Spatial Dynamics of Cod-Capelin Associations off Newfoundland

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Abstract
Statistical analysis of large-scale (1-1,000 km) predator-prey associations between cod (*Gadus morhua*) and capelin (*Mallotus villosus*) is difficult because the spatial distributions of both species are heterogeneous and temporally dynamic. Statistics based on Ripley’s *K*-function were used to describe the spatial association between cod and capelin off Newfoundland. The number of capelin prey around cod predators (potential contact) was computed from acoustic survey data for a range of possible cod ambits, from 5 to 100 km. Potential contact between cod and capelin varied seasonally in Placentia Bay, southeastern Newfoundland in 1998, being highest in June and lowest in January. This seasonal difference was largely attributable to an increase in the spatial association of cod and capelin at scales of 10-50 km in spring. A similar pattern was observed off the northeast Newfoundland shelf in 1991-1994 where postspawning cod migrated inshore in spring and encountered groups of capelin. As a consequence of this migration pattern, spatial association and potential contact between cod and capelin were dependent on survey timing relative to the timing of cod spawning.

Introduction
The interaction between cod (*Gadus morhua*) and capelin (*Mallotus villosus*) is one of the best studied predator-prey interactions, and arguably the most important, in the northwest Atlantic ecosystem. Until the 1992 moratorium on fishing, cod were the most valuable commercial species in Atlantic Canada, and capelin are a major prey (review in Lilly 1987). Despite the importance of this interaction, relatively little is known about the association between cod and capelin distributions at large (>10 km) spatial
scales. Previous studies have used schematics (Akenhead et al. 1982) or expanding symbol plots (Lilly 1994) to graphically compare cod and capelin distributions with no formal statistical analysis. These and other studies suggest that the interaction between cod and capelin is spatially and temporally dynamic. The inshore movement of cod in spring (Rose 1993) coincides with the inshore spawning migration of capelin (Akenhead et al. 1982), and it has long been suggested that cod “follow” the movements of capelin at this time (Templeman 1965). At other times of the year (e.g., Turuk 1968) and in other areas (e.g., Casas and Paz 1996) consumption of capelin by cod is low, and little or no spatial association might be expected.

Previous quantitative studies of the association between cod and capelin were carried out at small spatial scales (<20 km), inshore, during the summer. In their study in southern Labrador, Rose and Leggett (1990) found that spatial associations were scale-dependent. Capelin and cod were positively correlated at the largest scales examined (>4-10 km), and negatively correlated at smaller scales, except when cod were actively pursuing capelin. Horne and Schneider (1994, 1997) did not detect spatial association between cod and capelin at any scale from 20 m to 10 km in 16 of 19 transects in Conception Bay, Newfoundland, and suggested that cod were not aggregating in response to capelin at these scales in this area (Horne and Schneider 1994). The dependence of association on spatial scale is typical of predator-prey interactions (Schneider 1992). Analysis at large scales may reveal patterns that would not be detected at smaller scales (Thrush 1991).

Our first aim in this study was to develop a statistical methodology to examine large-scale associations between cod and capelin from a variety of distributional data sets. Our second aim was to expand the temporal and spatial scales over which capelin-cod interactions have been examined.

**Methods**

**Acoustic Data**

Acoustic data on cod and capelin distributions were collected during research surveys in June 1991-1994, and in January (winter), March (early spring) and June (spring) 1998. Surveys in 1991-1994 mapped cod and capelin distributions on the northeast Newfoundland shelf (Fig. 1) using a Biosonics 102 dual-beam 38-kHz echo sounder calibrated with a tungsten carbide standard target. Surveys in 1998 covered Placentia Bay (Fig. 1) using a similarly calibrated Simrad EK500 split-beam 38-kHz echo sounder. Signals from cod and capelin were distinguished based on signal characteristics (LeFeuvre et al. 1999) and information from targeted fishing sets made using midwater and bottom trawls. Acoustic data were integrated in 100-m bins and scaled by target strength (TS) to give estimates of areal density (fish per square meter) of cod and capelin in each 100-m bin. Mean target strengths were calculated from fishing set length-frequency data
using the relationship $TS = 20 \log L - 67.5$ (G.A. Rose, unpubl. data) for cod, and $TS = 20 \log L - 73.1$ for capelin (Rose 1998) where $L$ is total length in centimeters. Areal density estimates were grouped into larger bins corresponding to 0.05 degrees of latitude by 0.05 degrees of longitude (equivalent to ~5.6 km by ~3.7 km at 49°N) prior to statistical analysis to reduce computational time and to compensate for differences in sampling intensity between areas.

**Statistical Analysis**
Potential contact is defined as the product of predator and prey abundance within the limits of some unit area (Schneider 1994). The general expression for potential contact is:

$$PC(r) = \frac{\sum_{x=1}^{n} (A_x B_x)}{\sum A_x}$$

(1)
is the number of individuals of type \( A \) within an area \( x \) of size \( r \), \( B_x \) is the number of individuals of type \( B \) within the same area \( x \), \( \Sigma A_x \) is the total number of individuals of type \( A \), and \( \sum_{x=1}^{n} \) is a summation over all areas \( x = 1 \ldots n \) of size \( r \).

Acoustic data provide estimates of density (fish per square meter) rather than numbers of individuals. The expected density of type \( B \) individuals (capelin) within distance \( t \) of any type \( A \) individual (cod), \( E[b(t)] \) is:

\[
E[b(t)] = \frac{\sum_{i=1}^{n} a_i(b_{ij})}{\sum_{i=1}^{n} a_i} \quad (2)
\]

where

\[
(b_{ij}) = \frac{\sum_{j=1}^{n} l_i(u_{ij})b_j}{\sum_{j=1}^{n} l_i(u_{ij})} \quad (3)
\]

For each point \( i \) for which density estimates are available, all capelin densities \( (b_j) \) within distance \( t \) (indicator function \( l_i(u_{ij}) = 1 \) where distance \( ij < t \), \( l_i(u_{ij}) = 0 \) otherwise) are averaged, and scaled by the density of cod at point \( i \) \( (a_i) \). This is repeated for all \( n \) points sampled. The result is then divided by the sum of the individual cod densities. It can be demonstrated (O’Driscoll et al. 2000) that equation 2 is analogous to the expectation term of Ripley’s bivariate \( K \) function (Ripley 1981) for a spatial point pattern. Equation 2 is also equivalent to Lloyd’s index of mean crowding for a single species (Lloyd 1967). However, unlike Lloyd’s index of mean crowding, potential contact may be calculated at increasing spatial scales (increasing \( t \)) without arbitrarily grouping data (O’Driscoll et al. 2000).

By multiplying \( E[b(t)] \) by the area enclosed by the circle with radius \( t (= \pi t^2) \), we obtain a measure of the potential contact between cod and capelin at scale, \( t \).

\[
PC(t) = \pi t^2 E[b(t)] \quad (4)
\]

\( PC(t) \) is the average number of potential capelin prey within an ambit of radius \( t \) of any cod. Potential contact increases as ambit size increases and is determined by the spatial association between cod and capelin as well as the overall density of capelin. Note that our definition of potential contact is based only on the relative spatial arrangement of cod and capelin and does not imply that cod encounter, or even have the ability to detect all capelin within their ambit. We assume, however, that at spatial scales similar to the foraging ambit of the predator that potential contact is a measure of feeding opportunity.
To test the hypothesis that there was association between cod and capelin at distance scale $t$, independent of capelin density, we generated 99 further realizations of the cod data by randomly reallocating cod density values to different points in the spatial distribution and recalculating $PC(t)$ for the randomized data. The results are expressed as the “extra contact” at distance $t$, $XC(t)$:

$$XC(t) = PC(t) - PC(t)_{\text{ran}}$$

$PC(t)_{\text{ran}}$ is the average potential contact from the random realizations. $XC(t)$ is the average number of “extra” capelin within an ambit of radius $t$. “Extra” capelin are those which are not expected if the cod sample densities were distributed randomly throughout the study area. $XC(t)$ has an expected value of 0 when there is no association between cod and capelin, $XC(t) > 0$ when cod and capelin are positively associated (correlated), and $XC(t) < 0$ when there is negative association. The upper and lower confidence intervals for $XC(t)$ were determined from the randomizations.

$$XC(t)_{95} = PC(t)_{95} - PC(t)_{\text{ran}}$$

$$XC(t)_{5} = PC(t)_{5} - PC(t)_{\text{ran}}$$

$PC(t)_{5}$ and $PC(t)_{95}$ are the values of the 5th and the 95th percentiles of potential contact from the random realizations.

**Results**

The distributions of cod and capelin in Placentia Bay in 1998 were spatially and temporally variable (Fig. 2). In January peak capelin densities were observed on the eastern side of the outer bay while cod were concentrated in the inner bay. In March the highest densities of both capelin and cod occurred in the inner bay. In June both species were present in large numbers in the outer bay. Average densities of cod and capelin in the study area in June 1998 were an order of magnitude higher than in the other two surveys.

In Fig. 3 potential contact with capelin is plotted as a function of ambit radius $t$ for cod ambits of 5, 10, 15, ... 100 km. Little is known about the foraging ambit of cod, but Rose et al. (1995) measured mean swimming speeds of between 6.6 and 24 km per day, with a peak of 59 km per day during the spring migration. At ambits of radii <60 km, potential contact between cod and capelin was highest in June, intermediate in March, and lowest in January (Fig. 3). These seasonal differences in potential contact were due to changes in spatial association between cod and capelin (Fig. 4) and changes in capelin density (Fig. 2). In January the association between
Figure 2. Expanding symbol plots of capelin and cod distributions from three acoustic surveys in Placentia Bay in 1998; + indicates no fish were detected.
cod and capelin was negative over a range of spatial scales (Fig. 4), reflecting the segregated spatial distributions of predator and prey (Fig. 2). In March potential for contact between cod and capelin increased (Fig. 3), despite a decrease in the density of capelin in the bay, because the distributions of the remaining cod and capelin were similar (Fig. 2). There was positive association between the two species at spatial scales <20 km with a peak (maximum association) of 15 km in March (Fig. 4). Potential contact was highest in June when cod were positively associated with high densities of capelin. Spatial association was detected at scales of 10-50 km in June, with maximum association at 45 km (Fig. 4).

There was interannual variation in potential contact between cod and capelin off the northeast Newfoundland shelf in June 1991-1994 (Fig. 5). In 1991 and 1992 cod were observed offshore in spawning aggregations (Fig. 6). Because these large aggregations of cod were spatially segregated from areas of high capelin density (Fig. 6), there were fewer capelin surrounding each cod than would be expected in a random arrangement of cod (negative association, Fig. 7). Cod spawning was earlier in 1993 and cod were observed farther inshore (Fig. 6). There was positive spatial association (although not above the 95% confidence interval) between cod and capelin at scales <250 km (Fig. 7) and potential contact was high (Fig. 5). In 1994 densities of cod were very low (Fig. 6) and most fish were immature. There

Figure 3. Seasonal variation in potential contact with capelin in Placentia Bay in 1998 over a range of possible cod ambits.
Figure 4. Seasonal variation in spatial association between cod and capelin in Placentia Bay. Plots show extra contact as a function of scale (solid line). Values greater than zero indicate positive association and values less than zero indicate negative association (segregation). Dashed lines are the 5% and 95% bounds for a random arrangement of cod generated from 100 randomizations of density increments.
Figure 5. Interannual variation in potential contact between cod and capelin on the northeast Newfoundland shelf, June 1991-1994.
Figure 6. Expanding symbol plots of capelin and cod distributions on the northeast Newfoundland shelf from acoustic surveys in June 1991-1994. Key as for Fig. 2.
Figure 7. Interannual variation in spatial association between cod and capelin on the northeast Newfoundland shelf. See Fig. 4 for details.
was positive spatial association between cod and capelin at large scales (250-400 km, Fig. 7), but potential for contact between cod and capelin was lower in 1994 than in 1993 (Fig. 5).

**Discussion**

The predator-prey interaction between cod and capelin off Newfoundland was dynamic because of seasonal and interannual variability in the spatial distribution and abundance of both species. Potential contact provided a robust, quantitative measure of the overall influence of predator and prey distributions and prey abundance on potential encounter rates. A related measure, extra contact, assessed spatial association across a range of scales independent of density. Unlike alternative covariance-based methods such as spectral analysis (Rose and Leggett 1990; Horne and Schneider 1994, 1997), contact statistics are not sensitive to the presence of zero values and can be applied to areas with irregular sampling and/or boundaries. The statistical outputs are easily interpreted biologically as the potential for contact between predator and prey.

Our equation for potential contact (equation 4) is not corrected for edge effects. Edge effects arise when a sample point is within distance of a survey boundary. In these instances, part of the predator ambit centered on point is outside the survey area and prey densities within the ambit cannot be evaluated without a certain bias (Haase 1995). Edge bias increases with increasing ambit size. Our method used capelin densities within the portion of the cod ambit which was inside the survey area to estimate densities beyond the boundary. The implicit assumption is that capelin densities outside the surveyed area were similar to densities inside. This is clearly not the case when the survey area is bordered by land (e.g., Placentia Bay). We conducted simulations by adding zero values beyond the survey boundaries and found that at small cod ambits (t < 40 km) there was little evidence of edge bias. At larger cod ambits absolute values of PC(t) overestimate potential contact when there are no capelin outside the survey area. Comparisons of relative values of potential contact at these larger ambits are still valid. Because the same assumptions are made for the data and for the random realizations, our measure of spatial association XC(t) (equation 5) was not biased by edge effects.

Our data from Placentia Bay provide support for the hypothesis that cod “follow” capelin in spring (Templeman 1965). Between March and June 1998 there was an influx of both cod and capelin into Placentia Bay from outside the study area. Tagging studies also show that there is a postspawning migration from the inner bay spawning grounds to the outer bay (Lawson 1999). Potential contact was very high in June because there were high densities of capelin closely associated with cod. However, it should be noted that spatial association does not necessarily indicate cause and effect. There are at least three cod spawning sites in Placentia Bay and
spawning also occurs in spring (Lawson 1999). Some movements of cod may have been driven by reproduction rather than feeding.

Interannual differences in spatial association between cod and capelin off the northeast Newfoundland shelf were explained by differences in the timing of the acoustic surveys relative to the inshore postspawning migration of cod (Rose 1993). Although surveys in 1991-1994 were conducted at the same time of year, cod spawning was delayed in 1991 and 1992, possibly because of very cold water temperatures in these years. In 1993, spawning was earlier and the cod migration was more advanced. Cod were observed farther inshore and were associated with capelin. Little can be concluded from the 1994 survey because densities of cod were very low and the size structure of the population was different from previous years. These data emphasize the importance of understanding seasonal patterns in spatial association before attempting to quantify long-term trends in potential contact between predators and prey.

The observed movement patterns of cod on the northeast Newfoundland shelf and in Placentia Bay led to increased opportunities for feeding on capelin in spring. This is consistent with what is known about seasonality of feeding by cod. Templeman (1965) found that consumption of capelin by cod captured inshore at St. John's increased from May to June, was highest (capelin 88-99% of total cod food by volume) between mid-June and early August, and decreased again in the fall. Offshore, on the northeast slope of the Grand Banks, Turuk (1968) also recorded peak feeding on capelin from June to August. Little is known about cod diet in Placentia Bay, but our preliminary analysis of cod stomachs indicates that consumption of capelin is greater in spring than in late fall or winter. We intend to examine cod stomach data in more detail to compare our predicted contact rates with capelin consumption.

The statistical techniques described in this paper are applicable to any survey data where there are estimates of predator and prey density, providing the minimum separation between sample points is smaller than the spatial scale of interest (O'Driscoll et al. 2000). Sampling design is an important consideration when calculating contact statistics, as it is for any statistical method that relies on sample data. The separation between adjacent sampling points determines the minimum spatial scale at which potential contact can be assessed and also the precision with which we can describe association.

Contact statistics may also be calculated to describe scale-dependent spatial pattern in a single species (O'Driscoll et al. 2000) or to determine association with abiotic features such as habitat type (Bult et al. 1998).

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References


Spatial Patterns of Pacific Hake (*Merluccius productus*) Shoals and Euphausiid Patches in the California Current Ecosystem

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Abstract

In the summer, along the California Current Ecosystem (CCE) off the coastline of California, Oregon, and Washington, the battle line between actively feeding Pacific hake (*Merluccius productus*) shoals and large patches of euphausiids is drawn at the shelf break. In this paper we examine the summer spatial distribution of shoals of the dominant fish predator in this ecosystem (88% of trawl catch by volume) and its major prey species and suggest that the spatial proximity of these groups is dominated by their overlap at or near the shelf break (between 150 and 250 m depth).

Based on acoustic survey data collected by the National Marine Fisheries Service, Alaska Fisheries Science Center during summer 1995 and 1998, I used image processing methods and acoustic backscatter theory to distinguish patches of plankton from shoals of fish. Having multiple transects marching south to north from California to British Columbia provided a degree of pseudoreplication and gave us the ability to compare fish and plankton distributions over both space and time. I found evidence for an inverse relationship between fish and plankton over some regions. Of particular interest is the apparent northward shift of Pacific hake during the 1998 El Niño year and the accompanying increase in plankton abundance over part of the region (California, Oregon, and Washington). Two proximity-related tests were applied on a transect-by-transect basis. One, a nonparametric model of fish shoal biomass as a function of proximate plankton biomass, indicated a high degree of overlap in some regions and times, between high-abundance fish shoals and high-abundance plankton patches proximate to these shoals. This proximity has predator-prey implications, in that it suggests that the shelf break may be a dominant zone...
for hake predation on euphausiids because high-abundance euphausiid patches and high-abundance fish shoals were most consistently found together near the shelf break.

Introduction

This paper distills results from acoustic surveys in summer 1995 and 1998 along the northern California, Oregon, and Washington continental shelf-break regions, concerning the spatial distribution of fish shoals, primarily Pacific hake (*Merluccius productus*), and euphausiids, which are their major prey over this region. (Fish and plankton are used interchangeably with Pacific hake and euphausiids, respectively. Pacific hake dominated the fish abundance with 90% [1995] and 89% [1998] of the targeted Aleutian wing trawl catch by weight [Wilson and Guttormsen 1997, 1998]. Euphausiids, because they are the largest plankton, dominated the plankton backscatter at 120 kHz [McKelvey 2000]. Much higher densities of smaller zooplankton would be necessary to be “seen” at 120 kHz.) While results are specific to this area, we hope that the methods and findings will be generally applicable to studies of shelf-ecosystem predator-prey spatial distributions and interactions.

Predator-prey dynamics in the nearshore ocean are played out in a labile, three dimensional space. This space also features mesoscale oceanographic features, such as fronts, jets, and eddies, and bathymetric features such as shelf breaks, trenches, and rises (Hickey 1998). In this extensive, but far from featureless, habitat, both fish and plankton form aggregations, which may provide them with advantages in either finding and utilizing their prey or escaping from their predators (Partridge 1982, Pitcher and Parrish 1993) or both. Recent improvements in ocean sensing, including satellite imagery (Simpson and Harkins 1993), low-frequency sonar systems, acoustic doppler current profilers (Pierce et al. 1999), and long-lived buoy-based hydrographic monitors (Hickey et al. 1997), have improved our understanding of the importance of ocean features in structuring nutrient, temperature, phytoplankton, and current dynamics. Still, our understanding of biological interactions in the highly productive shelf regions of our world’s oceans is far from mature. Attempts have been made to model such explicit spatial phenomena as larval drift (Hermann et al. 2001) and juvenile fish feeding by adding passively moving biota onto mesoscale-level ocean models, which can resolve, but not predict, such features as jets, fronts, and eddies (i.e., they are mimics rather than predictors of observed oceanic phenomena). Predation by fish, another spatially explicit process, is clearly an active process where both the fish and their prey (be it fish or zooplankton) use their mobility to maintain or change position within the environment. At fine temporal scale (diurnal) euphausiids often exhibit diel migration, moving down in the water column during the daytime and up at night (Fulton and LeBrasseur 1984), presumably to avoid predation during the daytime and to feed during nighttime and crepuscu-
lar periods. At larger scales fish migrate, presumably to utilize higher seasonal production, and may also orient themselves around such productive features as ocean fronts and eddies (Shinomiya and Tameishi 1988). To examine how effectively these strategies work for the fish and plankton would require observation through the water column at a spatial and temporal scale currently unattainable. We are left with either monitoring smaller areas more extensively or larger areas occasionally and not simultaneously (i.e., we cannot cover the entire study area synoptically and instantaneously). As such, we must be content with repeated three-dimensional snapshots of the same area at selected time periods and make brave assumptions. Such is the case with this study. Yet, I hope to demonstrate that the spatial proximity between feeding fish shoals and their plankton prey is remarkably consistent in the face of the spatial complexity of continental shelf ecosystems. Here I will use the large number of survey transects as pseudo-replicates to suggest certain patterns that repeat over given spatial areas in the California Current Ecosystem (CCE) through much of the summer, and some that do not.

Data

The data used in this study were collected by the National Marine Fisheries Service, Alaska Fisheries Science Center (AFSC) acoustics group during summer, from July 1 to September 1, 1995, and July 6 to August 27, 1998. A hull-mounted SIMRAD EK-500 split beam sonar system with BI500 software (Knudsen 1994) and with two transducers at 38 and 120 kHz was used along survey transects from Monterey, California, to Queen Charlotte Islands, British Columbia in both years (Fig. 1). Survey tracks were parallel, generally oriented east-west, and spaced at 10-nmi intervals. This study uses the data from the latitude of Cape Mendocino, California to the Washington–British Columbia border at the Strait of Juan de Fuca because there were almost identical transects within this region in both study years. Large-net midwater and bottom trawls (anchovy and otter trawls) were used to corroborate fish distribution in the backscatter, and smaller “plankton nets” (Methot trawls) were used for species composition and size composition of the fish and plankton. The 120 kHz acoustic system has a range of not more than 250 m and, as such, data on plankton abundance below 250 m were not available. The fish shoals and plankton patches identified using the methods described below were not compared with the fish catch data (scrutinized) to give information about species composition. However, the catch data were dominated by Pacific hake and euphausiids, respectively. The survey was conducted during the daytime hours.

Methods

Fish shoal identification used the 38 kHz echograms, while plankton patch identification used both the 38 and 120 kHz data. The identification algo-
Figure 1. Shoal abundance (biomass per kilometer) shown by ovals and plankton abundance by rectangles for 1995 (left panel) and 1998 (right panel). Results for the offshore region (>250 m) are shown on the left side and shallow region results on the right side of each transect. Three coastal regions (North, Middle, and South) and the approximate location of the shelf break are identified.
rithms required that patches comprise contiguous pixels in the echogram images, with a clearly defined boundary, and with a backscatter range indicative of the target group (e.g., greater than –51 dB for Pacific hake shoals [Swartzman 1997] and between –62 and –45 dB for euphausiid patches). (The threshold levels for euphausiids were obtained after trial and error tests on individual transects. The best thresholds to use may vary depending on the project objective.) After applying the appropriate threshold to the 38 kHz echograms a morphological filter using a $3 \times 3$ (horizontal $\times$ vertical) binary structuring element was used according to methods from Swartzman et al. (1994, 1999).

Plankton patches were located by taking the difference between the 120 and 38 kHz images after the threshold filters for euphausiids were applied. A morphological closing followed by an opening (Haralick and Shapiro 1992) using a $3 \times 2$ structuring element was applied to the difference echogram after a +2 dB threshold was applied to it (Swartzman et al. 1999). This second threshold assured that all remaining pixels had backscatter at 120 kHz at least 2 dB higher than backscatter at 38 kHz, which is consonant with geometric backscatter models used for euphausiids (the bent cylinder model; Stanton et al. 1993). (The backscatter difference between 120 and 38 kHz for euphausiids may be higher than 2 dB. McKelvey (2000) found an average backscatter difference of about 10 dB for backscatter by euphausiids.) The resulting euphausiid patches and fish shoals were recorded in a table which describes parameters of the patches including shape, size, location, backscatter, and environmental parameters of the patches using a connected component algorithm to extract this information (Haralick and Shapiro 1992, Swartzman et al. 1999).

An index of abundance for fish shoals and plankton patches was derived from the processed images (Fig. 1). Because the shelf and offshore areas are so different bathymetrically and hydrodynamically in the CCE, we computed transect abundance (biomass per kilometer) separately for the shelf and offshore regions. We used the product of the patch area (in square meters) times the mean $s_A$ ($m^2/m^2$) for the patch. This was converted to an index of transect abundance by summing the abundance indices for all the patches in the transect and dividing by the length of the transect (in kilometers). The index was applied separately to deep, offshelf (offshore) regions (bottom > 250 m) and shelf regions (bottom < 250 m) within each transect (Fig. 1). The distance in the denominator was the part of the transect within each region (offshore and shelf). The study area was divided into three regions north to south (Fig. 1), to reflect differences in oceanographic conditions. These are the North region, from Cape Flattery to the Columbia River; the South region, from Cape Mendocino to Cape Blanco; and the Middle region, between these. Cape Blanco forms a natural oceanographic boundary, with a narrower shelf and more consistent wind-driven upwelling to the south (Hickey 1979, 1998). The Columbia River, the major river system along the U.S. West Coast, is used as another region boundary (Hickey et al. 1997). Having these regions gives us a way to sim-
plify broad spatial patterns in fish and plankton abundance. By assuming homogeneity within transects in a region we can treat the transects as replicates and quantify large-scale distribution patterns.

To examine the spatial proximity of fish shoals and plankton patches two complementary approaches were used. A nonparametric regression generalized additive model (GAM) approach was used to look at the relationship of several factors to shoal biomass, and a distance-based proximity index (Swartzman et al. 1999) to look at the proximity of fish shoals and plankton patches.

In the GAM model (Hastie and Tibshirani 1990) fish shoal abundance was modeled as an additive sum of smooths of shoal depth, bottom depth, and plankton abundance proximate to the fish shoals. This model was used on a transect-by-transect basis for both 1995 and 1998. To compute the plankton abundance proximate to each fish shoal we chose a distance range of 1 km, an estimate of the short-term fish feeding range. The GAM model, run in S-Plus software, used a spline smoother with a range set by cross-validation (Venables and Ripley 1994) and assumed the abundance data were normally distributed.

A distance-based proximity index, computed for 1995 and 1998, measured the plankton abundance index at different distances from each fish shoal from 0 m (i.e., the patch overlaps the shoal) to 1 km, in intervals of 100 m. The measure was compared with results obtained by randomly translating the plankton patches within the transect a large number of times (20) and recomputing the measure. This provided error bounds to determine the distance range over which the plankton were uniformly distributed around the fish shoals (the empirical proximity index was within the 95% error bounds), more regular than uniform (below the lower error bound), or clustered (above the upper error bound). The proximity measure is based on Ripley’s $K$, used in spatial statistics to test for randomness of points in space (Diggle 1983). We modified Ripley’s $K$ to include the size of the fish shoal and the plankton patches, using distance from the edge (instead of from the center) of each shoal as the measure of distance and summing the plankton patch abundance within each distance range from each fish shoal instead of just counting the number of points (e.g., patch centers) within that range (Swartzman et al. 1999). The proximity index was calculated separately for each transect both for fish shoals over bottom depths less than 250 m (shelf shoals) and those over bottom depths greater than 250 m (offshore shoals).

These two indexes examined different aspects of proximity. The GAM model tested whether there was a significant change in the abundance of fish shoals with changes in the total abundance of plankton patches within 1 km of the edge of the shoals. The proximity index showed whether, for a given distance range from the edge of fish shoals, the plankton abundance was randomly distributed or whether it was more clustered (i.e., more plankton abundance than expected from a random distribution of plankton patches around the fish shoals at small distance ranges) or regularly dis-
tributed (i.e., less plankton abundance than expected from a random distribution of plankton patches around the fish shoals at small distance ranges). The GAM model looked at the effect on shoal abundance of plankton within a single distance range, while the proximity index was a multiscale effect, but did not tell anything about the size of the shoals.

Results

The distribution of fish differed markedly between 1995 and 1998 over the study region. Hake abundance was greater further north in 1998 and over half the hake biomass in that year was in Canada (Wilson and Gutormsen 1997, 1998). Similarly the north-south distribution of euphausiids was different between the 2 years, with plankton highest offshore in the North in 1995 and the South in 1998 (Figs. 1 and 2, Tables 1 and 2).

Hake abundance in 1995 was highest in the South region (abundance >2 × 10^{-2} m²/km for all transects), especially in offshore water (>250 m depth) but also, somewhat along the shelf. This was accompanied by consistently low plankton abundance offshore over the same region (Figs. 1 and 2). In 1998, an El Niño year, fish abundance, especially over the shelf, was consistently low in the South (abundance < 5 × 10^{-3} m²/km for 11 of 12 transects; median abundance = 2 × 10^{-3} m²/km) while plankton tended to be elevated (Fig. 2).

Figures 3, 4, and 5 show fish shoal and plankton patch distributions along matching transects for 1995 and 1998 in the South, Middle, and North regions, respectively. In these figures the intensity of the shading is proportional to the biomass of the shoal or patch. The intensity scaling is on a per transect basis, so relative abundance can only be ascertained within, not between, transects. These transects are fairly typical of transects in each region. Some of the observable features of note are: (1) consistent overlap of large plankton patches and larger fish shoals in the neighborhood of the shelf break; (2) a consistent “layer” of plankton between 150 and 250 m depth in the shelf break and offshore regions, generally more pervasive in 1995 than in 1998; and (3) more variable plankton patch and fish shoal abundance from transect to transect along the shelf than offshore.

Results from the GAM regressions and the Ripley’s proximity tests are summarized in Tables 1 and 2 for 1995 and 1998, respectively. The tables also give the median fish and plankton abundance for each region on the shelf and offshore. In some cases the Ripley’s clustering test did not work, because there were insufficient fish or plankton in a region to give a result, which accounts for there being fewer tests reported in some regions than numbers of transects in that region.

Tables 1 and 2 show the number of transects in each region having significant clustering of plankton patches around fish shoals (i.e., the empirical mean of Ripley’s K was above the upper 95% confidence limit for randomness for a distance range up to 1 km) for both the shelf and offshore.
Figure 2. Box plots for relative abundance (m²/km) of fish shoals and plankton patches on the shelf and offshore in the South, Middle, and North regions for 1995 and 1998.

Figure 3. Distribution of plankton patches (light-shaded polygons) and fish shoals (dark-shaded polygons) for transects at 42.14°N in the South region. Shading is proportional to biomass. The bottom contour and plankton patches at the shelf break are also shown.
Table 1. Distribution in 1995 of shelf and offshore fish and plankton abundance (m²/km) and results of proximity index and GAM tests.

<table>
<thead>
<tr>
<th>Region</th>
<th>Transects</th>
<th>Median shelf plankton</th>
<th>Median shelf fish</th>
<th>Median offshore plankton</th>
<th>Median offshore fish</th>
<th>Transects showing offshore clusters</th>
<th>Transects showing shelf clusters</th>
<th>Transects with GAM signif.</th>
</tr>
</thead>
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<tr>
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<td>16</td>
<td>9×10⁻³</td>
<td>6×10⁻³</td>
<td>2.5×10⁻³</td>
<td>3.2×10⁻²</td>
<td>5/16</td>
<td>4/11</td>
<td>14/16</td>
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<tr>
<td>Middle</td>
<td>14</td>
<td>8×10⁻³</td>
<td>2×10⁻³</td>
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<td>12/14</td>
<td>9/14</td>
</tr>
<tr>
<td>North</td>
<td>20</td>
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<td>1×10⁻³</td>
<td>5×10⁻³</td>
<td>1.5×10⁻³</td>
<td>5/16</td>
<td>15/16</td>
<td>6/20</td>
</tr>
</tbody>
</table>

Table 2. Distribution in 1998 of shelf and offshore fish and plankton abundance (m²/km) and results of proximity index and GAM tests.

<table>
<thead>
<tr>
<th>Region</th>
<th>Transects</th>
<th>Median shelf plankton</th>
<th>Median shelf fish</th>
<th>Median offshore plankton</th>
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<th>Transects with GAM signif.</th>
</tr>
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<tr>
<td>South</td>
<td>16</td>
<td>1×10⁻²</td>
<td>2×10⁻³</td>
<td>1.5×10⁻²</td>
<td>5×10⁻³</td>
<td>6/16</td>
<td>8/13</td>
<td>9/16</td>
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<tr>
<td>Middle</td>
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<td>7×10⁻³</td>
<td>3×10⁻³</td>
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<td>8×10⁻³</td>
<td>6/14</td>
<td>7/14</td>
<td>9/14</td>
</tr>
<tr>
<td>North</td>
<td>19</td>
<td>7×10⁻³</td>
<td>3×10⁻³</td>
<td>8×10⁻³</td>
<td>1.1×10⁻²</td>
<td>9/17</td>
<td>9/19</td>
<td>14/19</td>
</tr>
</tbody>
</table>
Figure 4. Distribution of fish shoals (dark-shaded polygons) and plankton patches (light-shaded polygons) for a transect in the Middle region at 43.8°N. Intensity of shading of the polygons is proportional to biomass.

Figure 5. Fish shoal (dark-shaded polygons) and plankton patch (light-shaded polygons) distribution for a transect at 46.1°N latitude in the North region. Intensity of polygon shading is proportional to biomass.
Figure 6. Results of GAM model for the effect of plankton patch abundance proximate to fish shoals on fish shoal abundance for transects in the South, Middle, and North regions.
regions. They also show the number of transects in each region having significant GAM relationships for the effect of plankton abundance within 1 km of fish shoals and the abundance (biomass) of the fish shoals.

In all regions GAM results (e.g., Fig. 6) indicate that, in every transect, the most significant covariate for fish shoal abundance was the abundance of plankton patches within 1 km of the fish shoal. The other covariates (shoal depth and bottom depth under the shoal) were rarely significant at $P < 0.05$. Figure 6 shows the effect of proximate plankton abundance on fish shoal abundance for the same transects in each region depicted in Figs. 3-5. Five of 6 cases shown gave significant results at $P < 0.01$. In all significant cases shown here fish shoal abundance increased with increasing proximate plankton abundance only for higher abundance of plankton. This is seen in the ascending right limb in all significant transects in Fig. 6. The tick marks along the x-axes in Fig. 6, termed the “rug,” indicate where data points were located. The rugs show that the ascending right limb was based on a relatively small number of shoals.

Figure 6 shows the effect of plankton patch abundance on fish shoal abundance, conditional on the effects of other covariates (mostly insignificant) and with the overall mean shoal abundance subtracted. This accounts for the curves having negative as well as positive values on the y-axis. Examination of the plots of plankton and fish abundance as a function of distance along the transects in this region (e.g., Figs. 3-5 and other transects not shown here) suggests that for almost all transects where the GAM results were significant (e.g., 13 of the 14 significant transects in 1995 and all 9 significant transects in 1998 in the South region) there was clear visual evidence for proximity of high-abundance plankton patches near the shelf break with larger biomass fish shoals in the area. Furthermore, for transects in the South region, where there was no significant GAM effect of proximate plankton abundance on fish shoal abundance, there was generally no observable proximity of fish and large plankton patches near the shelf break (e.g., 1 of 2 transects in 1995 and 6 of 7 transects in 1998). This pattern also held for the other regions.

In the Middle region, the abundance of fish and plankton were at intermediate levels for both 1995 and 1998 (Fig. 2). However, for 9 of 14 transects in both years (Tables 1 and 2) the GAM model showed a significant effect of plankton abundance near fish shoals on fish shoal abundance, with the relationship being due to high-abundance fish shoals associated with high-abundance plankton patches (Fig. 4). All transects having significant GAMs in this region in both years had visual evidence of large fish shoal-plankton patch proximity near the shelf break (e.g., Fig. 6).

The North region had a plankton-fish relationship in the shelf region which differed between 1995 and 1998. In 1995 most transects had low fish abundance and relatively high plankton abundance (Figs. 1 and 2) along the shelf (median fish abundance was $1 \times 10^{-3}$ m$^2$/km and plankton abundance was $9 \times 10^{-3}$ m$^2$/km; Table 1). In 1998, both fish and plankton abundance along the shelf were variable, with fish shoal abundance higher than
the overall region median and plankton abundance lower than the region median south of 47.3°N and vice versa north of this latitude (median plankton abundance = \(4 \times 10^{-3}\) m\(^2\)/km south and \(1.1 \times 10^{-2}\) m\(^2\)/km north of that latitude; median fish abundance = \(1.8 \times 10^{-2}\) m\(^2\)/km south and \(4 \times 10^{-3}\) m\(^2\)/km north of that latitude; Fig. 1). Offshore, both plankton and fish abundance were higher in 1998 than in 1995 in this region (Fig. 2).

The GAM relationship of large-abundance plankton patches and fish shoals in the North region also differed between 1995 and 1998. In 1995, when fish abundance was low both on the shelf and offshore, only 6 of 20 transects showed a significant GAM relationship between plankton abundance proximate to fish shoals and fish shoal abundance. In 1998, a year of higher fish and lower plankton abundance along the shelf in this region, 14 of 19 transects showed a significant effect of plankton abundance on fish abundance from the GAMs. The example transect shown in this region (Figs. 5 and 6) showed a significant GAM relationship for large plankton and fish in 1998, but not in 1995. In 1995, although high abundance plankton patches appeared near the shelf break, there were no high biomass fish shoals close by (e.g., Fig. 5).

Results from the proximity-index test for the possible clustering of plankton patches around fish shoals (irrespective of the biomass of the fish shoals) showed a strong clustering relationship on the shelf in 1995 for all transects in the Middle and North regions. In the shelf area, 27 of 30 transects showed significant clustering of plankton patch abundance around fish shoals. Offshore, there was less clustering of plankton patches around fish shoals, with somewhat less than half the transects showing clustering (somewhat more than half in the Middle region). The proximity picture was different in 1998. As in 1995, the number of transects showing clustering over the shelf area was higher than offshore (although only marginally so). There was significant clustering along the shelf in 16 of 33 transects in the Middle and North and in 8 of 13 transects in the South (Table 2). This was a much less striking contrast than in 1995, and, unlike 1995, clustering along the shelf was more prevalent in the South than in the Middle and North regions. In the offshore region there was significant clustering in 15 of 31 transects in the Middle and North and 6 of 16 transects in the South (Table 2). Clustering offshore in 1998 was about the same as in 1995 in all regions (12 of 29 transects showing significant clustering in the Middle and North and 5 of 13 transects in the South in 1995). Clustering on the shelf in the South was higher in 1998 than in 1995 (only 4 of 11 transects showed significant clustering in the South in 1995, while 8 of 13 did in 1998; Tables 1, 2).

**Discussion**

The large number of transects having GAMS with a significant overlap between large-biomass fish shoals and higher levels of proximate plankton abundance and visual observation of these transects suggests that high-
abundance fish shoals were often close to the high-abundance plankton patches when the plankton patches were close to the shelf break and were, arguably, easier to locate by grazing hake shoals. This pattern occurred pervasively over the study region in both 1995 and 1998, and apparently independent of changes in the relative abundance of fish shoals and plankton patches. The only exception occurred in the North region in 1995, where fish abundance was, for most transects, exceptionally low (Fig. 5, Table 1). Perhaps the migration of hake did not go as far as the North region in 1995, or perhaps the high-biomass fish shoals in the North region were so patchy that they were not frequently encountered along the survey transects. Almost all transects in the North region in 1995 showed large patches of plankton near the shelf break, but few if any fish shoals along the transect (e.g., Fig. 5).

In the South region, irrespective of whether plankton abundance was high and fish abundance low (1998) or vice versa (1995), there was, for a majority of transects, a clear association between high-abundance fish shoals and high-abundance plankton patches. Furthermore high-abundance plankton patches were commonly found on the shelf break. In 1995, the proximity of high-abundance fish shoals to high-abundance plankton patches near the shelf break, despite the relatively low plankton abundance in this region, might reflect the effect of intense predation on euphausiids by Pacific hake such as to reduce the euphausiid abundance. The persistence of larger euphausiid patches near the shelf break in this region when plankton abundance was lower, as in 1995, suggests that these may be a favored habitat for euphausiids, maintained despite heavy predation. The shelf break might be a preferred euphausiid habitat because it provides a stable summer feeding environment and may also have hydrodynamic features that allow the euphausiids to remain in the area despite high alongshore currents (Mackas et al. 1997). While the spatial overlap of high-abundance fish shoals and plankton patches was marked in 1995, it was also apparent in the South (although not as prevalent) in 1998, a year when plankton were high and fish abundance low. However, in 1998, there was also consistent overlap of high-abundance fish shoals and plankton patches in the North region, where both shelf and offshore fish densities were higher than in 1995 (Table 2).

Because of the apparent importance of the shelf break, separation of this region from the offshore and shelf regions seems desirable. This was not done here, mainly because locating the boundaries of the shelf break by algorithm was difficult due to variability of shelf break bathymetry and the existence of bathymetric features (e.g., ocean rises and canyons) that can be confounded with the shelf break. This remains as future work.

The proximity measure examined how close shoals in general were to food resource patches without regard to the size of the fish shoals. Thus, although in the North in 1995 prey patches on the shelf were distributed around fish shoals in a nonrandom, clustered fashion in almost every transect (Table 1), the high-abundance shoals were not often associated
with high-abundance plankton patches over the entire transect. The major difference in fish-plankton proximity between 1995 and 1998 was in the shelf areas, which had more clustering in the Middle and North in 1995 (27 of 31 transects) but more clustering South in 1998 (8 of 13 transects). The high degree of clustering of plankton patches around fish shoals on the shelf in 1995 in the Middle and North regions may be due to the higher plankton abundance in this region than in the South and the effectiveness of hake in locating and grazing on plankton patches in this area. The lower (about 50% of transects) incidence of clustering of plankton patches around fish shoals in 1998 in the Middle and North regions over the shelf may be due to the hake being younger in this area in 1998 than in 1995 and therefore less effective grazers. For example, 95% of the Pacific hake caught in trawls off Washington in 1995 were above 42 cm fork length, while only 50% in 1998 were in this size category (Wilson and Guttormsen 1997, 1998).

Results from the GAM and cluster proximity tests frequently do not agree (Tables 1 and 2). Because the hake biomass is dominated by larger shoals, the GAM results give a more apt interpretation of what is happening for most of the fish in a region. However, for the shelf areas, where hake shoals tended to be smaller, the cluster results have provided additional insight into fish-plankton dynamics.

We have focused effort in this paper on fish-plankton relationships off the U.S. coast. In both years, the survey went farther north, to the neighborhood of the Queen Charlotte Islands, Canada (latitude 50°N). Significantly, large aggregations of Pacific hake were found off Vancouver Island in 1998, suggesting that one of the features of El Niño years was a northward shift of Pacific hake (Wilson and Guttormsen 1998). A similar pattern was found for acoustic surveys run during previous El Niño years (Dorn 1991, Dorn 1995).

It is unclear whether the higher than average northward migration in 1998 was driven primarily by physical factors, such as enhanced northward flowing current at depths between 150 and 400 m, where the hake were primarily found, or due to a lack of food resources farther south. This study showed regional reversals between 1995 and 1998 in fish and plankton abundance, with the South region having high fish abundance and low plankton abundance in 1995 and shifting to the reverse in 1998. Generally, fish abundance throughout the U.S. California Current Ecosystem (CCE) region was higher in 1995 than in 1998 and plankton was higher in 1998 than in 1995 (except for the region around the Columbia River; Fig. 1). That zooplankton abundance in 1998 was generally higher than in 1995, despite the expected reduction in primary production due to lowered wind-driven upwelling, which usually accompanies El Niño, leads to the hypothesis that movement of hake farther north during 1998 may not have been due to reduced food availability, but to enhanced northward flow. This can be investigated using ADCP data currently being processed (Pierce et al. 1999; M. Kosro, Oregon State University, pers. comm.) and also from current meters deployed during 1998 off Coos Bay, Oregon (B. Hickey,
University of Washington, unpubl. data). Because the zooplankton condition earlier in the summer, when many of the hake passed through the southern region, is not available, the question about the source of higher plankton abundance in 1998 remains unresolved. Does the larger euphausioid abundance in 1998 reflect reasonable food availability for and growth by euphausiids, or does it reflect the effects of reduced hake predation due to northward shift of the hake population in an El Niño year?

Another striking observation, which has not been further investigated, is the presence of large layers of plankton in the offshore region. The layers may be continuous or more patchy (Figs. 3-5). However, it is not clear how the plankton can remain in patches in the face of the large shear found offshore at a depth near the maximum northward flowing California undercurrent (Pierce et al. 1999). Perhaps the higher-production shelf break region is saturated and the plankton remain in the undercurrent until they encounter regions of higher food availability. Perhaps they remain offshore to avoid predation along the shelf break. Alternatively, they may be diel migrating such as to maintain position (surface waters in the summer CCE are generally southward flowing) in anticipation of higher production eddies or jets. Clearly, more work is waiting in this area.

The above discussion illustrates part of the difficulty in trying to ascertain patterns of grazing from the spatial configuration of predator and prey at a given time and place. We do not know the movement history of the animals prior to their observation and we do not know the production history of the euphausiids and their food resources. Nonetheless, some of the patterns are compelling and provide insight. Others serve to raise questions that may be addressed in the future through process studies.

Acknowledgments

This work is entirely indebted to Chris Wilson from the Alaska Fisheries Science Center, who cooperated with me both in freely making data available and in stimulating discussions. Neil Williamson, Steve DeBlois, and Taina Honkalehto also helped with data transfer. I appreciate discussions with and feedback from Mark Saunders, Robert Kieser, and Kenneth Cooke from the Pacific Biological Station in Nanaimo, B.C., Canada. This paper is the result of research funded by the National Oceanic and Atmospheric Administration Coastal Ocean Program under award # NA96OP0238 to the University of Washington.

References


Spatial Patterns in Species Composition in the Northeast United States Continental Shelf Fish Community during 1966-1999

Lance P. Garrison
National Marine Fisheries Service, Northeast Fisheries Science Center, Woods Hole, Massachusetts

Abstract
I evaluated spatial structure in the northeast United States continental shelf groundfish community based on a 30-year time series of bottom trawl survey data. Four major faunal regions were identified based on similarity in species composition. The faunal regions had consistent geographic boundaries across the time series. There were significant changes in species composition within faunal regions through time, reflecting changes in both species abundances and spatial patterns. Species that declined in abundance tended to contract their spatial range while those that increased tended to expand the total area covered by the population. However, the more general pattern in this community was a northward shift in spatial distribution observed in many exploited and unexploited species. The major changes in community structure and spatial distributions associated with both fishing pressure and climate variation have important implications for the trophic dynamics of this ecosystem.

Introduction
Fishery harvest and overexploitation have driven dramatic changes in ecosystem structure and dynamics in fish communities on a global scale (Jennings and Kaiser 1998). Predicting the response of fish communities to overexploitation requires a greater understanding of the ecosystem-wide effects of fishing on the interactions between species and the resulting
community dynamics (Fogarty and Murawski 1998, Jennings and Kaiser 1998). These “ecosystem” and multispecies approaches to fishery assessment and management require an improved understanding of the processes that regulate the strength of species interactions in fish communities.

The fish predators in continental shelf ecosystems are characterized by a high degree of dietary generalism and opportunistic feeding (Jennings and Kaiser 1998, Garrison and Link 2000). Selection of a given prey is largely determined by encounter rates and prey abundance, and high spatial overlap between predator and prey can significantly influence predation rates (Jennings and Kaiser 1998). The processes influencing spatial patterns in community structure therefore play an important role in driving variability in trophic interactions.

Fish spatial distributions are sensitive to environmental factors, particularly temperature and depth (Overholtz and Tyler 1985, Mountain and Murawski 1992), and species with similar habitat preferences have high spatial overlap (Murawski and Finn 1988, Garrison 2000). Environmental gradients drive the formation of species assemblages at regional scales in continental shelf fish communities (Gabriel 1992, Gomes et al. 1995). These associations are typically stable through time, and the species within them typically show a similar response to interannual variations in temperature (Gabriel 1992).

Exploitation patterns may also influence fish spatial distributions and species composition. There is a general relationship between population size and the spatial range of fish species. As population abundance declines, spatial ranges generally decrease and the species is concentrated into smaller areas (Atkinson et al. 1997). Alternatively, management restrictions on fishing effort, such as marine protected areas, or refugia from fishing gear may alter species distributions and concentrate fish in localized areas. Changes in spatial distributions associated with variations in population size, fishing pressure, and climate variability influence the spatial associations between species and therefore the strength of trophic interactions.

In the northeast United States continental shelf fish community, there have been significant changes in the population sizes of both over- and underexploited stocks. Over the last three decades, there has been a general decline in the abundance of heavily exploited species including gadids and flatfish. There has been a concomitant increase in less-utilized species including elasmobranchs and small pelagic fish (Fogarty and Murawski 1998, NEFSC 1998). In the current study, I examine temporal variability in the spatial structure of the northeast United States continental shelf fish community associated with these changes in population size. I document decadal-scale changes in the spatial pattern of species composition and identify major changes in spatial distributions associated with both fishery exploitation and environmental variability. I discuss the implications of observed changes in spatial structure and species composition for the trophic dynamics of this system.
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Methods

The data for this study were drawn from seasonal bottom trawl surveys conducted by the Northeast Fisheries Science Center (NEFSC). The surveys employ a stratified random sampling design with strata defined by depth and latitude. Sample depths ranged between 8 and 400 m on the North American continental shelf between Cape Hatteras, North Carolina and Nova Scotia (Fig. 1). Typically 300-400 stations are occupied during each seasonal survey. At each station, a 36-Yankee or similar bottom trawl is towed for 30 min at a speed of 6.5 km per hr. All species within the sample are identified, weighed (kg), and subsampled to determine catch in numbers per 1-cm size classes. Catch correction factors were applied to account for changes in vessels and gears across the time series. Details of the survey sampling design, execution, and efficiency are available in NEFC (1988).

The current study included trawl tows from the northwest Atlantic continental shelf between 39° and 45° north latitude including areas of southern New England, Georges Bank, the Gulf of Maine, and the southwest Nova Scotian shelf (Fig. 1). The analyses were conducted using data from autumn (September-October) bottom trawl surveys conducted from 1966 to 1999. Patterns in spatial structure were evaluated in 5-year time blocks, and species abundance and distribution patterns were generally homogenous within 5-year blocks. Data from alternating time blocks are presented for brevity including the periods 1966-1970 (1,016 stations), 1976-1980 (1,455 stations), 1986-1990 (925 stations), and 1996-1999 (837 stations). The spatial pattern of sampling has remained consistent throughout the time series with the exception of reduced sampling in the Scotian shelf region in recent years (Fig. 1). Twenty-seven predator species were included in the study, including two squids (Table 1). These are numerical and biomass dominants, commercially valuable, and/or ecologically important species in the northwest Atlantic.

Species abundance data were aggregated into 0.5°-square grid cells for each time block to quantify spatial patterns. The average catch (in kilograms per square kilometer) of each species was calculated across tows collected within each grid cell. A swept-area biomass estimate was then calculated by multiplying catch per square kilometer by the total area of the cell (2,275 km²) and the proportion of the cell area available to the survey (e.g., proportion of cell not covered by land). This level of spatial and temporal resolution captured the major features of the spatial patterns in species distributions (Garrison, unpubl. data). Because I have not accounted for the catch efficiency of the gear in these calculations, the swept-area biomass should be considered an index of relative abundance rather than an absolute biomass value.

The 0.5° cells were clustered based upon their similarity in species composition. The biomass estimate in each cell (tons) was transformed by taking the fourth root to reduce the influence of highly abundant species (Pielou 1984). The proportional similarity in species composition between
Figure 1. Bottom trawl survey strata on the northeast United States continental shelf and sample locations during four time periods: (A) 1966-1970, (B) 1976-1980, (C) 1986-1990, and (D) 1996-1999. Inset map shows the eastern coast of North America and the study area.
Table 1. Fish and squid species included in the current study.

<table>
<thead>
<tr>
<th>Common name</th>
<th>Scientific name</th>
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</thead>
<tbody>
<tr>
<td>Smooth dogfish</td>
<td><em>Mustelus canis</em></td>
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<tr>
<td>Spiny dogfish</td>
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<td>Little skate</td>
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<td>Shortfin squid</td>
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<td>Longfin squid</td>
<td><em>Loligo pealeii</em></td>
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</tbody>
</table>
grid cells was calculated using the Bray-Curtis (Bray and Curtis 1957) similarity index,

\[ S_{ij} = 1 - \frac{\sum_{k=1}^{N} |n_{ik} - n_{jk}|}{\sum_{k=1}^{N} (n_{ik} + n_{jk})}, \]  

(1)

where \( N \) is the total number of species and \( n_{ik} \) and \( n_{jk} \) are the transformed biomass of species \( k \) in cells \( i \) and \( j \) respectively. Based upon this similarity index, grid cells were clustered with a hierarchical agglomerative clustering algorithm using unweighted group average clustering (Pielou 1984). The resulting dendrograms and the identified spatial clusters were not sensitive to different data transformations or clustering methods. Spatial gradients in species composition were also quantified using a detrended correspondence analysis (DCA, Hill and Gauch 1980). Based upon these analyses, in each time block I identified “faunal regions” defined as geographic areas with similar species composition in that time period. I examined changes in the species composition within these faunal regions through time.

In addition, I present example maps of changes in species distributions across time and discuss three types of spatial distribution shifts that occurred in this community: range contraction, range expansion, and range shifts. To further elucidate general patterns of latitudinal shifts in species distributions, I calculated the weighted mean latitude of occurrence for 18 example species in each 5-year time block from 1966 to 1999. The biomass data was lognormally distributed, and was therefore transformed (\( \ln[y+1] \)) prior to calculating the mean latitude to prevent large values from skewing the mean. For each species, the mean latitude of occurrence was calculated,

\[ \bar{X} = \frac{\sum_{i=1}^{N} y_i x_i}{\sum_{i=1}^{N} y_i}, \]  

(2)

where \( y_i \) is the log-transformed biomass of the species in latitude \( x_i \) for each of \( N 0.5^\circ \) latitude cells. The variance was then calculated as,

\[ s^2_{\text{lat}} = \frac{\sum_{i=1}^{N} y_i (x_i - \bar{X})^2}{\sum_{i=1}^{N} y_i}. \]  

(3)
The mean latitude is interpreted as a "center of mass" for the population being considered, and trends (with 95% CI) through time were evaluated to assess decadal scale shifts in species distributions.

**Results**

**Faunal Regions**

In all four time blocks examined, there were clear geographic patterns in species composition based on both the cluster analysis and the DCA ordination. The grid cells clustered into faunal regions at similarity levels ranging between 45% and 60%. The faunal regions were geographically contiguous and were generally consistent through time (Fig. 2). Grid cells clustered into four major faunal regions based upon their similarity in species composition in all four time blocks: Offshore, Georges Bank/Southern New England, Gulf of Maine, and Scotian Shelf (Fig. 2). During the 1976-1980 and 1986-1990 periods an additional faunal region was identified: Inshore Southern New England (Fig. 2b,c).

The DCA analysis also indicated important gradients in species composition, and cell groups in the ordination space defined by the first two DCA axes were similar to those identified in the cluster analysis (Fig. 3). The first two axes explained 50-53% of the total variation in the species data. The first axis organized locations along a latitudinal gradient. Cells in the southern portion of the sampling area had low scores on this axis, while those in the Gulf of Maine and Scotian Shelf regions had higher scores (Figs. 2 and 3). Species abundant in southern habitats such as smooth dogfish, summer flounder, butterfish, and longfin squid had low scores on this axis while those abundant in northern habitats including redfish, witch flounder, haddock, and pollock had higher scores. The second axis organized locations along a depth gradient. The deepwater, offshore locations had lower scores while those in shallower habitats on Georges Bank and the Scotian Shelf area had higher scores (Figs. 2 and 3). Species abundant in deep water, including offshore hake, shortfin squid, and goosefish, had low scores on this axis while species abundant in shallower water, including summer flounder, winter skate, and windowpane, had higher scores.

The offshore faunal region was characterized by a high biomass of longfin and shortfin squids during the early portion of the time series (Fig. 4a,b). During these periods, these two species accounted for over 50% of the biomass, and butterfish, silver hake, and white hake were also important components in offshore habitats. However, during the 1986-1990 and 1996-1999 periods, the relative importance of the squid species declined to total approximately 30% of the biomass while that of spiny dogfish increased to 24% and 27% in 1986-1990 and 1996-1999, respectively (Fig. 4c,d). In addition, silver hake was an important component of the biomass (22%) during the 1986-1990 time period.
Figure 2. Faunal region maps based on cluster analyses for four time periods: (A) 1966-1970, (B) 1976-1980, (C) 1986-1990, and (D) 1996-1999. Grid cells that were not members of a cluster were identified as outliers. Blank cells indicate areas where no samples were collected.
Figure 3. DCA ordination plots showing the distribution of grid cells in the ordination space defined by the first two axes in four time blocks: (A) 1966-1970, (B) 1976-1980, (C) 1986-1990, and (D) 1996-1999. Percentage of total inertia in species data explained by each axis is indicated in parentheses. Dashed circles enclose grid cells within the faunal regions identified in Fig. 2: ■ Offshore, ▲ Inshore SNE, ● Georges Bank/Southern New England, ♦ Gulf of Maine, □ Scotian Shelf.
Figure 4. Proportion of total fish biomass by species in grid cells in the Offshore faunal region in (A) 1966-1970, (B) 1976-1980, (C) 1986-1990, and (D) 1996-1999. Other is the sum of all species accounting for <1% of the biomass.
The Inshore Southern New England faunal region was only identified during the 1976-1980 and the 1986-1990 time periods. During the earlier time block, the region was dominated by spiny dogfish (49% of biomass) along with longfin squid (25%) and smooth dogfish (8%, Fig. 5a). The importance of spiny dogfish was much lower (4%) during the later time period, and the region was dominated by longfin squid (42%), smooth dogfish (19%), and butterfish (19%, Fig. 5b).

The Georges Bank/Southern New England faunal region was characterized by a greater number of species than other assemblages. Spiny dogfish was the dominant biomass component throughout the time series (Fig 6). During the two earlier time periods, spiny dogfish accounted for 48% and 40% of the biomass in this region (Fig. 6a,b). In the 1966-1970 time block, haddock (7%), yellowtail flounder (8%), and cod (4%) were also important biomass components (Fig. 6a). In the 1976-1980 time period, the importance of these gadids and flatfish declined and winter skate (8%), little skate (7%), longfin squid (7%), and butterfish (11%) became more important (Fig. 6b). During the 1986-1990 period, spiny dogfish declined to 27%, while the importance of winter skate (22%) and longfin squid (11%) increased (Fig. 6c). In the most recent period, spiny dogfish was again the dominant species in this region (54%), winter skate remained important (8%), and haddock also increased (7%, Fig. 6d).

The Gulf of Maine region was dominated by redfish, haddock, cod, and pollock during the 1966-1970 and 1976-1980 time periods (Fig. 7a,b). Spiny dogfish accounted for a relatively small proportion of the biomass during these time periods (12% and 11% respectively), and both silver hake and white hake were also important species (Fig. 7a,b). During the 1986-1990 period, spiny dogfish was much more important and accounted for 44% of the biomass in the region (Fig. 7c). Redfish, haddock, cod, and pollock were each <8% of the biomass during this period, and silver hake (8%), white hake (8%), and winter skate (6%) were also important (Fig. 7c). During the 1996-1999 period, spiny dogfish declined to 31% of the biomass while redfish increased to 27% (Fig. 7d). Silver hake (12%) and white hake (6%) remained important while haddock, cod, and pollock each accounted for <6% of the regional biomass (Fig. 7d).

The southwest Scotian Shelf was characterized by a high proportion of haddock throughout the time series (Fig. 8). During the 1966-1970 and 1976-1980 periods, haddock accounted for 47% and 75% of the biomass in this region, and cod (24%) and pollock (13%) were the other important species during the 1966-1970 period (Fig. 8a,b). During the 1986-1990 period, haddock remained important (35%), but spiny dogfish became the biomass dominant (42%) and both cod (7%) and pollock (2%) were less important (Fig. 8c). In the 1996-1999 period, the proportion of spiny dogfish declined (9%), haddock (41%) and pollock (14%) were the dominant species, and winter flounder and redfish were also important species (Fig. 8d).
Figure 5. Proportion of total fish biomass by species in grid cells in the Inshore Southern New England faunal region in (A) 1976-1980 and (B) 1986-1990. Other is the sum of all species accounting for <1% of the biomass.
Figure 6. Proportion of total fish biomass by species in grid cells in the Georges Bank/Southern New England faunal region in (A) 1966-1970, (B) 1976-1980, (C) 1986-1990, and (D) 1996-1999. Other is the sum of all species accounting for <1% of the biomass.
Figure 7. Proportion of total fish biomass by species in grid cells in the Gulf of Maine faunal region in (A) 1966-1970, (B) 1976-1980, (C) 1986-1990, and (D) 1996-1999. Other is the sum of all species accounting for <1% of the biomass.
Figure 8. Proportion of total fish biomass by species in grid cells in the Scotian Shelf faunal region in (A) 1966-1970, (B) 1976-1980, (C) 1986-1990, and (D) 1996-1999. Other is the sum of all species accounting for <1% of the biomass.
Temporal Changes in Species Distribution

The changes in species composition within faunal regions reflect changes in both species biomass and spatial distribution across time. There were three general patterns of changes in spatial distribution in the northwest Atlantic fish community. First, as population sizes declined, there was a reduction in the total area covered by a species, defined as a “range contraction.” As an example, during the 1960s, haddock were abundant throughout Georges Bank, the Gulf of Maine, and the Scotian Shelf (Fig. 9a), and the total estimated biomass of haddock was $2.9 \times 10^5$ tons. The haddock biomass index declined to $0.9 \times 10^5$ tons in the 1986-1990 time period, and haddock distributions were restricted to the Scotian Shelf and the Great South Channel on Georges Bank during this period (Fig. 9c). Haddock estimated biomass has recently increased to $1.4 \times 10^5$ tons, and their range has expanded slightly in recent years (Fig. 9d). Similar contraction of ranges occurred in many species that experienced declines in biomass including cod, pollock, and yellowtail flounder.

Conversely, species whose population sizes increased through time have increased their spatial range, termed a “range expansion.” For example, the estimated biomass of Atlantic herring during the 1966-1970 was $4.5 \times 10^3$ tons and declined to only $0.5 \times 10^3$ tons during the 1976-1980 period. During this period, their range contracted and became restricted to small areas of the Gulf of Maine (Fig. 10a,b). The herring biomass index increased during the 1986-1990 period and increased to $61 \times 10^3$ tons during the 1996-1990 period. Their range expanded during the 1990s to cover the majority of the Gulf of Maine (Fig. 10c,d). A similar pattern of range expansion occurred in Atlantic mackerel and butterfish as their estimated biomass increased through time.

Finally, many species have exhibited significant “range shifts” through time and have become relatively more abundant in northern habitats. For example, spiny dogfish was abundant primarily in southern New England during the 1966-1970 time period (Fig. 11a). The spiny dogfish population shifted north through time, and their estimated biomass declined in southern regions and increased in northern regions including the Gulf of Maine and the Scotian Shelf through the 1976-1980 and 1986-1990 time periods (Fig. 11b,c). During the 1996-1999 period, the spiny dogfish population has again shifted south, becoming less abundant in the Scotian Shelf area and more abundant in southern regions (Fig. 11d).

Across decadal time scales, many species have exhibited northward distribution shifts, and these were indicated by trends in their mean latitude of occurrence across the time series (Fig. 12). Northward shifts of $0.5^\circ - 1.0^\circ$ of latitude occurred in fourspot flounder, butterfish, winter skate, yellowtail flounder, herring, mackerel, red hake, silver hake, spiny dogfish, ocean pout, longhorn sculpin, and sea raven (Fig. 12). This reflects a very significant shift in spatial distribution. For example, during 1966-1970 81% of the total estimated spiny dogfish biomass occurred in the Offshore and
Figure 9. Estimated biomass of haddock in 0.5° cells in four time blocks: (A) 1966-1970, (B) 1976-1980, (C) 1986-1990, and (D) 1996-1999.
Figure 10. Estimated biomass of Atlantic herring in 0.5° cells in four time blocks: (A) 1966-1970, (B) 1976-1980, (C) 1986-1990, and (D) 1996-1999.
Figure 11. Estimated biomass of spiny dogfish in 0.5° cells in four time blocks: (A) 1966-1970, (B) 1976-1980, (C) 1986-1990, and (D) 1996-1999.
Figure 12. Mean latitude of occurrence for 18 species of fish across 5-year time blocks from 1966 to 1999. Error bars indicate 95% CI.
Georges Bank/Southern New England faunal regions while during 1986-1990 only 21% of the spiny dogfish biomass was in the southern regions and 79% of the biomass occurred in the Gulf of Maine and Scotian Shelf regions. This shift was manifested in a change of 0.5° of mean latitude (Fig. 12). Similar latitudinal shifts were not observed in many southern species (e.g., smooth dogfish, little skate, windowpane; Fig. 12) and did not occur in primarily northern and deep-water species including redfish, haddock, cod, witch flounder, and white hake (not shown).

Discussion
The spatial patterns and faunal regions in this community have remained generally stable over the last three decades despite major changes in species composition. These patterns are consistent with previous studies both within this community (Overholtz and Tyler 1985, Gabriel 1992) and in the groundfish community of the Canadian Atlantic continental shelf (Gomes et al. 1995). These generally stable patterns are related to similarities in habitat preferences among species. Spatial overlap between species on Georges Bank was strongly related to similarities in habitat preferences, particularly preferred depth and temperature ranges (Murawski and Finn 1988, Garrison 2000). As habitat characteristics, primarily temperature, change on an interannual basis, species with similar habitat preferences alter their spatial distributions in similar ways (Mountain and Murawski 1992). The distinct regional geographic boundaries in species composition observed in the current study therefore reflect spatial boundaries in habitat characteristics.

The most notable change in the northwest Atlantic groundfish community over the last three decades is the general decline in the abundance of heavily exploited species including gadids and flatfish and an increase in the abundance of less-exploited elasmobranchs, in particular spiny dogfish (Fogarty and Murawski 1998). In recent years, a large fishery for adult female spiny dogfish developed, and the stock has experienced severe declines in biomass over the last 5 years (NEFSC 1998). The changes in the biomass of spiny dogfish through time are reflected in changes its spatial distribution and the species composition within faunal regions observed in the current study. Prior to 1980, spiny dogfish was a dominant component of the biomass only in the Georges Bank/Southern New England region, and the majority of its biomass was concentrated in southern and offshore habitats. During the 1980s and early 1990s, spiny dogfish became a biomass dominant in all of the faunal regions on the northwest Atlantic continental shelf. The increase of spiny dogfish populations and its movement north into Scotian Shelf and Gulf of Maine habitats represents a major change in the trophic dynamics of this system. Spiny dogfish is a pelagic predator feeding on ctenophores and shrimp taxa in smaller size classes and pelagic fish and squids in larger sizes (Garrison and Link 2000). Spiny dogfish is among the major predators of pelagic fish biomass.
in the northwest Atlantic (Overholtz et al. 1999), and it exerts a major influence on community dynamics due to its high abundance and predatory nature.

Concomitant with the increases in spiny dogfish biomass, there has been a decline in the populations of heavily exploited species, including Atlantic cod, yellowtail flounder, and haddock. These species have experienced a contraction of ranges, associated with their overall decline in abundance and have become only minor components of the fish biomass in the Georges Bank and Gulf of Maine faunal regions. Similar declines in species area with declines in population size are well documented in other fish communities (Atkinson et al. 1997). During the early 1960s, prior to the time-frame of the current study, these species were biomass and numerical dominants on Georges Bank and throughout the northwest Atlantic (Overholtz and Tyler 1985, Fogarty and Murawski 1998). Both yellowtail flounder and haddock are benthivorous species feeding upon polychaetes, amphipods, and echinoderms while Atlantic cod is a generalist predator feeding upon both pelagic and benthic invertebrates and fish in larger size classes (Garrison and Link 2000). The change from dominance by these primarily demersal species to the more pelagic spiny dogfish represents a major change in the structure of this ecosystem. In addition, spiny dogfish has replaced large Atlantic cod as the major piscivore in this community (Link and Garrison 2001).

In the last decade, the biomass estimates for small pelagic species, including Atlantic herring and mackerel, increased by nearly an order of magnitude, and this increase in biomass was accompanied by an expansion of ranges for these species. The dramatic increase in pelagic biomass influences the trophic dynamics of this community in two ways. First, small pelagic species are important prey items for the many piscivores in this community. During the period of depressed abundance of small pelagic fish, the diets of piscivores including silver hake, cod, and spiny dogfish were composed of other species and squids. As herring populations have increased and expanded into the Gulf of Maine, the diets of major piscivores have included higher proportions of herring (Link and Garrison 2001). The increase in herring biomass significantly alters the prey field available to piscivores in this system. Second, these small pelagic fish are important consumers of zooplankton, and their increased abundance may result in a greater removal of water column secondary production prior to its export to benthic communities. Herring is also a potentially important predator of larval fish, particularly haddock and cod on Georges Bank (Garrison et al. 2000). The impact of elevated pelagic biomass on the recovery of demersal fish stocks remains an important area for continuing research.

The most general change in the spatial distributions of fish species was an increase in the mean latitude of occurrence for a large number of species. These included both exploited and unexploited species, suggesting that directed fishery removals are not the major cause of this pattern. The observed northward distribution shifts suggest a community-wide re-
response to increases in temperature (Mountain and Murawski 1992, Murawski 1993). There has been a notable increase in bottom temperatures in the northwest Atlantic over the last three decades; the 1990s were significantly warmer than the 1960s. The majority of this temperature change occurred during the early portion of the time series (Holzwarth and Mountain 1990), and the majority of the northward shift in species distributions observed in the current study also occurred during the earlier period. While the broad changes in spatial distribution are consistent with a community-wide response to temperature change, changes in population size, geographic patterns in fishing effort, and changes in the survey sampling intensity through time may also influence the observed patterns of biomass distribution (Murawski 1993). Assessing the importance of climate variations in altering spatial distributions and the underlying mechanisms remain important areas for further investigation.

The major changes in community structure and spatial distributions associated with both fishing pressure and climate variation have important implications for the trophic dynamics in this ecosystem. This community has generally shifted from one dominated by demersal species to one dominated by more pelagic predators and planktivores (Link 1999). In addition, the changes in spatial patterns documented in the current study will influence the strength of species interactions. The northward shift observed in many species in this community along with the range expansion observed in small pelagic species influences predator and prey fields and potential competitive interactions. Continuing efforts will directly evaluate the impact of observed spatial patterns on species interactions by using spatial overlap and selectivity models to assess trophic interactions between species and compare them across the time series.

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