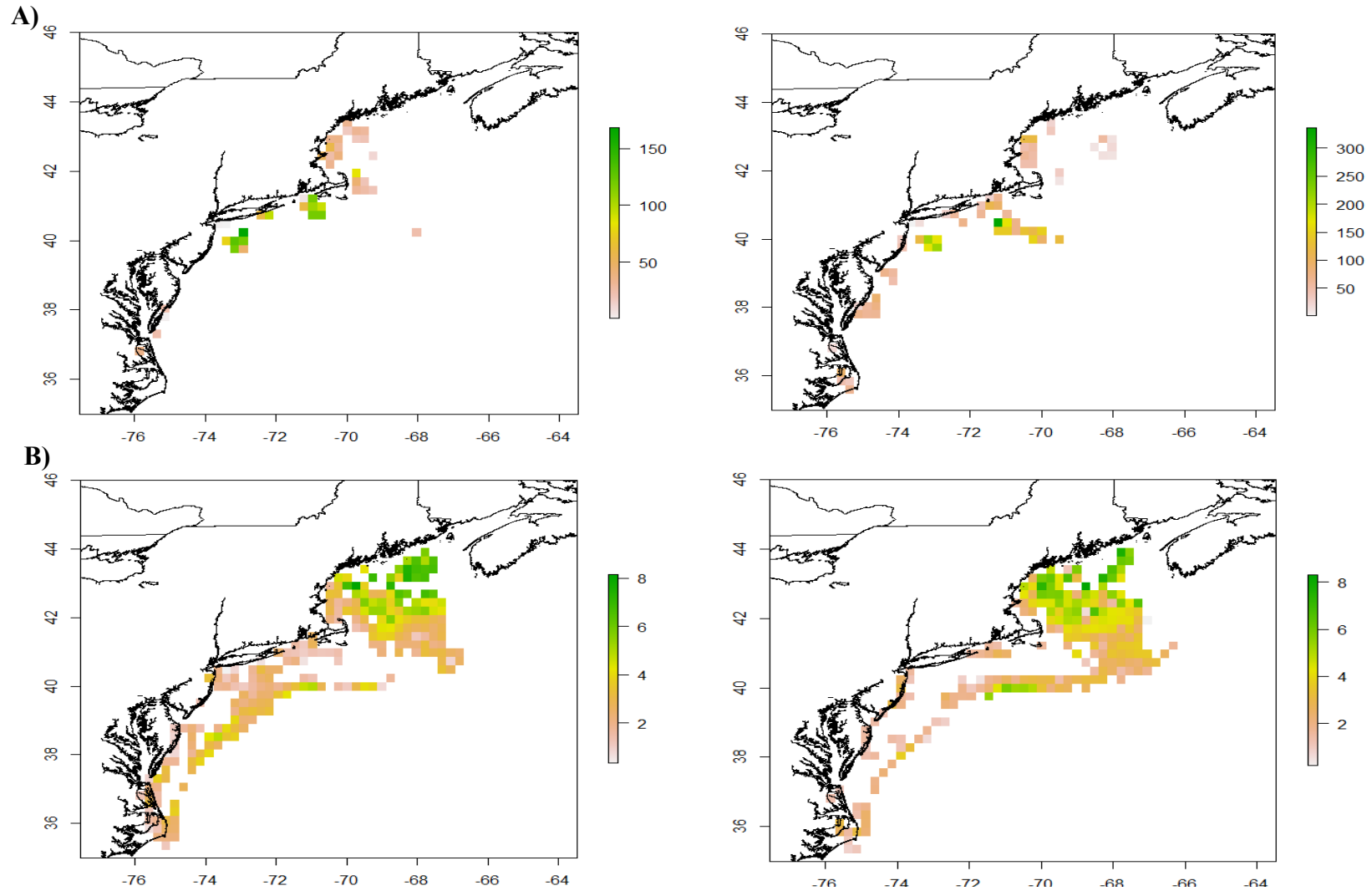


Figure 5E.21. Spatial distribution of fishing effort in the Northeast (US) shelf large marine ecosystem during autumn (left panel) and spring (right panel) of 2009 for the domestic A) sink gill net and B) otter trawl fisheries. Cell size $\sim 560 \text{ km}^2$ where values reflect the average effort (number of hours fished) obtained through rasterization of the original fisheries observer data.



Appendix 5F. Spatial Distribution of Spiny Dogfish Catch by Fisheries and the NEFSC Survey

Table 5F.1. Ordinary kriging model performance for predicting the spatial distribution of spiny dogfish from the otter trawl and sink gill net fisheries during autumn and spring between 1989 and 2009 based on mean predicted values and 100-fold cross validation (CV). Var = variance, SE = standard error, *RMSE* = root mean square error of prediction, *AVE* = average error, Resid = residuals. - indicates no data available.

	Sink Gill Net							Otter Trawl						
	Mean Prediction				100-fold CV			Mean Prediction				100-fold CV		
	Var	SE	<i>RMSE</i>	<i>AVE</i>	Var	SE	Resid	Var	SE	<i>RMSE</i>	<i>AVE</i>	Var	SE	Resid
<u>AUTUMN</u>														
1989	6.90	2.63	0.35	-0.14	4.71	2.17	0.010	9.65	3.11	0.99	-0.69	8.57	2.93	0.004
1990	4.69	2.17	0.32	-0.13	3.82	1.95	-0.003	13.27	3.64	0.81	0.00	12.26	3.50	-0.002
1991	6.18	2.49	0.53	-0.29	4.27	2.07	0.003	10.93	3.30	1.43	-0.84	8.22	2.87	0.002
1992	5.81	2.41	0.89	-0.80	4.40	2.10	0.002	10.88	3.30	1.00	-0.54	4.56	2.00	0.025
1993	7.14	2.67	0.98	-0.80	5.08	2.25	0.001	11.30	3.36	0.69	-0.09	4.79	2.05	0.006
1994	5.06	2.25	1.90	-1.86	0.34	0.53	-0.002	12.77	3.54	1.78	-1.67	4.37	2.09	-0.002
1995	7.45	2.72	1.53	-1.40	3.34	1.83	0.006	11.74	3.32	1.69	-1.44	3.91	1.98	-0.008
1996	8.97	2.99	1.12	-0.88	3.46	1.86	0.000	9.42	3.05	1.68	-1.40	5.07	2.25	0.008
1997	8.25	2.87	1.34	-1.18	4.27	2.07	0.002	7.17	2.65	1.89	-1.74	3.63	1.91	-0.002
1998	11.05	3.31	1.23	0.58	3.99	2.00	-0.002	13.28	3.64	1.53	0.12	2.18	1.44	-0.014
1999	9.13	3.02	1.17	-0.62	3.28	1.81	0.001	9.46	3.07	1.61	-1.32	4.22	2.05	-0.005
2000	1.58	1.25	2.63	-2.62	0.50	0.70	-0.001	4.94	2.20	2.23	-2.15	1.87	1.37	0.000
2001	2.40	1.55	2.51	-2.48	0.58	0.76	0.000	10.48	3.15	1.61	-1.33	3.84	1.96	-0.004
2002	6.67	2.58	2.13	-2.09	0.27	0.43	0.006	7.30	2.69	1.57	-1.28	3.41	1.85	0.006
2003	8.59	2.93	1.56	-1.45	4.47	2.11	0.005	9.57	3.05	1.61	-1.35	4.69	2.17	0.004
2004	6.02	2.44	1.00	-0.41	3.25	1.80	0.000	10.78	3.20	1.38	-0.73	4.67	2.16	0.001
2005	5.27	2.29	1.20	-0.95	4.06	2.01	-0.001	11.12	3.21	1.71	-1.36	3.29	1.81	0.001
2006	3.43	1.85	1.97	-1.87	2.24	1.50	0.004	9.40	3.06	1.25	-0.73	5.88	2.42	0.004
2007	5.08	2.25	1.88	-1.80	0.62	0.71	-0.020	11.85	3.40	1.40	-0.98	8.25	2.87	0.000
2008	5.69	2.38	1.54	-1.47	0.60	0.69	-0.003	9.65	3.01	1.97	-1.74	3.71	1.93	0.001
2009	8.55	2.92	0.71	-0.33	0.61	0.68	-0.007	10.23	3.14	1.80	-1.37	6.60	2.57	0.000

	Sink Gill Net							Otter Trawl						
	Mean Prediction				100-fold CV			Mean Prediction				100-fold CV		
	Var	SE	RMSE	AVE	Var	SE	Resid	Var	SE	RMSE	AVE	Var	SE	Resid
<u>SPRING</u>														
1989	-	-	-	-	-	-	-	9.34	3.06	1.37	-1.07	7.23	2.69	0.004
1990	0.87	0.93	2.67	-2.66	0.07	0.25	-0.003	14.92	3.86	1.36	0.24	6.70	2.56	0.010
1991	2.15	1.47	2.17	-2.13	0.36	0.54	-0.035	9.16	3.03	1.31	-1.07	7.02	2.65	0.003
1992	6.43	2.48	1.69	-1.62	1.04	1.02	0.003	9.23	3.04	1.40	-1.04	7.59	2.76	0.006
1993	3.92	1.92	2.27	-2.21	0.92	0.96	0.000	8.71	2.95	1.73	-1.60	4.28	2.05	-0.012
1994	2.79	1.62	2.42	-2.21	0.61	0.78	0.003	7.37	2.72	1.71	-1.61	7.37	2.72	0.000
1995	4.41	2.00	2.25	-2.10	1.18	1.09	0.000	6.29	2.51	1.65	-1.33	4.24	2.06	0.004
1996	4.13	1.88	2.35	-2.17	0.58	0.76	-0.001	5.96	2.41	1.91	-1.58	2.55	1.60	-0.001
1997	5.81	2.32	1.97	-1.80	1.40	1.18	-0.001	5.68	2.38	1.61	-1.32	3.36	1.83	0.007
1998	5.54	2.33	1.84	-1.70	2.73	1.65	-0.001	4.51	2.12	1.99	-1.93	4.51	2.12	0.000
1999	5.86	2.42	1.67	-1.57	0.60	0.69	-0.016	3.05	1.75	2.02	-1.91	3.05	1.75	0.000
2000	6.80	2.51	2.16	-2.11	2.72	1.65	-0.001	6.85	2.62	1.58	-1.33	5.03	2.24	0.015
2001	1.27	1.12	2.76	-2.74	0.05	0.21	0.004	7.75	2.78	1.44	-1.22	4.57	2.14	-0.002
2002	5.27	2.28	2.41	-2.35	0.60	0.77	0.011	8.67	2.94	0.81	-0.34	4.22	2.05	0.003
2003	1.38	1.18	2.73	-2.72	1.38	1.18	0.000	5.01	2.24	1.63	-1.43	4.03	2.01	0.002
2004	2.58	1.61	2.45	-2.43	2.59	1.61	0.000	6.00	2.45	1.58	-1.27	4.51	2.12	-0.001
2005	1.72	1.31	2.66	-2.65	0.10	0.27	0.006	4.53	2.13	2.06	-1.93	4.01	2.00	0.000
2006	1.17	1.08	2.67	-2.66	1.17	1.08	0.000	5.48	2.34	1.80	-1.66	3.88	1.97	-0.002
2007	1.78	1.33	2.48	-2.44	1.16	1.08	-0.001	6.58	2.53	1.86	-1.22	4.02	2.00	0.001
2008	1.78	1.31	2.44	-2.41	0.01	0.01	15440.000	5.40	2.32	1.81	-1.38	4.65	2.16	0.004
2009	2.12	1.44	2.27	-2.20	0.05	0.18	0.009	4.73	2.17	2.10	-1.44	3.70	1.92	0.002

Table 5F.2. Ordinary kriging model performance for predicting the spatial distribution of spiny dogfish from the NEFSC bottom trawl survey during autumn and spring between 1989 and 2009 based on mean predicted values and 100-fold cross validation (CV). Var = variance, SE = standard error, *RMSE* = root mean square error of prediction, *AVE* = average error, Resid = residuals.

	Mean Prediction				100-fold CV			Mean Prediction				100-fold CV			
	Var	SE	<i>RMSE</i>	<i>AVE</i>	Var	SE	Resid	Var	SE	<i>RMSE</i>	<i>AVE</i>	Var	SE	Resid	
<u>SPRING</u>								<u>AUTUMN</u>							
1989	7.89	2.74	139.76	-9.07	2.90	1.70	0.028	5.10	2.22	29.13	-3.47	2.40	1.55	-0.002	
1990	7.96	2.70	309.12	-12.97	2.03	1.40	0.024	6.39	2.51	58.83	-5.13	4.35	2.08	-0.017	
1991	8.04	2.71	90.94	-7.61	1.84	1.33	0.004	6.00	2.41	108.86	-8.53	2.87	1.69	0.011	
1992	8.41	2.81	89.23	-8.48	2.57	1.58	0.003	5.81	2.33	88.06	-6.50	1.77	1.32	-0.008	
1993	7.97	2.68	63.03	-5.78	1.70	1.27	0.001	5.19	2.24	53.23	-4.30	2.31	1.52	-0.013	
1994	8.96	2.86	180.14	-14.58	2.09	1.42	0.000	5.44	2.28	43.44	-4.49	2.31	1.51	0.003	
1995	8.34	2.83	39.02	-4.64	3.81	1.92	-0.023	5.83	2.37	107.64	-6.95	2.62	1.61	0.029	
1996	8.02	2.73	99.61	-8.46	2.16	1.44	-0.023	7.30	2.60	101.36	-5.64	2.58	1.60	0.012	
1997	8.14	2.81	43.53	-5.01	3.75	1.93	0.001	5.98	2.39	58.86	-4.64	2.47	1.56	0.003	
1998	6.73	2.56	34.09	-3.79	3.47	1.85	0.018	7.50	2.67	92.84	-6.20	3.00	1.73	0.003	
1999	8.07	2.82	48.72	-4.63	4.76	2.17	0.013	7.50	2.63	51.07	-3.91	2.22	1.48	-0.011	
2000	6.89	2.60	28.50	-3.05	3.78	1.94	-0.018	7.03	2.50	36.73	-3.94	1.42	1.18	-0.021	
2001	6.54	2.50	42.29	-3.71	2.72	1.64	0.017	8.24	2.76	72.45	-6.40	2.71	1.64	-0.006	
2002	6.93	2.59	56.69	-4.25	3.34	1.82	0.011	7.42	2.66	49.65	-3.98	3.13	1.77	0.004	
2003	7.42	2.67	84.51	-5.92	3.08	1.74	0.032	7.24	2.65	78.64	-4.68	4.03	2.01	0.008	
2004	6.28	2.44	46.27	-4.68	2.25	1.49	0.013	9.57	2.97	55.32	-6.16	3.00	1.73	0.003	
2005	6.19	2.47	68.57	-5.84	3.79	1.94	-0.009	8.18	2.76	94.89	-7.66	2.54	1.58	-0.029	
2006	7.03	2.60	85.31	-7.87	3.03	1.72	0.017	8.77	2.84	72.39	-6.34	3.11	1.76	-0.014	
2007	7.03	2.58	45.62	-5.57	2.56	1.59	-0.016	8.46	2.74	71.29	-6.36	2.08	1.44	-0.019	
2008	7.04	2.58	46.04	-5.90	2.73	1.62	0.028	7.97	2.75	53.40	-5.42	3.22	1.79	-0.020	
2009	8.54	2.85	143.12	-13.19	3.31	1.81	0.002	8.48	2.88	85.35	-6.90	4.54	2.13	0.010	

Figure 5F.1. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during autumn of 1989 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

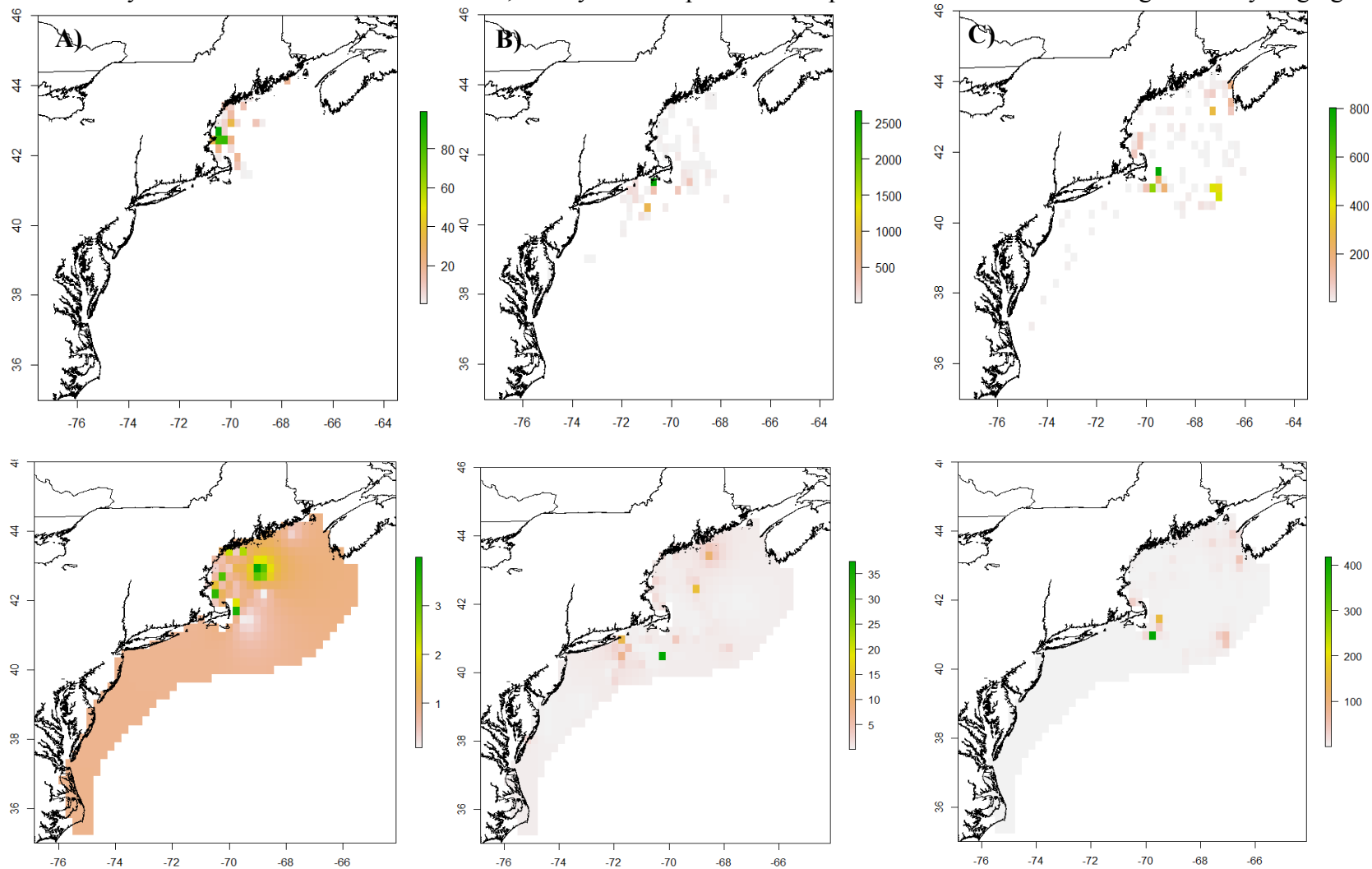


Figure 5F.2. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during autumn of 1990 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

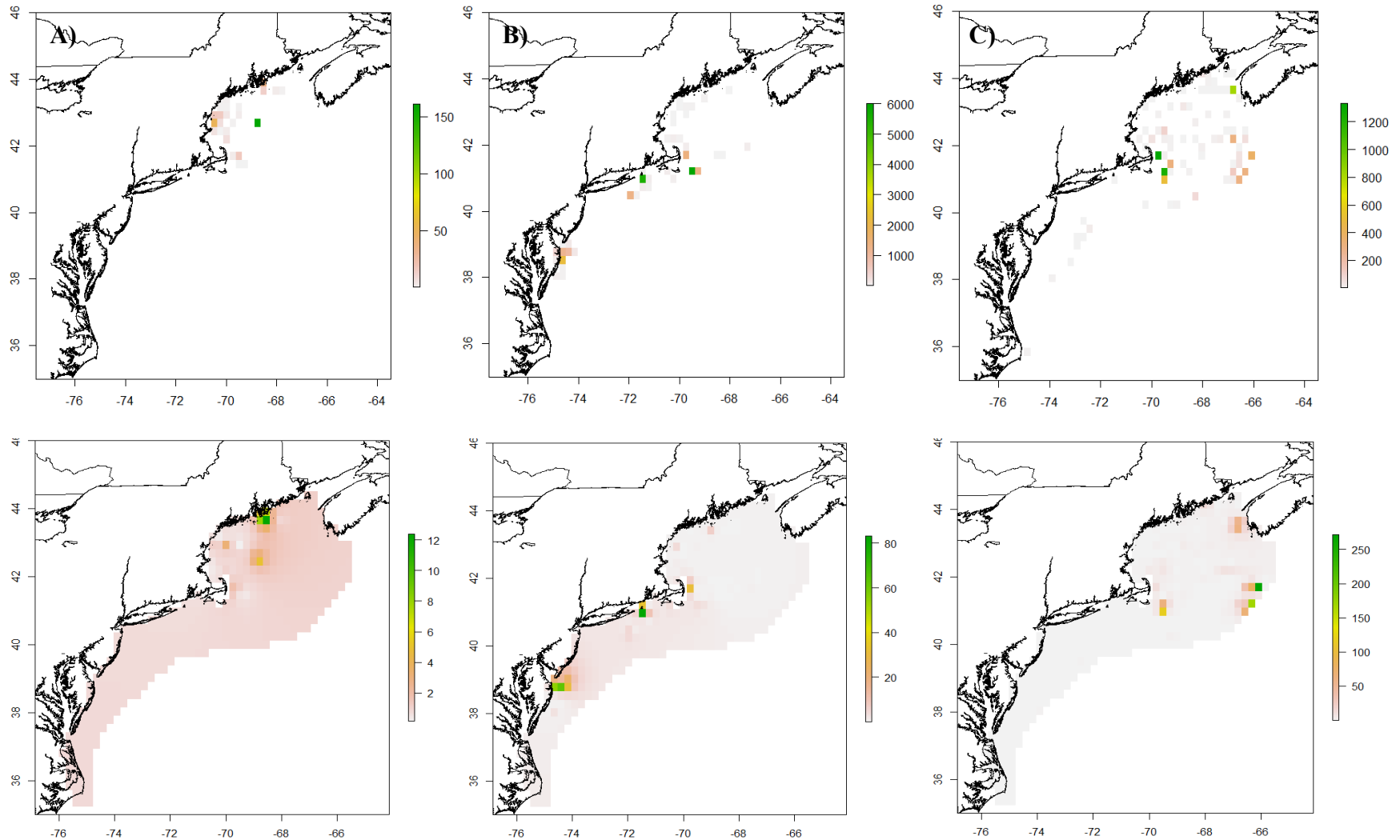


Figure 5F.3. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during autumn of 1991 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

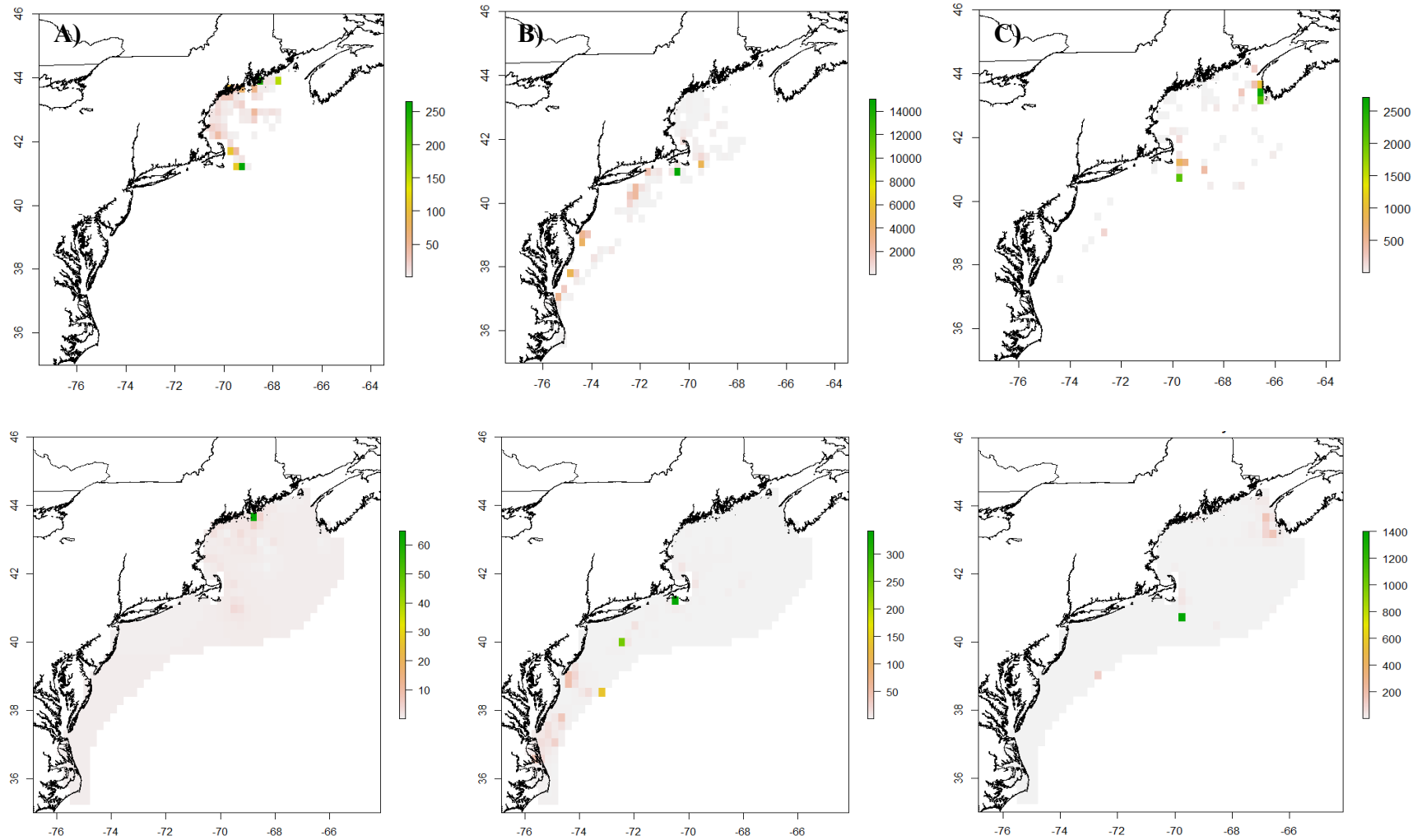


Figure 5F.4. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during autumn of 1992 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

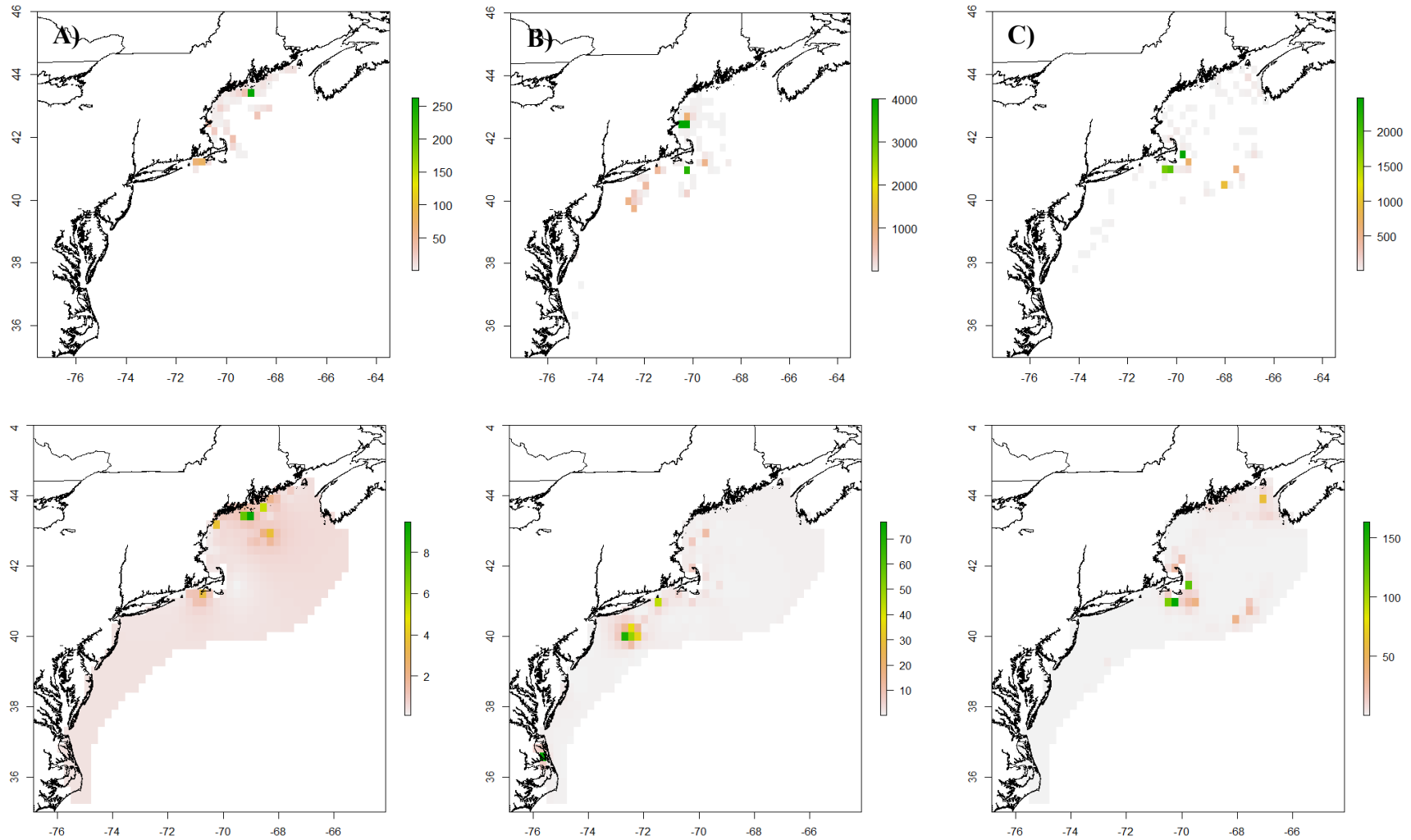


Figure 5F.5. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during autumn of 1993 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

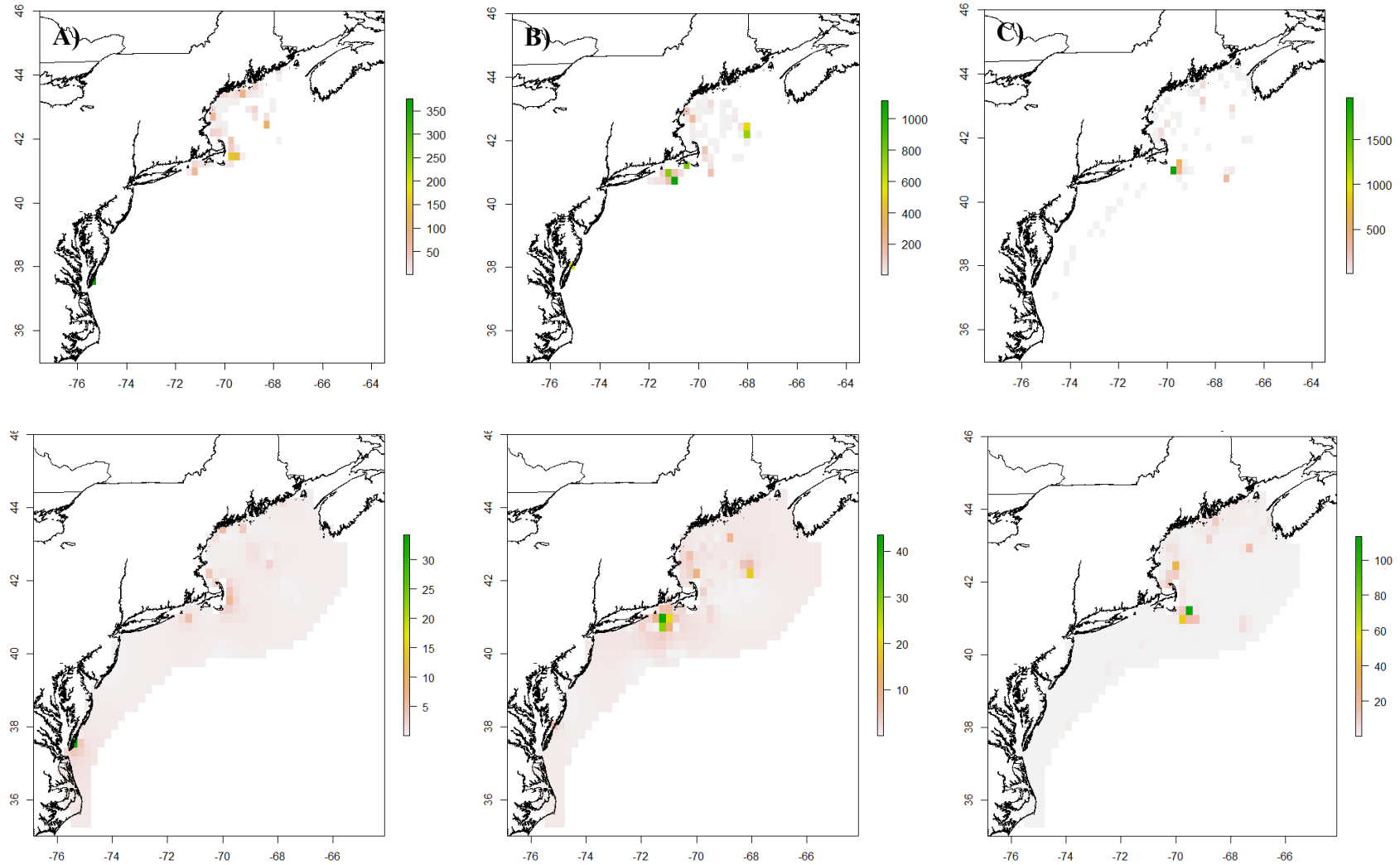


Figure 5F.6. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during autumn of 1994 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

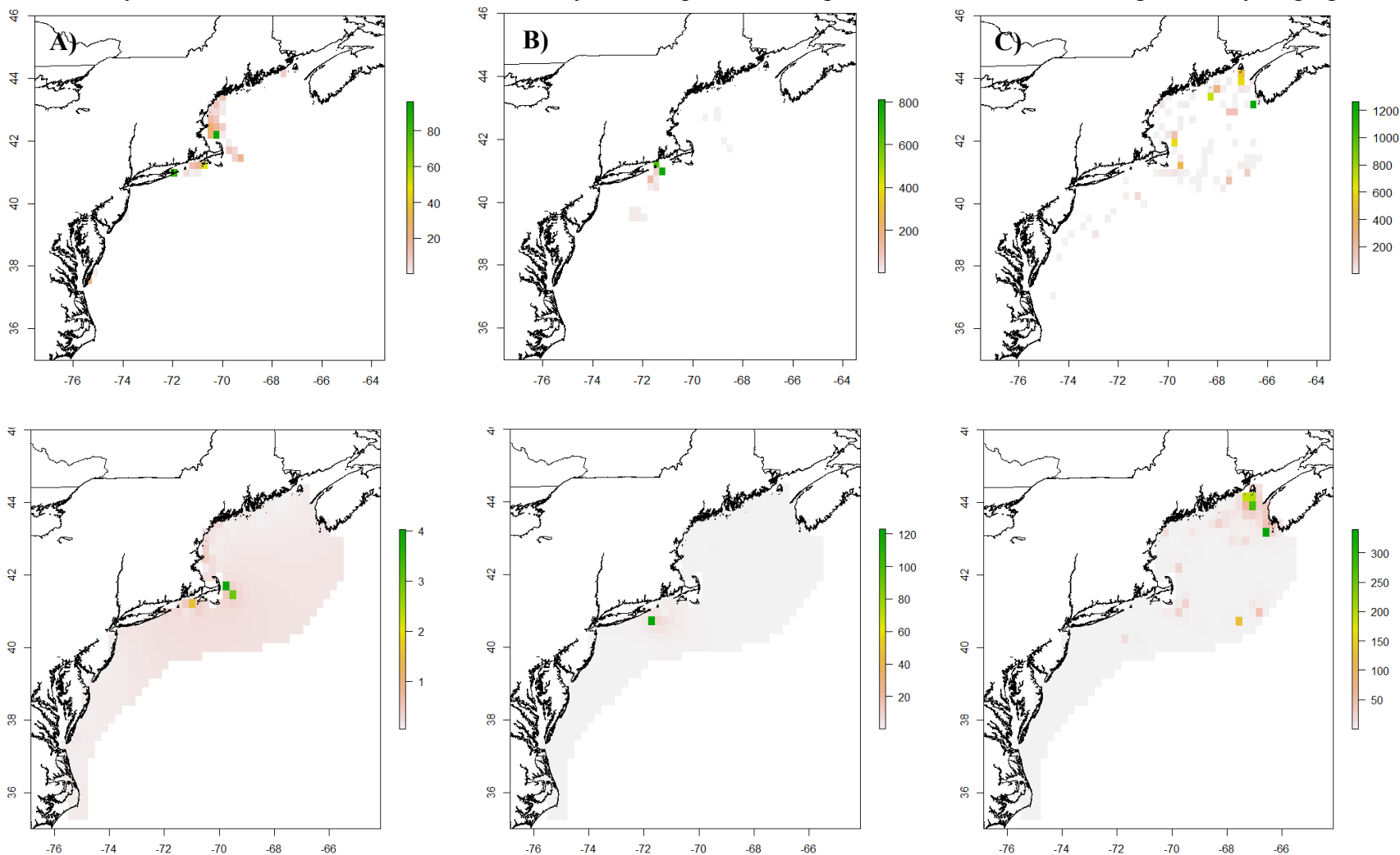


Figure 5F.7. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during autumn of 1995 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

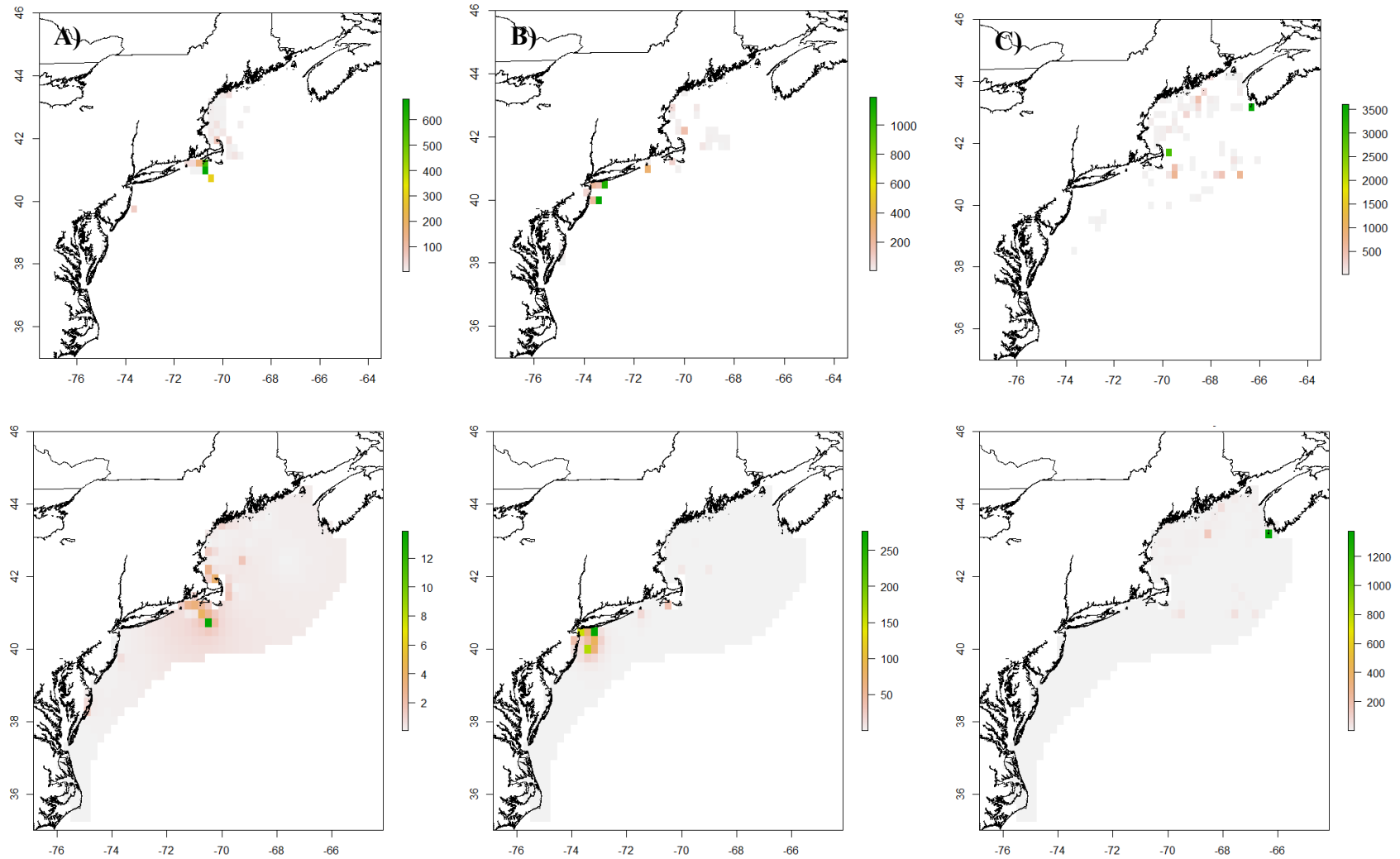


Figure 5F.8. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during autumn of 1996 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

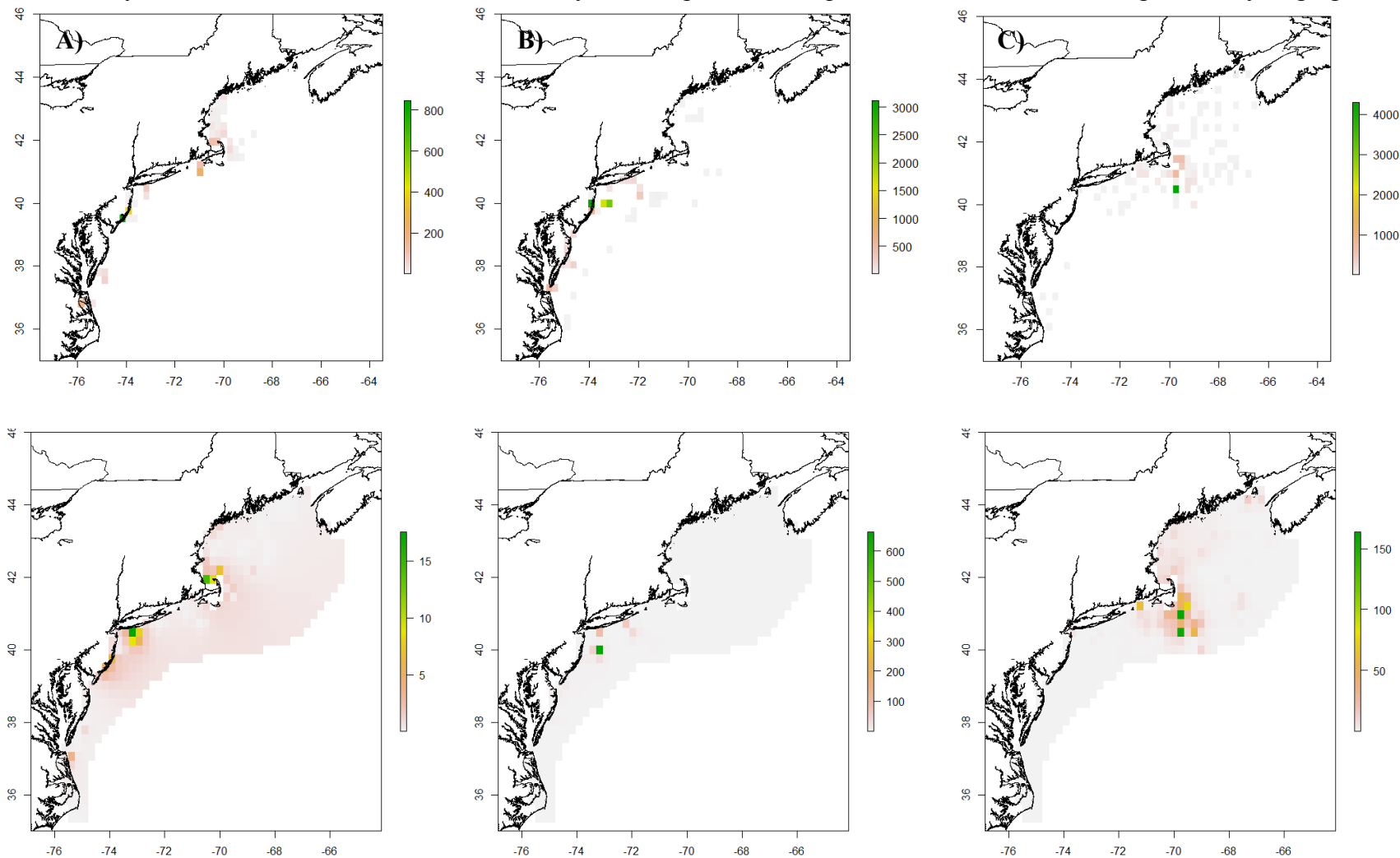


Figure 5F.9. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during autumn of 1997 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

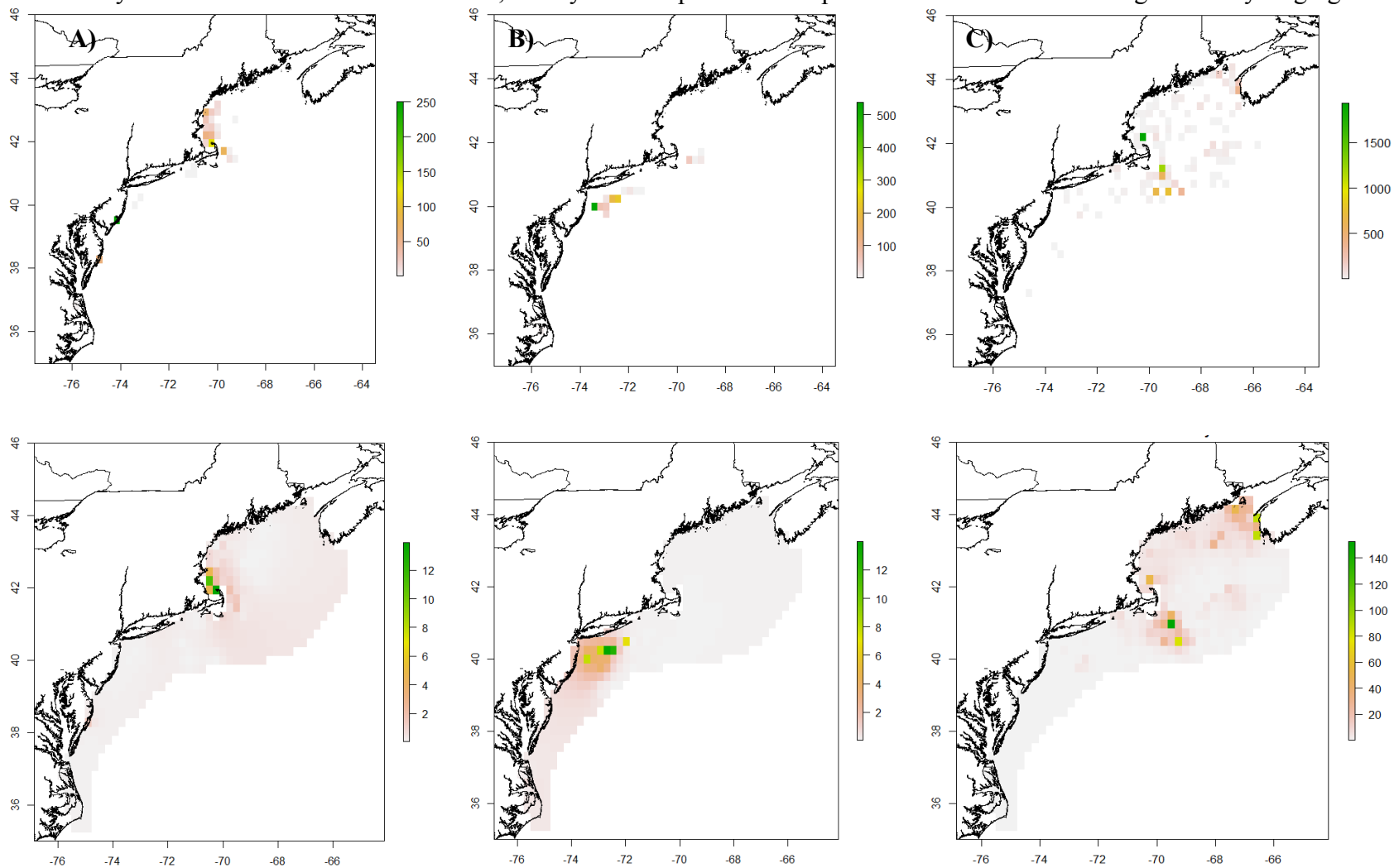


Figure 5F.10. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during autumn of 1998 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

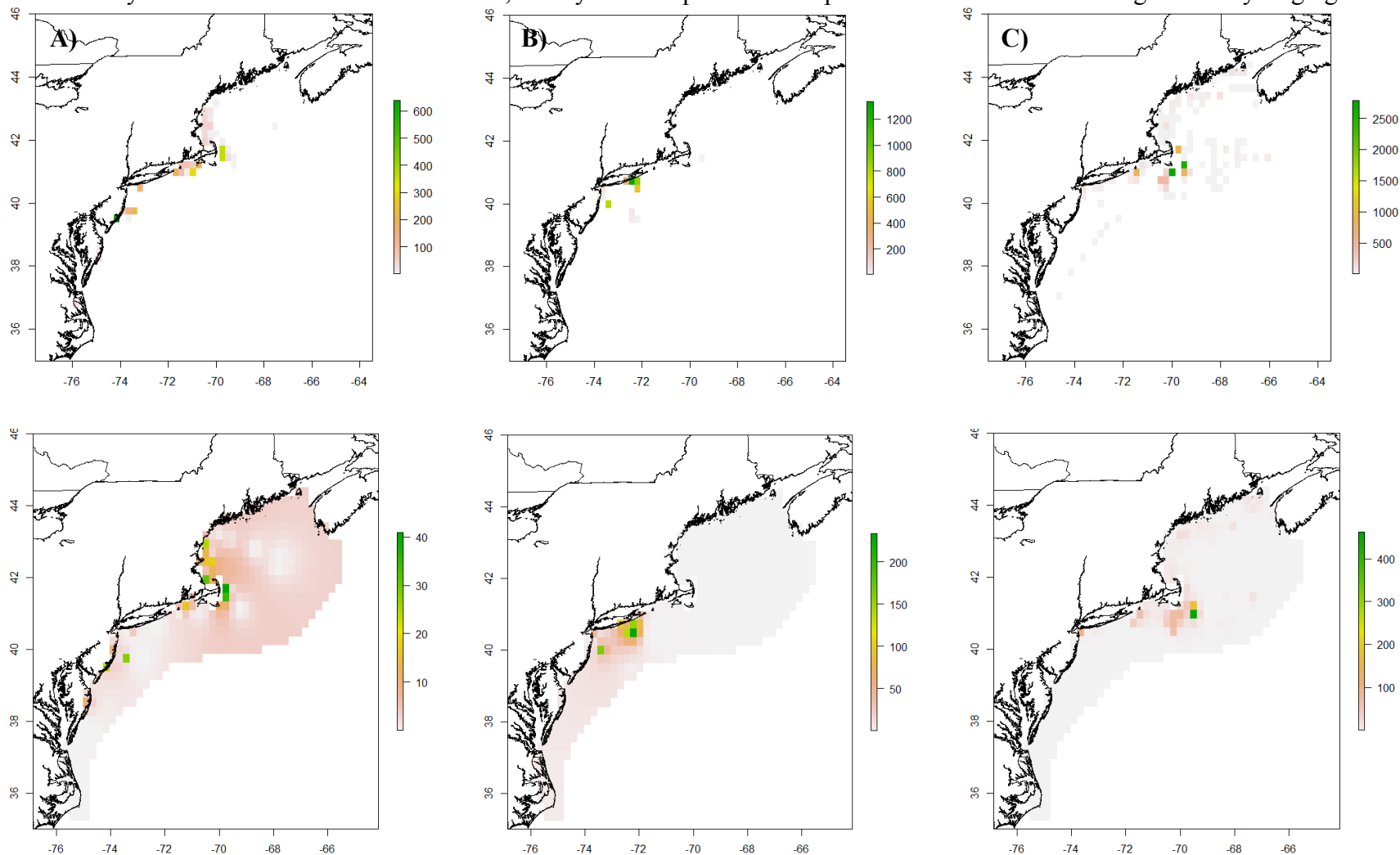


Figure 5F.11. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during autumn of 1999 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

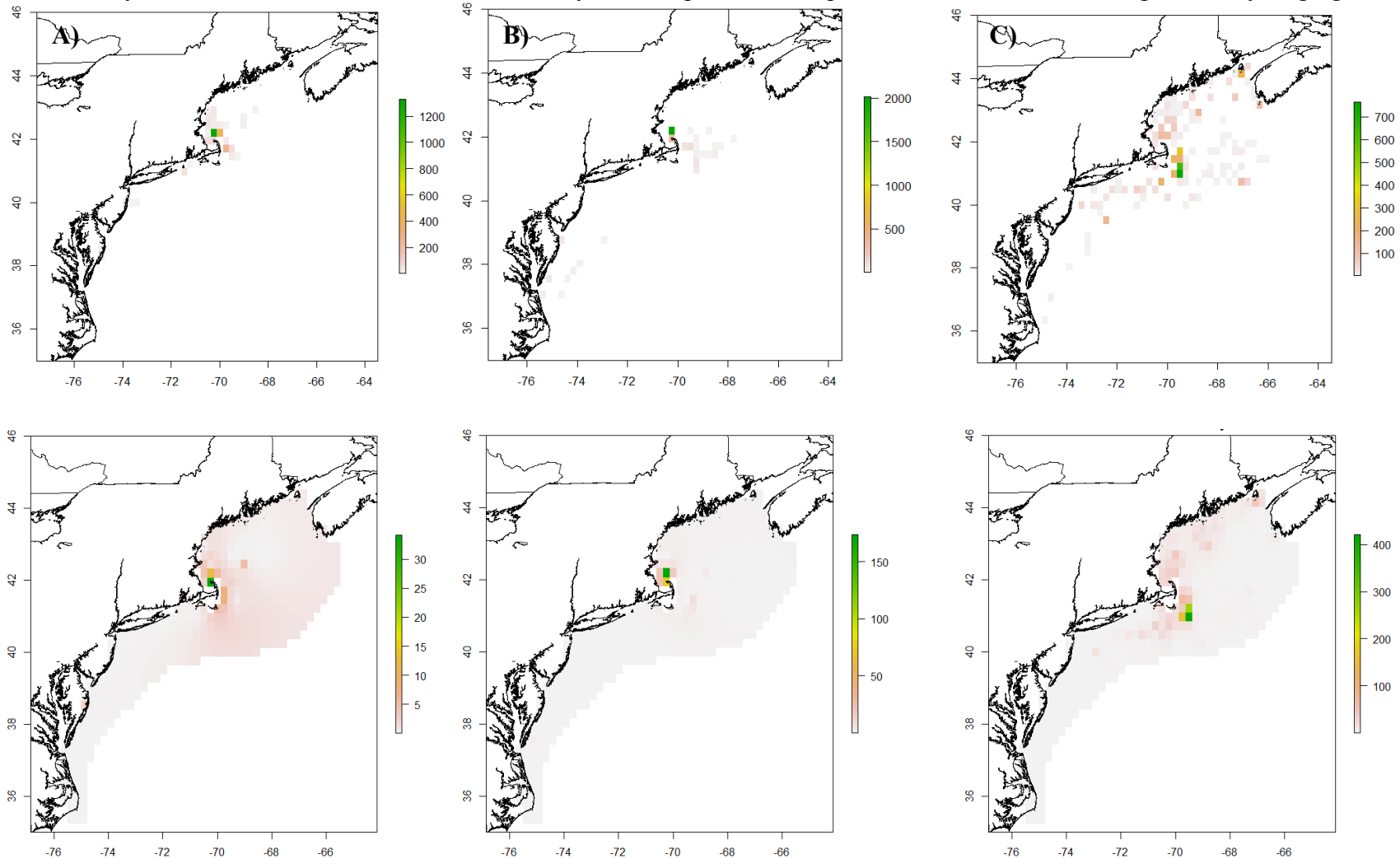


Figure 5F.12. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during autumn of 2000 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

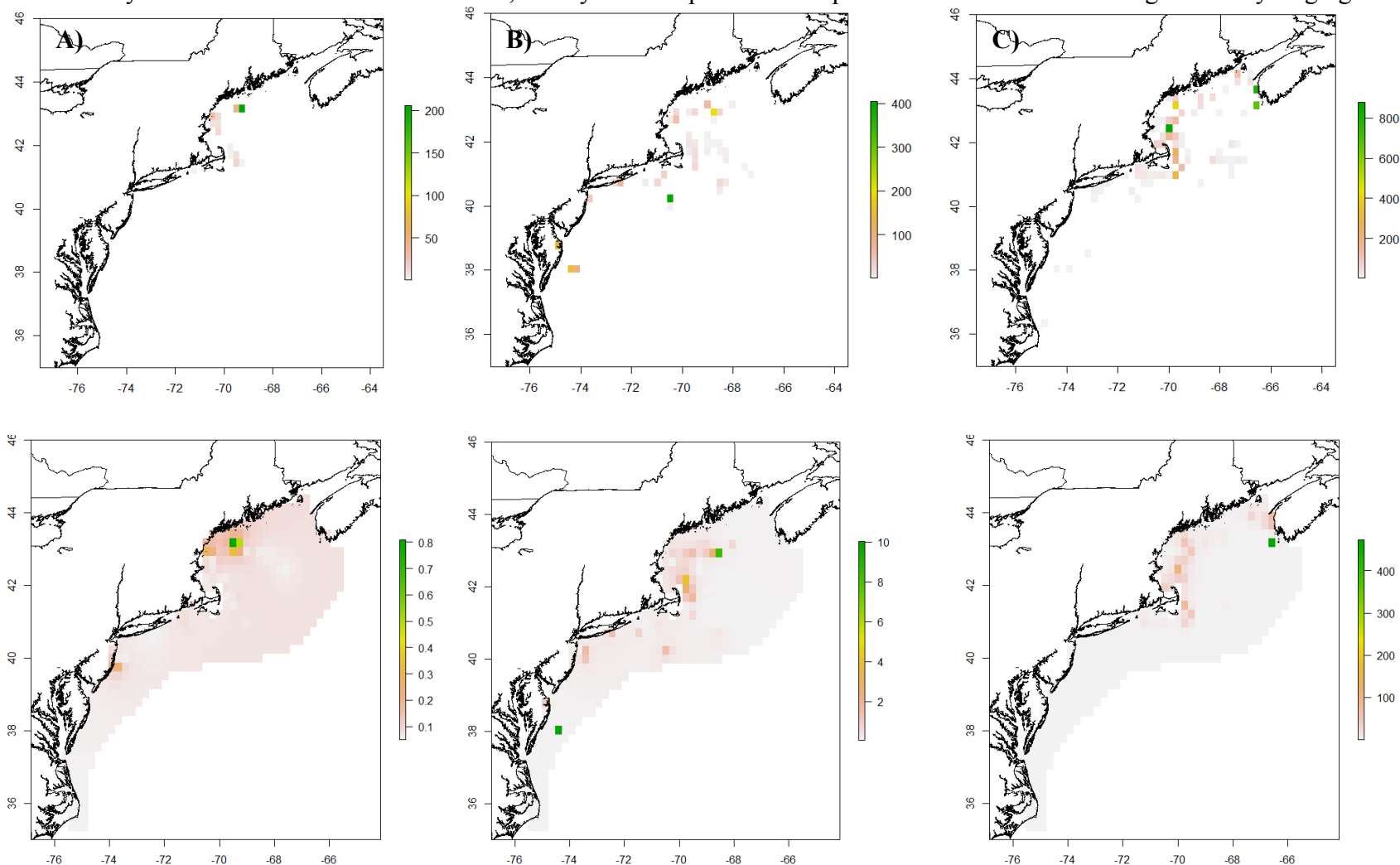


Figure 5F.13. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during autumn of 2001 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

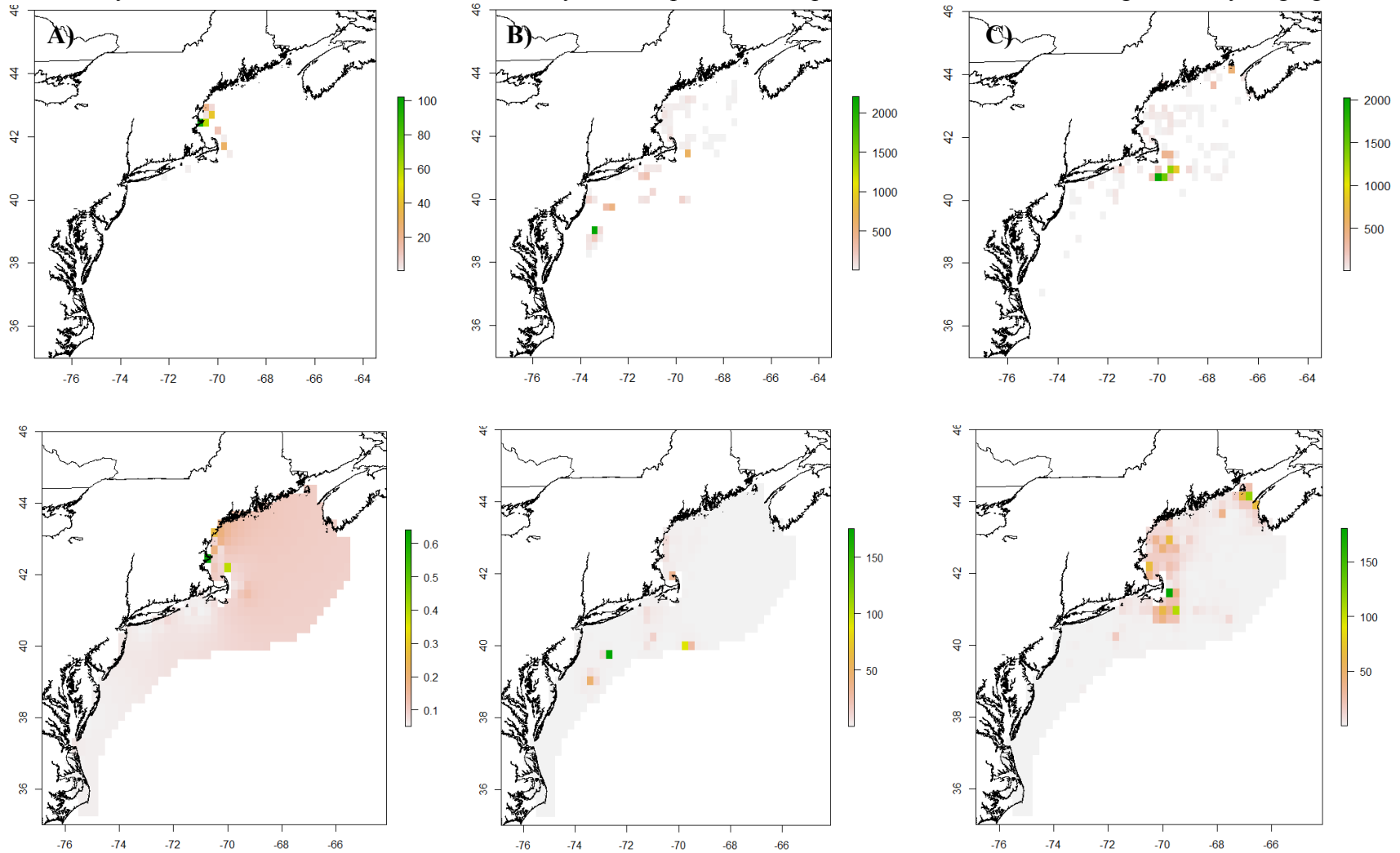


Figure 5F.14. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during autumn of 2002 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

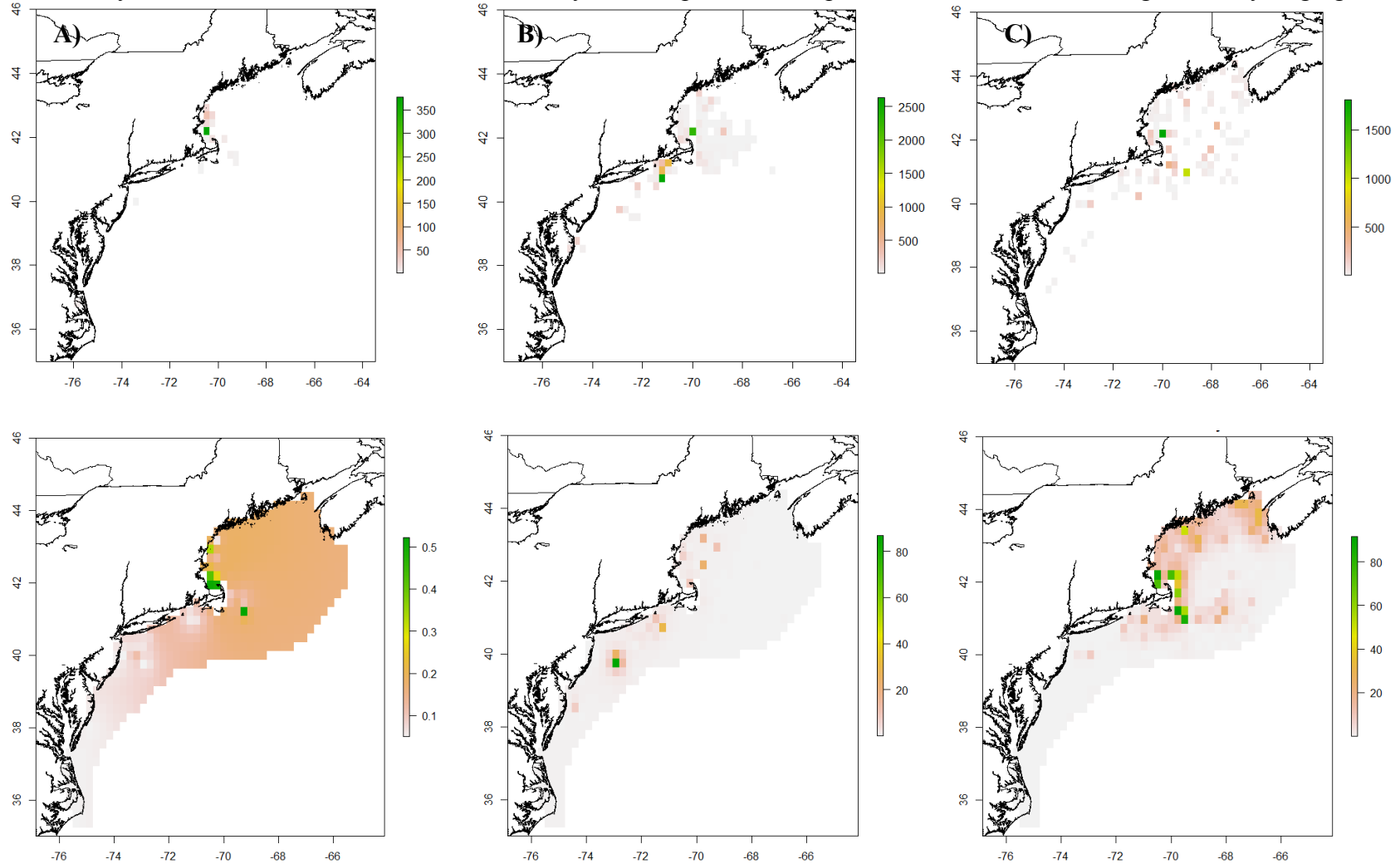


Figure 5F.15. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during autumn of 2003 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

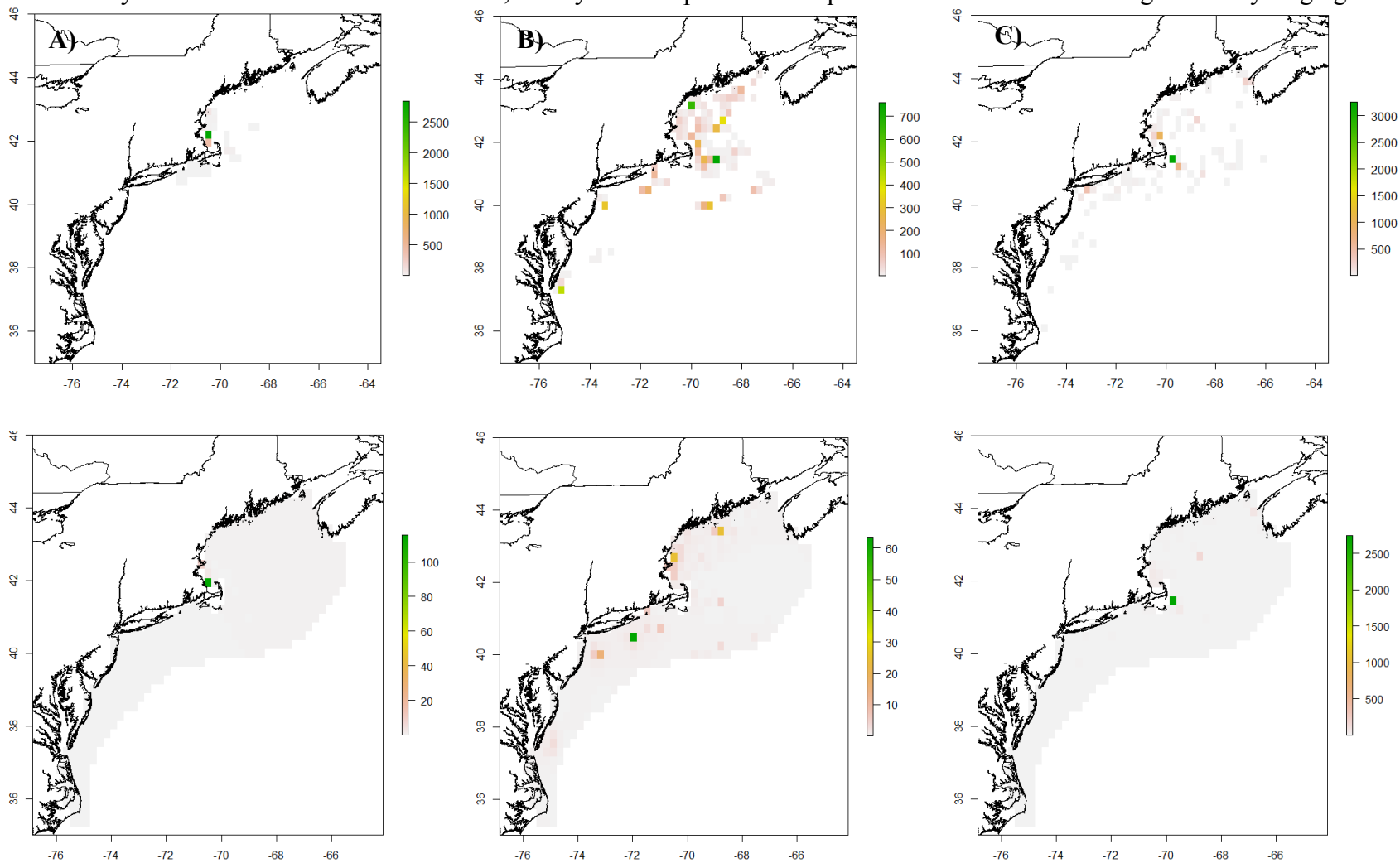


Figure 5F.16. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during autumn of 2004 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

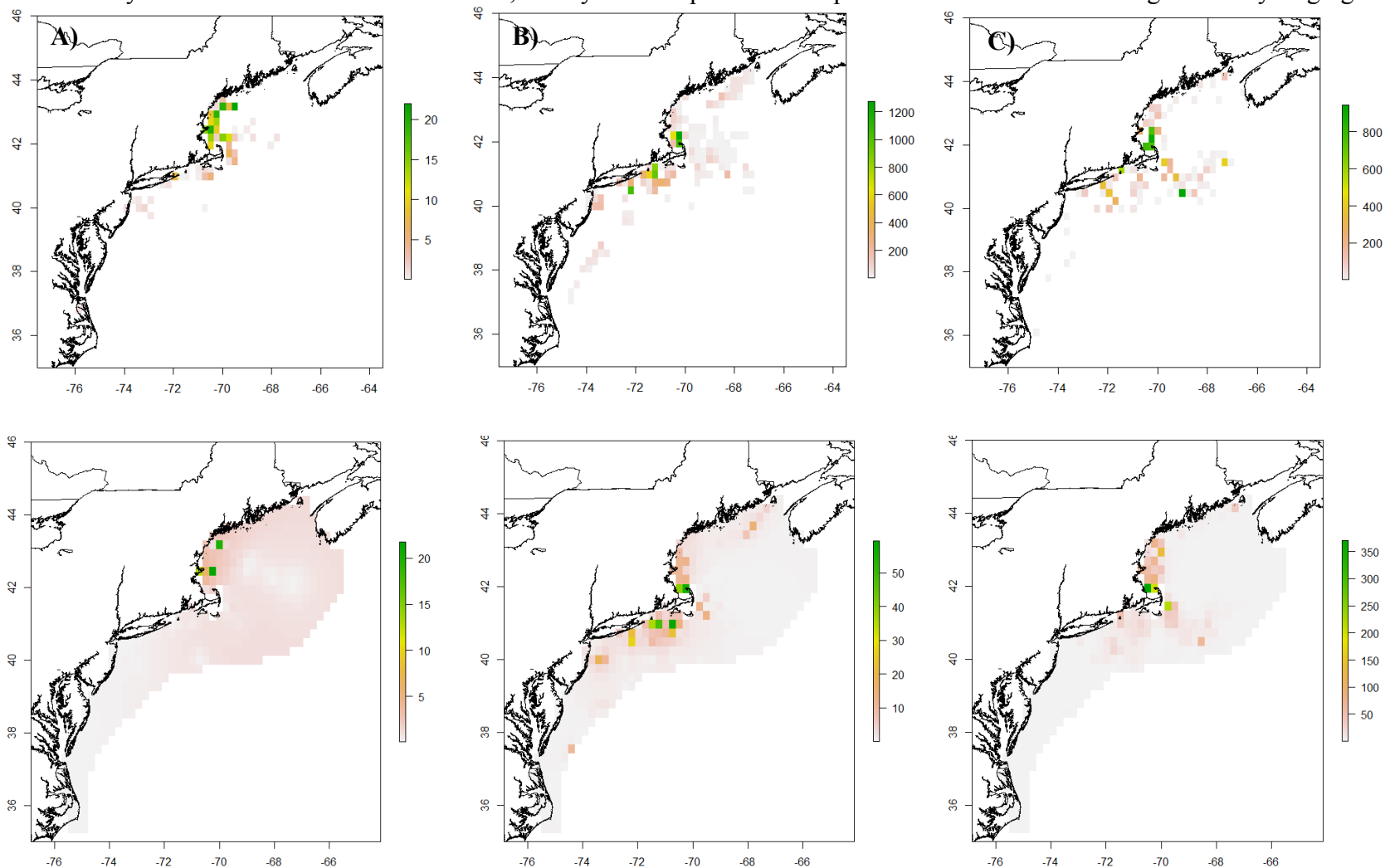


Figure 5F.17. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during autumn of 2005 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

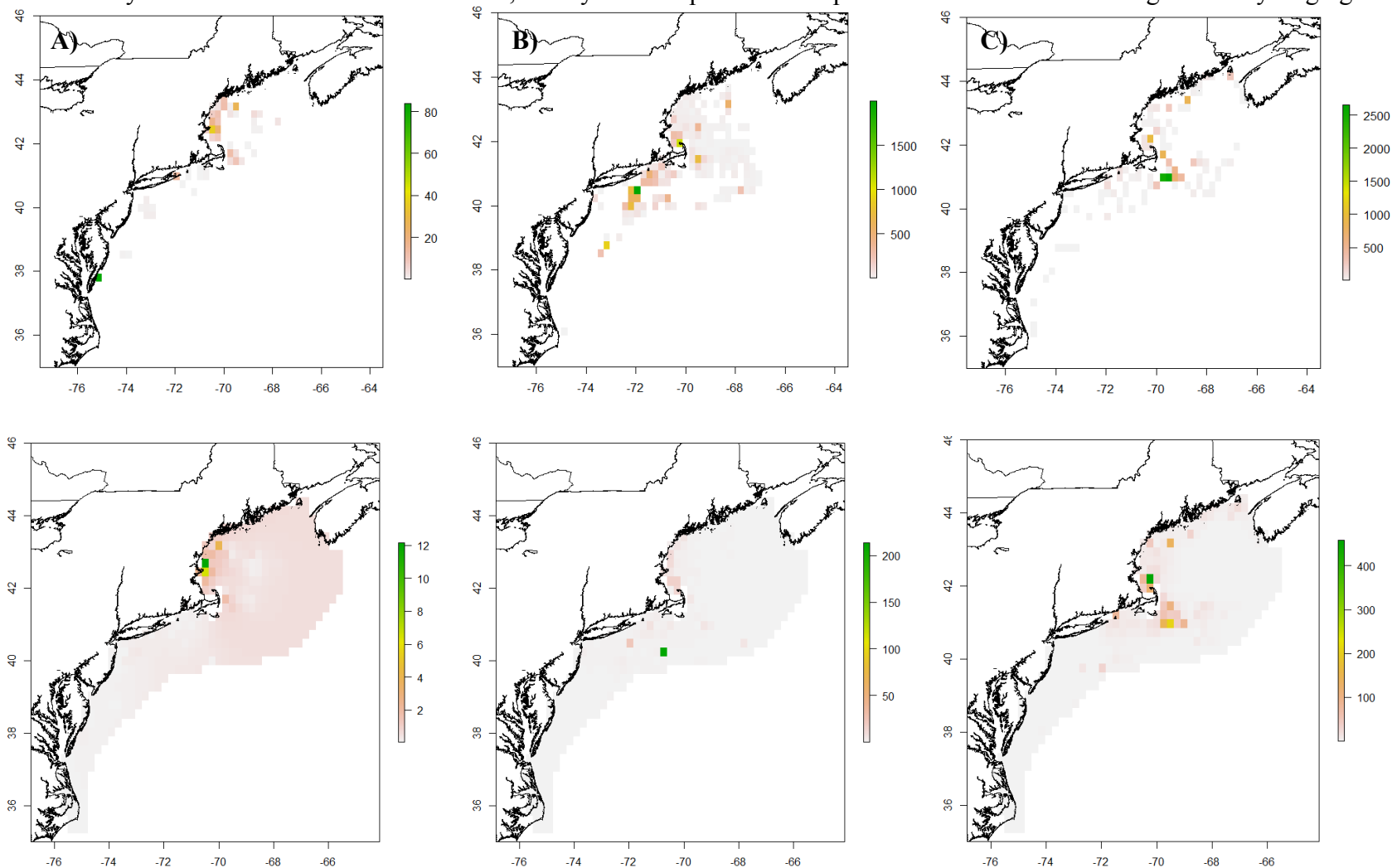


Figure 5F.18. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during autumn of 2006 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

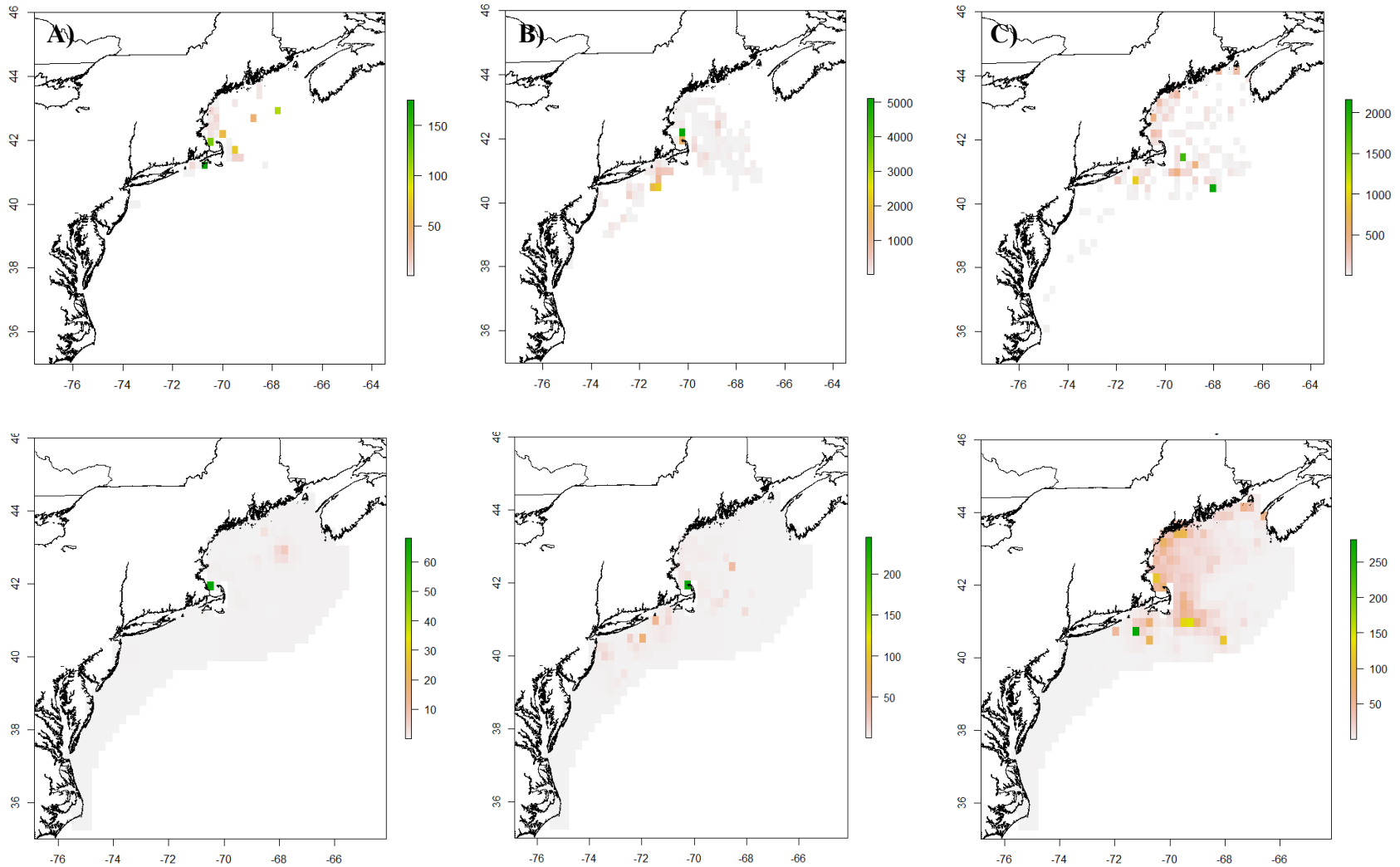


Figure 5F.19. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during autumn of 2007 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

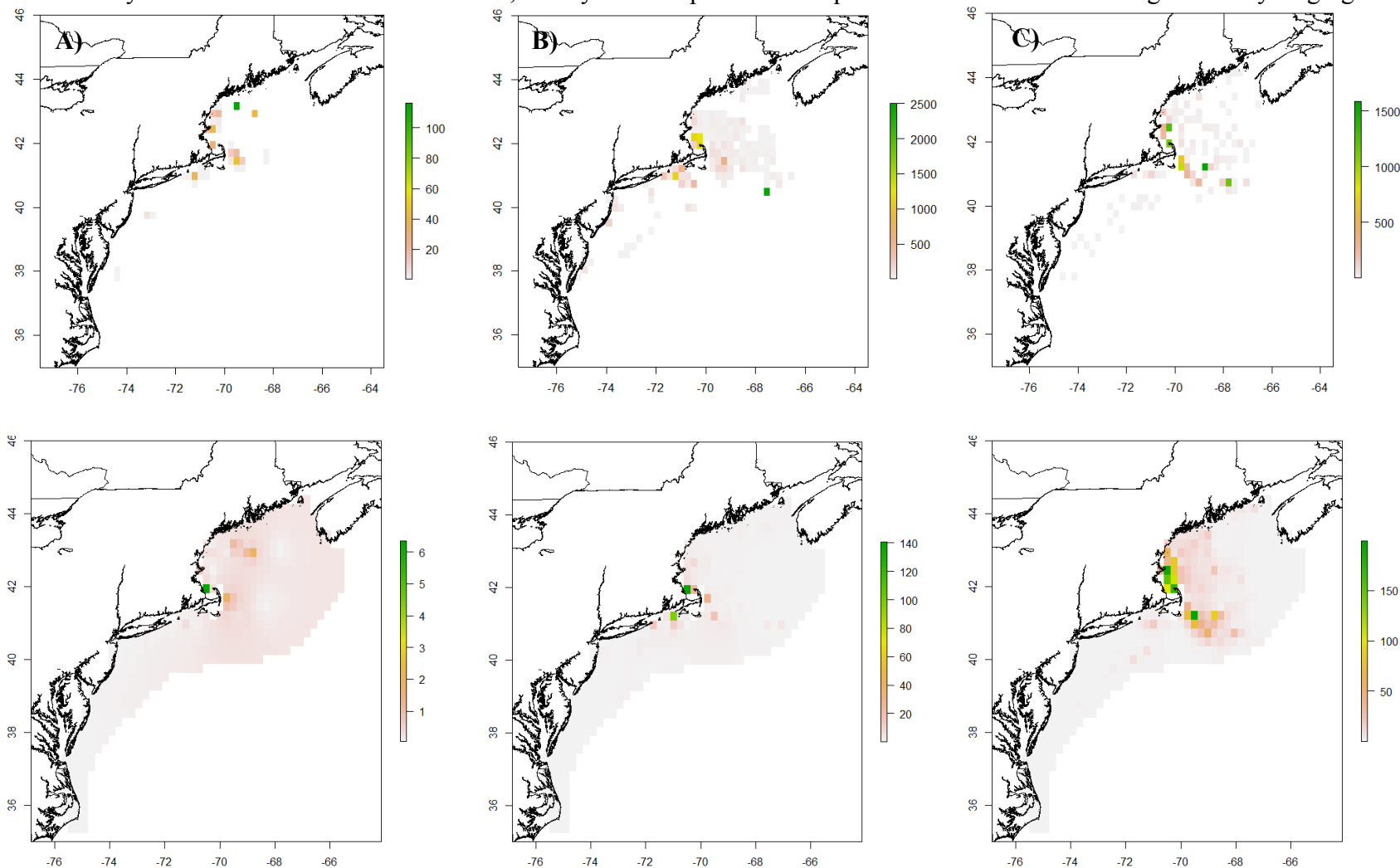


Figure 5F.20. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during autumn of 2008 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

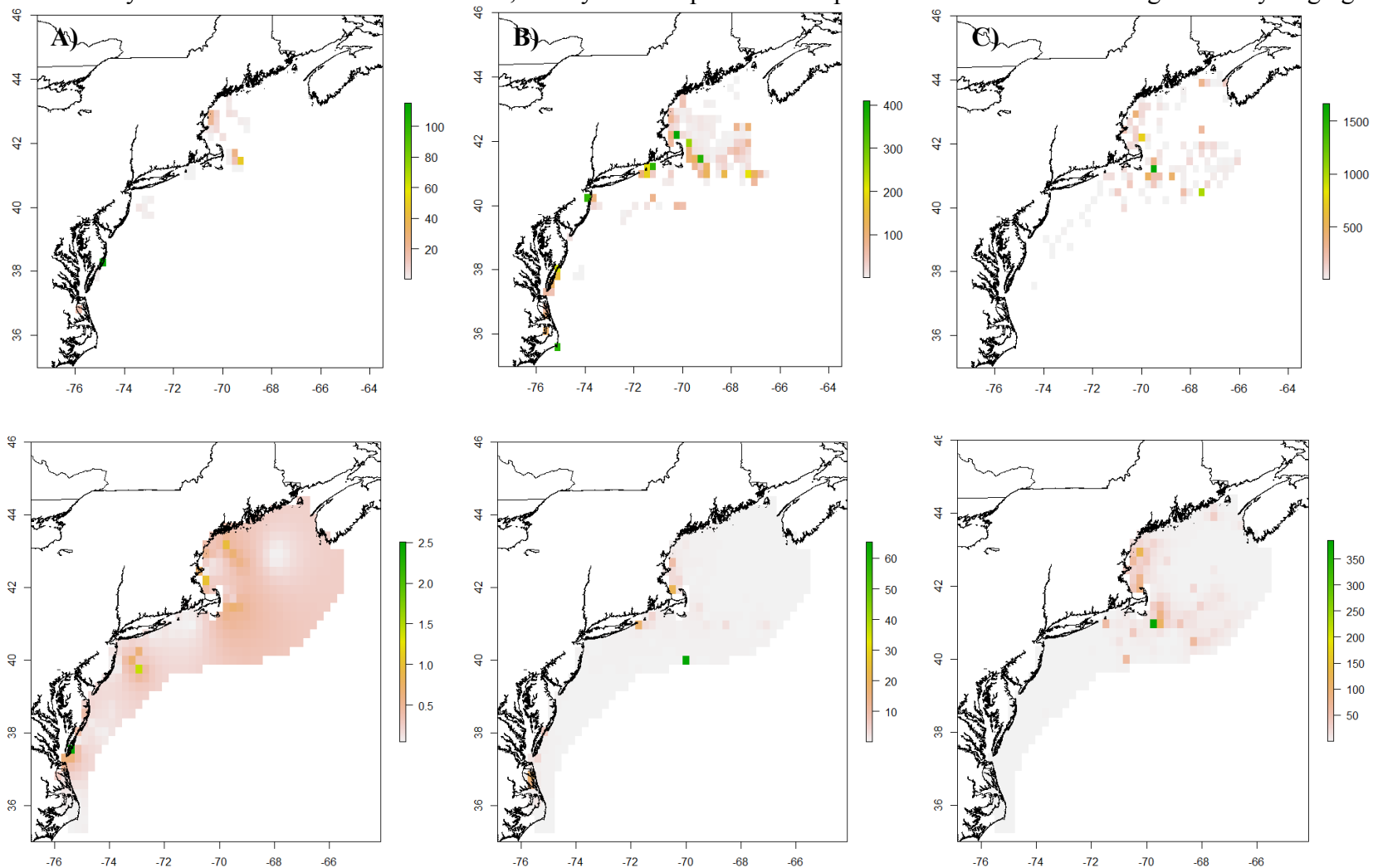


Figure 5F.21. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during autumn of 2009 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

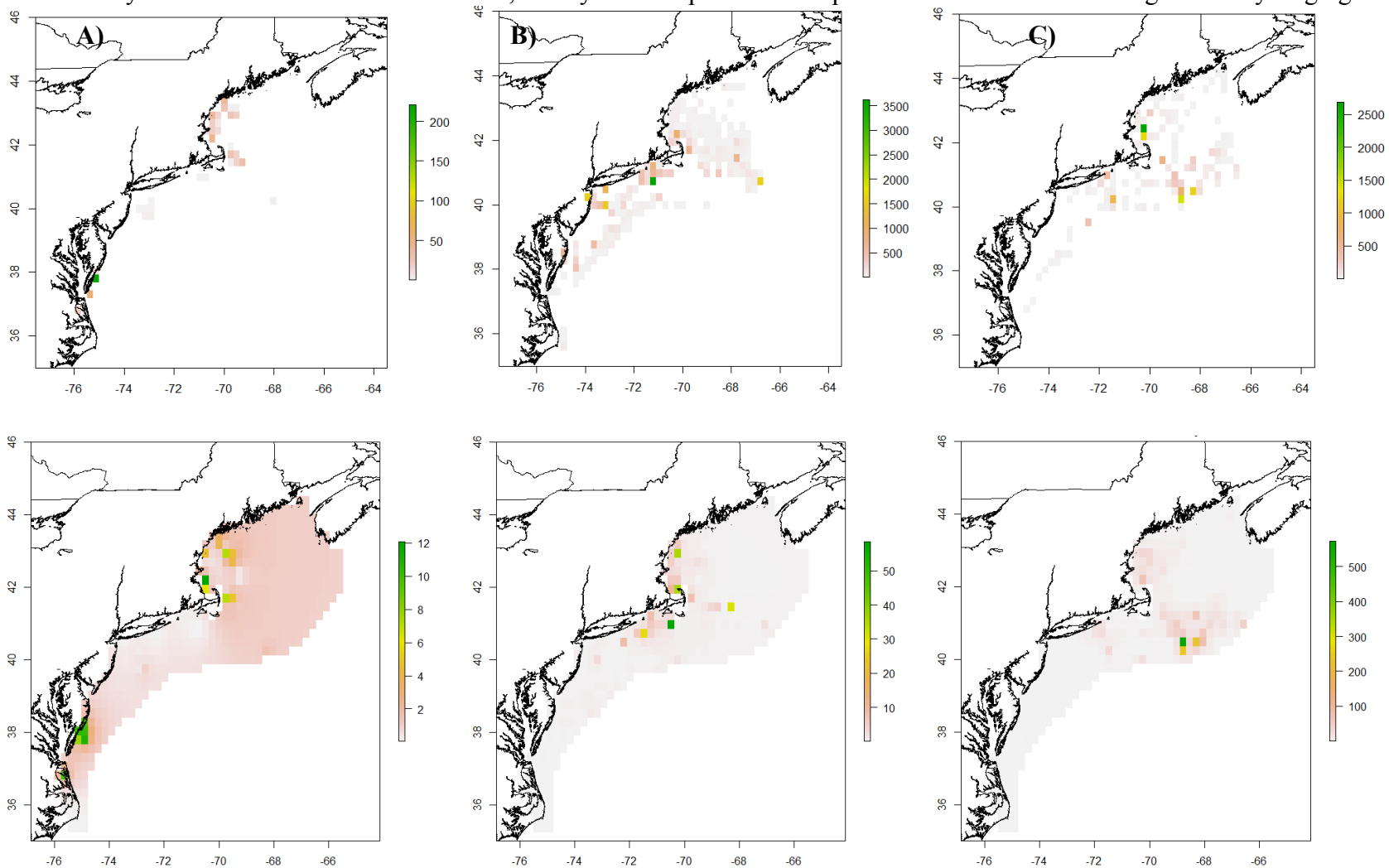


Figure 5F.22. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring of 1989 for the domestic A) otter trawl and B) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

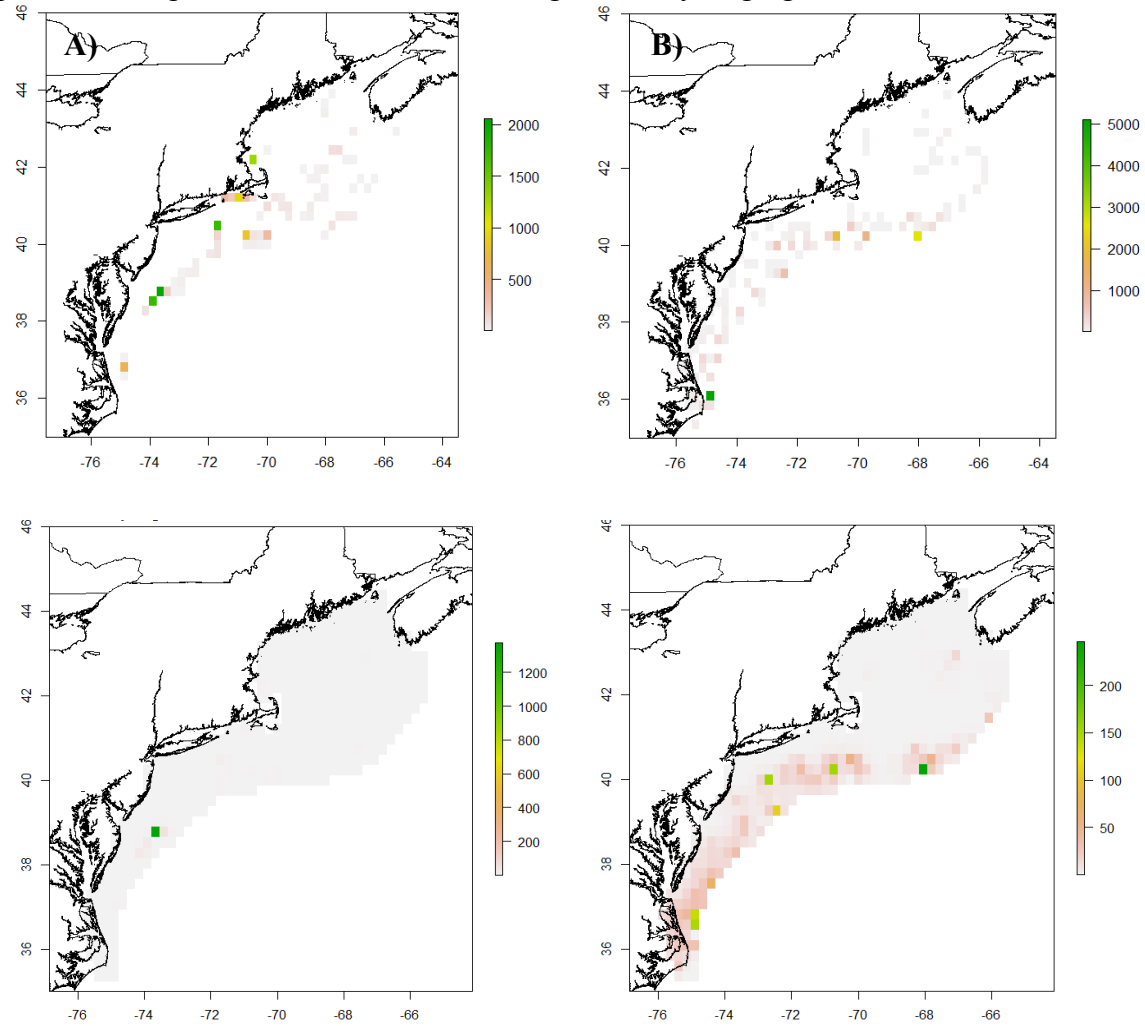


Figure 5F.23. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring of 1990 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

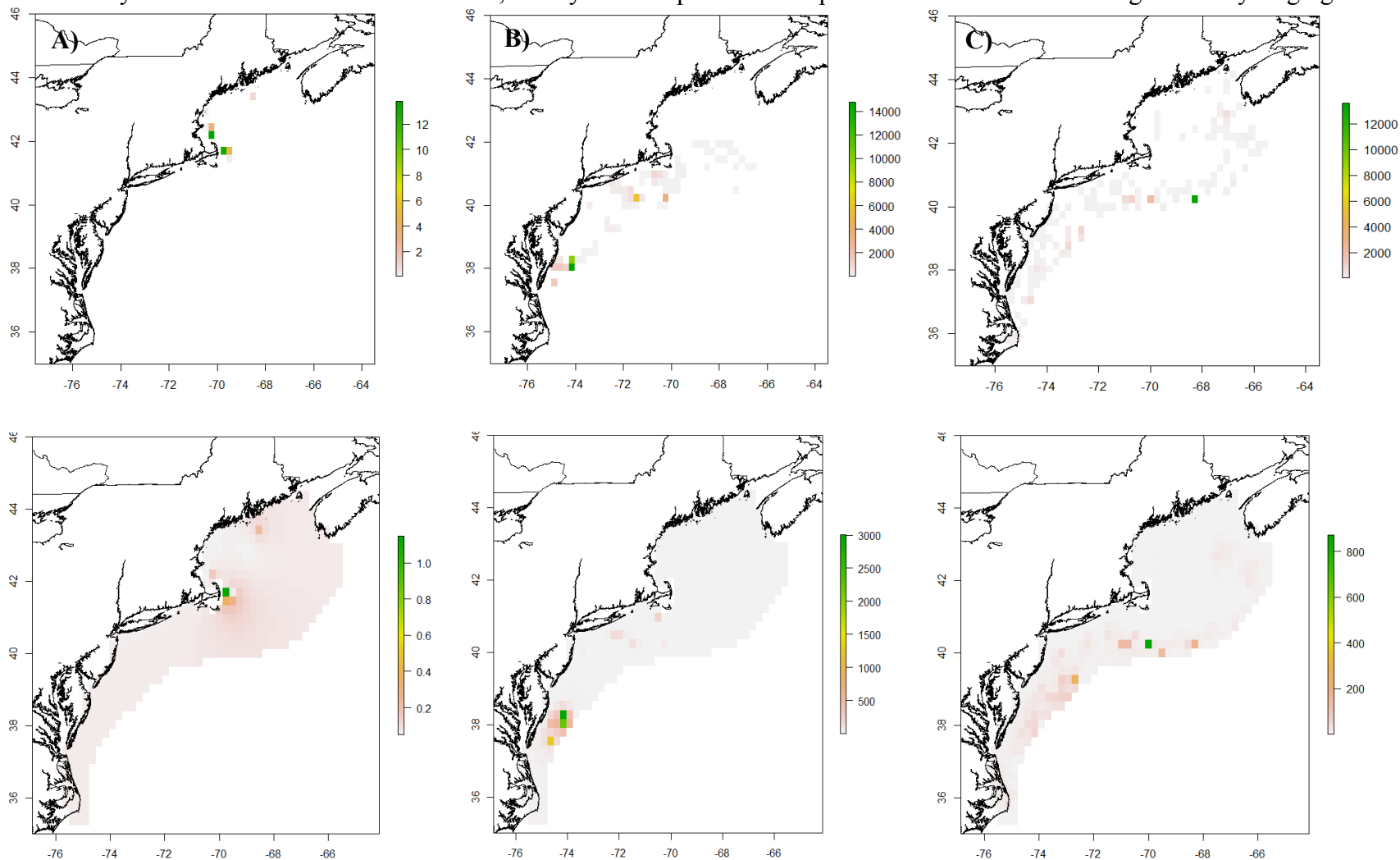


Figure 5F.24. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring of 1991 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

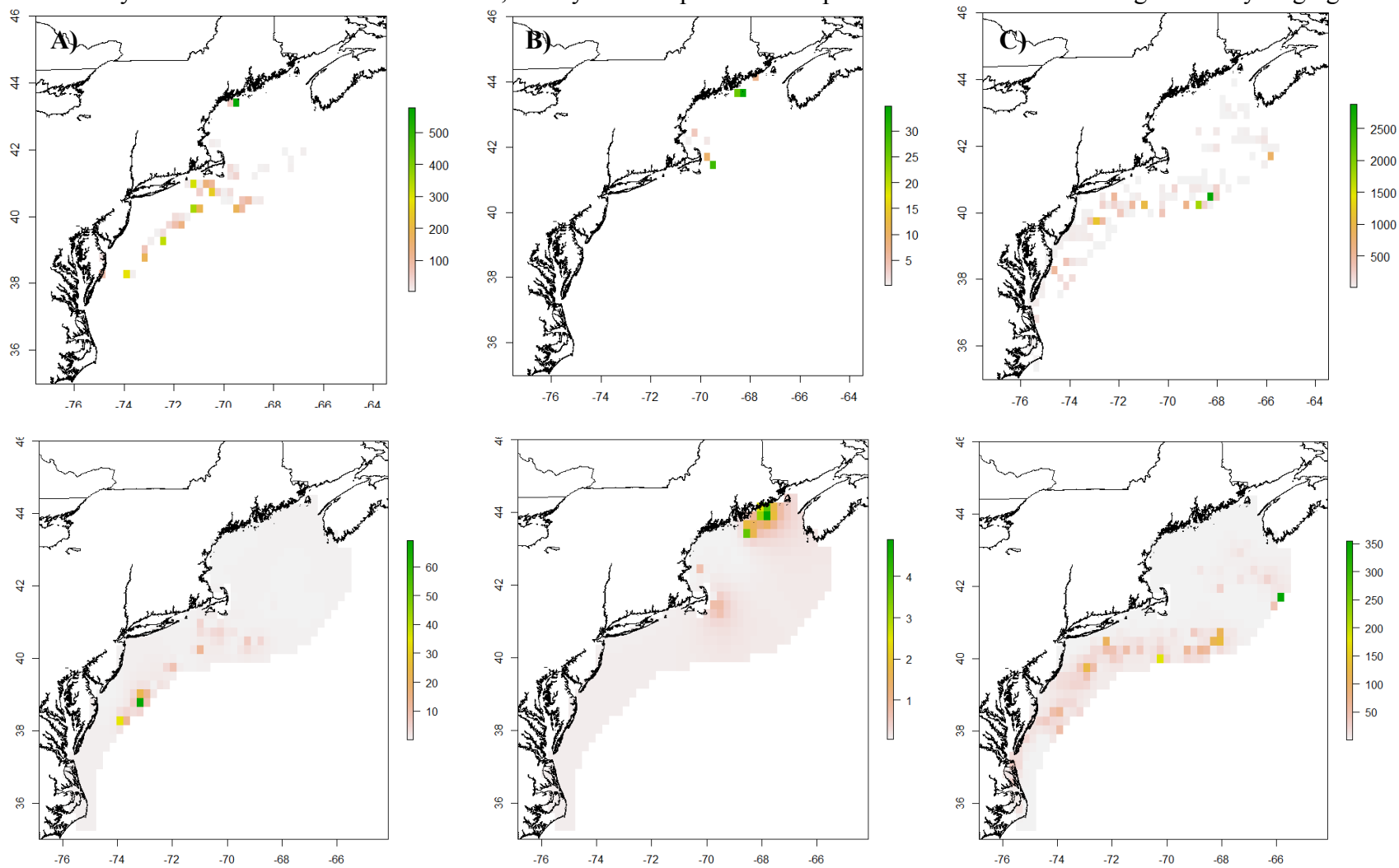


Figure 5F.25. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring of 1992 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

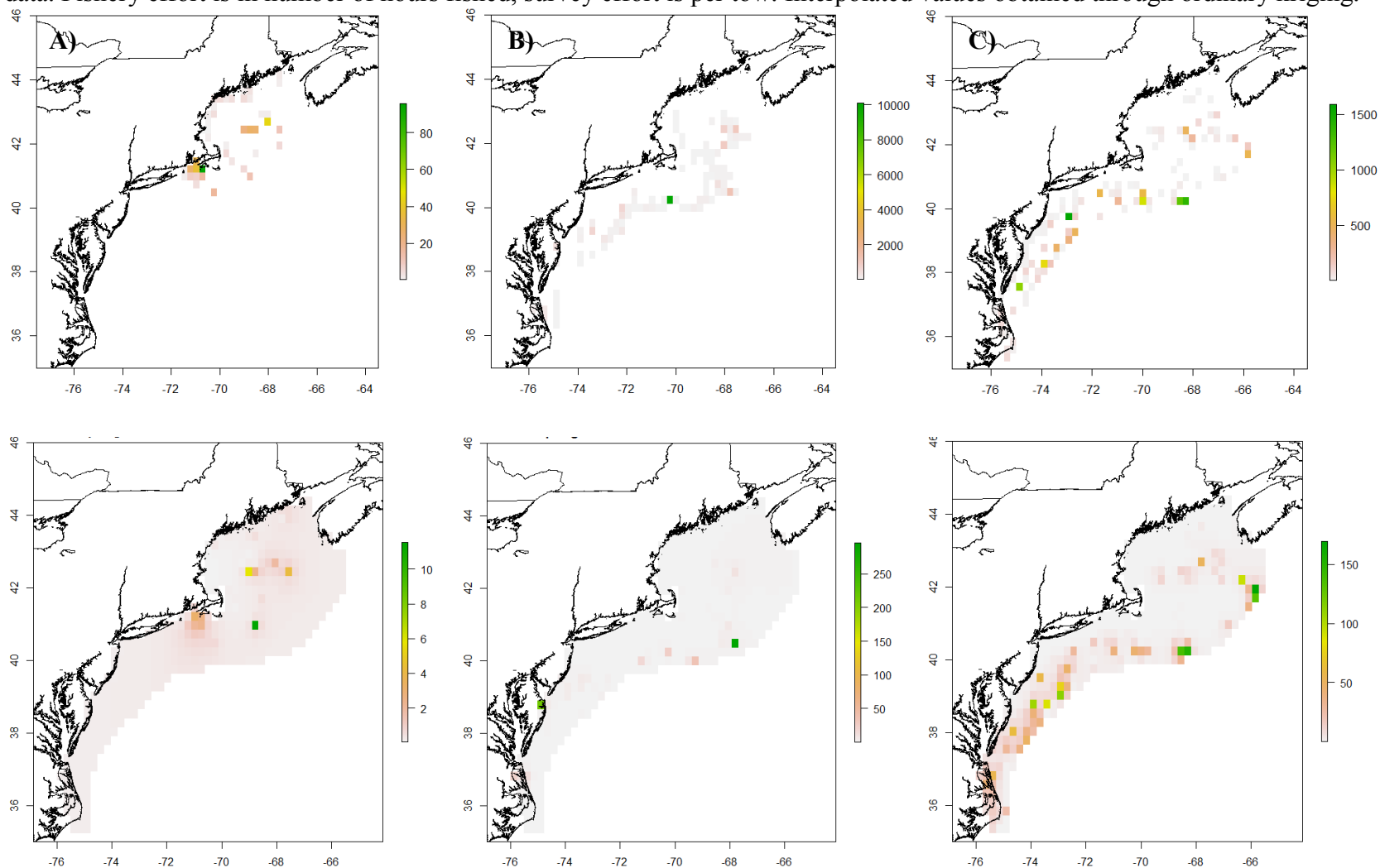


Figure 5F.26. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring of 1993 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

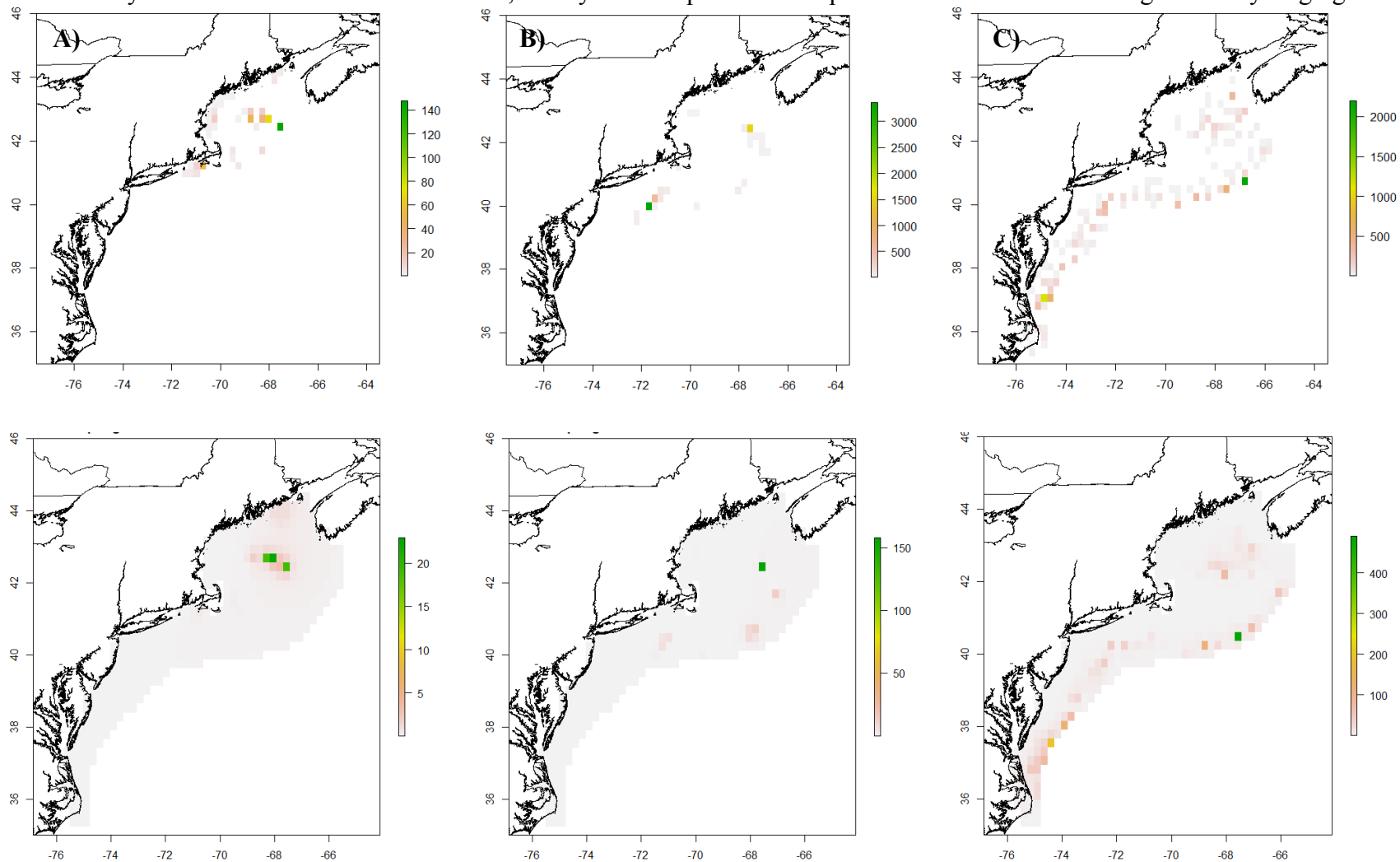


Figure 5F.27. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring of 1994 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

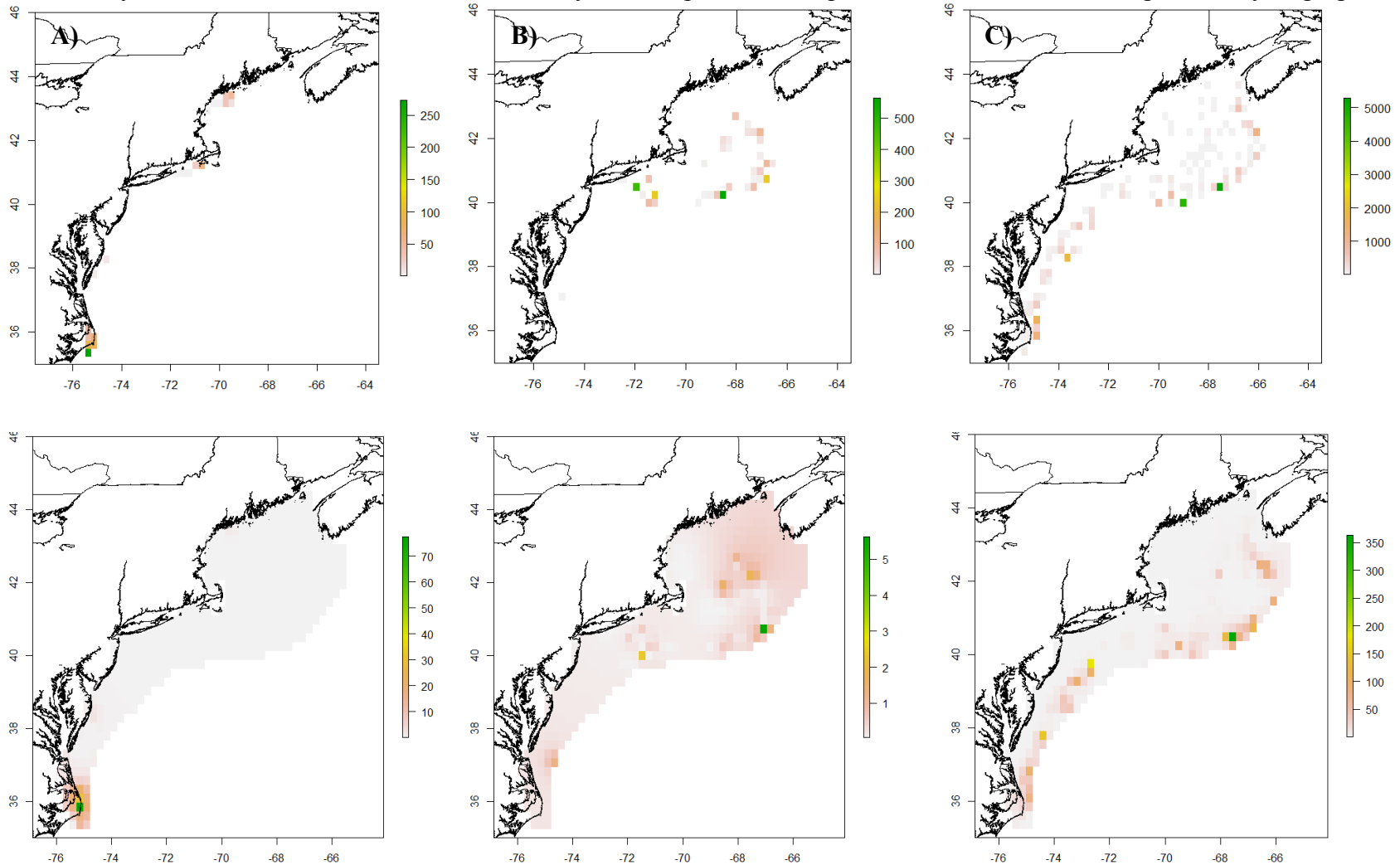


Figure 5F.28. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring of 1995 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average CPUE (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

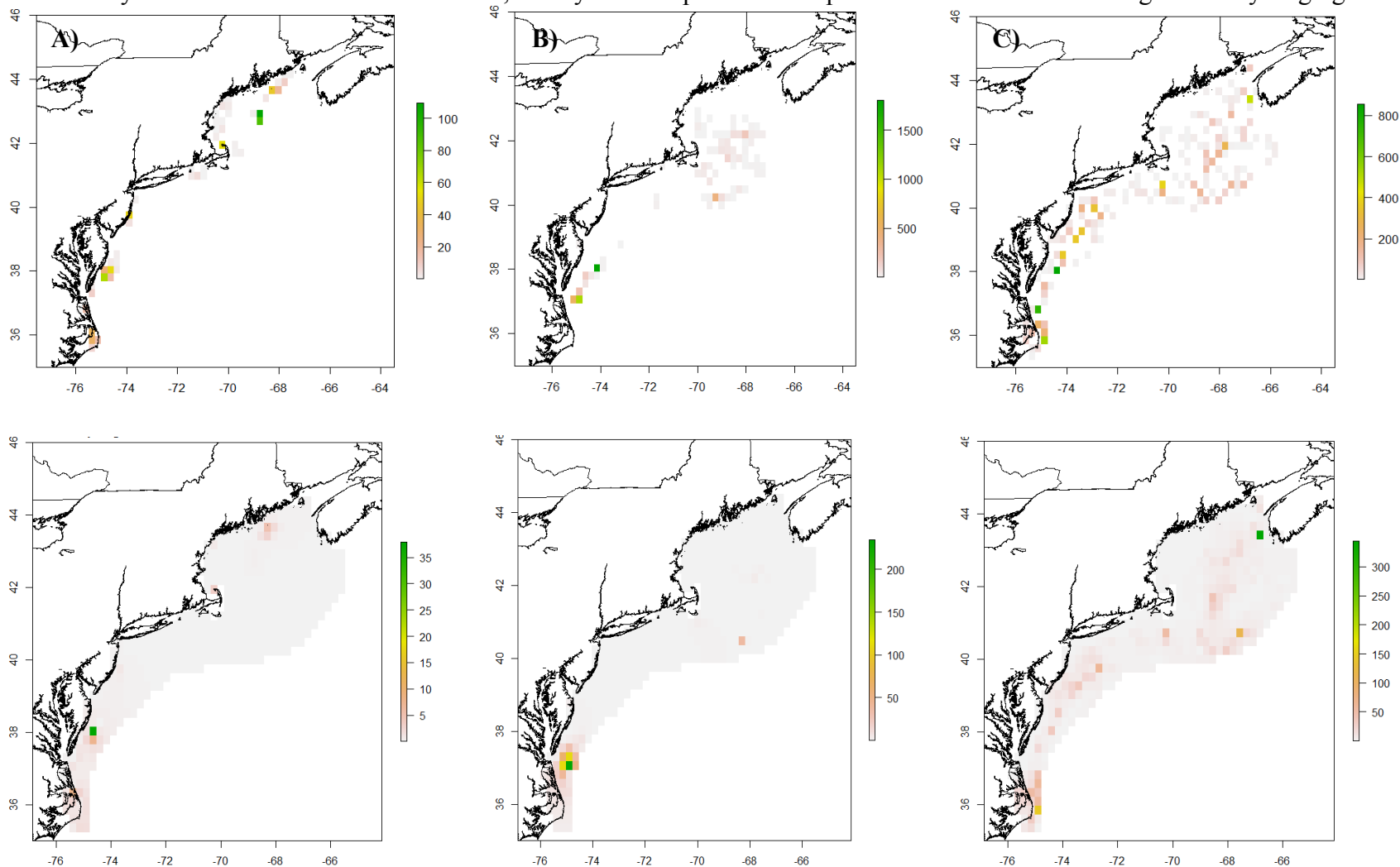


Figure 5F.29. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring of 1996 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

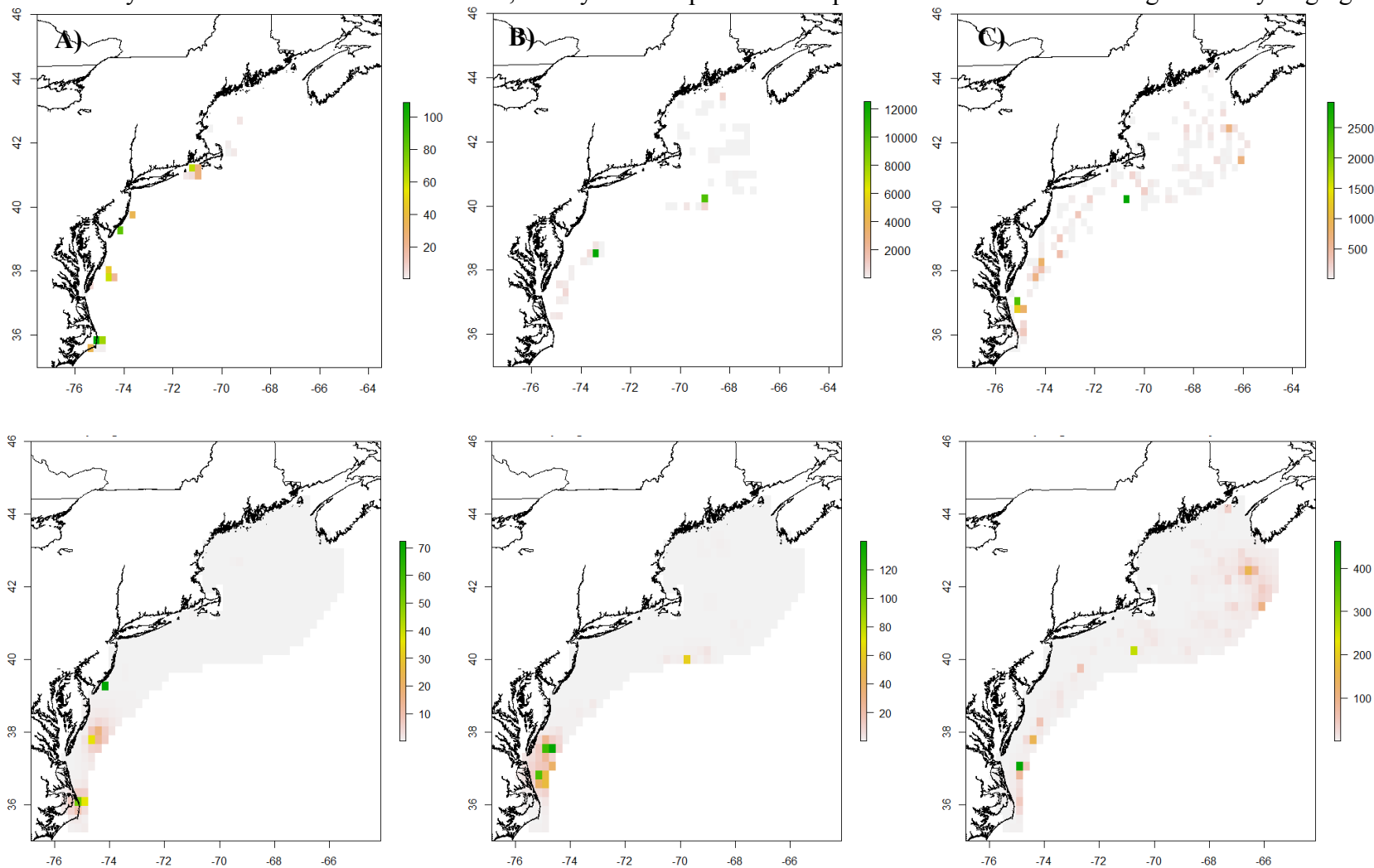


Figure 5F.30. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring of 1997 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

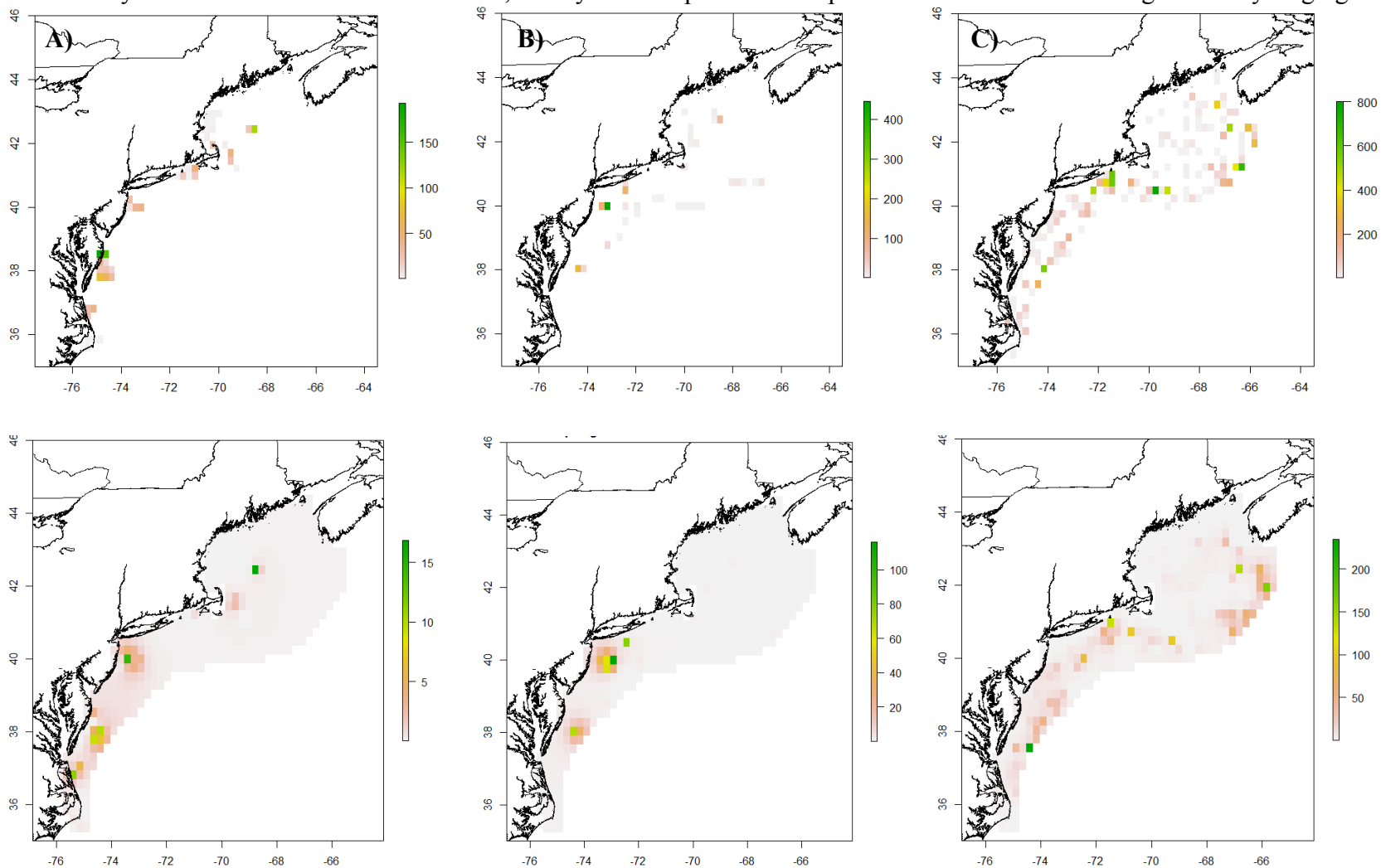


Figure 5F.31. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring of 1998 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

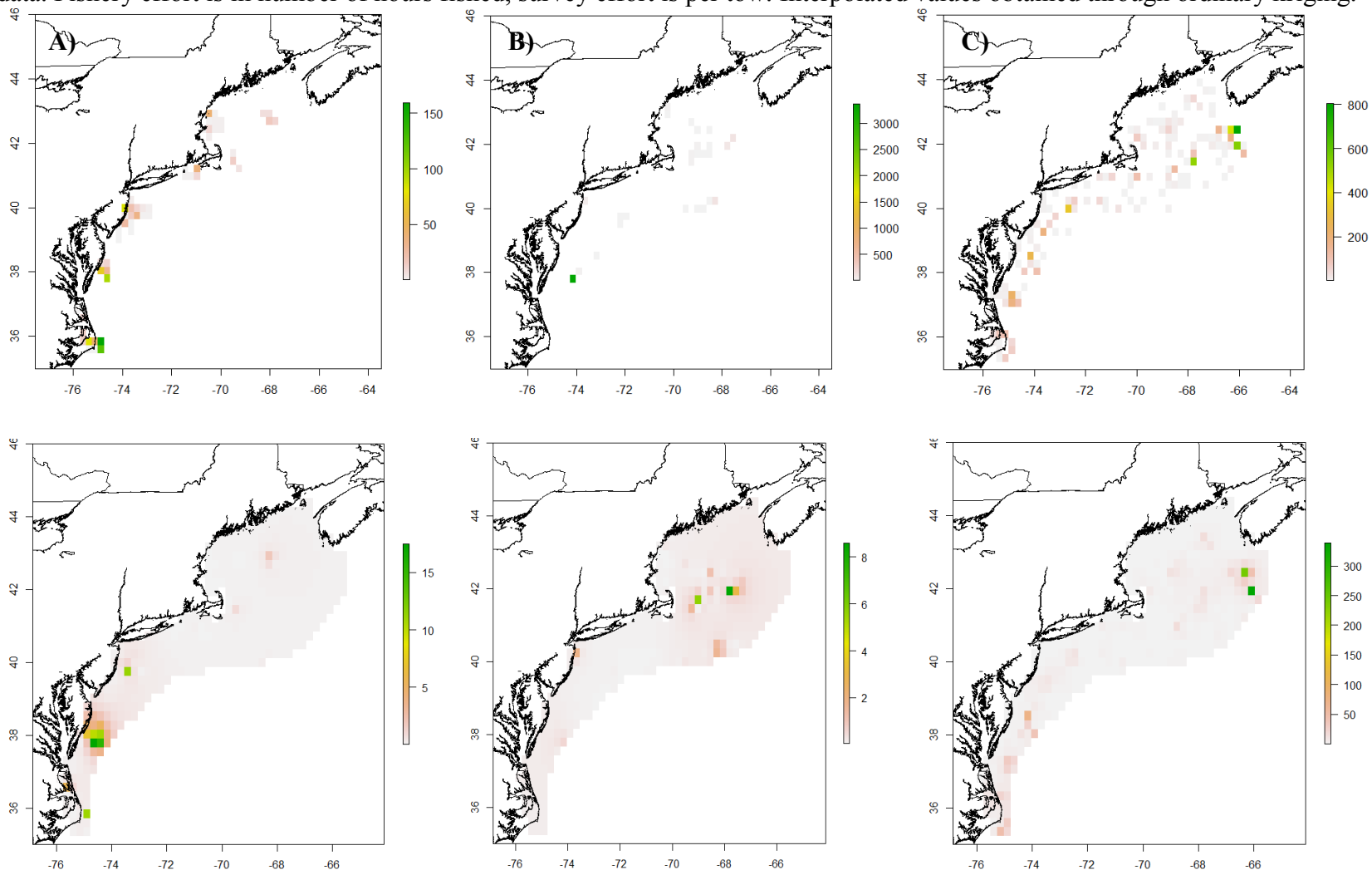


Figure 5F.32. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring of 1999 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

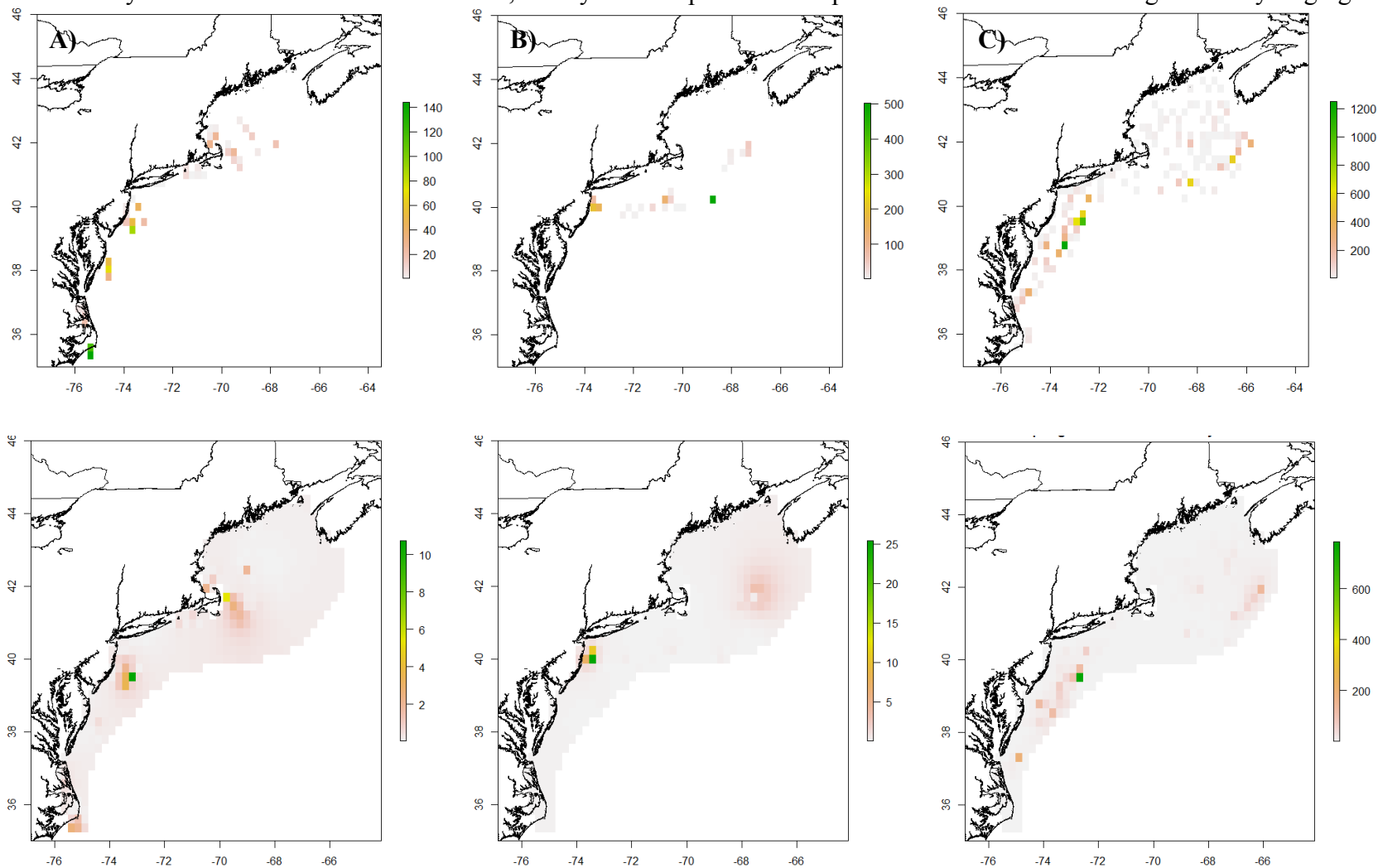


Figure 5F.33. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring of 2000 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

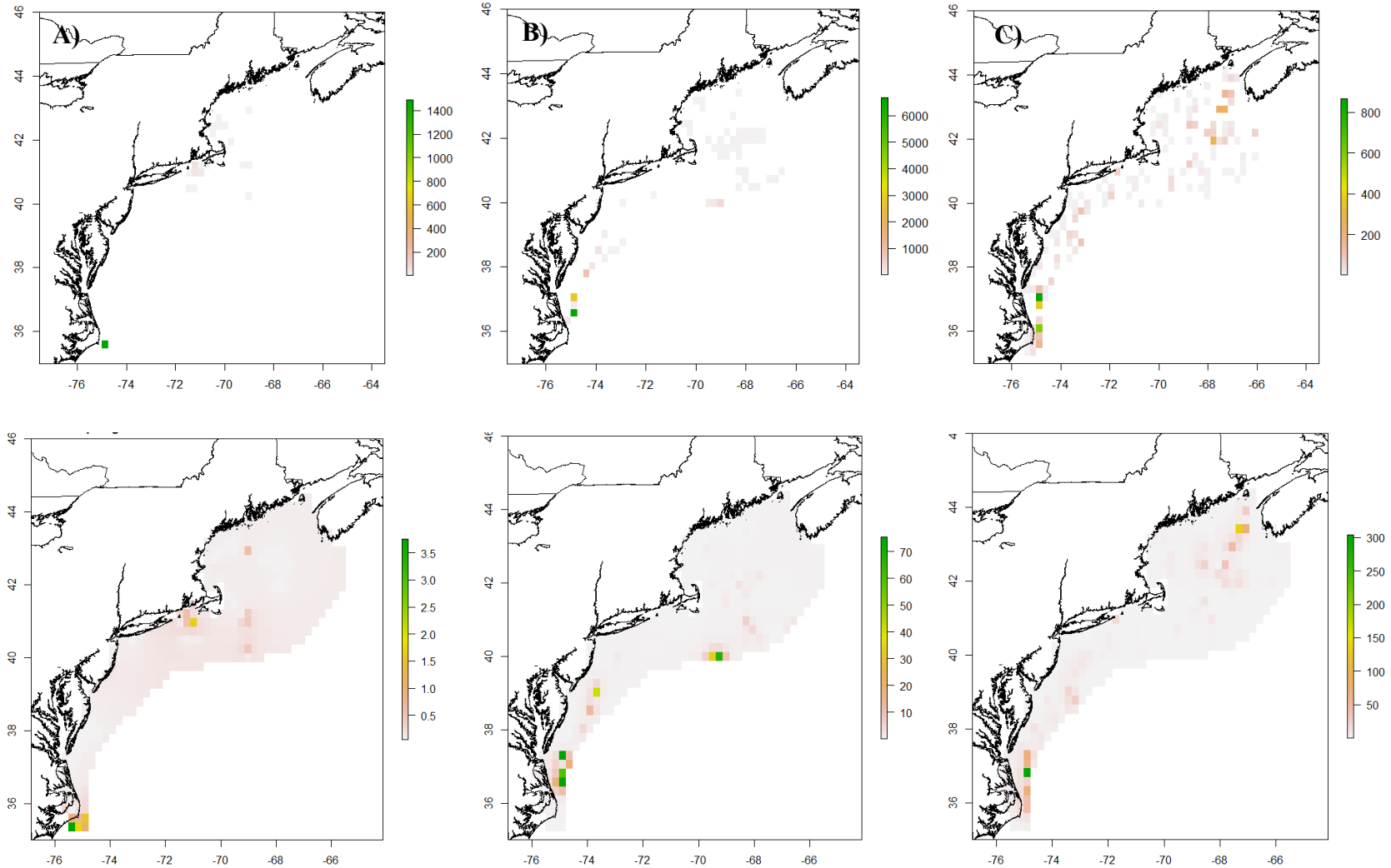


Figure 5F.34. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring of 2001 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

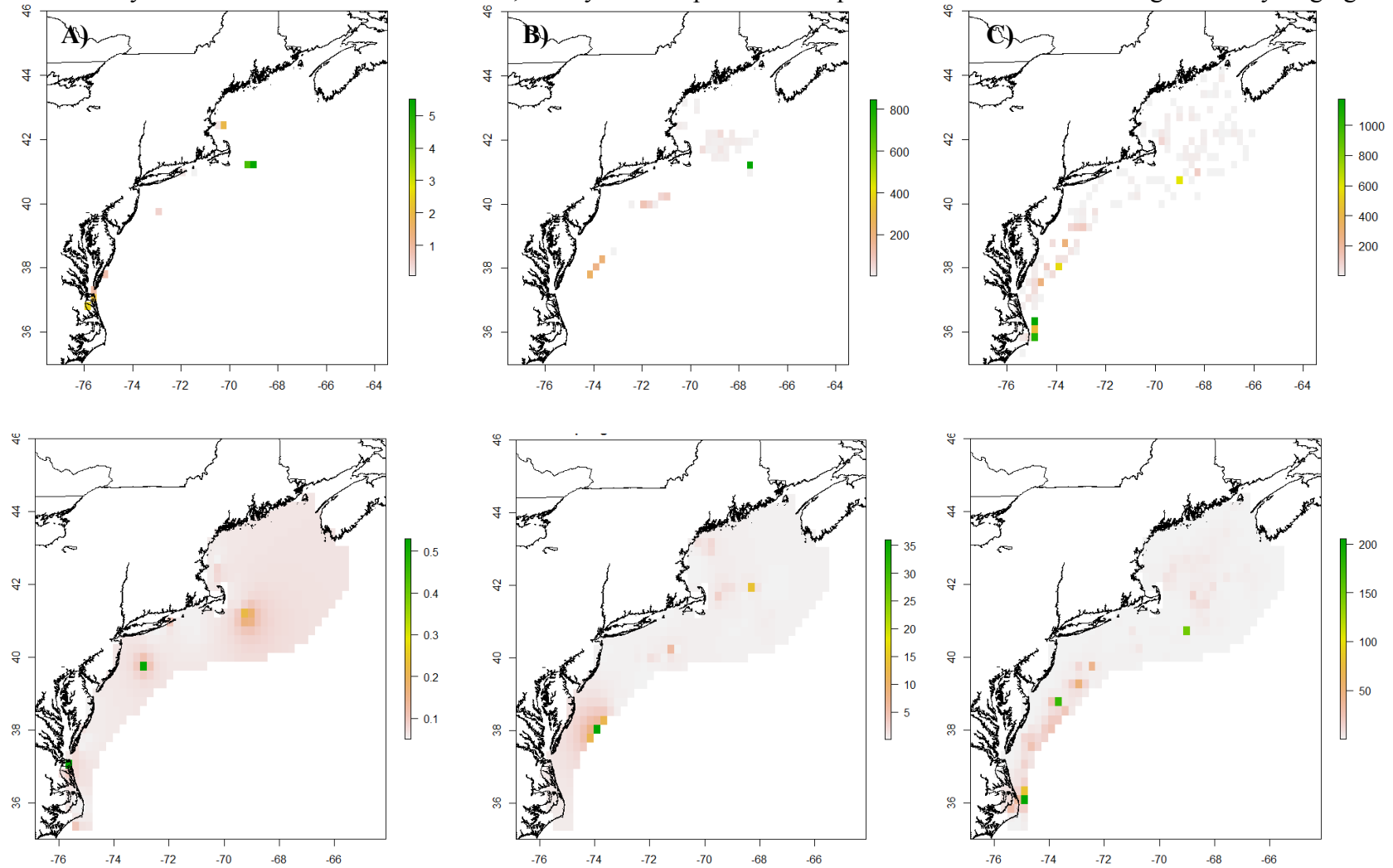


Figure 5F.35. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring of 2002 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

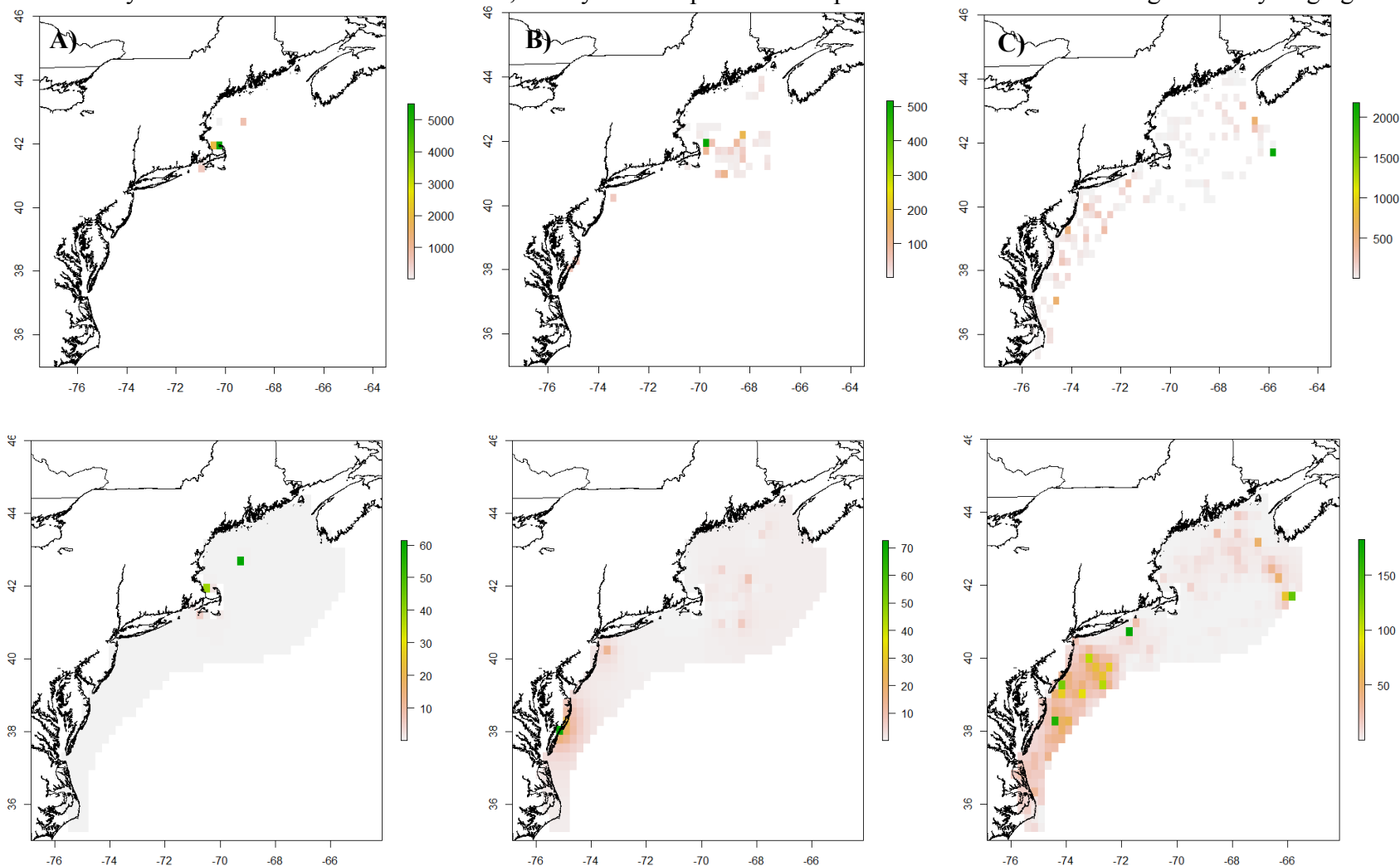


Figure 5F.36. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring of 2003 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

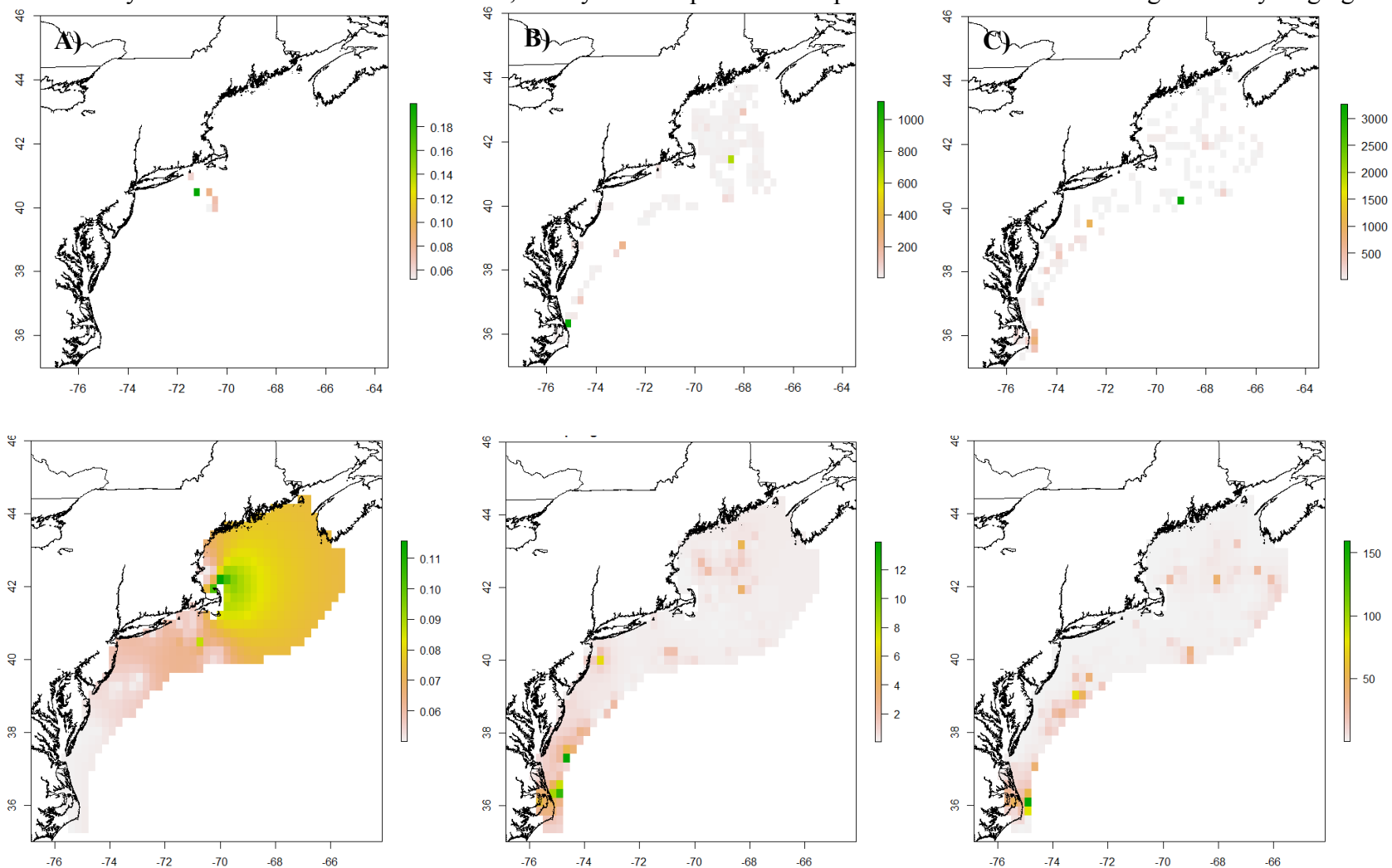


Figure 5F.37. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring of 2004 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

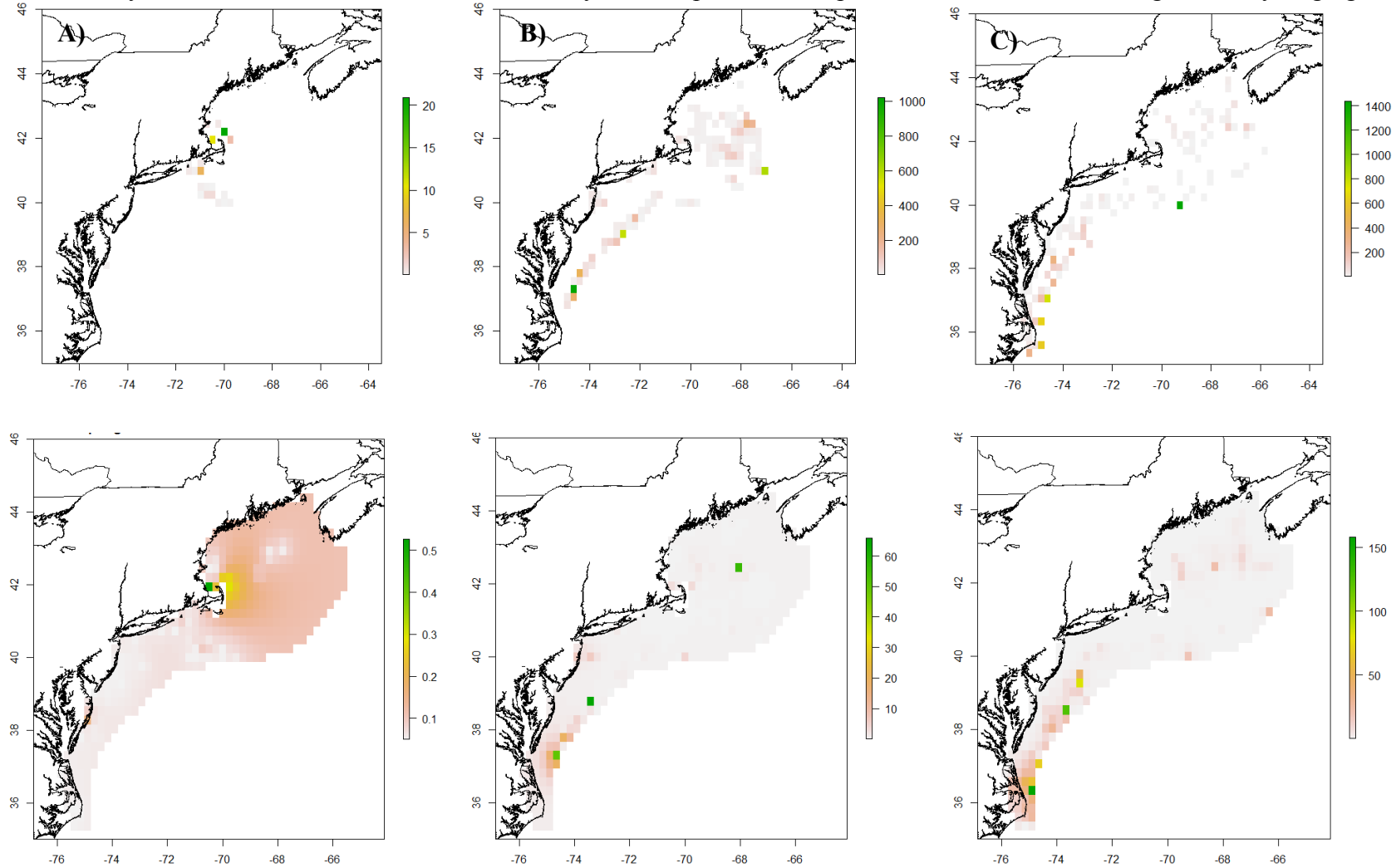


Figure 5F.38. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring of 2005 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

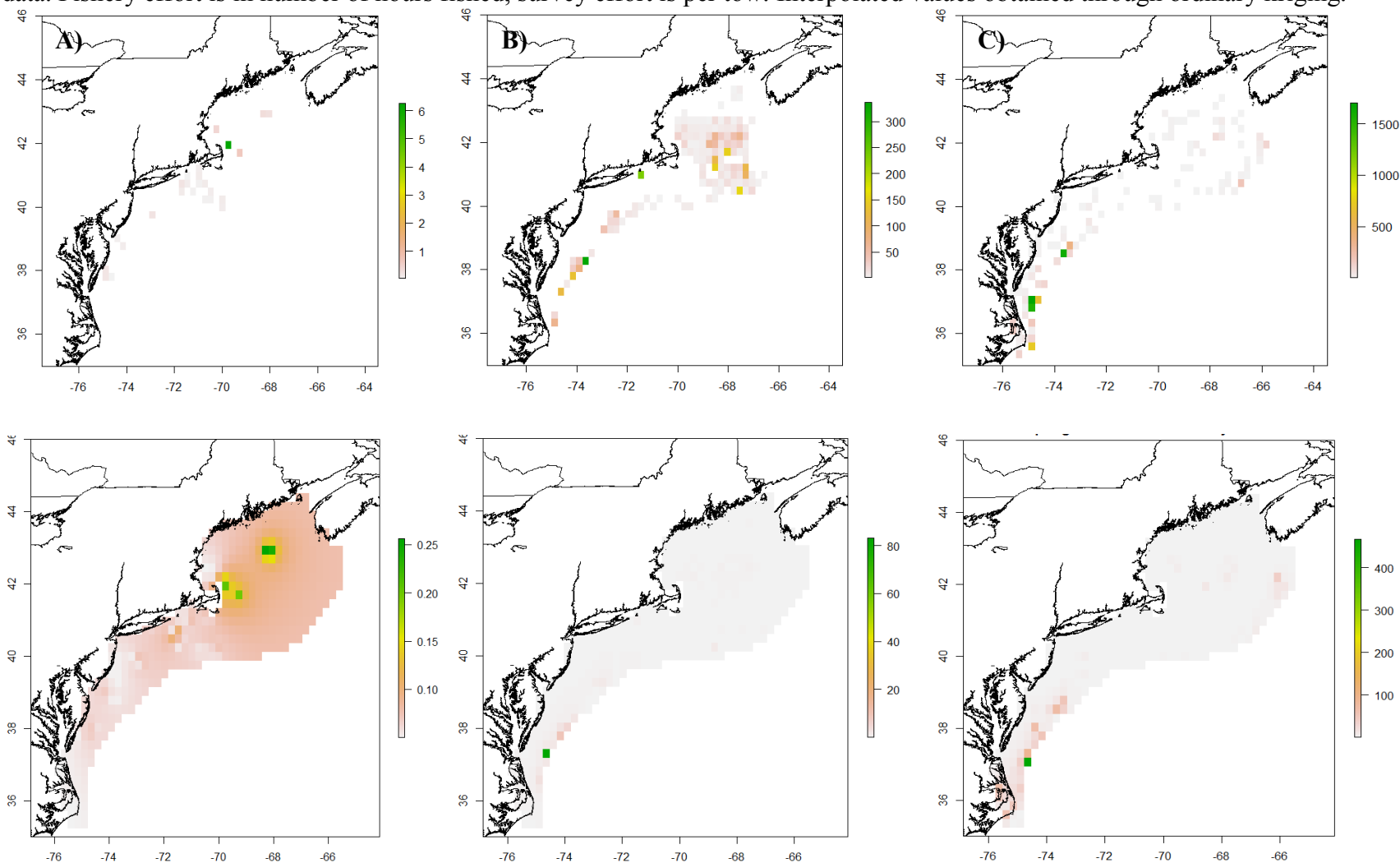


Figure 5F.39. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring of 2006 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

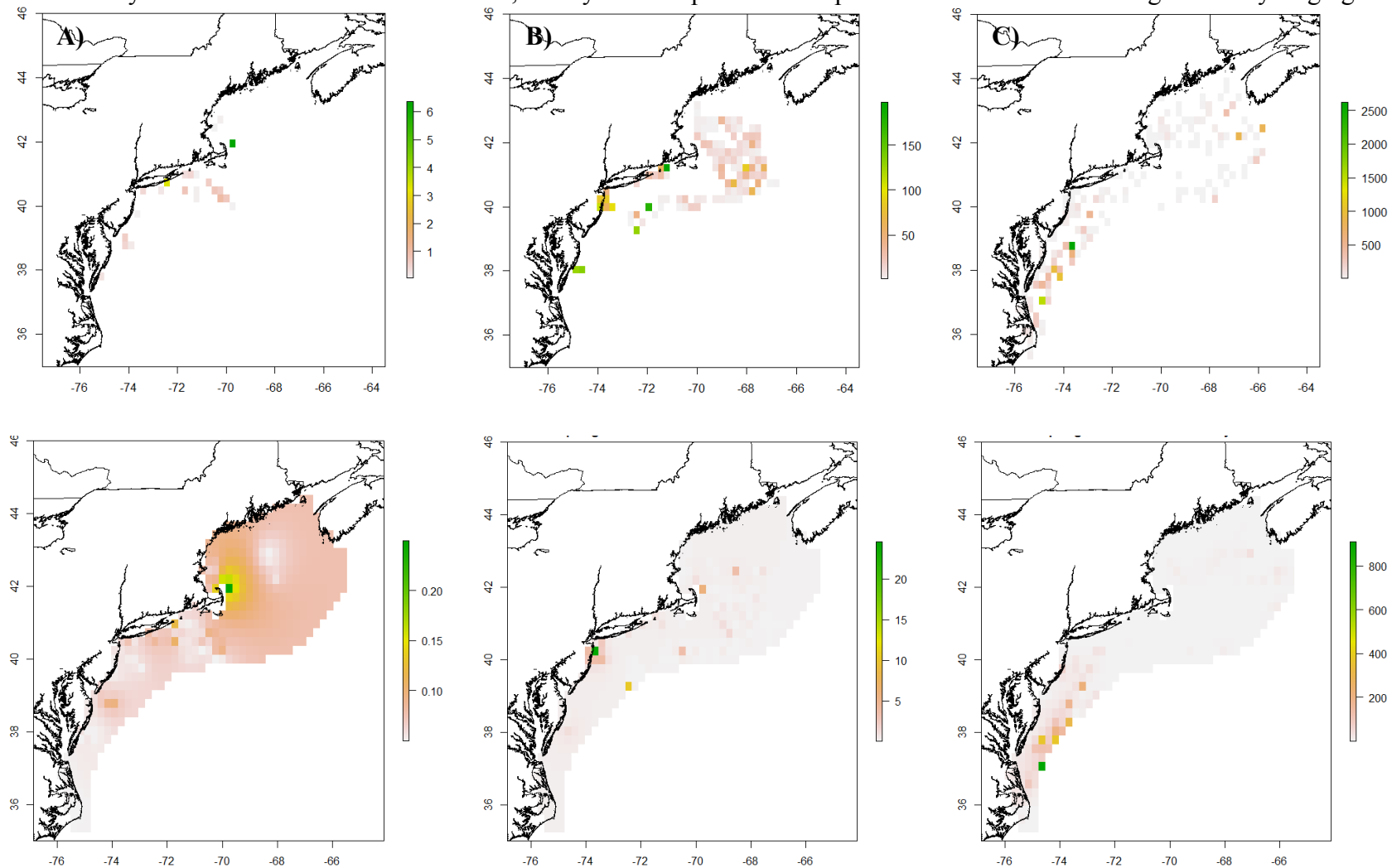


Figure 5F.40. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring of 2007 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

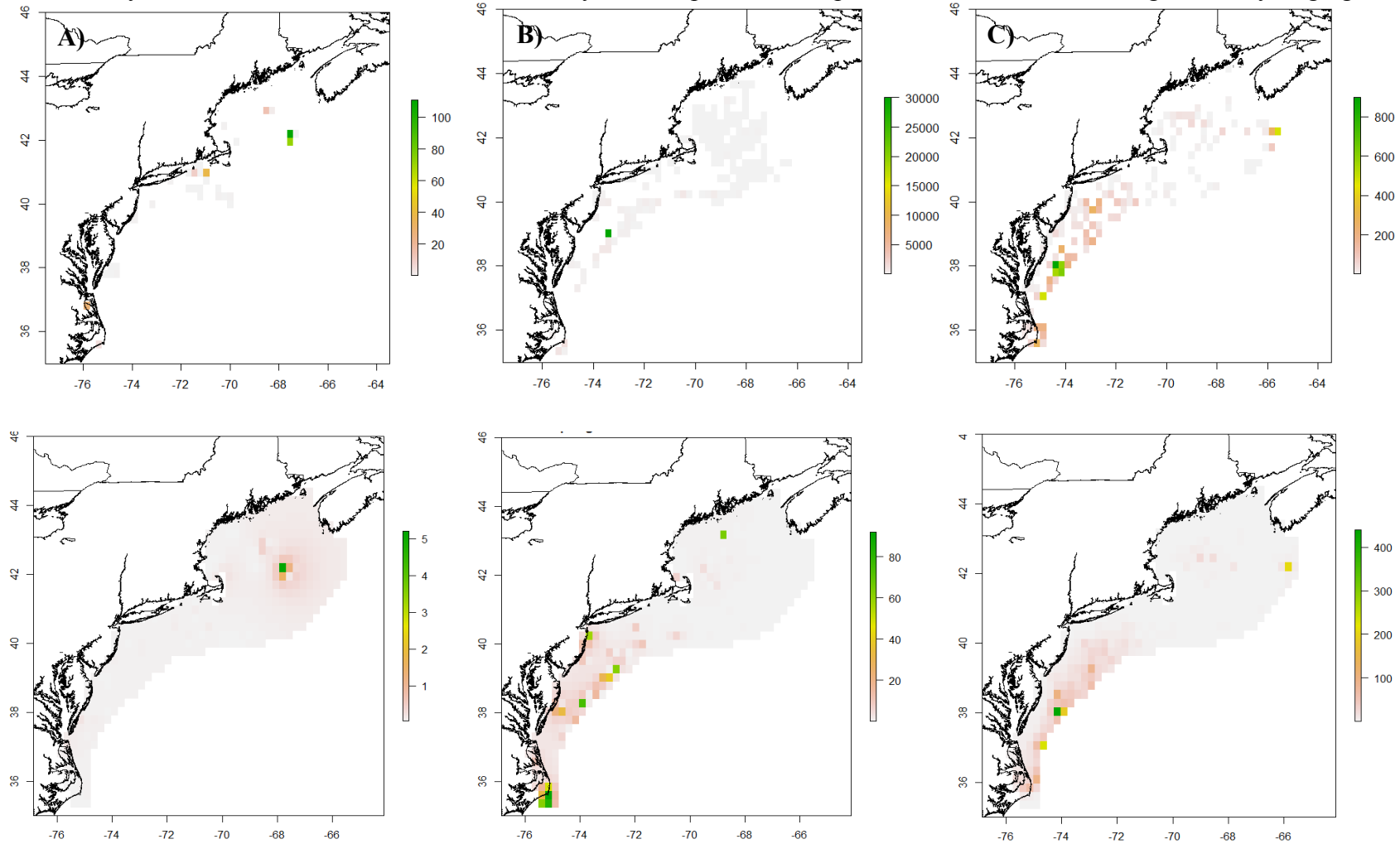


Figure 5F.41. Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring of 2008 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

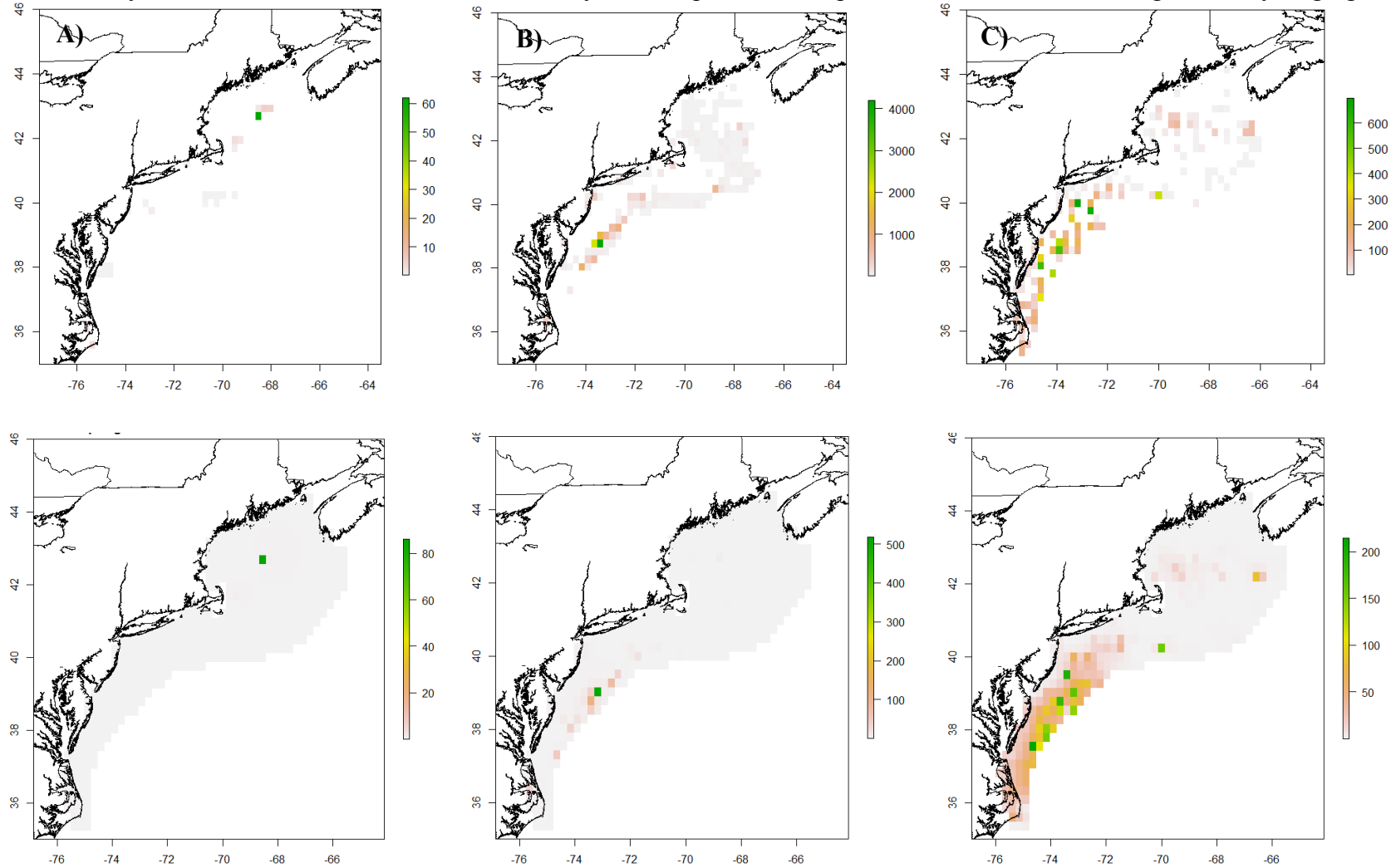


Figure 5F.42 Observed (top) and interpolated (bottom) spatial distribution of spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring of 2009 for the domestic A) sink gill net and B) otter trawl fisheries and the C) NEFSC trawl survey. Cell size $\sim 560 \text{ km}^2$ where values reflect the average *CPUE* (number caught per unit effort) obtained through rasterization of the original data. Fishery effort is in number of hours fished, survey effort is per tow. Interpolated values obtained through ordinary kriging.

