SEASONAL PATTERNS OF DIVERSITY IN MARINE FISH COMMUNITIES

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AUGUSTINE JAPIENI MUNGKAJE

SEASONAL PATTERNS OF DIVERSITY IN MARINE FISH COMMUNITIES

BY

© AUGUSTINE JAPIENI MUNGKAJE, B.Sc.(Hons.)

A thesis submitted to the School of Graduate Studies in partial fulfilment of the requirements for the degree of Master of Science

Department of Biology
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ABSTRACT

This study used exploratory analysis to discover and describe seasonal patterns of diversity in marine fish communities. Many small-scale studies have shown that seasonal patterns of diversity do exist in fish communities; there have been no comparisions to investigate large-scale patterns.

The specific objectives of this comparative study were to: (i) use published data sets to discover seasonal patterns of diversity in marine fish communities; (ii) describe these seasonal patterns; (iii) separate general seasonal patterns from specific ones; (iv) develop further testable hypotheses about the possible causes and mechanisms of these patterns of diversity; and (v) discuss these seasonal patterns and any relationships among richness, heterogeneity and equitability components of diversity in order to enable researchers in applied fields such as fisheries management and marine pollution, where diversity statistics are often used, to design and execute more sensitive tests.

Published fish catch data sets were compiled and analysed for seasonal patterns in the diversity indices S, H' and E which measure richness, heterogeneity and equitability, respectively. Three principal patterns were observed.

A broad geographical pattern was that two major seasonal peaks in the three indices occurred in fish communities from

higher latitudes (> 41°10'N) while two to three such peaks were frequent at lower latitudes (≤ 41°10'N) in the North American East Coast. The time of occurrence of the first peaks in H' and E showed a latitudinal trend in this region; the first peaks in H' and E occurred earlier at lower latitudes than at higher latitudes.

Two major patterns of seasonal tracking in S, H' and E observed were an `in-phase' (peaks in species number coincide with peaks in H' and E) and an `out-of-phase' pattern (peaks do not coincide). The `in-phase' pattern was more prevalent than the `out-of-phase' pattern, which typically results from the influx of large numbers of one or two species. An additional pattern observed was that the means of S and H' within studies were higher in data sets with more species while that of E was higher in those with fewer species.

Autocorrelation analysis of the temporal resolution of the peaks in the seasonal patterns showed that for all data sets that had `smooth correlograms', the time interval between peaks was longer (≥ five months) at latitudes ≥ 33°37'N than at latitudes < 33°37'N.

Two hypotheses were formulated from these results: (i) "Plankton and Fish Phenology" hypothesis; and (ii) "Instability-Dominance" hypothesis. The potential application of these patterns and hypotheses in fisheries management and marine pollution monitoring are discussed.

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1 INTRODUCTION

Seasonal patterns of diversity in animal communities reflect changes in community structure with time. Temporal variation in community structure results from changes in species composition and their relative abundances in the community over time. In trying to understand the structure of communities and the patterns of change in the structure with time, ecologists have traditionally looked at measures of diversity of communities to try to understand such change in structure. Reviews by Pianka (1966), Peet (1974), and Washington (1984) covered the developments in the concept of diversity and the diversity indices that have been used to measure diversity in communities of organisms. Pielou (1966) described and classified types of biological collections one can get by sampling any community. A key for the classification of the type of collection and which index of diversity is suitable for the collection was also presented. Pielou (1969) and Magurran (1988) provide a good coverage of indices of diversity which are in use and also discuss their relative merits.

Diversity measures have two components; the measure of the variety and richness of communities is one whilst the measure of the relative abundances of the different species in communities is the other. Indices such as the total numbers of species present, S, measures the former while indices such as

the Shannon-Wiener index of diversity H', attempts to measure both (Peet, 1974; Magurran, 1988). Furthermore, indices such as the species evenness index E, which is a ratio of observed diversity H', to the maximum diversity of the community (H_{max}), where $H_{max}=\ln S$ (Peet, 1974), are often used to measure the relative magnitude of the two components of diversity measured, compared to the maximum possible (Magurran, 1988). That is, E measures the relative abundance of each species in the community; an evenness value of 1.0 means all species are equally abundant. For the purposes of consistency and clarity the terms "richness", "heterogeneity", and "equitability" will be used throughout the text in association with the three diversity indices; S, H' and E respectively. This terminology follows that of Peet (1974).

Seasonal patterns of diversity in marine fish communities are the primary interest of this thesis. If seasonal patterns of variation in diversity can be discerned, then these should be useful for purposes of predicting changes in community structure. If seasonal patterns of diversity can be predicted, this should be useful for applied purposes such as fisheries management and aquatic ecosystems management. In pollution management studies in aquatic ecosystems, fish data have been used to assess pollution and habitat degradation (Bechtel and Copeland, 1970; McErlean et al., 1973; Haedrich and Haedrich, 1974; Haedrich, 1975; Livingston, 1975; Hilman et al., 1977;

Potter et al., 1986). In such studies, fish diversity statistics are often used to describe seasonal patterns of diversity and community structure.

It is important in environmental management problems such as impact assessment that studies be appropriately designed to solve the specific problem(s) in question. Because natural variations within ecological systems can easily confound with variations incurred by anthropogenic causes, improper designs and irrelevant temporal and spatial scales selected for a study can fail to detect impacts (Green, 1989). Stressing the importance of proper design, Eberhardt and Thomas (1991) stated that unlike controlled experimentation, ecological and environmental research often do not meet the criteria of modern experimental design. In impact assessment studies the sampling design is often planned to accomplish two principal goals (Underwood and Peterson, 1988). The first goal is to formally detect and confirm that a change in the system has occurred. Secondly, the sampling design should allow the assessment of whether the observed change is due to the impact (e.g. pollution) or whether it is due to some other natural processes. To achieve the first goal often requires the execution of pilot studies or the utilization of existing baseline ecological data (Clarke and Green, 1988; Green, 1989). In situations where such baseline data are unavailable or financial resources for pilot studies are limited,

established patterns in community structure can become useful in this respect.

In studying seasonal patterns of diversity and community structure, the choice of what temporal scales to use depends on the nature of the problem being investigated and some knowledge of the biology and ecology of the species concerned. Quarterly and monthly time scales are commonly used in the study of seasonal patterns of diversity and community structure in fish communities. The finer resolutions of seasonal patterns are only adequately shown over monthly intervals. This has been assessed quantitatively for benthic invertebrate and fish data (Livingston, 1987).

The existence of seasonal patterns in diversity in fish communities is evident from various studies. Most of these earlier studies which looked at seasonal patterns in diversity and community structure in fish communities, have been on the east coast of United States (Merriman and Warfel, 1948; McFarland, 1963; Richards, 1963; Dahlberg and Odum, 1970; Tyler, 1971; Oviatt and Nixon, 1973; Haedrich and Haedrich, 1974; Subrahmanyam and Drake, 1975; Hilman et al., 1977; Hoff and Ibara, 1977). Besides studies on the east coast of the United States other studies have been done in California (Allen and Horn, 1975), Mexico (Warburton, 1978), Severn Estuary (U.K.) (Claridge et al., 1986), Sweden (Thorman, 1986), Australia (Quinn, 1980; Rainer, 1984), Kuwait (Wright,

1989), southern Iraq (Al-Daham and Yousif, 1990), and Cape Coast, South Africa (Bennett, 1989).

Published studies have shown considerable seasonal change in diversity. Species richness, which is measured in this study by the index S, has been reported to vary seasonally by several studies. It was generally reported to be low in colder months and high during warmer months (McFarland, 1963; Richards, 1963; Shuntov, 1971; Oviatt and Nixon, 1973; Hoff and Ibara, 1977; Warburton, 1978; Quinn, 1980; Rainer, 1984; Thorman, 1986). Variations do exist in terms of the specific timing of the occurrence of these seasonal highs and lows in species richness but not the general trend of more species in warmer months and a decline in species richness in the colder months. Studies by McFarland (1963) in Texas and Richards (1963) in New York, both showed that the richness component of diversity was low in the winter months and high in the summer months. Species richness was reported to be high in October and low in January in a study in Narragansett Bay (Oviatt and Nixon, 1973). Two more studies from the North American East Coast, also reported species richness to reach a maximum in the summer. These were reported from Florida (Subrahmanyam and Drake, 1975) and Massachusetts (Hoff and Ibara, 1977). This seasonal trend in species richness was also reported from California (Allen and Horn, 1975; Allen, 1982) and Mexico (Warburton, 1978). Further studies which reported this pattern

in areas other than North America were in Sweden (Thorman,1986); northern Australia (Shuntov, 1971; Quinn, 1980; Rainer, 1984); Kuwait (Wright, 1989) southern Iraq (Al-Daham and Yousif, 1990); South Africa (Bennett, 1989). One study reported a reverse seasonal pattern in species richness; species richness was higher in the colder months. This was shown by a study done in Severn Estuary, U.K. (Claridge et al., 1986).

The seasonal pattern of the heterogeneity component of diversity showed that peaks occurred in either warm and cold seasons of the year; usually one or the other occurred in any one study. Maximum values in the heterogeneity component of diversity in warmer months were reported by a number of studies (Oviatt and Nixon, 1973; Subrahmanyam and Drake, 1975; Allen and Horn, 1975; Warburton, 1978; Al-Daham and Yousif, 1990). Other studies reported maximum values in this component of diversity during the colder months (Hoff and Ibara, 1977; Allen, 1982; Claridge et al., 1986).

The equitability component of diversity showed a seasonal pattern similar to that for the heterogeneity component of diversity. That is, maximum values were observed in both warm seasons (Dahlberg and Odum, 1970; Warburton, 1978; Al-Daham and Yousif, 1990) as well as cold seasons of the year (Claridge et al., 1986).

The above studies indicate one pattern to be common. That

is the richness component of diversity reached maximum values in the warmer months. This ranged from March to about October in the northern hemisphere studies (McFarland, 1963; Richards, 1963; Warburton, 1978; Thorman, 1986; Wright, 1989; Al-Daham and Yousif,1990) and from December to March in the southern hemisphere studies (Quinn, 1980; Rainer, 1984; Bennett, 1989). Late spring into early autumn is generally regarded as warm months while late autumn to early spring can be generally regarded as cold months, within an annual cycle. The specific months for these warmer and colder conditions will be different in the two hemispheres hence this difference should be borne in mind when referring to seasonal patterns reported by seasons (i.e spring, summer, autumn and winter). That is the summer in the northern hemisphere is from about June to late early September while in the southern hemisphere this period is winter. Unlike species richness which appeared to show a fairly consistent warm-cold trend, the heterogeneity and equitability components of diversity seemed to show either pattern in different studies. This implies that all three components of diversity can either track each other, or that the heterogeneity and equitability components of diversity can show an opposite seasonal pattern to that of species richness. Whenever the peaks and troughs in the three diversity indices, S, H' and E, closely follow each other, this represents an equitable influx and efflux of species. An equitable influx

occurs when S, H' and E increase together. If S shows a peak while H' and E decrease, this trend represents an inequitable influx and efflux of species due to one or two dominant species. A schematic illustration of the two types of tracking of the three indices is given in Figure A1, Appendix A.

From the above descriptions of seasonal variation in diversity, it is evident that seasonal patterns in diversity do exist in fish communities. Species distributions and compositions, as well as environmental factors which are often found to influence them, vary geographically. Thus, one asks whether one can differentiate between general patterns (those occurring over large geographical scales) and those specific to particular types of fish communities (those occurring over local scales). This question deals with large spatial scales and can only be sufficiently addressed by a comparative approach. If large scale patterns do exist, then this should be useful in applied fields such as impact and pollution assessment as well as fisheries management.

From this review of the literature on studies on seasonal patterns of diversity and community structure of fish communities, it is evident that although numerous small scale or single study investigations on the subject have been published, no major large scale comparative studies have been reported. One recent study used published data sets for fish captures on power station intake screens from twelve sites

throughout England and Wales to study the seasonal patterns of diversity and community structure of inshore fish communities (Henderson, 1989). This study demonstrated both temporal (seasonal) as well as spatial (latitudinal) trends in diversity and community structure. I aim to integrate both local and large scale seasonal patterns of diversity and community structure of fish communities in this study, which if accomplished, will be useful for applied purposes.

The information reviewed above can be summarized as a working hypothesis that seasonal patterns in diversity in marine fish communities exist, and these patterns are regulated by processes influenced by the interaction of a range of biotic and abiotic variables operating in concert. The principal objective of this study is to analyse this hypothesis and propose further testable ones. The study will specifically involve firstly, using published data sets to discover seasonal patterns of diversity in marine fish communities. Any apparent patterns discovered will be described, to allow general seasonal patterns (patterns occurring over large geographical scales) to be separated from ones that are specific to local scales. These described patterns will be used to propose further hypotheses about the processes and mechanisms regulating seasonal patterns of diversity in marine fish communities. Finally, these seasonal patterns, any relationships among the three components of

diversity (richness, heterogeneity, and equitability), and the proposed hypotheses will be used to illustrate examples of how these information can be used by researchers in applied fields that use diversity statistics derived from fish catch data, such as fisheries management and marine pollution, to design and execute more sensitive tests.

To achieve these objectives, two analytical techniques will be used to identify seasonal patterns of diversity. These are: (1) a graphical technique; and (2) the use of statistics (means, variances and autocorrelation coefficients) of the indices S, H' and E. The graphical technique will allow for a visual display of any seasonal patterns as well as any possible trends in these patterns. In the use of sample statistics, the ranks of the means, variances, and the autocorrelation functions of the time series of each index for different data sets will be used. These ranks will be analysed with respect to major explanatory variables such as habitat type, type of gear, and latitude, within geographical regions with similar climatic regimes, to determine whether any relationships exist among the ranks of the different statistics and the explanatory variables.

2 MATERIALS AND METHODS

2.1 Data acquisition

Data used in this study were obtained through published sources. Literature search for relevant publications was done by using computer search methods, searching through the contents of every volume of key journals, and following up relevant references from every appropriate article. The key journals searched were: Marine Biology; Bulletin of Marine Science; Marine Ecology Progress Series; Estuarine Coastal and Shelf Science; Estuaries; Journal of the Marine Biological Association of the United Kingdom; Journal of the Marine Biological Association of India; Environmental Biology of Fishes; Canadian Technical Reports of Fisheries and Aquatic Sciences. Additional journals searched to some extent were: Fishery Bulletin (U.S.); Australian Journal of Marine and Freshwater Research; Canadian Journal of Fisheries and Aquatic Sciences; Journal of Fish Biology.

Throughout the search, the selection criteria for articles were that: (1) the study should involve monthly or fortnightly sampling for six months or more; (2) all data presented should be sampled by a single sampling gear or where more than one gear type is used, data from each type of gear should be separable; (3) taxonomic information should be complete to species level or if species are unidentified, they should be distinguished from other related species and be

consistently recorded by a tentative identification; and (4) the sampling procedures used should be sufficiently and accurately described to allow for the calculation of catch per unit effort (CPUE) statistics. Based on these criteria, a total of 22 data sets were selected for this study.

Data sets were either obtained directly from the publications whenever these were presented or were requested from the authors. From an initial attempt of thirteen requests, only one author responded by sending original data. This poor response resulted in abandoning this method of obtaining data. The twenty-two data sets used in this study were largely compiled from published sources; they are available for use upon request.

2.2 Data processing

All data sets acquired were stored as ASCII files using Memorial University's mainframe (VAX/VMS) computer. The data sets were separated by sampling stations and by type of sampling gear used. These data files were the parent files from which subsequent manipulations and specific analyses were done.

2.3 Data analysis

Data analysis was done with three computer software packages. Graphical analyses were performed with SIGMA PLOT

and MATHCAD. Statistical analyses were performed with MINITAB, which was available on the University's mainframe computer. Two analytical techniques were used in data analysis; the use of graphical analysis was one technique and the use of statistics (means, variances and autocorrelation coefficients) was the other.

Graphical methods are often useful in exploratory data analysis as they display any patterns existing in the data. This enables the researcher to extract visually any possible relationships between the pattern in the data and the variables concerned. It also allows the researcher to decide on appropriate methods of data analysis to use for testing these relationships statistically.

The statistical technique used was the analysis of the autocorrelation coefficients, and the ranks of the means and variances of S, H' and E. These statistics were analysed with respect to a number of explanatory variables. Habitat type, gear type, and latitude within major geographical regions grouped according to similarities in climatic patterns, were the main explanatory variables used. The ranks of means and variances for each index were checked against each of the explanatory variables to uncover any relationships that existed. Similarly, the autocorrelation coefficients of the three indices of diversity were analysed by testing the types of correlograms of different data sets with the explanatory

variables for any relationships.

Several major indices of diversity are available and their descriptions and merits have been discussed in a number of publications (Pielou, 1969; Legendre and Legendre, 1983; Washington, 1984; Magurran, 1988). Statistical properties of these major indices have been compared using data from a copepod community by Heip and Engels (1974). They showed that the Shannon-Wiener index H', was the index that gave a better measure of the diversity of the copepod community in terms of the variability and conformity of values calculated for individual samples and that of all samples pooled. No consensus exists as to which indices are better and which are not (Washington, 1984; Magurran, 1988). Besides this lack of consensus, there are also limitations to the biological interpretations among values of the different diversty indices. This is because many indices are ratios of meaningful biological variables such as species richness and relative abundance, and therefore share information (Poole, 1974). The problem arises when these two types of information about a community are compounded into a single numerical measure (Poole, 1974) as in the Shannon-Wiener index H'. Many such indices are in use today (Washington, 1984; Magurran, 1988). To guard against this problem one must carefully consider the suitability of sampling methods and designs planned for collecting species diversity data from a particular community

(Green, 1979), and select appropriate indices for the samples collected respectively (Pielou, 1966; Poole, 1974).

Despite this limitation, paying critical attention to sampling and statistical aspects of selected indices can give information about the biology of the system studied. This has been shown with data from bird, benthos and plankton communities (Webb, 1974). My reasons for using the above indices are as follows. (1) Species richness that is measured by the index S, is based on the total counts of the number of species in a collection. It is an absolute and fundamental measure of species diversity (Magurran, 1988) since it measures directly the species content of a sample. (2) The Shannon-Wiener index has been widely used in diversity studies in fish communities and so it is used here to enable comparisons of seasonal patterns of this index in this study with previous ones if necessary. (3) The Shannon-Wiener index combines both the number of species present in the sample as well as the apportionment of the number of individuals into the different species (Peet, 1974; Magurran, 1988). (4) A common observation in animal and plant communities is that often most individuals in a community belong to a small number of dominant species while a large number of species are represented by a small number of individuals (Margalef, 1958; Hughes, 1986; Lawton, 1990). This generally means that the number of individuals per species in most animal and plant

communities tend to be a logarithmic function of the rank in abundance of the constituent species of the community. According to information theory (Shannon and Weaver, 1949) the Shannon-Wiener index H', has properties that approximate properties of theoretical models of species distribution such as the log series and log-normal distributions. Therefore, the Shannon-Wiener index is chosen for use in this study. (5) The evenness index E, which measures the equitability component of diversity, is also selected because it is a measure of the ratio of the heterogeneity H' of the sample to the maximum heterogeneity possible if all the species were equally represented (Peet, 1974; Magurran, 1988). Therefore, this index gives us a handle on whether or not the species in the community from which the samples were obtained, are numerically equally represented. (6) Because each of the three indices looks at a different aspect of diversity, they were all used here in order to describe the overall structure of the community.

2.3.1 Calculation of diversity indices

The diversity indices calculated were: the total number of species S, recorded for a station on each sampling date; the Shannon-Wiener index of diversity H'; the species evenness index of diversity E. The formulae for these indices were as follows:

S = total number of species recorded at a site on a sampling date;

$$H' = - \Sigma\ p_i\ \ln\ p_i \qquad \text{(Equation 1)}$$

where p_i = the proportion of the ith species in the sample ($p_i = n_i/N$);
n_i is the total number of individuals of the ith species;
N is the total number of individuals of all species in the sample.

$$E = H'/\ln S \qquad \text{(Equation 2)}$$

where ln S is equal to the maximum diversity (H_{max}) of the community (Peet, 1974).

H' and E were both calculated using the MINITAB statistical package. Computation routines saved as macros (a saved set of executable MINITAB commands) were executed sequentially to obtain each index for each data set.

The sequence of the computations to obtain H' was as follows: (1) the proportion of each species (p_1, p_2,...p_i) for each sampling date was calculated; (2) the natural logarithm (ln) of each p was calculated and stored; (3) the product of the values in (1) and (2) respectively were then computed,

giving a value corresponding to each species for each sampling date in the data set; and (4) summing up the values obtained in (3) for each sampling date finally gave the respective H' values (see equation 1).

To calculate the species evenness values E, for each sampling date, the natural logarithm of the number of species S, for each date was computed. This was then divided into the corresponding value of H' obtained in (4) above, to give the respective evenness value (see equation 2). All values of S, H' and E for each sampling date for each study were then saved for the subsequent analyses of seasonal patterns.

2.3.2 Effect of sampling bias on seasonal patterns

In any sampling programme, regardless of the type of gear used, the catchability of the gear varies for different species as a result of factors such as gear efficiency, distributional patterns of the different species, and their response to the gear (Taylor, 1953; Kenchington, 1980; Byrne et al., 1981; Gulland, 1983). Catchability is conventionally designated as q in the fisheries literature, and is also termed a "catchability coefficient" (Ricker, 1975; Kjelson and Johnson, 1978; Gulland, 1983; Blaber et al., 1990). This coefficient q, in the instance of trawling gear, is defined as the ratio of individuals of a certain species caught by the trawl to the total number of that species in the path of the

trawl (Ricker, 1975; Kjelson and Johnson, 1978). Mathematically, this relationship can be represented by the equation:

$$q = c/n \qquad \text{(Equation 3)}$$

where q = the proportion of individuals of a species in the path of the gear, represented in the catch;
c = the number of individuals of a species in the catch;
n = the total number of individuals of a species in the path of the gear.

This study used catch data obtained from published studies. All data sets used in this study used a single gear type, except one (Allen, 1982), which was collected by multiple gear types. This data set was accepted for use in this study because a common effort was possible to calculate for the different methods used, enabling the standardization of the catch in terms of this common effort. It was important to observe the above criteria in compiling the data sets because the catchability of different gears for different species differ and never have a perfect catchability of q = 1.0 (Taylor, 1953; Kenchington; 1980; Byrne et al., 1981; Gulland, 1983). Therefore, it was important to determine whether keeping any imperfect catchabilities in gear ($q < 1.0$)

for the different species constant, among samples within a study, would give comparable seasonal patterns for H' and E to those discerned under situations of perfect catchability (q = 1.0) for all species. If the two patterns are the same, then one can assume that as long as the sampling design and the sampling programme were constant within a study, the seasonal patterns discerned from the catch data are not biased by differential catchability of species.

To assess the above question, the data set of Macdonald et al. (1984) (see Tables B1 and B2, Appendix B) was arbitrarily chosen to analyse whether imperfect catchability affected the interpretation of the seasonal patterns observed; q = 1.0 would imply that c = n. From the catch (c) in this data set 300 data sets were simulated, each to represent possible total numbers (n) for each species exposed to the gear. In each simulation different values of q were randomly generated for each species in the data set. Within each simulation these values of q were kept constant for each species. This simulation procedure was as follows: (1) MINITAB was used to generate random values between 0.2 and 1.0 for q from a uniform probability distribution for each species in the data set; (2) the catch c, in the original data set for each species was divided by the corresponding q to give a simulated data set which represented the simulated n for each species (see equation 3); (3) H' and E for this simulated data

set were then calculated following the computational sequence for calculating the two indices described in 2.3.1 above; and (4) the values for H' and E were then saved. This routine was repeated 300 times.

The 300 values of H' and E were then graphically analysed. This was done to see if the seasonal pattern of diversity from the original data set differed significantly from that for the 300 data sets simulated with constant randomly generated catchabilities for each species, throughout all sampling dates. To assess the dispersion of the values of both H' and E calculated for each sampling date from the simulated data sets, "Box and Whiskers" plots were done for each index. These were plots of the quartiles of the distribution of the 300 values for each index for each sampling date. The values for H' and E calculated from the original data set were then superimposed on the "Box and Whiskers" plot. This was done to display the variability in the values of each index from the 300 simulated data sets, in relation to the corresponding values of the two indices from the original data set. Values of H' and E of the original data for each sampling date were further compared with the values of the two indices obtained from data from two of the 300 simulations. This was done by comparing the graphs of H' and E calculated from the original data and the values of the two indices calculated from data from two of the three hundred

simulations. The two simulations used for the comparison were arbitrarily chosen. From this comparison, it was determined whether the seasonal pattern of diversity changed when n was varied at each simulation by a new set of random catchabilities for each species.

2.3.3 Approximate randomization test

A randomization test was used to determine whether H' and E calculated from these simulated values of n differed significantly from the values of the two indices calculated from the original catch (c) data. The simulated data sets were obtained by randomly generated catchabilities as described in 2.3.2 above. This procedure is called an "approximate randomization test" (Noreen, 1989). It involves randomly generating samples from a pool of all possible values of a variable which are obtainable by complete permutation and then calculating the required statistic from these samples. In this case n was the variable sampled and H' and E were the required statistics. For each simulated data set obtained from randomly generated catchabilities, H' and E were calculated by executing macros that carried out the computations described in 2.3.1 above. The values of the two indices corresponding to each simulation were saved together. To compute the descriptive statistics for the 300 sets of values for H' and E which were obtained from simulated values of n, it was

necessary to separate each set of values for each index from the 300 files in which they were stored. The 300 files containing H' and E from each simulation were retrieved in batches of fifty files at a time into MINITAB and the values for H' and E were then resaved separately. Fifty files were sorted at a time by repeatedly executing a macro which conveniently did the sorting because randomization methods are often lengthy and time consuming. Repeating this procedure six times resulted in six such files each for H' and E, all with a data matrix of fifty columns (corresponding to fifty simulations of random catchability) x sixteen rows (corresponding to sixteen sampling dates). Finally, these six files for H' and E respectively, were combined to give the final 300 x 16 matrix for each index. The descriptive statistics for the 300 values for each index for each date obtained from the simulated data sets were calculated from these two final matrices. These descriptive statistics were then used to analyse and compare the dispersion of the 300 values of H' and E for the simulated data sets with respect to the values for each index for the original data set.

2.3.4 Analysis of seasonal patterns of diversity from sigma-plot graphs

Graphical analysis for seasonal patterns in S, H' and E was done using SIGMA PLOT. Visual inspection of these graphs

was done to identify major peaks and troughs and to look for general seasonal patterns in the three diversity indices. Those plots of S, H' and E, were all plotted onto a single page, each index with a suitable y-axis and all indices with a common x-axis. Exact dates were plotted, or where such was not possible from the data, Julian dates corresponding to the middle of each month were used. This arrangement of graphs allowed for simultaneous comparisons of seasonal patterns in the three indices.

2.3.5 Visual analysis of sigma-plot graphs

The graphs drawn with SIGMA PLOT were ordered by latitude within four major geographical regions from which the data sets were collected. The four regions were: (1) Europe; (2) North American East Coast; (3) Mediterranean, South Africa, and North American West Coast; and (4) Tropics/Subtropics. Marine biogeographic regions mapped according to the distributional patterns of shore and shallow sea fauna (Hedgpeth, 1957) were used to group the above regions. Hedgpeth's biogeographic regions were based on littoral provinces of the world classified by Ekman (Ekman, 1953 op cit. Hedgpeth, 1957). Those provinces were: Arctic-Antarctic; Boreal-Antiboreal; Warm Temperate; Tropic. They reflected temperature regimes associated with latitude. According to this scheme, the appropriate biogeographic provinces for the

respective regions were: Europe - Boreal; North American East Coast - Arctic, Boreal, Temperate; Mediterranean, South Africa and North American West Coast - Warm Temperate, Boreal/Antiboreal; Tropics/Subtropics - Tropic. Within each region the data sets were ordered latitudinally from north to south and the seasonal patterns of S, H' and E from data sets from the respective regions were inspected for patterns with the various explanatory variables. The main explanatory variables were latitude, habitat type and gear type.

To carry out the analysis, a form was drawn up to record the location of each study, position (latitude/longitude) and months of sampling. By visual inspection each major cycle of increase and decrease in each index, S, H' and E, was identified. Months of highest and lowest values of each index in each major cycle were then recorded on the form. This information on the timing of the peaks and troughs of each index were then plotted. To ensure consistency in the analysis, definitions for `peak' and `trough' were necessary. A `peak' is defined here as the highest point which is approached by a series of progressively increasing data points and departed from it by a series of progressively decreasing points, in a time series plot of any of the three indices. A change within either an overall increasing or decreasing trend by a minimum of one data point was not considered a change in the general trend. A `trough' is defined as the lowest point

between any two adjacent peaks in a time series plot of any of the three indices. Peaks and troughs as defined here are graphically illustrated in Figure A2 (Appendix A). These definitions excluded any peaks and troughs at the start and end of any time series in the analysis because those were often not represented in a complete cycle.

Graphs of all data sets from the three geographical regions were latitudinally ordered and each index was separately plotted. Visual inspections of these plots enabled comparison of major seasonal as well as latitudinal patterns in each index within each of the major geographical areas. Patterns related to possible influence of sampling gear and type of habitat were also explored.

2.3.6 Spline analysis of seasonal patterns in S, H' and E

Spline analysis for the diversity indices S, H' and E, of all data sets were done with the MathCAD software package. This method was also used besides the visual method because it is more quantitative and explicit. That is, different people using the technique would obtain similar results for any data set. On the other hand, the visual method may give slightly different results in this respect, it has the advantage of permitting intelligent judgements about `outliers' in the data, allowing one to appropriately plot seasonal trends in the data. Spline analysis works best when serial data are

collected at equal intervals of time or space. Splines were found to be highly sensitive to serial data collected at unequal intervals. Hence, using both methods serves to cross check the methods of analysis and their results.

The spline analysis involved fitting linear splines between knots. A spline is a line of best-fit through the data points within a pre-determined interval (i.e. the resolution) while a `knot' in a spline plot is an imaginary line perpendicular to the x-axis, the time axis in this case, that marks the point at which splines on either side of it are connected. When adjacent lines are connected at successive knots, an overall line or a curve results; whether this spline is straight or curved depends on the power of the function that describes the relationship between the two variables plotted. Detailed descriptions and examples of spline analysis is given in Wold (1974). Figure A2 (Appendix A) shows plots of both visual and spline analysis with respect to the original data, for the time series for each of the three indices.

The resolution (i.e. the interval between successive knots) in my analysis was pre-determined to span two data points, giving resolutions of: sixty days on average for all data sets collected over monthly intervals; thirty days on average for those collected at variable time intervals that ranged between weekly to monthly intervals; and fifteen days for data sets collected at a weekly time interval or less. The

average resolution in each data set was computed using the formula:

$$R_m = k\, n^{-1}\, (t_i - t_1) \qquad \text{(Equation 4)}$$

where R_m is the resolution at knot m;

k is the number of data points spanned (2);

t_i is time at sampling in Julian days of the ith sample;

t_1 is time at sampling in Julian days of the first sample;

n is the sample size.

Using the above formula: seventeen data sets had a resolution of sixty days on average; four data sets had a resolution of thirty days; and one data set had a resolution of fifteen days, in the spline analysis for each index in the data sets.

The analysis resulted in spline plots at appropriately selected resolutions for each index in each data set. The peaks and troughs were analysed in the same manner as was done in section 2.3.5, according to their respective definitions. For plots of each index of all data sets, the months and corresponding Julian dates for each peak and trough in the time series were tabulated. This data was compared with latitude, habitat type and sampling gear, to determine any relationships in the peaks and troughs with these variables.

2.3.7 Patterns of seasonal tracking of S with H' and E

In order to determine the differences in the type of seasonal patterns of species richness S, the heterogeneity index H' and the equitability index E in different data sets, the major peaks and troughs visible from the original sigma-plot graphs of each index for each data set were used. The peaks and troughs of each index for each data set were examined to display the pattern of tracking of H' and E with respect to the peaks in and troughs in species richness, S. The major pattern(s) of tracking in each data set observed from this analysis were tabulated.

2.3.8 Ranks of variances and means of S, H' and E

Variances and means of the three diversity indices within each of the data sets were analysed by ranking and checking to see whether these statistics were related to any of the variables used in the analysis. Using MINITAB, the variances and the means of S, H' and E of each study were calculated. The means and variances for each index for each data set were then ranked and tabulated separately, resulting in two sets of tables. One set was for the variances of each index while the other was for the means. In each set of tables, the type of habitat for each study; latitude for each study; the total number of species recorded in the data; the type of sampling gear(s) used; the sampling interval; and the duration of

sampling, were recorded. These tables were then used to determine whether the ranks in the variances and means for each index in each data set showed any relationships with any of the variables listed above. For example, was high variance in species number associated with a particular habitat, such as the nearshore?

The variables that appeared to be related on a rank scale to the three indices were then analysed in more detail. Ranks of the variances and means of S, H' and E were also examined in relation to latitude and the total number of species in the data sets, to further describe the pattern with respect to these variables.

2.3.9 Autocorrelation analysis of S, H' and E

Autocorrelation functions measure the correlation of any pair of observations that are k lags apart (Montgomery and Johnson, 1976) in a series of time-oriented observations (Montgomery, 1991), called a time series (Montgomery and Johnson, 1976). The seasonal values of diversity indices analysed in this study is an example of such a series. Autocorrelation coefficients, also called serial correlation coefficients (Poole, 1974), measure the relative strength of association of pairs of observations formed by the original time series sliding by one observation each time beside a copy of itself (Platt and Denman, 1975) until the lag k_{n-1} is

reached. Generally, when observations k lags apart have values of similar magnitudes their autocorrelation coefficients will be close to 1.0, while those with a large value succeeded by a small value results in the coefficient having a value close to -1.0. However, if such observations have very little relationship, the coefficient would be approximately zero (Montgomery and Johnson, 1976).

The formula for the autocorrelation functions according to Legendre and Legendre (1983) is:

$$r_{yy}(k) = S_{yy}(k) / S_{yy}(0) \qquad \text{(Equation 5)}$$

= autocovariance at k / variance at zero lag;

k is the lag ($k_1 \ldots\ldots k_{n-1}$);

$r_{yy}(k)$ is the autocorrelation coefficients at k and ranges between -1 and +1. The signs indicate the direction of the relationship.

Autocorrelation functions for the values of each index in each data set were calculated with the MINITAB statistical package by executing the autocorrelation function command. Autocorrelation coefficients for the first lag and the highest value for each series, for S, H' and E for all data sets, were tabulated. Five explanatory variables which included latitude, habitat type, type of gear used, the resolution of the time

series for each index, and the duration of sampling, were also included in the table. Besides computing autocorrelation coefficients for each lag of each series, MINITAB also plotted correlograms of the computed values.

A correlogram is a plot of the values of the autocorrelation coefficients versus lags in the series (Poole, 1974; Box and Jenkins, 1976; Legendre and Legendre, 1983). When the oscillations in a correlogram rapidly dampens to zero as k increases, this indicates that the oscillations in the indices with time are not occurring in a "regular and periodic" manner (Poole, 1974). If they are sinusoidal this indicates that a regular periodic phenomenon exists (Stephenson, 1978).

Three main patterns in correlograms for S, H' and E were identified. A `sinusoidal pattern' with each successive coefficient being sequentially related both by magnitude and direction, was the first kind. In this pattern, connecting the sequence of coefficients resulted in a sinusoidal curve. The second pattern was one with each successive coefficients being generally of a similar magnitude, and with a constant direction. This pattern resulted in a `uniformly linear pattern' when each coefficient in the sequence was connected. For the purposes of testing for relationships of these two patterns in the correlograms with the five variables listed above, they were classified together as `smooth pattern'.

Thirdly, there was the type with the magnitude and direction of the coefficients being highly variable, giving a `spiky pattern'. That is, a plot of the coefficients in the correlogram appeared as spikes projecting in an irregular manner either in a positive or negative direction in relation to lags plotted on the x-axis.

The correlograms of S, H' and E for each data set were inspected to determine the type of pattern as well as to classify whether the autocorrelation pattern was `smooth' or `spiky'. Subsequently, the appropriate pattern of autocorrelation for each index for each data set was recorded with each of the five explanatory variables. For the purposes of clarity in reporting these results, particularly when not all indices of a data set were classified together under one or the other of the two classes of autocorrelation patterns, the data sets were divided into three categories. The first category was `all indices with smooth correlograms'. This category contained all the data sets in which the correlograms for all three indices had a `smooth pattern'. Secondly, there was the category, `all indices with spiky correlograms'. It contained the data sets whose correlograms for all three indices had a `spiky pattern'. The third one was the `mixed' category; it contained data sets with one or two of the three indices belonging to either the first or second category.

A `smooth correlogram' for any index means that the index

is correlated with a series of previous values. The sinusoidal pattern that is characteristic of `smooth correlograms' indicates that there is strong seasonality in the indices (Stephenson, 1978). `Spiky correlograms' indicate that the values of the index concerned are correlated with few of the previous values. This implies little or no seasonality in the index.

3 RESULTS

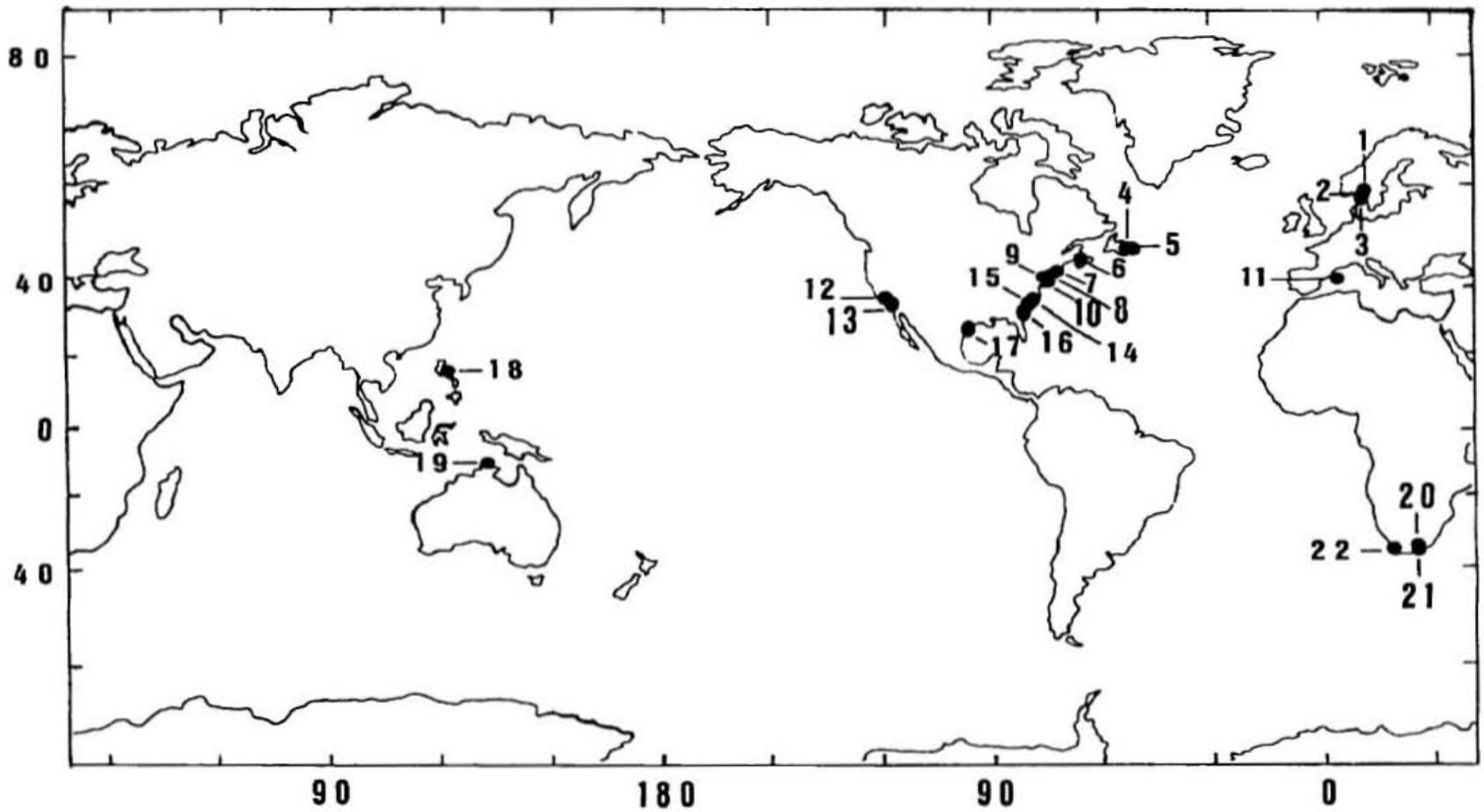
3.1 Data sets compiled for this study

All suitable data sets acquired for this study are listed in Table B1 and Table B2 (Appendix B). The ordering in the two tables is by latitude from north to south. Figure 1 shows the geographical locations of the various studies from which the data sets were compiled. Table B1 (Appendix B) lists the different data sets, their geographical position in terms of latitude and longitude, and the source reference for each study. The type of habitat and the sampling gear(s) used for each study are presented in Table B2 (Appendix B). Most of these studies are from either estuarine or inshore marine habitats, and mostly used seine and trawl gear. The 22 data sets compiled fulfiled all four criteria: monthly or fortnightly samples were collected for a period of six months or more; gear used for collecting data were specified; sampling procedures were accurately described to permit calculation of CPUE; taxonomic information was complete to species level. It is apparent from Figure 1 that the North American East Coast as a single geographical region, is relatively well represented.

3.2 Effect of variation in catchability of gear

The seasonal pattern of diversity from the catch data was found not to be distorted by biases in catchability, as long

Figure 1. Geographical distribution of data sets compiled from the literature for this study. The numbers representing the different data set correspond to the numbers given in Tables B1 and B2 (Appendix B).


80
40
0
40
90
180
90
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22

as the bias was constant within study. The dispersion of 300 values for the Shannon-Wiener index of diversity H', and the species evenness index E, calculated from 300 data sets simulated with randomly generated catchability coefficients q, were plotted in Figure 2 and Figure 3, respectively. All the values for the two indices representing the original data fell within the middle boxes that encompassed 26%-75% of the values in the respective frequency distributions for each 300 simulation for each sampling date. Most of those values for the original data in both figures were very close to the median.

The seasonal pattern for H' and E are shown in Figure 4 and Figure 5, respectively. These figures compare the seasonal pattern for each index calculated from the original data of Macdonald et al. (1984) with those of two of the 300 simulations. From the comparison of the two graphs it was apparent that the seasonal patterns of H' and E in the catch data did not differ from that of the two simulations.

3.3 Visual analysis of graphs of seasonal patterns in S, H' and E

Visual analysis of sigma-plot graphs of the three indices showed general seasonal and latitudinal patterns to exist in fish communities. These seasonal patterns were more apparent for the North American East Coast; a geographical region that

Figure 2. Graph for H' calculated from the original data (Macdonald et al., 1984) (—●—●—) and "Box and Whiskers" plots (⊢□□⊣) representing quartiles for the dispersion of 300 values of H' calculated for each month from data simulated with a constant catchability for each species. The dashed lines (- - - -) indicate no monthly samples being taken.

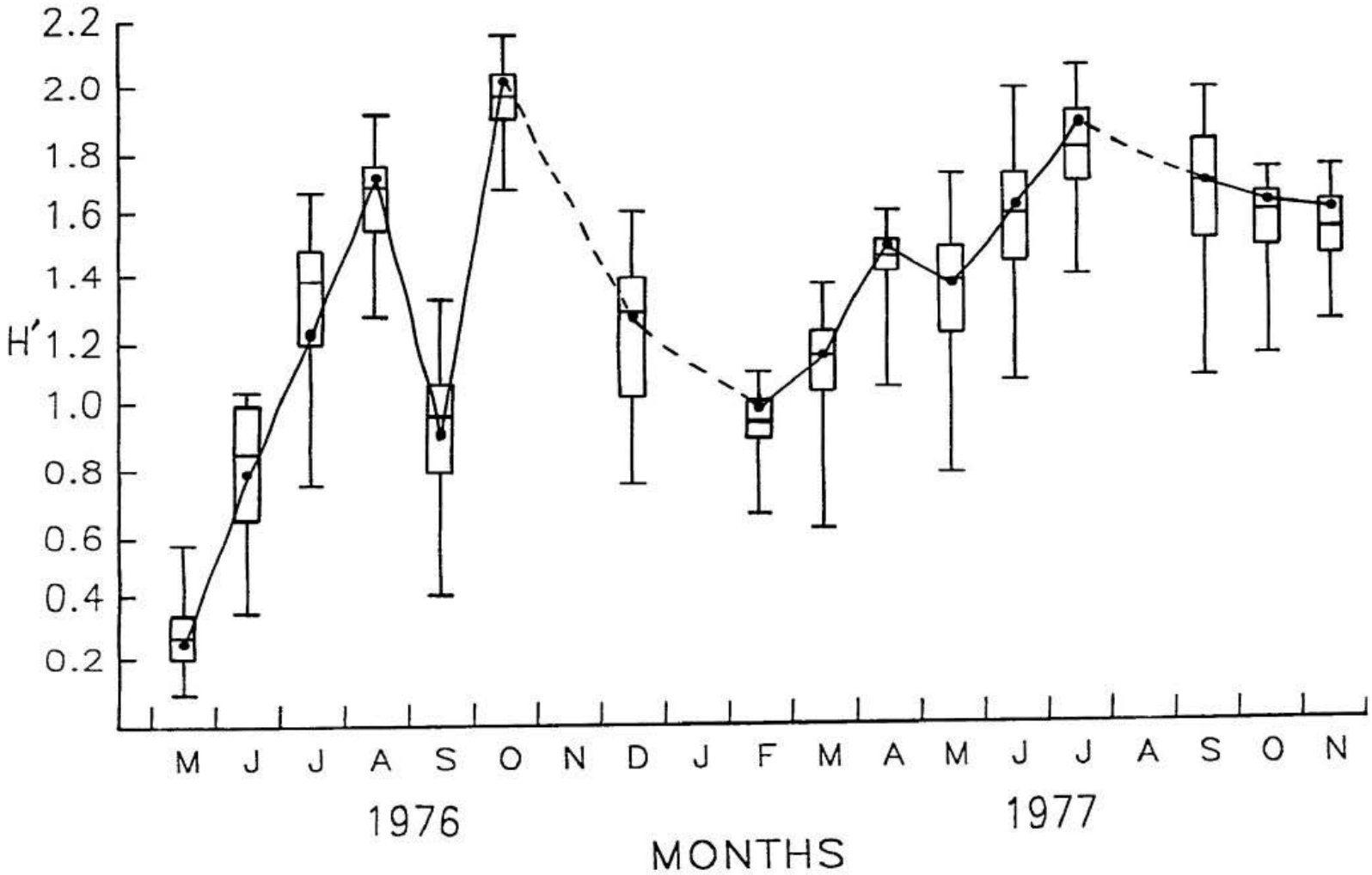

2.2
2.0
1.8
1.6
1.4
H' 1.2
1.0
0.8
0.6
0.4
0.2
M J J A S O N D J F M A M J J A S O N
1976
1977
MONTHS

Figure 3. Graph for E calculated from the original data (Macdonald et al., 1984) (—●—●—) and "Box and Whiskers" plots (|—□□—|) representing quartiles for the dispersion of 300 values of E calculated for each month from data simulated with a constant catchability for each species. The dashed lines (- - - - -) indicate no monthly samples being taken.

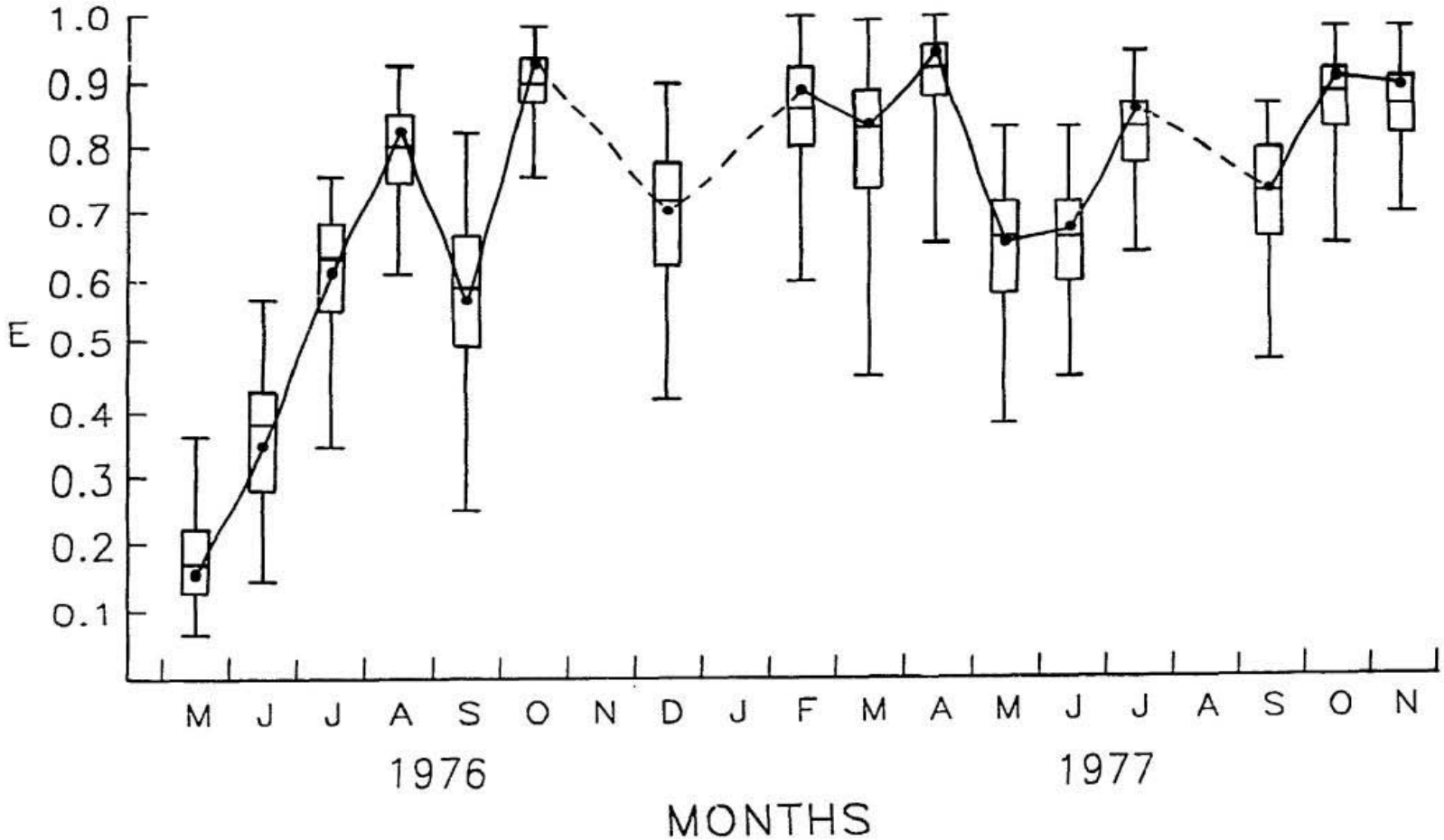

1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
E
M J J A S O N D J F M A M J J A S O N
1976
1977
MONTHS

Figure 4. Seasonal pattern of H' versus time (months) for H' of original data (Macdonald et al., 1984) and for H' of two other of the 300 simulations. The two simulations used for the comparison were arbitrarily chosen; the comparision was done to show that the seasonal pattern of H' from simulated data is comparable to that of the original data.

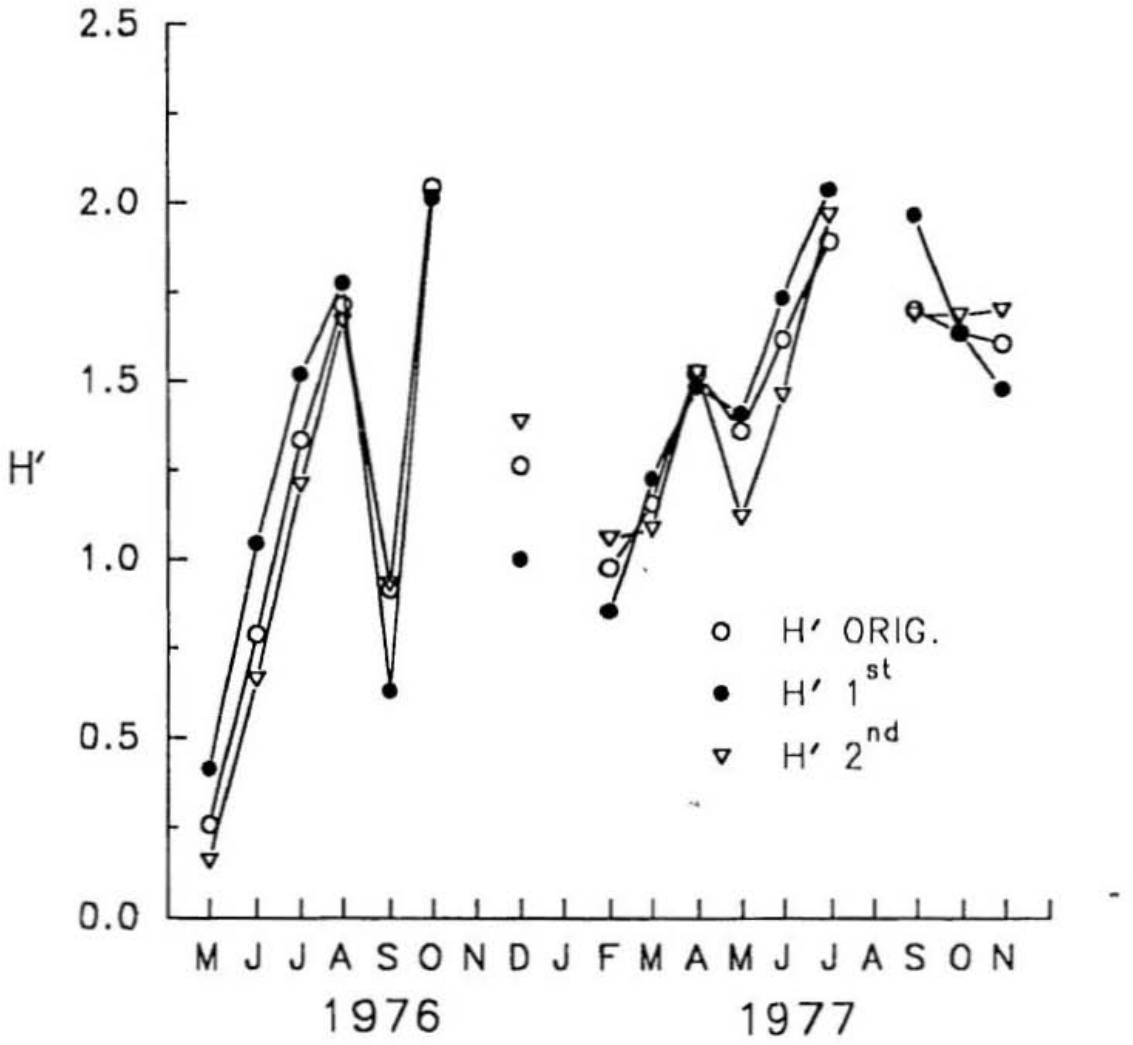
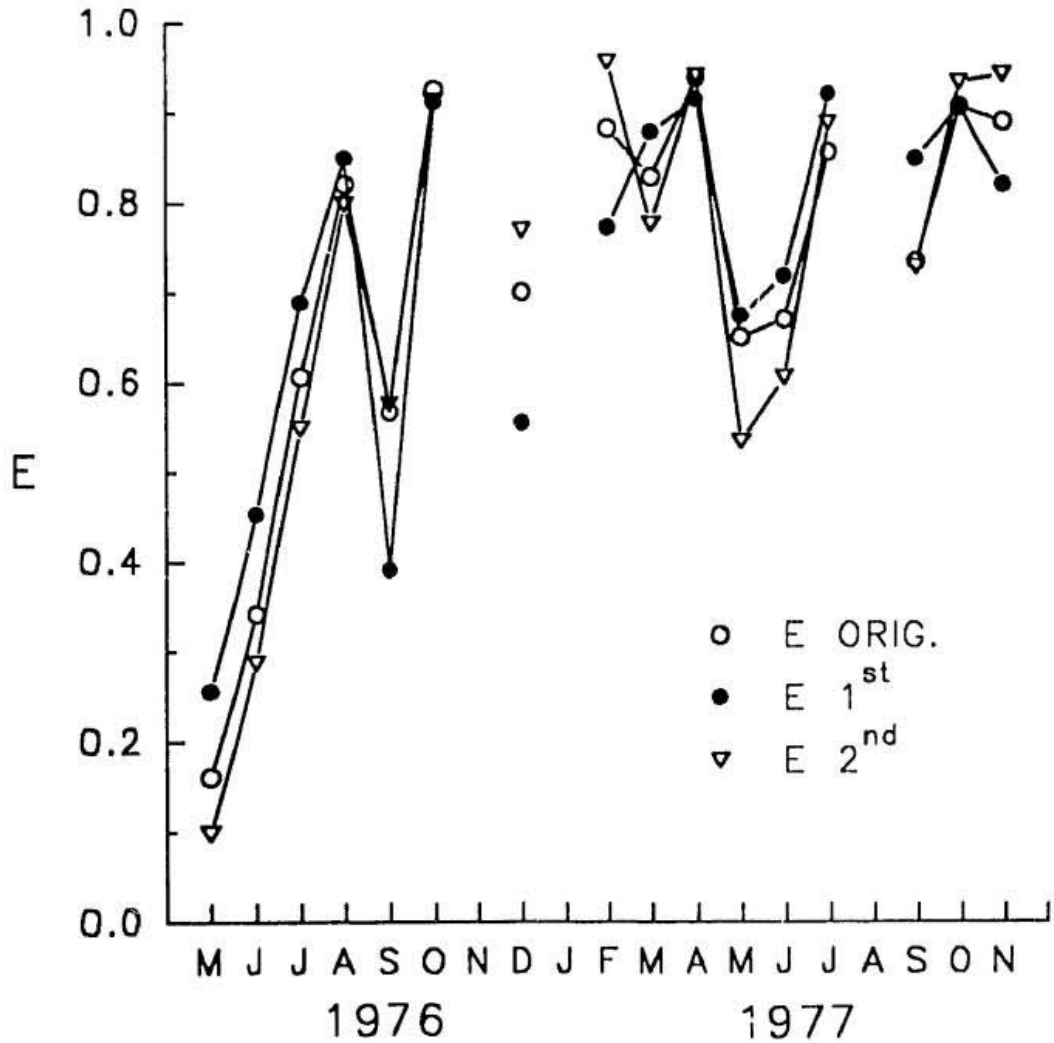

2.5
2.0
1.5
1.0
0.5
0.0
H′
M J J A S O N D J F M A M J J A S O N
1976
1977
H′ ORIG.
H′ 1st
H′ 2nd

Figure 5. Seasonal pattern of E versus time (months) for E of original data (Macdonald et al., 1984) and for E of two other of the 300 simulations. The two simulations used for the comparison were arbitrarily chosen; the comparison was done to show that the seasonal pattern of E from simulated data is comparable to that of the original data.


1.0
0.8
0.6
0.4
0.2
0.0
E
E ORIG.
E 1st
E 2nd
M J J A S O N D J F M A M J J A S O N
1976
1977

is relatively well represented in terms of data sets, in this study. A total of eleven data sets represented this region.

Table 1 and Figure 6 summarize the results of the analysis of the timing and number of peaks in the species richness index S, within an annual cycle. The analysis showed that the richness component of diversity, measured by the index S, showed a single peak within an annual cycle for locations at latitudes between 41°30'N or higher in the North American East Coast region. Those single peaks occurred between late spring and early fall. In Logy Bay, Newfoundland (47°38'N) they occurred between early summer and early fall. Further south, the first peak in S occurred in spring in Passamaquoddy Bay, New Brunswick (45°N) and as one moves south to Slocum River, Massachusetts (41°30'N) the peak occurred in the fall (Figure 6).

Two to three peaks in species richness within an annual cycle was common for sites extending from Block Island Sound, New York (41°15'N) to areas as further south as Mustang Island, Texas (27°45'N). At Block Island Sound, there were three annual peaks in the species richness index S. The first occurred in the middle of summer while the second and third occurred in early and late fall, respectively (Figure 6). Seven data sets comprised this second group. In the two data sets from Long Island Sound, New York (41°10'N) the first annual peak in species richness occurred in the middle of

Table 1. Numbers and Julian dates of major peaks in the index S, determined by visual analysis of sigma-plot graphs. The peaks are classified by latitude and major geographical regions: (1) Europe; (2) North American East Coast; (3) Mediterranean, South Africa, and North American West Coast; (4) Tropics/Subtropics.

Data set	Latitude	Region	Julian day of peak 1	2	3	Total # of peaks
1. Thorman	58°24'N	1	258			1
2. Thorman	58°22'N	1	289			1
3. Thorman	58°19'N	1	289			1
4. Pepper	47°38'N	2	296			1
5. Pepper	47°38'N	2	192			1
6. Macdonald	45°06'N	2	165			1
7. Hoff	41°30'N	2	228			1
8. Merriman	41°15'N	2	225	304	352	3
9. Richards	41°10'N	2	147	289		2
10. Richards	41°10'N	2	147	289		2
11. Cain	33°19'N	2	99	247		2
12. Dahlberg	31°35'N	2	136	289		2
13. Livingston	30°00'N	2	45	258		2

Table 1. Continued.

14. McFarland	27°45'N	2	145	238		2
15. Sebatés	41°-42°N	3	166			1
16. Allen	33°45'N	3	166			1
17. Allen	33°37'N	3	197			1
18. Lasiak	33°56'S	3	105	319		2
19. Lasiak	33°56'S	3	105	289	350	3
20. Bennett	34°08'S	3	350			1
21. Pinto	14°03'N	4	75	228	258	3
22. Davis	12°22'S	4	50	280	355	3

Data set	Latitude	Months of major peaks in S											P
		J	F	M	A	M	J	J	A	S	O	N	D	
Thorman	58°24'N									■				1
Thorman	58°22'N										■			1
Thorman	58°19'N										■			1
Pepper	47°38'N										■			1
Pepper	47°38'N							■						1
Macdonald	45°06'N						■							1
Hoff	41°30'N								■					1
Merriman	41°15'N								■		■		■	3
Richards	41°10'N					■					■			2
Richards	41°10'N					■					■			2
Cain	33°19'N				■					■				2
Dahlberg	31°35'N							■			■			2
Livingston	30°00'N		■							■				2
McFarland	27°45'N					■			■					2
Sebatés	40°-42°N						■							1
Allen	33°45'N						■							1
Allen	33°37'N							■						1
Lasiak	33°56'S				■							■		2
Lasiak	33°56'S				■						■		■	3
Bennett	34°08'S												■	1
Pinto	14°03'N			■					■		■			3
Davis	12°22'S		■								■		■	3

Figure 6. Timing of major peaks in S with latitude by region, determined by visual analysis of sigma-plot graphs. The four regions separated by the horizontal lines are, from top to bottom: Europe; North American East Coast; Mediterranean, South Africa and North American West Coast; and Tropics/Subtropics, respectively. P = Total number of annual peaks.

spring and the second occurred in early fall. Similar peaks for the data set from North Inlet, South Carolina (33°19'N) occurred a little earlier; the first in early spring and the second in late summer. The fifth data set in this second group was from Sapelo Sound and St. Catherine's Sound, Georgia (31°35' N) where the species richness peaked in early summer and again in early fall. In the study from Apalachee Bay, North Florida (30°N) the first of the two annual peaks occurred in late summer and the second occurred in the middle of winter. The last of the seven data sets in this second group was from Mustang Island, Texas (27°45'N). The two annual peaks in species richness occurred in the middle of spring and the middle of summer respectively.

The above descriptions of seasonal and latitudinal patterns of species richness, as indicated by the species richness index S, can be summarised as follows: (1) studies at latitudes greater than and equal to 41°15'N exhibited only one peak in species richness within an annual cycle while between two to three such peaks were apparent for studies from latitudes between 41°15'N and as far south as 27°45'N; (2) the occurrence of the first and second peak in the latter group did not vary in the length of the interval (approximately five months on average) between the two peaks, but did vary in the timing of the occurrence of the peaks (Figure 6). The first peak occurred as late as the middle of spring at Long Island

Sound, New York (41°10'N) and as early as the middle of winter further south at Apalachee Bay, North Florida (30°N). A general conclusion is that the seasonal peaks in species richness occurred earlier at lower latitudes than at higher latitudes within an annual cycle in the North American East Coast geographical region. Another conclusion is that the number of peaks decreased with increasing latitude.

The heterogeneity component of diversity, measured by the index H', varied from one to three peaks within an annual cycle. Two peaks within an annual cycle was the most frequent pattern; it occurred in six out of the eleven data sets from the North American region (Table 2 and Figure 7). Figure 7 showed that the interval (in months) between the peaks was variable and showed no apparent latitudinal trend. However, the occurrence of the first peaks in H' within an annual cycle did show a general latitudinal trend; the first peaks occurred earlier at lower latitudes and later at higher latitudes. That is, the occurrence of the first peak in H' was in late winter in the data set from Texas (27°45'N), with the trend generally progressing over the annual cycle with increasing latitude to early summer and early fall respectively, in the two data sets from Newfoundland (47°38'N) (Table 2 and Figure 7).

The occurrence of peaks in the equitability component of diversity within an annual cycle, as measured by the index E, is shown in Table 3 and Figure 8. The number of peaks within

Table 2. Numbers and Julian dates of major peaks in the index H', determined by visual analysis of sigma-plot graphs. The peaks are classified by latitude and major geographical regions: (1) Europe; (2) North American East Coast; (3) Mediterranean, South Africa, and North American West Coast; (4) Tropics/Subtropics.

Data set	Latitude	Region	Julian day of peak 1	2	3	Total # of peaks
1. Thorman	58°24'N	1	228			1
2. Thorman	58°22'N	1	166			1
3. Thorman	58°19'N	1	166			1
4. Pepper	47°38'N	2	296			1
5. Pepper	47°38'N	2	192			1
6. Macdonald	45°06'N	2	180			1
7. Hoff	41°30'N	2	258	350		2
8. Merriman	41°15'N	2	255	352		2
9. Richards	41°10'N	2	198			1
10. Richards	41°10'N	2	116	275		2
11. Cain	33°19'N	2	99	218		2
12. Dahlberg	31°35'N	2	45	105		2
13. Livingston	30°00'N	2	45	258		2

Table 2. Continued.

14. McFarland	27°45'N	2	69	145	230	3
15. Sebatés	41°-42°N	3	166			1
16. Allen	33°45'N	3	105	166		2
17. Allen	33°37'N	3	136			1
18. Lasiak	33°56'S	3	228			1
19. Lasiak	33°56'S	3	16			1
20. Bennett	34°08'S	3	16	136		2
21. Pinto	14°03'N	4	45	166		2
22. Davis	12°22'S	4	50	309		2

Data set	Latitude	Months of major peaks in H'												P
		J	F	M	A	M	J	J	A	S	O	N	D	
Thorman	58°24'N								▮					1
Thorman	58°22'N						▮							1
Thorman	58°19'N						▮							1
Pepper	47°38'N										▮			1
Pepper	47°38'N							▮						1
Macdonald	45°06'N						▮							1
Hoff	41°30'N									▮			▮	2
Merriman	41°15'N									▮			▮	2
Richards	41°10'N							▮						1
Richards	41°10'N				▮						▮			2
Cain	33°19'N				▮				▮					2
Dahlberg	31°35'N		▮		▮									2
Livingston	30°00'N		▮							▮				2
McFarland	27°45'N			▮		▮			▮					3
Sebatés	40°-42°N						▮							1
Allen	33°45'N				▮		▮							2
Allen	33°37'N					▮								1
Lasiak	33°56'S								▮					1
Lasiak	33°56'S	▮												1
Bennett	34°08'S	▮				▮								2
Pinto	14°03'N		▮					▮						2
Davis	12°22'S		▮									▮		2

Figure 7. Timing of major peaks in H' with latitude by region, determined by visual analysis of sigma-plot graphs. The four regions separated by the horizontal lines are, from top to bottom: Europe; North American East Coast; Mediterranean, South Africa and North American West Coast; and Tropics/Subtropics, respectively. P = Total number annual of peaks.

Table 3. Numbers and Julian dates of major peaks in the index E, determined by visual analysis of sigma-plot graphs. The peaks are classified by latitude and major geographical regions: (1) Europe; (2) North American East Coast; (3) Mediterranean, South Africa, and North American West Coast; (4) Tropics/Subtropics.

Data set	Latitude	Region	Julian day of peak 1	2	3	4	Total # of peaks
1. Thorman	58°24'N	1	228				1
2. Thorman	58°22'N	1	136				1
3. Thorman	58°19'N	1	166				1
4. Pepper	47°38'N	2	256	305			2
5. Pepper	47°38'N	2	129				1
6. Macdonald	45°06'N	2	100	283			2
7. Hoff	41°30'N	2	166	319			2
8. Merriman	41°15'N	2	51	299			2
9. Richards	41°10'N	2	36	198	318		3
10. Richards	41°10'N	2	101	204	303		3
11. Cain	33°19'N	2	99	218			2
12. Dahlberg	31°35'N	2	16	105			2
13. Livingston	30°00'N	2	166	350			2

Table 3. Continued.

14. McFarland	27°45'N	2	31	145	188	230	4
15. Sebatés	41°-42°N	3	136				1
16. Allen	33°45'N	3	44	105			2
17. Allen	33°37'N	3	136				1
18. Lasiak	33°56'S	3	197				1
19. Lasiak	33°56'S	3	16	350			2
20. Bennett	34°08'S	3	16	136			2
21. Pinto	14°03'N	4	45	105	166		3
22. Davis	12°22'S	4	62	309			2

Data set	Latitude	Months of major peaks in E												P
		J	F	M	A	M	J	J	A	S	O	N	D	
Thorman	58°24'N								▮					1
Thorman	58°22'N					▮								1
Thorman	58°19'N							▮						1
Pepper	47°38'N									▮		▮		2
Pepper	47°38'N					▮								1
Macdonald	45°06'N				▮						▮			2
Hoff	41°30'N						▮					▮		2
Merriman	41°15'N		▮								▮			2
Richards	41°10'N		▮					▮			▮			3
Richards	41°10'N				▮			▮						3
Cain	33°19'N								▮					2
Dahlberg	31°35'N		▮		▮									2
Livingston	30°00'N						▮						▮	2
McFarland	27°45'N	▮				▮		▮	▮					4
Sebatés	40°-42°N					▮								1
Allen	33°45'N		▮		▮									2
Allen	33°37'N					▮								1
Lasiak	33°56'S							▮						1
Lasiak	33°56'S		▮										▮	2
Bennett	34°08'S	▮				▮								2
Pinto	14°03'N		▮		▮			▮						3
Davis	12°22'S			▮								▮		2

Figure 8. Timing of major peaks in E with latitude by region, determined by visual analysis of sigma-plot graphs. The four regions separated by the horizontal lines are, from top to bottom: Europe; North American East Coast; Mediterranean, South Africa and North American West Coast; and Tropics/Subtropics, respectively. P = Total number of annual peaks.

an annual cycle ranged from one to four. As in H', two peaks within an annual cycle was the most common pattern. That is, of the eleven data sets from the North American East Coast region: two peaks within an annual cycle were observed in seven data sets; one peak in one data set; three peaks in two data sets; and four peaks in one data set. Unlike S and H', E did not show any apparent latitudinal trends in the seasonal patterns of the occurrence of peaks within an annual cycle (Figure 8). The same information in each index (date of occurrence of peaks and number of peaks within an annual cycle) tested for patterns with habitat type (Tables 4, 5 and 6) and type of gear (Tables 7, 8 and 9) showed no apparent pattern.

3.4 Spline analysis of seasonal patterns in S, H' and E

The timing and number of annual peaks in species richness S, as measured by spline analysis, showed a general latitudinal trend in the North American East Coast region. The occurrence of first peaks was earlier at lower latitudes than at higher latitudes. This trend was not progressive with latitude within each latitudinal division. Generally, the first peaks occurred earlier (between January and May) at lower latitudes (27°N to 41°10'N) while at higher latitudes (> 41°10'N), the peaks occurred later (between June and September) (Figure 9). Within the higher-latitude division,

Table 4. Numbers and Julian dates of major peaks in the index S, determined by visual analysis of sigma-plot graphs. The peaks are classified by habitat and major geographical regions: (1) Europe; (2) North American East Coast and Europe; (3) Mediterranean, South Africa, and North American West Coast; (4) Tropics/Subtropics.

Data set	Habitat	Region	Julian day of peak 1	2	3	Total # of peaks
1. Thorman	River	1	258			1
2. Pinto	River	4	75	228	258	3
3. Thorman	Estuary	1	289			1
4. Thorman	Estuary	1	289			1
5. Hoff	Estuary	2	228			1
6. Allen	Estuary	3	197			1
7. Cain	Estuary	2	99	247		2
8. Dahlberg	Estuary	2	136	289		2
9. Davis	Estuary	4	50	280	355	3
10. Pepper	Inshore	2	296			1
11. Pepper	Inshore	2	192			1
12. Macdonald	Inshore	2	165			1
13. Merriman	Inshore	2	225	304	352	3

Table 4. Continued.

14. Richards	Inshore	2	147	289		2
15. Richards	Inshore	2	147	289		2
16. Allen	Inshore	3	166			1
17. McFarland	Surf-zone	2	145	283		2
18. Lasiak	Surf-zone	3	105	319		2
19. Lasiak	Surf-zone	3	105	289	350	3
20. Bennett	Surf-zone	3	350			1
21. Livingston	Salt marsh	2	45	258		2
22. Sebatés	Shelf/Pelagic	3	166			1

Table 5. Numbers and Julian dates of major peaks in the index H', determined by visual analysis of sigma-plot graphs. The peaks are classified by habitat and major geographical regions: (1) Europe; (2) North American East Coast; (3) Mediterranean, South Africa, and North American West Coast; (4) Tropics/Subtropics.

			Julian day of peak			Total # of
Data set	Habitat	Region	1	2	3	peaks
1. Thorman	River	1	228			1
2. Pinto	River	4	45	166		2
3. Thorman	Estuary	1	166			1
4. Thorman	Estuary	1	166			1
5. Hoff	Estuary	2	258	350		2
6. Allen	Estuary	3	136			1
7. Cain	Estuary	2	99	218		2
8. Dahlberg	Estuary	2	45	105		2
9. Davis	Estuary	4	50	309		2
10. Pepper	Inshore	2	296			1
11. Pepper	Inshore	2	192			1
12. Macdonald	Inshore	2	180			1
13. Merriman	Inshore	2	225	352		2

Table 5. Continued.

14.	Richards	Inshore	2	198			1
15.	Richards	Inshore	2	166	275		2
16.	Allen	Inshore	3	105	166		2
17.	McFarland	Surf-zone	2	69	145	230	3
18.	Lasiak	Surf-zone	3	228			1
19.	Lasiak	Surf-zone	3	16			1
20.	Bennett	Surf-zone	3	16	136		2
21.	Livingston	Salt marsh	2	45	258		2
22.	Sebatés	Shelf/Pelagic	3	166			1

Table 6. Numbers and Julian dates of major peaks in the index E, determined by visual analysis of sigma-plot graphs. The peaks are classified by habitat and major geographical regions: (1) Europe; (2) North American East Coast and Europe; (3) Mediterranean, South Africa, and North American West Coast; (4) Tropics/Subtropics.

Data set	Habitat	Region	Julian day of peak 1	2	3	4	Total # of peaks
1. Thorman	River	1	228				1
2. Pinto	River	4	45	105	166		3
3. Thorman	Estuary	1	136				1
4. Thorman	Estuary	1	166				1
5. Hoff	Estuary	2	166	319			2
6. Allen	Estuary	3	136				1
7. Cain	Estuary	2	99	218			2
8. Dahlberg	Estuary	2	16	105			2
9. Davis	Estuary	4	62	309			2
10. Pepper	Inshore	2	256	305			2
11. Pepper	Inshore	2	129				1
12. Macdonald	Inshore	2	100	283			2
13. Merriman	Inshore	2	51	299			2

Table 6. Continued.

14. Richards	Inshore	2	36	198	318		3
15. Richards	Inshore	2	101	204	303		3
16. Allen	Inshore	3	44	105			2
17. McFarland	Surf-zone	2	31	145	188	230	4
18. Lasiak	Surf-zone	3	197				1
19. Lasiak	Surf-zone	3	16	350			2
20. Bennett	Surf-zone	3	16	136			2
21. Livingston	Salt marsh	2	166	350			2
22. Sebatés	Shelf/Pelagic	3	136				1

Table 7. Numbers and Julian dates of major peaks in the index S, determined by visual analysis of sigma-plot graphs. The peaks are classified by gear type and major geographical regions: (1) Europe; (2) North American East Coast; (3) Mediterranean, South Africa, and North American West Coast; (4) Tropics/Subtropics.

Data set	Gear	Region	Julian day of peak			Total # of peaks
			1	2	3	
1. Merriman	Trawl	2	225	304	352	3
2. Richards	Trawl	2	147	289		2
3. Richards	Trawl	2	147	289		2
4. Dahlberg	Trawl	2	136	289		2
5. Pinto	Trawl	4	75	228	258	3
6. Macdonald	Seine	2	165			1
7. Hoff	Seine	2	228			1
8. Allen	Seine	3	166			1
9. Allen	`Mixture'*	3	197			1
10. McFarland	Seine	2	145	238		2
11. Lasiak	Seine	3	105	319		2
12. Lasiak	Seine	3	105	289	350	3
13. Bennett	Seine	3	350			1

Table 7. Continued.

14.	Thorman	Drop net	1	258			1
15.	Thorman	Drop net	1	289			1
16.	Thorman	Drop net	1	289			1
17.	Davis	Flood trap	4	50	280	355	3
18.	Sebatés	Bongo net	3	166			1
19.	Pepper	Scuba census	2	296			1
20.	Pepper	Scuba census	2	192			1
21.	Cain	Poison	2	99	247		2
22.	Livingston	Poison	2	45	258		2

* A mixture of sampling gears with known effort were used. The gears included a Bag seine, Seine, Drop net and Enclosure net.

Table 8. Numbers and Julian dates of major peaks in the index H', determined by visual analysis of sigma-plot graphs. The peaks are classified by gear type and major geographical regions: (1) Europe; (2) North American East Coast; (3) Mediterranean, South Africa, and North American West Coast; (4) Tropics/Subtropics.

Data set	Gear	Region	Julian day of peak 1	2	3	Total # of peaks
1. Merriman	Trawl	2	225	352		2
2. Richards	Trawl	2	198			1
3. Richards	Trawl	2	116	275		2
4. Dahlberg	Trawl	2	45	105		2
5. Pinto	Trawl	4	45	166		2
6. Macdonald	Seine	2	180			1
7. Hoff	Seine	2	258	350		2
8. Allen	Seine	3	105	166		2
9. Allen	'Mixture'*	3	136			1
10. McFarland	Seine	2	69	145	230	3
11. Lasiak	Seine	3	228			1
12. Lasiak	Seine	3	16			1
13. Bennett	Seine	3	16	136		2

Table 8. Continued.

14. Thorman	Drop net	1	228		1
15. Thorman	Drop net	1	166		1
16. Thorman	Drop net	1	166		1
17. Davis	Flood trap	4	50	309	2
18. Sebatés	Bongo net	3	166		1
19. Pepper	Scuba census	2	296		1
20. Pepper	Scuba census	2	192		1
21. Cain	Poison	2	99	218	2
22. Livingston	Poison	2	45	258	2

* A mixture of sampling gears with known effort were used The gears included a Bag seine, Seine, Drop net and Enclosure net.

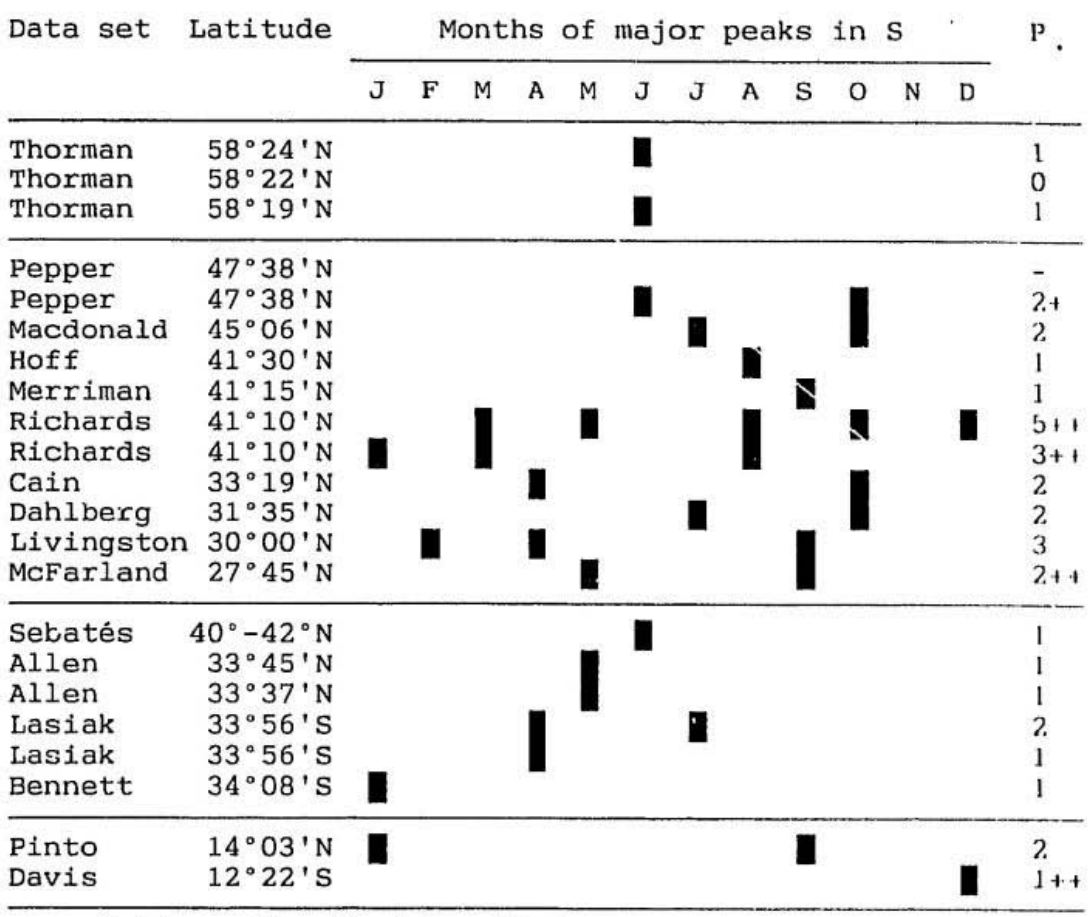
Table 9. Numbers and Julian dates of major peaks in the index E, determined by visual analysis of sigma-plot graphs. The peaks are classified by gear type and major geographical regions: (1) Europe; (2) North American East Coast; (3) Mediterranean, South Africa, and North American West Coast; (4) Tropics/Subtropics.

			Julian day of peak				Total # of
Data set	Gear	Region	1	2	3	4	peaks
1. Merriman	Trawl	2	51	299			2
2. Richards	Trawl	2	36	198	318		3
3. Richards	Trawl	2	101	204	303		3
4. Dahlberg	Trawl	2	16	105			2
5. Pinto	Trawl	4	45	105	166		3
6. Macdonald	Seine	2	100	283			2
7. Hoff	Seine	2	166	319			2
8. Allen	Seine	3	44	105			2
9. Allen	`Mixture'*	3	136				1
10. McFarland	Seine	2	31	145	188	230	4
11. Lasiak	Seine	3	197				1
12. Lasiak	Seine	3	16	350			2
13. Bennett	Seine	3	16	136			2

Table 9. Continued.

14. Thorman	Drop net	1	228		1
15. Thorman	Drop net	1	136		1
16. Thorman	Drop net	1	166		1
17. Davis	Flood trap	4	62	309	2
18. Sebatés	Bongo net	3	136		1
19. Pepper	Scuba census	2	256	305	2
20. Pepper	Scuba census	2	129		1
21. Cain	Poison	2	99	218	2
22. Livingston	Poison	2	166	350	2

* A mixture of sampling gears with known effort were used. The gears included a Bag seine, Seine, Drop net and Enclosure net.



\+ Splines fitted with a 15 days resolution;
++ Splines fitted with a 30 days resolution;
All others were fitted with a 60 days resolution.

Figure 9. Timing of major peaks in S with latitude by region, determined by spline analysis. The four regions separated by the horizontal lines are, from top to bottom: Europe; North American East Coast; Mediterranean, South Africa and North American West Coast; and Tropics/Subtropics. P = Number of annual peaks.

the first peaks occurred earlier at higher latitudes and later at lower latitudes (Figure 9). This contrasts with the general pattern of earlier peaks at lower latitudes and later peaks at higher latitudes, observed between the two latitudinal divisions. The position of this change in the timing of the occurrence of the first peak in S between the two latitudinal divisions seem to be at about 41°10' N (Figure 9). In addition to differences in the timing of the first annual peaks in the index S, there were generally two or more peaks in the index within an annual cycle at latitudes less than and equal to 41°10'N, while at latitudes greater than 41°10'N there were between one and two peaks within an annual cycle.

The timing of the first peak in heterogeneity H', also appeared to occur earlier at lower latitudes (27°N to 41°15'N) than at higher latitudes (> 41°15'N) in the North American East Coast region (Figure 10). In comparison to the latitude of separation between higher and lower latitudes in S, which is 41°10'N, the latitude of 41°15'N for H' is comparable in this respect. The occurrence of the first peaks ranged between January and April at lower latitudes (27°45'N to 41°15'N) in this region while at the higher latitudes (> 41°15'N) it ranged between July and October (Figure 10). As in the species richness index S, there was a tendency for the data sets from higher latitudes (> 41°15'N) in the North American East Coast region to have up to two peaks within an annual cycle while two

Data set	Latitude	Months of major peaks in H'												P
		J	F	M	A	M	J	J	A	S	O	N	D	
Thorman	58°24'N								▮					1
Thorman	58°22'N						▮							1
Thorman	58°19'N						▮							1
Pepper	47°38'N													-
Pepper	47°38'N							▮			▮			2+
Macdonald	45°06'N							▮		▮				2
Hoff	41°30'N										▮			1
Merriman	41°15'N	▮								▮				2
Richards	41°10'N							▮			▮			2++
Richards	41°10'N			▮				▮			▮		▮	4++
Cain	33°19'N				▮				▮					2
Dahlberg	31°35'N				▮									1
Livingston	30°00'N					▮				▮				2
McFarland	27°45'N	▮			▮		▮		▮			▮		5++
Sebatés	40°-42°N						▮							1
Allen	33°45'N				▮						▮			2
Allen	33°37'N					▮					▮			2
Lasiak	33°56'S	▮			▮				▮				▮	4
Lasiak	33°56'S		▮											1
Bennett	34°08'S	▮												1
Pinto	14°03'N			▮							▮			2
Davis	12°22'S		▮											1++

\+ Splines fitted with a 15 days resolution;
++ Splines fitted with a 30 days resolution;
All others were fitted with a 60 days resolution.

Figure 10. Timing of major peaks in H' with latitude by region, determined by spline analysis. The four regions separated by the horizontal lines are, from top to bottom: Europe; North American East Coast; Mediterranean, South Africa and North American West Coast; and Tropics/Subtropics. P = Number of annual peaks.

or more peaks appeared to occur at lower latitudes (≤ 41°15'N).

The equitability component of diversity measured by the index E also showed a trend similar to S and H', regarding the timing of the occurrence of the first peak (Figure 11). At lower latitudes (≤ 41°15'N) the months of first peaks ranged between January and April. Similar peaks at higher latitudes (> 41°15'N) ranged between March and April (Figure 11). Three annual peaks in the equitability index E was more common in the North American East Coast region.

The latitudinal trend in the time of occurrence of the first peak in all three indices was more obvious than that for the number of major peaks in the three indices, in the North American East Coast region. That is, the first annual peaks in S, H' and E generally occurred earlier at lower latitudes (≤ 41°10'N) than at higher latitudes (> 41°10'N) within an annual cycle (Tables 10, 11 and 12; Figures 9, 10 and 11). This trend in the time of occurrence of the peaks with latitude was more apparent in the heterogeneity H' and equitability E components of diversity but less so in the species richness S component of diversity. This is evident form the regressions of Julian dates of first peaks in each index with latitude (Figures 12, 13 and 14). The coefficients of determination (r^2), which are measures of explained variances in the regressions, were 0.11 ($p = 0.351$), 0.28 ($p = 0.114$), and 0.25 ($p = 0.145$) for S, H'

Data set	Latitude	Months of major peaks in E												P
		J	F	M	A	M	J	J	A	S	O	N	D	
Thorman	58°24'N								■					1
Thorman	58°22'N						■							1
Thorman	58°19'N						■							1
Pepper	47°38'N													-
Pepper	47°38'N			■					■				■	3+
Macdonald	45°06'N				■						■			2
Hoff	41°30'N				■							■		2
Merriman	41°15'N	■		■						■				3
Richards	41°10'N		■		■			■				■		4++
Richards	41°10'N			■					■		■			3++
Cain	33°19'N				■				■					2
Dahlberg	31°35'N				■									1
Livingston	30°00'N	■				■		■						3
McFarland	27°45'N	■			■				■					3++
Sebatés	40°-42°N						■							1
Allen	33°45'N				■						■			2
Allen	33°37'N				■								■	2
Lasiak	33°56'S	■			■		■		■					4
Lasiak	33°56'S		■				■							2
Bennett	34°08'S	■												1
Pinto	14°03'N			■								■		2
Davis	12°22'S		■											1++

\+ Splines fitted with a 15 days resolution;
++ Splines fitted with a 30 days resolution;
All others were fitted with a 60 days resolution.

Figure 11. Timing of major peaks in E with latitude by region, determined by spline analysis. The four regions separated by the horizontal lines are, from top to bottom: Europe; North American East Coast; Mediterranean, South Africa and North American West Coast; and Tropics/Subtropics. P = Number of annual peaks.

Table 10. Number and Julian dates of major peaks in the index S, determined by spline analysis. The peaks are classified by latitude and major geographical regions: (1) Europe; (2) North American East Coast; (3) Mediterranean, South Africa, and North American West Coast; (4) Tropics/Subtropics.

Data set	Latitude	Region	Julian day of peak					Total # of peaks
			1	2	3	4	5	
1. Thorman	58°24'N	1	166					1
2. Thorman	58°22'N	1	0					0
3. Thorman	58°19'N	1	166					1
4. Pepper	47°38'N	2	-					-
5. Pepper	47°38'N	2	206	297				2+
6. Macdonald	45°06'N	2	194	283				2
7. Hoff	41°30'N	2	228					1
8. Merriman	41°15'N	2	255					1
9. Richards	41°10'N	2	81	147	226	289	338	5++
10. Richards	41°10'N	2	18	83	226			3++
11. Cain	33°19'N	2	99	290				2
12. Dahlberg	31°35'N	2	197	289				2
13. Livingston	30°00'N	2	45	105	258			3
14. McFarland	27°45'N	2	145	258				2++

Table 10. Continued.

15. Sebatés	40°-42°N	3	166	1
16. Allen	33°45'N	3	136	1
17. Allen	33°37'N	3	136	1
18. Lasiak	33°56'S	3	105 319	2
19. Lasiak	33°56'S	3	105	1
20. Bennett	34°08'S	3	16	1
21. Pinto	14°03'N	4	16 258	2
22. Davis	12°22'S	4	355	1++

\+ Splines fitted with a resolution of 15 days;
++ Splines fitted with a resolution of 30 days;
All others were fitted with a resolution of 60 days.

Table 11. Number and Julian dates of major peaks in the index H', determined by spline analysis. The peaks are classified by latitude and major geographical regions: (1) Europe; (2) North American East Coast; (3) Mediterranean, South Africa, and North American West Coast; (4) Tropics/Subtropics.

Data set	Latitude	Region	Julian day of peak 1	2	3	4	5	Total # of peaks
1. Thorman	58°24'N	1	228					1
2. Thorman	58°22'N	1	166					1
3. Thorman	58°19'N	1	166					1
4. Pepper	47°38'N	2	-					-
5. Pepper	47°38'N	2	206	297				2+
6. Macdonald	45°06'N	2	194	261				2
7. Hoff	41°30'N	2	289					1
8. Merriman	41°15'N	2	23	253				2
9. Richards	41°10'N	2	164	289				2++
10. Richards	41°10'N	2	81	191	275	338		4++
11. Cain	33°19'N	2	99	218				2
12. Dahlberg	31°35'N	2	105					1
13. Livingston	30°00'N	2	136	258				2
14. McFarland	27°45'N	2	18	118	166	230	319	5++

Table 11. Continued.

15. Sebatés	40°-42°N	3	166	1
16. Allen	33°45'N	3	105 289	2
17. Allen	33°37'N	3	136 289	2
18. Lasiak	33°56'S	3	16 105 228 319	4
19. Lasiak	33°56'S	3	45	1
20. Bennett	34°08'S	3	16	1
21. Pinto	14°03'N	4	75 289	2
22. Davis	12°22'S	4	50	1++

\+ Splines fitted with a resolution of 15 days;
++ Splines fitted with a resolution of 30 days;
All others were fitted with a resolution of 60 days.

Table 12. Number and Julian dates of major peaks in the index E, determined by spline analysis. The peaks are classified by latitude and major geographical regions: (1) Europe; (2) North American East Coast; (3) Mediterranean, South Africa, and North American West Coast; (4) Tropics/Subtropics.

Data set	Latitude	Region	Julian day of peak 1	2	3	4	Total # of peaks
1. Thorman	58°24'N	1	228				1
2. Thorman	58°22'N	1	166				1
3. Thorman	58°19'N	1	166				1
4. Pepper	47°38'N	2	-				-
5. Pepper	47°38'N	2	129	241	341		3+
6. Macdonald	45°06'N	2	100	283			2
7. Hoff	41°30'N	2	105	319			2
8. Merriman	41°15'N	2	23	83	253		3
9. Richards	41°10'N	2	36	116	191	318	4++
10. Richards	41°10'N	2	81	226	303		3++
11. Cain	33°19'N	2	99	218			2
12. Dahlberg	31°35'N	2	105				1
13. Livingston	30°00'N	2	16	136	197		3
14. McFarland	27°45'N	2	13	118	230		3++

Table 12. Continued.

15. Sebatés	40°-42°N	3	166				1
16. Allen	33°45'N	3	105	289			2
17. Allen	33°37'N	3	105	350			2
18. Lasiak	33°56'S	3	16	105	166	228	4
19. Lasiak	33°56'S	3	45	166			2
20. Bennett	34°08'S	3	16				1
21. Pinto	14°03'N	4	75	319			2
22. Davis	12°22'S	4	50				1++

\+ Splines fitted with a resolution of 15 days;
++ Splines fitted with a resolution of 30 days;
All others were fitted with a resolution of 60 days.

Figure 12. Regression of Julian day of first peak in S with latitude. The coefficient of determination (r^2) of the regression is 0.11 ($p=0.351$).

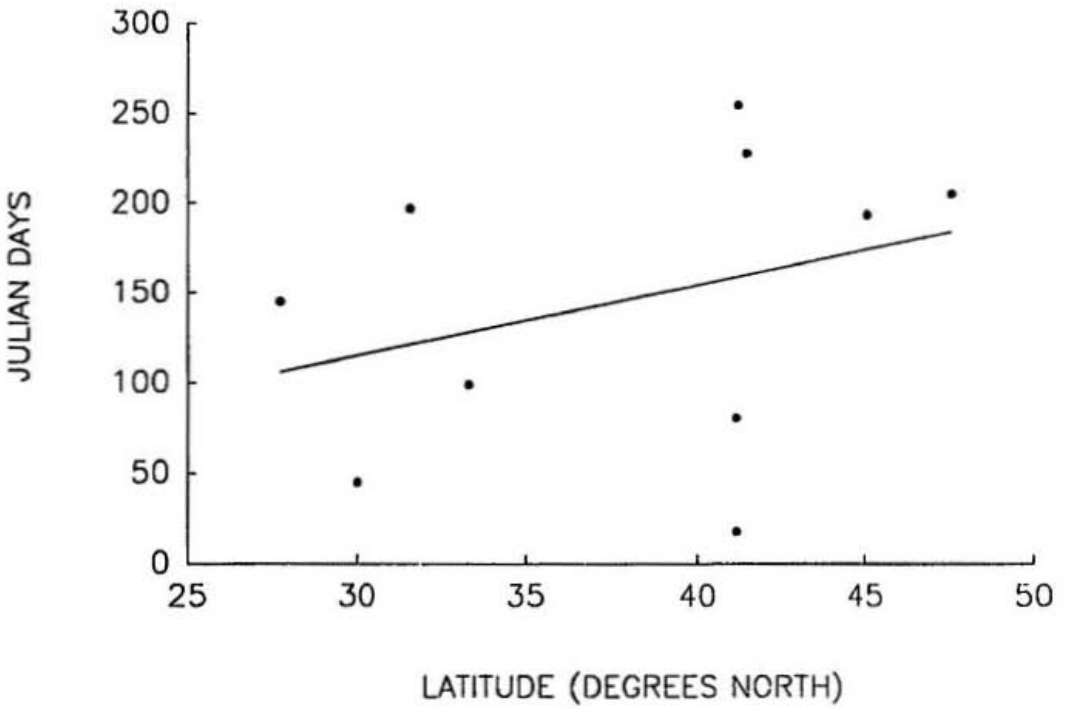

300
250
200
150
100
50
0
JULIAN DAYS
25
30
35
40
45
50
LATITUDE (DEGREES NORTH)

Figure 13. Regression of Julian day of first peak in H' with latitude. The coefficient of determination (r^2) of the regression is 0.28 ($p=0.114$).

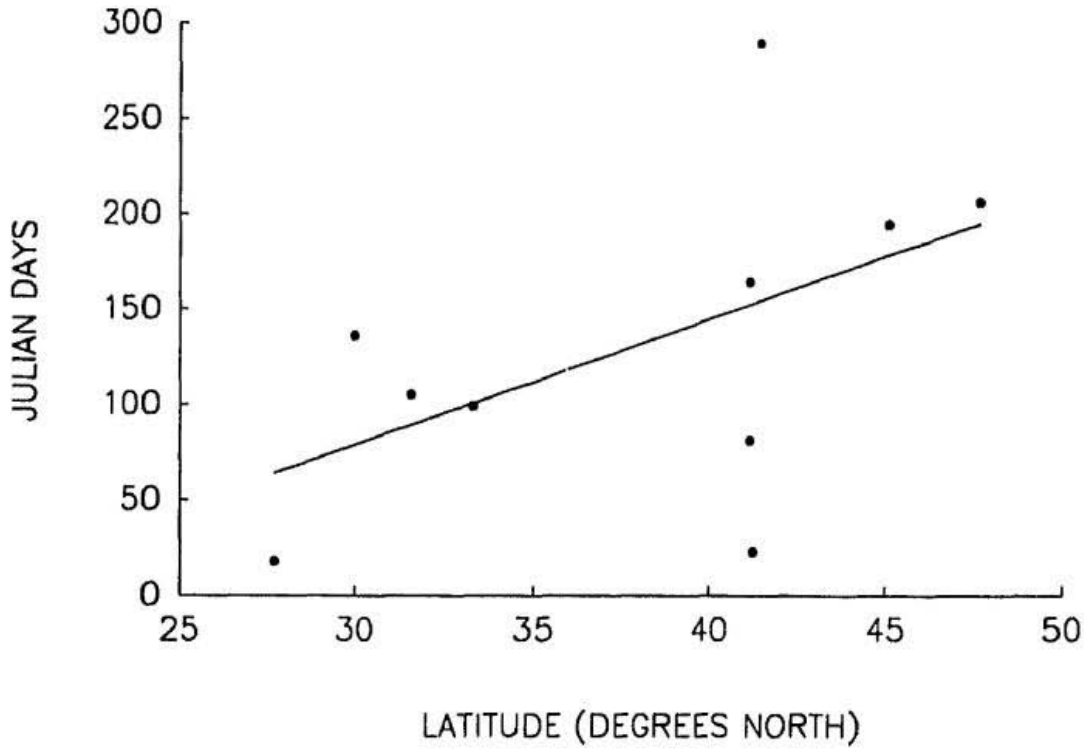
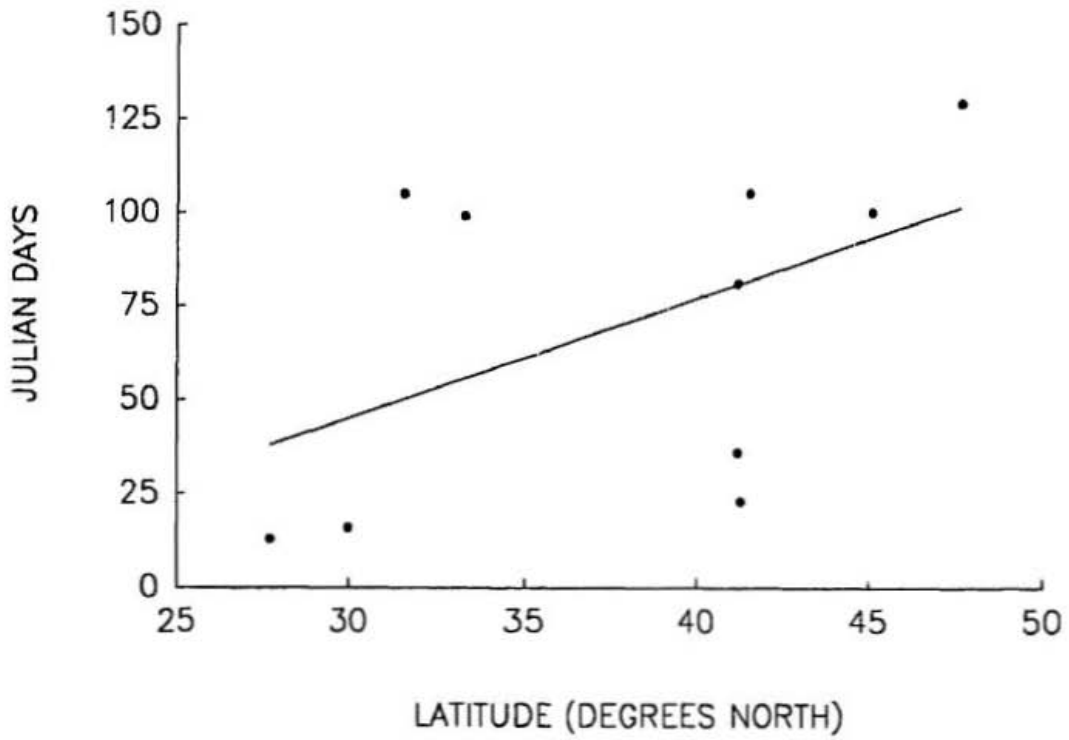

300
250
200
150
100
50
0
JULIAN DAYS
25
30
35
40
45
50
LATITUDE (DEGREES NORTH)

Figure 14. Regression of Julian day of first peak in E with latitude. The coefficient of determination (r^2) of the regression is 0.25 ($p=0.145$).


150
125
100
75
50
25
0
JULIAN DAYS
25
30
35
40
45
50
LATITUDE (DEGREES NORTH)

and E, respectively. Taking into account the fact that the data used for the regressions were from an inevitably limited number of field, not experimental, studies an $\alpha \leq 0.15$ is accepted as significant. A significance criterion of $\alpha \leq 0.15$ was used in this exploratory analysis, in order to reduce Type II error, failure to detect a true pattern. Even if taking $\alpha \leq 0.05$, a conservative level traditionally accepted in hypothesis testing, renders these regressions non-significant, Figures 12, 13 and 14 do indicate a latitudinal trend in the northward progression of the dates of first peaks in S, H' and E.

The slope of the regressions for H' and E were 6.58 and 3.19 days per degree north, respectively. These slopes can be interpreted as the rate of northward progression of the occurrence of first peaks in heterogeneity and equitability in an annual cycle. As evident from the coefficients of determination, only dates of occurrence of first peaks in heterogeneity H' and equitability E showed a trend with latitude but not species richness S. The number of peaks was variable between lower and higher latitudes. On the whole, two annual peaks in species richness S, heterogeneity H' and equitability E commonly occurred at higher latitudes in the North American East Coast region. Two to three peaks were generally noted in the three indices at lower latitudes in this regard.

The position of the latitudinal division for `northern' and `southern' latitudes was lower (41°10'N) for S, while forH' and E it was at 41°15'N. This difference by only 5' is a minor one. However, this latitudinal position does coincide with the approximate latitudinal range (41°N - 42°N) at which the cooler (5°C - 10°C) "boreal" water masses separate from the warmer (10°C - 25°C) "warm temperate" waters (Hedgpeth, 1957; Colton, 1964 op cit. Colton et al., 1979; Backus, 1986); the temperature ranges given for the two water masses are taken from Figure 5 of Hedgpeth (1957). The trend for the number of peaks to be more than two within an annual cycle at lower latitudes was stronger for S and H' than E.

Tables 10, 11, and 12 summarize the timing and number of annual peaks in S, H' and E respectively, which were determined by spline analysis. The timing and number of annual peaks are compared with respect to latitude. Similar summaries for S, H' and E are given for the testing for relationships with habitat (Tables 13, 14, and 15) and type of gear (Tables 16, 17, and 18). The information in Tables 10, 11, and 12 agreed with the patterns described above using Figures 9, 10, and 11. There was no apparent relationship in the timing of seasonal peaks in S, H' and E with habitat type (Tables 13, 14, and 15) or type of gear used (Tables 16, 17, and 18). However, there was a relationship in the two variables with the total number of peaks in an annual cycle for all

Table 13. Number and Julian dates of major peaks in the index S, determined by spline analysis. The peaks are classified by habitat and major geographical regions: (1) Europe; (2) North American East Coast; (3) Mediterranean, South Africa, and North American West Coast; (4) Tropics/Subtropics.

Data set	Habitat	Region	Julian day of peak					Total # of peaks
			1	2	3	4	5	
1. Thorman	River	1	166					1
2. Pinto	River	4	16	258				2
3. Thorman	Estuary	1	0					0
4. Thorman	Estuary	1	166					1
5. Hoff	Estuary	2	228					1
6. Allen	Estuary	3	136					1
7. Cain	Estuary	2	99	290				2
8. Dahlberg	Estuary	2	197	289				2
9. Davis	Estuary	4	355					1++
10. Pepper	Inshore	2	-					-
11. Pepper	Inshore	2	206	297				2+
12. Macdonald	Inshore	2	194	283				2
13. Merriman	Inshore	2	255					1
14. Richards	Inshore	2	81	147	226	289	338	5++

Table 13. Continued.

15. Richards	Inshore	2	18	83	226		3++
16. Allen	Inshore	3	136				1
17. McFarland	Surf-zone	2	145	258			2++
18. Lasiak	Surf-zone	3	105	319			2
19. Lasiak	Surf-zone	3	105				1
20. Bennett	Surf-zone	3	16				1
21. Livingston	Salt marsh	2	45	105	258		3
22. Sebatés	Shelf/Pelagic	3	166				1

\+ Splines fitted with a resolution of 15 days;
++ Splines fitted with a resolution of 30 days;
All others were fitted with a resolution of 60 days.

Table 14. Number and Julian dates of major peaks in the index H', determined by spline analysis. The peaks are classified by habitat and major geographical regions: (1) Europe; (2) North American East Coast; (3) Mediterranean, South Africa, and North American West Coast; (4) Tropics/Subtropics.

Data set	Habitat	Region	Julian day of peak 1	2	3	4	5	Total # of peaks
1. Thorman	River	1	228					1
2. Pinto	River	4	75	289				2
3. Thorman	Estuary	1	166					1
4. Thorman	Estuary	1	166					1
5. Hoff	Estuary	2	228					1
6. Allen	Estuary	3	136	289				1
7. Cain	Estuary	2	99	289				2
8. Dahlberg	Estuary	2	105					1
9. Davis	Estuary	4	50					1++
10. Pepper	Inshore	2	-					-
11. Pepper	Inshore	2	206	297				2+
12. Macdonald	Inshore	2	194	261				2
13. Merriman	Inshore	2	23	253				2
14. Richards	Inshore	2	164	289				2++

Table 14. Continued.

15. Richards	Inshore	2	81	191	275	338		4++
16. Allen	Inshore	3	105	289				2
17. McFarland	Surf-zone	2	18	118	166	230	319	5++
18. Lasiak	Surf-zone	3	16	105	228	319		2
19. Lasiak	Surf-zone	3	45					1
20. Bennett	Surf-zone	3	16					1
21. Livingston	Salt marsh	2	136	258				2
22. Sebatés	Shelf/Pelagic	3	166					1

\+ Splines fitted with a resolution of 15 days;
++ Splines fitted with a resolution of 30 days;
All others were fitted with a resolution of 60 days.

Table 15. Number and Julian dates of major peaks in the index E, determined by spline analysis. The peaks are classified by habitat and major geographical regions: (1) Europe; (2) North American East Coast; (3) Mediterranean, South Africa, and North American West Coast; (4) Tropics/Subtropics.

Data set	Habitat	Region	Julian day of peak 1	2	3	4	Total # of peaks
1. Thorman	River	1	228				1
2. Pinto	River	4	75	319			2
3. Thorman	Estuary	1	166				1
4. Thorman	Estuary	1	166				1
5. Hoff	Estuary	2	105	319			1
6. Allen	Estuary	3	105	350			1
7. Cain	Estuary	2	99	218			2
8. Dahlberg	Estuary	2	105				1
9. Davis	Estuary	4	50				1++
10. Pepper	Inshore	2	-				-
11. Pepper	Inshore	2	129	241	341		3+
12. Macdonald	Inshore	2	100	283			2
13. Merriman	Inshore	2	23	83	253		3

Table 15. Continued.

14. Richards	Inshore	2	36	116	191	318	4++
15. Richards	Inshore	2	81	226	303		3++
16. Allen	Inshore	3	105	289			2
17. McFarland	Surf-zone	2	13	118	230		3++
18. Lasiak	Surf-zone	3	16	105	166	228	4
19. Lasiak	Surf-zone	3	45	166			2
20. Bennett	Surf-zone	3	16				1
21. Livingston	Salt marsh	2	16	136	197		3
22. Sebatés	Shelf/Pelagic	3	166				1

\+ Splines fitted with a resolution of 15 days;
++ Splines fitted with a resolution of 30 days;
All others were fitted with a resolution of 60 days.

Table 16. Number and Julian dates of major peaks in the index S, determined by spline analysis. The peaks are classified by gear type and major geographical regions: (1) Europe; (2) North American East Coast; (3) Mediterranean, South Africa, and North American West Coast; (4) Tropics/Subtropics.

Data set	Gear type	Region	Julian day of peak					Total # of peaks
			1	2	3	4	5	
1. Merriman	Trawl	2	255					1
2. Richards	Trawl	2	81	147	226	289	338	5++
3. Richards	Trawl	2	18	83	226			3++
4. Dahlberg	Trawl	2	197	289				2
5. Pinto	Trawl	4	16	258				2
6. Macdonald	Seine	2	194	283				2
7. Hoff	Seine	2	228					1
8. Allen	Seine	3	136					1
9. Allen	`Mixture'*	3	136					1
10. McFarland	Seine	2	145	258				2++
11. Lasiak	Seine	3	105	319				2
12. Lasiak	Seine	3	105					1
13. Bennett	Seine	3	16					1
14. Thorman	Drop net	1	166					1

Table 16. Continued.

15. Thorman	Drop net	1	0	0
16. Thorman	Drop net	1	166	1
17. Davis	Flood trap	4	355	1++
18. Sebatés	Bongo net	3	166	1
19. Pepper	Scuba census	2	-	-
20. Pepper	Scuba census	2	206 297	2+
21. Cain	Poison	2	99 290	2
22. Livingston	Poison	2	45 105 258	3

\+ Splines fitted with a resolution of 15 days;
++ Splines fitted with a resolution of 30 days;
All others were fitted with a resolution of 60 days.
* A mixture of gears with known effort were used. The gears included a Bag seine, Seine, Drop net, and Enclosure net.

Table 17. Number and Julian dates of major peaks in the index H', determined by spline analysis. The peaks are classified by gear type and major geographical regions: (1) Europe; (2) North American East Coast; (3) Mediterranean, South Africa, and North American West Coast; (4) Tropics/Subtropics.

Data set	Gear type	Region	Julian day of peak					Total # of peaks
			1	2	3	4	5	
1. Merriman	Trawl	2	23	253				2
2. Richards	Trawl	2	164	289				2++
3. Richards	Trawl	2	81	191	275	338		4++
4. Dahlberg	Trawl	2	105					1
5. Pinto	Trawl	4	75	289				2
6. Macdonald	Seine	2	194	261				2
7. Hoff	Seine	2	289					1
8. Allen	Seine	3	105	289				2
9. Allen	'Mixture'*	3	136	289				2
10. McFarland	Seine	2	18	118	166	230	319	5++
11. Lasiak	Seine	3	16	105	228	319		4
12. Lasiak	Seine	3	45					1
13. Bennett	Seine	3	16					1
14. Thorman	Drop net	1	228					1

Table 17. Continued.

15. Thorman	Drop net	1	166		1
16. Thorman	Drop net	1	166		1
17. Davis	Flood trap	4	50		1++
18. Sebatés	Bongo net	3	166		1
19. Pepper	Scuba census	2	-		-
20. Pepper	Scuba census	2	206	297	2+
21. Cain	Poison	2	99	218	2
22. Livingston	Poison	2	136	258	2

\+ Splines fitted with a resolution of 15 days;
++ Splines fitted with a resolution of 30 days;
All others were fitted with a resolution of 60 days.
* A mixture of gears with known effort were used. The gears included a Bag seine, Seine, Drop net, and Enclosure net.

Table 18. Number and Julian dates of major peaks in the index E, determined by spline analysis. The peaks are classified by gear type and major geographical regions: (1) Europe; (2) North American East Coast; (3) Mediterranean, South Africa, and North American West Coast; (4) Tropics/Subtropics.

Data set	Gear type	Region	Julian day of peak 1	2	3	4	Total # of peaks
1. Merriman	Trawl	2	23	83	253		3
2. Richards	Trawl	2	36	116	191	318	4++
3. Richards	Trawl	2	81	226	303		3++
4. Dahlberg	Trawl	2	105				1
5. Pinto	Trawl	4	75	319			2
6. Macdonald	Seine	2	100	283			2
7. Hoff	Seine	2	105	319			2
8. Allen	Seine	3	105	289			2
9. Allen	'Mixture'*	3	105	350			2
10. McFarland	Seine	2	13	118	230		3++
11. Lasiak	Seine	3	16	105	166	228	4
12. Lasiak	Seine	3	45	166			2
13. Bennett	Seine	3	16				1
14. Thorman	Drop net	1	228				1

Table 18. continued.

15. Thorman	Drop net	1	166			1
16. Thorman	Drop net	1	166			1
17. Davis	Flood trap	4	50			1++
18. Sebatés	Bongo net	3	166			1
19. Pepper	Scuba census	2	-			-
20. Pepper	Scuba census	2	129	241	341	3+
21. Cain	Poison	2	99	218		2
22. Livingston	Poison	2	16	136	197	3

\+ Splines fitted with a resolution of 15 days;
++ Splines fitted with a resolution of 30 days;
All others were fitted with a resolution of 60 days.
* A mixture of gears with known effort were used. The gears included a Bag seine, Seine, Drop net, and Enclosure net.

indices. Tables 13, 14, and 15 showed that two or more peaks were more frequent in inshore and surf-zone habitats than in other habitats. Regarding relationships with gear type, there was a similar relationship in the number of peaks with trawling and seining (Tables 16, 17, and 18). That is, there were two or more peaks in the three indices in an annual cycle for data sets collected with trawls and seines but there was no obvious pattern with any of the other gears used.

3.5 Patterns of seasonal tracking of S with H' and E

The analysis of the type of tracking of the seasonal patterns of S, H' and E showed two patterns: an `in-phase' pattern and an `out-of-phase' pattern. The more frequent of the two patterns is the `in-phase' pattern of tracking (Table 19). In this pattern, the major seasonal peaks and troughs in species richness S coincided with corresponding peaks and troughs in the heterogeneity H' and equitability E components of diversity. The second and less frequent pattern was the `out-of-phase' pattern of tracking where the seasonal peaks and troughs in species richness S coincided with opposite patterns (i.e. troughs) in the heterogeneity H', and equitability E components of diversity. This resulted in the seasonal patterns of peaks and troughs in S to be mirror-imaged by the corresponding peaks and troughs in H' and E. Figure A1 (Appendix A) gives a schematic illustration of the

Table 19. Summary of type of seasonal tracking of the heterogeneity H', and the equitability E, components of diversity with respect to species richness S. Two major patterns of this tracking analysed from sigma-plot graphs are 'in-phase' tracking (I.p) and 'out-of-phase' tracking (O.p) (see text and Figure A1). Names of dominant species associated with the major troughs in H' and E in each data set are also listed; names of species for the data sets from North American East Coast are from Scott and Scott (1988).

			Dorminant species	
Data set	I.p	O.p	Family	Scientific name
1. Thorman		X	Gobiidae	Pomatoschistus microps
2. Thorman	X			P. microps
3. Thorman	X			P. microps
4. Pepper	X		Cottidae	Myoxocephalus scorpius
5. Pepper	X		Cyclopteridae	Liparis atlanticus
			Stichaeidae	Stichaeus punctatus
6. Macdonald	X		Gadidae	Pollachus virens
			Gasterosteidae	Gasterosteus aculeatus
7. Hoff	X	X	Atherinidae	Menidia menidia

Table 19. Continued.

8. Merriman	X	X	Pleuronectidae	Pseudopleuronectes americanus
9. Richards	X		Ammodytidae	Ammodytes americanus
			Pleuronectidae	P. americanus
10. Richards	X		Bothidae	Scopthalmus aquosus
			Pleuronectidae	P. americanus
11. Cain	X		Atherinidae	Menidia menidia
12. Dahlberg	X		Sciaenidae	Stellifer lanceolatus
13. Livingston	X		Clupeidae	Brevoortia patronus
14. McFarland	X		Atherinidae	Menidia beryllina
15. Sebatés	X	X	Gonostomatidae	Cyclothone braueri
16. Allen	X		Engraulidae	Anchoa delicatissima
				Engraulis mordax
17. Allen		X	Atherinidae	Atherinops affinis
18. Lasiak	X		Haemulidae	Pomadasys olivaceum
			Sparidae	Sarpa salpa
19. Lasiak		X	Haemulidae	P. olivaceum
20. Bennett		X	Sparidae	Lithognathus mormyrus
			Atherinidae	Atherinia breviceps
21. Pinto		X	Centropomidae	Ambassis kopsi
22. Davis	X		Centropomidae	Ambassis gymnocephalus
			Scatophagidae	Selenotoca multifasciata

two types of tracking.

The dominant species recorded in the original data sets for the dates of major troughs in H' and E were also recorded in this analysis. Generally, most of those dominant species appeared to be species known to occur simultaneously in large numbers or are schooling species (Table 19).

3.6 Variances and means of S, H' and E

Table 20 summarizes whether the ranks in the variances and means of S, H' and E in different data sets showed strong, weak, or no trend, with total number of species in the data sets, latitude, habitat, gear type, and sampling frequency. This summary shows that the ranks in the variances and means of S, H' and E all showed relatively strong trends with the total number of species in the data sets. Trends in the ranks in the variances and means of the three indices with latitude was, by comparison, weaker. This trend with latitude was noticeable within regions, especially the North American East Coast region; it was the latitudinally most well represented region. Habitat, sampling gear, and frequency of sampling did not show any relationships with the ranks in the variances and means of the three indices (Table 20).

The relative strengths of the trends in the ranks of thevariances of the three indices with total number of species and latitude, can be seen from Tables 21, 22 and 23. Similar

Table 20. Summary of strength of trend in the ranks in the variances and means of S, H' and E with five explanatory variables. The relative strength of trend is based on whether or not an obvious trend existed among the ranks of the variances and means of the three indices with the explanatory variables.

	Variance			Mean		
Explanatory variable	S	H'	E	S	H'	E
Total number of species	++	++	++	++	++	++
Latitude	+	+	0	+	+	+
Habitat	0	0	0	0	0	0
Sampling gear	0	0	0	0	0	0
Frequency of sampling	0	0	0	0	0	0

++ Strong trend with variable;
+ Weak trend with variable;
0 No pattern.

Table 21. Ranks of the variances of the index S, of different data sets with total number of species and latitude, in different regions. n is the sample size.

Data set	Variance (n)	# Spp.	Latitude	Region *
1. Hoff	65.6100 (23)	54	41°30'N	2
2. Cain	62.8849 (16)	51	33°19'N	2
3. McFarland	37.2100 (25)	47	27°45'N	2
4. Dahlberg	23.8144 (13)	70	31°35'N	2
5. Livingston	22.6576 (18)	47	30°00'N	2
6. Lasiak	15.3899 (26)	50	33°56'S	3
7. Davis	14.2129 (12)	38	12°22'S	4
8. Merriman	13.6604 (31)	33	41°15'N	2
9. Lasiak	11.5668 (13)	37	33°56'S	3
10. Allen	10.2400 (12)	23	33°45'N	3
11. Thorman	9.3025 (7)	15	58°19'N	1
12. Richards	9.1930 (21)	36	41°10'N	2
13. Allen	7.3984 (13)	32	33°37'N	3
14. Macdonald	5.8516 (16)	23	45°06'N	2
15. Richards	5.8419 (20)	25	41°10'N	2
16. Thorman	5.1438 (7)	13	58°22'N	1
17. Pinto	4.5753 (18)	20	14°03'N	4
18. Bennett	3.7442 (13)	20	34°08'S	3

Table 21. Continued.

19. Sebatés	1.8660 (6)	12	40°-42°N	3
20. Pepper	1.3783 (74)	7	47°38'N	2
21. Pepper	1.2814 (33)	5	47°38'N	2
22. Thorman	1.2388 (7)	7	58°24'N	1

* The geographical regions numerically coded are:
1: Europe;
2: North American East Coast;
3: Mediterranean, South Africa, and North American West Coast;
4: Tropics/Subtropics.

Table 22. Ranks of the variances of the index H', of different data sets with total number of species and latitude, in different regions. n is the sample size.

Data set	Variance (n)	# Spp.	Latitude	Region *
1. Livingston	0.4942 (18)	47	30°00'N	2
2. Hoff	0.4122 (23)	54	41°30'N	2
3. McFarland	0.3919 (25)	47	27°45'N	2
4. Thorman	0.3399 (7)	15	58°19'N	1
5. Cain	0.2959 (16)	51	33°19'N	2
6. Dahlberg	0.2927 (13)	70	31°35'N	2
7. Sebatés	0.2591 (6)	12	40°-42°N	3
8. Lasiak	0.2098 (13)	37	33°56'S	3
9. Macdonald	0.2098 (16)	23	45°06'N	2
10. Pepper	0.2036 (74)	7	47°38'N	2
11. Lasiak	0.1956 (26)	50	33°56'S	3
12. Allen	0.1927 (13)	32	33°37'N	3
13. Pepper	0.1823 (33)	5	47°38'N	2
14. Bennett	0.1739 (13)	20	34°08'S	3
15. Thorman	0.1648 (7)	13	58°22'N	1
16. Pinto	0.1569 (18)	20	14°03'N	4
17. Allen	0.1490 (12)	23	33°45'N	3
18. Davis	0.1421 (12)	38	12°22'S	4

Table 22. Continued.

19. Merriman	0.1359 (31)	33	41°15'N	2
20. Richards	0.0782 (21)	36	41°10'N	2
21. Thorman	0.0439 (7)	7	58°24'N	1
22. Richards	0.0381 (20)	25	41°10'N	2

* The geographical regions numerically coded are:
1: Europe;
2: North American East Coast;
3: Mediterranean, South Africa, and North American West Coast;
4: Tropics/Subtropics.

Table 23. Ranks of the variances of the index E, of different data sets with total number of species and latitude, in different regions. n is the sample size.

Data set	Variance (n)	# Spp.	Latitude	Region *
1. Thorman	0.0718 (7)	15	58°19'N	1
2. Thorman	0.0656 (7)	13	58°22'N	1
3. McFarland	0.0581 (25)	47	27°45'N	2
4. Bennett	0.0510 (13)	20	34°08'S	3
5. Livingston	0.0504 (16)	47	30°00'N	2
6. Macdonald	0.0488 (16)	23	45°06'N	2
7. Sebatés	0.0391 (6)	12	40°-42°N	3
8. Hoff	0.0356 (20)	54	41°30'N	2
9. Allen	0.0325 (13)	32	33°37'N	3
10. Allen	0.0303 (12)	23	33°45'N	3
11. Thorman	0.0296 (7)	7	58°24'N	1
12. Dahlberg	0.0254 (13)	70	31°35'N	2
13. Lasiak	0.0247 (13)	37	33°56'S	3
14. Pinto	0.0239 (18)	20	14°03'N	4
15. Lasiak	0.0223 (26)	50	33°56'S	3
16. Merriman	0.0197 (31)	33	41°15'N	2
17. Pepper	0.0193 (32)	7	47°38'N	2
18. Cain	0.0180 (16)	51	33°19'N	2

Table 23. Continued.

19. Richards	0.0180 (20)	25	41°10'N	2
20. Richards	0.0178 (21)	36	41°10'N	2
21. Davis	0.0171 (12)	38	12°22'N	4
22. Pepper	0.0170 (30)	5	47°38'N	2

* The geographical regions numerically coded are:
1: Europe;
2: North American East Coast;
3: Mediterranean, South Africa, and North American West Coast;
4: Tropics/Subtropics.

strengths in the ranks of the means of S, H' and E with the two variables can be noted from Tables 24, 25 and 26.

The ranks in the variances in S and H' were generally higher in the data sets that recorded greater than thirty species (Tables 21 and 22, respectively). Conversely, the order in the ranks of the variance of E showed an inverse relationship in this respect (Table 23). That is, the data sets with greater than thirty species generally had lower ranks in E. Similar patterns were observed in the ranks in the means of S, H' and E (Tables 24, 25 and 26, respectively) with total number of species recorded in the data sets. That is, the ranks in the means of species richness S, and heterogeneity H', of data sets with greater than thirty species recorded, generally tended to be ranked higher than those with thirty or less number of species recorded. This pattern was again reversed in the equitability index E; the data sets that had greater than thirty species tended to have lower ranks in the means of E.

A relatively weaker trend in the ranks of the variances and means in S, H' and E with latitude was observed. It was difficult to confirm an overall latitudinal trend (i.e. pattern among regions) in this respect. However, latitudinal comparisons within regions, especially the North American East Coast region, showed a pattern weaker than that shown with numbers of species recorded in the data sets. This region is

Table 24. Ranks of the means of the index S, of different data sets with total number of species and latitude, in different regions. n is the sample size.

Data set	Mean (n)	# Spp.	Latitude	Region *
1. Dahlberg	29.1500 (13)	70	31°35'N	2
2. Davis	19.0000 (12)	38	12°22'N	4
3. Cain	17.8800 (16)	51	33°19'N	2
4. Lasiak	14.3080 (13)	37	33°56'S	3
5. Lasiak	14.1150 (26)	50	33°56'S	3
6. Pinto	13.8890 (18)	20	14°03'N	4
7. McFarland	12.6000 (25)	47	27°45'N	2
8. Hoff	12.5200 (23)	54	41°30'N	2
9. Merriman	12.5160 (31)	33	41°15'N	2
10. Allen	11.6920 (13)	32	33°37'N	3
11. Sebatés	10.3330 (6)	12	40°-42°N	3
12. Richards	9.0950 (21)	36	41°10'N	2
13. Livingston	8.9400 (18)	47	30°00'N	2
14. Allen	8.3330 (12)	23	33°45'N	3
15. Thorman	7.4300 (7)	15	58°19'N	1
16. Macdonald	7.1250 (16)	23	45°06'N	2
17. Bennett	7.0770 (13)	20	34°08'S	3
18. Richards	6.9500 (20)	25	41°10'N	2

Table 24. Continued.

19. Thorman	6.1430 (7)	13	58°22'N	1
20. Thorman	4.2860 (7)	7	58°24'N	1
21. Pepper	2.9700 (33)	5	47°38'N	2
22. Pepper	1.7300 (74)	7	47°38'N	2

* The geographical regions numerically coded are:
1: Europe;
2: North American East Coast;
3: Mediterranean, South Africa, and North American West Coast;
4: Tropics/Subtropics.

Table 25. Ranks of the means of the index H', of different data sets with total number of species and latitude, in different regions. n is the sample size.

Data set	Mean (n)	# Spp.	Latitude	Region *
1. Dahlberg	1.9450 (13)	70	31°35'N	2
2. Lasiak	1.8309 (26)	50	33°56'S	3
3. Pinto	1.6917 (18)	20	14°03'N	4
4. Sebatés	1.6390 (6)	12	40°-42°N	3
5. Cain	1.5470 (16)	51	33°19'N	2
6. Merriman	1.3756 (31)	33	41°15'N	2
7. Macdonald	1.3600 (16)	23	45°06'N	2
8. Richards	1.3583 (21)	36	41°10'N	2
9. Livingston	1.3440 (18)	47	30°00'N	2
10. Richards	1.3221 (20)	25	41°10'N	2
11. Hoff	1.3100 (23)	54	41°30'N	2
12. Davis	1.2920 (12)	38	12°22'S	4
13. Thorman	1.2560 (7)	15	58°19'N	1
14. McFarland	1.2450 (25)	47	27°45'N	2
15. Lasiak	1.0650 (13)	37	33°56'S	3
16. Allen	1.0210 (13)	32	33°37'N	3
17. Bennett	0.8550 (13)	20	34°08'S	3
18. Thorman	0.8124 (7)	7	58°24'N	1

Table 25. Continued.

19. Thorman	0.7080 (7)	13	58°22'N	1
20. Allen	0.5800 (12)	23	33°45'N	3
21. Pepper	0.8687 (33)	5	47°38'N	2
22. Pepper	0.3594 (74)	7	47°38'N	2

* The geographical regions numerically coded are:
1: Europe;
2: North American East Coast;
3: Mediterranean, South Africa, and North American West Coast;
4: Tropics/Subtropics.

Table 26. Ranks of the means of the index E, of different data sets with total number of species and latitude, in different regions. n is the sample size.

Data set	Mean (n)	# Spp.	Latitude	Region *
1. Pepper	0.8528 (30)	5	47°38'N	2
2. Pepper	0.8398 (32)	7	47°38'N	2
3. Macdonald	0.7207 (16)	23	45°06'N	2
4. Richards	0.7205 (20)	25	41°10'N	2
5. Lasiak	0.7067 (26)	50	33°56'S	3
6. Sebatés	0.6996 (6)	12	40°-42°N	3
7. Livingston	0.6941 (16)	47	30°00'N	2
8. Richards	0.6545 (21)	36	41°10'N	2
9. Pinto	0.6486 (18)	20	14°03'N	4
10. Thorman	0.6350 (7)	15	58°19'N	1
11. Hoff	0.6091 (20)	54	41°30'N	2
12. Thorman	0.5888 (7)	7	58°24'N	1
13. Dahlberg	0.5790 (13)	70	31°35'N	2
14. Merriman	0.5578 (31)	33	41°15'N	2
15. Cain	0.5436 (16)	51	33°19'N	2
16. McFarland	0.5336 (25)	47	27°45'N	2
17. Bennett	0.4579 (13)	20	34°08'S	3
18. Davis	0.4418 (12)	38	12°22'S	4

Table 26. Continued.

19. Thorman	0.4393 (7)	13	58°22'N	1
20. Allen	0.4249 (13)	32	33°37'N	3
21. Lasiak	0.4015 (13)	37	33°56'S	3
22. Allen	0.2759 (12)	23	33°45'N	3

* The geographical regions numerically coded are:
1: Europe;
2: North American East Coast;
3: Mediterranean, South Africa, and North American West Coast;
4: Tropics/Subtropics.

the only region for which such a comparison can be made because the within-region latitudinal coverage is more complete than the other three regions. There were larger variances and means for S and H' in data sets from lower temperate latitudes (30°N to 42°N) than at higher latitudes (> 42°N) in this region. This can be seen from Table 21 and Table 22 for the variances and Table 24 and Table 25 for the means. However, this latitudinal pattern was less strong in the ranks of the variances and means for the equitability index E. Generally, the variances for E were higher at higher temperate latitudes (> 42°N) than at lower temperate latitudes (Table 23). The means of E from data sets collected at latitudes from 41°N or higher in the North American East Coast region, appeared to be ranked higher (Table 26).

3.7 Autocorrelation analysis of S, H' and E

Ranges in the minimum and maximum values for the degree of autocorrelation (i.e. the magnitude of the regression coefficients), the category of autocorrelation (`spiky', `smooth', and `mixed'), and the number of lags in each series for S, H' and E are summarized in Tables 27, 28 and 29, respectively. The overall ranges, minimum and maximum respectively, for all three indices were: |0.000 to 0.676| for S; |0.000 to 0.734| for H'; |0.000 to 0.535| for E. Of the ranges of the autocorrelation coefficients of each index

Table 27. Summary of autocorrelation analysis for the index S, for the different data sets that were classified according to the category of their respective patterns in the correlograms of all three indices. The horizontal lines separate the three categories from top to bottom: all indices having `smooth correlograms'; all indices having `spiky correlograms'; and a `mixture' of both types of correlograms, respectively.

			Autocorrelation coefficient		
Data set	Latitude	# of lags	Min.	Lag 1	Max.
1. Pepper	47°38'N	18	0.000	0.291	0.319
2. Pepper	47°38'N	33	-0.018	0.391	0.490
3. Hoff	41°30'N	14	0.043	0.669	0.669
4. Cain	33°19'N	14	-0.028	0.676	0.676
5. Dahlberg	31°35'N	7	-0.018	-0.265	0.469
6. Allen	33°45'N	11	0.069	0.611	0.611
7. Allen	33°37'N	12	0.045	0.532	0.532
8. Pinto	14°03'N	14	0.021	0.348	-0.515
9. Thorman	58°24'N	6	-0.027	-0.049	-0.217
10. Thorman	58°22'N	6	0.069	0.069	-0.378

Table 27. Continued.

11. Thorman	58°19'N	6	0.070	0.148	-0.358
12. Macdonald	45°06'N	5	-0.152	-0.305	0.438
13. Richards	41°10'N	14	0.012	0.078	-0.388
14. Richards	41°10'N	14	0.008	0.072	-0.284
15. Lasiak	33°56'S	12	0.048	0.059	-0.337
16. Lasiak	33°56'S	15	-0.002	-0.011	-0.192
17. Davis	12°22'S	11	0.000	-0.564	-0.564
18. Merriman	41°15'N	14	0.033	0.504	0.504
19. Livingston	30°00'N	14	-0.002	0.352	-0.391
20. McFarland	27°45'N	14	-0.015	0.672	0.672
21. Bennett	34°08'S	12	-0.040	0.615	0.615

Table 28. Summary of autocorrelation analysis for the index H', for the different data sets that were classified according to the category of their respective patterns in the correlograms of all three indices. The horizontal lines separate the categories from top to bottom: all indices having `smooth correlograms'; all indices having `spiky correlograms'; a `mixture' of both types of correlograms, respectively.

			Autocorrelation coefficient		
Data set	Latitude	# of lags	Min.	Lag 1	Max.
1. Pepper	47°38'N	18	-0.010	0.236	0.370
2. Pepper	47°38'N	33	0.031	0.232	0.459
3. Hoff	41°30'N	14	0.031	0.479	0.479
4. Cain	33°19'N	14	-0.025	0.734	0.734
5. Dahlberg	31°35'N	7	-0.006	0.449	-0.449
6. Allen	33°45'N	11	-0.027	0.291	-0.358
7. Allen	33°37'N	12	-0.036	0.410	0.410
8. Pinto	14°03'N	14	0.019	0.333	-0.378
9. Thorman	58°24'N	6	-0.063	-0.646	-0.646
10. Thorman	58°22'N	6	0.009	0.009	-0.395

Table 28. Continued.

11. Thorman	58°19'N	6	-0.033	-0.182	-0.567
12. Macdonald	45°06'N	5	0.006	0.006	-0.375
13. Richards	41°10'N	14	-0.004	-0.030	0.230
14. Richards	41°10'N	14	-0.062	0.104	0.277
15. Lasiak	33°56'S	12	0.000	0.287	-0.436
16. Lasiak	33°56'S	15	0.002	-0.384	0.401
17. Davis	12°22'S	11	-0.008	-0.079	0.290
18. Merriman	41°15'N	14	-0.013	0.186	-0.244
19. Livingston	30°00'N	14	0.005	0.209	-0.292
20. McFarland	27°45'N	14	0.015	-0.097	0.365
21. Bennett	34°08'S	12	-0.011	-0.049	0.243

Table 29. Summary of autocorrelation analysis for the index E, for the different data sets that were classified according to the category of their respective patterns in the correlograms of all three indices. The horizontal lines separate the categories from top to bottom: all indices having `smooth correlograms'; all indices having `spiky correlograms'; a `mixture' of both types of correlograms, respectively.

Data set	Latiude	# of lags	Autocorrelation coefficient		
			Min.	Lag 1	Max.
1. Pepper	47°38'N	18	-	-	-
2. Pepper	47°38'N	33	-	-	-
3. Hoff	41°30'N	14	-	-	-
4. Cain	33°19'N	14	-0.010	0.362	-0.365
5. Dahlberg	31°35'N	7	-0.027	0.493	0.493
6. Allen	33°45'N	11	0.032	0.150	-0.435
7. Allen	33°37'N	12	-0.033	0.402	0.402
8. Pinto	14°03'N	14	0.003	0.376	-0.390
9. Thorman	58°24'N	6	-0.036	-0.535	-0.535
10. Thorman	58°22'N	6	0.039	0.215	-0.315

Table 29. Continued.

11. Thorman	58°19'N	6	0.030	-0.195	0.223
12. Macdonald	45°06'N	5	0.043	0.225	-0.355
13. Richards	41°10'N	14	-0.031	-0.283	-0.283
14. Richards	41°10'N	14	0.021	-0.309	-0.407
15. Lasiak	33°56'S	12	0.003	0.295	-0.481
16. Lasiak	33°56'S	15	0.020	-0.302	-0.250
17. Davis	12°22'S	11	0.001	0.033	-0.292
18. Merriman	41°15'N	14	-0.022	0.266	-0.417
19. Livingston	30°00'N	14	-	-	-
20. McFarland	27°45'N	14	0.001	0.065	-0.233
21. Bennett	34°08'S	12	0.018	-0.058	-0.210

given above, it can be noted that the maximum values for S and H' were from the `all indices with smooth correlograms' category (Tables 27 and 28, respectively). The maximum value for E was from the `all indices with spiky correlograms' category (Table 29). Generally, whenever the maximum autocorrelation coefficient for any of the indices in any data set was about 0.4 or greater, the maximum value was often that at lag 1.

Latitude, habitat type, the length of the time series, and the lag for maximum autocorrelation (i.e. the lag with the highest autocorrelation coefficient in the time series), showed a relationship with whether patterns of the correlograms of S, H' and E were `smooth' or `spiky'. There was no relationship with gear type in this respect. Whether the time series for any of the three indices had `smooth' or `spiky' correlograms seemed to show a relationship with the length of the time series (Tables 30 and 31). Seven out of eight data sets in the `all indices with smooth correlograms' category were those that had autocorrelation analysis done on a time series covering a period of one year or greater (Table 30). The data sets in the `all indices with spiky correlograms' category (Table 31) did not show a strong relationship in this respect. Four out of nine data sets were those that had autocorrelation analysis done on a time series covering greater or equal to one year while five out of nine

Table 30. Data sets with `smooth correlograms' in the indices S, H' and E and the explanatory variables: habitat; gear type; length of time series; average lag of series. The data sets are ordered by latitude from north to south within each region. These regions separated by horizontal lines are from top to bottom: North American East Coast; Mediterranean, South Africa and North American West Coast; and Tropics/Subtropics, respectively.

Data set	Habitat	Gear type	Length (Months)	Av. lag (Days)
1. Pepper	Inshore	Scuba census	15	6 +
2. Pepper	Inshore	Scuba census	12	10 +
3. Hoff	Estuary	Seine	23	67 +
4. Cain	Estuary	Poison	12	42
5. Dahlberg	Estuary	Trawl	8	60
6. Allen	Inshore	Seine	12	56
7. Allen	Estuary	Mixed gear ++	13	56
8. Pinto	River	Trawl	18	57

\+ Autocorrelation of E was not done due to breaks in the series.

++ `Mixed' gear: included a Bag seine, Seine, Drop net, and Enclosure net; all gear types with a known effort.

Table 31. Data sets with `spiky correlograms' in the indices S, H' and E and the explanatory variables: habitat; gear type; length of time series; average lag of series. The data sets are ordered by latitude from north to south within each region. These regions separated by horizontal lines are from top to bottom: Europe; North American East Coast; Mediterranean, South Africa, and North American West Coast; Tropics/Subtropics, respectively.

Data set	Habitat	Gear type	Length (Months)	Av. lag (Days)
1. Thorman	River	Drop net	7	53
2. Thorman	Estuary	Drop net	7	53
3. Thorman	Estuary	Drop net	7	53
4. Macdonald	Inshore	Seine	6	70
5. Richards	Inshore	Trawl	13	35
6. Richards	Inshore	Trawl	13	37
7. Lasiak	Surf-zone	Seine	13	56
8. Lasiak	Surf-zone	Seine	26	59
9. Davis	Estuary	Flood trap	6	27

data sets were those covering a time series of less than one year (Table 31). Whether a data set had both types of correlograms among the three indices, where any two indices may have either `smooth' or `spiky' correlograms, seemed to be related to habitat. That is, the data sets in the `mixed' category were data collected either in a surf-zone or an estuarine marsh habitat (Table 32). Two other surf-zone data sets were included in the `all indices with spiky correlograms' category (Table 31).

The lag with the maximum autocorrelation in all data sets with `smooth correlograms' in S, H' and E showed a relationship with latitude (Table 33). Apparently the lags with maximum autocorrelation are between five to six months after, in the time series at higher latitudes for all three indices. At lower latitudes the lag with the maximum autocorrelation is often less than five months (Table 33).

3.8 Summary of results

1. Differential catchability of species did not affect the seasonal pattern of diversity if catchability was constant within a study.

2. Visual and spline analysis showed that there was no latitudinal difference in the number of annual peaks in species richness S, heterogeneity H' and equitability E within the North American East Coast region. Although the number of

Table 32. Data sets with both `smooth'(sm) and `spiky'(sp) correlograms in S, H' and E, and the explanatory variables: habitat; gear type; length of time series; average lag of series. Data sets are ordered by latitude within regions; the regions separated by horizontal lines are from top to bottom: North American East Coast; Mediterranean, South Africa, and North American West Coast, respectively.

Data set	S	H'	E	Habitat	Gear	Length (Months)	Av. lag (Days)
1. Merriman	sm	sp	sm	Inshore	Trawl	17	66
2. Livingston	sm	sp	-	Salt marsh	Poison	18	65
3. McFarland	sm	sp	sp	Surf-zone	Seine	8	33
4. Bennett	sm	sp	sp	Surf-zone	Seine	13	56

Table 33. Latitudinal trend in the time lag of maximum autocorrelation of pattern in S, H' and E for data sets with `smooth correlograms'. The time (t) at maximum lag is in months.

Data set	Latitude	Index	Autocorrel. coeffs. Lag 1	Max.	t
1. Pepper	47°38'N	S	0.291	0.319	0.75
2. Pepper	47°38'N	S	0.391	0.464	0.50
3. Hoff	41°30'N	S	0.669	-0.544	6
4. Merriman	41°15'N	S	0.504	-0.466	6
5. Allen	33°45'N	S	0.661	-0.576	5
6. Allen	33°37'N	S	0.532	-0.473	5
7. Cain	33°19'N	S	0.676	0.610	1
8. Dahlberg	31°35'N	S	-0.265	0.469	3
9. Livingston	30°00'N	S	0.352	-0.391	8
10. McFarland	27°45'N	S	0.672	0.617	1
11. Pinto	14°03'N	S	0.352	-0.515	3
12. Bennett	34°08'S	S	0.615	-0.525	5
1. Pepper	47°38'N	H'	0.232	0.459	0.50
2. Hoff	41°30'N	H'	0.479	0.401	12
3. Allen	33°45'N	H'	0.291	-0.358	7

Table 33. Continued.

4. Allen	33°37'N	H'	0.410	-0.230	8
5. Cain	33°19'N	H'	0.734	-0.577	3
6. Dahlberg	31°35'N	H'	0.449	-0.437	4
7. Pinto	14°03'N	H'	0.333	-0.378	14
1. Merriman	41°10'N	E	0.266	-0.417	5
2. Allen	33°45'N	E	0.150	-0.435	7
3. Allen	33°37'N	E	0.402	-0.202	4
4. Cain	33°19'N	E	0.362	-0.365	1
5. Dahlberg	31°35'N	E	0.493	-0.430	4
6. Pinto	14°03'N	E	0.376	-0.390	14

annual peaks were variable in this region, two peaks within an annual cycle was found to be common by both analyses. That is all data sets had at least two peaks within an annual cycle. The time interval between the first and second peak for the eleven data sets from this region was five months on average. On the other hand, the analysis for time of occurrence of seasonal peaks in S, H' and E showed a relationship with latitude within the North American East Coast region. That is, the peaks within an annual cycle occurred earlier at lower latitudes ($\leq$ 41°15'N) and later at higher latitudes ($>$ 41°15'N). Regression analysis of this latitudinal trend in the time of occurrence of the first peak for all the data sets from this region was stronger in heterogeneity H' and equitability E, than in species richness S.

3. Analysis of peaks and troughs showed that there were two major patterns of seasonal tracking of species richness S by heterogeneity H' and equitability E in marine fish communities; an `in-phase' pattern is one, an `out-of-phase' pattern is another. In-phase changes in S, H' and E occur more than the out-of-phase pattern.

4. Seasonal variability in S, H' or E was not related to geographical region, habitat type, sampling gear and frequency of sampling (Table 20).

5. The seasonal variability in the three indices measured by the means and variances was related to species richness S

of individual data sets (Table 20). Variances and means in species richness S (Tables 21 and 24) and heterogeneity H'(Tables 22 and 25) tended to be higher in data sets with more species and lower in data sets with fewer species. On the other hand, the variance and mean of equitability E (Tables 23 and 26) showed an opposite pattern in this respect. There was also some relationship with latitude within the North American East Coast region.

6. Results of autocorrelation analysis showed that, in data sets with `smooth correlograms', the lag of maximum autocorrelation for S, H' and E was longer at latitudes ≥ 33°37'N than at latitudes < 33°37'N. In higher latitudes it was five months or greater; this length of time was generally shorter than five months at latitudes < 33°37'N.

4 DISCUSSION

4.1 Data sets used in this study

The principal objective of this study was to use available research fish catch data, collected over time, to discover and describe seasonal patterns of diversity in fish communities. Such research requires large suitable databases; the data have to be quantitative and collected by consistent sampling procedures. Twenty-two data sets which fulfilled these conditions were compiled for use in this study. Eleven of these data sets were from the North American East Coast region, making this region the best represented region in the study. This enabled within study as well as among study comparisions of seasonal patterns of diversity to be made for this region.

The limitation in terms of global and regional coverage reflects firstly historical and current research interests in the subject in different regions. Secondly, the small number of data sets compiled for this study is the result of inaccessibility of any available data as well as the unsuitability of data based on the above criteria. That is, for inclusion the data sets have to be collected by clearly specified sampling gear(s), the sampling procedures have to be accurately described and the taxonomic information of species caught had to be complete to species level.

4.2 Effect of bias by sampling gears

A wide range of fishing gears for large scale commercial purposes are described in FAO (1978) and Strange (1981). Rounsefell (1975) provided descriptions and illustrations of a fairly complete range of fishing gears. He classified these range of gears according to types of species which can be suitably captured with particular gear types as well as the types of habitats in which the gears are suitable for use. Often ecological or fisheries researchers rely on modified and appropriately adapted miniature versions of such fishing gears to obtain samples for studying biological and ecological aspects of fish.

Different sampling gears have different efficiencies in catchability (Taylor, 1953; Kenchington, 1980; Byrne et al., 1981; Gulland, 1983). Gears such as seines, traps set for migrating species, electrofishing and poisoning with compounds such as rotenone are more complete (Huntsman, 1948); their efficiency can be increased with repeated usage in a set area. On the other hand, gears such as trawls (Taylor, 1953; Kjelson and Johnson, 1978; Gibbs and Mathews, 1982; Engås and Godø, 1989(a, b)) and gillnets (Hamley, 1975) are less complete. It is known that regardless of the type of gear or design, the existence of a certain degree of bias in any research sampling protocol is inevitable (Byrne et al., 1981). Therefore, any research sampling design should aim to eliminate or control

any bias as much as possible. One has to take into account the possible biases of the sampling gear(s) and any underlying assumptions of the design of the sampling procedure(s) in interpreting the data (Byrne et al., 1981; Collie and Sissenwine, 1983).

Because research catch data available from published sources were used to study seasonal patterns of diversity of fish communities in this study, it was necessary to assess if biases in sampling affected seasonal patterns of diversity discerned from the data. The results of the simulation using the "approximate randomization test" procedure (Noreen, 1989) showed that as long as any bias that existed within studies was constant, it does not affect the seasonal patterns of diversity discerned from the data in relative terms. Figures 2 and 4, and Figures 3 and 5 demonstrate this conclusion for the heterogeneity H' and equitability E components of diversity, respectively.

As demonstrated by the above simulation analysis, as long as biases were constant within each study, conclusions from any comparisions of seasonal patterns of diversity among studies should be valid. Furthermore, most of the data sets used in this study were collected largely in similar habitats (inshore and estuary) and by related sampling gears (trawling and seining) (Table B2, Appendix B), using sampling designs planned for research purposes. Problems of gear selectivity

and among-study biases were carefully guarded against by screening and selecting the data sets, based on the efficiency and consistency of the design of the sampling protocol (see section 2.1). Although sampling biases may not be perfectly controlled in this manner, such considerations would minimize its effects and that of any interaction among latitude, habitat and gear type, enabling true patterns due to these variables to be exposed.

The among-study comparisions of the ranks in the variances and means of the indices can also be argued to suffer from variabilities due to biases in sampling gear among studies because of problems discussed in Green (1979, pp. 32-35). However, my results consistently showed strong trends in the ranks in all indices with the total number of species recorded in each study (Table 20). There was no trend associated with gear. Hence, I conclude that the influences of any biases in gear on the variability in the variances and means in the indices among studies are relatively negligible, at least at the spatial scales involved in this comparative study (Figure 1), than that due to the influence of species numbers.

With respect to gear selectivity, it is also necessary to clarify here that the term `fish community' used in the text in the context of this study, refers specifically to species of a certain size range and to individuals of certain size

ranges of particular species which, as a result of their size and behaviour, are susceptible to the sampling gear used. Therefore, `fish community', as used in this context, does not represent truely natural communities; I define a natural fish community to be one that comprises of all individuals of the different species that coexist and interact within a defined geographical area.

4.3 Seasonal patterns of diversity in fish communities

Fish communities from the North American East Coast generally tended to have two peaks in species richness S, heterogeneity H', and equitability E over an annual cycle at latitudes > 41°10'N and two to three peaks at latitudes ≤ 41°10'N. However, two annual peaks in the three indices is the most common pattern (Figures 9, 10, and 11). The peaks, indicating an influx of species into the communities, are separated by troughs which indicate an efflux, respectively. Consequently, seasonal patterns of peaks and troughs appear in the three indices, which are either `in-phase' or `out-of-phase' (Figure A1, Appendix A).

It has been calculated from Julian dates that the time interval between the two peaks, or that of the first two peaks in data sets with more than two peaks, was five months on average. Of the 22 data sets analysed, the index S from data sets from higher temperate latitudes (> 33° north or south)

that had 'smooth correlograms' appeared to have a time interval of five or six months between lag 1 and the lag of maximum autocorrelation (Table 33). This indicates that there is a better chance of predicting the seasonal pattern of any of the three indices five or six months later at higher latitudes. An interval of such magnitude coincides with the time interval between spring and fall peaks in primary production in temperate latitudes as proposed by the "match-mismatch" hypothesis (Cushing, 1967; 1975; 1990). Several examples using autocorrelation techniques to analyse temporal and spatial cycles in ecological data have been reviewed (Platt and Denman, 1975). They stated that spectral analysis using autocorrelation techniques is a relevant method of verifying any predictions in the periodicity of such cycles.

The results of the spline analysis (Figures 9, 10, and 11) show that the number of peaks in S, H' and E within an annual cycle fall into two main clusters in the North American East Coast region; one cluster is more a warm-months cluster while the other is a cold-months cluster. This implies that there are two major events of influx and efflux of species within an annual cycle in this region; one is associated with the warming of the sea during early spring into late summer while the other is associated with its cooling during early fall till late winter.

As reviewed in the introduction, many studies on seasonal

patterns of diversity in fish communities have reported peaks and troughs in species richness S, heterogeneity H' and equitability E to be associated with warm and cold seasons of the year. Species richness S was reported to be low in colder months of the year and high during the warmer months (McFarland, 1963; Richards, 1963; Shuntov, 1971; Oviatt and Nixon, 1973; Hoff and Ibara, 1977; Warburton, 1978; Quinn, 1980; Rainer, 1984; Thorman, 1986). Unlike species richness S, the heterogeneity component of diversity H' was found to be high during both the colder and warmer seasons of the year. Species heterogeneity H' was reported to be high during the warmer seasons of the year by a number of studies (Oviatt and Nixon, 1973; Subrahmanyam and Drake, 1975; Allen and Horn, 1975; Warburton, 1978; Al-Daham and Yousif, 1990). On the other hand, some studies reported this index to be high during the colder seasons of the year (Hoff and Ibara, 1977; Allen, 1982; Claridge et al., 1986). Similarly, the equitability index of diversity E was also reported to have maximum values during both the warmer (Dahlberg and Odum, 1970; Warburton, 1978; Al-Daham and Yousif, 1990) and colder seasons of the year (Claridge et al., 1986).

Therefore, it can be concluded that the seasonal changes in patterns of diversity in fish communities, as described above, are associated with major influxes and effluxes of species into and out of those respective communities. My

analysis of the major seasonal `troughs' in H' and E from the 22 data sets used in this study showed that the `troughs' were associated with the influx into the different communities by dominant species. This was also observed from a study of small flatfishes and other demersal fishes at seven stations inshore of Heceta Bank, Oregon (Pearcy, 1978). A decline in the heterogeneity index H' in Pearcy's study was found to be associated with the predominance in the catch (86 % by number) by the Pacific sanddab, Citharichthys sordidus, a dominant species in inshore (74-102 m) waters. In this regard, the species associated with the major `troughs' observed in the data sets used in my study are recorded in Table 19, many of them are either schooling species or those that have some form of aggregating behaviour.

When a species with an aggregating behaviour, or one that is numerically dominant in a community occurs, there is a proportionately greater contribution to the total numbers of fish in the community by this species. However, there is no corresponding increase in S with increase in total numbers. Consequently, the hetergeneity (H') and equitability (E) indices drop, resulting in the occurrence of `troughs' in these two indices, and an `out-of-phase' pattern in the overall seasonal pattern of diversity. However, when the fluxes are equitable for all species, the overall seasonal pattern would be `in-phase' (Figure A1, Appendix A).

4.4 Processes regulating seasonal patterns of diversity

The seasonal influx and efflux of fish species that is responsible for the two major peaks in the indices S, H' and E observed in data sets from the North American East Coast region, can be due to a number of processes. Some idea of what these processes are can be attained by thinking of variables and factors that are known to influence and regulate fish populations on a seasonal basis. In studies on fish population dynamics it is known that the number of fish at a given time in a given area is the result of an integration of the influences of both abiotic (environmental) and biotic variables. Abiotic variables include temperature, light and motion (water circulation and currents) (Skud, 1982; Longhurst, 1984; Rothschild, 1986). Cushing (1982) discussed some of these factors under the general topic "climate" and how it influences marine fisheries production. Biotic variables include fecundity, growth, age at maturity (Rothschild, 1986; Daan et al., 1990; Rijnsdorp et al., 1991), larval nutrition and larval predation (Longhurst, 1984; Rothschild, 1986; Pepin, 1990). Besides these, anthropogenic factors such as impact from fishing and water pollution also influence fish population dynamics (Rothschild, 1986). Because of the complexity of the relationships among these variables and their influences on fish population dynamics, the separation of the effects of fishing from that of any of the

other factors has been difficult for exploited fish populations (Rothschild, 1986; Daan et al., 1990).

In this study, I have collated time series data on fish catches from which the indices S, H' and E were calculated, as well as data on habitats sampled and gear used. Based on the patterns shown by my analyses of these data, as well as published information, I propose the following processes to be possible contributors to the observed seasonal patterns of diversity in fish communities of the North American East Coast region. The proposed processes would serve as starting points from which to investigate accurately which of them are involved, by collecting further data on variables such as reproductive condition, age composition, diet, body condition, as well as direct measurements of physical variables such as sea temperature and motion. This will allow one to integrate and identify accurately what processes are responsible for the observed patterns.

4.4.1 Recruitment variability

Seasonal reproductive and recruitment patterns (i.e. recruitment variability) (Longhurst, 1984) of different species of fish can influence the seasonal patterns of diversity in fish communities as analysed in this study. Ricker (1975) defines recruitment as the addition of new fish to the vulnerable population by growth from among smaller size

categories. "Vulnerable population" in this context implies the size classes of fish in the population that are susceptible to capture by any appropriate fishing gear. A definition of recruitment more specific to fisheries scientists is "adding a new cohort of individuals to an exploitable stock", rather than to a biologically defined population (Holt, 1990). On the other hand, a definition more suitable to ecology is the addition of a cohort of young individuals to a population (Sale, 1990). Ricker's definition, which is intermediate between that by Holt and Sale and too that it is appropriate to the context of this study, will be implied throughout the text where no further clarification is given.

In temperate latitudes, physical factors such as temperature and photoperiod undergo apparent seasonal variations in their magnitudes, being lowest and shortest in winter and highest and longest in summer, respectively. These variations provide external cues for the timing of seasonal reproductive activity in many temperate species of fish (Fry, 1971; DeVlaming, 1972, 1975; Lam, 1983) to coincide with seasons which can potentially enhance recruitment through increased larval and juvenile food, their survivorship and dispersal.

The regulation of reproductive activity by temperature and photoperiod has been observed in both freshwater and

marine fishes. DeVlaming (1972) critically reviewed the effect of these two environmental factors in controlling teleost reproductive cycles in six major orders. It was reported in the green sunfish, Lepomis cyanellus (Kaya, 1973), the cyprinid, Notemigonus crysoleucas (DeVlaming, 1975), and the pumpkinseed, Lepomis gibbosus (Burns, 1976). Data from Colton et al. (1979) and Sherman et al. (1984; 1987) showed spawning seasons in many marine fishes from the North American East Coast to be occurring either during the `cold months'(October-March) or the `warm months'(April-September) of the year. From their data from Georges Bank and the Middle Atlantic Bight the `cold months' spawners included examples such as: Gadidae- Gadus morhua, Pollachius virens, Melanogrammus aeglefinus; Clupeidae- Clupea harengus; Ammodytes sp.. Examples of the `warm months' spawners included: Gadidae- Merluccius bilinearis, Urophyscis spp.; Scombridae- Scomber scombrus; Labridae- Tautogolabrus adspersus (this species undergoes torpor during the `cold months').

The influence of such cues on the reproductive cycles of marine fishes is important, especially in temperate regions, where major pulses of primary production are also seasonal. It allows for the synchronization of spawning and the emergence of larval fish with events of high primary production (blooms) in the oceanic and shelf waters, and to enable larvae to successfully locate and exploit this primary production.

Spring blooms, which are examples of such high primary production, are associated with the warming of the sea after the winter, an increase in the day length, and the shallowing of the mixed layer (Wroblewski, 1989). These cycles of increased primary production over the shelf waters in temperate and boreal regions can deliver as much as 50% of the total annual input of organic carbon to the benthos (Townsend and Cammen, 1988). Such quantities of organic matter (phytoplankton and the associated zooplankton, and benthic heterotrophs) produced over the shelf waters within a brief period over the annual cycle is important. According to the "match-mismatch" hypothesis (Cushing, 1967; 1975; 1990), this organic matter can be important sources of food for the larvae and juveniles of many fish species that can synchronize their reproduction with these seasonal cyles of primary production in the sea.

Many examples of synchronization in reproductive cycles in fish with cycles of primary production in the marine environment exist. The synchronization of peaks in the reproductive cycles of various North Sea fishes with different production cycles (spring, autumn, and summer blooms) were discussed in Cushing (1975). In the continental shelf waters of northern United States, between Cape Sable and Cape Hatteras, several important species of fish have been found to synchronize their peak spawning periods with peaks in the

abundance of their copepod prey (Sherman et al., 1984; 1987). A coincidence in the occurrence of large numbers of fish larvae with an increased zooplankton production in spring and summer was reported from Georges Bank (Sherman et al., 1987). Iverson (1990) reported marine fish production to be sensitive to variations in phytoplankton production in oligotrophic marine environments. The year-class strengths of the anchovy and horse mackeral in the Black Sea were found to be correlated with the seasonal abundance of copepods and phytoplankton biomass (Arkhipov, 1990). Time series analysis of recruitment data of North Sea fish stocks have revealed short term fluctuations in these stocks to be associated with plankton abundance (Pepin, 1990).

4.4.2 Sea water temperature tolerence

The physiological tolerence by different species of fish to seasonal fluctuations in sea water temperatures is another process that can influence seasonal patterns of diversity in fish communities. Teleostean body-fluid systems are highly sensitive to temperature shock. Both heat and cold stress trigger variations in the status of the body fluids (Houston, 1973). Temperature has been reported by a number of studies in the North American East Coast to be an important factor influencing the abundance and distribution of groundfish (Massman, 1962; Tyler, 1971; Colvocoresses and Musick, 1984;

Horne and Campana, 1989; Morgan and Brodie, 1991).

In the context of phenotypic plasticity in teleosts (Warner, 1991), species which are more mobile with wide dispersal abilities would tend to be more tolerent over wide ranges of temperature change than species which have narrow dispersal abilities and are less mobile. Therefore, different species have different ranges of tolerence to fluctuations in temperature. They can respond either behaviourally, physiologically or some intermediate adaptation between these extremes, when encountered with such changes. This was evident in fish communities from temperate and boreal latitudes of the North American East Coast region during summer and winter, resulting in seasonal groups in the ichthyofauna (Tyler, 1971; Colton et al., 1979; Colvocoresses and Musick, 1984; Jeffries and Terceiro, 1985).

Behaviourally, fish can move away from areas of unfavourable temperatures to ones where tolerable ranges of temperature prevail. Many studies have reported such behavioural responses in fish communities along the North American East Coast. In summer in Conception Bay, Newfoundland, Canada, juvenile Atlantic cod, G. morhua, migrated into shallower and warmer waters during the day, and migrated to deeper and colder waters during the night (Clark and Green, 1990). Nearshore distributions of cod were found to be associated with sea temperatures ranging from - 0.5°C to +

8.5°C in the Gulf of St. Lawrence, Canada (Rose and Leggett, 1988). This study also reported highest cod densities in July (summer). The distribution pattern of American plaice, Hippoglossoides platessoides, in NAFO Division 3L on the Grand Banks was reported to be more aggregated in winter, avoiding waters with temperatures ≤ minus 1.2°C (Morgan and Brodie, 1991). Furthermore, demersal fish species studied from a trap fishery in the Middle Atlantic Bight indicated dominant species in the community to be migrating inshore in spring and going offshore in autumn (Eklund and Targett, 1991). Tyler (1971) has shown seasonal groups of fish to change their relative abundances in response to seasonal changes in temperature in Passamaquoddy Bay, New Brunswick, Canada. Seasonal dispersal and habitat selection by the cunner, T. adspersus, and young tautog, Tautoga onitis, in Long Island, New York has been found to be related to seasonal changes in water temperature (Olla, et al., 1979). In summer, some portion of the population of these two species would move from their resident (perennial) habitats to the seasonal (summer) habitats, moving back to the former in the fall, where they over winter in torpor.

Of course, not all fish need to migrate in order to cope with seasonal changes in temperature. Some species of fish are physiologically adapted to very cold temperatures by their ability to lower respiration and growth rates (DeVeries, 1971)

through physiological processes such as torpor (Green and Farwell, 1971; Pottle and Green, 1979(a&b)). Others evolve abilities to lower freezing temperatures of plasma and body fluids (DeVeries, 1971). Species with such adaptations are usually residents in temperate and boreal fish communities where freezing temperatures are normally experienced during the winter and the overall seasonal temperature fluctuations are minimal (Auster, 1988).

Examples of both of the above physiological adaptations have been reported from boreal marine environments. In Newfoundland waters it has been reported that the cunner, T. adspersus undergoes torpor to survive the cold winter temperatures (Green and Farwell, 1971; Pottle and Green, 1979(a&b)). During torpor the cunner remains under loose rock and boulders until water temperatures reach 5-6°C from April to late May, by which time they become active again (Green and Farwell, 1971; Pottle and Green, 1979(a&b)). Another study looked at the relative abilities of different species of fish in lowering freezing temperatures of plasma and body fluids, and their seasonal patterns of occurrence, in response to changes in sea temperature. This was investigated in a subarctic fish community in Izembek Lagoon, Bering Sea (Smith and Paulson, 1977). They noted that seven species out of 23, which were year-round residents, had winter serum osmotic concentrations of about 60% above that of summer values.

Whether a behavioural or a physiological response is the strategy of adaptation for different species of fish when unfavourable temperatures are encountered, is dependent on their relative ranges of tolerence. Species with wider ranges of tolerence, which generally have wider dispersal abilities and greater mobility (Warner, 1991), are likely to respond bahaviourally. On the other hand, species with narrower ranges of tolerence, narrower dispersal abilities, and are less mobile are likely to respond physiologically.

Which of these two strategies are attained by a particular species inhabiting any given temperate or boreal marine fish community, will determine whether it will migrate or not during changes in sea water temperature in early spring and early autumn. These extreme responses to temperature together with their many intermediate modifications that fulfil microhabitat thermal requirements by different species, will affect the relative numbers of residents and seasonally migrant species of fish in the respective communities. Consequently, such changes in the relative composition of these groups of fish will affect the seasonal patterns of diversity in these communities. The peaks and troughs in S, H' and E will be `in-phase' if the influx and efflux of the different species are equitable. However, if only a few abundant species shift seasonally in response to seasonal temperature changes then an `out-of-phase' pattern is

expected.

4.4.3 Avoidance of competition and predation

A third process that can also influence the seasonal patterns of diversity is due to the ecological adaptation by different species of fish to avoid competition and/ or predation. In the context of the theory of competitive exclusion (Hardin, 1960), large numbers of species can utilize a common resource (food or habitat) by varying their timing and strategies of utilizing these resources in order to avoid competition. Studies from the North American East Coast region have shown different species of fish to be abundant at different seasons and substituted each other, resulting in seasonal groups in the fauna, namely: spring, summer, fall, winter, resident, and transient groups (Massman, 1962; Tyler, 1971; Jeffries and Johnson, 1974; Colvocoresses and Musick, 1984; Jeffries and Terceiro, 1985). Winter flounder, Pseudopleuronectes americanus, a dominant and normally resident species in Narragansett Bay, Rhode Island has been shown to be replaced by migrant species when its numbers declined (Jeffries and Terceiro, 1985). This influx of migrants, following a decline in the winter flounder population, was thought to be attracted by the abundant food resources which are normally utilized by the winter flounder.

This `substitution' by different seasonal groups of fish

at different times of the year may be a strategy evolved to avoid competition and predation pressures. Daan (1980) used the term "replacement" to describe this phenomenon stating that two or more species undergoing replacement must be functionally related in exploiting a common resource base (food or habitat). This has been studied in some of the world's major fisheries over time scales of many years (Daan, 1980). One such example is the study by Skud (1982), which looked at the changes in the relative abundances of the Atlantic herring, Clupea harengus, and the Atlantic mackerel, Scomber scombrus. These two species alternated as dominant and subordinate species depending on their relative abundances.

Predation on eggs and larval fish is a density-dependent mortality factor that all fish must endure. This has been identified for the recruitment of herring in the Gulf of Maine (Campbell and Graham, 1991) and coral reef fishes (Hixon, 1991). To be successful evolutionarily different species of fish, especially those that do not offer parental care to their young, must be able to identify and utilize spawning grounds and seasons that minimize the impact of this factor on recruitment. It is evident from section 4.4.1 that at temperate and boreal latitudes of the North American East Coast, different species of fish spawn during two distinct seasons; one is during the `warm months' (April-September) and the other is during the `cold months' (October-March) of the

year. This separation can allow different species of fish to minimize both competition for larval food sources as well as larval and egg predation. For example, in a study on the trophic structure within the Bristol Channel, United Kingdom, the abundance of cohorts of Sprattus sprattus was found to vary within seasons between years. This was thought to influence the predatory pressures of Merlangius merlangus (Henderson et al., 1992).

Therefore, it is evident that the avoidance of competition and predation pressures can be another process that could be responsible for major seasonal influxes and effluxes in temperate and boreal marine fish communities, influencing their seasonal patterns of diversity.

In a fish community, it is unlikely for one to find large numbers of species responding similarly to any given set of biological and environmental variables. Similarly, it would be unlikely to find only one of the above processes to be responsible in influencing the influx and efflux of species in any community, affecting its seasonal patterns of diversity. Furthermore, not all the processes described above would operate over the same temporal and spatial scales.

However, it may be possible to rank the different processes in terms of their importance in determinig the seasonal patterns of diversity of a particular fish community. This can be done by properly identifying the variables to

measure, the appropriate spatial and temporal scales at which these variables are relevant, and appropriately designing field studies to investigate the relative importance of each process. The use of comparative studies, as attempted in this study, as well as the use of ecological models (Campbell and Graham, 1991) can be very useful tools in this regard. Through constant use of field data with the above methods, more accurate insights into the processes involved can be attained.

4.5 Hypotheses on seasonal patterns of diversity

One of the objectives of this study was to formulate hypotheses using seasonal patterns discerned from the analysis. The spatial scale of this work was intended to cover local, regional and global scales. Among-region comparisions of patterns was limited due to fewer data sets from the three other regions (Europe: three data sets; Mediterranean, South Africa and North American West Coast: six data sets; Tropics/Subtropics: two data sets) in comparision to the North American East Coast which alone was represented in the study by eleven data sets (Figures 1; Tables 1, 2, 3, 10, 11, and 12; Tables B1 and B2, Appendix B). Therefore, detailed analysis at regional scales was only restricted to the latter.

4.5.1 Plankton and Fish Phenology hypothesis

From the North American East Coast data a major

latitudinal pattern in the number and timing of seasonal peaks in the three indices (S, H' and E) was observed. Generally, two major seasonal peaks in the three indices occurred at latitudes > 41°10'N while two to three peaks occurred at latitudes ≤ 41°10'N. The heterogeneity index H' and the equitability index E, showed a steady progression with latitude where the first peaks in the two indices occurred earlier at lower latitudes and later at higher latitudes. This trend was shown to be significant by regression analysis (Figures 13 and 14). Their respective slopes were 6.58 and 3.19, and these slopes can be interpreted as rates of northward progression of the production cycle, expressed as days per degree north. A similar latitudinal trend was noted from a study on food supply and the phenology of migrating shorebirds along the North American East Coast, where their pattern of northward movement was related to the "poleward moving bloom of benthic marine invertebrates" (Schneider, 1981).

The demarcation at 41°10'N may not be accidental. It is within the latitudinal range (40°N - 42°N) at which the cooler "boreal" water masses (5°C - 10°C) separate from the warmer "warm temperate" waters (10°C - 25°C) (Hedgpeth, 1957; Colton, 1964 op cit. Colton et al., 1979; Backus, 1986); the temperature ranges for the two water masses is taken from Figure 5 of Hedgpeth (1957). It is also proximal to the

latitude (40°) poleward from which the production cycle becomes seasonally marked in the two hemispheres (Cushing, 1989; Angel and Hargreaves, 1992), as a consequence of the large scale patterns in both vertical and horizontal heat flux in the ocean (Longhurst, 1984). This pattern revealed by the eleven data sets representing the entire east coast of North America ranging from Texas (27°45'N) to Newfoundland (47°38'N) (Figure 1; Tables 1, 2, 3, 10, 11 and 12; Tables B1 and B2, Appendix B) signals the existence of a process that is influencing the seasonal abundance and diversity of marine fishes over a large spatial scale in this region.

From the list of processes proposed in section 4.4 above, it seems that recruitment variability (section 4.4.1) is the process that would be most relevant at this regional scale. Throughout this latitudinal range seasonality in physical factors such as sea water temperature, photoperiod, wind forcing and the stability of the water column (stratification regimes) exist. Successful recruitment is dependent on the enhancement of larval and juvenile suvivorship and their subsequent inclusion in the adult population.

Seasonal peaks in diversity in fish communities result from an influx of fish into these communities. Major peaks in recruitment would also be seasonal throughout this latitudinal range within the North American East Coast, in relation to major seasonal cycles in the reproductive biology of marine

fishes. Reproductive variability has been suggested to be more important than density-dependent factors in regulating the numerical strengths of cohorts of North Sea plaice, sole and cod (Rijnsdorp et al., 1991). In the documentation by Sherman et al. (1984; 1987) of the seasonal reproductive activity of principal groups of marine fishes of the shelf waters of northeastern United States, different species were shown to be reproductively active either in the `cold months' or the `warm months' of the year (see section 4.4.1). However, appearance of juveniles from the two reproductive seasons in their respective communities is reversed; juveniles of `cold months' spawners appear in `warm months' and those of `warm months' appear in `cold months'. This reversal is due to the duration of the larval phase which generally is equivalent to the time interval between the two seasonal periods. For the Atlantic herring (Clupea harengus harengus) stocks along the North American East Coast, this duration ranges between four to five months (Sinclair and Tremblay, 1984), with the more northerly stocks spawning in the `warm months'(spring-summer) and the southerly stocks in the `cold months' (autumn-winter). This time period corresponds with the time interval between lag 1 and the lag of maximum autocorrelation (Table 33), which was interpreted to be the time interval between spring and fall peaks in primary production at temperate latitudes.

The availability of food resources is very important for

fish larvae as soon as the yolk is totally reabsorbed. Food supply was one of two primary factors identified to be controlling recruitment of herring populations in the coastal waters of Maine during years when the larval stage was critical (Campbell and Graham, 1991). Phytoplankton production is fundamental to the trophic requirements of marine communities and ecosystems (Ryther, 1969; Townsend and Cammen, 1988; Urban et al., 1992). Its development is dependent on the total amount of light and photoperiod (Tarzwell, 1970), both of which are aspects of radiant energy (Hedgpeth, 1957). Therefore, the seasonal cycles in phytoplankton and the associated zooplankton, from hereon to be referred to as `plankton', at higher latitudes which follow variations in these variables may be regulating similar cycles in secondary and tertiary production such as fish biomass. The seasonalities in the reproductive biology of various high latitude marine fishes and their recruitment may be evolutionarily linked with these seasonal production cycles of plankton. Hence, I propose the hypothesis that the recruitment variability, influenced by evolutionary mechanisms that link the timing of major reproductive seasons of marine fishes with seasonal pulses in marine primary production, is the major process regulating the described trend in the number and timing of occurrence of seasonal peaks in the diversity indices S, H' and E in the North American East Coast.

This hypothesis is theoretically very similar to Cushing's "match-mismatch" hypothesis (Cushing, 1967; 1975; 1990). However, in Cushing's hypothesis the seasonal cycles in absolute abundance of fish populations, formulated largely from herring data, were matched with similar cycles in plankton. In my "plankton and fish phenology" hypothesis the relative abundances of different species of fish in entire communities, measured by diversity indices, are considered. Thus, the results reflect seasonal changes in the structure of these ichthyofaunal communities over large spatial scales in response to the seasonal cycles in plankton productivity, rather than seasonal changes in single populations to such productivity. These two hypotheses pertain to similar ecological phenomena but look at two different levels of ecological organization. They are complemetary and are both relevant over large spatial scales, in contrast to the "larval retention" hypothesis (Iles and Sinclair, 1982; Sinclair and Tremblay, 1984).

The "larval retention" hypothesis states that marine fishes spawn in areas where local oceanographic features facilitate the retention of larvae that hatch in these areas which also serve as rich larval feeding grounds (Iles and Sinclair, 1982; Sinclair and Tremblay, 1984). Considering the heterogeneity of the marine environment (Longhurst, 1984) such areas would be patchy as a consequence of the local

variability in bathymetric and oceanographic features. Such hypothesis would not be relevant to explain the large scale seasonal patterns in diversity described for the North American East Coast in my study. However, the proposed "plankton and fish phenology" hypothesis or the "match-mismatch" hypothesis can be used to explain such patterns at their respective level of ecological organization.

4.5.2 Instability-Dominance hypothesis

The use of indices such as S, H' and E can serve as an univariate approach (Clarke and Green, 1988) to the measurement of community structure. Diversity encompasses two components of ecological communities, namely their richness and the relative abundances of their constituent species. Indices such as S measures the former while H' measures both (Peet, 1974; Magurran, 1988). The equitability index E, measures the magnitude of the two components of diversity relative to the maximum possible (Peet, 1974; Magurran, 1988).

Therefore, the seasonal patterns in S, H' and E described in this study can be interpreted as seasonal patterns of change in structure in marine fish communities along the North American East Coast. Theoretically, peaks in the three indices indicate an influx of species into a community and the troughs are associated with an efflux. Two major patterns of peaks and troughs were described in this study. One was an `in-phase'

pattern where all three indices (S, H' and E) either approach peaks or fall into troughs simultaneously, while the other was an 'out-of-phase' pattern where when S approaches a peak, H' and E fall into troughs and vice versa (Figure A1, Appendix A). Of the twenty two data sets analysed, the 'in-phase' pattern was more common than the 'out-of-phase' pattern (Table 19).

In searching for patterns in the seasonal occurrence of the two patterns among the different data sets, one relationship became apparent. The 'out-of-phase' pattern was found to be associated with the predominance of schooling species, or species with any other form of aggregating behaviour, in the catch (Table 19). That is, it occurred when the community was swamped by one or two dominant species. A recent study reporting the structure of ichthyoplankton communities in the Celtic Sea stated similar influences on the heterogeneity and equitability indices by the predominance of the larvae of the mackerel, Scomber scombrus, in the catches (Hortsman and Fives, 1994). On the other hand, the 'in-phase' pattern occurred when there were no single numerically dominant species in the catch, resulting in a relatively equitable species composition in the catch.

An important aspect of communities is the stability in their structure. The stability of a community is dependent on whether or not all variables return to the initial equilibrium

levels after a perturbation in the system (Pimm, 1984). Related to stability is resilience which is how fast a community attains this stability (Pimm, 1984). Perturbations in ecological communities often result in the appearance of dominant species (e.g. during early succession), and when they stabilize the situation tends towards equitable species compositions (e.g. in climax communities) (May, 1986; 1988). Once the structure of a community has stabilized by having a well established set of species of different trophic levels (Pimm, 1980; 1984; Cohen, 1989; May, 1986; 1988), any dynamics and instability in its structure would be the result of factors such as: (i) natural perturbation; (ii) seasonal changes in environmental conditions; (iii) recruitment variability of dominant species (section 4.4.1); and (iv) any anthropogenic causes (e.g. pollution and habitat destruction).

Having discussed the interrelationships between diversity, and community structure and stability above, I propose the hypothesis that in any marine fish community, whenever the seasonal pattern of diversity of S, H' and E appear to be `out-of-phase' it indicates the occurrence of dominant species in the community. Hence, this implies any of the four above factors to be operating. Where anthropogenic causes are known to occur in an area, this could signal the need to execute an impact study (section 4.6.2). With a knowledge of possible factors responsible, as listed above,

appropriate test variables, sampling designs and statistical tests can be selected. This will enable the definite cause(s) to be established using appropriate statistical analyses. Therefore, this hypothesis should serve as a useful basis for applied problems such as fisheries management and environmental monitoring in the marine environment. Detailed discussions in this respect is ebmbarked on below (section 4.6).

4.6 Applications for described patterns in S, H' and E

The description of existing patterns in structure of any ecological community is useful for purposes of developing predictions about the temporal and spatial dynamics of its structure. If predictions can be made, then this can provide a means to test for underlying processes and mechanisms responsible for observed patterns in community structure (Gaston, 1990; Lawton, 1990). Once the underlying processes are understood, they can be used in applied research. The use of diversity indices S, H' and E is a univariate approach to studying community structure (Clarke and Green, 1988). In this study it enabled the determination of seasonal patterns of diversity of fish communities, reflecting also the seasonal patterns of change in their structure. The seasonal patterns of the three indices described in this study can be applied in fisheries management, environment monitoring and impact

assessment.

As discussed in section 4.4, seasonal patterns of diversity in fish communities reflect the temporal dynamics of the populations of their constituent species. These dynamics can be attributed to processes to which the different species respond. For example, the principal processes that have been proposed in this study for the North American East Coast region are: (1) recruitment variability; (2) sea water temperature tolerence; and (3) avoidance of competition and predation (section 4.4).

In the present study, two major seasonal patterns of diversity were described, largely from data from the North American East Coast. Firstly, there are two seasonal peaks in the three indices (S, H' and E) at latitudes > 41°10'N and two to three peaks at latitudes ≤ 41°10'N (see sections 3.8.2 and 4.3) over an annual cycle. These peaks separate into two clusters, one for those that occur during the cold-months of the year and the other for those that occur during the warm-months. Secondly, the peaks in the three indices are either `in-phase' or `out-of-phase' (Figure A1, Appendix A), indicating an equitable influx or a non-equitable influx (i.e. dominance by a few, usually one or two species), respectively (see sections 3.8.3 and 4.3).

The number and relative abundance of species are of interest in the context fisheries management, environment

monitoring, and impact assessment. Spatial and temporal patterns in the number and relative abundance of species (S, H' and E) can be used to determine: (1) the amount of spatial and temporal variability; (2) the timing of the major peaks and troughs within/between latitude and region; and (3) the sampling frequencies needed to resolve seasonal variation in the abundance of different species within each community. This allows the design of appropriate sampling programmes which will enable sensitive and statistically powerful tests to be done. Consequently, a knowledge of spatial and temporal patterns in S, H' and E augment the reliability of monitoring and management decisions.

4.6.1 Application in fisheries management

An important aspect of the dynamics of fish populations relevant to fisheries management is the timing of peaks in their abundance and their subsequent decline. The timing of such peaks described in this study, largely from data from temperate and boreal latitudes from the North American East Coast, indicate that these occur during early spring into late summer, and during early fall till late winter. If these periods are confirmed to coincide with the proposed processes such as spawning and recruitment of fish stocks (see section 4.4) in this region, managers can use this information to ensure that vulnerable stocks are not fished during these

periods or are only fished under restricted quotas. This will allow the populations of such stocks to recover to sustainable levels.

Such a management approach can be applied in other regions where similar seasonal patterns in abundance of fish populations also occur. Alternatively, if studies are needed in a different region to establish the timing of peaks and intervals between annual peaks within this region, the results from my comparative study could provide the basis for the design of such a study. For example, the decision on a suitable sampling interval can be directly adapted from my study which indicates that an interval of one month gives the resolution sufficient to show seasonal patterns. That is, where labour and financial constraints render regular sampling difficult, every effort must be made to secure a monthly interval of sampling when studying seasonal patterns; seasonal patterns would not be resolved at sampling intervals greater than one month.

Another important result from this study is the latitudinal trend in the dates (measured in Julian days) of occurrence of the first annual peak in diversity, which is the peak starting in early summer. In the North American East Coast region the first peaks in the three indices occurred earlier at lower latitudes and progressed steadily northwards. Regression analysis of this data was significant for the

heterogeneity H' and equitability E components of diversity (Figures 13 and 14, respectively).

This result has predictive value among latitudes within this region. These regressions can enable predictions to be made within region of the time of occurrence of peaks in the respective diversity indices in fish communities of interest. It can be useful to fisheries scientists and managers who are involved with the task of forcasting seasonal dynamics of fish populations. Additionally, it can be used by marine ecologists working in this region to study local processes that regulate the occurrence of the peaks, by comparing biotic and abiotic variables in localities that are successfully predicted and those that are not. Because the coefficients of determination (r^2) of these regressions are known, 0.11, 0.28 and 0.25 for S, H' and E respectively, an assessment of the expected variations in the predictions can be made. This will allow the determination of the degree of confidence in these estimates and predictions.

4.6.2 Application in environmental monitoring and impact assessment

In environmental monitoring and impact assessment proper sampling designs and sensitive testing are necessary in achieving desired objectives. Several important factors related to the goals of the study and the appropriate

analytical methods to use on the data when they are collected must be considered during the design of the sampling programme. These include: (i) the identification of appropriate test variables to be measured (Clarke and Green, 1988; Underwood and Peterson, 1988); (ii) proper designation of controls for these variables (Green, 1989; Eberhardt and Thomas, 1991); (iii) proper replications of samples (Hurlbert, 1984); (iv) appropriate spatial and temporal scales of study (Green, 1989; Livingston, 1987); (v) the classification of the structure of the variables measured; (vi) the assignment of appropriate degrees of freedom; and (vii) appropriate statistical tests to employ in the analysis (Clarke and Green 1988; Underwood and Peterson, 1988; Green, 1989; Eberhardt and Thomas, 1991). This list gives a general guide to what factors should essentially be considered in the design, sampling and analysis stage of an environmental monitoring and impact assessment study. These considerations reduce any analytical difficulties oi the data at the end of the study.

Environmental monitoring and impact assessment studies can be classified into three categories; baseline, impact and monitoring studies (Green, 1979). According to Green (1979) a basline study is, "one in which data are collected and analyzed for the purpose of defining the present state of the biological community, the environment or both. "Usually some environmental change is anticipated". He defines an impact

study as, "one whose purpose is to determine whether a specified impact causes change in a biological community and, if it does, to describe the nature of that change". Finally, "a monitoring study has the purpose of detecting a change from the present state". A decision key for determining what category an enviromental study comes under, the appropriate sampling designs and suitable tests of hypotheses necessary for each category is provided in Figure 3.4 (p. 72) of Green (1979).

In enviromental monitoring and impact assessment studies in aquatic environments fish is often a taxa of choice (e.g. Bechtel and Copeland, 1970; Haedrich and Haedrich, 1974; Livingston, 1975; Hilman et al., 1977), setting measures of its abundance as the response variable. I will discuss below how my results of seasonal patterns in diversity of marine fish communities can be applied in environmental studies, with examples for each of the above categories.

In a baseline study a programme of data collection is usually executed in anticipation of an impact at a particular site (Green, 1979). Here the spatial scale is relatively fixed since the site is known, however a decision on a suitable temporal scale over which sampling intervals are to be set have to be made.

The results of this study (Figure A2, Appendix A) showed that a temporal scale of one month gives sufficient resolution

to detect natural seasonal patterns of diversity (see also section 4.6.1). One month should be an appropriate temporal scale of resolution to analyse whether or not an impact has occurred, despite any natural seasonal variability in relative abundances of different species in any fish community. Hence, if an impact is anticipated and a chronic (e.g. prolonged discharge of sewage or thermal effluents) effect on fish communities is expected, the collection of monthly samples during the `baseline' phase of the study would be sufficient to resolve natural seasonal patterns of diversity, if diversity statistics are used. Decisions on whether an impact on fish communities has occurred in the area can then be made, based on testing for the significance of the differences in the variances of the seasonal patterns resulting from natural causes and that resulting from the impact.

Furthermore, the knowledge of the timing of seasonal peaks and troughs in S, H' and E as described for the North American East Coast region in section 4.3 above, can also be applied in baseline studies in this region. The seasonal peaks in the indices are found to occur during two principal seasons. Some peaks occur during the warm months from early spring to late summer while others occur during the cold months, starting in early fall till late winter. A knowledge of seasons of expected peaks and troughs, and processes (see section 4.4) regulating them, in a specific location must be

developed during baseline studies as points of reference to use to compare any alteration to this expectation when the anticipated impact occurs. For example, from the "Dahlberg" data set obtained at a latitude of 31°35'N, two peaks in S have been analysed by spline analysis (Figure 9) to occur in July and October. On the other hand, only a single peak was recorded for both H' and E, both occurring in April (Figure 10 and 11 respectively). This is an example of an 'out-of-phase' pattern since the peaks in S do not coincide with those of H' and E.

If such a pattern was established during a baseline study at the site of an anticipated impact, a deviation from this expected pattern should signal a perturbation in the system. If the deviation in the pattern occurs after the anticipated impact has occurred, appropriate statistical analyses should be undertaken to confirm if the change in pattern is due to the impact or any of the other factors listed in section 4.5.2.

In an impact study, the principal aim is to determine if a specific impact causes a change in the biological community, and to describe this change (Green, 1979). Here, the time the impact has occurred is known. A suitable control site has to be selected, ideally one in proximity to the impact site, must have similar environmental features, and it must be separated from the influences of the impact. For example, if an inshore

area is the site of impact due to the discharge of a pollutant, a site unlikely to be reached by this pollutant by known physical and oceanographic processes occurring in the area must be selected. With a proper sampling design, the impact and control sites can be sampled at the same points in time; immediately after impact, several months later and same time the following year. Calculating S, H' and E and statistically comparing their values can establish the relative differences in the community structure caused by the impact.

Furthermore, the analysis of the ranks in the means and variances of S and H' in my study showed a clearer relationship with the total number of species recorded in the data sets than with latitude (Tables 20, 21, 22, 23, 24, 25, and 26). Data sets with greater than thirty species recorded generally had higher ranks in the means and variances of the species richness index S and the heterogeneity index H'. There was a reverse trend in the equitability index E in this respect: means and variances were generally ranked higher for data sets that recorded fewer than thirty species.

Therefore, when impact analyses are planned for a site where the total number of species recorded is large, say greater than thirty from my analysis, one would expect the natural seasonal variability in H' to be high at this site. Thus, greater attention must be paid to the timing of peaks

and troughs in seasonal patterns of diversity as described above (see section 4.3). Besides the samples taken immediately after the impact and at the same time the following year, at least two samples must be taken `several months later', one during the time of a known peak and another during a known trough. This will enhance the sensitivity of the test by increasing the chances of detecting changes in seaonal diversity due to the impact despite the existence of greater natural variabilities in seasonal patterns. Seasonal variability in the data due to natural causes can mask any effect due to anthropogenic causes and so this requires proper sampling designs and sensitive tests (Hurlbert, 1984; Green, 1989).

Finally, I would like to consider an example of application of my results in a monitoring study, where the aim is to detect a change from the present state of the environment or biological community (Green, 1979). In such studies time series data of key variables are collected for the purpose of detecting a change in the trend of these variables in response to some perturbation. In my view, a monitoring study incorporates aspects of both a baseline study and an impact study.

The particular results from this study that I think can be used in a monitoring study of marine fish communities is the `in-phase' and `out-of-phase' patterns of diversity,

described in section 3.5 and Figure A1, Appendix A. As concluded from Table 19, the `in-phase' pattern is the more commonly occurring pattern in fish communities. The `out-of-phase' pattern is less common, and is concluded (Table 19) to be associated with the occurrence of only a few dominant species in the community.

Therefore, if an `out-of-phase' pattern is detected from monitoring data, a swamping of the fish community by a few dominant species is implied. Such swamping indicates that an ecological perturbation, either anthropogenic or natural, has occurred. The cause may or may not be immediately known. However, in either case a properly designed impact study (see this section) with careful consideration of key variables, and natural and artificial processes that may be responsible, the cause(s) of the `out-of-phase' pattern in diversity can be established (see section 4.5.2).

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6 APPENDICES

6.1 Appendix A: Illustrative figures

Figure A1. A schematic illustration of seasonal tracking in the three components of diversity; `in-phase' tracking of species richness S by heterogeneity H' and equitability E (left) and `out-of-phase' tracking of S by H' and E (right).

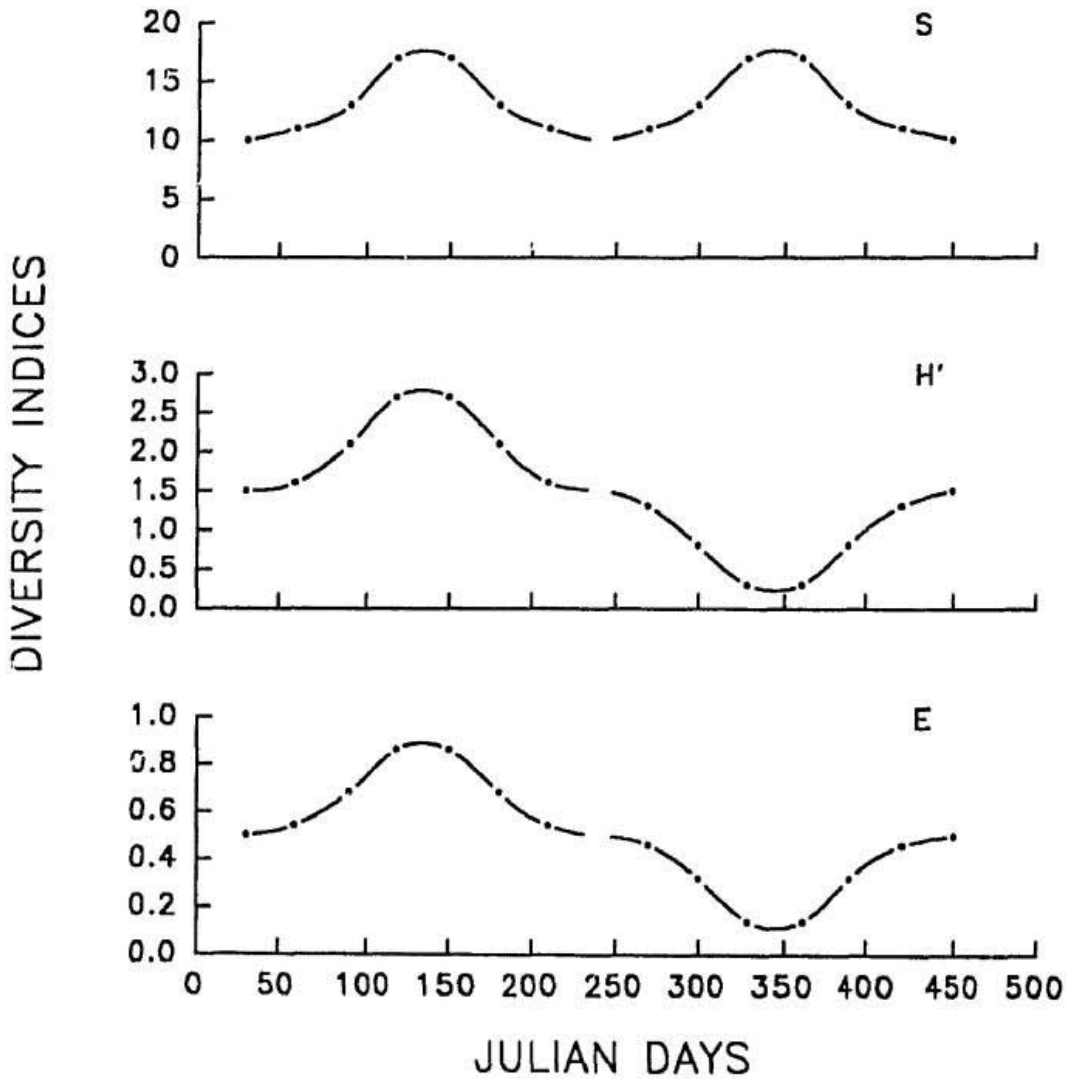
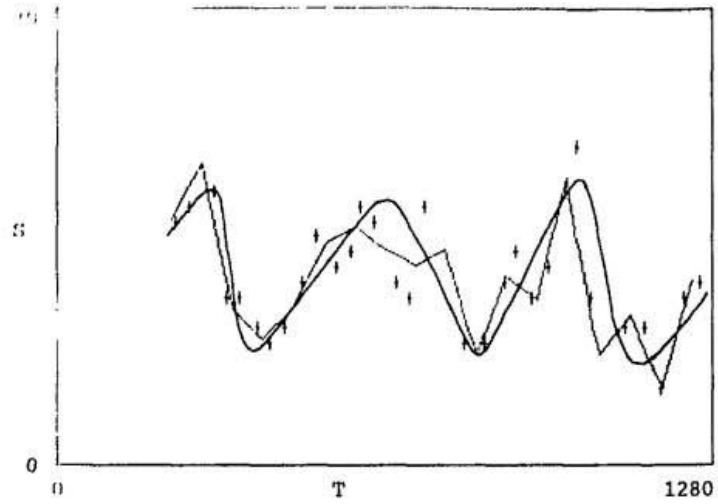
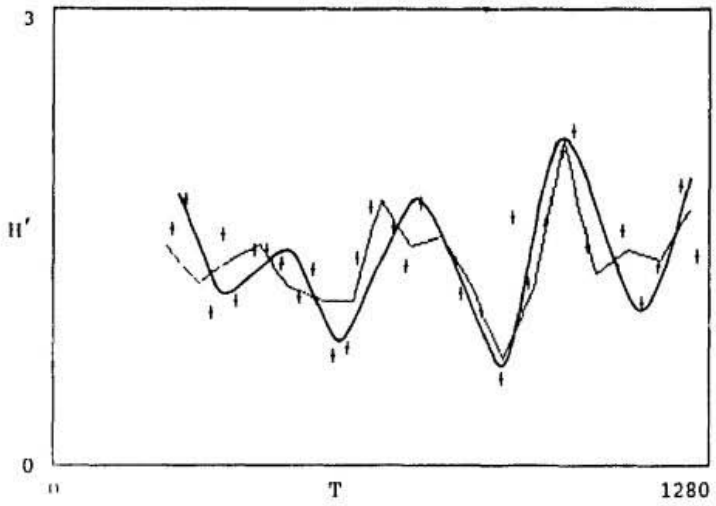
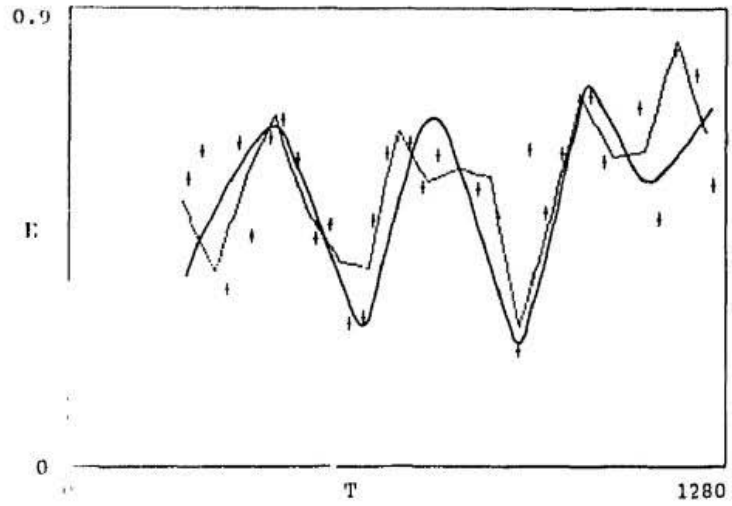

DIVERSITY INDICES
S
H'
E
20
15
10
5
0
3.0
2.5
2.0
1.5
1.0
0.5
0.0
1.0
0.8
0.6
0.4
0.2
0.0
0
50
100
150
200
250
300
350
400
450
500
JULIAN DAYS

Figure A2. Peaks and troughs determined by visual analysis (solid line) and spline analysis (jittery line), in comparison with the original data points (crosses). The x-axes in all plots is time in Julian days (T) while the y-axes are the three indices: S (top); H' (centre); and E (bottom). Both `in-phase' and `out-of-phase' patterns of tracking in S, H' and E, illustrated in Figure A1 can be seen in this figure from original data of Merriman and Warfel (1948).


S
0
0
T
1280


3
H'
0
0
T
1280


0.9
E
0
T
1280

6.2 Appendix B: Summary of data sets compiled for this study

Table B1. A summary of data sets compiled for this study showing locality of study and source of data.

Location	Lat./Long.	Source
1. Broälven Estuary, Sweden (Site RR)	58°24'N 11°26'E	Thorman & Fladvad, 1981
2. Broälven Estuary, Sweden (Site R)	58°22'N 11°26'E	Thorman & Fladvad, 1981
3. Broälven Estuary, Sweden (Site Z)	58°19'N 11°26'E	Thorman & Fladvad, 1981
4. Logy Bay, Newfoundland (Smaller species)	47°38'N 52°40'W	Pepper, 1974
5. Logy Bay, Newfoundland (Larger species)	47°38'N 52°40'N	Pepper, 1974
6. Passamaquoddy Bay, New Brunswick	45°06'N 67°07'W	Macdonald, et al. 1984
7. Slocum River, Massachusetts	41°30'N 70°45'W	Hoff & Ibara, 1977

Table B1. Continued.

8. Block Island Sound	41°15'N 71° - 72°W	Merriman & Warfel, 1948
9. Long Island Sound, New York (Station 1)	41°10'N 72°15'W	Richards, 1963
10. Long Island Sound, New York (Station 3A)	41°10'N 72°15'W	Richards, 1963
11. Catalan Shelf, Western Mediterranean	40°-42°N 01°-04°W	Sebatés & Masó, 1990
12. Colorado Lagoon, California	33°45'N 118°10'W	Allen & Horn, 1975
13. Newport Bay, California	33°37'30"N 117°54'20"W	Allen, 1982
14. North Inlet, South Carolina	33°19'N 79°08'W	Cain & Dean, 1976

Table B1. Continued.

15. Sapelo & St. Catherine's Sounds, Georgia	31°35'N 81°15'W	Dahlberg & Odum, 1970
16. Apalachee Bay, N. Florida (Site 4A)	30°00'N 84°12'W	Livingston, 1975
17. Mustang Island, Texas	27°45'N 97°09'W	McFarland, 1963
18. Pagbilao Bay, Quezon, Philippines	14°03'N 121°45'E	Pinto, 1987
19. Leaner Swamp, Darwin, Australia	12°22'S 130°55'E	Davis, 1988
20. King's Beach, S. Africa (Coarse net)	33°56'S 25°39'E	Lasiak, 1984
21. King's Beach, S. Africa (Fine net)	33°56'S 25°39'E	Lasiak, 1984
22. Cape Coast, S. Africa	34°08'S 18°27'E	Bennett, 1989

Table B2. A summary of data sets compiled for this study showing locality, type of habitat, sampling gear used and duration of each study.

Location	Habitat Type	Sampling Gear	Duration Start	Duration End
1. Broälven Estuary, Sweden (Site RR)	River	Drop net	April 1978	Oct. 1978
2. Broälven Estuary, Sweden (Site R)	Estuary	Drop net	April 1978	Oct. 1978
3. Broälven Estuary, Sweden (Site Z)	Estuary	Drop net	April 1978	Oct. 1978
4. Logy Bay, Nfld. (Smaller species)	Inshore bay	SCUBA Census (Quadrat)	Aug. 1972	Dec. 1973
5. Logy Bay, Nfld (Larger species)	Inshore bay	SCUBA Census (Visual)	Aug. 1972	Dec. 1973
6. Passamaquoddy Bay, New Brunswick	Inshore cove	Seine	May 1976	Nov. 1977

Table B2. Continued.

7. Slocum River, Massachusetts	Estuary	Seine	June 1966	April 1968
8. Block Is. Sound,	Inshore	Otter trawl	Aug. 1943	July 1946
9. Long Is. Sound (Station 1)	Inshore	Otter trawl	July 1956	July 1957
10. Long Is. Sound (Station 3A)	Inshore	Otter trawl	July 1956	July 1957
11. Catalan Shelf, Western Mediterranean	Pelagic	Bongo net	April 1983	Oct. 1983
12. Colorado Lagoon, California	Lagoon	Seine	Jan. 1973	Dec. 1973
13. Newport Bay, California	Estuarine bay	Small seine Bag seine Drop net Enclosure net	Jan. 1979	Jan. 1980

Table B2. Continued.

14.	North Inlet, South Carolina	Estuary	Poison	June 1971	May 1972
15.	Sapelo & St. Cath. Sounds, Georgia	Estuary	Otter trawl	Jan. 1967	Feb. 1968
16.	Apalachee Bay, N. Florida (Site 4A)	Salt marsh	Seine Poison	April 1971	Sept. 1972
17.	Mustang Island, Texas	Surf-zone	Seine	May 1960	July 1961
18.	Pagbilao Bay, Quezon, Philippines	River	Otter trawl	March 1973	Aug. 1974
19.	Leaner Swamp, Darwin, Australia	Tidal swamp	Fyke net Poison	Oct. 1979	March 1980
20.	King's Beach, S. Africa (Coarse net)	Surf-zone	Coarse seine	Sept. 1978	Oct. 1980
21.	King's Beach, S. Africa (Fine net)	Surf-zone	Fine seine	Oct. 1979	Oct. 1980

Table B2. Continued.

22. Cape Coast, S. Africa	Surf-zone	Seine	May 1980	May 1981