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# The Quest for Lobster Stock Boundaries in the Canadian Maritimes

by

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## Abstract

Historical and recent data on lobsters (Homarus americanus) from the Canadian maritimes were examined for stock differences with the object of defining lobster population boundaries. Using pattern recognition techniques, historical lobster landings (1892-1981) from 32 areas resulted in grouping the landing trends into 7-8 areas.

Examination of morphometrics data, landing trends, population parameters (growth and size at maturity), movement of tagged lobsters, and general surface currents that might indicate larval drift, suggested the following general lobster stock areas:

1. Western maritimes which included the Bay of Fundy, inshore and possibly offshore) southwestner Nova Scotia (to Shelburne Co.),

2. The Eastern Coast of Nova Scotia (Queens to Cape Breton Counties) which seems to be a transition zone for lobsters between the Gulf of Maine and the Gulf of St. Lawrence, and

3. Southern Gulf of St. Lawrence.

STOCK DISCRIMINATION SYMPOSIUM

Key words: Homarus americanus; lobsters; stocks; population dynamics; morphometrics; landing statistics; electrophoresis; recruitment; tagging; movement.

## General Introduction

Historically, there have been various debates amongst biologists, fishery managers, and fishermen as to the geographic discreteness of lobster (Homarus americanus) populations on the Atlantic Coast of North America (eg. Aiken 1971; Wilder 1974; Dadswell 1979; Robinson 1979; Anthony and Caddy 1980). Crucial to the fisheries management of lobsters is the recognition of the significance and distribution of lobster populations that can be grouped into having common life history characteristics (eg. growth and mortality rates). The establishment of the number and identity of these groups and their distribution in both space and time is difficult. Indeed, the choice of a group or unit stock of lobsters may change with the methodology used and investigator involved, and as new data are obtained and population characteristics are measured more precisely.

Whether different lobster populations come from discrete gene pools or their population characteristics merely reflect their phenotypic plasticity to different environmental conditions these characteristics are still useful in defining stock identity. Even if population characteristics may only reflect spatial separation with only partial reproductive isolation among genetically similar stocks, these characteristics provide useful tools for stock identification. For the purpose of this paper a stock is broadly defined as a group of individuals that respond in a similar way to environmental changes within common geographic boundaries, and includes but not limited to, population groups that are isolated reproductively.

The purpose of this paper is to improve our understanding of the location of different lobster stocks in the Canadian maritimes. In an attempt to delineate lobster stock boundaries we analyzed historical commercial lobster landings to determine patterns which might indicate common lobster production areas. We also examined population dynamics characteristics and tag return data and studied samples of lobsters from several locations to characterize morphometric variation among groups of lobster. The literature was selectively reviewed to provide further indications of stock discreteness through electrophoretic, parasitic, morphometric, and movement studies on lobsters. No attempt was made to include all relevant data from the many studies on lobsters; rather, only data needed to illustrate statements were used. Extensive reviews on lobster biology and fisheries are present in Cobb and Phillips (1980) and Anthony and Caddy (1980).

The majority of the information used in this paper are from lobsters of a size range vulnerable to commercial fishing gear, which includes subadult and adult lobsters. Little information is available on the ecology, bionomics and chemical composition of juvenile benthic stages of H. americanus.

For convenience, the paper is divided into separage subject chapters. 1. Analysis of lobster landing trends; 2. Population parameters; 3. Tagging movement; 4. Morphometrics; 5. Parasites; 6 Electrophoresis; 7. Surface current patterns and possible larval recruitment; 8. Summary conclusion. Although some of our analyses included Newfoundland, Quebec and Maine, the main discussion is centered around lobster populations off New Brunswick, Nova Scotia and P.E.I.

## 1. ANALYSIS OF LOBSTER LANDING TRENDS

### Introduction

A number of previous Canadian workers have used landings to generally infer lobster stock units (eg. Wilder 1965; Robinson 1979). In this present study annual lobster commercial landings from 32 areas over a 90-yr period (1892-1981) were statistically analyzed to determine patterns which might indicate common lobster production area in the Canadian maritimes (Fig. 1). We assumed that effort was sufficiently high and probably in excess in most years to remove a substantial amount of the lobster biomass from the fishing grounds. Fishing effort is generally high in most areas where the American lobster are fished with 60-95% removal rates reported (Anthony 1980; Campbell 1980) suggesting a sufficiently large fraction of available biomass is removed each year. With constant excess effort, catch patterns would probably be dominated by lobster abundance; thus total catch will probably be a good index of lobster biomass in most areas.

If this assumption is correct then the changes of lobster biomass in an area will reflect its productivity for lobsters which can be influenced by a number of biotic and abiotic factors. A number of people have hypothesized that temperature (Flowers and Saila 1972; Dow 1977), river discharge (Sutcliffe 1973), changes in lobster recruitment patterns (Iles 1975;

Dadswell 1979; Robinson 1979) or algal productivity related to sea urchin abundance (Wharton and Mann 1981) as contributing factors to fluctuation in lobster landings in an area. This present paper does not attempt to explain in detail the reason for these fluctuations in any particular area. Rather the paper attempts to find a group of areas that have similar lobster landing trends which are geographical approximate that can be considered a lobster stock which is reacting similarly in biomass changes to environmental (biotic and abiotic) and/or man-induced perturbations.

Also, we assumed that the majority of commercial-sized lobsters that are fished out of an area had not previously moved appreciable distances (Wilder 1974).

Multivariate statistical methods, especially cluster and principal component analyses (PCA) were used to summarize the lobster landing trends to obtain general relationships between areas. Methods and aids for multivariate methods are well documented (Seal 1964; Morrison 1967; Spath 1980).

Because PCA is a general hypothesis developing multivariate analysis technique which assumes linear relationships and tends to lead to subjective interpretations, additional clustering techniques were used so that the trends could be more accurately described and grouped. As the results will show both methods produced similar groupings and interpretations.

## Methods

The lobster catch landing (MT) trends over the 90-yr period (1892-1981) were compiled for 32 areas from Maine (courtesy J.C. Thomas), New Brunswick, Prince Edward Island, Quebec and Newfoundland (Statistics Canada, Halifax). All offshore landings (eg., Browns Bank, Georges Bank) are excluded from the analyses. (Landings on either side of P.E.I. (Kings, Queens, and Prince Counties) were not reported. When data for a particular area were absent the hole was filled in by linearly interpolating the adjacent years, eg., if the hole was in 1892 the 1893 value for that area was used. The need for interpolation was quite rare and should not affect results. Lobster District 1 (Charlotte County, excluding Grand Manan and St. John County), Lobster District 1 (Grand Manan), and Annapolis and Kings Counties combined, Albert County were chosen to represent the landings from the Bay of Fundy.

Multivariate statistical methods were used to summarize the landing data and to obtain general relationships of trends among 32 areas: 1.

Principal component analyses of the raw landing data; 2. Cluster analysis of (a) 6-yr means and of (b) Chebyshev polynomials of the normalized data. Because the catch data showed a high year-to-year variability both the cluster analyses (a and b) were performed on catch data normalized with respect to the mean (Fig. 2). Thus, when the normalized catch had a value of 0.7, that year had a catch which was 70% of the mean for the 90-yr period. The data were normalized so that the pattern over the period was important, not its magnitude. Also, the sizes of the catch were hard to compare unless the carrying capacity or production potential for each area could be estimated.

1. Principal component analysis

We used a principal component analysis (PCA) program developed by Lee (1971) to analyze the raw landings data for 31 areas (Albert County not included) (Table 1). A sample was considered as the annual total MT landed for each area and year (1892-1981). Principal component analysis was performed on a correlation matrix; assuming that the linearity assumption implied in this analysis (Seal 1964) was met without any data transformations. Those principal components accounting for less than 8% of the total variation were not considered for interpretation.

2. Cluster analyses

Clustering is a technique for grouping multidimensional data such that objects within a group (or cluster) are more similar than objects in different clusters (Spath 1980). For this reason, clustering is sometimes referred to a similarity grouping. For the purposes of this section each of the 32 areas is referred to as a point in a multidimensional space. For the entire time series this would mean that the points are defined in a 90-dimensional space. The degree of similarity between two points is the distance squared in the multidimensional space. The distance is unweighted Euclidean. As a practical consideration for this type of clustering, the number of dimensions were reduced to as few as possible. Thus, time trends were expressed in as economical manner as possible before attempting to cluster the data.

Two methods are presented to reduce the number of terms associated with each areas: averaging and polymonial representation. The 90 annual values for each area are reduced to 15 six-year averages (Fig. 2). Six-year averages are chosen as a compromise between reducing the number of dimensions and retaining the detail of the data.

The Chebyshev polynomial (Kuo 1965) was chosen to represent the time series because of its efficiency, orthogonality, and relative meaningfulness of the coefficients. Without going too deeply into mathematical definitions the Chebyshev polynomials ,$T_n(x)$, may be used to represent a function ,$f(x)$, as an infinite series:

$$f(x) = \sum_{n=0}^{\infty} T_n(x)$$

if the infinite series is truncated the function may be approximated. For this study the series was truncated at the sixth order:

$$f(x) = \sum_{n=0}^{6} T_n(x)$$

The first few Chebyshev's are:

$$T_0(x) = 1$$

$$T_1(x) = x$$

$$T_2(x) = 2x^2-1$$

$$T3(x) = 4x3-3x$$

Therefore, the coefficient of the zeroth order term is the mean, the coefficient of the first order term is the linear trend, and of the second order term is the degree to which the data are domed or cupped. The coefficients are orthogonal which means that they are all independent of one another. This is not true for the usual polynomial approximation. The smooth curves in Fig. 2 are the Chebyshev approximations to the data.

The program used to find clusters in the data finds a fixed number of clusters which must be specified. If too few clusters are specified the clusters are large and will contain a range of patterns in each. If too many, each cluster will have only one or two elements and not find underlying patterns in the data. A range from 4 to 9 clusters was tried for each data set. As the final cluster is dependent upon the order in which the points are introduced to the program, 10 runs were made at each number of clusters. The result of the clustering are compared using the total distance of all points to their respective cluster center. This is equivalent to a residual. Both average total distance and minimum total distance are given.

Total distance of points to cluster centers

| No. of clusters | Chebyshev $D_{ave}$ | Chebyshev $D_{min}$ | Six-year average $D_{ave}$ | Six-year average $D_{min}$ |
|---|---|---|---|---|
| 4 | 9.8 | 9.1 | 43.7 | 40.1 |
| 5 | 8.3 | 7.8 | 37.9 | 30.4 |
| 6 | 7.4 | 6.8 | 32.7 | 30.1 |
| 7 | 6.3 | 5.5 | 31.2 | 26.0 |
| 8 | 5.6 | 4.5 | 24.1 | 19.3 |
| 9 | 5.0 | 3.8 | 20.2 | 16.4 |

As expected, the distances fall with increasing cluster number. Also, it is noted that the rate of improvement decreases from 8 to 9 clusters: therefore, 8 clusters will be used to define partitions. The clusters chosen are those from the grouping having the lowest total distance. As there are approximately 1 million starting combinations and exhaustive search for the absolute minimum would be impractical. The minimal clusters for the 8 centers are given below, and as the coefficients of the first and second order Chebyshev are easily interpreted, they are also included.

## Results and discussion

The following grouping of areas by the various analyses must be interpreted in relation to geographic and oceanographic considerations. For example, although Albert and Victoria Counties were grouped in the same cluster on the basis of catch history, no one would advocate that this represents a common stock. It is the coincidental similarity of catch trends due to presumably several independent forces. However, when neighbors or areas sharing a body of water are grouped it is suggested that the driving forces of the stock (effort, recruitment, and growth) are acting in concert.

### 1. Principal component analyses

The intercorrelations (Pearson product moment) among 31 variables are presented in Table 1. The correlation matrix was used in the PCA (Table 2). Principal component loadings $<0.20$ or $>-0.20$ were not considered for interpretation.

The first four principal components explained 81.3% of the variation

(Table 2, Fig. 3). The first principal component ($C_I$), accounting for 40.4% of the variation (all had negative loadings of -.2 to -.25) grouped most of the counties that had experienced major overall fluctuating declines in lobster landings during last 90 years. There are four main geographic areas representing currently collapsed or depressed lobster fisheries (1) North shore of Bay of Fundy, Lobster District 1, (2) East coast of Nova Scotia from Shelburne County (Co.) to Cape Breton Co., (3) Central Northumberland Strait, Colchester Co. to Westmorland Co. including Queens Co., P.E.I., (4) Duplessis Co., Northern Quebec. One county, Gloucester, which was included in $C_I$ could not be explained along with other areas (loading -0.24); although Gloucester had experienced steady decline in landings in recent years (8 yrs) has experienced a sharp increase in landings (Fig. 2).

The second component accounting for 14.1% of the variation produced two groupings (Table 2, Fig. 3). The first (high negative loadings) grouped many areas, some geographically separated, that have had relatively stable landings in the last 30 years, with some fluctuating declines and increases from 1892-1940, these were Maine Lobster District 2, Yarmouth Co., Shelburne Co., Kings Co., P.E.I., Newfoundland. (N.B. the overlap indication that Shelburne is also grouped with Yarmouth as well as Eastern Nova Scotia Counties). The second (high positive loadings) group Pictou Co. and Antigonish Co. are geographical adjacent to each other and had generally stable landings with recent decline and modest recovery. Why Guysborough had a high positive loading (0.21) was included, cannot be explained; although geographically close to Antigonish Co. the landings have fluctuated with general major declines.

The third component accounting for 9.4% of the variation produced one group all with positive loadings and showing relatively stable landings (Table 2, Fig. 2,3). However, the areas occurred in two general geographical distinct locations: (1) Western Nova Scotia (Maine and Lobster District 2), and (2) Gulf of St. Lawrence (Victoria Co., and Pictou Co.) with Kent Co., Northumberland Co., and Restigouche Co. especially grouped together because of very high loadings (0.47, 0.40 and 0.34, respectively). One exception in the third component was Duplessis, again kept separate from all other areas with a high negative loading (-0.26).

The fourth component accounting for 8.0% of the variation produced three groupings (Table 2, Fig. 3). The first showed high negative loadings indicating general lobster landing declines in areas of the inner Bay of Fundy (Lobster District 1 and Annapolis and Kings Counties) and Lunenburg. The second showed positive loadings with stable landings around Cape Breton area (Victoria Co., Inverness Co.) and western Northumberland Strait (Antigonish Co., Pictou Co., and Kings Co., P.E.I.). The third group had the highest positive loadings (0.30, 0.35) which were the Quebec provinces of Bonaventure and Gaspé.

2. Cluster analyses

If both clustering data sets, Chebyshev and six-year average, clustered the same neighboring areas this was considered as a stronger indication of relationship than for just one of the sets. Such association will be called strong and weak, respectively.

The southern Bay of Fundy has a strong association between Yarmouth Co. and Grand Manan with Maine, Annapolis-Kings Co., and Shelburne being loosely associated around them (Fig. 1). This group is typified by an initial long term downward with a recovery and generally stable landings during the last 30 years (Fig. 2).

On eastern Nova Scotia the Counties of Richmond, Guysborough and Halifax form a strong grouping with Lunenburg weakly associated to them (Fig. 1). This cluster has a linear trend which is strongly negative (Table 3, $T_1 = -1.5$).

In northern Nova Scotia, Inverness, Cape Breton and Antigonish Counties are strongly associated; but in this midst Victoria County is not even loosely associated (Fig. 1). This is because Victoria County showed an upward trend which was not shared by her neighbors (Fig. 2). However, as Victoria was linked to Kings County, P.E.I., and the Magdalen Islands linked to the Cape Breton group the whole group were considered weakly associated. This group shows little linear trend or cuppedness over the 90-year data period.

Along the Northumberland Strait, Westmorland, Cumberland, and Colchester Counties form a strong nucleus with Pictou and Queen's, P.E.I., forming a second strong nucleus weakly associated together (Fig. 1).

Prince and Kent Counties form a third strong linking along Northumberland Strait. All of these areas have similar linear and U-shaped trends.

Northumberland is weakly linked to the Kent Co.-Prince Co. pair, and the two northern most New Brunswick Counties, Gloucester Co., and Restigouche Co., are weakly associated to each other.

The Gaspé Co. and Bonaventure Co. areas are strongly associated, with Gloucester Co. and Newfoundland loosely linked to them. These areas have a relatively large coefficient of $T_2$, (Table 3) which indicates a large cupped or U-shaped component. On examining the catch data (Fig. 2) we see these areas have recovered in recent years.

Duplessis is not linked to any other area and is marked by a virtual collapse during the 1920's.

The first order Chebyshev coefficient, $T_1$, is analogous to a linear regression coefficient, and a negative value denotes a decreasing trend over the 90-yr period (Table 3). All clusters, except No. 8, have a negative coefficient. Indeed, of the 32 areas, only seven had positive coefficients. The second term is the amount of cuppedness, and a positive coefficient implies the end points tend to be higher than the middle of the series. Only Bonaventure and Gaspé show this strongly with what appears to be recovering fisheries. The large second-order term in Cluster 5 (Duplessis) is not a sign of recovery because of the domination of the downward linear trend. The first-order coefficient is the single most important entity in determining clusters using the Chebyshev representation; the second order is next in importance. For this reason all the areas are plotted using these two values to show the problem faced in clustering these data (Fig. 4). In the six-year average data representation the first six-year average and the last one are the most important.

Figure 5 shows the results of the two analyses (PCA and clustering) combined into general areas of similarly grouped lobster landing trends. The first group, the western maritimes (Lobster District 2, Annapolis and Kings Counties, Digby Co., Yarmouth Co., and Shelburne Co.) and Maine, U.S.A., in general showed similar lobster landing trends in the last 30 yrs. The landings on the N.B. side of the Bay of Fundy (Lobster District 1 and Albert Co.) did not show similar trends, however, during 1981 they constituted only 4% of the total lobster landings of the western maritimes.

The second group, Eastern Nova Scotia, (Queens, Lunenburg, Halifax, Guysborough and Richmond Counties) showed similar declining landing trends.

There seemed to be a transition zone in changing trends in Queens and Shelburne Counties on this shore line.

The third group, includes most of the Cape Breton Counties, part of eastern Northumberland Strait (Cape Breton, Victoria, Inverness, Antigonish, and Kings Counties) and the Magdalen Islands in a generally stable productive lobster area throughout the last 90 years.

The fourth group, includes central Northumberland Strait (Pictou, Colchester, Cumberland, Westmorland, and Queens Counties) as having shown declines in lobster landings in recent years.

Three other groups, were northern N.B. and Northumberland Strait combined (Prince, Kent, Northumerland, Gloucester, and Restigouche Counties), Bonaventure and Gaspé Counties combined, and Duplessis kept separate.

We kept Newfoundland lobster landings separate, although loosely associated with those of other areas in the Gulf of St. Lawrence, because we did not originally keep separate the landings from various lobster districts of Newfoundland.

## 2. POPULATION PARAMETERS

Population parameters of lobsters such as size frequencies, growth, size at maturity, fecundity, timing of egg hatch and larval settlement, level of recruitment, mortality, can all be influenced by environmental factors. Because population parameters are sensitive to extrinsic differences, they can usually be recognized as belonging to a particular area with its own environmental peculiarities. Regional differences in some population parameters can be used as evidence of discreteness of a lobster stock, although reproductive isolation with lobster populations from other areas is not necessarily implied. Crucial to lobster management is the knowledge of differences in population parameters from region to region so that each subset, if different, can be treated differently in terms of applying population models and assisting in determining the required fishing management regulations. Population parameters, however, do not provide information on the genetic discreteness of a stock and may limit the scope of practical management decisions based only on these characters. For example, a stock that is genetically coherent may encompass a large area because of mixing during part of its life cycle (eg., larval and mature adult stages). However, different subsets of the stock may have different population parameters which, without adequate information on the genetic discreteness of the stock and only partial information on population parameters (eg., larval recruitment), may make it seem advantageous to treat these subsets differently.

The following sections give information on some of the population parameters that differ regionally. This review is by no means exhaustive.

Size frequencies

There are many differences in the average sizes of lobsters caught in commercial traps in various areas of the Canadian maritimes (Fig. 6). These differences will reflect a variety of factors such as trap selectivity, minimum size regulations, variable exploitation rates, fishing season regulations, and catchability due to temperature (McLeese and Wilder 1958, Robinson 1979; Elner 1980; Campbell 1980). Lobsters caught are generally smaller in the Gulf of St. Lawrence than east Nova Scotia and inshore SW Nova Scotia. Lobsters are mostly large and mature in offshore SW Nova Scotia with few sublegal lobsters (81 mm CL) caught compared to inshore SW Nova Scotia lobsters (Wilder 1974, Stasko and Campbell 1980; Stasko and Pye 1980). In addition, egg-bearing females are caught more frequently in the offshore areas (eg. Browns Bank) than in the inshore SW Nova Scotia areas.

Growth

Growth of lobsters has been the subject of many studies. There are numerous reviews on lobster growth (eg. Ennis 1980a; Aiken 1980). Lobster growth is discontinuous due to the periodic shedding of the exoskeleton. Thus, lobster growth is usually measured in two separate components, molt increment and molt frequency in a group of equivalent sized individuals. The higher summer water temperatures in the Gulf of St. Lawrence generally allow lobsters to grow more rapidly, molting more frequently than in the cooler summer water temperatures of the Bay of Fundy and SW Nova Scotia. Tagged subadult lobsters were found to molt twice in Egmont Bay (Wilder 1963) and the Magdalen Islands (Munro and Therriault 1981) and about once off Port Maitland and Grand Manan (Wilder 1953). Templeman (1936) found that molting was about one week later for each degree lower summer temperature.

Size at maturity

The reproductive biology of lobsters was reviewed by Aiken and Waddy (1980). Lobsters mature at a smaller size in the Gulf of St. Lawrence and Newfoundland than in Fundy and SW Nova Scotia, due mainly to differences in water temperatures (Templeman 1936, 1944a,b; Robinson 1979; Ennis 1980b). From a recent study of physiological size at maturity, using a gonadal index (Aiken and Waddy 1980), we (Campbell, unpublished data) have shown that the Eastern Nova Scotia seems to be a transition area for the shift in size at maturities between Northumberland Strait and Fundy and SW Nova Scotia (Fig. 7). Differences in size at maturity has important implications on the reproductive potential of a population and at what recruitment size regulation should be adopted in a geographic area (Campbell et al. in preparation).

Fecundity

Fecundity increases with the size of lobster (eg., Saila et al. 1969). Although geographic differences in lobster fecundity have been shown, especially in Newfoundland waters (Ennis 1981), no pattern in fecundity is characteristic from one area to another. Females attain maturity and bear eggs at larger sizes and a wider size range in the Gulf of Maine than those in the Gulf of St. Lawrence.

## 3. TAGGING

Tagging studies can indirectly provide evidence of stock discreteness. The degree of mixing among lobster populations can be deduced by examining tag recoveries through time given tag release-recapture locations from which pattern of movement and ranges are estimated. To date tagging of lobsters have been restricted to sizes that are vulnerable to capture in traps (about 50-200 mm CL range) which includes subadult and mature adult lobsters. Earlier tagging studies indicated that tagged lobsters do not move appreciable distances and exhibit general random movements from the point of release in three geographic areas (Gulf of St. Lawrence, Bay of Fundy, SW Nova Scotia) (Templeman 1935b,1940; Simpson 1961; Squires 1970; Wilder 1963, 1974; Wilder and Murray 1958; see also reviews by Krouse 1980 and Stasko 1980). However, these earlier studies were generally designed to determine exploitation and growth rates so there were aspects in the experimental design that would not have allowed detection of seasonal migrations during summer months (June-October). The carapace tags used in most of these studies were released usually prior to the fishing season, recaptured by commercial fishermen during cold winter months when lobsters do not move as much (McLeese and Wilder 1958) or during the warmer summer months when molting occurred.

Tags were lost during the summer molting period. With the advent of the design of tags that could be retained through lobster molts (eg., Scarratt and Elson 1965) seasonal and long-term movements could be recorded. Also, most lobsters tagged by Wilder (1974) were immature, especially in the inshore fishery of SW Nova Scotia, and the majority are recovered by the fishery prior to reaching maturity. Recent tagging studies in the Bay of Fundy indicate that immature lobsters (eg., 60-94 mm CL) do not move greater than a mean 10.5 km from point of release, whereas mature lobsters ≳95 mm CL moved a mean 41.9 km (Table 4, Fig. 8, Campbell, unpublished data). Large, deepwater mature lobsters have a seasonal shoalward movement in May-August and move back into deep water during winter (Krouse 1980; Stasko 1980).

Evidence for many lobsters moving long distances (>100 km) and seasonally inshore-offshore (or shallow and deep waters) in the Gulf of Maine and in Georges Bank has been shown by a number of workers (eg. Cooper and Uzmann 1971; Cooper et al. 1975; Dow 1974; Krouse 1980, 1981; Saila and Flowers 1968). Seasonal movements of mature, large lobsters is significantly greater than immature lobsters in the Gulf of Maine (Dow 1974; Campbell and Stasko in preparation, cf. Table 4, Fig. 8). Although morphometric studies (Saila and Flowers 1969; this paper) suggest some segregation of inshore and offshore lobster stocks, tagging studies indicate that there are probably subpopulations of immature lobsters (60-94 mm CL) that do not move significant distances, but that a portion of mature (≳95 mm CL) lobsters populations can travel long distances and do exhibit seasonal mixing between inshore and offshore lobster populations. The long distance movement of mature lobsters suggests that size-specific genetic mixing may regularly occur within at least the large reproductively mature lobsters in the Gulf of Maine system.

There is hardly any published information on lobster movement along eastern Nova Scotia and Cape Breton. Wilder (1974), using carapace tags on lobsters to determine exploitation rates mainly, found little movement of lobsters on the Fourchu-Gabarus-L'Archevêque fishing grounds. No lobsters tagged with sphyrion tags released in southwestern Nova Scotia (west of Clarke's Harbour) have been recaptured along the eastern Nova Scotia (east of Clarke's Harbour) (Stasko and Graham 1976; Campbell, unpublished data).

In the Gulf of St. Lawrence which includes the Magdalen Islands, Northumberland Strait, Bay of Chaleur, tagged lobsters tended to move over smaller distances ( 15 km) (Wilder and Murray 1958), although short distance seasonal offshore-inshore movements have been noted (Bergeron 1967; Montreuil 1953,1954a; Axelson and Dubé 1978; Munro and Therriault 1981). In Newfoundland, lobsters are generally restricted to shallow waters, such as large bays, without any demonstrable movement from one bay to the next; although short distant seasonal movements from depth <10 m in summer to >15 m short in winter was observed in Bonavista Bay (Squires and Ennis 1968; Ennis, pers. comm. in Stasko 1980a).

Stasko (1980a) suggested that water temperature was the causative factor to explain both the lack of movement of Gulf of St. Lawrence lobsters and movement of lobsters off SW Nova Scotia. In the southern Gulf of St. Lawrence water temperatures are below 0°C down to about 100 m depth, whereas at 50-200 m temperatures remain <4°C throughout the year (Trites 1972) suggesting that long-distance movement to deep water would not increase growth rates (Stasko 1980a). In contrast, at 200 m off SW Nova Scotia water temperatures can remain about 7°C throughout the year, allowing lobsters to feed and grow during winter when surface waters are about 0°C (Stasko 1980a).

Tagging data are helpful in determining spatial discreteness of lobster stocks by measuring movements and estimating stock sizes but not, unfortunately, gene flow. Interpretation of patterns of lobster movements must be tempered by the fact that tag recovery locations and frequencies are biased by the distribution and amount of the fishing effort. Notwithstanding this caveat available evidence suggests that large, mature lobsters move sufficient distances to allow mixing of lobsters in the Gulf of Maine.

## 4. MORPHOMETRICS

### Introduction

Morphometric characters have been used to show that the shape of lobsters can vary between different geographic areas (Templeman 1935a,1944a,b; Rogers et al. 1968; Saila and Flowers 1969). The use of morphometrics in identification of lobster stocks is complicated because phenotypic variation may be induced by differences in environmental conditions from one area to another. At present little is know of the degree of heritability of morphological variation of lobsters and the relative contribution of the environment to modifying the genetic control of this morphological variation. Nevertheless given sufficient numbers of individuals and multivariate data, phenotypic differences among lobster populations can probably provide valuable information on stock characterization in terms of spatial separation, whether or not there is reproductive isolation and/or genetic similarity. Although morphological characters are influenced by geographically different environments, morphometrics are probably just as valuable in characterizing stock discreteness and overlap as other more genetically orientated measurements.

The present analysis includes external body measurements of only lobsters of sizes vulnerable to commercial fishing gear (traps). The measured lobsters were caught in four general areas on traditional fishing grounds off New Brunswick, Nova Scotia and P.E.I. (Fig. 9). The purpose of the study was to determine if there were differences in body measurements of lobsters between four general areas (Bay of Fundy and inshore southwestern Nova Scotia, offshore Nova Scotia, eastern shore of Nova Scotia and Northumberland Strait) which would indicate stock discreteness and/or the extent of overlap. Wilder (1974) claimed that the inshore and offshore SW Nova Scotia lobster populations were discrete. Saila and Flowers (1969), using multivariate analysis of morphological measurements obtained from geographically separated lobster samples, found differences between inshore and offshore samples in the Gulf of Maine and southeast to Hudson Canyon. Rogers et al. (1968) and Templeman (1935b,1948) showed morphometric characters also could be used to establish geographic population differences although only bivariate comparisons were made.

Materials and Method

Lobsters were trap-caught from four general areas: (1) Bay of Fundy and inshore southwestern Nova Scotia (sample areas were Alma, Grand Manan-Seal Cove and North Head, Chance Harbour, Port Maitland, Seal Island, during May-November 1979 and May 1980); (2) offshore SW Nova Scotia (SW Browns Bank, east Georges Bank, Truxton Swell, Crowell Basin, during March-November 1979 and May 1980); (3) eastern coastline of Nova Scotia (Port Mouton, Three-fathom Harbour and Fourchu, during April to July 1979, and May 1980); and (4) Northumberland Strait (Escuminac, Cape Tormentine, and Beach Point or Murray Harbour, during May-July 1979 and May 1980) (Fig. 9).

Fifteen morphometric characteristics were measured (Table 5) for both male and berried and unberried female lobsters. These measurements were similar but not all the same as those used by Saila and Flowers (1969). To minimize the effect of size on subsequent analyses, size ranges of 80-130 mm

CL for females and 90-130 mm CL for males that were common in lobster samples from all four areas; male and females (berried and unberried combined) were kept separate. To remove further variation in lobster size within these size ranges, body measurements were expressed as ratios of CL. This adjustment for size variation was successful for most samples with less than 10%, showing relationships significantly different from zero, with most $R^2$ values $\leq 0.30$, suggesting adjustments for CL within samples had minimum effect on further analyses. A stepwise discriminant function analysis (Klecka 1975) using all 15 characters (in variable/CL ratio form, cf. Table 6) to compare samples and classifying individual lobsters into groups. To visualize relationships among individuals of the groups, canonical discriminant functions were used to produce scatterplots.

Results and Discussion

The discriminant function analysis on adjusted body measurements gave significant differences between stock centroids (Table 7). The first two canonical discriminant functions were significant and accounted for 95.2% and 90.9% of total variance for female and male, respectively (Table 7). The five main measurements (ratios) giving the best discrimination, in order of importance, were ED, AW, T, CW, PCL for females, and ED, T, CCW, UR, PCB for males (Table 7). There were relatively larger eye diameters and abdominal widths, but smaller carapace widths and telsons in females from Northumberland Strait compared to those from the other three areas (Table 6). The telson was relatively smaller, but the ED, crusher and pincer claws were relatively larger in male lobsters from Northumberland Strait than those from the other three areas. Geographic differences in secondary sexual characteristics for AW in females and crusher claw size in males have been recorded by a number of Canadian workers (Templeman 1935, 1936, 1944a,b; Ennis 1980; Aiken and Waddy 1980).

A posteriori classification of individual lobsters was used to estimate the discriminating power and classification accuracy of the derived canonical discriminant functions. The total percent of 'grouped' cases correctly classified was 55.6% for females and 51.1% for males (Table 8, Fig. 9,10). The highest correct classification was for the lobsters from Northumberland Strait (76.4% for females and 73.9% for males), with very little overlap with lobsters from Fundy, inshore and offshore SW Nova Scotia. Lobsters from east Nova Scotia (especially Cape Breton area-Fourchu) were overlapped considerably in morphological characters with those from Northumberland Strait, and to a lesser extent with those from SW Nova Scotia. There seems to be a gradation in morphological lobster traits along the eastern Nova Scotia shore, with Fourchu lobsters being similar to those of Northumberland Strait, and Port Mouton lobsters similar to inshore SW Nova Scotia lobsters. (By removing lobsters from Port Mouton and Three-Fathom Harbour from the east Nova Scotia sample, the percent grouped cases correctly classified increased to 64%). There was considerable overlap in morphological characteristics also with lobsters from both the offshore and inshore SW Nova Scotia and Bay of Fundy area (Table 8, Fig. 9,10).

Although statistical differences among lobsters from the four general areas were obtained, the results of this morphological investigation did not furnish completely convincing evidence for biological differences between these populations. The extent of separation between the four populations was not as high as expected, except perhaps for that of Northumberland Strait. A number of possibilities exist, eg., (1) variation is not genotypic, (2) variation is genotypic but masked by phenotypic responses to the environment, (3) some or all of the samples were not representative of the populations. Sample sizes were small especially for males from all locatins except perhaps for that of Fundy and SW Nova Scotia. The size distribution of individuals varied between samples within a size range requiring correction (variable/CL). The suitability of this correction for discriminant function analysis may not be appropriate (R.K. Misra, pers. comm.). Indeed, any variation in size left after this correction may provide further error in the statistical analyses.

However, examining all parts of the morphological analysis, the main conclusion is that lobsters can be divided into two main groups. One group includes lobsters from the Bay of Fundy and inshore and offshore southwestern Nova Scotia and the southern half of eastern Nova Scotia. The other group includes lobsters from Northumberland Strait and the Cape Breton portion of eastern Nova Scotia.

The wide phenotypic "plasticity" of lobsters may confound these morphometric methods documenting differences in lobster stocks. Possible spatial overlap due to movement by mature lobsters between deep and shallow waters (cf. reviews by Krouse 1980 and Stasko 1980) during various parts of the year may also obscure stock discreteness among offshore and inshore stocks (Saila and Flowers 1969).

## 5. PARASITES

Examination of lobster parasite distribution and abundance could be used as a technique amongst others in assessing the degree of discreteness of lobster populations and lobster movements. To date there has not been a published comprehensive survey of lobster parasites throughout the Canadian Maritimes with the purpose of quantitavely assessing lobster stock discreteness. A number of workers have examined lobsters for parasites (eg. Herrick 1911; Montreuil 1954b; Uzmann 1967a,b, 1970; Gelder 1978; Boghen 1978; see also review by Stewart 1980). Uzmann (1970) found that the larval nematode, *Ascarophis* sp. was almost exclusively restricted to offshore lobsters and the juvenile acanthocephalan, *Corynosoma* sp., was found on coastal lobsters of the United States, eg, Gulf of Maine and off Cape Cod. Both these genera have also been found in the Gulf of St. Lawrence (Montreuil 1954; Boghen 1978). Wilder (1974) reported a small goose barnacle collected from offshore lobsters but none from lobsters inshore of SW Nova Scotia. Differences in geographical environmental conditions as well as the presence of alternate host species (eg. such gadoid fishes for *Ascarophis*) may influence the abundance of various parasite species on lobster populations. To date there are no clear indications that parasites can be used as effective indicators of discreteness in lobster stocks.

## 6. ELECTROPHORESIS

Horizontal starch-gel electrophoresis with zymogram staining has been used by a number of workers to obtain genetically detectable protein enzymes in various organs of naturally occurring *H. americanus* (benthic stage) (Barlow and Ridgeway 1971; Tracey et al. 1975; Odense and Annand 1978). Electrophoretic surveys of various lobster populations sampled from Prince Edward Island, inshore and offshore SW Nova Scotia to Hudson Canyon south of New York, U.S.A., indicated low levels of genetic variability, suggesting there are no significant differences between genotypes of lobster populations from these areas. Tracey et al. (1975) examining 44 loci found *H. americanus* populations from eight areas genetically homogenous with one exception; the malic enzyme (Me) locus could be used to differentiate between lobster populations. The Me enzyme was absent in lobsters sampled from P.E.I., but present in varying amounts from lobsters collected south of Cape Cod. Unfortunately, tests for $Me^{100}$ locus were not made in lobsters sampled from inshore SW Nova Scotia and Maine. In addition, the low numbers (N=20) of lobsters sampled from P.E.I. make adequate interpretation of genetic isolation of populations for the Me locus difficult on the basis of the data presented by Tracey et al. (1975). Further sampling of lobsters from these areas (Gulf of St. Lawrence, East Nova Scotia and Gulf of Maine) with larger sample numbers, electrophoretic examination of the Me locus would probably be useful. Because one locus was not found in the P.E.I. lobsters does not preclude the presence of Me locus in other lobsters from the Gulf of St. Lawrence. If in fact the absence of the Me locus is characteristic of the Gulf of St. Lawrence lobster stock and not of those lobsters from the Gulf of Maine this may imply that there is a lack of gene flow or infrequent gene exchange between the two stocks.

Odense and Annand (1978) found no genetic variability between lobsters sampled from SW Browns Bank and inshore SW Nova Scotia. They did not, however, look for the Me locus.

On the whole, the interpretation of electrophoretic data, to date, indicate that local populations of *H. americanus* are genetically similar. Electrophoretic surveys of other large decapods, e.g., *H. gammarus*, *Cancer magister*, *Jasus edwardsii* and *J. novaehollandiae* have shown similar low heterozygosities, indicating low levels of genetic variation (Gooch 1977; Hedgecock et al. 1976, 1977; Nelson and Hedgecock 1980; Smith and McKoy 1980). However, Menzies and Kerrigan (1979) and Menzies (1980), using polyacrylamide gel-electrophoresis, have examined the esterase systems in adult *Panulirus argus* from different geographic regions, and results suggest detectable genetic differences between populations of *P. argus* in Central America and those of the Florida Coast.

This homogeneity in *H. americanus* may be due to gene exchange between populations. Even if the lobster stocks are electrophoretically inseparable the stocks may have adapted differently to their local environments. As large mature mobile and generalized predators, lobsters may be adapted to varying environments through phenotypic plasticity rather than genetic variability. Although juvenile and subadult lobsters may not move appreciable distances isolating sub-populations, it is probably through the 1-2 mo long surface planktonic larvae and adult movements that regular genetic interchanges may occur.

## 7. SURFACE CURRENT PATTERNS

To-date there is little empirical information on lobster larval ecology and recruitment patterns in the Canadian maritimes (see review by Stasko 1980b). Most of our knowledge comes from inference from the available information on gross surface currents. Study of residual surface currents (Fig. 11) may give a general indication of the pattern of lobster larval drift and whether there are circular (or closed) currents that may maintain larvae within an area or longitudinal (or open) currents that transport larvae large distances from original area of release (hatching) (Menzies et al. 1978; Menzies and Kerrigan 1980). A number of workers have proposed larval recruitment hypotheses based on these types of surface current patterns. Stasko (1978) proposed that summer surface currents from Browns Bank move northward providing a transport mechanism delivering passively drifting larvae to inshore SW Nova Scotia area (Stasko and Campbell 1980). Dadswell (1979) proposed that about six lobster recruitment cells exist for the Canadian maritimes based mainly upon surface current trends and commercial landings. (Open cell: 1. W. Gulf of St. Lawrence; 2. Northumberland; 3. eastern Nova Scotia; 4. Fundy; closed cell: S. Magdalen Islands; 6. SW Nova Scotia). Harding et al. (1982) hypothesize that observed small-scale patchiness of lobster larvae is caused by langmuir circulation. Iles (1975) and Robinson (1979) suggested that collapse of the lobster fishery in central Northumberland Strait was due to a number of factors including overexploitation and reduced larval recruitment.

In gross terms, genetic exchange, by lobster larval drift, may occur within area of the Gulf of St. Lawrence and possibly the western part of Cape Breton (to Cape Breton County); larvae are probably swept out into the Atlantic ocean beyond Cape Breton. The Gulf of Maine has a distinctly different current system than that of Gulf of St. Lawrence. Both which may be closed systems for lobsters and which make lobster larval mixing between the two areas difficult. The Eastern shore of Nova Scotia seems to have a longitudinal open current and larval drift system, and may afford some genetic exchange of lobsters between the two Gulf systems perhaps over several lobster generations.

## 8. SUMMARY CONCLUSION

Historical lobster commercial landing trends (1892-1981) were compiled for 32 areas of the Canadian maritimes and Maine, U.S.A. Principal component analysis of the raw landing data and cluster analyses of 6-yr means and

Chebyshev polynomials of normalized data were used to obtain general relationships between areas. These pattern recognition techniques resulted in recognizing 7-8 areas that had different landing trends. The generally stable landings of western maritimes (Lobster District 2) N.S. side of Bay of Fundy, Yarmouth and Shelburne Counties) and Maine, U.S.A. were grouped together. The generally declining landings from eastern coast of Nova Scotia (Queens Co., east to Cape Breton Co.) were grouped together with transition zones of patterns at Queens and Cape Breton Counties. The Gulf of St. Lawrence logster landing trends were loosely related, but could be grouped into six separate areas: (1) Cape Breton Co. to Magdalen Is.; (2) Central Northumberland Strait; (3) Northern New Brunswick; (4) Gaspé; (5) Duplessis; and (6) Newfoundland.

Population parameters (eg., growth and size at maturity) vary with local environmental conditions. Lobsters in the Gulf of St. Lawrence grow more rapidly and mature at a smaller size than those in the Western Nova Scotia. There seems to be a gradient transition zone along the Eastern shore from the population characteristics of the Gulf of St. Lawrence to that of Western Nova Scotia.

Tagging studies indicate that immature lobsters move only short distances in all areas and that large mature lobsters can move large distances, probably allowing mixing in the Gulf of Maine. Tagged lobsters in the Gulf of St. Lawrence tend to move over smaller distances ( $<$15 km), although seasonal offshore-inshore movements have been noted.

Discriminant function analysis of 15 morphological characters of lobsters from four areas (Bay of Fundy and inshore SW Nova Scotia; (2) offshore SW Nova Scotia; (3) Eastern Nova Scotia; (4) Northumberland Strait) indicated significant differences between areas. There were relatively larger eye diameters and abdominal widths but smaller carapace widths and telsons in females and larger crusher and pincer claws, smaller telsons for males in Northumberland Strait compared to those in the other three areas. A posteriori classification of individual lobsters was used to estimate the discriminating accuracy of the derived canonical discriminant functions. The highest correct classification was for lobsters from Northumberland Strait (76.4% for females and 73.9% for males), with little overlap with lobsters from Fundy and SW Nova Scotia. Lobsters from East Nova Scotia (especially Fourchu) were overlapped considerably in morphological characters with those of Northumberland Strait, and to a lesser extent with those from SW Nova Scotia (especially those from Port Mouton and Three-Fathom Harbour). There was considerable overlap in morphological characteristics with lobsters from both offshore and inshore SW Nova Scotia and Bay of Fundy area.

Review of the literature indicates that use of parasites and electrophoresis as methods for delineating lobster stocks, although showing promise, require improvement in the number of lobsters and areas sampled. To-date interpretation of electrophoretic data indicate that local populations of H. americanus are genetically similar. Although low levels of genetic variation have been reported, the malic enzyme was found to be absent in a small sample of lobsters from P.E.I., but present in varying amounts in lobsters collected south of Cape Cod.

Examination of landing trends, some population parameters (growth and size at maturity), morphometrics, movement of tagged lobsters and general surface currents that might indicate larval drift, suggested the following general lobster stock areas:

1. Western maritimes which included the Bay of Fundy, inshore and possibly offshore) southwestern Nova Scotia (to Shelburne Co.),

2. The Eastern Coast of Nova Scotia (Queens to Cape Breton Counties) which seems to be a transition zone for lobsters between the Gulf of Maine and the Gulf of St. Lawrence, and

3. Southern Gulf of St. Lawrence.

At present, separation of these lobster stocks seems to depend mainly on the ability to detect differences in population parameters throughout the range of the species and not on genetically separate subgroups. Although commercial landing trends were grouped into distinctive areas, these groups alone cannot suggest genetic separation. In the Gulf of St. Lawrence, although 5 areas were clustered separately, most of these areas (except central Northumberland Strait) were closely related, and it is difficult to state they are different stocks. Lobster larval recruitment in general may only be a local phenomenon closely related to local reproductive patterns. However, larger scale larval drift would superimpose a large scale diffusion of lobster larvae making interpretation of larval recruitment patterns difficult.

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Table 1. Matrix correlation coefficients comparing annual lobster landings (MT) from 31 areas during 1892-1981. Co-efficients ≥0.21 are significant at the 1% level and ≥0.27 at the 5% level; decimal points are omitted (i.e., -25 = -025). Albert County not included.

| Variable | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. Maine | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 2. Lob. District 1 | 25 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 3. Lob. District 2 | 55 | 13 | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 4. Anna. and Kings | 37 | 33 | -10 | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 5. Yarmouth | 26 | 42 | -03 | 50 | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 6. Shelburne | 33 | 78 | 25 | 36 | 74 | | | | | | | | | | | | | | | | | | | | | | | | | |
| 7. Queens | 06 | 61 | -09 | 49 | 63 | 66 | | | | | | | | | | | | | | | | | | | | | | | | |
| 8. Lunenburg | 21 | 54 | 18 | 43 | 59 | 68 | 80 | | | | | | | | | | | | | | | | | | | | | | | |
| 9. Halifax | -20 | 73 | -13 | 26 | 46 | 67 | 71 | 59 | | | | | | | | | | | | | | | | | | | | | | |
| 10. Guysborough | -41 | 58 | -21 | 01 | 21 | 48 | 57 | 44 | 91 | | | | | | | | | | | | | | | | | | | | | |
| 11. Richmond | -19 | 69 | -09 | 64 | 20 | 54 | 60 | 52 | 84 | 92 | | | | | | | | | | | | | | | | | | | | |
| 12. Cape Breton | -30 | 56 | -19 | 11 | 16 | 41 | 55 | 38 | 73 | 84 | 82 | | | | | | | | | | | | | | | | | | | |
| 13. Victoria | 54 | -15 | 48 | -22 | -30 | -15 | -36 | -23 | -39 | -43 | -29 | -21 | | | | | | | | | | | | | | | | | | |
| 14. Inverness | -18 | 03 | 0 | -10 | 23 | 24 | 35 | 32 | 40 | 41 | 35 | 43 | -01 | | | | | | | | | | | | | | | | | |
| 15. Antigonish | -60 | -27 | -18 | -31 | -27 | -25 | 08 | -03 | 20 | 41 | 29 | 37 | -11 | 50 | | | | | | | | | | | | | | | | |
| 16. Kings, P.E.I. | 51 | 14 | 14 | 30 | 49 | 39 | 26 | 21 | 07 | -14 | -07 | 12 | 27 | 38 | -20 | | | | | | | | | | | | | | | |
| 17. Pictou | -23 | 28 | -18 | 18 | 09 | 20 | 55 | 44 | 64 | 73 | 72 | 65 | -19 | 43 | 61 | -05 | | | | | | | | | | | | | | |
| 18. Colchester | -20 | 03 | -35 | 38 | 29 | 33 | 45 | 35 | 61 | 64 | 56 | 50 | -30 | 29 | 32 | 11 | 74 | | | | | | | | | | | | | |
| 19. Cumberland | -29 | 42 | -35 | 27 | 34 | 37 | 73 | 52 | 78 | 80 | 75 | 63 | -47 | 39 | 39 | 06 | 83 | 76 | | | | | | | | | | | | |
| 20. Westmorland | 14 | 52 | -10 | 47 | 35 | 51 | 57 | 53 | 65 | 60 | 70 | 48 | -19 | 29 | 03 | 29 | 59 | 73 | 72 | | | | | | | | | | | |
| 21. Queen's, P.E.I. | -14 | 40 | -29 | 35 | 46 | 45 | 70 | 43 | 72 | 66 | 62 | 60 | -30 | 55 | 36 | 41 | 70 | 71 | 80 | 60 | | | | | | | | | | |
| 22. Kent | 28 | 05 | 28 | -01 | -15 | 02 | 05 | -05 | -01 | 02 | 10 | -02 | 38 | 13 | 21 | 23 | 25 | 15 | -07 | 30 | 06 | | | | | | | | | |
| 23. Prince, P.E.I. | -01 | 38 | -28 | 33 | 41 | 42 | 48 | 16 | 50 | 44 | 39 | 44 | -06 | 46 | 11 | 53 | 29 | 50 | 52 | 58 | 66 | 02 | | | | | | | | |
| 24. Northumberland | -06 | -20 | 52 | 74 | -23 | -26 | 01 | -12 | -10 | 01 | 01 | 10 | 09 | 05 | 40 | -16 | 33 | 14 | 08 | 08 | 07 | 55 | 05 | | | | | | | |
| 25. Gloucester | 64 | 54 | -32 | 49 | 57 | 57 | 63 | 35 | 68 | 55 | 50 | 51 | -30 | 43 | 05 | 47 | 39 | 61 | 61 | 70 | 75 | 20 | 83 | 05 | | | | | | |
| 26. Restigouche | 32 | 43 | 11 | 37 | 16 | 35 | 34 | 31 | 37 | 32 | 44 | 25 | 04 | 07 | -03 | 16 | 41 | 55 | 41 | 72 | 36 | 45 | 36 | 31 | 52 | | | | | |
| 27. Bonaventure | 13 | 48 | -14 | 07 | 41 | 49 | 31 | 13 | 42 | 35 | 38 | 34 | 02 | 31 | -16 | 49 | 47 | 28 | 30 | 39 | 49 | 02 | 66 | -34 | 65 | 19 | | | | |
| 28. Gaspé | -02 | 48 | -21 | 05 | 42 | 48 | 42 | 12 | 48 | 40 | 39 | 46 | -06 | 47 | -01 | 46 | 09 | 22 | 33 | 32 | 58 | 0 | 74 | -23 | 73 | 12 | 01 | | | |
| 29. Duplessis | -13 | -71 | -25 | 21 | 61 | 72 | 59 | 46 | 78 | 71 | 70 | 66 | -39 | 34 | -05 | 23 | 33 | 48 | 57 | 50 | 65 | -21 | 57 | -35 | 70 | 20 | 71 | 72 | | |
| 30. Magdalen Is. | 29 | 32 | -06 | 22 | 32 | 28 | 43 | 36 | 37 | 27 | 38 | 33 | 25 | 31 | -03 | 49 | 40 | 34 | 47 | 47 | 54 | 02 | 42 | -18 | 41 | 27 | 47 | 45 | 39 | |
| 31. Newfoundland | 30 | 72 | 11 | 24 | 46 | 73 | 43 | 38 | 62 | 48 | 59 | 46 | 02 | 25 | 18 | 36 | 16 | 25 | 30 | 51 | 44 | 11 | 53 | -31 | 66 | 41 | 70 | 70 | 71 | 44 |

Table 2. Principal component matrix based on the analysis of annual lobster landings (1892-1981). [a]Based on correlation matrix; n = 90, p = 31; decimal points are omitted (i.e., -35 = -0.35). (Albert County not included).

| Variable | Principal component (C) | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $C_I$ | $C_{II}$ | $C_{III}$ | $C_{IV}$ | $C_V$ | $C_{VI}$ | $C_{VII}$ | $C_{VIII}$ | $C_{IX}$ | $C_X$ | $C_{XI}$ | $C_{XII}$ |
| 1. Maine | 01 | -39 | 26 | -12 | 03 | 04 | 13 | -10 | -01 | -04 | 06 | 09 |
| 2. Lob. District 1 | -20 | -14 | -05 | -21 | 23 | -20 | -04 | -18 | 13 | -04 | -14 | 06 |
| 3. Lob. District 2 | 05 | -20 | 23 | -16 | 38 | 23 | -19 | 14 | -13 | -13 | 01 | 31 |
| 4. Anna. and Kings | -11 | -14 | 11 | -24 | -42 | -07 | 00 | -29 | -41 | 01 | -36 | 19 |
| 5. Yarmouth | -16 | -21 | -12 | -11 | -24 | 22 | -22 | 05 | 04 | -30 | 28 | -28 |
| 6. Shelburne | -20 | -22 | -05 | -18 | 12 | 07 | -22 | 11 | -02 | -24 | 01 | -16 |
| 7. Queens | -23 | -02 | 01 | -17 | -10 | 22 | -11 | -28 | 31 | 21 | 02 | 02 |
| 8. Lunenburg | -18 | -07 | 03 | -33 | 01 | 36 | -03 | 04 | 07 | 28 | 02 | -24 |
| 9. Halifax | -25 | 08 | -07 | -11 | 12 | -00 | -05 | 05 | 00 | -08 | -17 | 11 |
| 10. Guysborough | -23 | 21 | -07 | -06 | 19 | -07 | -01 | 05 | -06 | -07 | -16 | 03 |
| 11. Richmond | -23 | 14 | -00 | -10 | 28 | -07 | 08 | 01 | 10 | 05 | 02 | -00 |
| 12. Cape Breton | -21 | 17 | -05 | -00 | 23 | -04 | 01 | -39 | -34 | 03 | -01 | -24 |
| 13. Victoria | 09 | -19 | 29 | 21 | 28 | 08 | 26 | -19 | -18 | -17 | -09 | -35 |
| 14. Inverness | -14 | 08 | 05 | 29 | 08 | 43 | -19 | 18 | -34 | 39 | 03 | -10 |
| 15. Antigonish | -04 | 37 | 12 | 20 | 09 | 23 | -13 | 03 | -07 | -14 | -03 | 22 |
| 16. Kings, P.E.I. | -09 | -30 | 13 | 26 | -19 | 25 | -01 | 15 | 07 | -12 | -17 | 14 |
| 17. Pictou | -18 | 27 | 21 | -06 | 03 | 14 | 18 | -04 | 03 | -20 | -04 | 07 |
| 18. Colchester | -20 | 16 | 12 | -02 | -20 | -11 | 18 | 31 | -22 | -39 | 03 | -22 |
| 19. Cumberland | -23 | 19 | 03 | -05 | -10 | 06 | 16 | 07 | 32 | 04 | -02 | 06 |
| 20. Westmorland | -22 | -00 | 19 | -08 | -09 | -15 | 15 | 28 | -04 | 31 | -09 | -14 |
| 21. Queen's, P.E.I. | -24 | 08 | 03 | 13 | -15 | 14 | 05 | -06 | 01 | -24 | 09 | 38 |
| 22. Kent | -03 | -01 | 47 | 14 | 10 | -16 | -26 | 11 | 40 | -05 | -30 | -16 |
| 23. Prince, P.E.I. | -20 | -06 | 06 | 31 | -14 | -13 | -14 | -07 | 03 | 09 | -31 | -20 |
| 24. Northumberland | 02 | 19 | 40 | 02 | -08 | -09 | -33 | -42 | 03 | -10 | 38 | -06 |
| 25. Gloucester | -24 | -06 | 02 | 14 | -19 | -16 | -17 | -03 | -09 | 10 | 03 | 08 |
| 26. Restigouche | -14 | -04 | 34 | -12 | -02 | -31 | 06 | 24 | -15 | 24 | 48 | 11 |
| 27. Bonaventure | -17 | -19 | -14 | 30 | 08 | -15 | 06 | 06 | 11 | -05 | 19 | 00 |
| 28. Gaspé | -19 | -13 | -17 | 35 | 07 | -07 | -11 | -17 | 06 | 10 | 15 | 10 |
| 29. Duplessis | -24 | -05 | -26 | 02 | 07 | -07 | -03 | 02 | -04 | -19 | 11 | -16 |
| 30. Magdalen Is. | -16 | -12 | 09 | 14 | 00 | 21 | 59 | -21 | 14 | 03 | 13 | 01 |
| 31. Newfoundland | -20 | -21 | -05 | 05 | 23 | -16 | -03 | 03 | -15 | 06 | -02 | 28 |
| Variation explained | 40.4 | 14.1 | 9.4 | 8.0 | 6.3 | 4.9 | 3.6 | 2.2 | 1.5 | 1.3 | 1.2 | 1.0 |

Table 3. Inter-cluster distances and first and second order Chebyshev coefficients.

| Cluster No. | T * | $T_2$ | Inter-cluster distanc | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Chebyshev | | | | | | | | Six-year average | | | | | | | |
| | | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| 1 | -0.05 | -0.01 | 0 | | | | | | | | 0 | | | | | | | |
| 2 | -0.15 | 0.21 | 0.3 | 0 | | | | | | | 6 | 0 | | | | | | |
| 3 | -1.15 | 0.53 | 2.1 | 1.5 | 0 | | | | | | 5 | 3 | 0 | | | | | |
| 4 | -0.49 | 1.14 | 1.8 | 1.6 | 1.2 | 0 | | | | | 3 | 3 | 2 | 0 | | | | |
| 5 | -2.20 | 1.32 | 7.5 | 6.1 | 2.5 | .4 | 0 | | | | 21 | 14 | 8 | 10 | 0 | | | |
| 6 | -0.82 | 0.36 | 1.2 | 0.6 | 0.6 | 1.4 | 3.1 | 0 | | | 2 | 4 | 2 | 2 | 13 | 0 | | |
| 7 | -0.50 | 0.36 | 0.4 | 0.3 | 0.7 | 0.7 | 4.6 | 0.4 | 0 | | 14 | 18 | 24 | 13 | 38 | 17 | 0 | |
| 8 | 0.55 | 0.30 | 0.5 | 0.7 | 3.7 | 2.3 | 9.6 | 2.2 | 1.3 | 0 | 1 | 7 | 7 | 4 | 23 | 3 | 10 | 0 |

*is the Chebyshev coefficient of the linear term and $T_2$ of the second order or U-shaped component.

Table 4. Summary of movements of tagged lobsters released in six locations in the Bay of Fundy (Alma, St. Martins, Delap Cove, Chance Harbour, North Head and Seal Cove) during July 1977-September 1980, recaptured up to 31 September, 1981. Lobsters divided into physiologically immature (60-94 mm CL) and mature (≥95 mm CL) at release. (After Campbell and Stasko, in preparation).

| Details | Percent of total lobster recaptures | | |
|---|---|---|---|
| | Immature | Mature | Total |
| Distance moved (km) | | | |
| ≤18.5 | 87.1 | 56.5 | 75.9 |
| 18.5-36.9 | 6.6 | 12.3 | 8.7 |
| 37.0-92.6 | 2.6 | 14.3 | 6.9 |
| >92.6 | 0.9 | 14.0 | 5.7 |
| No location | 2.8 | 2.9 | 2.8 |
| Total % recaptures | 33.1 | 17.6 | 25.1 |
| Total number released | 9,517 | 10,473 | 20,190 |
| Mean distance (km) travelled | 10.5[a] | 41.9[a] | 21.9 |
| Max. distance (km) travelled | 389.7 | 590.1 | 590.1 |

[a]significantly different ($p<0.001$).

Table 5. List of lobster morphometric characters and acronyms used in the analyses. All measurements are linear distances in mm, length of setae excluded. For definition of terms, see Herrick (1911).

| Acronym | Description |
|---|---|
| CL | Carapace length measured from margin of eye socket to posterior margin of carapace in a line parallel to dorsal surface of carapace. |
| AW | Maximum width of second abdominal segment posterior to carapace. |
| TL | Total length measured from anterior tip of rostrum to posterior tip of telson when lobster held ventrally flat and fully extended. |
| CW | Maximum lateral width of carapace. |
| RL | Rostrum length from anterior tip to posterior edge of margin of curved eye socket. |
| T | Maximum length of telson. |
| UR | Maximum length of right uropod to end of second joint. |
| ED | Maximum diameter of right eye. |
| PER | Maximum length of the fourth segment of second left pereipod. |
| CCL | Crusher claw length from tip to proximal (Aiken and Waddy 1980). |
| CCW | Crusher claw width or height as maximum height from top of the protuberance over the terminal hing joint downwards, perpendicular to the axis of the propus occluding surface, to the margin of the manus (cf. Fig. 1 in Elner and Campbell 1981). |
| CCB | Maximum lateral breath of crusher claw (cf. Fig. 3, plate XLIII in Herrick 1911). |
| PCL | Pincer claw length from tip to proximal spur. |
| PCW | Pincer claw width or height as maximum height from top of the protuberance over the terminal hinge joint downwards, perpendicular to the axis of the propus occluding surface, to the margin of the manus. |
| PCB | Maximum lateral breath of pincer claw. |

Table 6. Summary of morphological measurements (means ±1 Standard Deviations). All measurements (except CL in millimeters) adjusted to ratios (variable x $10^2$/CL) for size range 80-130 mm CL for females and 90-130 mm CL for males.

| Variable | Fundy and SW Nova Scotia | Offshore SW Nova Scotia | East Nova Scotia | Northumberland Strait | Total |
|---|---|---|---|---|---|
| Female | | | | | |
| CL | 104.9±13.5 | 111.6±10.5 | 96.5±10.9 | 90.3±9.7 | 102.5±13.8 |
| AW | 65.9± 5.2 | 66.9± 4.7 | 66.4± 5.4 | 70.5±3.6 | 66.9± 5.2 |
| TL | 292.2± 5.4 | 291.9± 6.2 | 290.7± 5.4 | 290.8±5.3 | 291.7± 5.6 |
| CW | 63.7± 2.8 | 64.6± 2.6 | 61.9± 2.4 | 62.5±1.7 | 63.3± 2.7 |
| AL | 33.4± 2.6 | 32.4± 2.9 | 33.4± 2.9 | 33.5±2.2 | 33.2± 2.7 |
| T | 40.8± 1.3 | 40.5± 1.7 | 39.9± 1.4 | 39.5±1.1 | 40.4± 1.5 |
| UR | 43.9± 1.8 | 43.2± 2.2 | 43.5± 1.8 | 43.4±1.9 | 43.6± 1.9 |
| ED | 6.5± 0.6 | 6.1± 0.5 | 6.8± 0.5 | 7.1±0.5 | 6.6± 0.6 |
| PER | 42.4± 1.7 | 42.2± 1.8 | 41.8± 1.7 | 41.6±1.4 | 42.1± 1.7 |
| CCL | 124.0± 4.9 | 122.4± 5.0 | 122.1± 4.8 | 121.9±5.4 | 123.0± 5.0 |
| CCW | 57.1± 2.4 | 56.7± 2.8 | 56.3± 2.6 | 56.6±2.9 | 56.8± 2.6 |
| CCB | 30.1± 1.4 | 29.8± 1.6 | 29.6± 1.3 | 29.3±2.0 | 29.8± 1.5 |
| PCL | 135.1± 5.5 | 132.7± 6.3 | 131.9± 6.6 | 132.3±4.4 | 133.6± 5.9 |
| PCW | 47.8± 2.4 | 47.8± 2.6 | 46.9± 2.7 | 47.1±2.1 | 47.5± 2.5 |
| PCB | 27.3± 1.5 | 26.4± 1.9 | 26.7± 1.7 | 27.0±1.6 | 26.9± 1.7 |
| Male | | | | | |
| CL | 107.1±12.6 | 117.6±10.9 | 104.6±11.2 | 100.5±9.9 | 107.3±12.7 |
| AW | 54.5± 1.8 | 54.7± 2.0 | 54.5± 1.5 | 54.4±1.9 | 54.5± 1.8 |
| TL | 281.8± 5.0 | 281.8± 9.4 | 279.5± 5.1 | 278.6±6.9 | 281.0± 8.1 |
| CW | 62.0± 2.4 | 62.3± 1.7 | 61.0± 2.2 | 61.9±1.8 | 61.9± 2.3 |
| RL | 31.6± 2.4 | 30.9± 2.7 | 30.6± 2.5 | 30.8±2.1 | 31.2± 2.5 |
| T | 38.8± 1.3 | 39.7± 1.7 | 38.3± 1.2 | 37.6±1.0 | 38.7± 1.4 |
| UR | 41.9± 1.5 | 41.5± 1.9 | 41.8± 1.7 | 41.5±1.5 | 41.8± 1.6 |
| ED | 6.3± 0.6 | 6.1± 0.5 | 6.4± 0.5 | 6.8±0.4 | 6.3± 0.6 |
| PER | 42.4± 1.4 | 33.0± 1.6 | 41.9± 1.6 | 41.9±1.4 | 42.4± 1.5 |
| CCL | 126.7± 5.4 | 127.3± 4.7 | 127.5± 9.3 | 131.8±8.1 | 127.5± 6.7 |
| CCW | 60.4± 3.6 | 61.8± 3.3 | 61.9± 5.8 | 65.4±6.7 | 61.4± 4.7 |
| CCB | 32.4± 2.1 | 32.9± 1.9 | 33.1± 2.9 | 33.9±3.3 | 32.8± 2.4 |
| PCL | 136.2± 5.4 | 136.6± 5.0 | 135.4± 6.9 | 137.8±9.1 | 136.3± 6.1 |
| PCW | 48.9± 3.1 | 49.3± 1.9 | 48.7± 2.7 | 51.2±3.7 | 49.2± 3.1 |
| PCB | 27.6± 1.7 | 27.2± 1.1 | 27.6± 2.0 | 27.9±1.9 | 27.6± 1.7 |

Table 7. Canonical discriminant functions for lobster morphometrics data from four areas.

| Variable | Standardized discriminant function coefficients for function 1 | 2 | 3 |
|---|---|---|---|
| | Females | | |
| AW | 0.748 | -0.382 | 0.435 |
| TL | -0.030 | -0.309 | -0.253 |
| CW | -0.434 | -0.249 | 0.586 |
| RL | 0.056 | 0.340 | 0.033 |
| T | -0.528 | 0.112 | 0.190 |
| UR | 0.194 | 0.533 | -0.179 |
| ED | 0.864 | 0.039 | 0.293 |
| CCW | 0.154 | 0.229 | 0.118 |
| CCL | -0.159 | 0.139 | -0.117 |
| PCL | -0.208 | 0.039 | 0.361 |
| PCW | -0.162 | -0.264 | 0.026 |
| PCB | 0.108 | 0.365 | 0.325 |
| Percent variance | 86.38 | 8.82 | 4.79 |
| Canonical correlation | 0.713 | 0.309 | 0.233 |
| Wilk's $\lambda$ | 0.421* | 0.856* | 0.946* |
| | Males | | |
| CW | -0.127 | 0.105 | 0.621 |
| RL | -0.122 | -0.344 | 0.546 |
| T | -0.683 | 0.633 | -0.241 |
| UR | 0.289 | -0.502 | -0.177 |
| ED | 0.782 | 0.219 | 0.213 |
| PER | -0.215 | 0.142 | 0.089 |
| CCW | 0.572 | 0.583 | -0.469 |
| PCW | 0.092 | 0.389 | 0.653 |
| PCB | -0.232 | -0.450 | -0.039 |
| Percent variance | 73.26 | 17.63 | 9.11 |
| Canonical correlation | 0.584 | 0.333 | 0.246 |
| Wilk's $\lambda$ | 0.549* | 0.835** | 0.939$^{o}$ |

*$p < 0.001$ ; **$p < 0.01$ ; $^{o}p > 0.05$.

Table 8. Percent correct a posteriori classification to groups based on morphometric classification functions.

| Group | Percentage of cases classified into group | | | | |
|---|---|---|---|---|---|
| | Fundy & inshore SWNS | Offshore SWNS | East Nova Scotia | Northumberland Strait | No. of lobsters |
| | | | FEMALES | | |
| Fundy & inshore SW Nova Scotia | 52.1 | 28.5 | 17.7 | 1.7 | 351 |
| Offshore SWNS | 28.3 | 63.8 | 6.6 | 1.3 | 152 |
| East Nova Scotia | 22.7 | 6.1 | 41.7 | 29.4 | 163 |
| Northumberland Strait | 2.8 | 0.9 | 19.8 | 76.4 | 106 |
| Total percent of 'grouped' cases correctly classified = 55.6 | | | | | |
| | | | MALES | | |
| Fundy & inshore SW Nova Scotia | 45.2 | 21.0 | 28.2 | 5.6 | 124 |
| Offshore SWNS | 23.3 | 63.3 | 10.0 | 3.3 | 30 |
| East Nova Scotia | 15.9 | 11.4 | 47.7 | 25.0 | 44 |
| Northumberland Strait | 13.0 | 4.3 | 8.7 | 73.9 | 23 |
| Total percent of 'grouped' cases correctly classified = 51.1 | | | | | |

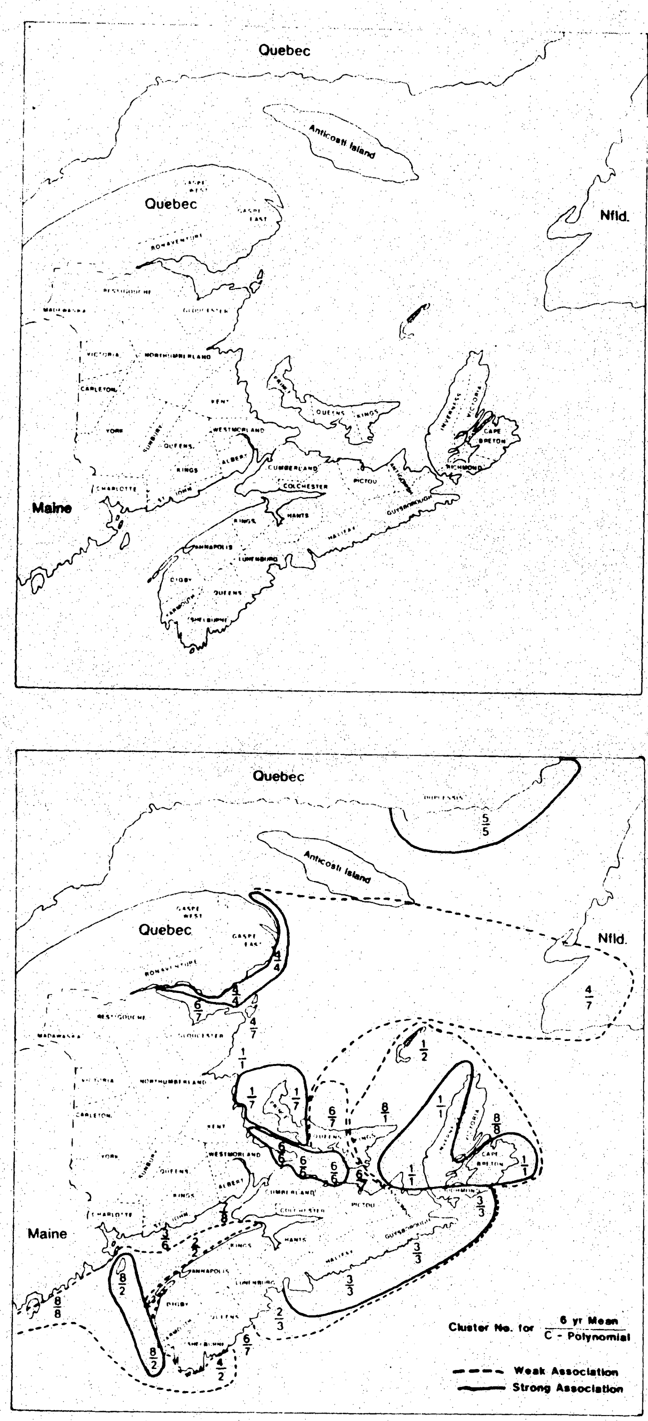


Fig. 1. Map of Canadian Maritimes showing provinces and counties with lobster landings grouped according to the cluster analyses on 6-yr means and Chebyshev polynomials of the normalized lobster landings by areas and/or counties.

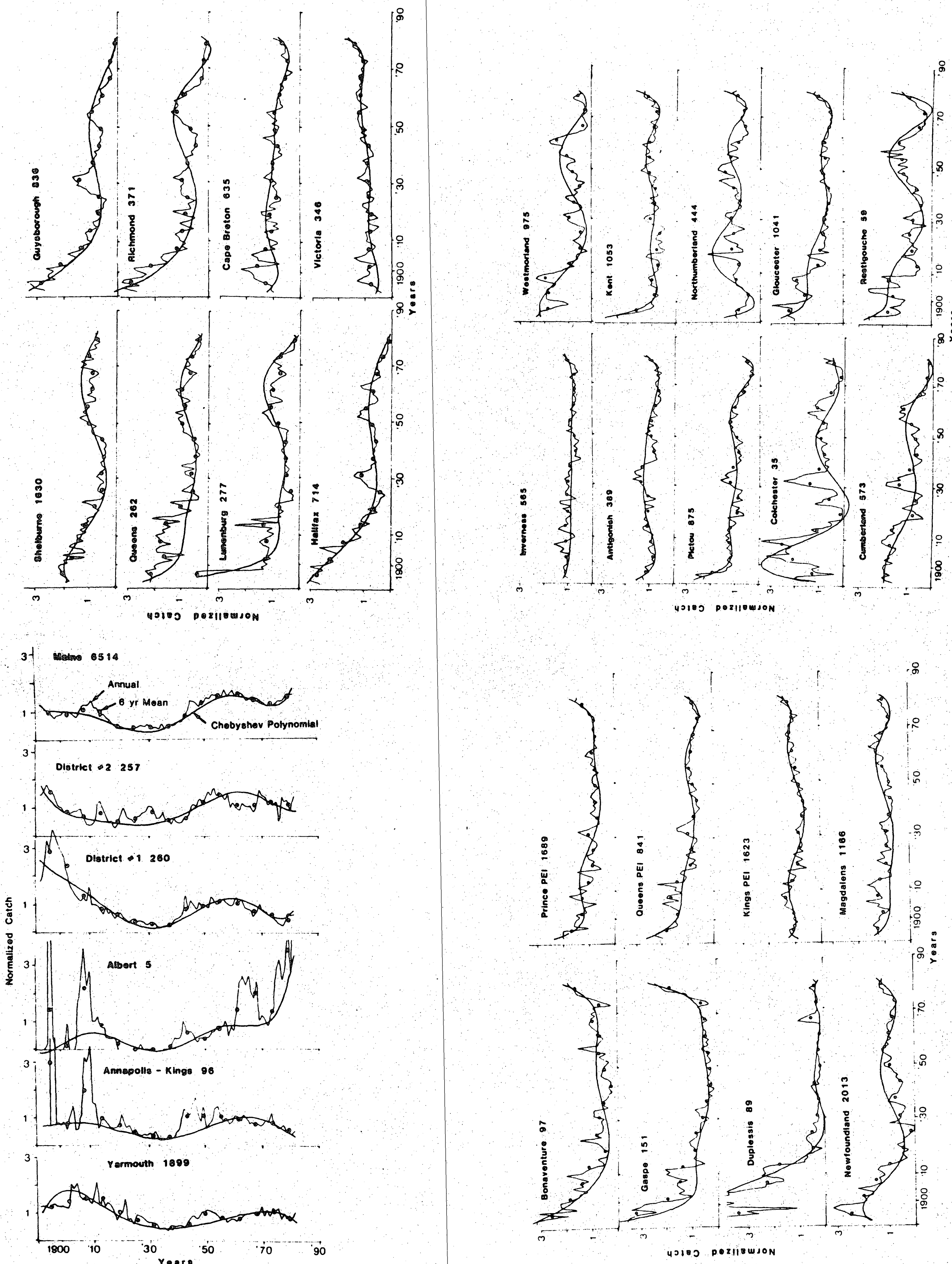


Fig. 2. Annual lobster landings normalized (thin line) with respect to the mean (shown on the right side of area or county name) for each area, 1892-1981. The dots represent 6-yr means and the smooth curves (thick lines) represent the Chebyshev polynomials fitted to the normalized landings.

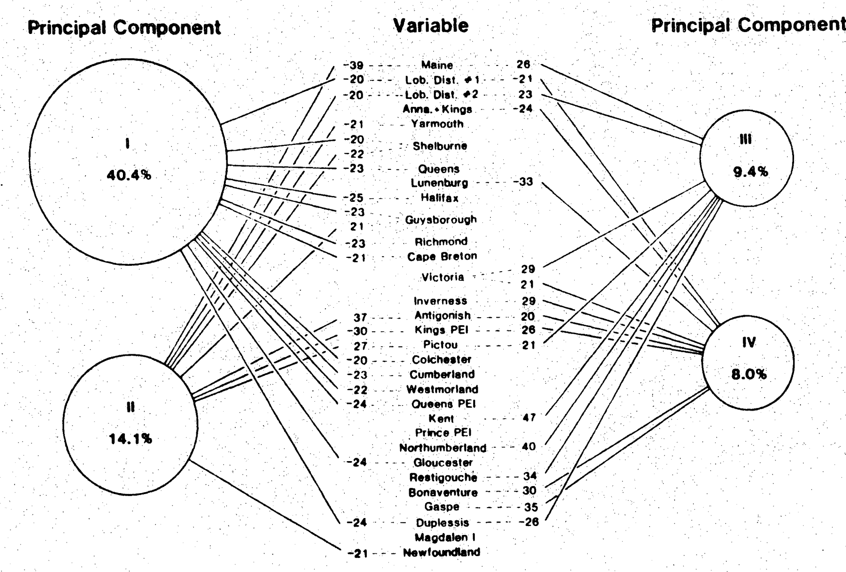


Fig. 3. Diagram illustrating effects of the first four principal components on the landing trends from 31 areas. The numbers at the inner ends of the lines represent the principal-component loadings of the variables; only the loadings ≥0.20 or ≤-0.20 are shown. The area of the circles enclosing the principal components is relative to the percentage variation explained by each principal component.

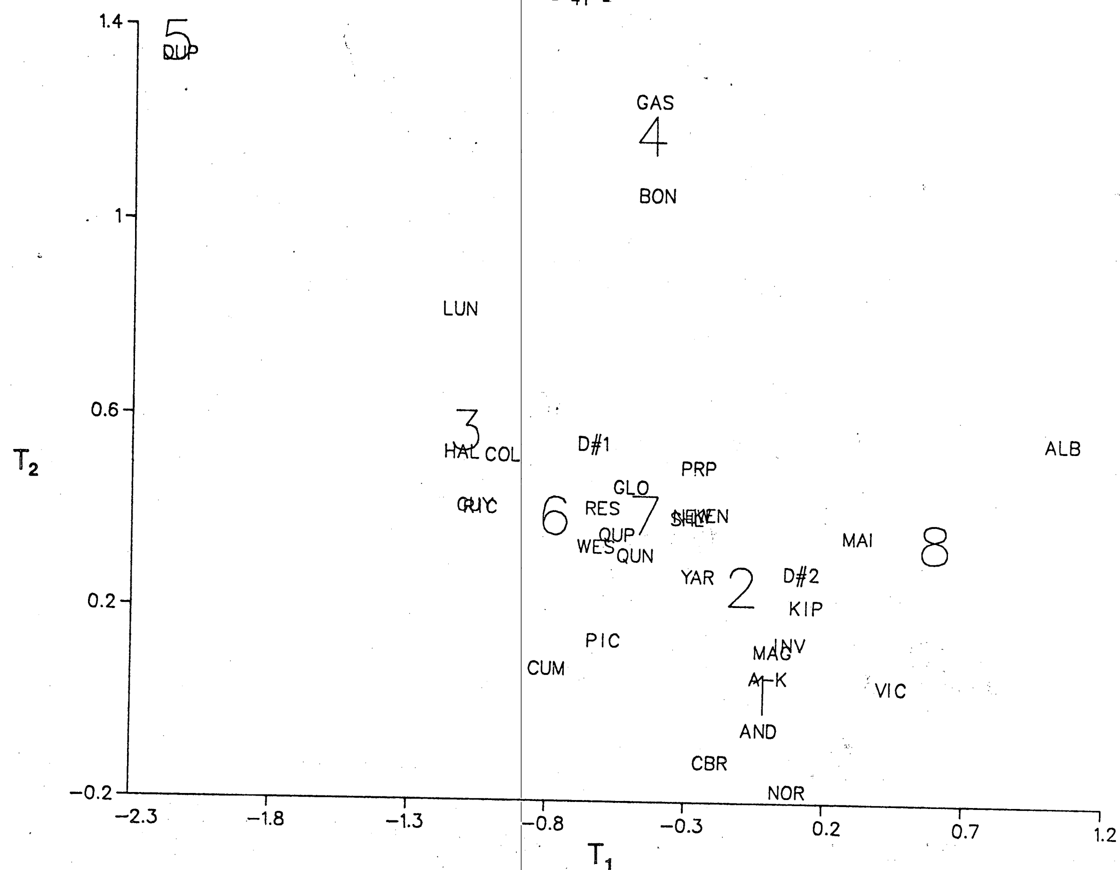


Figure 4a. Clusters using Chebyshev representation of data.

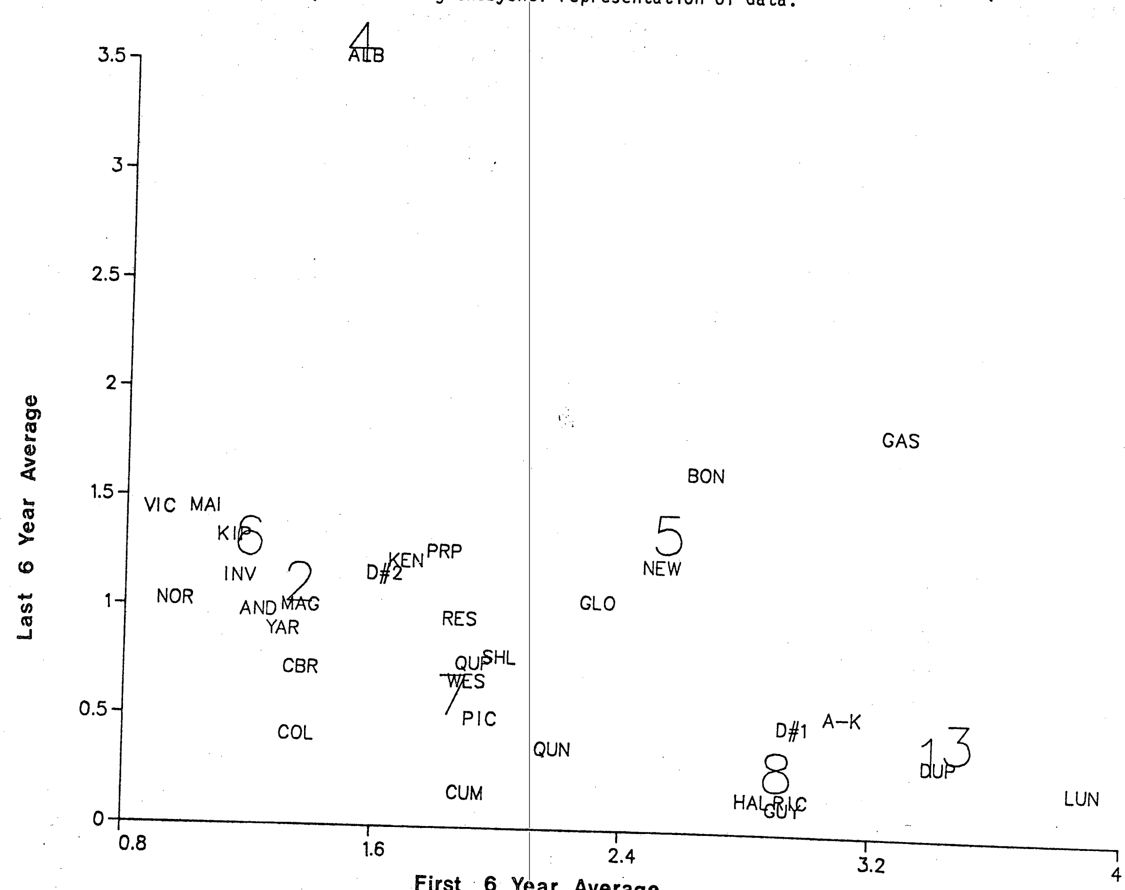


Figure 4b. Clusters and locations of statistical areas using 6-year average representation of data.

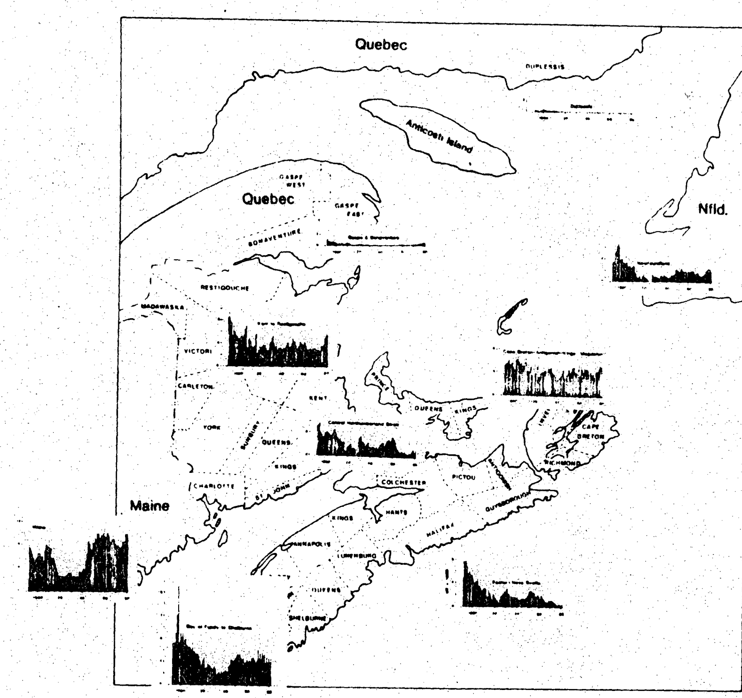


Fig. 5. Canadian and Maine, U.S.A., annual lobster landings (in MT for 1892-1981) combined into general areas recognized by the two methods of grouping similar landing trends (Principal component analysis and the two cluster analyses). (New Brunswick side of Bay of Fundy landings - generally declining - not shown).

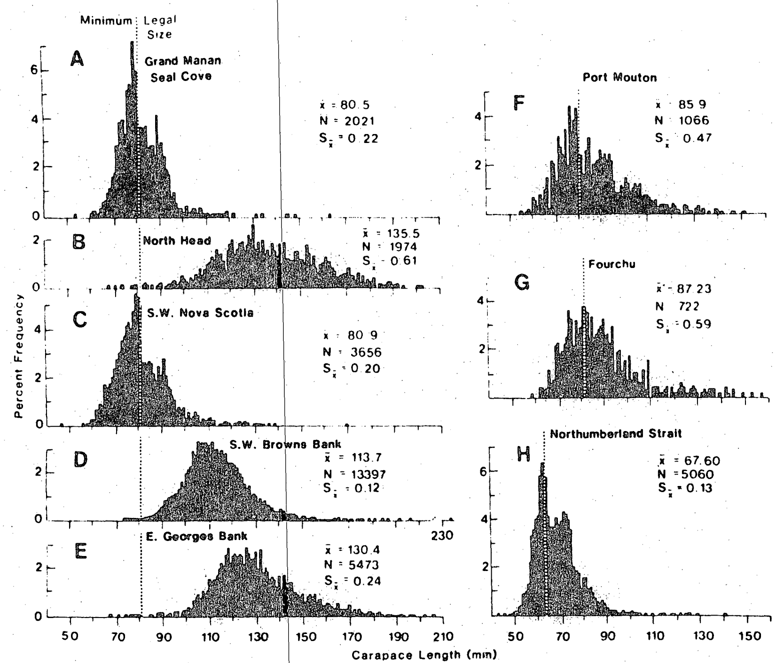


Fig. 6. Size frequencies (% of total in 1-mm groups) of lobsters caught in fishermen's traps for (A) Seal Cove, Grand Manan, 1978-80, (B) North Head, Grand Manan, 1978-80, (C) Port Maitland and Lower Argyle, 1978-79, (D) Southwest Browns Bank and Truxton Swell, 1977-79, (E) Southeast Browns Bank, Corsair Canyon, Georges Bank, 1977-79, (F) Port Mouton and Port Latour, 1978-79, (G) Fourchu, 1977-80, (H) Northumberland Strait, 1977-80. $\bar{X}$ = mean carapace length (mm), N = total number in sample, $S_{\bar{X}}$ = standard error of the mean carapace length.

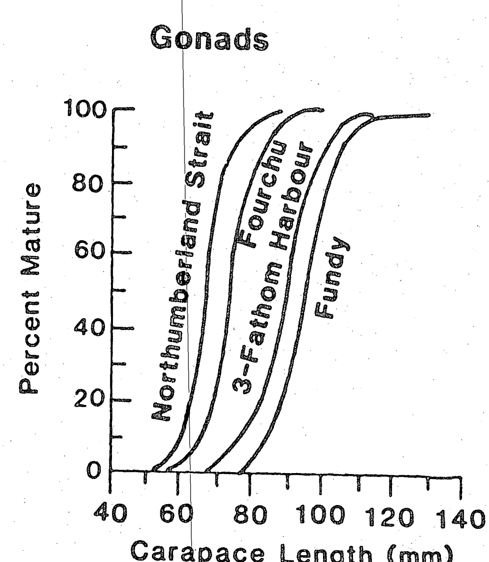


Fig. 7. Proportion 'physiological' maturity curves for female lobsters based on ovary examination for the Bay of Fundy and SW Nova Scotia, Three-Fathom Harbour, Fourchu and Northumberland Strait (A. Campbell, unpublished data).

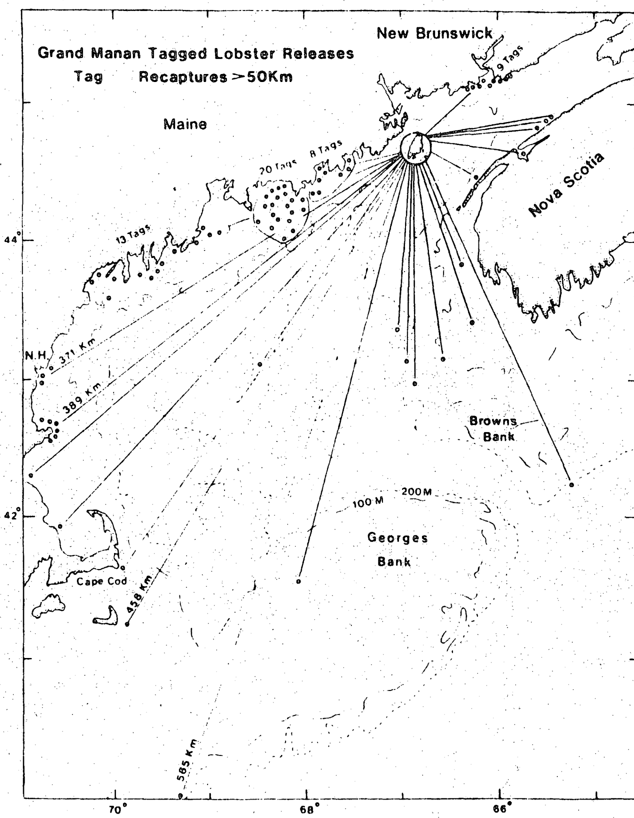


Fig. 8. 'Straight-line' movements of lobsters tagged off Grand Manan during 1977-80, returned up to 31 September, 1981. Only lobsters moving ≥50 km are included (After Campbell and Stasko, in preparation).

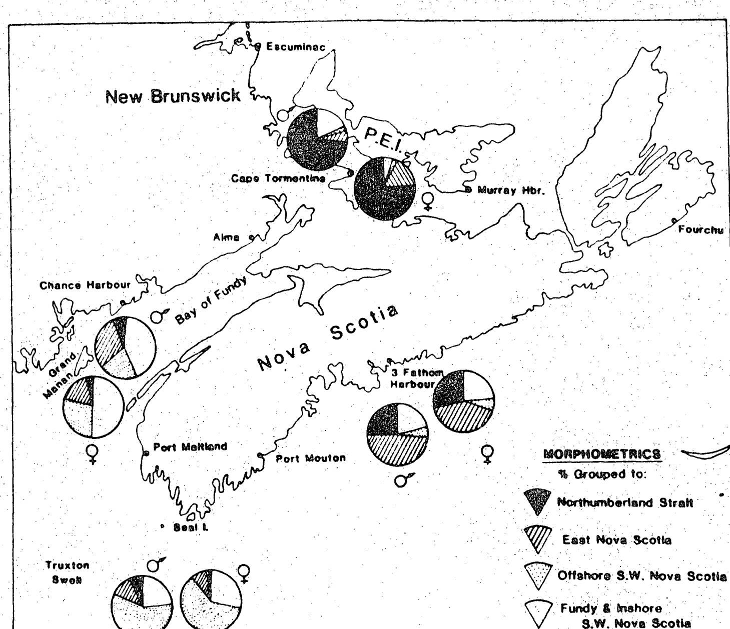


Fig. 9. Map of Canadian Maritimes showing general locations (ports) where lobsters were sampled for morphological measurements. Circles with shading indicate the percentage of individuals (males and females) from each area which were grouped to the four areas, using a posteriori classification derived from the canonical discriminant functions.

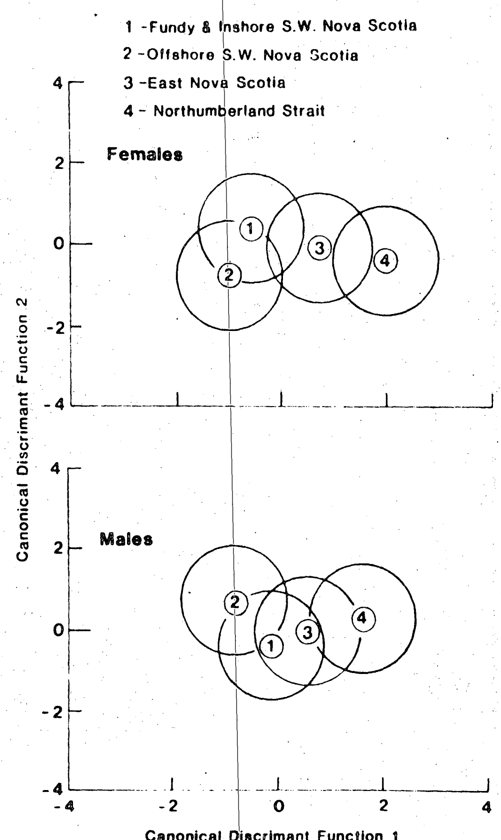


Fig. 10. Discriminant function scatterplots showing only centroids with 1 standard deviation based on morphometrics of male and female lobsters from (1) Bay of Fundy and inshore SW Nova Scotia, (2) offshore SW Nova Scotia, (3) East Coast of Nova Scotia, and (4) Northumberland Strait. Individual points not included because of their large number making graphs appear unclear and a mess (confused).

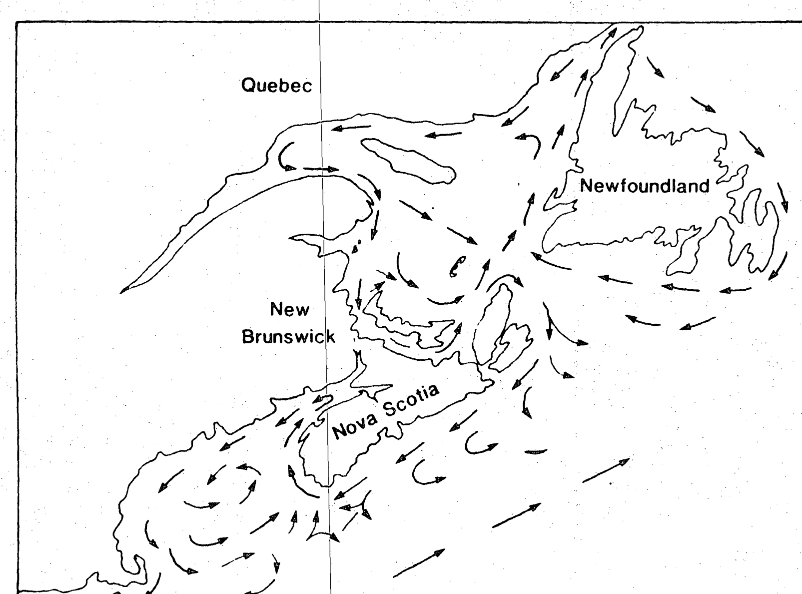


Fig. 11. Surface residual currents for Gulf of Maine and Gulf of St. Lawrence, during summer and fall, estimated from drift bottle data (after Bumpus and Lauzier 1965 and Trites 1982).