Identifying Habitat Associations of Marine Fishes Using Survey Data: An Application to the Northwest Atlantic

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We present an objective method for identifying associations between environmental (habitat) conditions and the distributions of marine fishes using survey data. The method tests the null hypothesis of a random association between fish distribution and habitat conditions. We apply this method to bottom depth, temperature, and salinity data and to the distributions of four groundfish species (yellowtail flounder (*Pleuronectes ferruginens*, previously *Limanda ferruginea*), haddock (*Melanogrammus aeglefinus*), silver hake (*Merluccius bilinearis*), and Atlantic cod (*Gadus morhua*)) from trawl surveys of the eastern Scotian Shelf (northwest Atlantic) conducted in winter/spring (March) and summer (July) 1979–84. Haddock and silver hake maintained similar temperatures in winter and summer by changing their depth distributions (temperature-keepers), with haddock generally at cooler temperatures than silver hake. Yellowtail flounder (a depth-keeper) maintained similar depths between seasons while tolerating a wide range of temperatures and salinities. Atlantic cod were not consistently associated with particular depths in either spring or summer, and we were unable to distinguish between temperature or salinity as a single factor modifying their distributions, perhaps because of age-related effects. Identification of persistent habitat associations of marine fishes provides an opportunity to improve fisheries management procedures.

Nous présentons une méthode objective permettant d'identifier les associations entre les conditions environnementales (habitat) et les distributions des poissons marins en utilisant les données fournies par des relevés. La méthode teste l'hypothèse nulle d'une association aléatoire entre la distribution des poissons et des conditions de l'habitat. Nous appliquons cette méthode à des données sur la profondeur au fond, la température et la salinité et à la distribution de quatre espèces de poisson de fond (limande à queue jaune (*Pleuronectes ferruginens*, auparavant le *Limanda ferruginea*), aiglefin (*Melanogrammus aeglefinus*), merlu argenté (*Merluccius bilinearis*) et morue franche (*Gadus morhua*)) à partir de relevés effectués au chalut sur l'est de la plate-forme néo-écossaise (Atlantique nord-ouest) à deux périodes : hiver/printemps (mars) et été (juillet) de 1979 à 1984. L'aiglefin et le merlu argenté se maintenaient à des températures similaires en hiver et en été en changeant de profondeur (préférence pour la température), l'aiglefin se tenant généralement à des températures plus basses que le merlu argenté. La limande à queue jaune (préférence pour la profondeur) se maintenait à la même profondeur d'une saison à l'autre mais tolérait une fourchette large de températures et de salinité. La morue franche n'était pas associée de façon régulière à une température donnée ni au printemps ni en été, et nous n'avons pas pu faire la différence entre la température ou la salinité comme facteur modifiant leur répartition, ce qui est peut-être causé par des effets liés à l'âge. La connaissance des associations stables avec l'habitat chez les poissons marins donne l'occasion d'améliorer les méthodes de gestion des pêches.

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Knowledge of the environmental conditions at which fish occur can lead to improved abundance estimates from trawl surveys (Smith 1990; Smith et al. 1991), identification of species assemblages (Mahon and Smith 1989), and understanding of environmental influences on fish distribution and migration patterns (e.g., Mysak 1986; Rose and Leggett 1988; Xie and Hsieh 1989). Reactions of freshwater fishes to temperature have received considerable attention, in particular regarding the impacts of thermal effluent (e.g., Coutant 1977; Richards et al. 1977). In the marine environment, the most common approach has been to determine environmental associations empirically using field studies and surveys. In the northwest (NW) Atlantic, Scott (1982a) examined depth, temperature, and salinity preferences of common groundfishes on the continental shelf off Nova Scotia from survey data collected during summer 1970–79. However, many fish species on the Scotian Shelf undertake seasonal migrations. Environmental conditions also change seasonally. It is unknown how fish in this area react to these changes, and whether associations with environmental conditions determined during summer can be applied to other seasons.

The objective of this paper is to identify significant associations between environmental (habitat) conditions and the

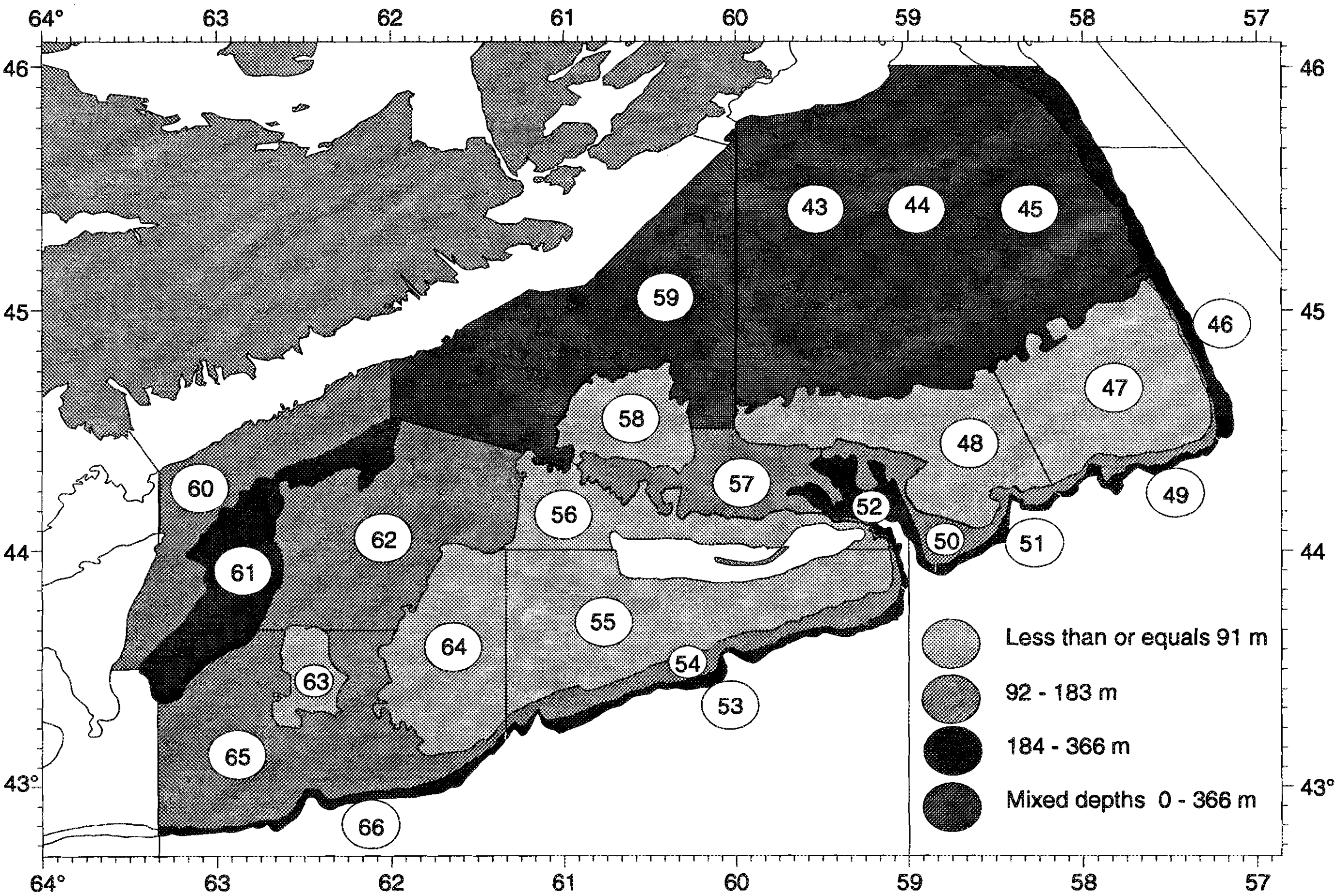

FIG. 1. Stratification scheme for spring and summer 1979–84 surveys of the eastern Scotian Shelf, NW Atlantic. Strata are identified by the numbers in circles and are based on the depth zones indicated.

distributions of four species of groundfish on the eastern Scotian Shelf in the NW Atlantic. To achieve this purpose, we develop an objective method to define fish–habitat associations which allows rigorous comparisons to be made with the ranges of environmental conditions available during the surveys. Strong associations with particular habitat conditions, especially those which may vary seasonally or interannually, will help predict changes in fish distributions as a response to changes in oceanographic conditions. For reasons of data availability, the habitat conditions we consider are temperature, salinity, and depth. The fish species we consider are yellowtail flounder (*Pleuronectes ferruginens*, previously *Limanda ferruginea*), haddock (*Melanogrammus aeglefinus*), silver hake (*Merluccius bilinearis*), and Atlantic cod (*Gadus morhua*). These are common groundfish species on the eastern Scotian Shelf and occur from shallow and intermediate depths with wide ranges of temperature and salinity (e.g., yellowtail flounder, Atlantic cod, haddock; mean conditions 60–90 m, 2–7°C, 31–34 psu) to deep depths and warm temperatures (e.g., silver hake; mean conditions 165 m and 7–10°C) (Scott 1982a; Smith et al. 1991).

Methods

Fish catch and hydrographic data were obtained from standard groundfish research trawl surveys of the eastern Scotian Shelf (NAFO Area 4VsW) conducted by the Marine Fish Division (Bedford Institute of Oceanography, Dartmouth, N.S., and Biological Station, St. Andrews, N.B.) of the Canadian Department of Fisheries and Oceans. The survey used a stratified random design, with strata based on depth boundaries of 91, 183, and 366 m (50, 100, and 200 fathoms) (Fig. 1). Inshore areas with bottom depths <28 m were not sampled. The survey sample unit was defined as the bottom area fished by a Western IIA trawl towed at a constant speed (3.5 kn) for a distance of 3.24 km (1.75 nautical miles). Locations of sample units (sets) were selected randomly within each stratum before each cruise. All species caught were identified, counted, and weighted to the nearest kilogram and expressed as catch per standard sample unit. Following each set, bottom-water samples were obtained with reversing bottles for measurements of temperature and salinity. Set depth was taken as the mean bottom depth during the tow determined from continuous echo sounder records. Further details of sample protocol are available in Halliday and Koeller (1981). Note that this protocol is unable to resolve variability and fish–environment associations at scales finer than the length of a tow, e.g., that might be caused by crossing frontal features. The summer survey has been conducted in July since 1970, while an additional survey was conducted in March (late winter/early spring) from 1979 to 1984. To compare seasons the analyses were restricted to the years 1979–84.

Our approach to identifying associations between catches of the four representative species and the environmental data from the surveys has three steps. First, we characterize

TABLE 1. Definitions of quantities associated with trawl survey calculations (Cochran 1977, p. 89–92; Smith 1988) and equations in the text.

n_h	=	number of hauls or sets in stratum h ($h = 1, \ldots, L$)
n	=	$\sum_{h=1}^{L} n_h$ (in the stratified case), total number of hauls
N_h	=	total number of possible sets in stratum h
N	=	$\sum_{h=1}^{L} N_h$, total number of possible sets overall
W_h	=	N_h/N, proportion of the survey area in stratum h
y_{hi}	=	number of fish of a particular species caught in set i ($i = 1, \ldots, n_h$) and stratum h; y_i is the same quantity but for the random (nonstratified) survey design
$\bar{y}_h$	=	estimated mean abundance of a particular species of fish in stratum h; $\bar{y}$ is the same quantity but for the random (nonstratified) survey design
$\bar{y}_{st}$	=	$\sum_{h=1}^{L} W_h \bar{y}_h$, estimated stratified mean abundance for a particular species of fish
x_{hi}	=	measurement for a hydrographic variable in set i of stratum h; x_{hij} indexes the measurement for hydrographic variable j in set i of stratum h when more than one hydrographic variable is considered simultaneously

the general frequency distribution of the habitat variable (depth, temperature, or salinity) by constructing its empirical cumulative distribution function (cdf). Commonly, the probability associated with each observation in a cdf is $1/n$, but the stratified random survey design results in a probability of $1/n_h$ within each stratum (all symbols are defined in Table 1). Therefore the cdf for any habitat variable (x_{hi}) is constructed to incorporate the survey design as (Chambers and Dunstan 1986)

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

with the indicator function

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

Here, t represents an index, ranging from the lowest to the highest value of the habitat variable at a step size appropriate for the desired resolution. Equation 1 is calculated over all values of t for each habitat measurement (x_{hi}) available. The cumulative distribution functions derived from equation 1 (e.g., depth; Fig. 2a) can be used to identify the proportion within any range of the habitat variable during the survey. For example, the range of depths that occurred within the central 50% (between the 25th and 75th percentiles) or the central 95% (between the 2.5th and 97.5th percentiles) of the area surveyed can be easily calculated from Fig. 2a.

Including the survey stratification scheme via the W_h/n_h terms ensures that we have an unbiased estimate of the frequency distribution for the habitat measurement. Ignoring the stratification by replacing W_h/n_h with $1/n$ would result in either under- or overestimating the area associated with any particular value of the habitat measurement. However, the term W_h/n_h does simplify to $1/n$ when the number of sets allocated to each stratum is proportional to the size of the stratum (i.e., $n_h = nW_h$). That is, stratification can be ignored when the allocation of sets is strictly proportional to stratum size.

Second, we associate the catch of fish (in numbers) of a particular species in each set with the habitat conditions at that set as a weight in the form

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

Scaling the number of fish caught (Y_{hi}) by the stratified mean number of fish caught ($\bar{y}_{st}$) in equation 2 results in $g(t)$ summing to 1 over all values of t. If large values of $y_{hi}/\bar{y}_{st}$ are consistently associated with particular habitat conditions, then this suggests a strong association between the fish species and those habitat conditions. The cumulative distribution functions calculated from equation 2 illustrate the range of conditions at which the species occurred and can be compared with the habitat conditions available in the sampled area as calculated with equation 1. For example, 50% of the depths surveyed in March 1984 (curve $f(t)$, Fig. 2a) were less than 110 m, while 50% of the yellowtail flounder (curve $g(t)$, Fig. 2a) were caught at depths less than 60 m. The curve $g(t)$ can differ widely from the habitat curve $f(t)$ depending on the range of conditions occupied by the fish. At one extreme, if the fish were associated with one depth only (e.g., 100 m), $g(t)$ would be zero for $t < 100$ and equal to 1.0 for $t \ge 100$. If there was no particular association between fish distributions and the habitat variable within the area surveyed, for example if the fish were randomly distributed with respect to the habitat variable, then $g(t)$ and $f(t)$ would be almost identical.

The third step is to determine the strength of the association between catch and the habitat variable by assessing the degree of difference between the two curves, $g(t)$ and $f(t)$. Our test statistic is similar to that used for comparing empirical cdf's in Kolmogorov–Smirnov tests (see Conover 1980). We calculate the maximum absolute vertical distance between $g(t)$ and $f(t)$ as

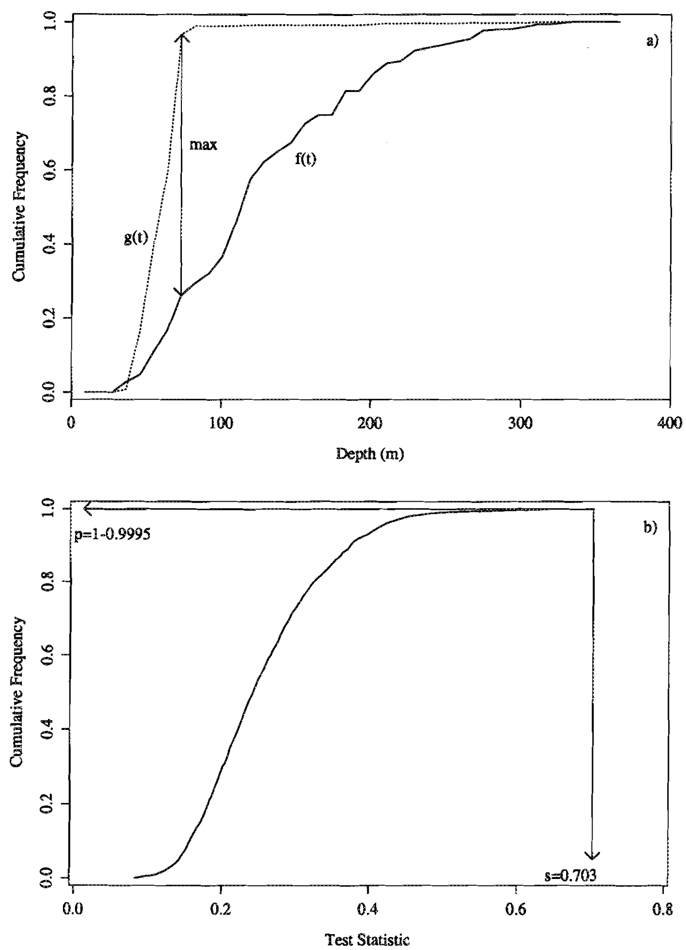

FIG. 2. (a) Cumulative distribution functions for observed depths ($f(t)$; equation 1) and depths as weighted by the number of yellowtail flounder caught ($g(t)$; equation 2) during the March 1984 bottom trawl survey on the eastern Scotian Shelf. The coordinate labelled "max" represents the depth at which the difference between the two curves ($|g(t) - f(t)|$) was maximum. (b) Cumulative distribution function for 2000 randomizations of the test statistic (equation 3) for yellowtail flounder depth distributions versus the observed depths from the March 1984 bottom trawl survey of the eastern Scotian Shelf. s represents the actual test statistic obtained from equation 3, while p represents its probability based on 2000 randomizations, i.e., a test statistic as large or larger than 0.703 was obtained in only 1 out of 2000 randomizations (see text for details).

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

where $|g(t) - f(t)|$ indicates the absolute value of the difference between $g(t)$ and $f(t)$ at any point t.

The stratified random survey design complicates distributional assumptions for the test statistic in equation 3, and therefore the standard tables for the Kolmogorov–Smirnov test, or indeed any goodness-of-fit test, cannot be used (see Rao and Thomas 1989). Instead, we developed a randomization procedure (Noreen 1989) to evaluate the significance of the test statistic. We modelled the distribution of the test statistic under the null hypothesis of random association between fish catch (numbers) and habitat variable through Monte-Carlo sampling. This was done by randomizing the pairings of $(W_h/n_h)[(y_{hi} - \bar{y}_{st})/\bar{y}_{st}]$ and x_{hi} over all h and i for the data within a survey and then calculating the test statistic in equation 3 for the new pairs. The x_{hi} for the pairings were obtained by sampling with replacement the observed x_{hi} with probability $W_h n_h$. This procedure was repeated a large number of times to give a pseudo-population of test statistics under the null hypothesis. The test statistic for yellowtail flounder and depth in March 1984 (Fig. 2b) was equal to 0.703 (also indicated as "max" in Fig. 2a) which was greater than or equal to 99.95% (2000 out of 2001) of the test statistics in the randomization distribution. There were 2001 test statistics when the original observed pairing of the data was included. Interpreting these results similar to a standard statistical hypothesis test, we note that the probability of obtaining a test statistic as large as 0.703 by chance is close to zero (p = 0.0005) and conclude that there was a very strong association by yellowtail flounder with a specific range of depths that was more restricted than the full range of depths available in the survey area during March 1984. This randomization test is a two-sided test, since it is the magnitudes of the absolute differences between $g(t)$ and $f(t)$ that are of interest.

However, environmental conditions are often correlated, for example where temperature decreases with increasing depth, which suggests that an association between a species and a particular depth range may also be confounded by an association with temperature. This problem can be explicitly considered by extending equations 2 and 3 to two (or more) habitat variables simultaneously. For k variables, equations 1 and 2 can be written as

$$(4)\quad \begin{aligned} f(\boldsymbol{t}) &= \sum_h\sum_i \frac{W_h}{n_h} I(\boldsymbol{x}_{hi}) \\ g(\boldsymbol{t}) &= \sum_h\sum_i \frac{W_h}{n_h}\frac{y_{hi}}{\bar{y}_{st}} I(\boldsymbol{x}_{hi}) \end{aligned}$$

where

$$I(\boldsymbol{x}_{hi}) = \begin{cases} 1, & \text{if } (x_{hi1} \le t_1, x_{hi2} \le t_2, \ldots, x_{hik} \le t_k); \\ 0, & \text{otherwise.} \end{cases}$$

Boldface type for $\boldsymbol{t}$ and $\boldsymbol{x}$ indicates vectors of habitat variables. In the two-variable case, $g(\boldsymbol{t})$ can be represented as a three-dimensional surface in which the cumulative frequency forms the vertical axis. The test statistic (equation 3) is modified as

$$(5)\quad \max_{\forall \boldsymbol{t}}\left|g(\boldsymbol{t})-f(\boldsymbol{t})\right| = \max_{\forall \boldsymbol{t}}\left|\sum_h\sum_i \frac{W_h}{n_h}\left(\frac{y_{hi}-\bar{y}_{st}}{\bar{y}_{st}}\right)I(\boldsymbol{x}_{hi})\right|.$$

Results

Univariate cdf Results

Associations between the four groundfish species and bottom depth varied with species during the March 1984 survey. Atlantic cod were distributed in proportion to the available depths (Fig. 3a), and the test statistic derived from equation 3 indicated little difference between the two cdf's ($p = 0.98$). We conclude that Atlantic cod had no association with bottom depth within the sampled depth range (30–300 m) in March 1984. Haddock were distributed at shallower depths than the total range available (Fig. 3a), and the test statistic indicated a moderate association of haddock with these shallow depths ($p = 0.096$) during spring 1984. Both yellowtail flounder and silver hake had cumulative frequency distributions that reflected very strong associations with particular depths ($p < 0.01$ for both). Yellowtail flounder were associated with shallow depths; 97.5% of the population on the eastern Scotian Shelf occurred at bottom depths <74 m, which represented the shallowest 25% of the survey area. Silver hake were associated with deep depths; 97.5% occurred where bottom depths were deeper than 118 m, which represented the deepest 40% of the eastern shelf.

Three of the four groundfish species showed strong associations with temperature in March 1984 (Fig. 3b). Yellowtail flounder were associated with cooler temperatures ($p < 0.01$), as 97.5% of the population occurred at <4.9°C, at the lower 50% of available temperatures. Silver hake were associated with warmer temperatures ($p < 0.01$), as 75% of the population occurred above 7.5°C, the warmest 25% of observed temperatures. Haddock were associated ($p = 0.01$) with intermediate temperatures (4–6°C), but Atlantic cod had no association with temperature ($p = 0.34$) during the March 1984 survey.

The patterns of salinity associations in March 1984 were similar to those for depth (Fig. 3c). Yellowtail flounder were associated with lower salinities ($p < 0.01$) and silver hake with higher salinities ($p < 0.01$). Almost all yellowtail flounder (97.5%) occurred at salinities <32.9 (the lower 45% of observed salinities) whereas 75% of silver hake occurred at salinities >34.2 (the upper 25% of salinities observed on the eastern shelf). Haddock were weakly associated with salinity ($p = 0.13$), whereas Atlantic cod showed no association ($p = 0.70$).

These trends in March 1984 were consistent for March cruises from 1979 to 1984 (Table 2). Yellowtail flounder were always different from a random depth distribution, and generally different from temperature and salinity. Haddock were not strongly associated with depth, but were more strongly associated with temperature and salinity, and silver hake were generally different from a random association with all three habitat variables. Atlantic cod rarely showed strong associations with bottom depth, temperature, or salinity. Much of the variability in these test results can be attributed to interannual variability in bottom temperature, salinity, and depth (where variability in depth resulted from differences in set locations and missed sets due to sea ice). For example, yellowtail flounder were very weakly associated with temperature in March 1983 ($p = 0.27$), but strongly associated ($p < 0.01$) in March 1984 (Table 2). These differences were due to cooler conditions in 1983, when the median temperature for both habitat and yellowtail flounder distributions was 2.7°C, compared with 1984 when the median habitat temperature was 4.8°C whereas it was 1.9°C for yellowtail flounder (Fig. 4a). These temperature shifts occurred without any difference in depth distributions of yellowtail flounder between years (Fig. 4b).

Interannual variability of temperature and salinity presents the problem of distinguishing species with absolute or relative associations with particular conditions, e.g.,

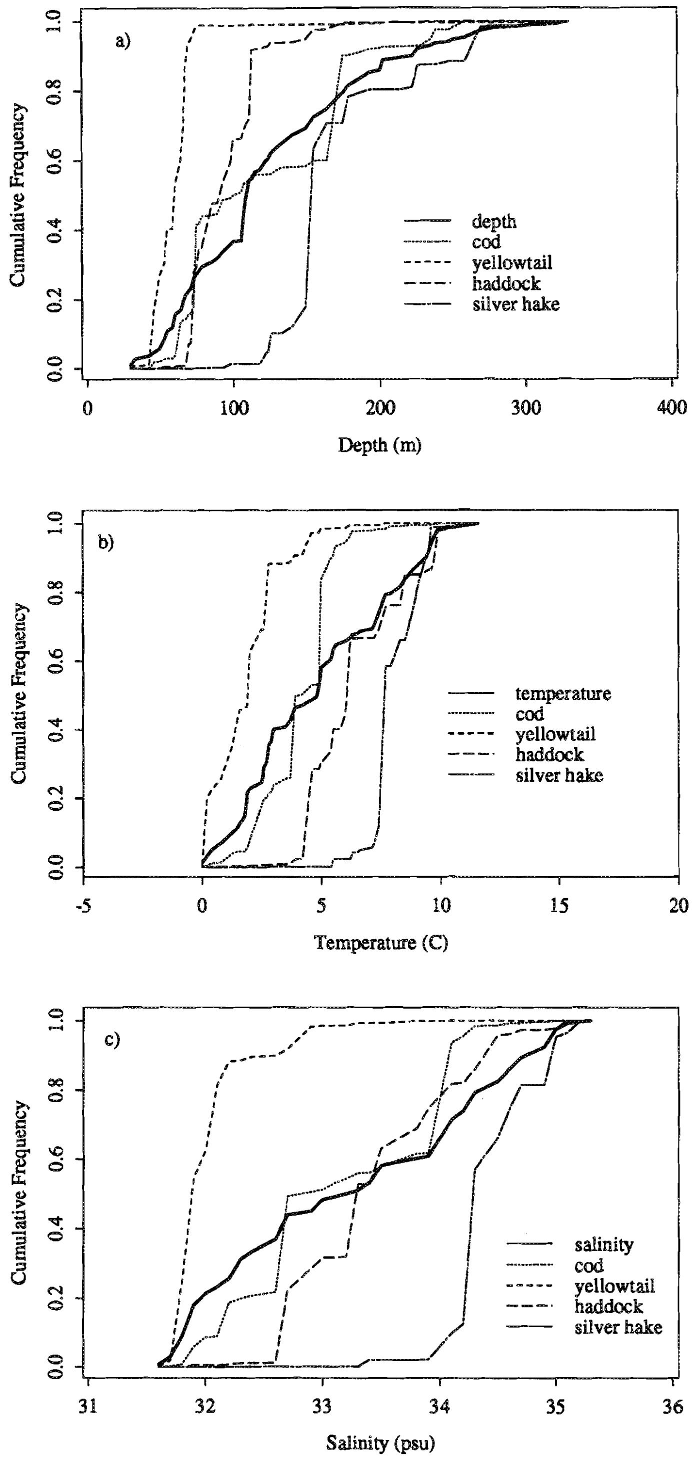

FIG. 3. Cumulative frequency distributions of habitat variables and catch-weighted data from the March 1984 trawl survey of the eastern Scotian Shelf for (a) bottom depth, (b) temperature, and (c) salinity. Test values for statistical significance are presented in Table 2.

species occur at relatively cooler or warmer temperatures rather than specific temperatures. Species having absolute associations should exhibit less variability among years compared with the variability of that habitat parameter itself. Three of the four species demonstrated such absolute associations with particular habitat conditions during the 1979–84 spring surveys. As shown by the relative error column of

TABLE 2. Test results for statistical differences in the catch-weighted cumulative frequency distributions compared with the unweighted cumulative frequency distributions of bottom depth, temperature, and salinity. Table entries are probability (p) values for having a test statistic (from the randomization procedure) as great or greater than that which was observed (equation 3).

		Atlantic cod		Yellowtail flounder		Haddock		Silver Hake	
Year	Habitat variable	March	July	March	July	March	July	March	July
1979	Depth	0.57	<0.01	<0.01	<0.01	0.97	0.01	0.02	0.02
1980		0.04	0.02	<0.01	<0.01	0.24	<0.01	<0.01	0.06
1981		0.53	0.13	<0.01	<0.01	0.22	0.16	0.54	0.20
1982		0.74	<0.01	<0.01	<0.01	0.33	0.02	0.20	0.01
1983		0.98	<0.01	<0.01	<0.01	0.10	<0.01	0.01	0.53
1984		0.98	0.52	<0.01	<0.01	0.10	<0.01	<0.01	0.40
1979	Temperature	0.24	0.25	<0.01	0.75	0.09	0.02	<0.01	<0.01
1980		0.32	0.02	<0.01	0.53	<0.01	0.08	<0.01	<0.01
1981		0.62	<0.01	0.02	0.46	0.25	<0.01	0.08	<0.01
1982		0.23	0.78	0.01	0.51	<0.01	0.02	0.02	<0.01
1983		0.66	0.47	0.27	0.17	0.02	0.09	<0.01	<0.01
1984		0.34	<0.01	<0.01	0.43	0.01	0.01	<0.01	<0.01
1979	Salinity	0.24	<0.01	<0.01	<0.01	0.08	0.02	<0.01	<0.01
1980		0.49	0.03	<0.01	<0.01	0.02	0.34	<0.01	<0.01
1981		0.11	<0.01	<0.01	<0.01	0.97	0.89	0.86	0.28
1982		0.33	0.42	0.21	<0.01	0.01	0.93	0.03	0.02
1983		0.67	<0.01	0.01	<0.01	<0.01	<0.01	<0.01	0.21
1984		0.70	0.15	<0.01	<0.01	0.13	0.60	<0.01	0.44

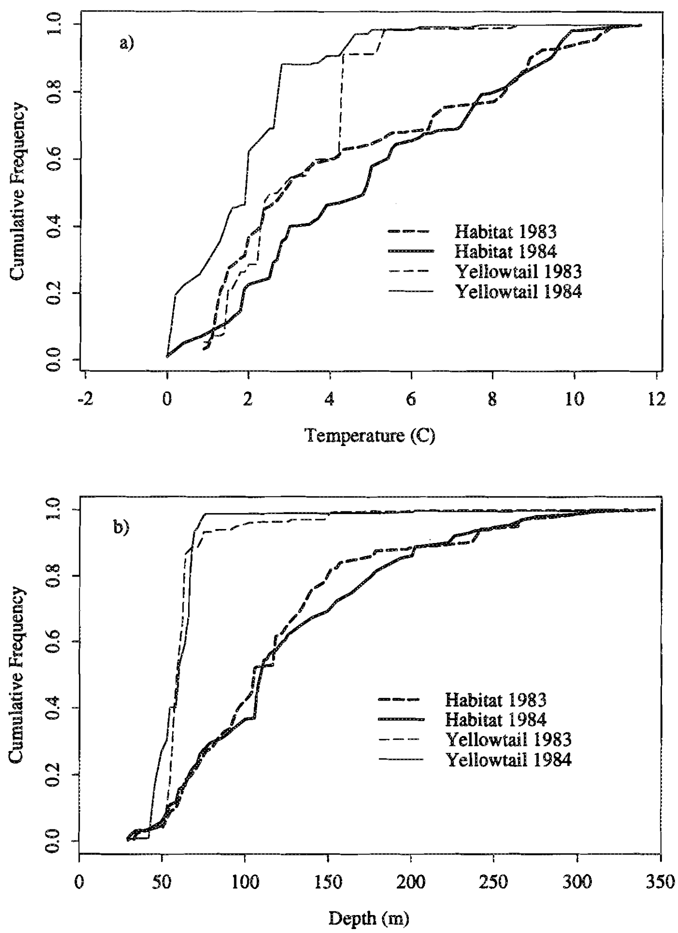

FIG. 4. Cumulative distribution functions for the observed (habitat) and yellowtail flounder (a) temperatures and (b) depths during surveys of the eastern Scotian Shelf in March 1983 and 1984.

Table 3, the median depth of yellowtail flounder was less variable than the median bottom depth, median temperatures for haddock and silver hake were less variable than the median available temperature, and the median salinity for yellowtail flounder was less variable than the median of the available salinities.

To investigate the effect of seasonal differences in fish behaviour (e.g., spring spawning versus summer feeding) on associations with water mass characteristics, the analysis was repeated using the summer (July) survey data for 1979–84. The cdf analysis clearly demonstrates the seasonal warming and freshening of bottom conditions during summer, the corresponding changes in temperature and salinity associations of yellowtail flounder despite little change of depth, and the movement of Atlantic cod to shallower depths in summer (Fig. 5). Yellowtail flounder showed strong associations with depth and salinity but not with temperature during summer, and haddock and silver hake were strongly associated with temperature (Table 2). However, Atlantic cod during the summer surveys were generally more associated with depth, temperature, and salinity than during the March surveys (Table 2). Variability and comparison of median conditions in summer (Table 4) were consistent with results from the spring surveys (Table 3). The median temperatures of haddock and silver hake varied less than the median of the available temperatures, and the median salinity of yellowtail flounder varied less than the median of the available salinities (Table 4). Although yellowtail flounder in summer were more variable with depth than the available habitat (larger relative error, Table 4), they were much less variable than the other three species, consistent with an absolute association with a particular depth range.

Bivariate cdf Results

The distributions of depth, temperature, and salinity on the eastern Scotian Shelf are not independent. The water mass

TABLE 3. Average value, standard deviation, and relative error (defined as the standard deviation/average value) of the median (50th percentile) of bottom depth, temperature, and salinity from the habitat and catch-weighted cumulative frequency curves calculated from March surveys over the period 1979–84. Asterisks indicate species–habitat associations for which the relative error was less than the habitat conditions.

Habitat variable	Habitat or species	Average value	Standard deviation	Relative error
Depth (m)	Habitat	116.2	8.8	0.0757
	Yellowtail flounder	61.1	2.9	0.0475*
	Atlantic cod	114.9	27.6	0.2402
	Haddock	92.4	10.6	0.1147
	Silver hake	147.5	15.2	0.1031
Temperature (°C)	Habitat	2.8	1.2	0.4286
	Yellowtail flounder	1.4	1.1	0.7957
	Atlantic cod	2.6	1.4	0.5385
	Haddock	5.0	1.4	0.2800*
	Silver hake	7.9	1.9	0.2405*
Salinity (psu)	Habitat	32.9	0.20	0.0061
	Yellowtail flounder	32.2	0.17	0.0053*
	Atlantic cod	32.8	0.42	0.0128
	Haddock	33.5	0.31	0.0093
	Silver hake	34.2	0.71	0.0208

TABLE 4. Average value, standard deviation, and relative error (defined as the standard deviation/average value) of the median (50th percentile) of bottom depth, temperature, and salinity from the habitat and catch-weighted cumulative frequency curves calculated from July surveys over the period 1979–84. Asterisks indicate species–habitat associations for which the relative error was less than the habitat conditions.

Habitat variable	Habitat or species	Average value	Standard deviation	Relative error
Depth (m)	Habitat	108.0	4.6	0.0426
	Yellowtail flounder	51.4	4.0	0.0778
	Atlantic cod	60.4	15.9	0.2632
	Haddock	63.3	19.0	0.3002
	Silver hake	142.2	38.6	0.2714
Temperature (°C)	Habitat	5.1	1.4	0.2745
	Yellowtail flounder	4.8	1.8	0.3750
	Atlantic cod	4.4	1.7	0.3864
	Haddock	6.7	1.1	0.1642*
	Silver hake	8.2	0.9	0.1098*
Salinity (psu)	Habitat	33.2	0.25	0.0075
	Yellowtail flounder	32.3	0.17	0.0056*
	Atlantic cod	32.5	0.25	0.0077*
	Haddock	32.8	0.68	0.0207
	Silver hake	34.0	0.84	0.0248

structure on the Scotian Shelf consists of an upper layer, a cold intermediate layer, and a warm deep layer (e.g., Hachey 1942), which leads to correlations among temperature, salinity, and depth. The effect of these correlated environmental variables on fish–habitat associations was examined using the bivariate form of the cdf analysis (equations 4 and 5).

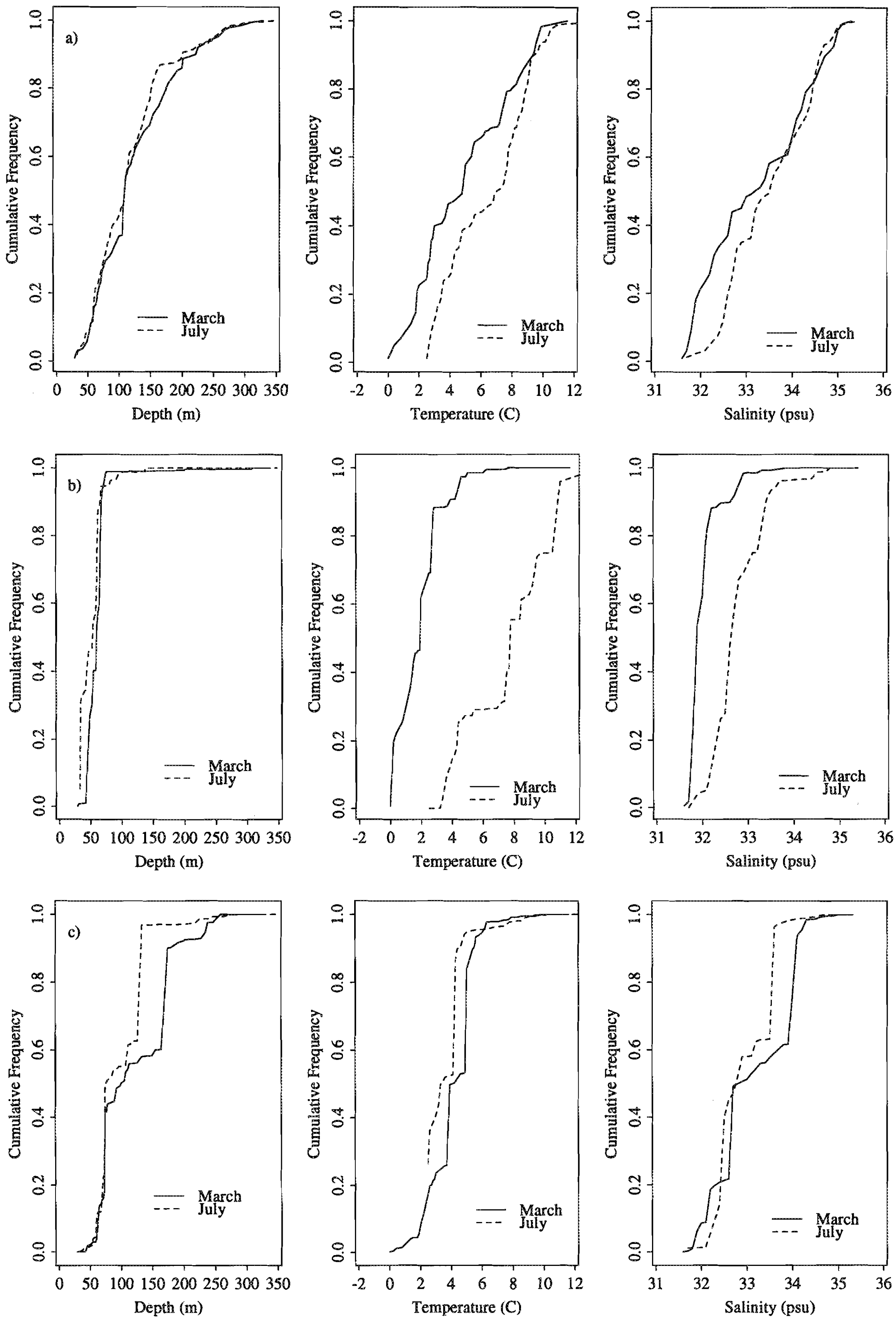

FIG. 5. Cumulative distribution functions for (a) observed (habitat) bottom depth, temperature, and salinity and as weighted by catches of (b) yellowtail flounder and (c) Atlantic cod from surveys of the eastern Scotian Shelf conducted in winter/spring (March) and summer (July) 1984.

The shapes and general locations of the bivariate cdf surfaces varied greatly among species within a season (Fig. 6). The available depths and temperatures were evenly distributed over the full range of conditions observed during March 1984, as indicated by the absence of large steps in the spring habitat panel of Fig. 6. In contrast, yellowtail flounder

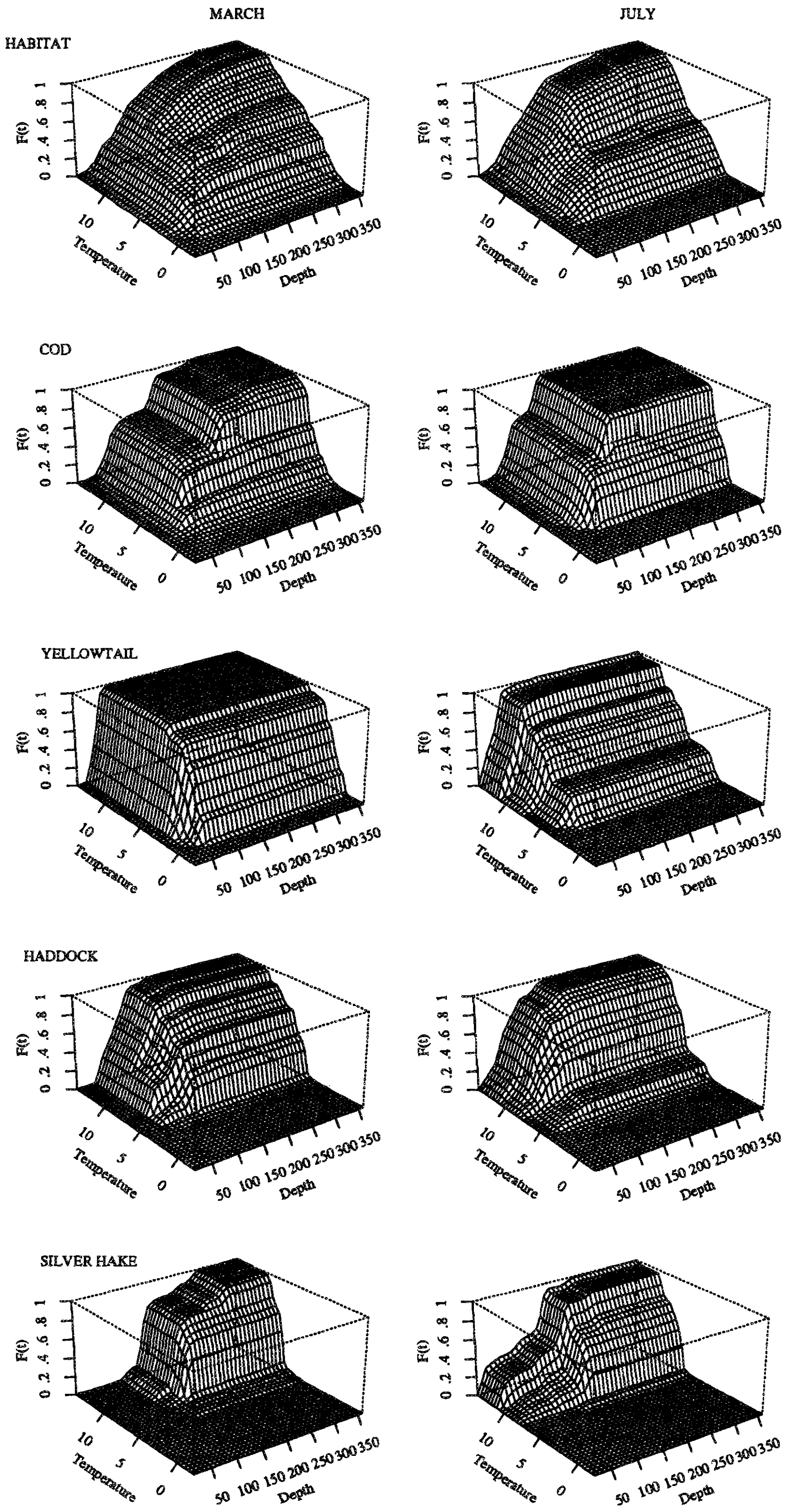

FIG. 6. Bivariate cumulative frequency surfaces (equation 4) for the habitat variables bottom depth and temperature and the four fish species from the March and July 1984 surveys of the eastern Scotian Shelf. Depths are in metres. "$F(t)$" refers to the bivariate cumulative frequency; $F(t) = 1$ represents the depth and temperature conditions up to which 100% of the fish populatin (or habitat) occurred as estimated by the survey. The back walls of the temperature or depth axes represent the same cumulative frequency distribution functions as calculated for the univariate cases (equations 1 and 2).

TABLE 5. Results from the randomization test (equations 4 and 5) for bivariate associations between catch and each of two hydrographic variables. Entries are p-values from tests which correspond to the probability of getting, by chance, a test statistic as large as was observed from the survey.

Year	Habitat variable	Atlantic cod March	Atlantic cod July	Yellowtail flounder March	Yellowtail flounder July	Haddock March	Haddock July	Silver Hake March	Silver Hake July
1979	Depth and temperature	0.92	<0.01	<0.01	<0.01	0.26	0.07	<0.01	0.01
1980		0.38	0.14	<0.01	<0.01	0.01	0.01	<0.01	0.04
1981		0.96	0.03	<0.01	<0.01	0.53	0.02	0.58	0.04
1982		0.58	<0.01	<0.01	<0.01	<0.01	0.12	0.18	0.01
1983		0.78	<0.01	<0.01	<0.01	0.10	<0.01	<0.01	0.06
1984		0.63	0.08	<0.01	<0.01	0.07	0.03	<0.01	0.04
1979	Depth and salinity	0.95	<0.01	<0.01	<0.01	0.28	0.06	<0.01	0.17
1980		0.38	0.15	<0.01	<0.01	0.24	0.03	<0.01	0.06
1981		0.96	<0.01	<0.01	<0.01	0.46	0.31	0.58	0.59
1982		0.58	0.02	<0.01	<0.01	0.14	0.32	0.19	0.12
1983		0.78	<0.01	<0.01	<0.01	0.02	<0.01	<0.01	0.46
1984		0.63	0.28	<0.01	<0.01	0.22	0.01	<0.01	0.29
1979	Temperature and salinity	0.63	0.01	<0.01	<0.01	0.18	0.03	<0.01	0.17
1980		0.71	0.12	<0.01	<0.01	<0.01	0.10	<0.01	0.02
1981		0.44	<0.01	<0.01	<0.01	0.40	<0.01	0.19	0.01
1982		0.42	0.55	<0.01	<0.01	<0.01	0.04	0.19	0.01
1983		0.60	<0.01	0.03	<0.01	<0.01	<0.01	<0.01	0.02
1984		0.41	0.05	<0.01	<0.01	0.02	0.02	<0.01	<0.01

occurred at low temperatures and shallow depths, silver hake occurred at high temperatures and deep depths, and haddock and Atlantic cod were intermediate (Fig. 6). For March 1984, these results indicate an association of yellowtail flounder with a narrow range of shallow depths (shown by the sharp increase without any "steps" in the shape of the cdf surface; Fig. 6) and an association with low temperatures although with a somewhat broader range than for depth. Silver hake in March 1984 were also associated with narrow ranges of temperature and depth, although the shape of the surface suggested that the association was stronger with temperature than with depth (i.e., the cdf surface was broader along the depth axis; Fig. 6). Haddock showed an association with depths between 50 and 100 m, but within this depth range there was also a relationship with temperature (the "step" shape of the surface along the temperature axis; Fig. 6). Atlantic cod was opposite to the results for haddock: most Atlantic cod were associated with a narrow (cool) temperature range, but there was also an effect of depth (Fig. 6). The strengths of these associations between fish catch and the joint distributions of depth and temperature were assessed by the bivariate randomization test (equation 5). Yellowtail flounder, silver hake, and haddock were all associated with particular ranges of depth and temperature ($p \leq 0.07$), but Atlantic cod appeared to be unrelated to the available combinations of the two variables ($p = 0.63$; Table 5).

The associations of these groundfish species with depth and temperature simultaneously during July 1984 are similar to those during March 1984. Yellowtail flounder were associated with shallow depths, but the association with temperature was weaker than in March 1984 (the more gradual slope along the temperature axis; Fig. 6). Silver hake were associated with temperature and depth, although more strongly with temperature; haddock were associated with ranges of depth and temperature similar to those during spring (Fig. 6). Atlantic cod were associated with shallower depths in summer than in spring (Fig. 6). The randomization test results for depth and temperature during July 1984 ($p \leq 0.04$; Table 5) were similar to those for March 1984 for yellowtail flounder, haddock, and silver hake but indicated that Atlantic cod were more strongly associated with particular ranges of temperature and depth during summer ($p = 0.08$; Table 5) than during spring.

The randomization test results for bivariate combinations of depth, temperature, and salinity from 1979 to 1984 (Table 5) refine the univariate habitat associations identified in Table 2. Yellowtail flounder were strongly associated ($p \leq 0.03$) with temperature and with salinity during spring and summer over all years when their joint distributions with depth were included (Table 5), in contrast with the univariate analysis (Table 2). Silver hake and haddock generally had stronger associations (smaller p-values; Table 5) with the joint distributions of temperature and depth, and with temperature and salinity, than with salinity and depth. However, the bivariate associations of Atlantic cod (Table 5) were similar to those from the univariate analysis (Table 2).

To identify which habitat variable was most influential in structuring the distributions of each of the four groundfish species in the presence of correlations among the habitat variables, we compared univariate and bivariate test results. The coordinates of the test statistic in equations 3 and 5 give the points of maximum difference between the catch-weighted cumulative curves and the cumulative curves for the habitat conditions (e.g., the point labelled "max" in Fig. 2a). In March 1984, the univariate cdf's for yellowtail flounder reached their maximum differences from the habitat cdf's at 75 m, 3.0°C, and 32.2 psu (Table 6a). However, when depth and temperature, and depth and salinity, were considered together in the bivariate analyses, the maximum differences increased for temperature and salinity but remained unchanged for depth (Table 6a). We assumed that the variable(s) with the strongest associations were those whose coordinates changed the least going from the univariate to the bivariate tests. Depth was the variable that changed the least for yellowtail flounder, followed by salinity (Table 6a). We conclude that depth was the most important variable because the salinities with which yellowtail flounder were associated were available at deeper depths, yet yellowtail flounder generally did not occur much deeper than 100 m. Haddock and silver hake were associated more with temperature than with salinity or depth (Tables 6b and 6c). In contrast, depth varied the most between univariate and bivariate analyses of Atlantic cod during March and July, but it is difficult to determine which of temperature or salinity was the least variable (Table 6d).

Discussion

Several methods have been used to identify habitat associations of marine fishes from survey data. Scott (1982a) defined habitat preferences of Atlantic groundfishes as those ranges of depth, temperature, and salinity with greater than 10% of the total species abundance. However, he took no account of the survey design (his data were derived from the same stratified-random design used in our study) or of the available habitat conditions. Murawski and Finn (1988) used data on fish catches, bottom depth, and temperature derived from a stratified-random survey to estimate habitat preferences of groundfishes on Georges Bank. Preferred conditions were defined as means and standard deviations of depth and temperature weighted by fish catch. Comparison of preferred conditions (i.e., weighted means) with available habitat conditions was done using scattergrams of the two habitat parameters (depth and temperature). Rose and Leggett (1988, 1989) compared the distributions of Atlantic cod and capelin (*Mallotus villosus*) (assessed acoustically) with temperature. They grouped data into 1°C categories and defined preference as those categories in which Atlantic cod occurrences were greater than expected based on the assumption of a random distribution with temperature. The observed distribution of Atlantic cod on temperature was compared with the expected (random) distribution using a χ^2-test. Rao and Thomas (1989) noted that in general, application of standard χ^2 tests to data from complex survey designs will result in the alternative hypothesis being rejected too often given the assumed type I error for the test.

The method we present has several advantages to estimating habitat associations of fish species. The use of cumulative distributions provides an objective method of estimating the proportion of a population that occurred within any range of habitat conditions, or conversely the conditions under which 50%, 95%, etc., of a population occurred. The method is nonparametric in the sense that no specific statistical distribution need be assumed for either the fish catch or habitat variables. It also allows quantitative comparisons with observed habitat conditions to identify species which are distributed randomly with respect to a particular habitat variable. The method takes explicit account of the survey design and can be applied to data collected with any sample-to-strata allocation scheme; it can therefore be used to estimate population-level responses. If the survey design is not stratified, using instead a simple random or regular scheme (or when a stratified design is used with proportional-to-area allocation), equations 1 and 2 for the calculation of the cumulative distribution functions reduce to

$$f(t) = \frac{1}{n}\sum_{i=1}^{n} I(\boldsymbol{x}_i)$$

$$g(t) = \frac{1}{n}\sum_{i=1}^{n} \frac{y_i}{\bar{y}} I(\boldsymbol{x}_i)$$

and

$$\max_{\forall t}\left|g(t) - f(t)\right| = \max_{\forall t}\left|\frac{1}{n}\sum_{i=1}^{n}\left(\frac{y_i - \bar{y}}{\bar{y}}\right) I(\boldsymbol{x}_i)\right|$$

where $I(\boldsymbol{x}_i)$ is the same as for equation 4 but without the stratification subscript h. This type of analysis could also easily be applied to fisheries data collected by other survey methods, for example acoustic surveys. Acoustic methods have the advantage of continuously monitoring fish biomass throughout the water column and, coupled with frequent water column measurements of hydrographic conditions, would be particularly important for assessing habitat associations of pelagic and semidemersal fish species.

One disadvantage of the method is that the randomization test (equations 3 and 5) is computationally more complex than applying any standard parametric or nonparametric test, but these can give erroneous results when applied to data from complex survey designs (Rao and Thomas 1989). In addition, Manly (1991) stated that randomization tests are often more powerful than their standard counterparts in nonstandard situations, such as the analyses we present here.

Several conclusions regarding winter/spring and summer habitat associations of the four eastern Scotian Shelf groundfish species examined in this study can be made based on the results of our analyses. Haddock and silver hake on the eastern Scotian Shelf can be considered as "temperature-keepers", in the sense that they maintained a similar temperature range between winter/spring and summer, but did this by changing their seasonal depth distributions. Yellowtail flounder, in contrast, can be considered as principally a "depth-keeper", implying that there was little alteration of their depth distribution between spring and summer and that they tolerated a wide range of temperature and salinity conditions. This relationship of yellowtail flounder with depth is consistent with the conclusions of Scott (1982a), who found that they tended to be located on the shallow banks on the eastern Scotian Shelf, and with the conclusions of Murawski and Finn (1988) for yellowtail flounder on Georges Bank. Murawski and Finn (1988) also concluded that silver hake on Georges Bank maintained a relatively narrow temperature range among seasons, but that haddock distributions on Georges Bank were more strongly related to depth than to temperature. The contrast with our results for haddock may be due to the reduced variation of depths sampled on Georges Bank (most full strata analysed by Murawski and Finn (1988) were <100 m) compared with the eastern Scotian Shelf.

In contrast, Atlantic cod were associated with particular ranges of depth, temperature, or salinity only during summer from 1979 to 1984, and we were generally unable to distinguish between temperature and salinity as the predominant single factor. The inability of the randomization test to detect consistent associations during March was likely due to the wider availability of the associated range of salinity during

TABLE 6. Coordinates of the test statistic for the univariate and bivariate randomization tests. The column labelled "Univ" under each habitat parameter represents the location of the maximum difference between the habitat and catch-weighted cumulative distribution functions in the univariate test (equation 3). The remaining two columns under each habitat parameter represent the locations of the maximum difference in the bivariate test (equation 5).

	Depth (m)			Temperature (°C)			Salinity (psu)		
Year	Univ	Temperature	Salinity	Univ	Depth	Salinity	Univ	Depth	Temperature
(a) Yellowtail flounder									
March									
1979	130	130	130	1.5	7.0	1.5	32.4	33.8	32.8
1980	90	90	90	1.5	2.5	1.5	32.2	32.4	32.4
1981	75	75	75	2.5	3.5	3.5	32.8	32.8	32.8
1982	90	90	75	0.0	0.0	0.0	32.4	32.6	32.8
1983	75	75	75	5.5	5.5	5.5	32.6	33.0	32.6
1984	75	75	75	3.0	5.0	3.0	32.2	33.0	32.2
July									
1979	75	90	90	2.5	9.5	9.5	32.8	33.4	32.8
1980	75	75	75	3.0	9.0	9.0	32.4	33.0	32.4
1981	90	90	90	8.0	12.0	12.5	32.8	33.6	32.8
1982	75	75	90	2.0	10.5	10.5	32.6	32.6	32.6
1983	75	75	75	2.5	8.5	8.5	32.8	33.2	32.8
1984	75	75	75	10.5	11.0	14.0	33.4	33.6	33.4
(b) Haddock									
March									
1979	90	300	240	2.5	2.5	2.5	33.2	33.2	35.0
1980	130	240	130	3.0	3.0	3.0	32.8	35.0	33.0
1981	110	110	110	3.0	7.5	3.0	33.8	34.2	33.8
1982	75	250	150	2.0	2.0	2.0	32.4	32.4	34.8
1983	110	275	250	3.0	3.0	3.0	32.8	32.8	32.8
1984	130	310	200	4.5	4.5	4.5	32.6	32.6	33.2
July									
1979	90	300	90	5.0	5.0	6.0	32.2	34.0	34.4
1980	75	75	75	4.5	8.0	4.5	32.6	34.0	34.0
1981	90	350	90	6.5	6.5	6.5	32.8	34.8	34.8
1982	130	240	130	2.0	2.0	2.0	32.6	34.4	33.2
1983	55	55	130	3.0	8.5	8.5	32.2	32.2	32.2
1984	110	110	110	7.0	11.0	7.0	34.2	34.4	35.0
(c) Silver hake									
March									
1979	150	350	275	8.0	8.0	8.0	34.4	34.4	35.0
1980	150	275	240	5.5	7.0	5.5	34.0	34.0	34.8
1981	130	310	130	3.5	3.5	3.5	32.6	33.4	33.8
1982	130	200	200	7.5	7.5	7.5	34.4	34.2	34.6
1983	110	250	310	6.0	6.0	6.0	33.6	33.6	34.6
1984	150	330	275	7.0	7.0	7.0	34.2	34.2	35.0
July									
1979	165	370	310	8.5	8.5	8.5	34.6	34.6	35.2
1980	90	310	240	6.5	6.5	6.5	33.6	33.6	34.8
1981	55	370	35	8.0	8.0	8.0	31.8	31.8	35.0
1982	130	250	290	5.5	6.0	5.5	34.0	34.0	34.8
1983	75	250	250	4.0	4.0	4.0	34.0	34.0	33.8
1984	35	310	35	7.5	7.5	7.5	33.2	32.4	35.0

March than during July. This is consistent with the widespread occurrence of Atlantic cod on the eastern Scotian Shelf (Scott 1988).

Age-specific differences and factors other than depth, temperature, or salinity can influence the distributions of marine fishes. These factors potentially include sediment type (e.g., Scott 1982b), oxygen (e.g., D'Amours 1993), and conceivably prey abundance and distribution. To some extent, depth may serve as a proxy for sediment type, while water mass (temperature and salinity) may act as a proxy for oxygen concentration and prey distributions. Therefore, while fish distributions may not be related to depth, tem-

TABLE 6. (*Concluded*)

Year	Depth (m) Univ	Depth (m) Temperature	Depth (m) Salinity	Temperature (°C) Univ	Temperature (°C) Depth	Temperature (°C) Salinity	Salinity (psu) Univ	Salinity (psu) Depth	Salinity (psu) Temperature
				(d) Atlantic cod					
March									
1979	110	240	240	7.0	7.0	7.0	33.4	33.4	34.6
1980	150	150	150	2.5	10.5	2.5	33.0	35.0	32.8
1981	90	275	275	7.5	7.5	7.5	34.0	34.0	34.0
1982	55	160	160	1.5	1.0	1.5	33.2	33.2	33.2
1983	130	240	240	4.5	4.5	4.5	33.6	33.6	33.6
1984	160	180	180	6.5	6.5	6.5	34.2	34.2	34.2
July									
1979	75	75	75	7.5	9.5	14.0	33.4	33.4	33.4
1980	75	250	55	6.0	6.0	6.0	34.0	32.6	34.0
1981	150	150	150	5.0	4.5	12.5	33.4	33.6	33.4
1982	55	55	55	2.5	5.5	5.5	32.6	32.6	32.6
1983	90	55	90	7.5	8.5	8.5	32.6	32.6	32.2
1984	150	150	150	4.5	4.5	4.5	32.6	33.6	33.6

perature, or salinity alone, these may serve as reasonable first approximations. Fish distributions can also differ substantially among different age classes (e.g., Tremblay and Sinclair 1985; Sinclair 1992). Smith et al. (1991), using a slightly different approach, found a relationship between age-4 Atlantic cod distributions and the intermediate (cold) water mass (defined as water with salinities in the range 32–33.5 psu) within a specific depth range on the eastern Scotian Shelf during the March surveys, 1979–84. Stronger relationships between Atlantic cod and the salinities associated with the intermediate cold layer might have been obtained in our study had we analysed separate age classes using the present methods.

Identification of consistent habitat associations of marine fishes offers the opportunity to improve fisheries management and stock assessment methods in several ways. It can provide oceanographic bases for understanding changes in fish distributions, which ultimately may be predictable in advance or assessed by monitoring a few selected oceanographic or habitat parameters, provide corrections to the assumption of homogeneous conditions and distributions of fish within strata, leading to corrections to survey estimates of abundance (e.g., Smith et al. 1991), and provide a basis for understanding oceanographic effects on variations of catchability (e.g., Murawski and Finn 1988; Gordoa and Hightower 1991). Finally, the identification of strong associations with particular habitat conditions, i.e., an improved definition of habitat "space", is a prerequisite for expansion of spatially explicit models of fish distribution and growth (e.g., Brandt et al. 1992; Swartzman et al. 1992) to the marine environment.

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