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Application of generalized additive models to examine ontogenetic and seasonal distributions of spiny dogfish (*Squalus acanthias*) in the Northeast (US) shelf large marine ecosystem

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Abstract: Increased commercial importance of spiny dogfish (*Squalus acanthias*) combined with an often debated, and controversial, ecological impact has warranted an investigation of the relationship among distribution, environment, and prey to better understand the species ecology and inform management. To elucidate mechanisms behind distributional changes, we modeled seasonal occurrence and abundance of neonate, immature, and mature spiny dogfish as functions of abiotic and biotic factors using generalized additive models and Northeast Fisheries Science Center bottom trawl survey data. Significant nonlinear relationships were widespread throughout dogfish stages and seasons. Seasonal occurrence was tightly linked to depth and bottom temperature, with year and Julian day influential for some stages. While these factors also influenced abundance, ecological factors (e.g., squid abundances) significantly contributed to trends for many stages. Potential impacts of climate change were evaluated by forecasting distributions under different temperature scenarios, which revealed higher regional probabilities of occurrence for most stages during a warmer than average year. Our results can be used to better understand the relationship between sampling periods and movement drivers to survey catchability of the population in the Northeast (US) shelf large marine ecosystem.

Résumé : L'importance commerciale croissante de l'aiguillat commun (*Squalus acanthias*), combinée à un impact écologique controversé faisant l'objet d'un débat soutenu, a motivé l'étude du lien entre répartition, milieu et proies dans le but de mieux comprendre l'écologie de cette espèce et d'en éclairer la gestion. Afin de faire la lumière sur les mécanismes qui sous-tendent les variations de la répartition, nous avons modélisé la présence et l'abondance saisonnières d'aiguillats communs nouveau-nés, immatures et matures en fonction de facteurs abiotiques et biotiques, à l'aide de modèles additifs généralisés et de données de levés au chalut de fond du Northeast Fisheries Science Center. Des relations non linéaires significatives étaient répandues pour tous les stades de vie de l'aiguillat et toutes les saisons. La présence saisonnière était étroitement reliée à la profondeur et la température au fond, l'année et le jour julien exerçant une influence pour certains stades. Si ces facteurs influençaient également l'abondance, des facteurs écologiques (p. ex. l'abondance de calmars) avaient une incidence significative sur les tendances pour de nombreux stades. Les impacts potentiels des changements climatiques ont été évalués en prédisant les répartitions pour différents scénarios de température, ce qui a révélé des probabilités régionales accrues de présence pour la plupart des stades durant les années plus chaudes que la normale. Nos résultats peuvent servir à une meilleure compréhension du lien entre les périodes d'échantillonnage et les facteurs influençant les déplacements dans l'évaluation de la capturabilité de la population dans le grand écosystème marin de la plate-forme du Nord-Est états-unien. [Traduit par la Rédaction]

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; Fig. 1), spiny dogfish (*Squalus acanthias*) play a key role in the structure and function of marine fisheries ecosystems (Fogarty and Murawski 1998; Link and Garrison 2002; Link and Ford 2006), drawing concern as both a consumer, poten-

tially competing with commercial fisheries, and as a species of conservation interest because of its vulnerable life history (Frisk et al. 2005, 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 and 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 sur-

2

Can. J. Fish. Aquat. Sci. Vol. 71, 2014

Fig. 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 Mid-Atlantic Bight (MA). Solid black line traces land masses. Lines reflect depth contours in metres. (For the coloured version of this figure, refer to the Web site at http://www.nrcresearchpress.com/doi/full/10.1139/cjfas-2013-0342.)
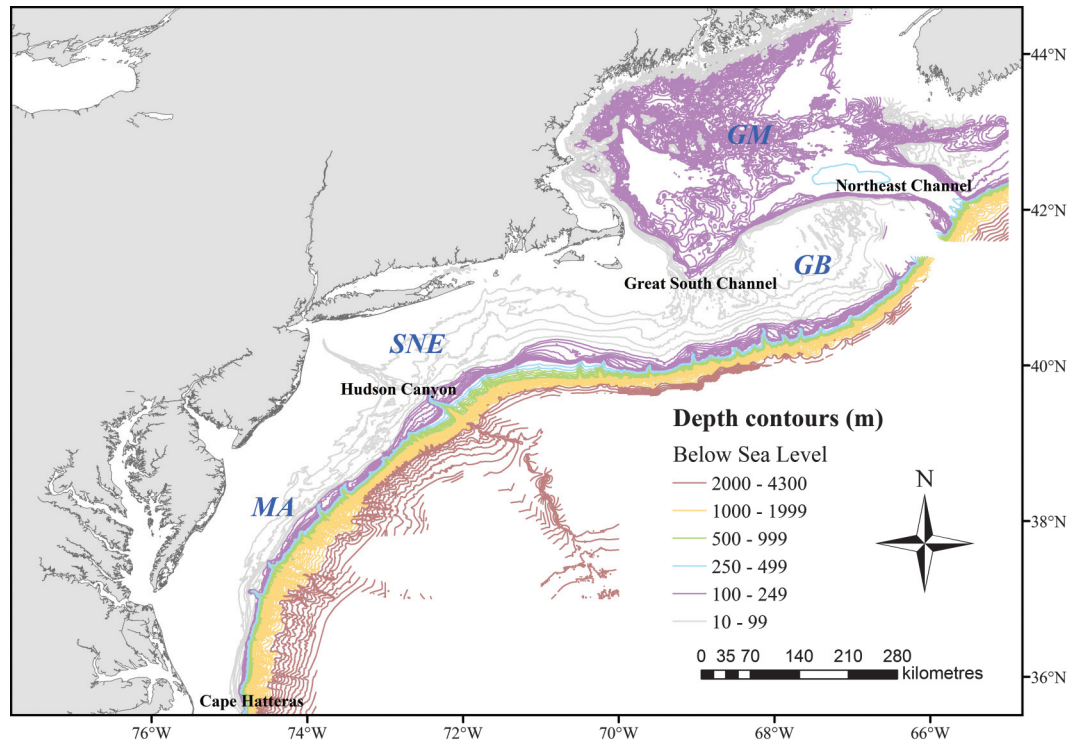
vey estimates of abundance. Estimation of these relationships, especially in the face of climate change (Hedger et al. 2004; Nye et al. 2009), will enhance forecasting ability (Link et al. 2011) and provide insight into species responses under both anthropogenic and natural alterations to the ecosystem.

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 and 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 and 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 and Smith 1994; Campana and 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.

In the Northwest Atlantic, decades of intensive foreign and domestic fishing effort reduced principal groundfish stocks in the 1970–1980s, altering not only the ecosystem structure but also the objectives of fishery and management targets (Murawski 1991; Fogarty and Murawski 1998). Species such as skates (e.g., winter skate (*Leucoraja ocellata*)) and dogfish that were traditionally discarded became commercially important as a means to offset the low catches of high valued groundfish (Murawski 1991; Fogarty and Murawski 1998; 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). For spiny dogfish, biologically unrealistic fluctuations in abun-

dance and assessment uncertainty (NEFSC 2006) further highlight the need to understand drivers of distribution and abundance, which are expected to vary between life-history stages owing to different seasonal migratory behavior (i.e., nursery grounds; Methratta and Link 2007; Cortés et al. 2011) or physiological demands (Macpherson and Duarte 1991). 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). Many factors complicate the assessment of this species, including seasonal transboundary movements and inconsistencies in both seasonal and decadal trends (Overholtz and Tyler 1985; Rago et al. 1998; Rago and Sosebee 2009). Spiny dogfish habitat utilization and movement are hypothesized to be driven by seasonal changes in temperature (Burgess 2002; Shepherd et al. 2002; Methratta and Link 2007). Their movements have also been suggested to reflect the distribution of prey, particularly during spring (Overholtz and Tyler 1985; Burgess 2002). Common prey items include squids, clupeids, scombrids, and other fishes (Fogarty and Murawski 1998; Link and Almeida 2000; Link and Garrison 2002).

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). The objectives of this study were to (*i*) analyze habitat preferences of spiny dogfish life-history stages using generalized additive models (GAMs) with a focus on the relationship of occupancy and abundance with ambient environmental, temporal, spatial, and ecological factors in the NES LME; (*ii*) identify key factors driving the distributions of dogfish stages and propose potential mechanisms; and (*iii*) forecast distributional changes under different bottom temperature scenarios encountered by a hypothetical survey, a driver assumed

important. 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 may 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.

Materials and methods

Data source

Data were collected from the NEFSC annual bottom trawl surveys conducted on the NES LME (Fig. 1) during autumn and spring since 1963 and 1968, respectively. These surveys sample the NES LME from Cape Hatteras, North Carolina, to Georges Bank and the Gulf of Maine using a stratified random design. 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 ± 13 stations (SE); N_{SPRING} = 346 ± 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 (Brown et al. 2007). 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 stages: aggregated male and female neonates (total length (TL) ≤ 26 cm), immature males (26 cm < TL < 60 cm), immature females (26 cm < TL < 80 cm), mature males (TL ≥ 60 cm), and mature females (TL ≥ 80 cm). Tow duration was standardized and represented by the number of dogfish caught per tow (CPUE). To account for zero-inflation, where the number of zero counts observed greatly exceeded those expected from standard statistical distributions (Welsh et al. 1996), the distribution of each dogfish stage was reported in two separate datasets: (*i*) occurrence (PA: 1 = present, 0 = absent) and (*ii*) abundance or zero-truncated presence (PRES) (Table 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 and 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 abundances) were selected based on their importance in spiny dogfish diet as reported from the National Marine Fisheries Service (NMFS) Food Webs Dynamic Program food habits database (Link and Almeida 2000). Prey species chosen included Atlantic butterfish (*Peprilus triacanthus*), Atlantic herring (*Clupea harengus*), shortfin squid (*Illex* spp.), longfin squid (*Doryteuthis* spp., formerly *Loligo* spp.), and Atlantic mackerel (*Scomber scombrus*). As for spiny dogfish, CPUE from the NEFSC survey was considered an appropriate proxy for prey abundance. If large correlations between any two variables occurred (i.e., $r > 0.6$), then one of the variables was excluded 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 Team 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, and the local index of collocation (LIC), which reflects the local overlap at sampling stations (Bez and 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 Bez and Rivoirard 2000 for equations), and was calculated as

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

where $\Delta \mathrm{CG}$ separates the CG of a dogfish stage (i.e., predator or conspecific) and a 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 Team 2010). The GIC index ranges from 0 (each population occupies a distinct location) to 1 (two CGs completely coincide) (Bez and Rivoirard 2000).

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

$$(2) \quad \mathrm{LIC}(t) = \frac{\sum_{i=1}^{N} z_i^{\mathrm{prey\ or\ conspecific}}(t)\, z_i^{\mathrm{dogfish\ stage}}(t)}{\sqrt{\sum_{i=1}^{N} \left[z_i^{\mathrm{prey\ or\ conspecific}}(t)\right]^2 \sum_{i=1}^{N} \left[z_i^{\mathrm{dogfish\ stage}}(t)\right]^2}}$$

This index represents the noncentered 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 and Rivoirard 2000).

Statistical analysis

Model fitting

The distributions of spiny dogfish were modeled separately for each stage and season using GAMs (Hastie and Tibshirani 1990; Wood 2006), a semiparametric extension of the generalized linear model (GLM) commonly applied to the spatial distributions of fishes (Feyrer et al. 2007; Murase et al. 2009; 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 nonlinear relationships and uncover hidden structure between variables missed by traditional linear methods (Hastie and Tibshirani 1990; Guisan et al. 2002). GAM analyses are often data-driven and can be either explanatory or predictive in nature (Yee and Mitchell 1991; Fewster et al. 2000; Guisan et al. 2002).

Two-stage (i.e., hurdle or delta method) models were constructed to account for zero-inflation and overdispersion (Potts and 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 and Stroup 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 and Elith 2006). All GAMs were built in R (R Core Development Team 2010) with the package "mgcv" (Wood 2011) using cubic regression splines and a maximum of 5 degrees of freedom (number of knots (k) = 5). The number of knots determines the smoothness or "wiggliness" of the curve; the more knots used, the less smooth the curve

4

Can. J. Fish. Aquat. Sci. Vol. 71, 2014

Table 1. Summarization of spiny dogfish occurrence (PA) and abundance (PRES) based on 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.

		PA			PRES			
Stage	$N_{OBS}{}^{*} = 0$	$N_{PA}{}^{*}$	Training	Test	$N_{PRES}{}^{*}$	Training	Test	+Tows (%)
Autumn								
Neo	14 220	14 395	10 077	4 319	175	123	53	1.22
ImmM	7 607	8 714	6 100	2 614	1 107	775	332	12.57
ImmF	6 415	8 714	6 100	2 614	2 299	1 609	690	26.08
MatM	6 720	8 714	6 100	2 614	1 994	1 396	598	22.88
MatF	7 301	8 714	6 100	2 614	1 413	989	424	16.22
Spring								
Neo	12 068	12 814	8 970	3 844	746	522	224	5.82
ImmM	7 449	8 869	6 208	2 661	1 420	994	426	16.22
ImmF	5 568	8 869	6 208	2 661	3 301	2 311	990	37.74
MatM	6 105	8 869	6 208	2 661	2 764	1 935	829	31.16
MatF	5 743	8 869	6 208	2 661	3 126	2 188	938	35.25

Note: Stages include neonate (Neo; TL ≤ 26 cm), immature male (ImmM; 26 cm < TL < 60 cm), immature female (ImmF; 26 cm < TL < 80 cm), mature male (MatM; TL < 60 cm), and mature female (MatF; TL ≥ 80 cm). $N_{OBS} = 0$ refers to the total number of zero observations. N is the number of observations for respective model. Tows is the overall percentage of tows where each dogfish stage was present (i.e., CPUE > 0).

*Depicts the number of observations after missing bottom temperatures were removed.

becomes (Zuur et al. 2009). Here, each predictor variable was divided a maximum of five times (defined by k) with each break spread evenly through its range (Wood 2006, 2011). A $k = 5$ was chosen based on expectations within explanatory variables and recommendations in the literature (Keele 2008; Zuur et al. 2009). In addition, each model formula included a "gamma = 1.4" to place a heavier penalty on each degree of freedom to counteract overfitting (Zuur et al. 2009; Wood 2011). The estimated smoothing parameters (i.e., estimated degrees of freedom) of the optimal model were chosen based on the lowest unbiased risk estimator score, an Akaike information criterion (AIC)-type statistic (Wood 2006, 2011).

Model selection

Because of the vast number of potential combinations of explanatory variables, GAMs were built in steps. The first submodel (abiotic) was a function of the temporal, spatial, and environmental variables, while the second submodel (biotic) was solely a function of ecological variables. Stepwise backward selection was implemented (Harrell 2001; Wintle et al. 2005), and the optimal submodel was chosen based on the lowest AIC (Fielding and Bell 1997; Pearce and 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, two-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. This combination was validated using tenfold 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) and through examination of the area under the receiver operating characteristic curve (AUC) solely for occurrence models (Hanley and 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 Team 2010) using the "gbm" package (Ridgeway 2010) supplemented with functions from Elith et al. (2008).

After submodel selection and identification of interactions, all main effects and interactions were combined into a single model. In situations where a variable was present as part of an interaction but was excluded from either submodel, 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 and variable combinations. Response curves were visually inspected for ecological realism (Wintle et al. 2005; Heinänen et al. 2008). The importance of each variable, and therefore its rank, was determined by estimating the magnitude of the smoothed function's range on the y axis.

Model evaluation

Unbiased estimates of each optimal model's predictive performance were obtained by evaluating a test dataset (Fielding and Bell 1997; Pearce and Ferrier 2000). PA models were tested for discrimination and accuracy in R (R Core Development Team 2010) using the packages "pROC" (Robin et al. 2011) and "Presence-Absence" (Freeman 2007), respectively, and for model behavior via bias using Bland–Altman plots (Bland and 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 and 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 and Altman 1986).

Validation of PRES models was assessed using typical model performance estimators, including calibration, correlations and mean error (Potts and Elith 2006; Heinänen et al. 2008), and Bland–Altman plots (Bland and 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 and

Table 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 (unit)	Type	Explanation
BFN (number·tow⁻¹)	Biotic	Relative abundance of *Peprilus triacanthus* captured per tow
HERN (number·tow⁻¹)	Biotic	Relative abundance of *Clupea harengus* captured per tow
ILLN (number·tow⁻¹)	Biotic	Relative abundance of *Illex* spp. captured per tow
DORN (number·tow⁻¹)	Biotic	Relative abundance of *Doryteuthis* spp. captured per tow
MACN (number·tow⁻¹)	Biotic	Relative abundance of *Scomber scombrus* captured per tow
Co	Biotic	Co-occurrence of specified stage (MatF, MatM; ImmF, ImmM): 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 (day)	Temporal	Julian day trawl was conducted
Region	Spatial	Georges Bank (GB), Gulf of Maine (GM), Southern New England (SNE), or Mid-Atlantic Bight (MA)

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 and 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 and Elith 2006). As misleading results are often obtained when relying solely on correlation coefficients (Bland and 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 in various temperature regimes

After documenting the importance of bottom temperature on the distributions of most stages, an a posteriori analysis was undertaken to investigate how temperature influenced the occurrence of spiny dogfish within the NES LME. A hypothetical dataset was created to mimic an annual survey ($n = 344$ stations) conducted during spring (Julian days 59–128) and autumn (Julian days 247–305). For each season, the frequency of daily tows conducted was determined from previous surveys trends, and the number of tows allocated to each Julian day was similar to past trends. For each hypothetical observation (i.e., station), average bottom temperature (BT_{avg}), depth, and zenith were assigned based on values averaged across all years for each Julian day (e.g., bottom temperatures for all stations conducted on Julian day 59 were set equal to the average bottom temperature across all years on Julian day 59).

Occurrence was predicted using optimal models identified in previous analyses. However, because of the uncertainty of how prey species would respond to the temperature changes, only the abiotic portion of the model was used. Different temperature scenarios were investigated by two bottom temperature variables, one to reflect a "warmer" than average year ($BT_{avg} + 1$ °C) and one a "cooler" than average year ($BT_{avg} - 1$ °C). Prediction maps were created by interpolating the predicted occurrence at hypothetical latitudes and longitudes based on the 2009 survey using inverse-distance weighted methods in the spatial analyst package extension of ArcMap (version 10, ESRI Corp).

Results

Data

Stations missing BT were excluded from all analyses. Occurrence and abundance of all dogfish stages were greater during spring compared with autumn (Table 1). During both seasons, immature females were present in the highest percentage of tows (autumn: 26.08%; spring: 37.74%) and neonates in the lowest percentage of tows (autumn: 1.22%; spring: 5.82%; Table 1).

Variable selection

Six biotic and six abiotic variables were available as candidate explanatory variables for describing occurrence and abundance of each dogfish stage based on perceived importance and data availability (Table 2). Julian day was selected to capture the seasonal track of the survey, which consistently runs from southerly latitudes to northerly latitudes. Intraspecific interactions were captured by the co-occurrence factor, which represented the presence or absence of the conspecific stage. For example, when modeling mature male distribution, co-occurrence was reflective of the presence or absence of mature female dogfish.

High correlations ($r > 0.6$) in both PA and PRES training datasets led to the exclusion of latitude and photosynthetically active radiation in all analyses. While depth and BT were occasionally highly correlated, both were retained because of 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. For prey species, the lowest GIC was displayed between neonates and herring during autumn (GIC = 0.22) and spring (GIC = 0.46) and between mature females and herring during spring (GIC = 0.46). For conspecifics, the lowest GIC was displayed between neonates and mature males during autumn (GIC = 0.26) and between neonates and mature females during spring (GIC = 0.61). 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). 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).

LIC

Locally, very little co-occurrence between spiny dogfish and prey species was observed during either season in contrast with higher co-occurrence of dogfish stages. LIC with prey species remained low during autumn for most predator–prey combinations and ranged from 0.01 (neonates with mackerel, mature females with *Illex* spp.) to 0.07 (females with *Doryteuthis* spp.). The lowest LIC was displayed between neonates and mature dogfish during autumn (LIC = 0.01) and between neonates and mature females during spring (LIC = 0.05). Compared with autumn, relatively higher LICs were observed with prey species during spring and ranged from 0.01 (neonates and immature males with herring) to 0.11 (all spiny dogfish combined with *Doryteuthis* spp.). The highest

LIC was observed for immature males and immature females during both autumn (LIC = 0.64) and spring (LIC = 0.69).

Statistical analysis

Model fitting and selection

General trends

During autumn, both PA and PRES models explained more deviance for mature dogfish and immature females compared with spring, whereas more error was explained during spring for immature males and neonates compared with autumn (Tables A1–A4). Deviance explained by PA models ranged from 53.0% for mature males to 21.8% for neonates during autumn (Tables A1–A2). For PRES models, deviance explained ranged from 59.0% for immature males during spring to 33.0% for neonates during autumn (Tables A3–A4). The addition of important two-way interactions identified by BRT analysis (see Sagarese 2013 for detailed results) reduced AIC values in both PA (range: 19–473) and PRES models (range: 78–467) and increased deviance explained during both autumn (PA: ≤5%, PRES: ≤18%) and spring (PA: ≤7%, PRES: ≤10%) (Tables A1–A4). While the addition of interactions to the neonate PRES model during autumn increased the AIC by 1 unit, they were retained because the deviance explained more than doubled.

PA models for all dogfish stages identified BT (Fig. 2), depth (Fig. 3), and (or) their interactions with region or the co-occurrence of the corresponding dogfish stage as highly influential during both seasons (Tables B1–B2). Temporal factors including year (Fig. 4), Julian day (Fig. 5), and (or) their interactions contributed greatly to mature male occurrence during autumn, immature female and neonate occurrence during autumn, and immature male and neonate occurrence during spring (Tables B1–B2). During autumn, Doryteuthis spp. abundance was also important to immature males, although the fitted smooth was not significant. PRES models also revealed an importance of depth, BT, and (or) their associated interactions for most dogfish stages during both seasons (Tables B3–B4). However, variable influence was more diverse within PRES models. During autumn, zenith (Fig. 6) was highly influential on the abundance of mature dogfish, temporal variables (i.e., Julian day, year) on all dogfish stages except neonates (Figs. 4–5), Doryteuthis spp. abundance (interacting with region) on mature females, and Illex spp. abundance (interacting with region) on neonates (Table B3). Prey species (and/or their interactions) frequently influenced abundance for most stages (Fig. 7). During spring, important variables were zenith for neonate abundance (Fig. 6), temporal (Julian day or year) for female dogfish (Figs. 4–5), and Illex spp. and Doryteuthis spp. abundances for mature females (Fig. 8).

During both seasons, the probabilities of occurrence and increasing abundance for all stages were influenced by abiotic and biotic factors and their interactions (Tables A1–A4). 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 and PRES models, region and (or) co-occurrence frequently interacted with environmental and (or) temporal variables. Unique to PRES models during autumn, the probability of increasing abundance for mature females and neonates was significantly influenced by regional interactions with prey abundances (Table B3). Many of the PA models displayed significant interactions between environmental and temporal variables during both autumn and spring (Tables B1–B2).

Environmental trends

Temperatures around 14 °C produced higher probabilities of occurrence for all dogfish stages except neonates during autumn but solely for immature males during spring (Fig. 2). For most dogfish stages, the probability of increasing abundance revealed significant relationships with temperature during both seasons (Fig. 2). Higher probabilities of both occurrence and increasing abundance were generally affiliated with specific depths for most dogfish stages during both autumn and spring (Fig. 3). Male dogfish generally possessed a greater probability of occurrence at low to moderate zenith angles during both seasons (Fig. 6). Higher probabilities of increasing abundance generally occurred at low zenith angles for many dogfish stages during both seasons.

Temporal trends

Many dogfish stages showed significantly higher probabilities of occurrence throughout the 1980s and (or) 2000s during autumn or spring (Fig. 4). In terms of increasing abundance, most dogfish stages displayed higher probabilities in the 2000s during autumn and throughout the 1980–1990s during spring. Significant nonlinear relationships with Julian day were frequently observed in both PA and PRES models during both seasons (Fig. 5).

Ecological trends

The importance of prey abundance was more pronounced in PRES models (Figs. 7–8) compared with PA models. Prey abundance occasionally influenced the probability of occurrence, whereas it frequently affected the probability of increasing abundance (Tables B1–B4). During autumn, herring and Doryteuthis spp. abundances influenced the occurrence of mature females and neonates and mature males, respectively, while PA models during spring revealed an importance of mackerel abundance to immature females and neonates, Doryteuthis spp. to immature males, and butterfish to neonates (Tables B1–B2). Multiple significant relationships concerning prey abundances were observed in PRES models for most dogfish stages during both autumn and spring.

Model evaluation

Generally, PA models displayed reasonable validation in terms of discrimination, calibration, and (or) bias (Table 3) and lacked autocorrelated and (or) spatially correlated residuals. In some instances, a 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). Most predicted probabilities of occurrence agreed with observed patterns (Figs. C1–C2) with the exception of neonates during both seasons.

The majority of PRES models also exhibited reasonable validation for most measures (Table 3) and displayed residuals lacking autocorrelation. However, some models did reveal contradictory agreement, poor calibration, moderate to strong bias (Table 3), and (or) spatial correlation in the form of slightly more frequent negative residuals throughout a specific region (autumn: MatF, ImmF; spring: MatF, MatM, ImmF). While some models underestimated the magnitude of abundance, most reasonably predicted where higher abundances were likely to occur (Figs. C3–C4) with the exception of neonates during autumn.

Forecasting of occurrence in various temperature regimes

Trends during spring revealed noticeable differences for all dogfish stages. Compared with 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 (Figs. 9a, D1). 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 (Figs. 9b, D1). 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. In contrast, occurrence trends were less pronounced during autumn (Fig. D2). During this season, mature dogfish and immature females were more likely to occur in the northern range

Fig. 2. Partial generalized additive model (GAM) plots identifying the additive effect of bottom temperature (°C) on the probabilities of occurrence (PA) and increasing abundance (PRES) for spiny dogfish life-history stages during autumn (Aut) and spring (Spr). Stages are as defined in Table 1. The *y* axis represents the degree of smoothing with its range indicative of the relative importance of the 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 because of a lack of data at the endpoints. Dashed lines reflect the 95% confidence intervals around response curves. Empty box indicates either lack of significance ($\alpha = 0.05$) or exclusion of that variable from the optimal model. Note that ranges on *x* and *y* axes differ among panels.
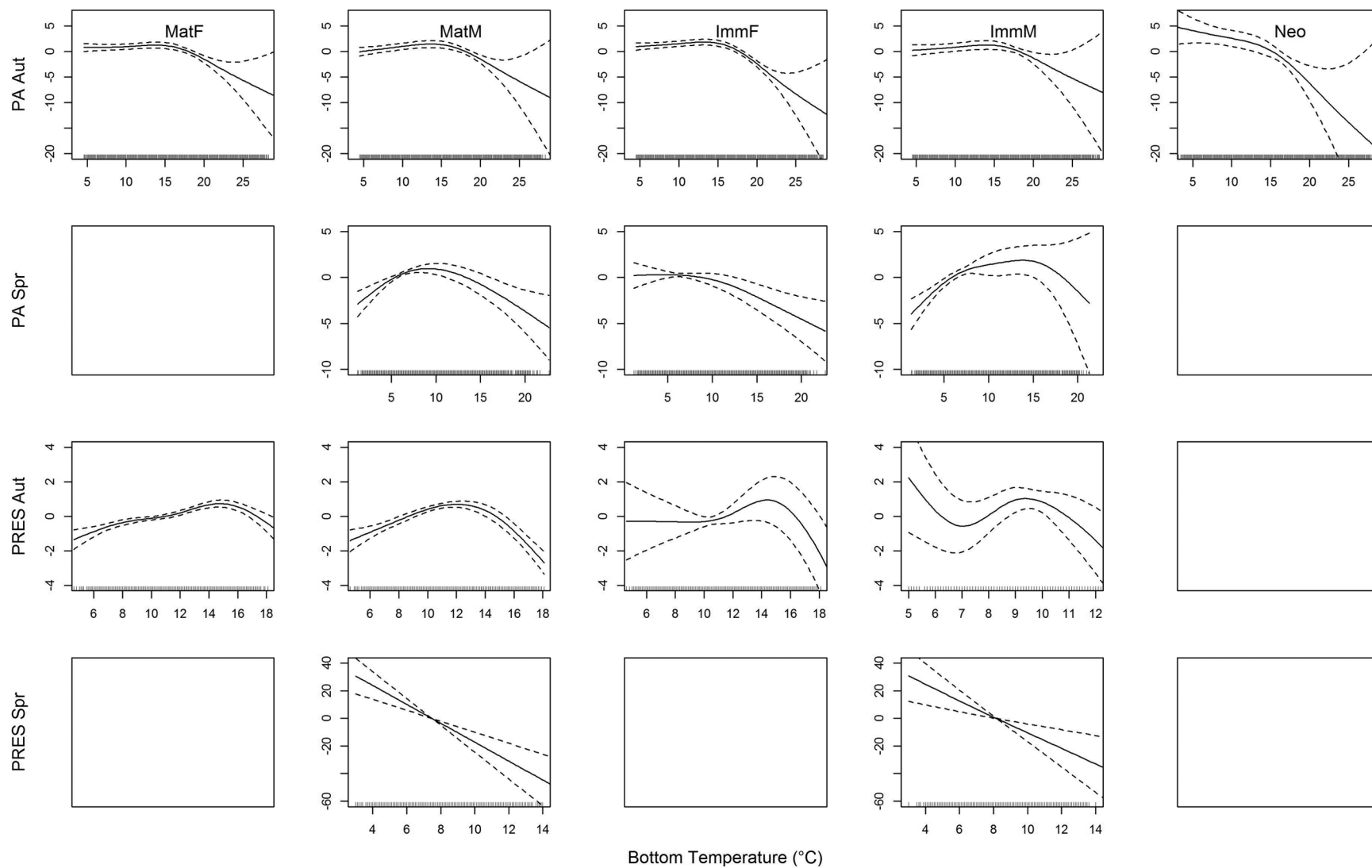
Fig. 3. Partial GAM plots identifying the additive effect of depth (m) on the probabilities of occurrence (PA) and increasing abundance (PRES) for spiny dogfish life-history stages during autumn (Aut) and spring (Spr). Stages are as defined in Table 1. Further details are given in Fig. 2 legend.
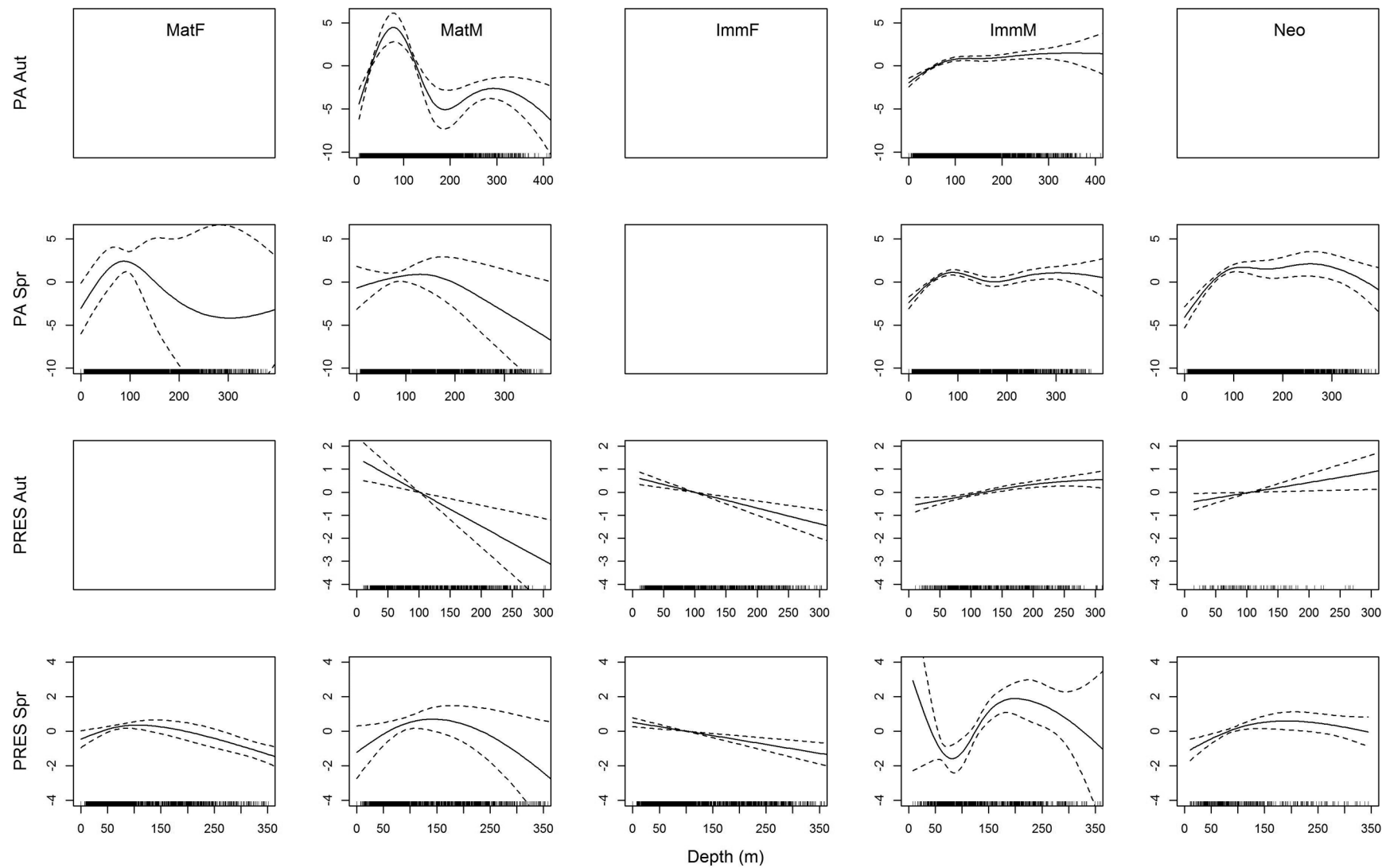
Fig. 4. Partial GAM plots identifying the additive effect of year on the probabilities of occurrence (PA) and increasing abundance (PRES) for spiny dogfish life-history stages during autumn (Aut) and spring (Spr). Stages are as defined in Table 1. Further details are given in Fig. 2 legend.
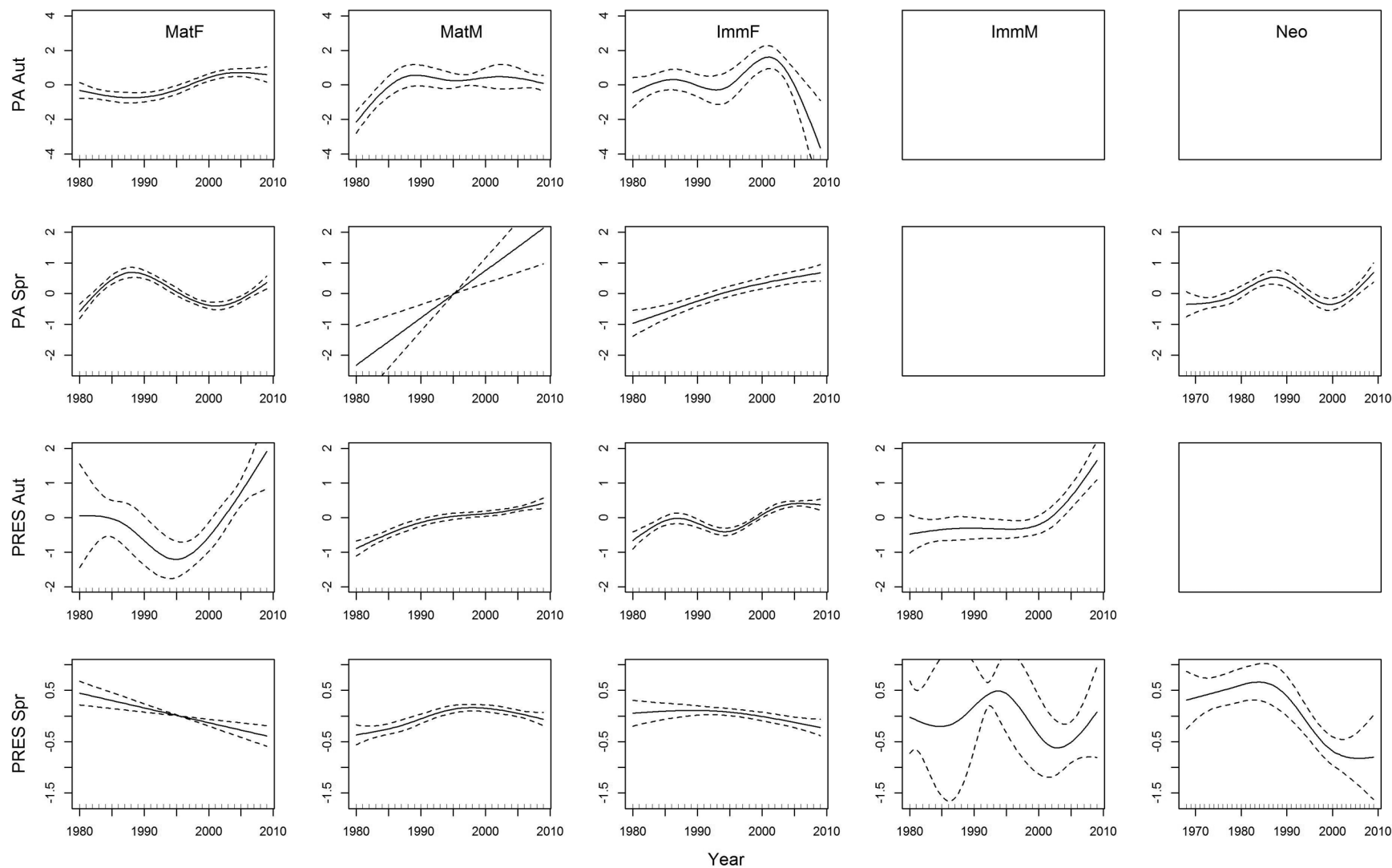
Fig. 5. Partial GAM plots identifying the additive effect of Julian day on the probabilities of occurrence (PA) and increasing abundance (PRES) for spiny dogfish life-history stages during autumn (Aut) and spring (Spr). Stages are as defined in Table 1. Further details are given in Fig. 2 legend.

Fig. 6. Partial GAM plots identifying the additive effect of zenith (°) on the probabilities of occurrence (PA) and increasing abundance (PRES) for spiny dogfish life-history stages during autumn (Aut) and spring (Spr). Stages are as defined in Table 1. Further details are given in Fig. 2 legend.
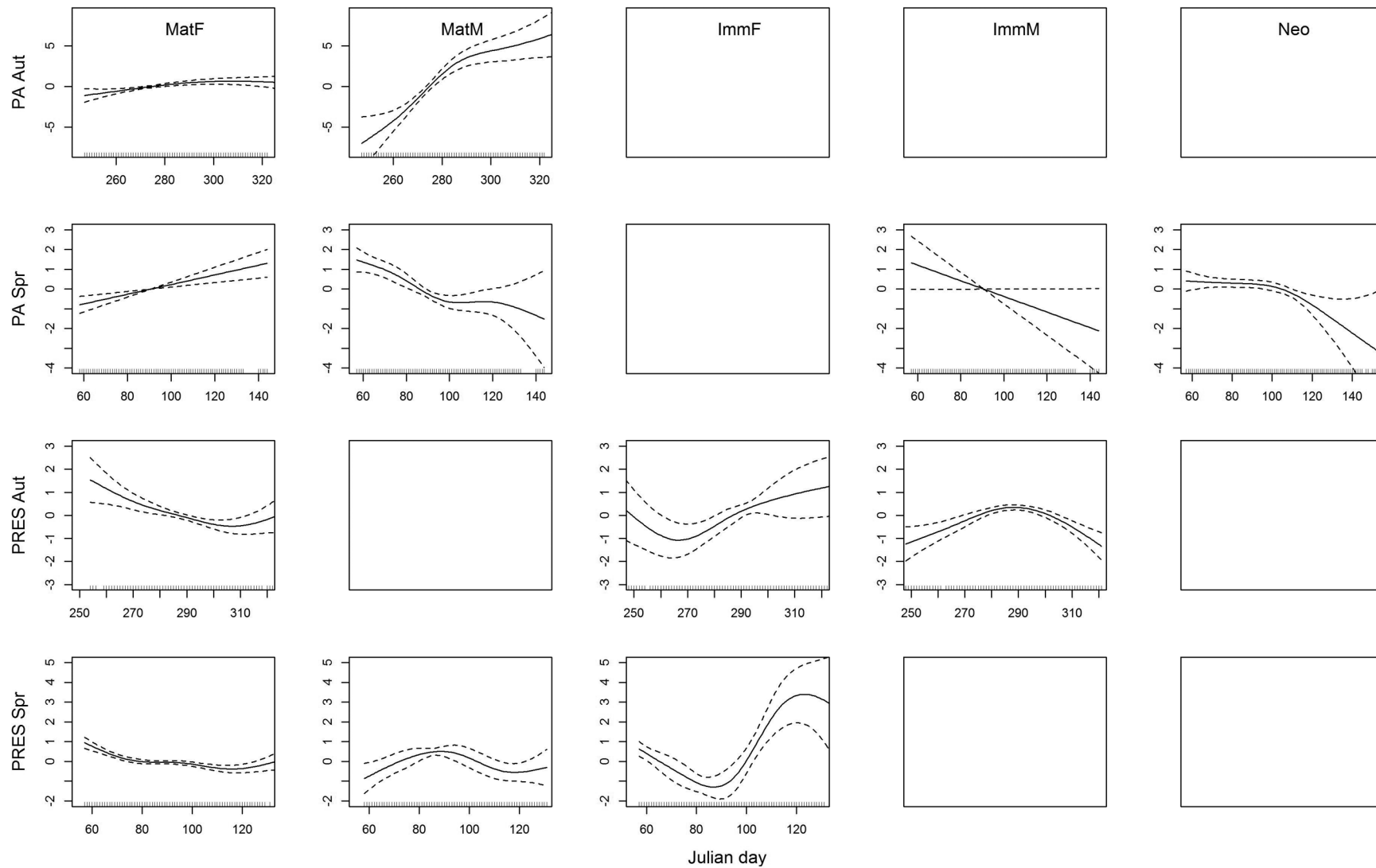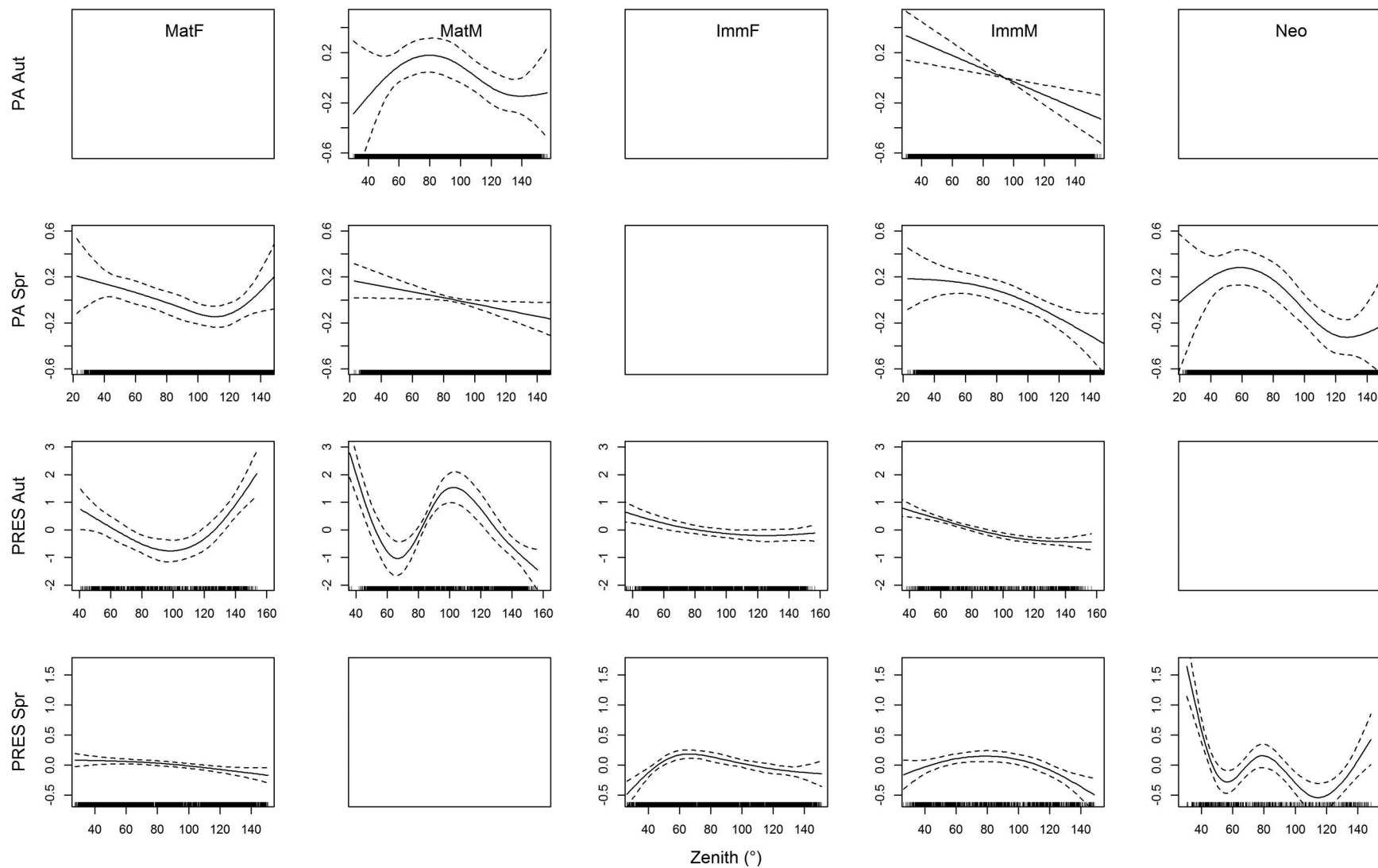
Fig. 7. Partial GAM plots identifying the additive effect of prey abundances (in numbers) on the probability of increasing abundance for spiny dogfish life-history stages during autumn. Stages and prey species are defined as in Tables 1 and 2, respectively. Further details are given in Fig. 2 legend. Note that neonate was excluded because of lack of significance or exclusion of variable from the optimal model.
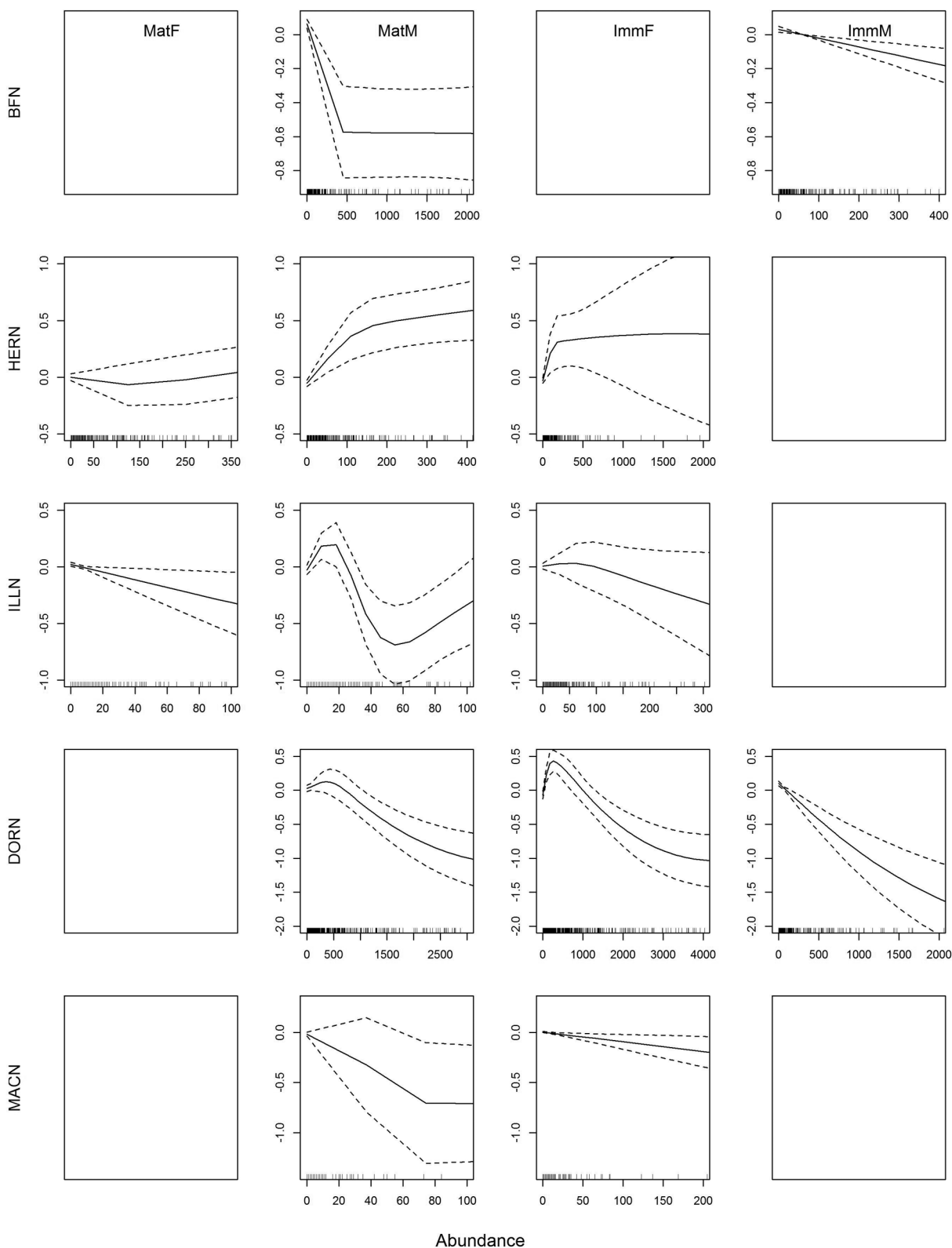
Fig. 8. Partial GAM plots identifying the additive effect of prey abundances (in numbers) on the probability of increasing abundance for spiny dogfish life-history stages during spring. Stages and prey species are defined as in Tables 1 and 2, respectively. Further details are given in Fig. 2 legend.
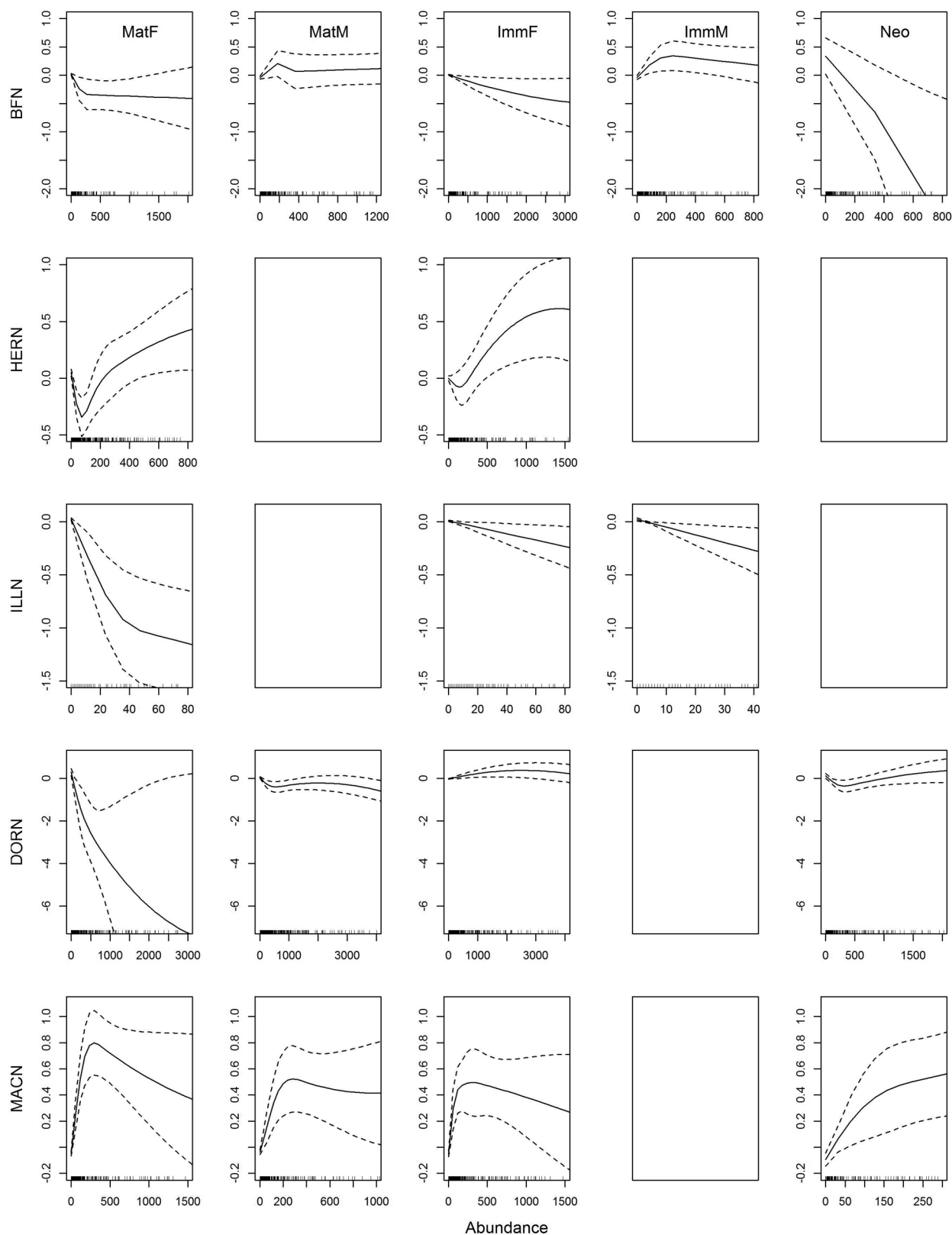
14

Can. J. Fish. Aquat. Sci. Vol. 71, 2014

Table 3. 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.

Stage	PA				PRES						
	AUC (%)	m	b	BA R^2	r	r_{sp}	m	b	RMSE	AVE	BA R^2
Autumn											
Neo	87.2±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±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±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±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±1.1	1.01	0.00	0.01 (+)	0.67	0.64	1.04	0.99	43.69	−1.72	0.54 (+)
Spring											
Neo	90.1±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±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±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±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±1.5	1.00	0.00	0.00 (+)	0.38	0.46	1.15	−1.35	64.33	−1.52	0.96 (+)

Note: Stages are as defined in Table 1. AUC = area under the receiver operating characteristic curve ± standard error; m = slope and b = y intercept of the fitted calibration line: observed = m(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.

during the warmer 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 and 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 and Garrison 2002). This study identified mechanisms behind the distribution of an understudied elasmobranch using a two-stage GAM. The utilization of 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.
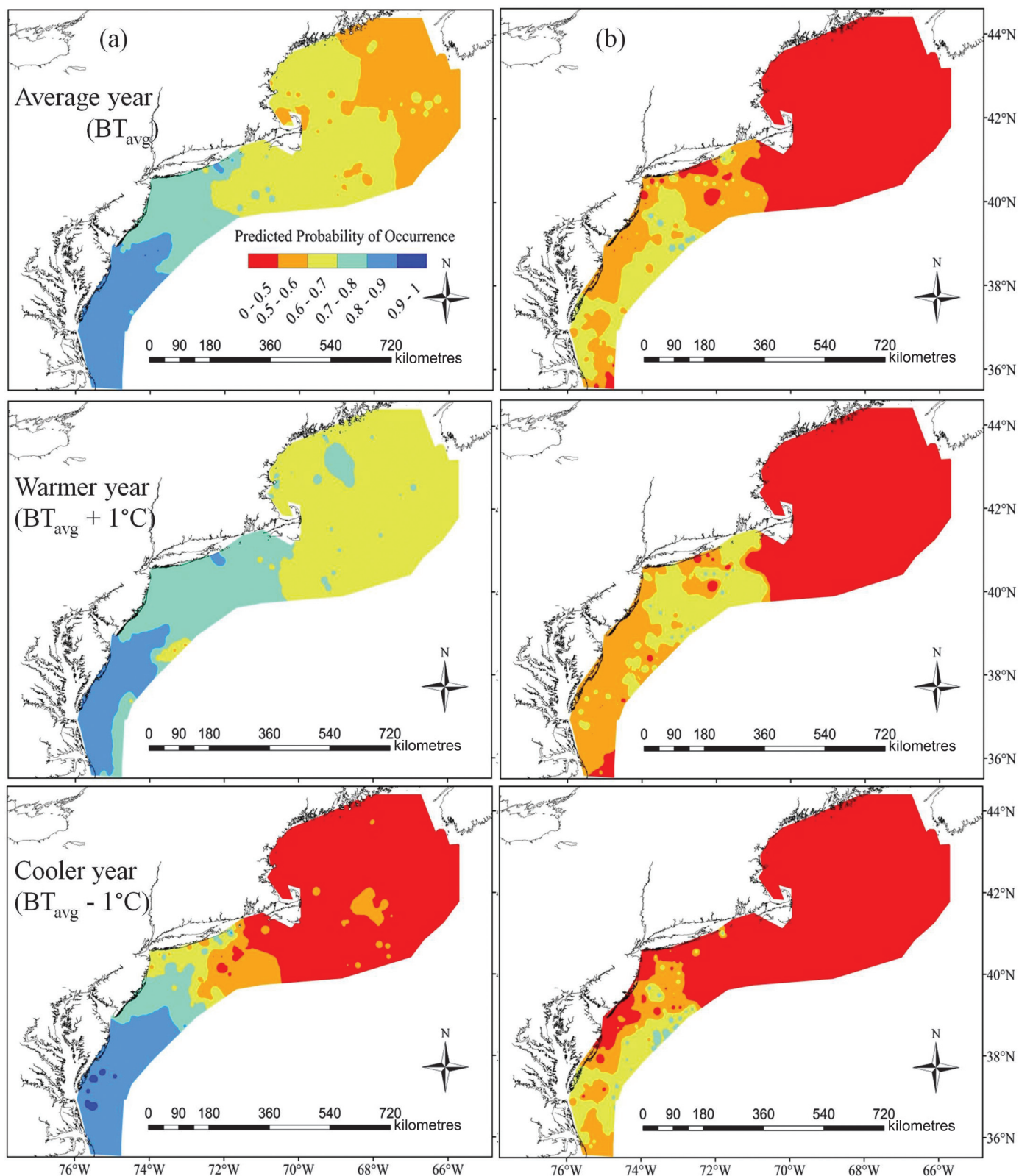
While two-stage GAMs have frequently been used to describe spatial distributions of commercially important fishes (Maravelias 1997; Bellido et al. 2001; Murase et al. 2009), this method also proved suitable for spiny dogfish showing that seasonal occurrence and abundance of most dogfish stages were driven by different processes. The importance of bottom temperature on occurrence during both seasons reinforced regional findings on the Scotian Shelf (Scott 1982; Shepherd et al. 2002) and Georges Bank – Gulf of Maine (Methratta and Link 2007), which suggested temperature was a migratory cue (Murawski and Finn 1988; Stehlik 2007). The strong temporal signal in occurrence estimated for younger dogfish and mature males may relate to the timing of movements that 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 as observed off the coast of Oregon (Brodeur et al. 2009), preferred habitat (e.g., Smith and Page 1996), 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 and Meadows 1964; Nammack et al. 1985; Jones and Ugland 2001) after an approximate 2-year gestation period (Hisaw and Albert 1947; Jones and Ugland 2001). During autumn, GAMs revealed a greater chance of encountering mature females around 240 m in SNE, a region that 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 and Ugland 2001), whereas those at greater depths may be pre- or postmated (Burgess 2002; Henderson et al. 2002) or searching for summer pupping grounds (Latham 1921; Hisaw and Albert 1947; Chatzispyrou and 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 and Sosebee 2009). In contrast the occurrence in the deep (~380 m) Mid-Atlantic Bight, which exceeds past preferred depth ranges (Jensen 1965), 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 (i) small immature males and females, (ii) medium-sized mature males or immature females, or (iii) large mature females (Jensen 1965). In the Gulf of Maine, greater probabilities of occurrence for mature dogfish and immature females during autumn support the theory that larger dogfish migrate northward during warmer

Fig. 9. Hypothetical predicted probability of (*a*) mature female and (*b*) 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 °C), and cooler (BT_{avg} − 1 °C) bottom temperatures. MA, Mid-Atlantic Bight; SNE, Southern New England; GB, Georges Bank; and GM, Gulf of Maine. Note that only the abiotic submodel was used for prediction because of uncertainty regarding how prey species would respond to temperature changes. (For the coloured version of this figure, refer to the Web site at http://www.nrcresearchpress.com/doi/full/10.1139/cjfas-2013-0342.)

16

Can. J. Fish. Aquat. Sci. Vol. 71, 2014

months (Hisaw and Albert 1947; Campana et al. 2007). In contrast, immature males and neonates were more likely encountered on Georges Bank and in SNE, respectively, corresponding to the findings of Methratta and Link (2007). During spring, more probable occurrence of females and neonates in the Mid-Atlantic Bight may be linked to parturition events, whereas the greater chance of encountering males on Georges Bank 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 that 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 that often aggregate together, co-occurrence may result from an overlap of resources between dogfish stages or enhanced protection from predators.

The perplexing behavior of spiny dogfish has attracted considerable skepticism regarding the utility of survey metrics to estimate population indices. Management of this resource is based on stock assessment models that assume survey abundance estimates reflect actual population trends (NEFSC 2006). Transboundary seasonal movements and highly variable interannual distribution and abundance trends contribute further to management uncertainty, particularly since an unknown portion of the population enters Canadian waters outside the NEFSC survey domain during autumn (Overholtz and Tyler 1985; Rago and 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. Usage of satellite tags may enable additional study of spiny dogfish distribution in relation to temperature.

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 Georges Bank, 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 because of small sample sizes, especially during autumn when neonates were rarely encountered. Future work should focus on neonate distribution, possibly through mid-water trawls to provide more accurate estimates of neonate abundance and recruitment potential.

Models displayed deviance and validation values comparable to, and in some cases better than, previous GAM studies (Bigelow et al. 1999; Cardinale and Arrhenius 2000; Feyrer et al. 2007); however, we were unable to remove weak residual patterns in about half of the occurrence and abundance models. Previous research has highlighted the need to understand predator–

prey dynamics in spring, justifying the added model complexity (Overholtz and 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 because of 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 recognizing these trends and 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 may 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.

Acknowledgements

References

Azarovitz, T.R. 1981. A brief historical review of the Woods Hole laboratory trawl survey time series. Can. Spec. Publ. Fish. Aquat. Sci. **58**: 62–67.

Azarovitz, T., Clark, S., Despres, L., and Byrne, C.J. 1997. The Northeast Fisheries Science Center bottom trawl survey program. ICES CM Doc No 1997/Y:33, Copenhagen, Denmark.

Bellido, J.M., Pierce, G.J., and Wang, J. 2001. Modelling intra-annual variation in abundance of squid *Loligo forbesi* in Scottish waters using generalised additive models. Fish. Res. **52**(1–2): 23–39. doi:10.1016/S0165-7836(01)00228-4.

Bez, N., and Rivoirard, J. 2000. Indices of collocation between populations. *In* Report of a workshop on the use of continuous underway fish egg sampler (CUFES) for mapping spawning habitat of pelagic fish. *Edited by* D.M. Checkley, J.R. Hunter, L. Motos, and C.D. von der Lingen. GLOBEC Rep. 14. pp. 48–52.

Bigelow, K.A., Boggs, C.H., and He, X. 1999. Environmental effects on swordfish and blue shark catch rates in the US North Pacific longline fishery. Fish. Oceanogr. **8**(3): 178–198. doi:10.1046/j.1365-2419.1999.00105.x.

Bland, J.M., and Altman, D.G. 1986. Statistical methods for assessing agreement between two methods of clinical measurement. Lancet, **327**(8476): 307–310. doi:10.1016/S0140-6736(86)90837-8.

Brander, K.M. 2007. Global fish production and climate change. Proc. Natl. Acad. Sci. U.S.A. **104**(50): 19709–19714. doi:10.1073/pnas.0702059104. PMID:18077405.

Brodeur, R.D., Fleming, I.A., Bennett, J.M., and Campbell, M.A. 2009. Summer distribution and feeding of spiny dogfish off the Washington and Oregon coasts. *In* Biology and management of dogfish sharks. *Edited by* V.F. Gallucci, G.A. McFarlane, and G.G. Bargmann. American Fisheries Society, Bethesda, Md. pp. 39–51.

Brotons, L., Thuiller, W., Araújo, M.B., and Hirzel, A.H. 2004. Presence–absence

versus presence-only modelling methods for predicting bird habitat suitability. Ecography, 27(4): 437–448. doi:10.1111/j.0906-7590.2004.03764.x.

Brown, R.W., Fogarty, M., Legault, C., Miller, T., Nordahl, V., Politis, P., and Rago, P. 2007. Survey transition and calibration of bottom trawl surveys along the Northeastern Continental Shelf of the United States. ICES CM Doc No 2007/Q:20, Copenhagen, Denmark.

Burgess, G.H. 2002. Spiny dogfishes: Family Squalidae. In Bigelow and Schroeder's fishes of the Gulf of Maine. 3rd ed. Edited by B.B. Collette and G. Klein-MacPhee. Smithsonian Institution Press, Washington, D.C. pp. 48–57.

Campana, S.E., and Joyce, W.N. 2004. Temperature and depth associations of porbeagle shark (Lamna nasus) in the northwest Atlantic. Fish. Oceanogr. 13(1): 52–64. doi:10.1111/j.1365-2419.2004.00236.x.

Campana, S.E., Gibson, A.J.F., Marks, L., Joyce, W., Rulifson, R., and Dadswell, M. 2007. Stock structure, life history, fishery and abundance indices for spiny dogfish (Squalus acanthias) in Atlantic Canada. DFO Can. Sci. Advis. Sec. Res. Doc. 2007/089.

Cardinale, M., and Arrhenius, F. 2000. The influence of stock structure and environmental conditions on the recruitment process of Baltic cod estimated using a generalized additive model. Can. J. Fish. Aquat. Sci. 57(12): 2402–2409. doi:10.1139/f00-221.

Chatzispyrou, A., and Megalofonou, P. 2005. Sexual maturity, fecundity and embryonic development of the spiny dogfish, Squalus acanthias, in the eastern Mediterranean Sea. J. Mar. Biol. Assoc. U.K. 85(05): 1155–1161. doi:10.1017/S0025315405012233.

Cortés, F., Jaureguizar, A.J., Menni, R.C., and Guerrero, R.A. 2011. Ontogenetic habitat preferences of the narrownose smooth-hound shark, Mustelus schmitti, in two Southwestern Atlantic coastal areas. Hydrobiologia, 661(1): 445–456. doi:10.1007/s10750-010-0559-2.

Damalas, D., Maravelias, C.D., Katsanevakis, S., Karageorgis, A.P., and Papaconstantinou, C. 2010. Seasonal abundance of non-commercial demersal fish in the eastern Mediterranean Sea in relation to hydrographic and sediment characteristics. Estuar. Coast. Shelf Sci. 89(1): 107–118. doi:10.1016/j.ecss.2010.06.002.

De'ath, G. 2007. Boosted trees for ecological modeling and prediction. Ecology, 88(1): 243–251. doi:10.1890/0012-9658(2007)88[243:BTFEMA]2.0.CO;2. PMID:17489472.

Denis, V., Lejeune, J., and Robin, J.P. 2002. Spatio-temporal analysis of commercial trawler data using general additive models: patterns of loliginid squid abundance in the north-east Atlantic. ICES J. Mar. Sci. 59(3): 633–648. doi:10.1006/jmsc.2001.1178.

Elith, J., Leathwick, J.R., and Hastie, T. 2008. A working guide to boosted regression trees. J. Anim. Ecol. 77(4): 802–813. doi:10.1111/j.1365-2656.2008.01390.x. PMID:18397250.

Faraway, J.J. 2006. Extending the linear model with R: generalized linear, mixed effects, and nonparametric regression models. Chapman & Hall/CRC, Boca Raton, Fla.

Fewster, R.M., Buckland, S.T., Siriwardena, G.M., Baillie, S.R., and Wilson, J.D. 2000. Analysis of population trends for farmland birds using generalized additive models. Ecology, 81(7): 1970–1984. doi:10.1890/0012-9658(2000)081[1970:AOPTFF]2.0.CO;2.

Feyrer, F., Nobriga, M.L., and Sommer, T.R. 2007. Multidecadal trends for three declining fish species: habitat patterns and mechanisms in the San Francisco Estuary, California, USA. Can. J. Fish. Aquat. Sci. 64(4): 723–734. doi:10.1139/f07-048.

Fielding, A.H., and Bell, J.F. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ. Conserv. 24(1): 38–49. doi:10.1017/S0376892997000088.

Fogarty, M.J., and Murawski, S.A. 1998. Large-scale disturbance and the structure of marine systems: fishery impacts on Georges Bank. Ecol. Appl. 8: S6–S22. doi:10.1890/1051-0761(1998)8[S6:LDATSO]2.0.CO;2.

Freeman, E. 2007. PresenceAbsence: An R package for presence-absence model evaluation. USDA Forest Service, Rocky Mountain Research Station, Ogden, Utah.

Frisk, M.G., Miller, T.J., and Dulvy, N.K. 2005. Life histories and vulnerability to exploitation of elasmobranchs: inferences from elasticity, perturbation and phylogenetic analyses. J. Northwest Atl. Fish. Sci. 35: 27–45. doi:10.2960/J.v35.m514.

Frisk, M.G., Miller, T.J., Martell, S.J.D., and Sosebee, K. 2008. New hypothesis helps explain elasmobranch "outburst" on Georges Bank in the 1980s. Ecol. Appl. 18(1): 234–245. doi:10.1890/06-1392.1. PMID:18372569.

Frisk, M.G., Duplisea, D.E., and Trenkel, V.M. 2011. Exploring the abundance-occupancy relationships for the Georges Bank finfish and shellfish community from 1963 to 2006. Ecol. Appl. 21(1): 227–240. doi:10.1890/09-1698.1. PMID:21516900.

Froeschke, J., Stunz, G.W., and Wildhaber, M.L. 2010. Environmental influences on the occurrence of coastal sharks in estuarine waters. Mar. Ecol. Prog. Ser. 407: 279–292. doi:10.3354/meps08546.

Gotway, C.A., and Stroup, W.W. 1997. A generalized linear model approach to spatial data analysis and prediction. J. Agricult. Biol. Environ. Stat. 2(2): 157–178. doi:10.2307/1400401.

Guisan, A., Edwards, T.C., and Hastie, T. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecol. Model. 157(2–3): 89–100. doi:10.1016/S0304-3800(02)00204-1.

Hanley, J.A., and McNeil, B.J. 1982. The meaning and use of the area under a receiver operating characteristic (ROC) curve. Radiology, 143: 29–36. PMID:7063747.

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

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

Hedger, R., McKenzie, E., Heath, M., Wright, P., Scott, B., Gallego, A., and Andrews, J. 2004. Analysis of the spatial distributions of mature cod (Gadus morhua) and haddock (Melanogrammus aeglefinus) abundance in the North Sea (1980–1999) using generalised additive models. Fish. Res. 70(1): 17–25. doi:10.1016/j.fishres.2004.07.002.

Heinänen, S., Rönkä, M., and Von Numers, M. 2008. Modelling the occurrence and abundance of a colonial species, the arctic tern Sterna paradisaea in the archipelago of SW Finland. Ecography, 31(5): 601–611. doi:10.1111/j.0906-7590.2008.05410.x.

Henderson, A.C., Flannery, K., and Dunne, J. 2002. Growth and reproduction in spiny dogfish Squalus acanthias L. (Elasmobranchii: Squalidae), from the west coast of Ireland. Sarsia, 87(5): 350–361. doi:10.1080/0036482021000155805.

Hisaw, F.L., and Albert, A. 1947. Observations on the reproduction of the spiny dogfish, Squalus acanthias. Biol. Bull. 92(3): 187–199. doi:10.2307/1538305. PMID:20249523.

Holden, M.J., and Meadows, P.S. 1964. The fecundity of the spurdog (Squalus acanthias L.). J. Cons. Int. Explor. Mer. 28(3): 418–424. doi:10.1093/icesjms/28.3.418.

Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., and Warner, R.R. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science, 293(5530): 629–637. doi:10.1126/science.1059199. PMID:11474098.

Jensen, A.C. 1965. Life history of the spiny dogfish. Fish. Bull. 65(3): 527–554.

Jones, T.S., and Ugland, K.I. 2001. Reproduction of female spiny dogfish, Squalus acanthias, in the Oslofjord. Fish. Bull. 99(4): 685–690.

Keele, L.J. 2008. Semiparametric regression for the social sciences. John Wiley & Sons Ltd., Chichester.

Latham, R. 1921. 1920 fish records from Orient, Long Island. Copeia, 1921(99): 72–73. doi:10.2307/1436984.

Leathwick, J.R., Elith, J., and Hastie, T. 2006. Comparative performance of generalized additive models and multivariate adaptive regression splines for statistical modelling of species distributions. Ecol. Model. 199(2): 188–196. doi:10.1016/j.ecolmodel.2006.05.022.

Leathwick, J.R., Elith, J., Chadderton, W.L., Rowe, D., and Hastie, T. 2008. Dispersal, disturbance and the contrasting biogeographies of New Zealand's diadromous and non-diadromous fish species. J. Biogeogr. 35(8): 1481–1497. doi:10.1111/j.1365-2699.2008.01887.x.

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

Link, J.S., and Ford, M.D. 2006. Widespread and persistent increase of Ctenophora in the continental shelf ecosystem off NE USA. Mar. Ecol. Prog. Ser. 320: 153–159. doi:10.3354/meps320153.

Link, J.S., and Garrison, L.P. 2002. Changes in piscivory associated with fishing induced changes to the finfish community on Georges Bank. Fish. Res. 55(1–3): 71–86. doi:10.1016/S0165-7836(01)00300-9.

Link, J.S., Bundy, A., Overholtz, W.J., Shackell, N., Manderson, J., Duplisea, D., Hare, J., Koen-Alonso, M., and Friedland, K. 2011. Northwest Atlantic ecosystem-based management for fisheries. In Ecosystem-based management for marine fisheries: an evolving perspective. Edited by A. Belgrano and C.W. Fowler. Cambridge University Press, New York. pp. 32–112.

Macpherson, E., and Duarte, C.M. 1991. Bathymetric trends in demersal fish size: is there a general relationship? Mar. Ecol. Prog. Ser. 71: 103–112. doi:10.3354/meps071103.

Maravelias, C.D. 1997. Trends in abundance and geographic distribution of North Sea herring in relation to environmental factors. Mar. Ecol. Prog. Ser. 159: 151–164. doi:10.3354/meps159151.

Martin, T.G., Wintle, B.A., Rhodes, J.R., Kuhnert, P.M., Field, S.A., Low-Choy, S.J., Tyre, A.J., and Possingham, H.P. 2005. Zero tolerance ecology: improving ecological inference by modelling the source of zero observations. Ecol. Lett. 8(11): 1235–1246. doi:10.1111/j.1461-0248.2005.00826.x. PMID:21352447.

Methratta, E.T., and Link, J.S. 2007. Ontogenetic variation in habitat association for four groundfish species in the Gulf of Maine – Georges Bank region. Mar. Ecol. Prog. Ser. 338: 169–181. doi:10.3354/meps338169.

Miller, J., and Franklin, J. 2002. Modeling the distribution of four vegetation alliances using generalized linear models and classification trees with spatial dependence. Ecol. Model. 157(2–3): 227–247. doi:10.1016/S0304-3800(02)00196-5.

Miller, T.J., Das, C., Politis, P.J., Miller, A.S., Lucey, S.M., Legault, C.M., Brown, R.W., and Rago, P.J. 2010. Estimation of Albatross IV to Henry B. Bigelow calibration factors. NEFSC Ref Doc 10-05. Available from National Marine Fisheries Service, 166 Water Street, Woods Hole, MA 02543-1026, USA.

Murase, H., Nagashima, H., Yonezaki, S., Matsukura, R., and Kitakado, T. 2009.

Pagination not final (cite DOI) / Pagination provisoire (citer le DOI)

18

Can. J. Fish. Aquat. Sci. Vol. 71, 2014

Application of a generalized additive model (GAM) to reveal relationships between environmental factors and distributions of pelagic fish and krill: a case study in Sendai Bay, Japan. ICES J. Mar. Sci. 66(6): 1417–1424. doi:10.1093/icesjms/fsp105.

Murawski, S.A. 1991. Can we manage our multispecies fisheries? Fisheries, 16(5): 5–13. doi:10.1577/1548-8446(1991)016<0005:CWMOMF>2.0.CO;2.

Murawski, S.A., and Finn, J.T. 1988. Biological bases for mixed-species fisheries: species co-distribution in relation to environmental and biotic variables. Can. J. Fish. Aquat. Sci. 45(10): 1720–1735. doi:10.1139/f88-204.

Nammack, M.F., Musick, J.A., and Colvocoresses, J.A. 1985. Life history of spiny dogfish off the Northeastern United States. Trans. Am. Fish. Soc. 114(3): 367–376. doi:10.1577/1548-8659(1985)114<367:LHOSDO>2.0.CO;2.

NEFSC. 1994. Report of the 18th Northeast Regional Stock Assessment Workshop (18th SAW). The plenary. NEFSC Ref. Doc. 94-23, Woods Hole, Mass.

NEFSC. 2006. 43rd Northeast Regional Stock Assessment Workshop (43rd SAW): 43rd SAW assessment report. US Dep. Commer. Northeast Fish. Sci. Cent. Ref. Doc. 06-25, Woods Hole, Mass.

Nye, J.A., Link, J.S., Hare, J.A., and Overholtz, W.J. 2009. Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. Mar. Ecol. Prog. Ser. 393: 111–129. doi:10.3354/meps08220.

O'Brien, L., and Rago, P. 1996. An application of the generalized additive model to groundfish survey data with Atlantic Cod off the Northeast Coast of the United States as an example. Northwest Atl. Fish. Organ. Sci. Counc. Stud. 28: 79–95.

Overholtz, W.J., and Tyler, A.V. 1985. Long-term responses of the demersal fish assemblages of Georges Bank. Fish. Bull. 83(4): 507–520.

Pearce, J., and Ferrier, S. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. Ecol. Model. 133(3): 225–245. doi:10.1016/S0304-3800(00)00322-7.

Perry, A.L., Low, P.J., Ellis, J.R., and Reynolds, J.D. 2005. Climate change and distribution shifts in marine fishes. Science, 308(5730): 1912–1915. doi:10.1126/science.1111322. PMID:15890845.

Perry, R.I., and Smith, S.J. 1994. Identifying habitat associations of marine fishes using survey data: an application to the Northwest Atlantic. Can. J. Fish. Aquat. Sci. 51(3): 589–602. doi:10.1139/f94-061.

Pikitch, E.K., Santora, C., Babcock, E.A., Bakun, A., Bonfil, R., Conover, D.O., Dayton, P., Doukakis, P., Fluharty, D., Heneman, B., Houde, E.D., Link, J., Livingston, P.A., Mangel, M., McAllister, M.K., Pope, J., and Sainsbury, K.J. 2004. Ecosystem-based fishery management. Science, 305(5682): 346–347. doi:10.1126/science.1098222.

Potts, J.M., and Elith, J. 2006. Comparing species abundance models. Ecol. Model. 199(2): 153–163. doi:10.1016/j.ecolmodel.2006.05.025.

R Core Development Team. 2010. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rago, P.J., and Sosebee, K.A. 2009. The agony of recovery: scientific challenges of spiny dogfish recovery programs. In Biology and management of dogfish sharks. Edited by V.F. Gallucci, G.A. McFarlane, and G.G. Bargmann. American Fisheries Society, Bethesda, Md. pp. 343–372.

Rago, P.J., Sosebee, K.A., Brodziak, J.K.T., Murawski, S.A., and Anderson, E.D. 1998. Implications of recent increases in catches on the dynamics of Northwest Atlantic spiny dogfish (Squalus acanthias). Fish. Res. 39(2): 165–181. doi:10.1016/S0165-7836(98)00181-7.

Renka, R.J., Gebhardt, A., Eglen, S., Zuyev, S., and White, D. 2009. tripack: triangulation of irregularly spaced data [online]. Available from http://cran.r-project.org/web/packages/tripack/index.html.

Ridgeway, G. 2010. gbm: generalized boosted regression models [online]. Available from http://cran.r-project.org/web/packages/gbm/index.html.

Robin, X., Turck, N., Hainard, A., Tiberti, N., Lisacek, F., Sanchez, J., and Müller, M. 2011. pROC: an open-source package for R and S+ to analyze and compare ROC curves. BMC Bioinform. 12: 77. doi:10.1186/1471-2105-12-77.

Sagarese, S.R. 2013. The population ecology of the spiny dogfish in the Northeast (US) shelf large marine ecosystem: implications for the status of the stock. Ph.D. dissertation, Stony Brook University, Stony Brook, N.Y.

Scott, J.S. 1982. Depth, temperature and salinity preferences of common fishes of the Scotian Shelf. J. Northwest Atl. Fish. Sci. 3: 29–39. doi:10.2960/J.v3.a2.

Shepherd, T., Page, F., and Macdonald, B. 2002. Length and sex-specific associations between spiny dogfish (Squalus acanthias) and hydrographic variables in the Bay of Fundy and Scotian Shelf. Fish. Oceanogr. 11(2): 78–89. doi:10.1046/j.1365-2419.2002.00191.x.

Smith, S.J., and Page, F.H. 1996. Associations between Atlantic cod (Gadus morhua) and hydrographic variables: implications for the management of the 4VsW cod stock. ICES J. Mar. Sci. 53(3): 597–614. doi:10.1006/jmsc.1996.0081.

Sosebee, K.A. 2005. Are density-dependent effects on elasmobranch maturity possible? J. Northwest Atl. Fish. Sci. 35: 115–124. doi:10.2960/J.v35.m492.

Stehlik, L.L. 2007. Essential fish habitat source document: spiny dogfish, Squalus acanthias, life history and habitat characteristics. 2nd ed. NOAA Tech Memo NMFS-NE-203, Woods Hole, Mass.

Stenberg, C. 2005. Life history of the piked dogfish (Squalus acanthias L.) in Swedish waters. J. Northwest Atl. Fish. Sci. 35: 155–164. doi:10.2960/J.v35.m525.

Stoner, A.W., Manderson, J.P., and Pessutti, J.P. 2001. Spatially explicit analysis of estuarine habitat for juvenile winter flounder: combining generalized additive models and geographic information systems. Mar. Ecol. Prog. Ser. 213: 253–271. doi:10.3354/meps213253.

Swets, J.A. 1988. Measuring the accuracy of diagnostic systems. Science, 240(4857): 1285–1293. doi:10.1126/science.3287615. PMID:3287615.

Welsh, A.H., Cunningham, R.B., Donnelly, C.F., and Lindenmayer, D.B. 1996. Modelling the abundance of rare species: statistical models for counts with extra zeros. Ecol. Model. 88: 297–308. doi:10.1016/0304-3800(95)00113-1.

Wintle, B.A., Elith, J., and Potts, J.M. 2005. Fauna habitat modelling and mapping: a review and case study in the Lower Hunter Central Coast region of NSW. Austral Ecol. 30(7): 719–738. doi:10.1111/j.1442-9993.2005.01514.x.

Wood, S.N. 2006. Generalized Additive Models: an Introduction with R. Chapman & Hall/CRC, Boca Raton, Fla.

Wood, S.N. 2011. Package 'mgcv'. [online]. Available from http://cran.r-project.org/web/packages/mgcv/index.html.

Yee, T.W., and Mitchell, N.D. 1991. Generalized additive models in plant ecology. J. Veg. Sci. 2(5): 587–602. doi:10.2307/3236170.

Zuur, A.F. 2010. AED: Data files used in mixed effects models and extensions in ecology with R. [Information and replacement coding can be found at http://www.highstat.com/book2.htm.]

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

Appendices A–D appear on the following pages.

Appendix A. Model selection

Table A1. Model selection for occurrence (PA) of spiny dogfish life-history stages during autumn (1963–2009).

Stage	Submodel	Optimal (sub) model	Dev (%)	AIC
MatF	A	PA ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region	37.9	3 376
	B	PA ~ s(HERN) + s(ILLN) + s(DORN) + s(MACN) + Co	37.7	3 378
	A + B	PA ~ A + s(DORN) + s(MACN) + Co	50.4	2 709
	Overall	PA ~ A + s(HERN) + s(DORN) + s(MACN) + Co + te(Zenith,Co) + te(Depth,Region) + te(Depth,Co) + te(Year,Co) + te(Julian,Depth)	52.1	2 645
MatM	A	PA ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region	38.1	4 145
	B	PA ~ s(BFN) + s(HERN) + s(ILLN) + s(DORN) + Co	33.5	4 436
	A + B	PA ~ A + B	48.5	3 473
	Overall	PA ~ A + B + te(Julian,Depth) + te(Depth,Year) + te(Julian,Co) + te(Year,Region)	53.0	3 206
ImmF	A	PA ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region	26.1	5 206
	B	PA ~ s(BFN) + s(HERN) + s(DORN) + s(MACN) + Co	21.9	5 502
	A + B	PA ~ s(Year) + s(Depth) + s(BT) + s(Julian) + Region + s(HERN) + s(MACN) + Co	40.8	4 186
	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	4 045
ImmM	A	PA ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region	16.3	3 898
	B	PA ~ s(ILLN) + s(DORN) + Co	31.7	3 167
	A + B	PA ~ A + s(DORN) + Co	38.9	2 854
	Overall	PA ~ A + s(DORN) + Co + te(Year,Co) + te(Depth,Co) + te(Julian,Co) + te(BT,Co)	39.7	2 835
Neo	A	PA ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region	15.2	1 215
	B	PA ~ s(BFN) + s(DORN) + s(ILLN) + s(HERN)	4.6	1 348
	A + B	PA ~ A + s(BFN) + s(DORN) + s(HERN)	16.8	1 205
	Overall	PA ~ A + s(BFN) + s(DORN) + s(HERN) + te(Year,Region) + te(Zenith,Year) + te(BFN,BT) + te(Depth,Year)	21.8	1 152

Note: A = optimal submodel consisting of abiotic main effects; B = optimal submodel consisting of biotic main effects; A + B = optimal submodel 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; s = cubic regression spline smooth; te = tensor product smooth; Dev = percent deviance explained; AIC = Akaike's information criterion. Spiny dogfish were not sexed consistently until 1980.

Table A2. Model selection for occurrence (PA) of spiny dogfish life-history stages during spring (1968–2009).

Stage	Submodel	Optimal (sub) model	Dev (%)	AIC
MatF	A	PA ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region	18.4	6 588
	B	PA ~ s(DORN) + s(MACN) + Co	18.4	6 563
	A + B	PA ~ A + B	28.2	5 802
	Overall	PA ~ A + B + te(BT,Depth) + te(Depth,Region) + te(Julian,Depth) + te(BT,Region)	32.4	5 520
MatM	A	PA ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region	26.3	5 725
	B	PA ~ s(BFN) + s(DORN) + s(MACN) + Co	19.3	6 248
	A + B	PA ~ A + B	36.1	4 981
	Overall	PA ~ A + s(BFN) + s(DORN) + Co + te(Julian,Year) + te(BT,Depth) + te(Depth,Region) + te(Depth,Year)	43.0	4 508
ImmF	A	PA ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region	23.8	6 315
	B	PA ~ s(BFN) + s(MACN) + Co	19.3	6 661
	A + B	PA ~ s(Year) + s(Depth) + s(BT) + s(Julian) + Region + s(MACN) + Co	33.4	5 523
	Overall	PA ~ s(Year) + s(Depth) + s(BT) + s(Julian) + Region + s(MACN) + Co + te(Julian,Depth) + te(BT,Depth) + te(Depth,Co) + te(Depth,Region) + te(Depth,Year)	37.9	5 222
ImmM	A	PA ~ s(Year) + s(Depth) + s(BT) + s(Zenith) + Region	27.9	4 002
	B	PA ~ s(BFN) + s(ILLN) + s(DORN) + Co	29.6	3 901
	A + B	PA ~ A + s(BFN) + s(DORN) + Co	44.2	3 116
	Overall	PA ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region + s(BFN) + s(DORN) + Co + te(Depth,Co) + te(Year,Co) + te(BT,Co) + te(Julian,BT)	46.1	3 043
Neo	A	PA ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region	30.5	2 825
	B	PA ~ s(BFN) + s(DORN) + s(ILLN) + s(MACN)	12.7	3 529
	A + B	PA ~ A + s(BFN) + s(DORN) + s(MACN)	31.3	2 807
	Overall	PA ~ A + s(BFN) + s(DORN) + s(MACN) + te(DORN,BT) + te(BT,Depth) + te(DORN,Depth) + te(BT,Region)	34.3	2 706

Note: A = optimal submodel consisting of abiotic main effects; B = optimal submodel consisting of biotic main effects; A + B = optimal submodel 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; s = cubic regression spline smooth; te = tensor product smooth; Dev = percent deviance explained; AIC = Akaike's information criterion. Spiny dogfish were not sexed consistently until 1980.

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20

Can. J. Fish. Aquat. Sci. Vol. 71, 2014

Table A3. Model selection for abundance (PRES) of spiny dogfish life-history stages during autumn (1963–2009).

Stage	Submodel	Optimal (sub) model	Dev (%)	AIC
MatF	A	PRES ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region	40.4	7 406
	B	PRES ~ s(HERN) + s(ILLN) + s(DORN) + Co	26.6	7 835
	A + B	PRES ~ A + B	48.4	7 167
	Overall	PRES ~ A + B + te(Zenith,Depth) + te(Zenith,Year) + te(Julian,Year) + te(DORN,Region) + te(Depth,Co)	56.9	6 946
MatM	A	PRES ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region	34.4	12 965
	B	PRES ~ s(BFN) + s(HERN) + s(ILLN) + s(DORN) + s(MACN) + Co	20.7	13 720
	A + B	PRES ~ A + B	41.0	12 627
	Overall	PRES ~ A + B + te(Zenith,Depth) + te(BT,Depth) + te(BFN,Depth) + te(Depth,Co) + te(Julian,Region)	45.6	12 433
ImmF	A	PRES ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region	19.2	13 802
	B	PRES ~ s(BFN) + s(HERN) + s(ILLN) + s(DORN) + s(MACN) + Co	23.0	13 606
	A + B	PRES ~ A + B	37.6	12 877
	Overall	PRES ~ A + B + te(BT,Co) + te(Zenith,Depth) + te(BT,Region) + te(Julian,Depth) + te(Julian,Co)	45.4	12 524
ImmM	A	PRES ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region	37.3	5 826
	B	PRES ~ s(BFN) + s(HERN) + s(ILLN) + s(DORN) + s(MACN) + Co	35.8	5 866
	A + B	PRES ~ A + B	49.4	5 497
	Overall	PRES ~ A + s(BFN) + s(ILLN) + s(DORN) + s(MACN) + Co + te(ILLN,BT) + te(BT,Region) + te(MACN,ILLN) + te(BT,Year)	54.9	5 377
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

Note: A = optimal submodel consisting of abiotic main effects; B = optimal submodel consisting of biotic main effects; A + B = optimal submodel 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; s = cubic regression spline smooth; te = tensor product smooth; Dev = percent deviance explained; AIC = Akaike's information criterion. Spiny dogfish were not sexed consistently until 1980.

Table A4. Model selection for abundance (PRES) of spiny dogfish life-history stages during spring (1968–2009).

Stage	Submodel	Optimal (sub) model	Dev (%)	AIC
MatF	A	PRES ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region	37.7	15 400
	B	PRES ~ s(BFN) + s(HERN) + s(ILLN) + s(DORN) + s(MACN) + Co	21.3	16 367
	A + B	PRES ~ A + B	46.2	14 931
	Overall	PRES ~ A + B + te(DORN,BT) + te(BT,Year) + te(BT,Depth)	48.8	14 820
MatM	A	PRES ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region	25.4	18 706
	B	PRES ~ s(BFN) + s(HERN) + s(ILLN) + s(DORN) + s(MACN) + Co	15.2	19 447
	A + B	PRES ~ A + s(HERN) + s(ILLN) + s(DORN) + s(MACN) + Co	31.7	18 270
	Overall	PRES ~ A + s(BFN) + s(HERN) + s(DORN) + s(MACN) + Co + te(BT,Region) + te(HERN,BT) + te(Julian,Depth) + te(Zenith,BT) + te(Depth,Region)	39.4	17 803
ImmF	A	PRES ~ s(Year) + s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region	29.7	19 787
	B	PRES ~ s(BFN) + s(HERN) + s(ILLN) + s(DORN) + s(MACN) + Co	25.0	20 142
	A + B	PRES ~ A + B	37.3	19 270
	Overall	PRES ~ A + B + te(Julian,BT) + te(BT,Depth) + te(BT,Region) + te(BT,Year) + te(BT,Co)	43.7	18 878
ImmM	A	PRES ~ s(Year) + s(Depth) + s(BT) + s(Zenith) + Region	45.8	7 689
	B	PRES ~ s(BFN) + s(HERN) + s(ILLN) + s(DORN) + s(MACN) + Co	26.9	8 394
	A + B	PRES ~ A + B	51.9	7 489
	Overall	PRES ~ A + 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	7 294
Neo	A	PRES ~ s(Depth) + s(BT) + s(Julian) + s(Zenith) + Region	30.9	3 341
	B	PRES ~ s(BFN) + s(HERN) + s(ILLN) + s(DORN) + s(MACN)	19.4	3 480
	A + B	PRES ~ A + B	40.0	3 261
	Overall	PRES ~ s(Year) + A + B + te(BT,Region) + te(ILLN,BT) + te(BFN,Julian) + te(BT,Depth) + te(BT,Year)	50.4	3 182

Note: A = optimal submodel consisting of abiotic main effects; B = optimal submodel consisting of biotic main effects; A + B = optimal submodel 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; s = cubic regression spline smooth; te = tensor product smooth; Dev = percent deviance explained; AIC = Akaike's information criterion. Spiny dogfish were not sexed consistently until 1980.

Appendix B. Generalized additive modeling results

Table B1. GAM results describing the occurrence (PA) of spiny dogfish life-history stages during autumn (1963–2009).

Stage	Variable	Range (rank)	EDF	Trend
MatF	Year	1.5 (7)	3.38	↓ 1987, ↑ (peak 2004), ↓
	BT	10 (2)	2.85	↑ (peak 13.5 °C), ↓
	Julian	1.7 (6)	2.18	↑ (peak day 308), ↓
	HERN	0.6 (10)	3.47	↑ (peak 275), ↓
	Zenith,CoP	1.2 (8)	1	↓
	Depth,SNE	34 (1)	3.63	↑ 45 m, ↓ 150 m, ↑ (peak 240 m), ↓
	RegionGM+	—	—	PA 1.93 higher than GB
	CoP+	—	—	PA 2.87 higher than CoA
MatM	Year	2.7 (6)	3.87	↑ (peak 1989), ↓ 1995, ↑ 2002, ↓
	Depth	9 (3)	4	↑ (peak 70 m), ↓ 180 m, ↑ 280 m, ↓
	BT	11 (2)	2.92	↑ (peak 13 °C), ↓
	Julian	12 (1)	3.64	↑ (peak day 320)
	Zenith	0.5 (11)	2.65	↑ (peak 80°), ↓ 140°, ↑
	DORN	1.5 (8)	1	↓
	Julian,CoP	3 (4)	3.27	(peak day 245), ↓ day 305, ↑
	Year,GB	2.8 (5)	2.56	(peak 1980), ↓ 1996, ↑
	Julian,Depth	—	5.61	Complex
	Depth,Year	—	4.10	Complex
	RegionGM+	—	—	PA 1.54 higher than GB
	RegionSNE+	—	—	PA 0.55 lower than GB
	CoP+	—	—	PA 2.94 higher than CoA
ImmF	Year	5.1 (2)	4	↑ 1986, ↓ 1993, ↑ (peak 2001), ↓
	BT	14 (1)	3.01	↑ (peak 13 °C), ↓
	Year,GB	1.4 (4)	1.45	↓ 1996, ↑ (peak 2009)
	Year,GM	1.6 (3)	3.76	↑ 1987, ↓ 1994, ↑ (peak 2003), ↓
	Year,SNE	1.1 (6)	1	↑
	Depth,Year	—	6.23	Complex
	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	Depth	3.4 (2)	3.67	↑ (peak 380 m)
	BT	9 (1)	2.83	↑ (peak 13 °C), ↓
	Zenith	0.65 (10)	1	↓
	Year,CoP	1.4 (6)	3.69	(peak 1980), ↓ 1987, ↑ 1994, ↓ 2003, ↑
	Depth,CoA	2.2 (4)	1.16	(peak 0 m), ↓
	BT,CoA	3.4 (3)	1	↓
	RegionGM+	—	—	PA 1.12 lower than GB
	CoP+	—	—	PA 3.57 higher than CoA
Neo	BT	25 (1)	2.7	(peak 3 °C), ↓
	HERN	1.5 (7)	1.91	↑ (peak 850), ↓
	Year,MA	7 (2)	3.79	(peak 1963), ↓ 1976, ↑ 1990, ↓ 1996, ↑
	BFN,BT	—	2.96	Complex
	Depth,Year	—	3.24	Complex
	RegionGM+	—	—	PA 1.18 lower than GB
	RegionSNE+	—	—	PA 0.68 higher than GB

Note: Range = *y* axis range for each smoothed term (with corresponding rank inside parentheses); EDF = estimated degrees of freedom; ↑ = increase; ↓ = decrease; + = trends for parametric term; dash (—) = not applicable; GB = Georges Bank; GM = Gulf of Maine; MA = Mid-Atlantic Bight; SNE = Southern New England. Stages and variables are as defined in Tables 1 and 2, respectively. Spiny dogfish were not sexed consistently until 1980; missing ranks are indicative of variables whose smooths were deemed insignificant ($\alpha = 0.05$).

Table B2. GAM results describing the occurrence (PA) of spiny dogfish life-history stages during spring (1968–2009).

Stage	Variable	Range (rank)	EDF	Trend
MatF	Year	1.3 (11)	3.84	↑ (peak 1988), ↓ 2001, ↑
	Depth	6 (3)	3.19	↑ (peak 85 m), ↓ 290 m, ↑
	Julian	1.8 (9)	1	↑
	Zenith	0.4 (13)	2.84	↓ 110°, ↑ (peak 150°)
	Depth,GM	3.5 (5)	2.26	↓ 120 m, ↑ (peak 375 m)
	Depth,MA	2 (8)	3.71	↑ (peak 40 m), ↓ 170 m, ↑ 280 m, ↓
	Depth,SNE	7 (2)	3.62	↑ 40 m, ↓ 170 m, ↑ (peak 375 m)
	BT,GM	14 (1)	1	↑
	BT,Depth	—	10.01	Complex
	Julian,Depth	—	5.64	Complex
	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	↑
	Depth	8 (3)	2.74	↑ (peak 130 m), ↓
	BT	6 (4)	2.58	↑ (peak 9 °C), ↓
	Julian	2.5 (8)	3.08	(peak day 60), ↓
	Zenith	0.32 (10)	1.03	↓
	Depth,MA	11 (1)	3.93	↑ 75 m, ↓ 160 m, ↑ (peak 380 m)
	Depth,SNE	6 (5)	2.86	↑ 85 m, ↓ 160 m, ↑ (peak 300 m), ↓
	Julian,Year	—	11.52	Complex
	BT,Depth	—	6.42	Complex
	Depth,Year	—	11.41	Complex
	RegionGM+	—	—	PA 1.43 lower than GB
	RegionSNE+	—	—	PA 0.52 lower than GB
	CoP+	—	—	PA 1.99 higher than CoA
ImmF	Year	1.6 (8)	1.57	↑ (peak 2009)
	BT	5 (2)	1.75	(peak 1–6 °C), ↓
	MACN	1.1 (9)	3.62	↑ (peak 200), ↓
	Depth,CoA	4.5 (3)	2.86	↓ 100 m, ↑ (peak 290 m), ↓
	Depth,CoP	8 (1)	1	↑
	Depth,GM	3.3 (5)	1	↑
	Depth,MA	4 (4)	3.98	↑ 70 m, ↓ 170 m, ↑ (peak 380 m)
	Depth,SNE	2.5 (7)	3.94	↑ 70 m, ↓ 170 m, ↑ (peak 280 m), ↓
	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
	CoP+	—	—	PA 2.22 higher than CoA
ImmM	Depth	3.6 (2)	3.86	↑ (peak 90 m), ↓ 165 m, ↑ 290 m, ↓
	BT	6 (1)	3.51	↑ (peak 13.5 °C), ↓
	Julian	3.4 (3)	1	↓
	Zenith	0.6 (8)	1.58	(peak 20°), ↓
	DORN	0.85 (7)	2.89	↓ 850, ↑ (peak 3500)
	Depth,CoP	2.7 (5)	2.6	↑ (peak 160 m), ↓
	Year,CoP	1.3 (6)	3.58	(peak 1980), ↓ 2003, ↑
	Julian,BT	—	8.07	Complex
	RegionGM+	—	—	PA 0.69 lower than GB
	CoP+	—	—	PA 2.54 higher than CoA
Neo	Year	0.95 (6)	3.89	↑ 1987, ↓ 1999, ↑ (peak 2009)
	Depth	6 (3)	3.88	↑ 115 m, ↓ 165 m, ↑ (peak 240 m), ↓
	Julian	3.8 (4)	2.57	(peak day 57), ↓
	Zenith	0.6 (8)	2.84	↑ (peak 60°), ↓ 125°, ↑
	BFN	0.8 (7)	3.56	↑ (peak 350), ↓
	MACN	0.5 (10)	3.64	↑ 200, ↓ 300, ↑ (peak 1500)
	BT,GB	12 (1)	1	↑
	BT,Depth	—	4.09	Complex
	RegionMA+	—	—	PA 3.03 higher than GB
	RegionSNE+	—	—	PA 2.78 higher than GB

Note: Range = y axis range for each smoothed term (with corresponding rank inside parentheses); EDF = estimated degrees of freedom; ↑ = increase; ↓ = decrease; + = trends for parametric term; dash (—) = not applicable; GB = Georges Bank; GM = Gulf of Maine; MA = Mid-Atlantic Bight; SNE = Southern New England. Stages and variables are as defined in Tables 1 and 2, respectively. Spiny dogfish were not sexed consistently until 1980; missing ranks are indicative of variables whose smooths were deemed insignificant ($\alpha = 0.05$).

Table B3. GAM results describing the abundance (PRES) of spiny dogfish life-history stages during autumn (1963–2009).

Stage	Variable	Range (rank)	EDF	Trend
MatF	Year	3.2 (1)	3.24	↓ 1995, ↑ (peak 2009)
	BT	2.1 (5)	3.86	↑ (peak 14.5 °C), ↓
	Julian	2.1 (6)	3.4	(peak day 254), ↓ day 305, ↑
	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), ↓
	DORN,GB	3 (2)	3.85	(peak 0), ↓ 200, ↑ 400, ↓
	DORN,SNE	1.7 (7)	3.05	(peak 0), ↓
	Depth,CoP	2.5 (4)	1	↓
	Zenith,Depth	—	8.35	Complex
	Zenith,Year	—	10.24	Complex
	Julian,Year	—	4.41	Complex
	RegionGM⁺	—	—	PRES 1.22 higher than GB
	RegionSNE⁺	—	—	PRES 1.47 higher than GB
	CoP⁺	—	—	PRES 1.15 higher than CoA
MatM	Year	1.3 (8)	2.79	↑ (peak 2009)
	Depth	3.9 (4)	1	↓
	BT	3.5 (5)	3.3	↑ (peak 12 °C), ↓
	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, ↑
	DORN	1.2 (9)	2.93	↑ (peak 250), ↓
	MACN	0.4 (15)	3.88	(peak 0), ↓
	Depth,CoP	1.05 (10)	2.34	↑ (peak 85 m), ↓ 225 m, ↑
	Julian,GB	14 (1)	3.83	↑ day 278, ↓ day 284, ↑ (peak day 296), ↓
	Julian,GM	4.1 (3)	2.24	(peak day 256), ↓
	Julian,SNE	3.2 (6)	2.84	↑ day 276, ↓ day 284, ↑ (peak day 302), ↓
	Zenith,Depth	—	14.93	Complex
	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	↑ 1987, ↓ 1994, ↑ (peak 2005), ↓
	Depth	2.1 (6)	1	↓
	BT	4 (2)	4	Constant (4–10 °C), ↑ (peak 14 °C), ↓
	Julian	2.2 (5)	3.26	↓ (day 265), ↑ (peak day 320)
	Zenith	0.9 (11)	2.25	(peak 40°), ↓ 120°, ↑
	HERN	0.3 (15)	2.83	↑ (peak ~1000)
	ILLN	0.35 (14)	2.49	↑ (peak 40), ↓
	DORN	1.4 (9)	3.85	↑ (peak 250), ↓
	MACN	0.1 (18)	1	↓
	BT,GB	4 (3)	3.94	↓ 8 °C, ↑ 11 °C, ↓ 15 °C, ↑ (peak 18 °C)
	BT,MA	6.8 (1)	2.63	(peak 4 °C), ↓ 10 °C, ↑ 11.5 °C, ↓ 14 °C, ↑
	Julian,CoP	1.9 (7)	2.21	↑ (peak day 290), ↓
	Julian,Depth	—	11.91	Complex
	RegionGM⁺	—	—	PRES 0.79 higher than GB
	RegionMA⁺	—	—	PRES 1.52 lower than GB
	CoP⁺	—	—	PRES 1.80 higher than CoA
ImmM	Year	2.1 (4)	3.44	↑ 1988, ↓ 1997, ↑ (peak 2009)
	Depth	1.05 (9)	1.88	↑ (peak ~300 m)
	BT	5.2 (3)	4	(peak 5 °C), ↓ 7 °C, ↑ 9.5 °C, ↓
	Julian	1.7 (6)	3.01	↑ (peak day 286), ↓
	Zenith	1.25 (8)	2.05	(peak 40°), ↓
	BFN	0.21 (12)	1	↓
	DORN	1.6 (7)	1.88	(peak 0), ↓
	BT,GM	7 (2)	3.56	↑ 8.5 °C, ↓ 10 °C, ↑ (peak ~13 °C)
	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
	CoP⁺	—	—	PRES 1.99 higher than CoA

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24
Can. J. Fish. Aquat. Sci. Vol. 71, 2014

Table B3 (*concluded*).

Stage	Variable	Range (rank)	EDF	Trend
Neo	Depth	0.7 (5)	1	↑
	ILLN,GB	3.2 (1)	1	↑
	RegionGM+	—	—	PRES 3.01 lower than GB
	RegionMA+	—	—	PRES 2.38 lower than GB
	RegionSNE+	—	—	PRES 1.97 lower than GB

Note: Range = *y* axis range for each smoothed term (with corresponding rank inside parentheses); EDF = estimated degrees of freedom; ↑ = increase; ↓ = decrease; + = identifies trends for parametric term; dash (—) = not applicable; GB = Georges Bank; GM = Gulf of Maine; MA = Mid-Atlantic Bight; SNE = Southern New England. Stages and variables are as defined in Tables 1 and 2, respectively. Spiny dogfish were not sexed consistently until 1980; missing ranks are indicative of variables whose smoothes were deemed insignificant (α = 0.05).

Table B4. GAM results describing the abundance (PRES) of spiny dogfish life-history stages during spring (1968–2009).

Stage	Variable	Range (rank)	EDF	Trend
MatF	Year	0.85 (5)	1	↓
	Depth	1.6 (2)	2.99	↑ (peak 100 m), ↓
	Julian	1.3 (3)	3.77	(peak day 57), ↓ day 115, ↑
	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), ↓
	DORN	5 (1)	2.62	(peak 0), ↓
	MACN	0.8 (6)	3.03	↑ (peak 225), ↓
	BT,Depth	—	6.8	Complex
	DORN,BT	—	12.76	Complex
	BT,Year	—	7.07	Complex
	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 1998), ↓
	Depth	3.3 (7)	2.42	↑ (peak 135 m), ↓
	BT	75 (3)	1	↓
	Julian	1.3 (10)	3.11	↑ (peak day 88), ↓ day 118, ↑
	BFN	0.26 (17)	3.85	↑ (peak 185), ↓ 370, ↑
	DORN	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 130 m), ↓ 290 m, ↑
	Depth,MA	3.5 (6)	2.57	↑ (peak 170 m), ↓
	Depth,SNE	2.9 (8)	3.98	↑ 130 m, ↓ 260 m, ↑ (peak ~400 m)
	HERN,BT	—	7.54	Complex
	Julian,Depth	—	14.63	Complex
	Zenith,BT	—	6.08	Complex
	RegionGM+	—	—	PRES 1.67 lower than GB
	RegionMA+	—	—	PRES 0.87 higher than GB
	CoP+	—	—	PRES 0.96 higher than CoA
ImmF	Year	0.32 (15)	1.77	↑ (peak 1988), ↓
	Depth	2 (4)	1	↓
	Julian	3.6 (2)	3.77	↓ day 85, ↑ (peak day 122), ↓
	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), ↓
	DORN	0.38 (14)	1.96	↑ (peak 2400), ↓
	MACN	0.58 (12)	3.7	↑ (peak 300), ↓
	BT,GM	34 (1)	3.86	(peak 3 °C), ↓ 7.5 °C, ↑ 9.5 °C, ↓
	BT,CoA	3.2 (3)	2.86	↑ (peak 11.5 °C), ↓
	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

Table B4 (*concluded*).

Stage	Variable	Range (rank)	EDF	Trend
ImmM	Year	1.2 (7)	4	↓ 1984, ↑ (peak 1994), ↓ 2002, ↑
	Depth	4.7 (6)	4	(peak 0 m), ↓ 75 m, ↑ 190 m, ↓
	BT	55 (3)	2	(peak 3 °C), ↓
	Zenith	0.65 (9)	2.37	↑ (peak 75°), ↓
	BFN	0.4 (11)	2.83	↑ (peak 250), ↓
	ILLN	0.32 (12)	1	↓
	BT,GB	60 (1)	2.92	↑ (peak 14 °C)
	BT,GM	41 (5)	2.84	↑ (peak 11.5 °C), ↓
	BT,MA	58 (2)	1	↑
	BT,SNE	54 (4)	3.86	↑ (peak 14 °C)
	BT,Year	—	12.91	Complex
	Julian,BT	—	2.38	Complex
	ILLN,Depth	—	11.99	Complex
	RegionGM+	—	—	PRES 2.60 lower than GB
	RegionMA+	—	—	PRES 0.44 lower than GB
	CoP+	—	—	PRES 1.92 higher than CoA
Neo	Year	1.5 (6)	3.61	↑ (peak 1983), ↓
	Depth	1.6 (5)	2.28	↑ (peak 175 m), ↓
	Zenith	2.1 (4)	4	(peak 34°), ↓ 55°, ↑ 78°, ↓ 114°, ↑
	BFN	1.3 (7)	2.51	(peak 0), ↓
	DORN	0.5 (11)	3.01	↓ 270, ↑ (peak 2000)
	MACN	0.6 (9)	2.75	↑ (peak 250)
	BT,MA	2.2 (3)	3.01	↑ (peak 10.5 °C), ↓
	ILLN,BT	—	6.68	Complex
	BFN,Julian	—	7.65	Complex
	BT,Year	—	7.08	Complex
	RegionGM+	—	—	PRES 2.88 lower than GB
	RegionSNE+	—	—	PRES 0.63 higher than GB

Note: Range = *y* axis range for each smoothed term (with corresponding rank inside parentheses); EDF = estimated degrees of freedom; ↑ = increase; ↓ = decrease; + = trends for parametric term; dash (—) = not applicable; GB = Georges Bank; GM = Gulf of Maine; MA = Mid-Atlantic Bight; SNE = Southern New England. Stages and variables are as defined in Tables 1 and 2, respectively. Spiny dogfish were not sexed consistently until 1980; missing ranks are indicative of variables whose smoothes were deemed insignificant (α = 0.05).

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26

Can. J. Fish. Aquat. Sci. Vol. 71, 2014
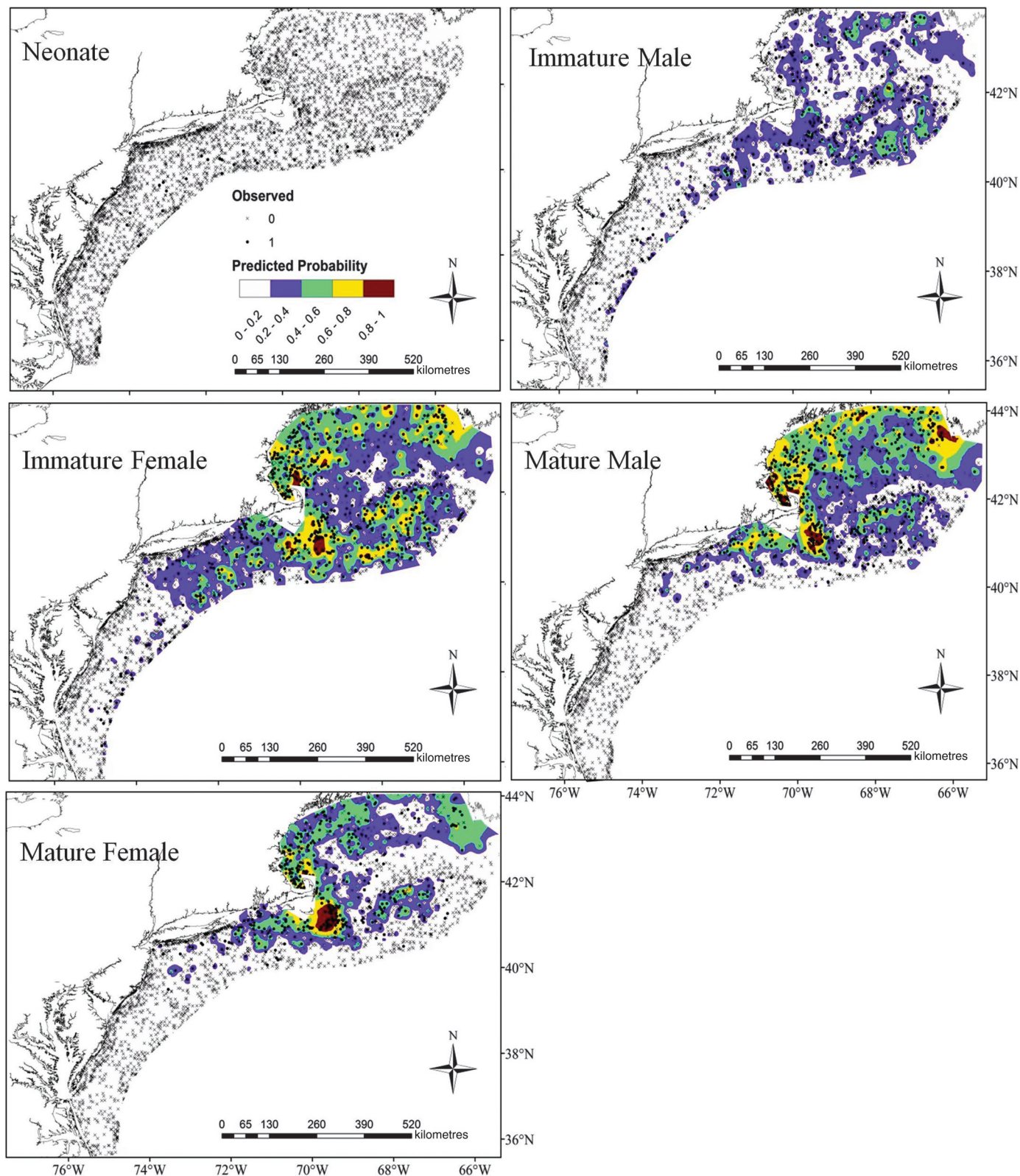
Appendix C. Model validation

Fig. C1. 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 autumn. Note that interpolation was carried out in ArcGIS using spatial analyst. (For the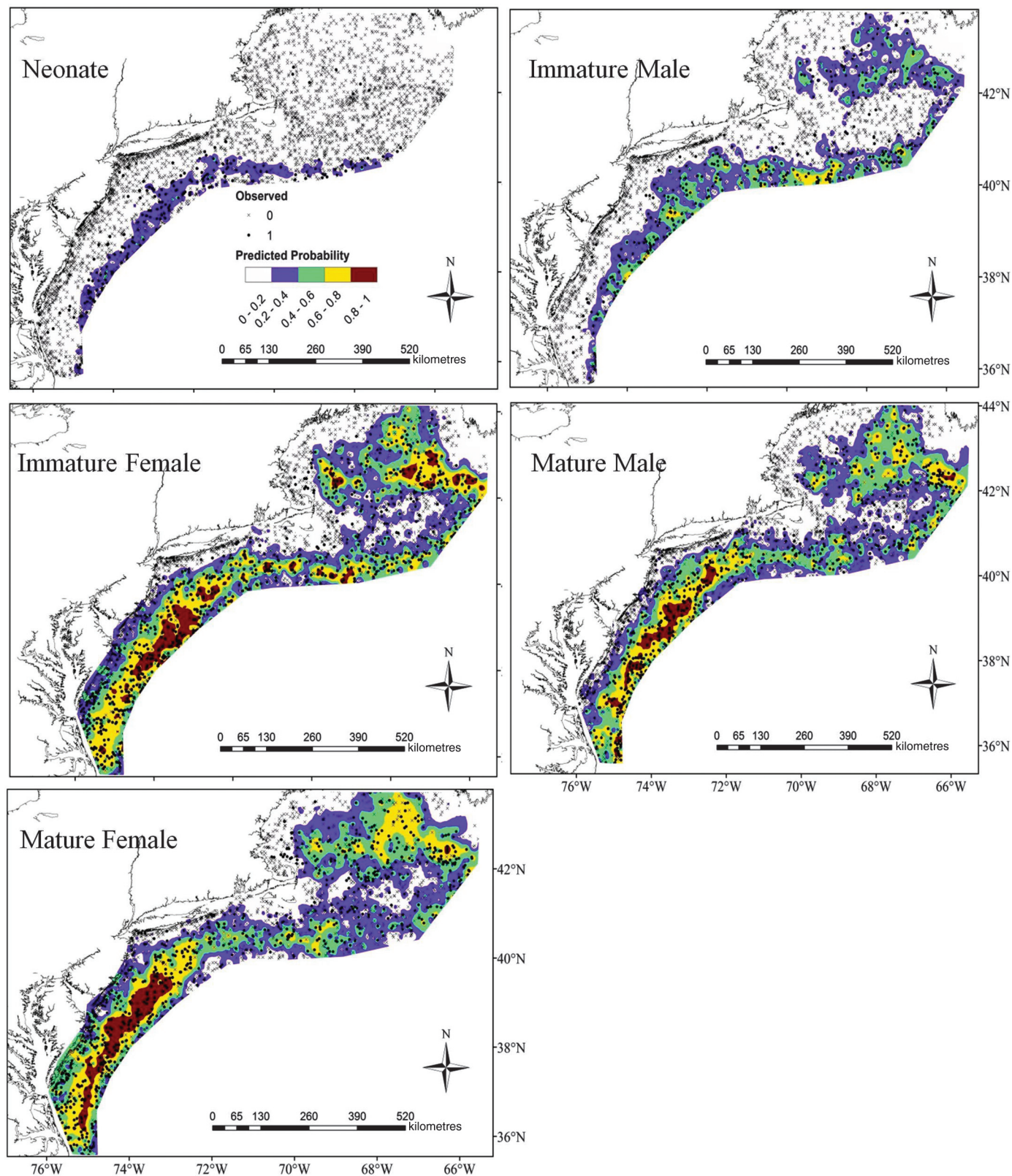 coloured version of this figure, refer to the Web site at http://www.nrcresearchpress.com/doi/full/10.1139/cjfas-2013-0342.)

Fig. C2. 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. Note that interpolation was carried out in ArcGIS using spatial analyst. (For the coloured version of this figure, refer to the Web site at http://www.nrcresearchpress.com/doi/full/10.1139/cjfas-2013-0342.)

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28

Can. J. Fish. Aquat. Sci. Vol. 71, 2014

Fig. C3. 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 spiny dogfish life-history stages during autumn. Note that interpolation was carried out in ArcGIS using spatial analyst. (For the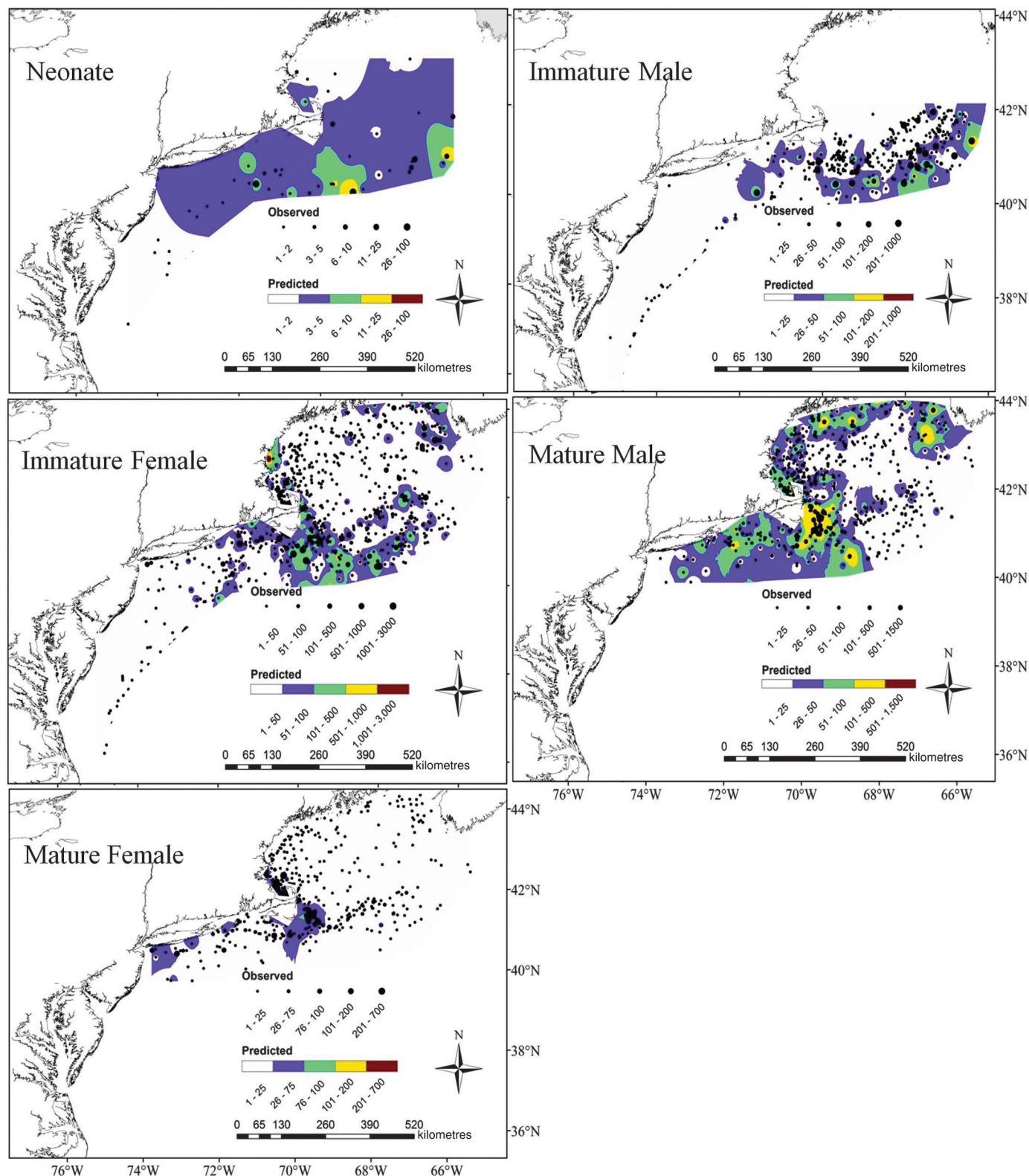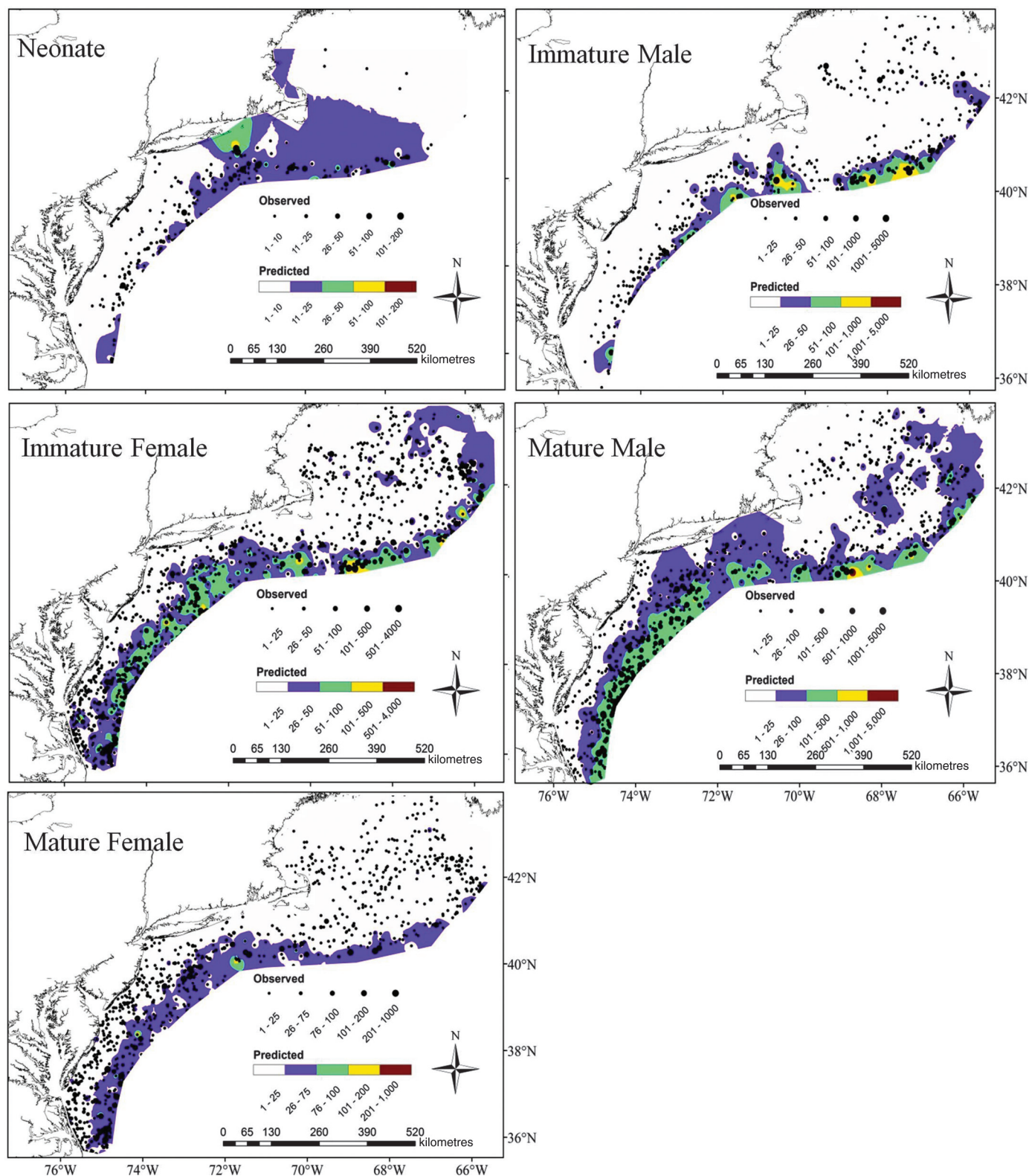 coloured version of this figure, refer to the Web site at http://www.nrcresearchpress.com/doi/full/10.1139/cjfas-2013-0342.)

Fig. C4. 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 spiny dogfish life-history stages during spring. Note that interpolation was carried out in ArcGIS using spatial analyst. (For the coloured version of this figure, refer to the Web site at http:// www.nrcresearchpress.com/doi/full/10.1139/cjfas-2013-0342.)

Appendix D. Model forecasts

Fig. D1. Hypothetical predicted probability of spiny dogfish occurrence during spring in the Northeast (US) shelf large marine ecosystem for a year exhibiting average (BT$_{avg}$), warmer (BT$_{avg}$ + 1 °C), and cooler (BT$_{avg}$ − 1 °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). (For the coloured version of this figure, refer to the Web site at http://www.nrcresearchpress.com/doi/full/10.1139/cjfas-2013-0342.) Note that only the abiotic submodel was used for prediction owing to uncertainty regarding how prey species would respond to temperature changes.
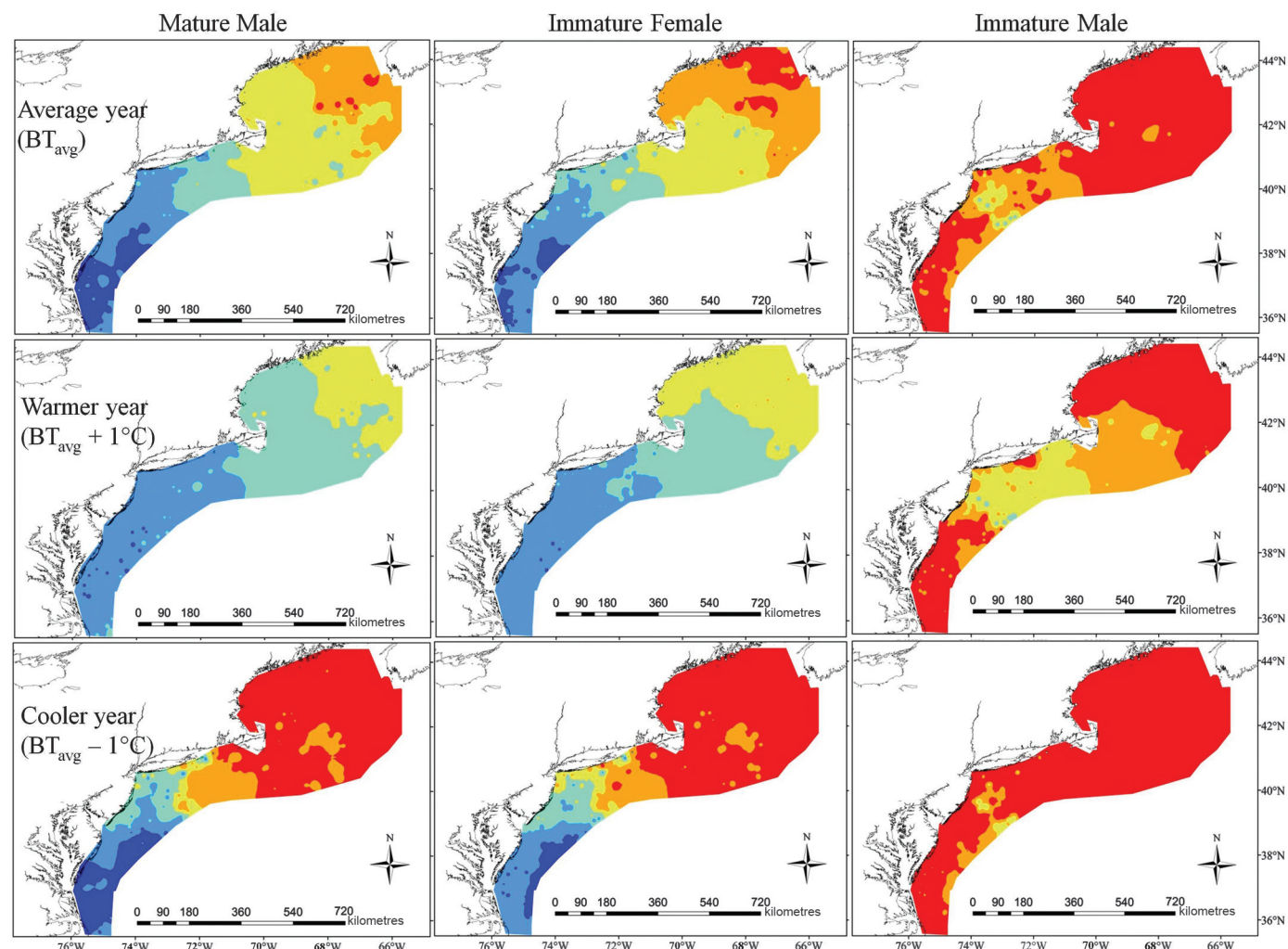
Fig. D2. Hypothetical predicted probability of spiny dogfish occurrence during autumn in the Northeast (US) shelf large marine ecosystem for a year exhibiting average (BT_{avg}), warmer (BT_{avg} + 1 °C), and cooler (BT_{avg} − 1 °C) bottom temperatures. Probabilities include <0.5 (red), 0.5–0.6 (orange), 0.6–0.7 (yellow), 0.7–0.8 (green), 0.8–0.9 (light blue), and 0.9–1.0 (dark blue). (For the coloured version of this figure, refer to the Web site at http://www.nrcresearchpress.com/doi/full/10.1139/cjfas-2013-0342.) Note that only the abiotic submodel was used for prediction owing to uncertainty regarding how prey species would respond to temperature changes.