Environmental Factors Influencing the Distribution of Juvenile Groundfish in Nearshore Habitats of Southwest Nova Scotia

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Eight nearshore (<20 m) marine habitats were surveyed to estimate the relative abundance of juvenile groundfish and to assess the environmental variables influencing their distribution. Surveys were conducted as part of a depth-stratified, random sampling design; at each site a small otter trawl was towed for 15 min at eight stations in each of three depth strata. A suite of 13 environmental variables were measured in association with each tow. A total of 1908 fish from 13 different species were caught at 191 completed trawl stations. Standardized centered principal components analysis, orthogonally rotated factor analysis, and detrended correspondence analysis (DCA) were used to delineate aggregations in the abundance data. DCA coupled with stepwise multiple regression best resolved the species' distributions and dominant gradients in the environment. The first two DCA axes reflected estuarine to coastal gradients (68% of the variance) and significant environmental variables were plotted as vectors in the ordination diagram. An estuarine assemblage of species, characterized by winter flounder (*Pseudopleuronectes americanus*) and white hake (*Urophycis tenuis*), was associated with waters that were warmer, less saline, more turbid, and overlying a finer grained substrate, than a coastal assemblage of species which included cod (*Gadus morhua*) and rock gunnel (*Pholis gunnellus*). The biologically significant gradients corresponded to those which dominated variation in the physical environment.

On a effectué des relevés dans huit habitats marins près du rivage (<20 m) afin d'estimer l'abondance relative des juvéniles de poisson de fond et d'évaluer les variables environnementales qui influencent leur répartition. Les relevés ont été réalisés dans le cadre d'un projet d'échantillonnage aléatoire, selon la profondeur; à chaque endroit, on a tiré un petit chalut à plateaux pendant 15 min à huit stations dans trois couches de profondeur. Une série de 13 variables environnementales a fait l'objet de mesures pour chaque remorquage. On a capturé un total de 1 908 poissons appartenant à 13 espèces différentes à 191 stations où les relevés ont été effectués. On a utilisé l'analyse en composantes principales, centrée, normalisée, l'analyse factorielle par rotation orthogonale, et l'analyse de correspondance indépendante des tendances pour cerner les aggrégats dans les données sur l'abondance. L'analyse de correspondance combinée à une régression multiple par étape a donné les meilleurs résultats en ce qui concerne la répartition des espèces et leurs gradients dominants dans l'environnement. Les deux premiers axes de l'analyse de correspondance reflètent les gradients estuariens à côtiers (68 % de variance), et les variables environnementales significatives apparaissent comme vecteurs sur l'axe des ordonnées. Un assemblage estuarien d'espèces, caractérisé par la plie rouge (*Pseudopleuronectes americanus*) et la merluche (*Urophycis tenuis*) a été observé dans des eaux plus chaudes, moins salées, plus turbides et recouvrant un substrat plus finement granulé, comparativement à celles arbritant un assemblage d'espèces côtières comprenant la morue (*Gadus morhua*) et la sigouine de roche (*Pholis gunnellus*). Les gradients biologiquement significatifs correspondent à ceux qui déterminent la variation dans l'environnement.

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In recent years, increased scientific effort has been focused on the role of nearshore marine environments in the recruitment of commercially important fish species. Typically, nearshore marine environments are believed to fulfill the role of nursery areas for the larvae and juveniles of some fish species (Subrahmanyam and Drake 1975; Rauck and Zijlstra 1978; Shenker and Dean 1979; Weinstein 1979; Blaber and Blaber 1980; Weinstein et al. 1980; Livingston 1982; Russel and Garret 1983; Riley and Parnell 1984; Blaber et al. 1985). In the Northwest Atlantic, and more specifically the Scotian Shelf, early life history and recruitment research have generally been focused on offshore areas. Groundfish and ichthyoplankton surveys have largely been prevented from sampling the nearshore environment because of vessel and gear size restrictions. The extent and use of the nearshore region by juvenile demersal fish species is only now being examined (e.g. Simon and Campana 1987).

The distribution of individuals in a fish population is assumed to be a result of an alignment with environmental gradients and/or biological features (Larson 1980; Sale 1980; Grossman 1982; Meffe 1984; Werner 1984). Numerous variables are reported to play a role in the habitat selection by fish: temperature (Col-

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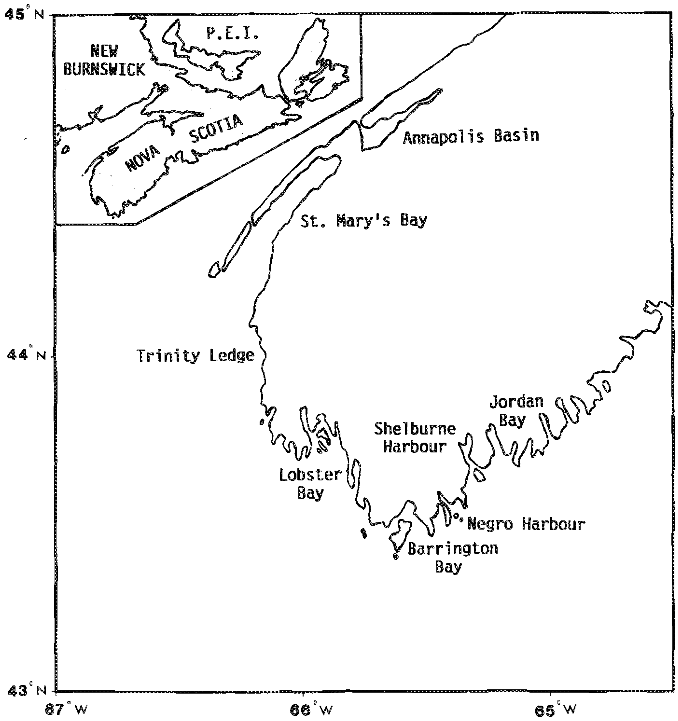

FIG. 1. Sample sites surveyed in Southwest Nova Scotia.

ton 1972; Subrahmanyam and Drake 1975; Sutcliffe et al. 1977; Scott 1982a; Blaber et al. 1985), salinity (Subrahmanyam and Drake 1975; Weinstein 1979; Scott 1982a; Riley and Parnell 1984; Blaber et al. 1985), depth (Sale 1969; Riley and Parnell 1984), turbidity (Blaber et al. 1985), and substrate characteristics (Sale 1969; de Sylva 1975; Mills 1975; Scott 1982b; McCormick and Aspinwall 1983; Keast 1985). Protection from predators (Riley and Parnell 1984; Keast 1985), competition (Larson 1980; Grossman 1982; Hansson 1984), and seasonal climate variation (Tyler 1971; Haedrich and Haedrich 1973; Quinn 1980) are also thought to play important roles in determining habitat utilization by fish species or assemblages.

The purpose of this study was to survey a number of nearshore (less than 20 m in depth) environments in southwestern Nova Scotia and, using multivariate techniques, describe the preferred habitat of juvenile demersal fish species. The study was designed to answer three primary questions: (1) How are juvenile groundfish distributed in nearshore marine environments in Southwest Nova Scotia? (2) Are species distributions related to specific environmental attributes or groups of attributes? (3) What is the most effective and robust technique to characterize species distributions?

Methods

Eight study sites were chosen to provide a broad geographic coverage of the Southwest Nova Scotia region and to reflect the range of habitat types available to juvenile groundfish. These included the Annapolis Basin, St. Mary's Bay, Trinity Ledge, Lobster Bay, Barrington Bay, Negro Harbour, Shelburne Harbour, and Jordan Bay (Fig. 1). Each study site was divided into three depth strata (2–6.9 m, 7–14.9 m, 15–20 m) which approximated the zonations of vegetation typically found in nearshore environments — intertidal (*Fucoid* and *Chondrus* species), kelp (*Laminaria* and *Alaria* species), and deep kelp (*Agarium* and *Ptilota* species). Eight stations in each depth stratum were randomly chosen from a rectangular (1.5 × 0.5 nautical mile) strip grid imposed on a navigational chart of the area. This design resulted in a total of 192 stations: eight survey sites, three depth strata, and eight stations within each stratum.

All sampling was conducted from the *Lebradelle*, a 9-m, 180 horse power, motor launch. The net used was a small otter trawl, commonly referred to as a "shrimp try net" (Gourock Industries Ltd., Halifax, Nova Scotia). The wings, body, and codend were 2.5-cm nylon stretch mesh with a liner of 5-mm nylon stretch mesh fitted to the codend. A 15-min tow at a speed of approximately 2 knots was conducted at each station, with tow time being measured from total warp out to beginning of haulback.

At the start of each tow, site number, day of sample, and a suite of environmental variables were measured and recorded. A Beckman RS5 salinometer was used to measure temperature (±0.1°C) and salinity (±0.1 ppt) at the water surface and just off bottom. A 30-cm Secchi disk was used to measure water clarity (±0.1 m). Depth, substrate, and vegetation type were monitored continuously using a Rayethon 719 chart recorder during the tow and verified using an Ekman grab sampler, samples from the otter trawl, and underwater diver observation when required. Minimum tidal amplitude (±0.01 m) was recorded for each station from a navigational chart.

Substrate, vegetation, and exposure were scored as categorical variables with values ranging from 1 to 5, according to criteria outlined in Table 1. An increase in substrate score paralleled an increase in the particle size of bottom sediments. Vegetation scores increased with canopy height and levels of vegetation. An exposure index categorizing fetch was adopted from Moore and Miller (1983) and expanded to include sheltered categories. Exposure was determined by using radar to measure the distance from the start location of a station to the nearest land mass (island or mainland) in the four cardinal compass directions. A simple tide scale with values ranging from 1 (ebbing) to 4 (high water) was developed to categorize the state of the tidal cycle.

The eight sites were sampled successively from the Annapolis Basin to Jordan Bay from July 11 to August 12, 1986. At the completion of the eight sites, low catch rates experienced in the Bay of Fundy area prompted the resampling of all stations in the Annapolis Basin and St. Mary's Bay from August 13 to August 21.

Analysis

The survey data were divided into two matrices — a suite of environmental measures and the abundance data for all species. To ensure species in the analysis were adequately represented and to avoid spurious effects of rare species, an initial filtering of the abundance data excluded species occurring in fewer than 5% of the stations (Gauch 1982, p. 213–214). This filter also removed stations which did not catch fish.

There were three steps in the analysis. The environmental data were initially analyzed to examine the dominant patterns of variation in the environment. Thirteen environmental variables were ordinated using a centered, standardized principal components analysis (PCA) (Hotelling 1933; Goodall 1954). In the second step, the species' abundance data were ordinated using three techniques: centered standardized principal components analysis (PCA), orthogonally rotated factor analysis (FA) (Harman 1967; Dagnelie 1978) and detrended correspondence analysis (DCA) (Hill 1979a; Hill and Gauch 1980). This

TABLE 1. Substrate, vegetation, and exposure indices.

Categorical score	Substrate	Vegetation	Exposure
1	Mud or clay	Barren	Enclosed A station having a land mass within 1 km on four cardinal compass points.
2	Sand	Low canopy	Sheltered A station having a land mass within 1 km on three sides of the four cardinal compass points.
3	Gravel	High canopy	Partially Open A station having a land mass within 1 km on two sides of the four cardinal compass points.
4	Cobble	Predominant low understory, high canopy	Open A station having a land mass within 1 km on one side of the four cardinal compass points.
5	Rock or boulder	Predominant high canopy, low understory	Oceanic A station greater than 1 km from any land mass on the four cardinal compass points.

facilitated a comparison between multivariate methods and oriented the species along biologically important gradients. DCA is a relatively new eigenanalysis ordination technique based on reciprocal averaging (Hill 1973, 1974) with two major changes: the arch effect is "eliminated" through a process of detrending (which places further constraints on the orthogonality criterion) and axes are rescaled to ensure a uniform species turnover rate along the length of the gradient. DCA analyzes a sample-by-species data matrix by simultaneously calculating sample and species ordination values, termed scores. The reciprocal averaging algorithm iterates to stabilized sample scores, which are weighted averages of the species scores that occur in them, and species scores which are the weighted averages of the samples they occur in. All axes but the first are detrended to avoid any systematic relation to the first axis and all axes are rescaled by forcing the mean within-sample dispersion of the species at all points along the gradient to unit variance. In the final step of the analysis, the biological gradients were analyzed in conjunction with the environmental data to reveal the variables which were correlated with the observed biological structure. Stepwise linear regressions (BMDP2R, Dixon 1983) of the station scores on the environmental data were computed for each axis using F-to-enter and F-to-remove values of 4.0 and 3.9, respectively. Vectors representing the variables extracted in the regressions were plotted in the DCA ordination diagram. The method of placement of environmental vectors is based on Gabriel's biplot theory (Gabriel 1971, 1981) and follows that of ter Braak (1986). Each vector represents an "axis" which can be obtained by extending the vector in both directions. If a perpendicular is drawn from each species point to an environmental vector or "axis," the intersections indicate the relative modal positions of the species distribution along that environmental gradient. Collectively, these species' endpoints establish the gradient of species along each vector.

The species abundance data were also tabulated using the polythetic divisive classification program TWINSPAN (Hill 1979b). TWINSPAN identifies differentiating "indicator" species and constructs ordered species-by-sample tables through binary division of successive ordinations. The resulting species and station classifications were compared with the DCA species ordination results. Qualitative station and species classification dendograms were plotted to illustrate the relationships among species. Each level of the dendogram corresponded to a level of division in the analysis.

Results

A total of 1976 fish comprising 25 different species were caught at 254 completed trawl stations. Species which did not fulfill the 5% occurrence criterion were removed from the data set. The remaining 191 stations and 1908 fish from 13 different species were included in the analysis (Table 2). Length frequency histograms for each species indicated 79% of the total catch were juveniles (young-of-the-year or age 1 fish).

Environmental

The results of the PCA are presented in Table 3. The first principal component accounted for 25.6% of the total variance and was labelled a depth-gradient axis. All variables contributing to this axis were highly correlated, indicating the general nature of the first principal component. The second axis reflected the depth stratification of the survey design and was labelled a water depth axis. The third and fifth principal axes were associated with substrate while the fourth axis was a tidal amplitude axis reflecting changes in bottom salinity and vegetation over the tidal cycle.

All station scores for the first two principal component axes were coded by site and plotted in Fig. 2. The station points from each site form unique clusters or "fingerprints" in the ordination diagram. Adjacent site clusters overlap, collectively forming a continuum of environmental conditions in both dimensions without discontinuities between sites.

Biological

The results of the three biological ordinations were compared to evaluate the ability of each method to effectively resolve differences between stations, and to orient stations along recognizable gradients. The PCA ordination clustered the vast majority of station points at the origin. Any resolution present on the first or second axis was a result of a few outlying points at the ends of both positive axes. In the FA ordination, resolution along the first axis was again limited by the clustering of station points at the origin. The range of the first factor was

TABLE 2. Total catch at site. In Annapolis Basin and St. Mary's Bay round 1 sampling is the left column, round 2 is the right column.

Species	Annapolis Basin		St. Mary's Bay		Trinity Ledge	Lobster Bay	Barrington Bay	Negro Harbour	Shelburne Harbour	Jordan Bay
Cod *Gadus morhua*	6	7	7	1	18	0	13	12	13	0
White Hake *Urophycis tenuis*	2	17	5	9	5	9	7	41	151	4
Pollock *Pollachius virens*	3	0	71	0	100	0	0	1	0	1
Winter Flounder *Pseudopleuronectes americanus*	29	316	71	193	11	148	36	90	51	21
Longhorn Sculpin *Myoxcephalus octodecemspinosus*	3	40	27	7	3	9	4	7	5	0
Shorthorn Sculpin *Myoxocephalus scorpius*	1	5	5	3	2	1	0	1	8	0
Sea Raven *Hemitripterus americanus*	9	12	2	7	6	9	3	2	3	1
Winter Skate *Raja ocellata*	2	4	4	4	0	8	2	1	2	2
Little Skate *Raja erinacea*	0	10	1	13	0	3	1	1	1	3
Cunner *Tautogolabrus adsersus*	0	0	18	23	0	33	15	0	0	0
Rock Gunnel *Pholis gunnellus*	0	1	2	1	0	0	11	13	2	0
Windowpane Flounder *Scophthalmus aquosus*	0	9	1	11	3	18	1	1	6	3
Lumpfish *Cyclopterus lumpus*	0	4	0	3	2	0	5	1	5	1

extended by two outliers at the positive end of the axis. A higher dispersion of station points and fewer outliers provided greater resolution along the second axis.

DCA was judged the most effective ordination technique. The ordination diagram (Fig. 3) was a much more "balanced" plot, providing a high degree of resolution along both axes. As DCA is a weighted averaging technique, the region of clustered points located in the second quadrant can be traced to the dominance of winter flounder (*Pseudopleuronectes americanus*) in the catch composition of many survey sites (see Table 2). The first and second axes of the DCA accounted for 42.4 and 25.7% of the explained variance, respectively.

Significant environmental variables extracted in the stepwise regressions of the standardized environmental data on the DCA station scores were plotted as vectors in the ordination diagram (Fig. 4). The first axis (DCA1) reflected a depth gradient of correlated environmental variables. Stations with low surface temperature, rock or boulder substrate and high water clarity dominated the positive end of the axis, whereas high surface temperature, mud or clay substrate and turbid water stations dominated the negative end of the axis. Day of sample is also incorporated in this axis but for reasons to be discussed later it is not included in the interpretation. Surface salinity was the only environmental variable extracted in the regression equation of the second axis (DCA2). Most of the resolution among species was located along the negative side of the axis, indicating variation in salinity preferences was greatest in brackish water conditions.

The third and fourth DCA axes (DCA3, DCA4) only accounted for 18 and 13.9% of the explained variance, respectively. The majority of station points were concentrated at or near the origin of the ordination diagram and did not significantly add to the ecological interpretation.

In the TWINSPAN analysis, stations were classified into 13 groups. Each group was characterized by one or two species which dominated the catch composition of stations within that group. The 13 groups formed by the classification of stations did not correspond to the 13 species used in the analysis. Longhorn sculpin (*Myoxocephalus octodecemspinosus*), *shorthorn sculpin (M. scorpius)*, and little skate (*Raja erinacea*) did not characterize any of the groups formed in the classification. In the species classification, four major groups were formed from the 13 species (Fig. 5). The first group contained seven species which corresponded to the species located on the left side of the DCA ordination plot. Cod and lumpfish formed satellite groups which joined the other two major groups. The remaining

TABLE 3. Summary of principal components analysis (PCA) environmental variable loadings, eigenvalues, and percent total variance.

Variable	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
Day	−0.165	0.444	0.457	0.163	−0.479
Surface temperature	−0.690	0.556	0.175	−0.091	0.098
Surface salinity	0.627	−0.449	0.277	0.195	−0.047
Bottom temperature	−0.530	−0.294	0.143	0.006	0.127
Bottom salinity	0.272	0.179	0.466	0.572	−0.307
Water clarity	0.768	0.000	0.247	−0.079	0.104
Exposure	0.614	0.108	−0.025	−0.165	−0.054
Substrate	0.271	−0.174	0.501	0.113	0.596
Vegetation	0.323	−0.281	0.332	−0.545	0.000
Depth	0.646	0.631	−0.209	−0.054	0.050
Tide	0.137	0.017	−0.387	0.633	0.396
Minimum depth	0.581	0.682	−0.153	−0.139	0.104
Site	−0.403	0.498	0.420	−0.066	0.462
Eigenvalue	3.33	2.06	1.37	1.17	1.11
% total variance	25.6	15.8	10.5	9.0	8.5

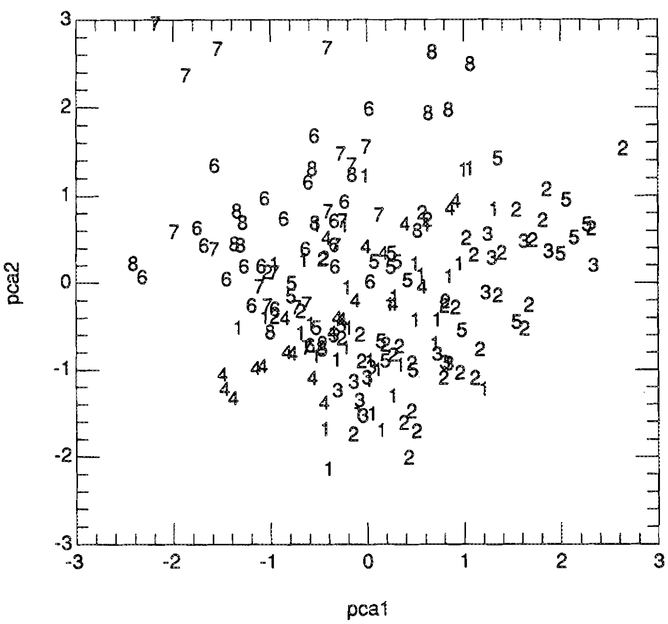

FIG. 2. Principal components analysis (PCA) ordination of station environmental data, axes 1 and 2. Each station is coded by site number: 1 = Annapolis Basin, 2 = St. Mary's Bay, 3 = Trinity Ledge, 4 = Lobster Bay, 5 = Barrington Bay, 6 = Negro Harbour, 7 = Shelburne Harbour, 8 = Jordan Bay.

four species corresponded to the species located on the right side of the DCA ordination plot. Overall, the order of species along the base of the dendogram closely reflected the position of the species points along the first axis of the DCA ordination.

Discussion

Environmental Analysis

The analysis of the environmental data revealed a high degree of collinearity among variables and a continuum of estuarine to coastal environmental conditions at each study site. Variables which contributed most to dominant gradients in the physical environment were also those which were most highly correlated with other environmental variables.

The first principal component was labelled a depth gradient axis. The actual depth gradient (the ratio of water depth to distance from shore) was not measured but paralleled the patterns of variation observed in the seven variables with the highest loadings. Stations with low depth gradients were generally sheltered and shallow with soft depositional substrates. The water column was characteristically turbid, with high surface and bottom temperatures, and low surface salinities. Stations with larger depth gradients were exposed, deeper stations with harder, larger particle sized substrates. Water clarity and surface salinities were higher, while surface and bottom temperatures lower. The transition from low depth gradient or estuarine stations, generally located near large freshwater inputs at the head of a bay, to high depth gradient or coastal stations, located along open coastlines or at the mouth of a bay, was present and consistent for each site in the survey. The second principal component, a depth axis, was expected as the survey design was depth stratified.

The presence of environmental gradients in coastal embayments is widely accepted and has often been used as a basis for estuarine classification schemes (e.g. Pritchard 1955; Ippen and Harleman 1961; Hansen and Rathray 1966). Using the most widely accepted definition of an estuary (Cameron and Pritchard 1965), the sites surveyed in this study, with the exception of Trinity Ledge, qualify as estuaries and would be classified as partially mixed estuaries. In conclusion, the sites in this survey were dynamic environments with distinct physical gradients extending from the head to the mouth of each bay.

Biological Analysis

The success of the DCA ordination is attributed to the suitability of the underlying species distributional model used in the analysis. DCA assumes a Gaussian model of species distribution which is equivalent to a normal distribution (Gauch and Whittaker 1972, 1976). Under this model, a species response curve reaches a single mode or optimum and declines to either side. Species differ in the location and height of the modes, as well as the width of dispersion along a gradient. Each species responds independently to the environmental gradient and while minor species have their modes randomly scattered, major species appear to form a continuum of changing species composition along the length of the gradient. This model was derived from Gause's competitive exclusion principle (Gauch and Whittaker 1972), as an example of species niche packing along an environmental gradient (May 1974).

Principal components analysis and factor analysis were unable to define distinct gradients in the biological ordination. The linearity assumptions used in these techniques were not appropriate for this data set. The juvenile groundfish species abundances were not normal in their distribution, nor were they uncorrelated. The violation of these assumptions prevented the differentiation of juvenile groundfish species along PCA or FA ordination axes. Both resulting ordination diagrams clustered the station points at the origin, which precluded biological and environmental interpretation of the results. The curvilinear distortion of the station points commonly encountered in PCA and FA was not present in either of the ordination diagrams. This

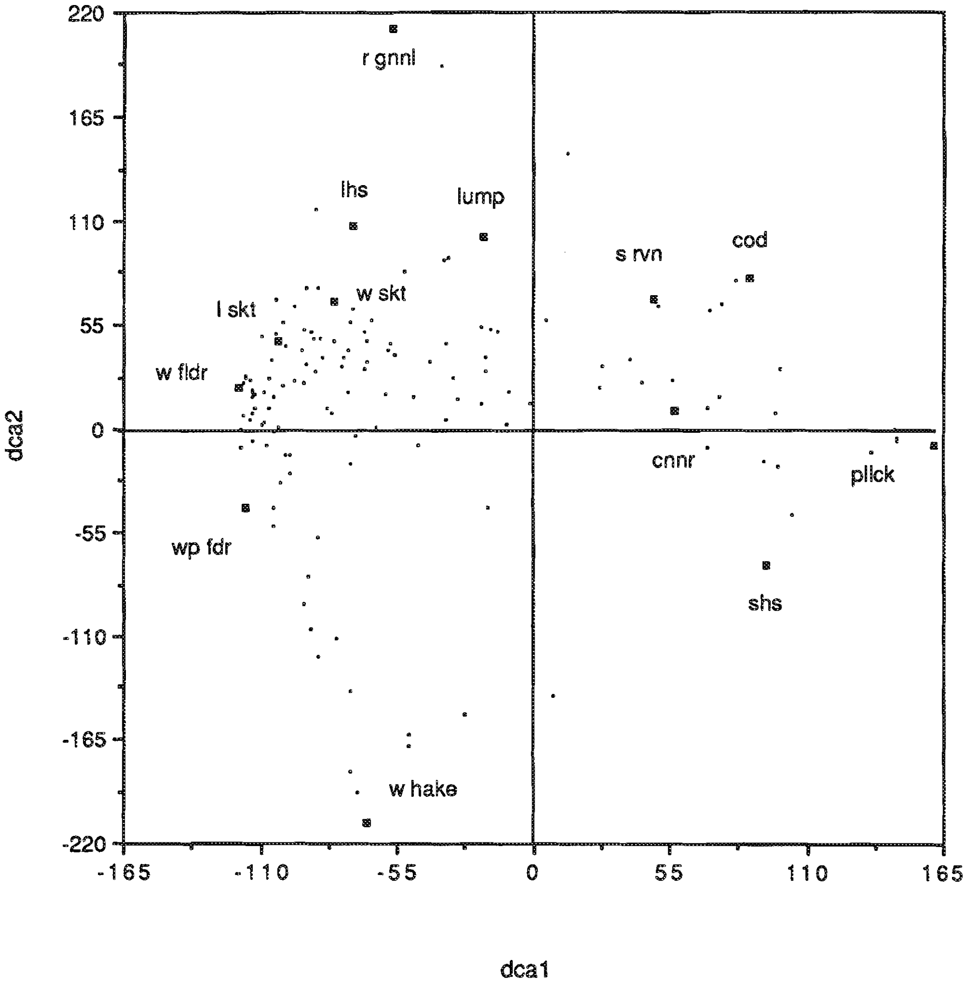

FIG. 3. Detrended correspondence analysis (DCA) ordination of station and species, axes 1 and 2. Species points are indicated by large boxes. Species labels used are: cod = cod, cnnr = cunner, lhs = longhorn sculpin, l skt = little skate, lump = lumpfish, pllck = pollock, r gnnl = rock gunnel, shs = shorthorn sculpin, s rvn = sea raven, w fldr = winter flounder, w hake = white hake, wp fdr = windowpane flounder, w skt = winter skate.

was probably a result of the failure of the methods to resolve species and station differences.

The monotonic distributional assumptions of nonmetric ordination techniques such as nonmetric multidimensional scaling (NMDS) (Kruskal 1964) were also rejected when assessing potential tools for use in this analysis. The underlying assumption of monotonicity is less stringent although related to the linearity assumptions of other eigenanalysis techniques. The use of abundance as an indicator of preference under a monotonic species response curve, implies that abundance should continuously increase to an optimum environmental value and no animals should be found beyond this value. Assuming each species has a physiological range, including a minimum and maximum value (Fry 1947), we expected species' abundances to be lower at the extremes of this range and increase to a maximum at a "preferred" value. This conceptual model approximates a bell shaped rather than a monotonic species response curve.

Although widely accepted, the Gaussian species response curve is not without its critics (Austin 1976, 1980, 1985; van der Maarel 1976). Occurrences of bimodal and non-Gaussian curves have frequently been published (for a review see Gauch 1982; Austin 1985) and are cited as evidence of the nonuniversality of the bell shaped curve. Whether the variety of response curve shapes are real, or an artifact of dimension reduction in a multidimensional hyperspace, has not been resolved (Pianka 1981; Austin et al. 1984).

A salient feature of the DCA ordination plot was the ability to divide the species and station points with a diagonal into two loosely defined species assemblages: a bottom dwelling estuarine assemblage and a more mobile coastal assemblage (Table 4). In Fig. 3, the proposed diagonal extends from the upper left side of the plot, through the lumpfish species point, to the lower right side of the plot. This grouping of species was based on the clustering of species' points in the ordination diagram (Fig. 3), and the relative positioning of species' endpoints along the environmental vectors (Fig. 4). This is a subjective division of species into groups but appears internally consistent. The estuarine assemblage was characterized by the more sedentary or brackish water residents whereas coastal assemblage species were typically found feeding on bottom or moving up to the water column of a more oceanic water mass. Lumpfish as a boundary species between the two assemblages was usually found clinging to kelp fronds up in the water column.

Environmental/Biological Integration

In the species and vectors ordination diagram (Fig. 4), the species endpoints formed a continuum along each vector in the

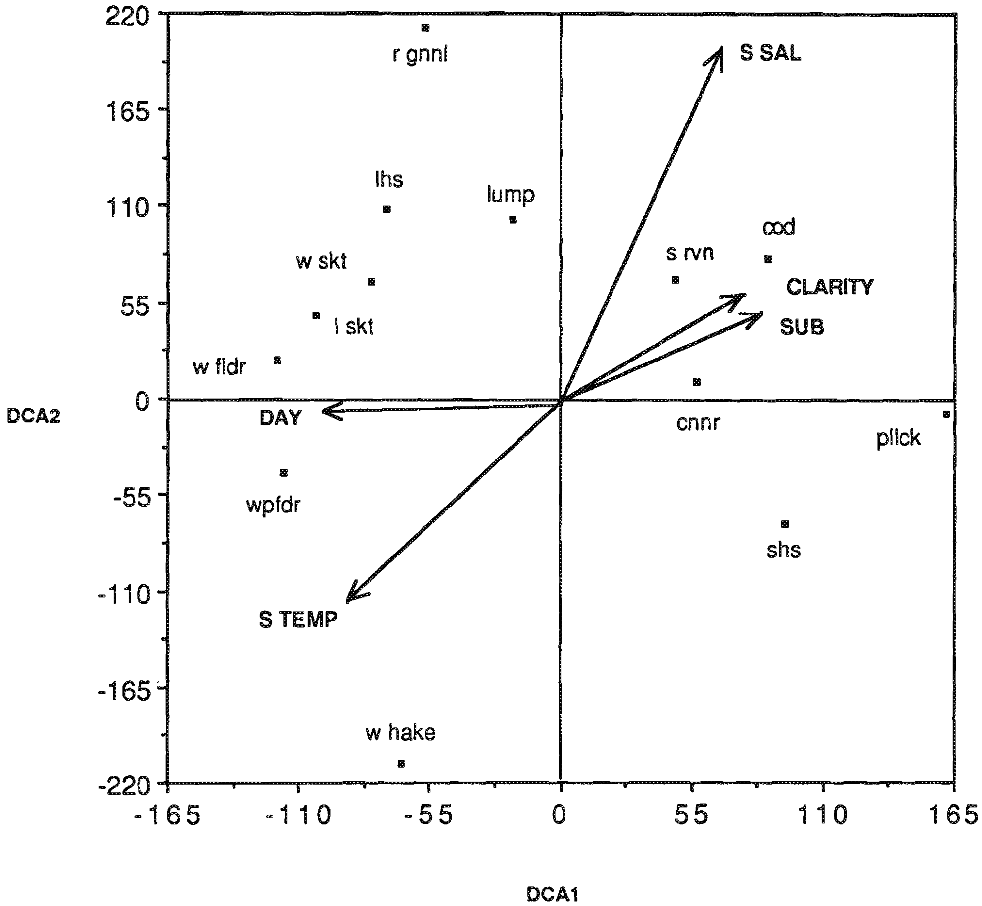

FIG. 4. Detrended correspondence analysis (DCA) ordination of species points and significant environmental vectors extracted in stepwise linear regressions of axes 1 and 2. Species labels correspond to those in Fig. 3. Vector labels used are: DAY = day of sampling, CLARITY = water clarity, S SAL = surface salinity, S TEMP = surface temperature, SUB = substrate.

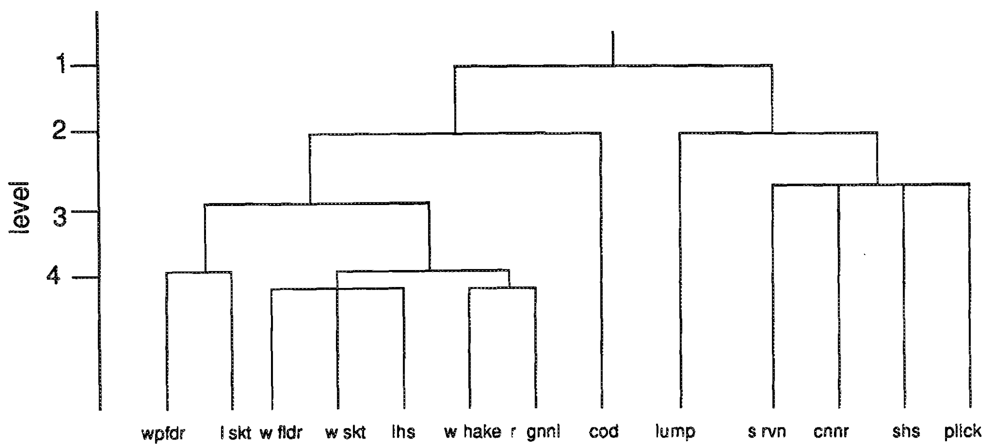

FIG. 5. Species dendogram of TWINSPAN species classifications. Species labels correspond to those in Fig. 3.

ordination diagram. However the species endpoint distributional patterns, grouped as estuarine and coastal species assemblages, were consistent for all environmental variables. The estuarine assemblage endpoints were clustered toward the head of the surface temperature and date of sample vectors indicating a preference for habitats with higher surface temperatures and later dates of sample. The coastal species endpoints clustered toward the heads of the surface salinity, water clarity, and substrate vectors. These species were characterized by habitats with higher surface salinity, higher water clarity and larger particle sized substrate than the estuarine species.

The proposed gradation of estuarine to coastal assemblages of juvenile groundfish species was supported by the division of species in the divisive classification program. Species relationships observed in the DCA ordination diagram (Figs. 3 and 4) were maintained in the species dendogram (Fig. 5) and supported through the labelling of geographic site maps with TWINSPAN station classifications. Estuarine assemblage spe-

TABLE 4. Estuarine and coastal species assemblages derived from detrended correspondence analysis.

Estuarine	Coastal
Winter Flounder	Rock Gunnel
Windowpane Flounder	Sea Raven
Little Skate	Cod
Winter Skate	Cunner
Longhorn Sculpin	Shorthorn Sculpin
White Hake	Pollock
	Lumpfish

cies were found near the head of bays and harbours or in sheltered areas in the vicinity of freshwater input sources. Species from the coastal assemblage were found at the mouth of bays and harbours or along exposed stretches of coastline. The gradient of estuarine to coastal groundfish species consistently matched the environmental cline from the head to the mouth of each bay or harbour.

The environmental variables which contributed most to the underlying structure of the observed biological gradients were largely the same variables which dominated the loadings on the first and second axes of the environmental PCA. Variables common to the first two axes of both analyses included surface temperature, water clarity, and surface salinity. The first axis of both analyses accounted for a large portion of the variance and was interpreted as a depth gradient axis.

A notable difference between the variables loading on the first two axes of the environmental PCA and the variables extracted in the regressions of the DCA axes was the inclusion of the depth and minimum depth variables in the PCA but not in the DCA regressions. Depth preferences are often cited as one of the primary environmental variables structuring the distribution of many fish species in a variety of habitats (e.g. Sale 1968, 1969; Riley 1973; Werner et al. 1977; Iglesias 1981; Riley et al. 1981; Scott 1982a; Mahon et al. 1984; Riley and Parnell 1984). It was assumed that depth preferences would also be evident in nearshore areas of Southwest Nova Scotia. This, in part, led to the adoption of a depth stratified survey design. There are two possible reasons which account for this inconsistency: (1) the depth range sampled in the survey was biologically homogeneous to the juvenile groundfish. (2) Depth is highly correlated with other environmental variables and juvenile groundfish make multidimensional trade-offs among stresses within the sampled depth range. Both of these factors are believed to contribute to the integration of depth with other environmental variables.

All environmental variables extracted in the regressions have been correlated independently with estimates of abundance in a variety of habitats. The effects of temperature on the physiological processes of poikilotherms have been clearly demonstrated both in the laboratory (Fry 1947, 1971; Brett 1970) and on the Scotian Shelf (Tyler 1971; Scott 1976, 1982a; Sutcliffe et al. 1977; Macdonald et al. 1984; Mahon et al. 1984). Extraction of day of sampling as a significant variable probably reflected the growth and movement of juvenile fish in nearshore areas. Temporal shifts in the community composition of fish species are well documented (Tyler 1971; Macdonald et al. 1984; Mahon et al. 1984) but the short sampling period in this study prevents direct comparison. The significance of the substrate variable may have been related to the link with diet (Sale 1969; de Sylva 1975). If the availability and distribution of benthic and epibenthic organisms are determined by the nature of the sea bottom (Gray 1974) and the foraging of fish is species specific, a typical fish fauna should also be identified with a characteristic bottom type. Water clarity has also been shown to play a role in habitat selection. As vision appears to be the dominant sense in feeding of many near-surface teleosts (Blaxter 1980), turbid water detracts from feeding ability and may deter foraging fish from these areas. Alternatively, turbid water provides a degree of protection from predators (Blaber and Blaber 1980) and may be used as a refuge by juvenile groundfish. Salinity as a significant environmental variable is often proposed as the primary environmental gradient in coastal areas (de Sylva 1975; Weinstein et al. 1980). The distribution of fish species may be regulated or influenced by salinity gradients (Khlebovich 1968). Because juvenile groundfish are reported to be more tolerant of salinity fluctuations than adults of the same species (Gunter 1967; Claridge and Potter 1984), movement into less saline water may also provide protection from potential predators.

Although extracted in the regression equation, day of sample can not be considered an entirely independent variable. This variable was closely correlated with other environmental variables which may have resulted in autocorrelation among error terms. The resulting regression coefficients would still be unbiased but the variance of error terms and the standard deviation of estimated regression coefficients may have been underestimated (Neter et al. 1983). However, variables extracted in the regression equations were only used qualitatively to identify biologically important, environmental gradients. Quantitative interpretation of the regression results were not included in the analysis.

In this study, single environmental variables have not been observed to determine an individual's or species' distribution. Scott (1982a) calculated depth, temperature, and salinity preferences of common adult groundfish species of the Scotian Shelf. Preference trends existed in the data for some species, but Scott concluded "the evidence indicates that there is no single abiotic controlling influence." The results of this study support this conclusion and illustrate the need for a multivariate approach. Univariate statistics which treat biological or environmental variables as uncorrelated quantities, discard the covariation among variables (Orlóci 1975). Therefore, conclusions drawn from the analysis are limited to a single variable at a time (Orlóci 1978). Further, the characterization of an ecological habitat by single environmental variables may contribute to false interpretations (Pielou 1984). A multivariate approach has the advantage of identifying primary and secondary gradients within the environment as well as indicating the underlying environmental structure of known or observed biological gradients. In addition, multivariate techniques minimize noise, summarize redundancy, elucidate relationships, and identify outliers (Gauch 1982).

In summary, the distributions of 13 juvenile groundfish species were aligned to gradients in the environment. These biologically significant gradients corresponded to those which dominated the variation in the physical environment. Use of these biological and environmental gradients allowed the separation of the juvenile groundfish into two species assemblages. Multivariate DCA ordination coupled with stepwise regression techniques was an effective and robust method to characterize species distributions.

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