

Influence of environmental, spatial, and ontogenetic variables on habitat selection and management of spiny dogfish in the Northeast (US) shelf large marine ecosystem

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Abstract: Declines in abundance of commercially valuable groundfish have highlighted the ecological and commercial importance of previously underutilized elasmobranchs in the Northeast (US) shelf large marine ecosystem (NES LME). Seasonal distributions and ontogenetic habitats of one such species, spiny dogfish (*Squalus acanthias*), were investigated using Northeast Fisheries Science Center (NEFSC) bottom trawl survey data (1963–2009). Neonate, immature, and mature dogfish all selected warmer, more saline, and more southerly locations during spring compared with available locations. During autumn, larger dogfish occupied relatively warmer, shallower, and less saline waters while neonates selected higher salinities. There were strong ontogenetic patterns in habitats occupied. Contrary to expectation, geographic range contracted as abundance increased during autumn. This suggests that niche constraints override density-dependent effects, although detection of relationships within stages was limited by low statistical power. The proportion of mature female survey catch within the Mid-Atlantic Bight was significantly related to temperature, suggesting that environmental conditions surveyed may impact population trends. Collectively, these results highlight critical habitats, suggest mechanisms behind ontogenetic habitat selection, and provide insight into how changing environmental conditions may impact stock assessment.

Résumé : Les baisses d'abondance de poissons de fond à valeur commerciale soulignent l'importance écologique et commerciale d'élasmobranches auparavant sous-utilisés dans le grand écosystème marin de la plateforme continentale du nord-est des États-Unis (NES LME). Les répartitions saisonnières et les habitats ontogéniques d'une de ces espèces, l'aiguillat commun (*Squalus acanthias*), ont été examinés à la lumière de données de relevés au chalut de fond (1963–2009) du Northeast Fisheries Science Center (NEFSC). Parmi les sites disponibles, les aiguillats nouveau-nés, immatures et matures choisissaient tous des emplacements relativement chauds, salins et méridionaux au printemps. À l'automne, les aiguillats plus grands occupaient des eaux relativement chaudes, moins profondes et moins salines, alors que les nouveau-nés choisissaient des eaux de plus forte salinité. L'occupation des habitats définissait des motifs ontogéniques marqués. Contrairement aux attentes, l'aire de répartition géographique diminuait parallèlement à l'augmentation de l'abondance à l'automne, ce qui donne à penser que les contraintes touchant à la niche l'emportent sur les effets dépendants de la densité, bien que la faible efficacité statistique limite la détection de relations pour des stades donnés. La proportion de femelles matures capturées dans le cadre des relevés dans le golfe Médio-atlantique était significativement reliée à la température, donnant à penser que les conditions ambiantes pourraient avoir une incidence sur les tendances des populations. Collectivement, ces résultats font ressortir des habitats essentiels et des mécanismes possibles de sélection d'habitats ontogéniques et jettent un éclairage sur l'incidence de l'évolution des conditions ambiantes sur l'évaluation des stocks. [Traduit par la Rédaction]

Introduction

Understanding the habitat preferences of marine fishes is important when describing their spatial distribution and ecology (Perry and Smith 1994; Smith and Page 1996; Shepherd et al. 2002) and is a prerequisite for effective fisheries management (Reynolds 2003). If distributions vary in response to environmental conditions, then estimates of abundance derived from fishery-independent surveys whose spatial domain is fixed may mislead stock assessments (Perry and Smith 1994; Smith and Page 1996; Shepherd et al. 2002). Such concerns are especially likely for highly migratory species for which environmental conditions may dictate the tim-

ing of migrations and therefore alter availability within surveyed regions (Shepherd et al. 2002; Peer and Miller 2014). For example, in the Northeast Atlantic, albacore (*Thunnus alalunga*) and bluefin tuna (*Thunnus thynnus*) have adapted the timing of their migrations in response to climate change with earlier arrivals in recent warmer years (Dufour et al. 2010). Moreover, a species' environmental preference may vary during its life history, resulting in diverse distributional patterns over broad spatial scales at the population scale (Methratta and Link 2007). Ontogenetic shifts in habitat use, resulting from change in morphology, physiology, ecological function, and (or) predation risk, have been frequently documented in marine fishes (e.g., Fry 1971; Swain 1993; Methratta

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and Link 2007), with older individuals generally favoring deeper depths (Macpherson and Duarte 1991). Density-dependent effects can also influence habitat selection (Swain and Kramer 1995; Swain 1999; Spencer 2008), with larger population sizes exhibiting a more widespread spatial distribution covering more habitats (MacCall 1990) as competition forces individuals beyond the core of their environmental optima.

In the Northwest Atlantic, the increasing harvest pressure on elasmobranchs resulting from fishers seeking to supplement income has necessitated research to enhance stock assessment of these understudied species, particularly for the spiny dogfish (*Squalus acanthias*) (Rago et al. 1998; McMillan and Morse 1999). Spiny dogfish is a small, slow-growing, long-lived elasmobranch that occurs in oceanic and coastal environments throughout the world (Compagno et al. 2005; Veríssimo et al. 2010). In the Northwest Atlantic, maturity occurs at age 6 (~60 cm total length, TL) for males and age 12 (~80 cm TL) for females (Burgess 2002; Sosebee 2005). Longevity is estimated to be 45 years (Campana et al. 2006). Spiny dogfish are yolk-sac viviparous and deposit pups in nursery areas. Overall, spiny dogfish occupy multiple habitats throughout their life history, with sex-specific habitat selection likely related to metabolic processes and reproductive behavior. Traditionally, their low commercial value has rendered efforts to understand their population dynamics unnecessary; now with important fisheries supported by previously undesirable elasmobranchs, it is imperative that research is conducted on habitat selection and distribution to better inform stock assessment.

Habitat preference studies in the Northwest Atlantic have generally focused on commercially important teleosts, including Atlantic cod (*Gadus morhua*) (Scott 1982; many others), haddock (*Melanogrammus aeglefinus*) (Scott 1982; Perry and Smith 1994; Methratta and Link 2007), American plaice (*Hippoglossoides platessoides*) (Scott 1982; many others), yellowtail flounder (*Limanda ferruginea*) (Scott 1982; Perry and Smith 1994), and silver hake (*Merluccius bilinearis*) (Murawski and Finn 1988; Perry and Smith 1994; Methratta and Link 2007). Far less attention has been paid to elasmobranchs. However, many variables have proven influential in determining the distribution and abundance of various elasmobranchs in other regions, including temperature, salinity, depth, dissolved oxygen concentration, and surface chlorophyll (Vögler et al. 2008; Craig et al. 2010; Cortés et al. 2011).

Spiny dogfish display variable distributional trends at seasonal and decadal scales (Templeman 1984; Overholtz and Tyler 1985; Rago et al. 1998) in the Northeast (US) shelf large marine ecosystem (NES LME). During seasonal movements, spiny dogfish are often locally abundant for several months at a time and display large interannual variations. Distinguishing changes in true abundance from variations in seasonal movements is essential for stock assessment, but can be challenging. Local concentrations have been blamed for the declines or suppressed recovery of important commercial species and have blurred stock structure in both federal (NEFSC 2006) and transboundary management (TRAC 2010). The classic depiction of the spiny dogfish life cycle involves overwintering in the Mid-Atlantic Bight and feeding in the Northwest Atlantic during summer. In early spring, females lead the population north (Templeman 1944; Hisaw and Albert 1947), reaching Georges Bank in March and April (Fig. 1) (Hisaw and Albert 1947; Burgess 2002). Between May and June the population spreads into the Gulf of Maine or onto the Scotian Shelf (Burgess 2002). During summer, some spiny dogfish move inshore into Canadian bays and estuaries (Rago et al. 1998; Campana et al. 2007), with females arriving first (Burgess 2002). Reportedly, parturition occurs during winter (Nammack et al. 1985; Jones and Ugland 2001; Henderson et al. 2002) after an approximate 2-year gestation period (Hisaw and Albert 1947; Jones and Ugland 2001). Although spiny dogfish are managed as a single unit stock between North Carolina and Newfoundland (NEFSC 2006), the stock structure remains uncertain, with multiple stocks hypothesized

and an unknown proportion of dogfish undergoing seasonal movements (Campana et al. 2007; TRAC 2010).

It has been hypothesized that the movements of spiny dogfish in the Northwest Atlantic reviewed above are driven by seasonal changes in temperature (Burgess 2002; Shepherd et al. 2002; Methratta and Link 2007). A consideration of spiny dogfish general life history suggests that the effects of environmental factors on their distribution are expected to vary between life-history stages because of diverse seasonal migratory behavior (i.e., nursery grounds) (Methratta and Link 2007; Cortés et al. 2011) or physiological demands (Macpherson and Duarte 1991). However, it remains unclear whether temperature operates exclusively and (or) whether various life-history stages are influenced in a similar manner. The available evidence suggests that in the Gulf of Maine and on Georges Bank, spiny dogfish prefer shallow, warm waters in autumn and deep, warm waters in spring (Methratta and Link 2007). Shepherd et al. (2002) showed sex- and length-specific differences in spiny dogfish habitat preference on the Scotian Shelf relative to temperature (6.6–9.2 °C), salinity (32.7–34.4 ppt), and depth (89–185 m). If the availability of different habitats impacts ontogenetic distribution and abundance, seasonal shifts and environmental changes resulting from climate change may lead to increased vulnerability of certain stages to inshore fisheries, as suggested for mature dogfish in shallow coastal waters during autumn (Shepherd et al. 2002).

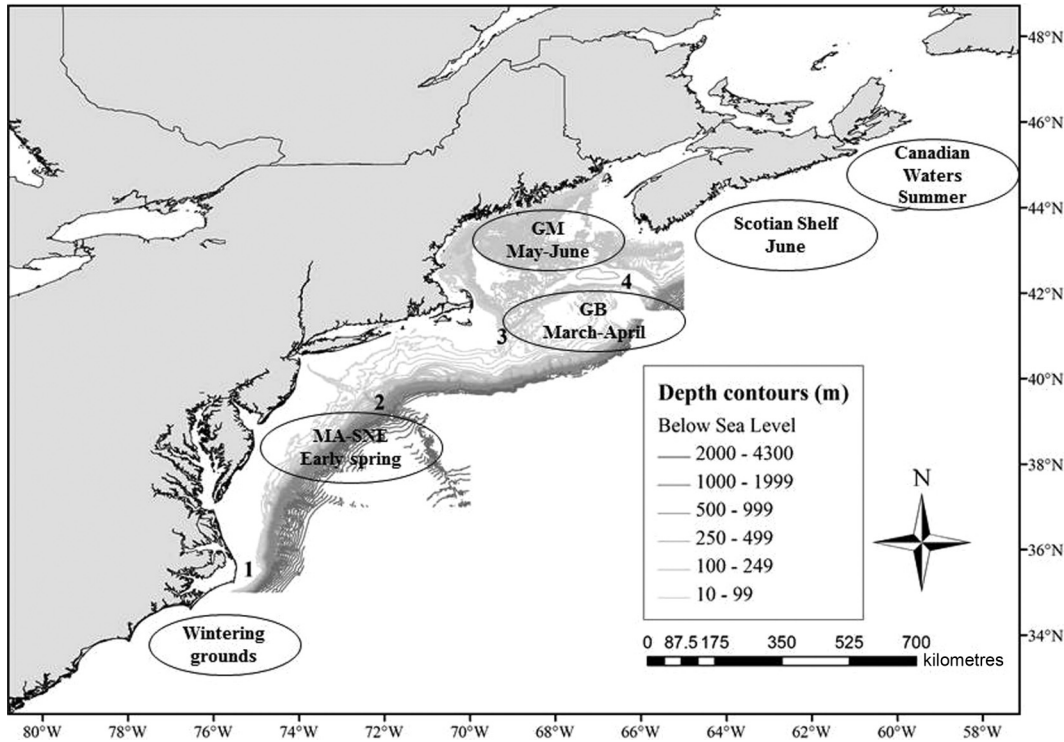
Seasonal habitat associations and geographic distribution were examined for spiny dogfish life-history stages to clarify and identify drivers behind ontogenetic movement and distribution in the NES LME using Northeast Fisheries Science Center (NEFSC) annual bottom trawl survey data (1963–2009). While generalized linear models (Maunder and Punt 2004) are frequently used to standardize catch rates, these models are discouraged for migratory species such as spiny dogfish, which traverse multiple habitats (Maunder et al. 2006). Here, stage-specific associations with bottom temperature, bottom salinity, depth, and latitude were used to evaluate hypothesized habitat selection resulting from reproductive and (or) feeding behavior (Shepherd et al. 2002; Methratta and Link 2007). Changes in ontogenetic distribution were examined in relation to changes in population size with the expectation of geographic range expansion at higher abundances (MacCall 1990). The implications of complex and stage-specific movement patterns identified herein are discussed as is their potential to impact vulnerability to capture fisheries. While these results focus on spiny dogfish, physiological and ecological mechanisms discussed extend to other migratory species where the environment may influence seasonal movements and therefore availability to commercial fisheries.

Materials and methods

Data

All analyses used fishery-independent data obtained from the NEFSC annual autumn and spring bottom trawl surveys. These surveys sample the NES LME from Cape Hatteras, North Carolina, USA, to Georges Bank and the Gulf of Maine using a stratified random design. Offshore and inshore strata are depicted in Figs. 1 and 2 of NEFSC (2006). The autumn survey has been conducted in offshore areas since 1963, and inshore strata were added in 1972. The spring survey began sampling offshore areas in 1968, and inshore strata were added in 1973. Survey strata comprise about 64 000 n.mi.² (1 nautical mile = 1.852 km). The number of stations sampled per stratum was proportional to its area but inshore strata were sampled at approximately three times the sampling rate of offshore strata. Approximately 300–400 stations were visited during autumn (mean ± SE = 344 ± 13 stations) and spring (mean ± SE = 346 ± 8 stations), with surveyed depths ranging from 5 to 500 m. Detailed descriptions of the survey design and changes in survey protocols over time can be found in Azarovitz (1981) and Azarovitz et al. (1997).

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



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

Species distribution

Tow duration was standardized and relative abundance was represented by the survey catch of spiny dogfish per unit effort (CPUE; number of spiny dogfish per tow). Mean values were calculated for all spiny dogfish combined and separately for each dogfish stage and season. Dogfish stages have been consistently reported in the survey since 1980 and were defined as follows: aggregated male and female neonates (TL ≤ 26 cm), immature males (26 cm < TL < 60 cm), immature females (26 cm < TL < 80 cm), mature males (TL ≥ 60 cm), and mature females (TL ≥ 80 cm). Neonate size was chosen based on a total length at birth of 26–27 cm (Hisaw and Albert 1947; Burgess 2002). Four regions were recognized within the survey domain: Georges Bank, Gulf of Maine, southern New England, and the Mid-Atlantic Bight (Fig. 1).

Distributional maps of spiny dogfish for autumn and spring, reflective of survey trends, were produced using ArcMap (version 10, ESRI Corp.). Decadal patterns of distributional trends were provided for the following decades: 1963–1969, 1970–1979, 1980–1989, 1990–1999, and 2000–2009. The proportion of survey catch in each of the four regions was reported to provide insight into highly variable decadal and seasonal trends.

Habitat selection and the degree of aggregation

Habitat selection for each dogfish stage was estimated following the nonparametric method developed by Perry and Smith (1994) using R (R Development Core Team 2010). First, the empir-

ical cumulative distribution function (CDF) of the available habitat $f(t)$ adjusted for unequal sampling effort within strata (W_h/n_h) was estimated with the following function:

$$(1) \quad f(t) = \sum_h \sum_i \frac{W_h}{n_h} I(x_{hi})$$

where

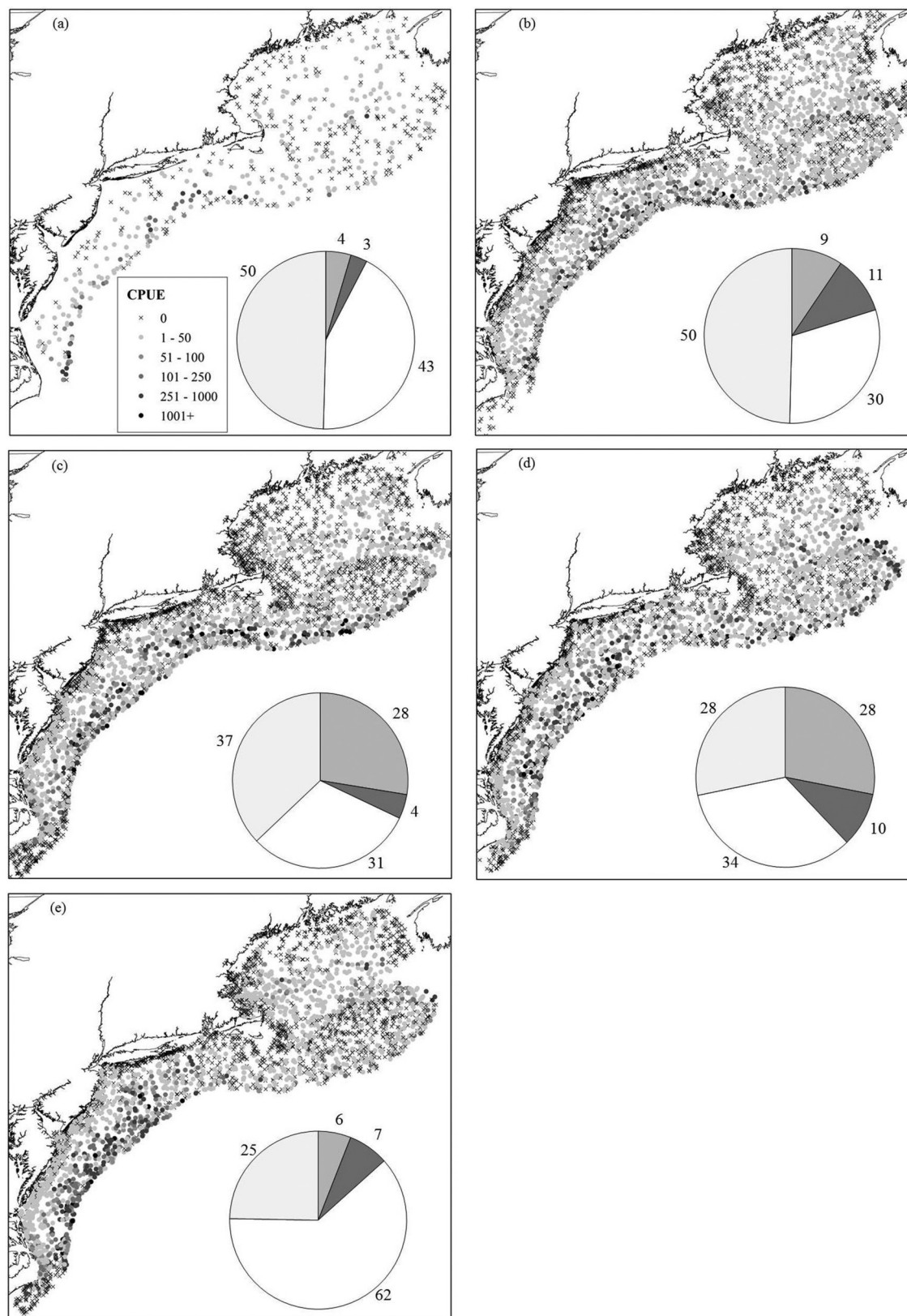
$$I(x_{hi}) = \begin{cases} 1, & \text{if } x_{hi} \leq t \\ 0, & \text{otherwise} \end{cases}$$

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

$$(2) \quad g(t) = \sum_h \sum_i \frac{W_h}{n_h} \frac{y_{hi}}{\bar{y}_{st}} I(x_{hi})$$

where y_{hi} is the number of spiny dogfish caught in trawl i and stratum h , and \bar{y}_{st} is the stratified mean catch (Perry and Smith 1994). Note that eq. 2 specifies the catch-weighted distribution of the habitat variable. For each habitat variable, the 5th, 50th (median), and 95th percentiles were determined. If spiny dogfish are randomly distributed with respect to the habitat covariate (x_{hi}), $f(t)$

Fig. 2. Decadal distribution and regional survey catch of spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring for the (a) 1960s, (b) 1970s, (c) 1980s, (d) 1990s, and (e) 2000s. The numbers of spiny dogfish per tow are plotted. Pie charts show regional proportion of survey catch from the Mid-Atlantic Bight (white), southern New England (light gray), Georges Bank (medium gray), and the Gulf of Maine (dark gray). Note that inshore sampling began in 1973, and data collection was limited during the 1960s.



and $g(t)$ would be identical. Thus, the strength of association between catch and habitat could be determined as the degree of difference between occupied ($g(t)$) and available ($f(t)$) habitat, with a Kolmogorov–Smirnov type test statistic (TS) for the absolute maximum vertical difference (DIF) between the two CDFs:

$$(3) \quad \max |g(t) - f(t)| = \max \left| \sum_h \sum_i \frac{W_h}{n_h} \left(\frac{y_{hi} - \bar{y}_{st}}{\bar{y}_{st}} \right) I(y_{hi}) \right|$$

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

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

$$(4) \quad \Phi_{i,h} = \frac{100 w_i y_{hi}}{\bar{y}_{st}}$$

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

$$(5) \quad A_i = 100 w_i$$

The Lorenz curve was obtained by plotting the cumulative A_i (abscissa) against the cumulative Φ_i (ordinate). The degree of concentration was quantified by the Gini index of inequality (Gini 1912), which measures the deviation of the Lorenz curve from a 45° line and ranges from 0 (equal distribution) to 1 (maximum heterogeneity) (Gini 1912; Temming et al. 2007). The Gini index was calculated using the “RELDIST” package (Handcock 2013) in R (R Development Core Team 2010). It was expected that a higher index, indicative of a more aggregated distribution (Swain et al. 1998; Swain and Morgan 2001), would reduce the power of the randomization tests.

Comparison of habitat selection

To test whether dogfish stages occupied statistically different habitats, cumulative distributions of occupied habitat were calculated for all dogfish stages and compared using a Kolmogorov–Smirnov type of statistic (Swain et al. 1998). Equation 2 was used to estimate the CDF of occupied habitat for each dogfish stage, while eq. 3 was used to estimate the statistic for significance testing with one slight difference. Here, DIF was calculated using the $g(t)$ for each dogfish stage. We evaluated the null hypothesis that differences in habitat distribution were due to chance alone.

Density-dependent analysis

The relationship between stock area and abundance was examined for density dependence using an index of geographic range,

the minimum area containing 95% of the target species (D_{95}) (Swain and Sinclair 1994). This index was calculated for all spiny dogfish combined and separately for each dogfish stage during both seasons. The cumulative frequencies of spiny dogfish catch in each year were determined with the following function:

$$(6) \quad F(c) = 100 \frac{\sum_{h=1}^L \sum_{i=1}^{n_h} \frac{A_h}{n_h} y_{hi} I(y_{hi})}{\sum_{h=1}^L \sum_{i=1}^{n_h} \frac{A_h}{n_h} y_{hi}}$$

where

$$I(y_{hi}) = \begin{cases} 1, & \text{if } y_{hi} \leq c \\ 0, & \text{otherwise} \end{cases}$$

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

$$(7) \quad G(c) = \sum_{h=1}^L \sum_{i=1}^{n_h} \frac{A_h}{n_h} I(y_{hi})$$

where

$$I(y_{hi}) = \begin{cases} 1, & \text{if } y_{hi} \leq c \\ 0, & \text{otherwise} \end{cases}$$

D_{95} was calculated with the following equation:

$$(8) \quad D_{95} = A_T - G(c_{05})$$

where A_T is total survey area (n.mi.²), and $G(c_{05})$ is the area over which density was less than or equal to the 5th percentile level. D_{95} decreases as the proportion of a population's spatial distribution at very low densities increases and increases as its distribution becomes more concentrated. D_{95} can remain constant if abundance changes at the same rate in all areas (Swain and Sinclair 1994; Swain and Benoit 2006). The relationship between annual D_{95} and \log_e -transformed abundance (i.e., survey CPUE) was explored using regression and correlation (r). The power (β) of each correlation was estimated as a function of sample size (N) and a significance level of $\alpha = 0.05$ in the “PWR” package (Champely 2009) of R (R Development Core Team 2010). To explore the strength of the relationship between environmental conditions and distribution, we assessed both Pearson and Spearman correlations between annual D_{95} and mean annual bottom temperature and salinity.

Link between environment and seasonal movements

To investigate the influence of environmental conditions on the timing of spiny dogfish movements, and therefore on the ability of the survey to encounter them, we explored the relationship between proportional catch of mature females against mean bottom water temperature. This analysis focused on mature females because they are expected to shift northward first, and their survey-derived abundance serves as a proxy for spawning stock biomass for stock assessment purposes. We restrict our analysis to the Mid-Atlantic Bight region on the assumption that spiny dogfish remain in the southern extent of their range during spring. It is expected that during years exhibiting colder temperatures, a greater proportion of mature females will be south in relatively warmer waters, possibly outside the survey area. We calculated

Table 1. Habitat associations of spiny dogfish life-history stages in the Northeast (US) shelf large marine ecosystem during spring (1968–2009) and autumn (1963–2009).

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

Note: Stages include neonate (Neo; total length (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). Data shown include habitat percentiles (5th, 50th (median), 95th), DIF (range of absolute vertical distances between distributions), TS (test statistic), and *p* value (probability). Significance (bolded) is based on an a priori $\alpha = 0.05$. Note that spiny dogfish were not sexed consistently until 1980, and *p* = 0.000 does not mean *p* = 0.

the proportion of mature females caught in the Mid-Atlantic Bight during Julian days 65–74 (i.e., 6–15 March) on an annual basis, assuming this temporal interval captured beginning survey trends. We then compared this proportion with the log_e-transformed mean bottom temperature conditions where each annual value was treated as an observation.

Results

Life-history data indicate that a portion of the spiny dogfish population is likely outside of the survey domain in autumn. Therefore, to conserve space, results from the decadal shifts from autumn surveys and information on the temporal patterns in environmental drivers and on the Lorenz curve analyses are presented in online Supplemental Information and are referred to as Figs. S1–S3 when appropriate below¹.

Spatiotemporal distributions of spiny dogfish

Spring surveys generally encountered spiny dogfish in the Mid-Atlantic Bight and southern New England, with these regions accounting for 62%–93% of the total survey catch depending upon the decade (Fig. 2). Survey trends in distribution during autumn were highly variable for all regions with the exception of the Mid-Atlantic Bight, where spiny dogfish were rarely encountered (0%–10%; Fig. S1¹), because some spiny dogfish are present in Canadian waters during autumn and therefore outside the area surveyed. As a result, slight changes in the fraction occurring north and east of the NEFSC survey area could greatly alter the fractions elsewhere.

Habitat selection and degree of aggregation

Survey conditions

The range of environmental and spatial (i.e., latitude) conditions sampled remained similar between years for both seasons

(Fig. S2¹). Exceptions occurred during the 1960s and early 1970s when only offshore strata were sampled.

Temperature

Associations with temperature were common throughout both seasons for most dogfish stages examined (Table 1). During spring, all dogfish stages avoided temperatures below 5 °C or above 14 °C (Fig. 3A). Within these limits, the distributions of all dogfish stages indicated that spiny dogfish were selecting significantly warmer waters (i.e., $g(t) - f(t) > 0$) than those surveyed (Table 1; Fig. 3A). Ontogenetic differences were evident as younger dogfish (neonate and immature male) occupied significantly warmer temperatures compared with other stages (Table 2; Fig. 3A). During autumn, spiny dogfish were absent at stations where temperatures fell below 5 °C or exceeded 17 °C (Fig. 4A). Mature spiny dogfish and immature females were significantly ($p < 0.05$) associated with warmer waters than those surveyed (Table 1; Fig. 4A). Ontogenetic differences were observed for mature females who occupied significantly warmer waters compared with male and neonate dogfish (Table 2; Fig. 4A).

Salinity

Associations with salinity were also common throughout both seasons for most dogfish stages (Table 1). During spring, all dogfish stages occupied significantly ($p < 0.05$) higher salinities than those surveyed (Table 1; Fig. 3B). Ontogenetic differences were found for immature males who associated with higher salinities compared with mature dogfish (Table 2; Fig. 3B). During autumn, neonates and mature spiny dogfish displayed significant ($p < 0.05$) salinity associations compared with those available, with neonates and mature dogfish occupying more and less saline habitats, respectively (Table 1; Fig. 4B). Younger dogfish (neonate and

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2013-0259>.

Fig. 3. Cumulative distributions of available and occupied habitat for spiny dogfish life-history stages in the Northeast (US) shelf large marine ecosystem during spring between 1968 and 2009. Habitat variables include (a) bottom temperature (°C), (b) bottom salinity (ppt), (c) depth (m), and (d) latitude (°N). Note that spiny dogfish were not sexed consistently until 1980, and salinity data has been collected consistently since 1996.

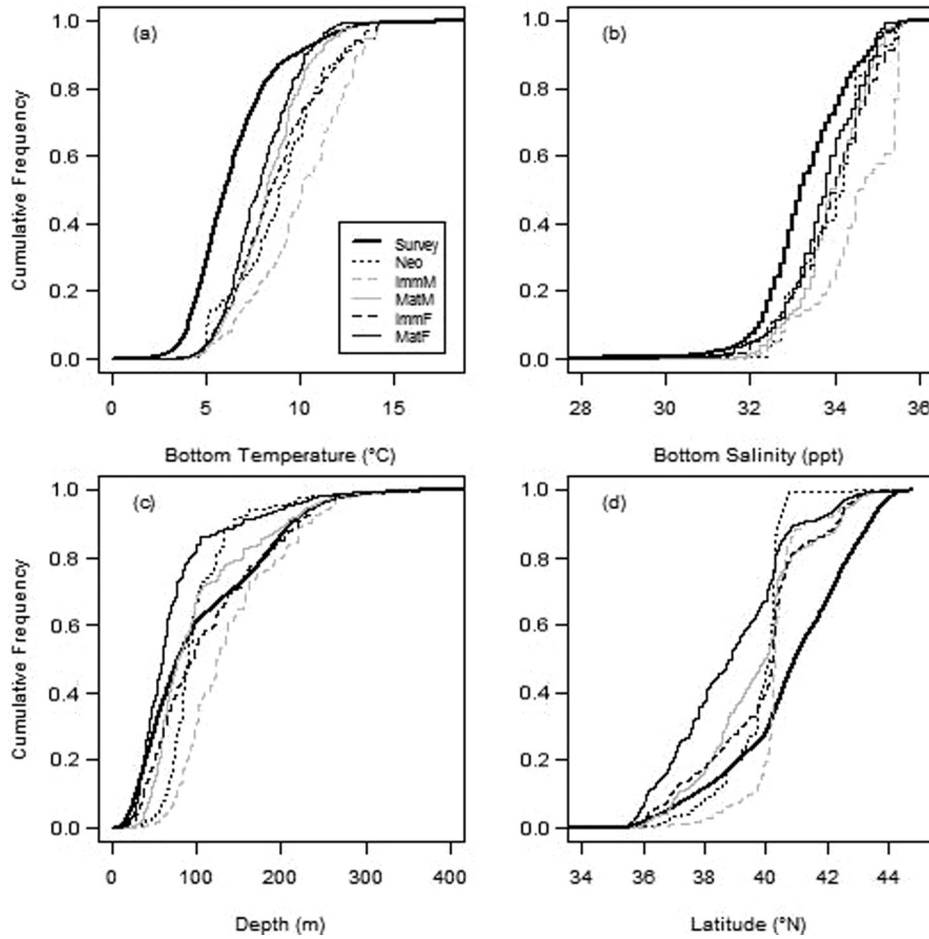
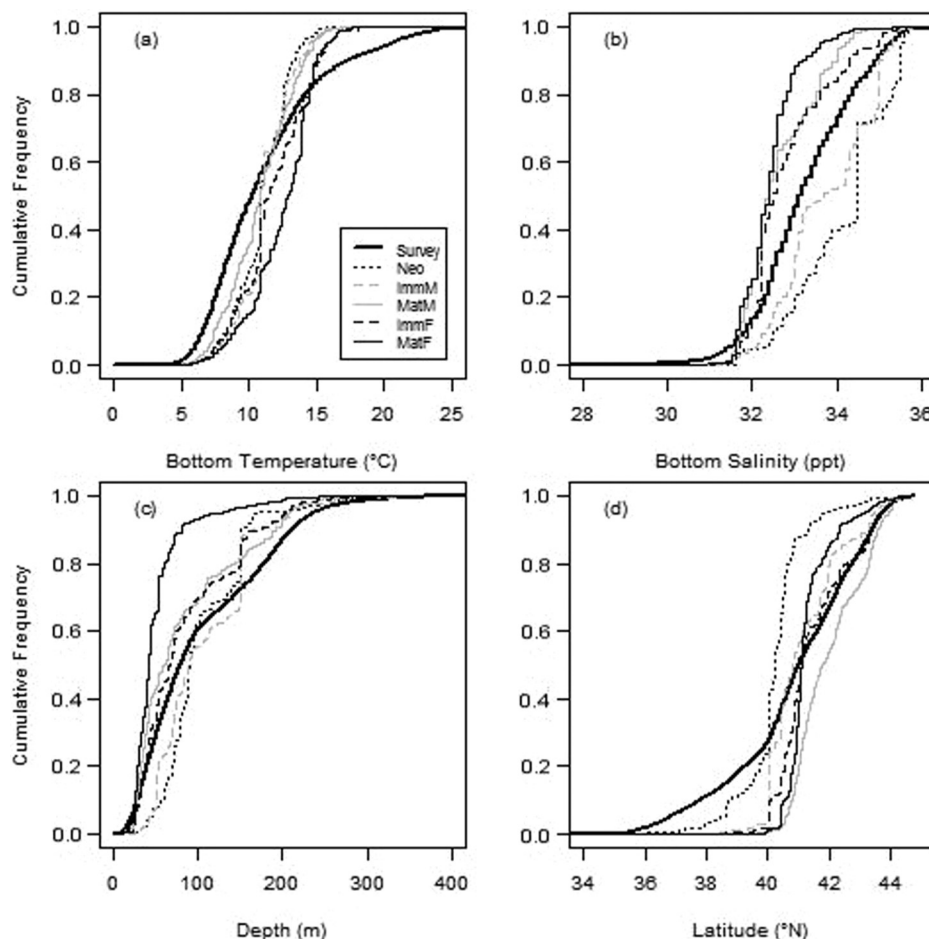


Table 2. Seasonal habitat comparisons for spiny dogfish life-history stages in the Northeast (US) shelf large marine ecosystem during spring (1968–2009) and autumn (1963–2009).

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

Note: Stages and data statistics are as defined in Table 1. Significance (bolded) is based on an a priori $\alpha = 0.05$. Spiny dogfish were not sexed consistently until 1980, and $p = 0.000$ does not mean $p = 0$.

Fig. 4. Cumulative distributions of available and occupied habitat for spiny dogfish life-history stages in the Northeast (US) shelf large marine ecosystem during autumn between 1963 and 2009. Habitat variables include (a) bottom temperature (°C), (b) bottom salinity (ppt), (c) depth (m), and (d) latitude (°N). Note that spiny dogfish were not sexed consistently until 1980, salinity data has been collected consistently since 1996, and temperature range on the x axis differs from Fig. 3.



immature male) selected higher salinities compared with mature dogfish (Table 2; Fig. 4B).

Depth

Associations with depth were prevalent throughout both seasons, with the exception of immature spiny dogfish (Table 1). During spring, immature males and mature females occupied significantly deeper and shallower depths, respectively, than those surveyed (Table 1; Fig. 3C). Ontogenetic differences in depth selection were found for all dogfish stages, with the exception of immature females and mature males (Table 2). During autumn, mature spiny dogfish and immature females occupied significantly shallower depths than those surveyed (Table 1; Fig. 4C). As observed during spring, ontogenetic differences were widespread. Mature females occupied shallower depths, whereas deeper depths were occupied by younger dogfish (Table 2; Fig. 4C).

Latitude

Associations with latitude were common throughout both seasons, with the exception of immature males (Table 1). During spring, all dogfish stages occupied significantly ($p < 0.05$) lower latitudes than those surveyed (Table 1; Fig. 3D). Neonates exhibited the shortest latitudinal range, while mature females displayed the largest. Ontogenetic differences in latitude association were widespread (Table 2), with mature females inhabiting the southernmost area (Fig. 3D). During autumn, trends were more diverse (Table 1; Fig. 4D). Mature males significantly ($p < 0.05$)

Table 3. Gini index quantifying the degree of aggregation for spiny dogfish in the Northeast (US) shelf large marine ecosystem during spring (1968–2009) and autumn (1963–2009).

Stage	Spring	Autumn	DOM	DEV
All	0.925	0.951	Aut	0.026
Neo	0.987	0.994	Aut	0.007
ImmM	0.984	0.988	Aut	0.004
MatM	0.965	0.976	Aut	0.011
ImmF	0.950	0.973	Aut	0.023
MatF	0.950	0.983	Aut	0.033

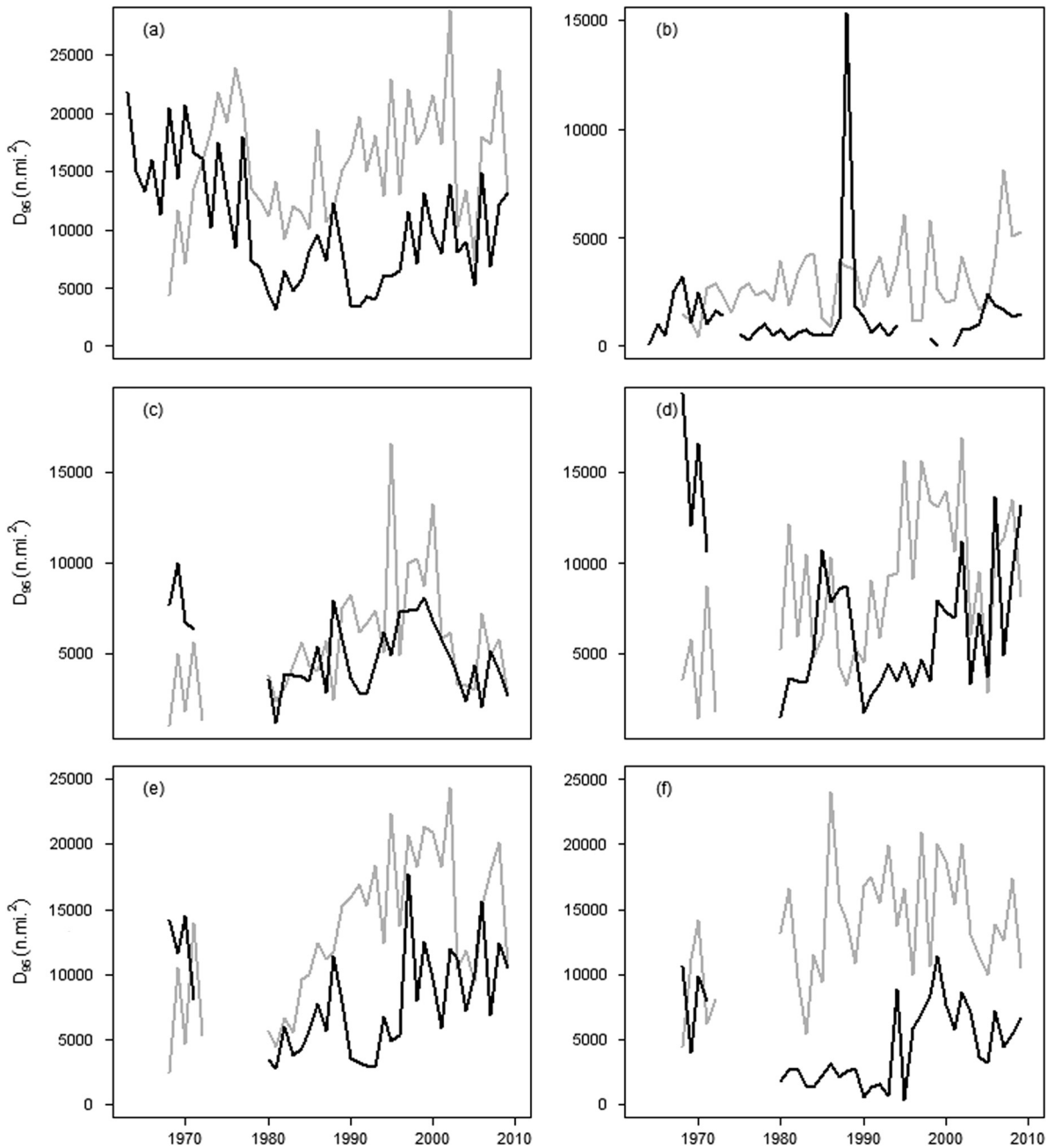
Note: Stages are as defined in Table 1. DOM refers to which season exhibited a higher aggregation index (Aut = autumn). DEV quantifies the deviation between seasonal Gini indices. Spiny dogfish were not sexed consistently until 1980.

occupied more northerly locations, while neonates selected more southerly regions compared with most dogfish stages (Table 2; Fig. 4D).

Degree of aggregation

Overall, all dogfish stages were more aggregated in distribution during autumn than spring, as evident by higher Gini indices (Table 3) and increased concavity (Fig. S3¹). Males and neonates revealed a relatively similar degree of aggregation between seasons (Fig. S3¹) as reflected by small deviations in Gini indices

Fig. 5. Annual variation in the distribution index (D_{95} , or minimum area (1 nautical mile = 1.852 km) over which 95% of the spiny dogfish population is spread) during spring (gray line) and autumn (black line) in the Northeast (US) shelf large marine ecosystem from 1963 to 2009. (a) All spiny dogfish, (b) neonates, (c) immature males, (d) mature males, (e) immature females, and (f) mature females. Note that y axes differ between panels, and the gap between 1973 and 1979 is due to inconsistencies in sexing of spiny dogfish.



(0.004–0.011; Table 3). Upon examination of DIF values, nonsignificant values during autumn were as great or greater than those deemed significant during spring, suggesting that the degree of aggregation interfered with the power of detecting a significant association (see Table 1). As an example, an identical range of DIF (0.04–0.43) for neonates during both seasons was significant during spring ($p = 0.000$) but not autumn ($p = 0.091$).

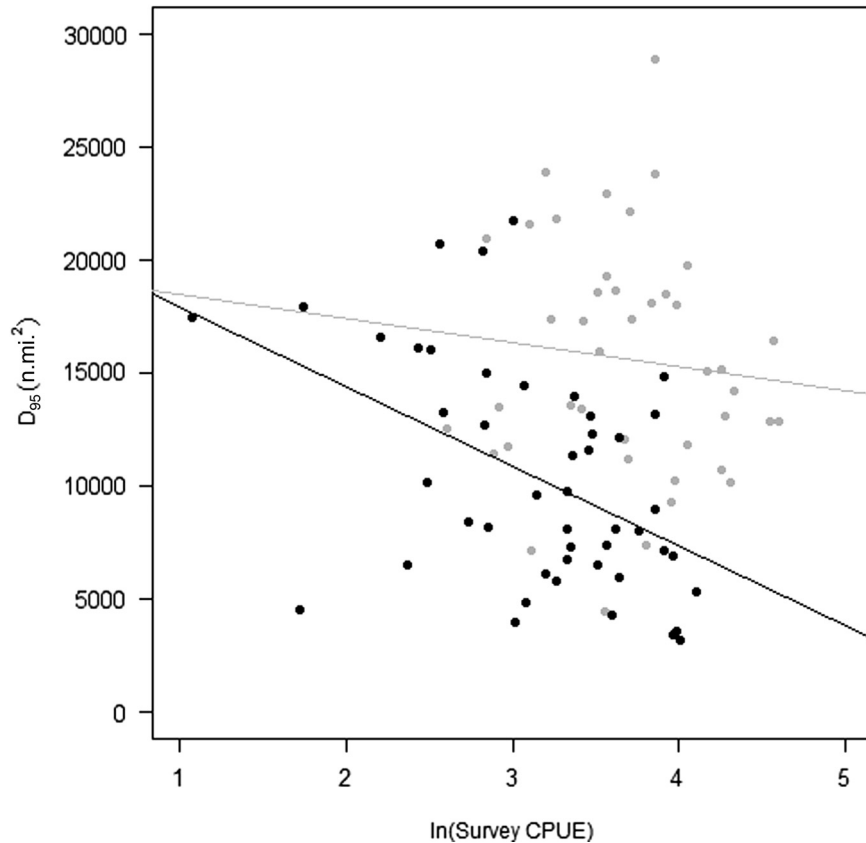
Density dependence

Based on collections from the NEFSC surveys, the D_{95} of spiny dogfish in the NES LME varied substantially throughout the time series during both seasons (Fig. 5). The area occupied during spring generally increased for most stages until the early to mid-

dle 2000s (Fig. 5). During autumn, D_{95} values remained relatively higher during the 2000s compared with other decades for all stages except immature males and neonates (Fig. 5).

No strong relationships were detected between geographic range (D_{95}) and abundance (survey CPUE) for any dogfish stage during either spring or autumn. However, significant negative relationships were found for all spiny dogfish combined during autumn through both regression ($D_{95} = -3520.8 \text{ CPUE} + 21\,433.8$; $R^2 = 0.22$, $p < 0.05$) and correlation analyses ($N = 47$; $r_p = -0.47$, $p < 0.05$, $\beta = 0.92$) (Fig. 6). Unfortunately the ability to detect significant relationships for individual dogfish stages appeared to be limited by low statistical power (i.e., $\beta < 0.70$).

Fig. 6. Relationship between annual abundance (survey CPUE) of all spiny dogfish and the distribution index (D_{95} , or minimum area (1 nautical mile = 1.852 km) over which 95% of the spiny dogfish population is spread) for spring (gray data) and autumn (black data) in the Northeast (US) shelf large marine ecosystem. D_{95} was regressed against the \log_e -transformed index of abundance (CPUE). Linear regression lines are shown for autumn (black; $D_{95} = -3520.8 \text{ CPUE} + 21\,433.8$; $R^2 = 0.22$, $p < 0.05$) and spring (gray; $D_{95} = -1071.0 \text{ CPUE} + 19\,540$; $R^2 = 0.01$, $p > 0.05$).



Correlations between \log_e -transformed environmental variables and distribution revealed opposing seasonal trends for all dogfish stages combined. During spring, analyses detected, with substantial power ($\beta = 0.84$), a positive association between the distribution and bottom temperature ($N = 42$, $r_p = 0.44$, $r_{sp} = 0.37$, $p < 0.05$) but not salinity. In contrast, distribution during autumn was negatively associated with bottom temperature ($N = 47$, $r_p = -0.56$, $r_{sp} = -0.41$, $p < 0.05$, $\beta = 0.99$) but positively associated with bottom salinity ($N = 14$, $r_p = 0.60$, $r_{sp} = 0.54$, $p < 0.05$, $\beta = 0.63$). We note the cause for concern over the power of the test for the second analysis reported above.

Link between environment and seasonal movements

The proportion of mature female catch within the Mid-Atlantic Bight was significantly related to mean bottom temperature conditions (proportion of catch = $-0.6550 \text{ BT}^2 + 0.7324 \text{ BT} + 0.7200$; $R^2 = 0.47$; $p < 0.05$) (Fig. 7). The proportion of mature females caught increased until mean bottom temperature exceeded approximately 10°C .

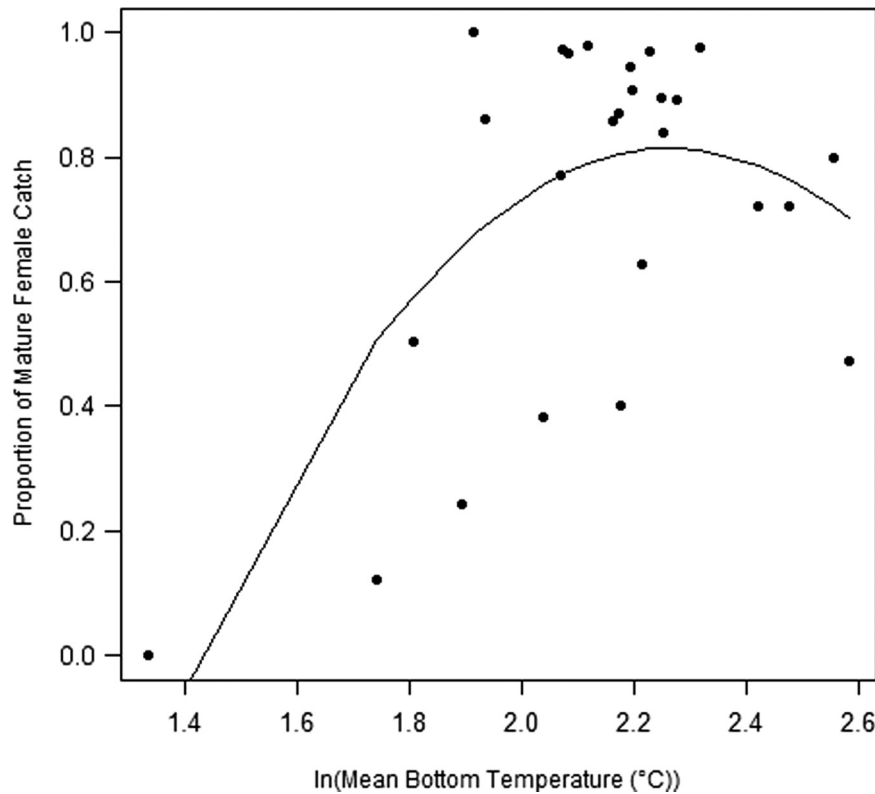
Discussion

The quantification of environmental preference is an essential first step towards effective management as it improves knowledge of the stock's distribution and increases the reliability of trends and forecasts (Perry and Smith 1994; Smith and Page 1996). Here we have shown how environmental preferences affect the distributions of spiny dogfish throughout its life history. Specifically, latitudinal associations provided the first quantitative evidence of north–south shifts in distribution by stage. During spring, selection for warmer, more saline, southerly regions was common

among all dogfish stages. In contrast, trends were more diverse during autumn, a season when an unknown proportion of spiny dogfish enter Canadian waters and therefore are unavailable to the NEFSC survey. During this season, larger spiny dogfish generally occupied warmer, shallower, and less saline waters compared with those surveyed. Strong ontogenetic selection of habitat highlights the need for management to consider stage-dependent trends, for example in defining essential habitat for conservation purposes. The proportion of mature female survey catch in the Mid-Atlantic Bight was significantly influenced by bottom temperature, suggesting a link between survey timing and environmental conditions.

The distinct seasonal ontogenetic latitudinal associations displayed by spiny dogfish may substantially affect the vulnerability of certain dogfish stages to harvest, thereby disproportionately impacting reproductive potential. Of particular concern is the selection of shallow inshore waters by mature females during autumn, a stage that is preferentially targeted for their larger size and profit (NEFSC 2006). Their close proximity to shore may increase the proportion vulnerable to fishers; if fishery interactions (i.e., spatial overlap) increase but are unaccounted for, artificially high densities may misrepresent true population dynamics. Given recent fisher accounts of large spiny dogfish aggregations in local areas (e.g., Gulf of Maine), research is needed to determine if these observations are reflective of regional trends (i.e., widespread increases in abundance) or if high densities remain local, either because of environmental conditions or prey distribution. Fishing within high-density areas can result in artificially high biomass estimates due to hyperaggregation or the aggregation of fish at low abundances (Rose and Kulka 1999). Spiny dogfish have been

Fig. 7. Relationship between the annual proportion of mature female catch (PC) in the Mid-Atlantic Bight and the mean bottom temperature (BT, °C) in the Northeast (US) shelf large marine ecosystem between Julian days 65–74. The annual proportion of catch was plotted against the \log_e -transformed mean bottom temperature (°C). The function shows a second-order polynomial with the following equation: $PC = -0.6550 BT^2 + 0.7324 BT + 0.7200$ ($R^2 = 0.47$; $p < 0.05$).



ranked as a species of greatest concern for targeted overexploitation because of their high potential for nonlinear catchability combined with a slow life history (Frisk et al. 2011). A comparison of ideal dogfish habitat with fishery behavior (via observer data) using spatial techniques such as kriging could investigate whether controversial increases in local abundance reflect increased spatial overlap in recent years.

The complex life history, seasonal movements, and apparent ubiquitous abundance of spiny dogfish poses a challenge for understanding catchability and developing robust estimates of stock trends for implementation of single-species and ecosystem-based management. Unfavorable environmental conditions (e.g., impinging cold water masses) may reduce the availability of a species to trawls and bias derived abundance estimates (Smith and Page 1996; Shepherd et al. 2002). It is commonly assumed that catchability and its subcomponents, availability and efficiency, are fixed in time (Walters and Martell 2004). However, for a species like spiny dogfish whose range shifts seasonally, timing of sampling and interannual variation in environmental drivers may bias results as shown by regression analysis, which revealed higher proportions of mature female catch in the Mid-Atlantic Bight during warmer temperatures. This issue will likely become more important as temperatures continue to increase with climate change.

During the development of stock assessments, catch rates are often standardized using generalized linear models (GLMs) (Maunder and Punt 2004), which relate a species' distribution to environmental conditions at the time of capture via environmental covariates (O'Brien and Rago 1996). In addition to assuming linearity of the response variable (i.e., abundance), these models assume a continuous and known distribution of the target species and generally do not take into account any relative habitat selectivity within a heterogeneous environment (Maunder et al. 2006).

If the full distribution is not sampled, as suspected for spiny dogfish whose distribution extends beyond the boundaries of the NEFSC survey (Nye et al. 2009), relative habitat choices may bias approaches to standardizing relative abundance estimates, thereby misrepresenting stock dynamics. Further, concern regarding distributional assumptions inherent in GLMs is augmented by strong ontogenetic habitat selection coupled with large-scale seasonal movements driven by environmental conditions hypothesized herein. Given these concerns, efforts aimed at standardizing relative abundance estimates may reduce apparent variability due to environmental conditions at the cost of introducing bias related to the behavior of spiny dogfish during spring.

It has been postulated that rates of colonization remain high for viviparous species for taxa ranging from reptiles to teleosts because of in utero transport of offspring across environmental extremes (Clutton-Brock 1991; Shine 1995; Goodwin et al. 2005). Such a process has previously been identified for many families of viviparous elasmobranchs (Goodwin et al. 2005). Spiny dogfish carry young for almost 2 years, traversing enormous distances and environments before returning to release pups in habitats similar to their neonate origins. This behavior may convey an evolutionary advantage for bearing young in warm protected habitat where survival and growth are maximized, at the adult's energetic expense, and has been linked to the selective pressure of competition, predation, and physiological trade-offs (Cushing 1976; Helfman 1978; Macpherson and Duarte 1991). During spring, recently impregnated females (stage A; Hisaw and Albert 1947) may inhabit different latitudes than females possessing more developed young (stage C; Hisaw and Albert 1947) or reproductively dormant females searching for mates. During autumn, mature females actively seek shallow warm waters where growth rates of internal embryos may be enhanced (Moore 1998). The utilization of low temperatures by

mature spiny dogfish during spring may help reduce energetic costs while enabling maximum reproductive potential for spawning events. Research is needed to connect habitat selection and in utero development to determine trade-offs between occupied habitat and reproductive success during the extended gestation period of spiny dogfish. The species “slow” life history (Musick 1999) and medium size combined with an iteroparous reproductive strategy (Frisk et al. 2002, 2005) highlight the potential for strong adult female habitat selection related to in utero growth (Moore 1998) to optimize lifetime fitness. Producing larger pups in protected environments likely contributes more towards first year survivability than would producing larger litter sizes.

An increase in exploitation of spiny dogfish necessitated the development of the Interstate Fishery Management Plan in 2000 to rebuild female spawning stock biomass (ASMFC 2002). Although it was initially expected that the stock would be rebuilt by 2020 (ASMFC 2002), in fact target reference points were met in 2010 (Rago and Sosebee 2010), partly the result of an abnormally large spawning stock estimate (i.e., mature female abundance) in the 2006 spring bottom trawl survey (NEFSC 2006). Specifically, mature female abundance was abnormally high from days 2 through 4 of the 2006 survey in relatively warmer temperatures, highlighting the importance and sensitivity of the survey to timing. This anomaly underlines the challenge of obtaining reliable abundance estimates from bottom trawl surveys when catchability varies with the environment (e.g., Smith and Page 1996) and with changes in population size (Frisk et al. 2011). While broad-scale movement in the Northwest Atlantic appears to be strongly dependent upon physical properties, food availability and (or) competition (Shepherd et al. 2002; Methratta and Link 2007) may also contribute towards observed trends in distribution and abundance. Additional consideration of ecological factors such as prey distributions may help to connect foraging behavior with population dynamics.

Ontogenetic movements related to habitat selection are widespread across marine taxa (Roff 2002; Jørgensen et al. 2008). Often, larval and juvenile stages inhabit shallow warm waters where food supply and growth rates are enhanced, while older fish occupy deeper, colder depths for lower metabolic costs and an increased life-span (Love 1970, 1980; Macpherson and Duarte 1991). Interestingly, spiny dogfish display an opposing pattern in that the species shifts from deeper depths during early life to shallower regions throughout adulthood (Shepherd et al. 2002; Methratta and Link 2007). Within the Northwest Atlantic, both goosefish (*Lophius americanus*) (Caruso 2002) and witch flounder (*Glyptocephalus cynoglossus*) (Markle 1975; Smith et al. 1975) also utilize continental slope waters as nursery grounds. For these species, this pattern likely reduces resource competition or intraspecific predation between stages and may relate to differences in dietary preferences (Shepherd et al. 2002). This pattern also adds to the complexity of spiny dogfish management; neonate spiny dogfish are generally found offshore and outside survey areas, making it difficult to assess their dynamics. During spring, neonates displayed the narrowest latitudinal range along the relatively warmer offshore waters of the eastern shores of Virginia and Georges Bank, suggesting this locality may be of importance to the survival and growth of young. By providing a preliminary understanding of neonate habitat, our results suggest neonate abundance, which serves as a proxy for recruitment in stock assessment models, may be strongly influenced by environmental conditions.

Although attempts to investigate density dependence within CPUE of dogfish stages were limited by statistical power, overall relative abundance (i.e., survey CPUE) increased as the geographic range contracted during autumn. The seasonal distribution of all stages combined was also significantly influenced by the environment. During spring, distribution indices were significantly correlated with temperature. This result may stem from seasonal

movements driven by temperature, where warmer waters could indicate an increase in the amount of optimal habitat. In contrast, during autumn warmer waters resulted in lower distribution indices. While this initially suggests range collapse, possibly due to widespread temperatures exceeding preferred thermal limits, it seems more likely an artifact of movement outside the survey area. In addition to environmental conditions, behavioral responses of solitary versus aggregated spiny dogfish to bottom trawls likely affects survey catchability as was observed for cod (Godø et al. 1999). Mature females during autumn were more aggregated as determined by Lorenz curves, possibly as a way to reduce potentially harmful mating advances from mature males (Veríssimo et al. 2011).

Our study provided critical information regarding ontogenetic habitat selection and distribution, which have important implications for stock assessment, particularly regarding survey utility and abundance estimates. Collectively, these results caution against the reliance on population trends derived solely from survey estimates of spiny dogfish recruitment (i.e., neonate CPUE) and spawning stock biomass (i.e., mature female CPUE) without taking environmental influences into account. Seasonal north-south movements, likely cued by bottom temperature, determine when spiny dogfish are detected by survey gear. Enhanced understanding of the joint effects of environmental factors, population biology, and harvests on the dynamics of exploited populations may provide additional insight into spiny dogfish dynamics, particularly in a changing climate.

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