PREDICTIONS UNDER UNCERTAINTY:
FISH ASSEMBLAGES AND FOOD WEBS ON THE GRAND BANK OF NEWFOUNDLAND

MANUEL DO CARMO GOMES, M.Sc.

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FISH ASSEMBLAGES AND FOOD WEBS ON THE GRAND BANK OF NEWFOUNDLAND

BY

© Manuel do Carmo Gomes, M.Sc.

A thesis submited to the School of Graduate
Studies in partial fulfillment of the
requirements of the degree of
Doctor of Philosophy

Department of Biology
Memorial University of Newfoundland
August 1991

St. John's Newfoundland

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ISBN 0-315-73330-6

If the Lord Almighty had consulted me
before embarking on creation I should have
recommended something simpler

Attributed to Alphonso X the Wise (1221-1284),
King of Castile and Leon. From Murray (1989).

Abstract

Six broad zoogeographic areas on the Grand Bank, each characterized by a relatively homogeneous and persistent species composition, are identified, described, and mapped. The contours of these areas consistently recurred around the same geographic positions year after year (1971-82, 1984-87) and were found to be strongly aligned with bottom depth and oceanographic circulation on the Bank. Consideration of their overall biological coherence led to the reformulation of the original six areas into four major regions that are suggested to define an appropriate scale for studies at the community level on the Grand Bank. Within the two major zoogeographic regions, Southern and Northeastern, there is a complex network of feeding interactions whose major year-round features have been summarized in the form of stereotyped community food webs. On average, the Grand Bank food chains are short, as is the case in other marine food webs, but they exhibit an uncommon degree of omnivory. Examination of diet overlap of predators on the Grand Bank suggests that body size is the most important structuring factor of niche space. Press perturbations, a modeling exercise in which individuals of a given species are continuously removed from the community, are used to investigate the consequences of two major sources of uncertainty (uncertainty about model structure and about parameter values) that plague attempts to make predictions about long term changes in species abundance. It is shown that long term predictions are highly sensitive to details of interactions in community models and therefore community dynamics must be, to a large extent, indeterminate over time.

Acknowledgments

I am very grateful to Dr. Richard Haedrich (MUN[1], OSC[2]) for his role as my Ph.D. supervisor. His guidance and council patiently helped to unfold perseverance into clear presentations of work and thoughts.

I am also grateful to Dr. Jake Rice (DFO[3]), Dr. David Schneider (OSC, MUN), Chris Bajdik (OSC), and Dr. George Lilly (DFO).

> Jake brought me to Canada, helped to lay the foundation for this work, shared his expertise on the Grand Bank, and fueled the encouragement that melt my initial hesitations.
>
> Dave is a scientist with the thoughtfulness, industry, and modesty that builds wisdom. I thank him for patiently entertaining my questions and reviewing my manuscripts.
>
> Chris is a skilled statistician with a unique gift to communicate with biologists. Much more than that, he is an excellent friend who made me feel at home in the land of Leonard Cohen and Stompin' Tom Connors.
>
> During our discussions, George was able to share his expertise and experience without giving up the healthy skepticism of a good fisheries biologist. I alsokp thank him for critically editing my manuscripts.

Very special thanks also to Prof. Campos Rosado (FCL[4]). No matter the geographical distance, his whole-hearted support and encouragement has been invaluable to me since 1980.

My thanks are also due to the staff of the Northwest Atlantic Fisheries Centre (DFO). Without their planning and long-term efforts in assembling the basic data, this work would have been impossible.

The Junta Nacional de Investigacao Cientifica e Tecnologica (JNICT), Lisbon, Portugal, has sponsored my work in Canada since 1986.

I dedicate this work to my son, Pedro Marco, and my late aunt Alice.

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Chapter 1

Introduction

One of the major goals of contemporary marine ecology is the prediction of changes in marine communities induced by natural phenomena and by human activities sustained over long periods of time. Directional changes in the physical environment and man's exploitation of living resources, for example, have persistent effects on population growth rates that affect the abundance of individual species and, ultimately, community structure. The comprehension of these effects and, more important, the ability to predict them, depends on understanding the community as a whole. What are the species involved and how do they interact ? How do the individual attributes of each species and the way communities are assembled determine the final outcome of a change taking place somewhere in the system ? Finally, but perhaps less obvious, does comprehensive biological knowledge of the community guarantee unequivocal long term predictions ? My thesis addresses these questions in the context of a large commercially exploited marine ecosystem on a boreal continental shelf – the Grand Bank of Newfoundland, Canada.

The quest to understand a complex system is a search for pattern and for the reduction of complexity to a number of easily comprehensible rules. However, as aquatic ecologists have long recognized (Powell 1989), pattern is largely dependent on scale and can be found at any level of investigation. Depending on the scale of observation adopted, the same variables can be perceived either changing so slowly that they can be assumed constant, or changing so fast that only their statistical properties are relevant. Piscivorous fish operate at larger scales and slower rates than do planktivorous fish which, in turn, operate at larger scales and slower rates than plankton. The formal recognition that complex systems in general, and ecosystems in particular, usually enclose a hierarchy of levels of organization, each with its characteristic rates associated with a given scale of observation, dates back to Simon (1962), has been formalized into a consistent body of principles by O'Neill et al. (1986) and can be understood within a much broader, dialectical view of the world (Levins and Lewontin 1985). More than just to provide a conceptual framework however, considerations of scale are increasingly important in ecology (O'Neill 1989) and the questions that they raise should be dealt with at the beginning of any sensible community study (Underwood 1986).

This thesis has been arranged in three parts that are suggested to follow a logical order of approach in community ecology (see also Sugihara 1983). Chapter 2 is an attempt to define a spatial scale for studies at the community level on the Grand Bank of Newfoundland. I have used a large data base (section 2.2) made available by the Department of Fisheries and Oceans (DFO) to define faunistically homogeneous areas that, year after year, are shown to form a regular geographic pattern on the Grand Bank (section 2.3). Some of the most abundant (and commercially important) fish species on the Bank are highly mobile and exhibit far-ranging movements. The areas defined are very large, in order to encompass these year-round movements (section 2.4), but their species composition remained reasonably persistent over a period of 17 years (section 2.5). It is reassuring that there seems to be some uniformity in major physical variables within each zoogeographic area identified. Section 2.6 provides evidence that these areas are not only aligned with the bottom depth of the Grand Bank but also with the major features of oceanographic circulation in the region.

Once the most abundant species within each zoogeographic area are identified, it becomes relevant to know how they interact. Chapter 3 synthesizes the most important features of feeding interactions on the southern and northern Grand Bank (sections 3.2, 3.3, 3.4) as inferred from available literature on species' diets.

The static food web structure emerging from this review can be compared with other marine food webs (section 3.5) but unfortunately static structure provides little insight into the dynamical aspects of species interactions. Feeding behaviour observed at the individual level does not translate directly into growth rates at the population level which, in turn, determine patterns of distribution and abundance. There is considerable uncertainty about the major determinants of population and community dynamics on the Grand Bank. I have handled this problem by building alternative topological configurations of the community, each meant to capture the main features of year-round community dynamics (section 3.7). These alternative models are all simple and biologically acceptable, but there is no information available to decide on which one is "better", i.e. more accurately represents the major determinants of community dynamics in the field.

Community structure, however, is not the only source of uncertainty when it comes to predicting dynamics. For each given structure, there is also considerable uncertainty concerning the values that parameters of population interaction should take. For example, what values should be attributed to the effect of cod density on the growth rate of capelin ? At the community level of observation, it is unlikely that we will ever be able to do better than take a probabilistic approach to this problem (May 1975, Yodzis 1989). Chapter 4 is aimed at investigating how these two main sources of uncertainty (community structure and population parameters) affect our ability to make long term predictions on the Grand Bank. Are there limits to knowledge when it comes to long term predictions even in well-defined simple situations ? To answer this question I simulate press experiments, a methodology of Bender et al. (1984), to represent the effect of environmental perturbations upon simple models of the Grand Bank community. Press experiments consist in removing individuals out of a population through a continuous period of time (section 4.3) and then examining the long term effect on all species in the community. It is shown that long term predictions about community dynamics are usually very sensitive to uncertainty in initial conditions (sections 4.6, 4.7) and therefore community behaviour is, to a large extent, indeterminate over time. The implications of these findings for the management of living resources are addressed in the discussion of Chapter 4 (section 4.8), although it is acknowledged that they extend far beyond the original scope of this thesis.

Chapter 2

Fish Assemblages on the Grand Bank

2.1. Purpose and History

2.1.1. Spatial scale, temporal scale, and fish assemblages

Whatever standpoint one adopts in the controversy about the relative role played by biotic and abiotic factors in determining species distributions (Saarinen 1982, McIntosh 1985), any sensible approach to a biological community should start by defining a spatial and temporal scale for the study envisioned (Underwood 1986). The purpose of Chapter 2 is to define an appropriate spatial scale for studies of community dynamics on the Grand Bank of Newfoundland. As Powell (1989) points out, the spatial scale of a problem can be defined on the basis of the significant variation of some quantity of interest. If we are interested in the biotic component of a continental shelf ecosystem, then a reasonable initial approach is to identify zoogeographic areas on the shelf that are characterized by a relatively homogeneous and persistent species composition. In this study, scale definition on the Grand Bank will be based on the identification and description of such areas. They should encompass the main year-round movements of the species there enclosed, and their boundaries should have some geographic consistency year after year. I map the areas, describe their species composition and, following common practice, identify the groups of species inhabiting them as fish assemblages. The criterion adopted for the definition of a fish assemblage is therefore "solely on the basis of geographic distribution" (Tyler et al. 1982), irrespective of whether species within the same assemblage area influence each other's growth rate or not.

The identification of fish assemblages and the study of their structure is heavily dependent on the choice of an appropriate time scale. There are two main reasons for this. The first has to do with statistical validation of the assemblage. The techniques of multivariate analysis used to identify fish assemblages eventually involve less objective decisions, for example in the choice of clusters in a dendrogram or in the number of axes to be retained after a factorial method has been used. These decisions can influence conclusions in terms of reported assemblages and respective geographic contours. One wants to make sure that the pattern of species co-occurrence observed one year is not a mere artifact of the methods used. A rational way of checking for the authenticity of the observed patterns of co-occurrence is to examine if they recur over a period of years. In this study I analyse a time period extending over 17 years, a time span that should be sufficient to guard against this sort of situation.

The second, perhaps more important reason for using an adequate time frame stems from the need to validate the assemblages themselves. If two species co-occur in a given area only during a short period of time, say one or two years, and then do not, there is usually little sense in including them in the same assemblage. Persistence, that is the ability of an assemblage to maintain its species composition, is an important requirement for assemblage validation. Persistence is not to be confused with stability (see a review of definitions in Pimm 1984) and the time scale required to deem an assemblage persistent is not necessarily the same needed to deem it stable. A strict interpretation of the definition of stability (e.g. Lewontin 1969) would require following the assemblage over at least two complete turnovers, one to check if it is at equilibrium and the other to follow how it responds to perturbations (Connell and Sousa 1983, Sutherland 1990). The time period required to deem an assemblage persistent appears yet more prone to subjective interpretations, but should probably encompass at least one complete turnover of the assemblage. If one defines this time period as being the longevity of the species with the longest life span in the community, then even the 17 years covered by the present study might not be long enough to guarantee one complete community turnover. However, if the time scale required to establish persistence is the generation time of the species in the community, then 17 years should be enough.

2.1.2. The past experience

Before the 1970's, studies embracing entire fish assemblages and extending over vast oceanic regions were uncommon, and rarely went beyond the compilation of species lists for given areas. By the end of the 1960's, the accumulation of data collected on continental shelves by fisheries-related activities and by scientific surveys, allied to the increasing availability of computational means, created conditions for the beginning of a comprehensive analysis of distribution patterns of fish assemblages over all the world ocean. The papers by Fager and Longhurst (1968) and Day and Pearcy (1968) should be mentioned as pioneer landmarks in the introduction of objective mathematical tools for the identification of large scale patterns of species co-occurrence on continental shelves.

In the past twenty years an increasing number of authors used different kinds of multivariate methods to identify demersal fish assemblages (Haedrich and Krefft 1978, Gabriel and Tyler 1980, Gabriel 1983, Overholtz 1983, Colvocoresses and Musick 1984, Mahon et al. 1984, Gomes 1987, Serrao 1989). These methods rely upon the initial construction of a proximity matrix between sites and/or species and range from simple Trellis diagrams to Cluster Analysis and various kinds of eigenvalue analyses (Orloci 1966, 1975; Clifford and Stephenson 1975, Chandon et Pinson 1981, Lebart et al. 1982, Gauch 1982). The data analysed have been either commercial catch statistics or samples from research surveys. The geographic areas covered have usually been large, extending over continental shelves and the upper part of the slopes.

Overall, multivariate techniques have proven to be useful tools in revealing the existence of relatively homogeneous fish assemblages covering large areas of continental shelves and slopes. Most of these studies concentrated on short-term aspects of fish assemblages (one to three years), but at least three studies covered a time period with the same order of magnitude as the life span of most fishes in the assemblage, presenting evidence of an overall constancy of the assemblages through time. Colvocoresses and Musick (1984) dealt with a 10-year period of surveys. In spite of some changes in assemblage composition and distribution from year to year, they found it to be very consistent in time. Mahon et al. (1984), dealing with 12 years of surveys on the Scotian Shelf, pointed out the dependence of the distribution patterns emerging on the scale of approach used to cluster their data. A large-scale approach resulted in a division of the Scotian Shelf into three regions. Discrimination of smaller regions within the larger ones remained the same through time. At a finer scale, 15 groups could be distinguished although with less constancy. Overholtz (1983) analysed a 15-year data series and stressed the importance of this long-term investigation for ecological and management purposes. He identified five main fish assemblages on Georges Bank whose spatial distribution remained remarkably constant despite strong variations in species richness and relative abundance.

As in most applications of multivariate methods, the question of cluster validity remains an important one. Any dissimilarity level can be chosen for establishing clusters in a dendogram. The delimitation of clouds of points in factorial planes may be a rather subjective matter as well. Some authors have resorted to special techniques aimed at lessening the subjectivity involved. Gabriel and Tyler (1980) partitioned their dendogram of site clumps into 12 groups based on the geographically contiguous location of the clumps. Colvocoresses and Musick (1984) used a method in the same spirit of mapping plots to obtain more objective partitioning decisions. They defined minimal groups in the dendogram of sites, then mapped and fused them if no significant differences in geographic distribution were found. Another possible method is the use of longer time series of data, allowing for a better judgment of the objectivity of the clusters identified. Both ideas have been applied in this study.

Most authors have attempted to relate environmental factors to the observed distribution of fish assemblages. Depth was almost unanimously found to be consistently associated with the greatest proportion of biological variation. In most instances depth is more or less associated with other environmental variables, some of which are routinely measured both in fixed stations of small areas and in trawl surveys. Variables like temperature (Fager and Longhurst, 1968, Haedrich and Krefft 1978, Mahon et al. 1984), salinity (Mahon et al. 1984, Overholtz 1983), type of bottom sediment (Day and Pearcy 1968, Mahon et al. 1984), or even latitude (Fager and Longhurst 1968, Gabriel and Tyler 1980, Overholtz 1983, Gomes 1987, Serrao 1989), were found to be associated with observed biological change.

2.2. Data and Methods

2.2.1. Data

Since 1971 the Department of Fisheries and Oceans (DFO) has been conducting Spring groundfish surveys off Newfoundland and Labrador in sub-areas 2 and 3 of the Northwest Atlantic Fisheries Organization (NAFO). I have analysed data collected during these Spring surveys (mostly April-May) in the three divisions of NAFO sub-area 3 that cover the Grand Bank of Newfoundland, divisions 3L, 3N and 3O (i.e. 3LNO - see Fig. 2). The time period covered by my study spans 17 years (1971-1987), although only 16 years of data were analysed (1971-82, 1984-87) because no groundfish surveys were conducted in 3LNO in 1983. Table 1 summarizes, year by year, the sources of the information analysed in 3LNO with respect to the research vessels, the time of the year, and the number of sampling stations. The research vessel "A.T. Cameron" conducted most of the surveys analysed up until 1984 (Table 1), at which time it was replaced by the "W. Templeman". The sampling plan of the groundfish surveys follows the stratified random method with stratification by latitude, longitude and depth. Sampling stations are allocated to strata according to area, with all strata containing at least two stations. Tows are for 30 minutes at 2.5 knots and water temperatures (surface and bottom) are recorded at each station. Table 1 shows the total number of stations conducted every spring in divisions 3LNO, and the number of stations actually analysed. Some of the stations had to be discarded because they had null catches of all the groundfish species selected for the study.

Every survey yields a two-way data matrix (stations x species) whose entry (i, j) is the catch in weight of species j at station i. For every year (1971-82, 1984-87) I have pooled the data of all surveys conducted during the corresponding Spring into one single matrix of groundfish catches. Species were included in the analysis if their biomass comprised at least 0.1% of the total catch in a given Spring survey. The number of species varied between 29 and 34, with 30 species (Table 2) almost always included.

TABLE 1. Data sources year by year in the three NAFO divisions covered by this study (3LNO). The data were collected by the research otter trawlers "A.T. Cameron" (Cam), "Gadus Atlantica" (Gadus), "A. Needler" (Need), and "W. Templeman" (Templ). Underneath the vessel's names are the months (roman numbers) during which surveys were conducted. "Stations" are the number of stations analysed each year (all divs. 3LNO pooled). "Total" is the total number of stations actually done during the survey. Some stations were discarded due to null catches of the species selected for each particular year.

NAFO div	1971	1972	1973	1974	1975	1976	1977	1978
3L	Cameron VI	Cameron V	Cameron IV, V	Cameron III,IV,V	Cameron V	Cameron IV, V	Cameron V	Cam, Gadus IV, V
3N	Cameron VI	Cameron V	Cameron IV, V	Cameron V	Cameron V	Cameron IV, V	Cameron V, VI	Cameron V, VI
3O	Cameron VI	Cameron V	Cameron IV, V	Cameron V	Cameron V	Cameron IV	Cameron V, VI	Cameron V, VI
Stations	122	80	110	125	111	146	192	187
Total	123	83	125	127	117	152	193	188

NAFO div	1979	1980	1981	1982	1984	1985	1986	1987
3L	Cam, Gadus V, VI	Cam, Gadus IV,V,VI	Cameron IV, V	Cameron III,IV,V	Needler V	Needler IV, V	Templ IV, V	Templ IV, V
3N	Cameron IV, V	Cam, Gadus IV, V	Cameron IV, V	Cameron III,IV,V	Needler IV, V	Need, Templ IV, V	Templ IV, V	Templ IV, V
3O	Cameron IV, V	Cam, Gadus IV, V	Cameron IV, V	Cameron III,IV,V	Needler IV, V	Needler IV	Templ IV, V	Templ IV, V
Stations	329	264	162	251	156	377	414	393
Total	338	264	165	256	158	377	423	399

TABLE 2. List of species used in the analysis of groundfish surveys.

Common name	Scientific name
Angler, Common	*Lophius americanus*
Argentine, Atlantic	*Argentina silus*
Capelin	*Mallotus villosus*
Cod, Atlantic	*Gadus morhua*
Eelpouts	*Lycodes sp.*
Eelpout, Vahl's	*Lycodes vahlii*
Eelpout, Arctic	*Lycodes reticulatus*
Greenland halibut	*Reinhardtius hippoglossoides*
Haddock	*Melanogrammus aeglefinus*
Hake, Longfin	*Urophycis chesteri*
Hake, Silver	*Merluccius bilinearis*
Hake, White	*Urophycis tenuis*
Halibut	*Hippoglossus hippoglossus*
Lumpfish, Common	*Cyclopterus lumpus*
Marlin-spike	*Nezumia bairdi*
Plaice, American	*Hippoglossoides platessoides*
Pollack	*Pollachius virens*
Redfish	*Sebastes sp.*
Roughhead grenadier	*Macrourus berglax*
Sea raven	*Hemitripterus americanus*
Sculpin, Longhorn	*Myoxocephalus octodecemspinosus*
Sculpin, Shorthorn	*Myoxocephalus scorpius*
Skate, Smooth	*Raja senta*
Skate, Thorny	*Raja radiata*
Spiny dogfish	*Squalus acanthias*
Witch flounder	*Glyptocephalus cynoglossus*
Wolffish, Broadhead	*Anarhichas denticulatus*
Wolffish, Spotted	*Anarhichas minor*
Wolffish, Striped	*Anarhichas lupus*
Yellowtail flounder	*Limanda ferruginea*

2.2.2. Cluster analysis

Cluster analysis was applied to investigate if there were groups of species that tended to occur together in the catches of groundfish surveys year after year. For each of the 16 Springs (1971-82, 1984-87), the data in the corresponding stations-by-species matrix was transformed (step 1), two algorithms of cluster analysis were applied (step 2), and three techniques were used to validate the clusters found (step 3). A step-by-step description of the operations follows, as well as justifications for the methods used.

1. The biological data (catch of species *j* at station *i*) were log-transformed ($ln(x+1)$) before every cluster analysis. The transformation is not aimed at achieving multivariate normalization, an ambitious goal with matrices usually so full of zero entries. As Gauch (1982) points out, differences in population abundance tend to be of an exponential nature. The variance of the most abundant species can easily dominate the results of multivariate analysis if the data are not transformed to correct for the influence of these species. Previous experience with groundfish data (Gomes 1987, Serrao 1989; see also Gauch 1982) indicated that the reduction of information to one-digit values (after the logarithm transformation) did not alter the results significantly.

2. All computations in this step were carried out using the CLUSTAN package (Wishart 1978). Stations were clustered using two agglomerative algorithms of cluster analysis. Two crucial decisions have to be taken at the outset of every cluster analysis (Chandon et Pinson 1981). The first (step 2.1) concerns the definition of a measure of proximity (similarity or dissimilarity) between the members of every pair of observations. A square matrix of proximities between observations is then built based on this measure. The second decision (step 2.2) concerns the choice of a process of automatic clustering that begins with the proximity matrix and derives a classification from it.

2.1. The semi-metric distance of Bray and Curtis, otherwise known as

Czekanowski's quantitative index, was used as a measure of dissimilarity between catches at any two fishing stations:

$$D_{ik} = \frac{\sum_j^p |x_{ij} - x_{kj}|}{\sum_j^p (x_{ij} + x_{kj})}$$

where D_{ik} is the dissimilarity between fishing stations i and k; x_{ij} is the catch of species j in station i and x_{kj} is the catch of the same species in station k; p is the total number of species in the data matrix. Notice that the denominator equals the sum of the total catch in the two stations. This coefficient ranges from zero (identical stations) to unity (totally dissimilar stations) and has previously been used for the analysis of groundfish surveys (Gabriel 1983, Overholtz 1983, Gomes 1987, Serrao 1989). Apart from performing well in measuring overlap in simple simulated situations (Bloom 1981) the coefficient has some appealing properties in the fisheries context, namely its sensitivity to abundant species. Since the denominator is constant for any pair of stations, the value of the coefficient is ultimately determined by species that give rise to outstanding differences in the numerator. One might then expect a clustering of stations mainly driven by abundant species, which are also the ones usually important for the fishery. However, these do not overshadow the less abundant species completely, given the balancing effect of the logarithmic transformation.

2.2. Observations (i.e. fishing stations) were clustered by two agglomerative polythetic methods: Group Average and Ward's Minimum Error Sum of Squares. Group Average (Sokal and Mitchener 1958, cit. in Chandon et Pinson 1981) begins by joining the pair of stations with the lowest dissimilarity value in the matrix of Bray-Curtis distances. The matrix is then rebuilt by evaluating the Bray-Curtis distance between any station and this new cluster as the average of the distances between the station and each constituent of the cluster. The same rationale is used when measuring the distance between any two clusters in further steps of the clustering process. Ward's method of Error Sum of Squares (Ward 1963) fuses those clusters (or station and station, or station and cluster) that yield the smallest total error sum of squares possible in each step of the clustering process. This error sum of squares is defined as the sum of the Bray-Curtis distances from each observation (fishing station) to the centroid of its current cluster, therefore it is a total within-clusters sum of squares. Since the total sum of squares is constant, a minimal within-clusters sum of squares implies a maximal between-clusters sum of squares. Even though Ward's method was originally developed for use with Euclidian distances, considerable empirical and formal evidence suggests that it performs well even with non-metric distances (cf. Batagelj 1988) such as the Bray- Curtis.

3. The validity of clusters of stations identified by cluster analysis was assessed by three methods:

i. Mapping the clusters and checking for geographical continuity of stations belonging to the same cluster.

ii. Visual confirmation of clusters coherence in the two-way table yielded by TWINSPAN (see below).

iii. Matrices randomly chosen were analysed by using the relocation procedure available in procedure RELOCATE of CLUSTAN and results were compared with those previously found by Group Average and Ward's method. RELOCATE was initiated with a random allocation of stations to 10 clusters. The method repeatedly scans these clusters by measuring the dissimilarity of each station to every cluster. Eventually the station is relocated if it is found closer to a cluster other than its own, causing a recalculation of the cluster's centroids. Once relocations stop, the less dissimilar clusters are fused and the scanning process starts again. Convergence of the results of this technique with those of Group Average and Ward's method was taken as good evidence that a global optimum had been found (Wishart 1978).

Usually considered "well-behaved" methods, Group Average and Error Sum of Squares have significant differences in clustering "intensity" (for a thorough discussion see Clifford and Stephensen 1975 and Boesch 1977) that were also explored for purposes of cluster validation. Joint use of the two methods was conducted by first identifying clusters yielded by Group Average that were geographically contiguous. The conservative properties of this method resulted in a considerable number of stations "laid-off" by chaining effect. These stations were often atypical, but a quick inspection of the tight clusters of Ward's dendrogram (with its relatively few lay-offs) provided a clue to the similarity between those stations and clusters in the Group Average dendrogram.

2.2.3. Interpretation method

Different techniques have been suggested for the interpretation of results of cluster analysis. Examples are inverse clustering of variables followed by nodal analysis (Lambert and Williams 1962) and the computation of cluster diagnostics (procedure RESULT of CLUSTAN, Wishart 1978). However, inverse hierarchical clustering of species held little attraction because of the discrete nature of exclusive classifications that lead to the inclusion of each species into a single cluster, no matter how ubiquitous that species may be. Moreover, ecologists have defended the practical and theoretical advantages of using polythetic divisive methods as opposed to agglomerative ones (Lambert et al. 1973, Boesch 1977, Gauch and Whittaker 1981, Gauch 1982). "Polithetic divisive methods have theoretical advantages in that all the available information is used to make the critical topmost divisions" (Lambert et al. 1973), resulting in a classification less sensitive to influence by the random "noise" commonly found in ecological samples.

Hill, Bunce et al. (1975) proposed a polythetic divisive method based on an ordination technique under the name of "indicator species analysis". This method has been refined and computerized by Hill (1979) as TWINSPAN. The method makes an initial ordination of species and samples using correspondence analysis. A rough division of samples is done based on scores on the first factorial axis and "differential" species are identified by their preference to one or the other side of the dichotomy. A second, "refined", ordination is then achieved by using "differential" species and the new ordination is divided to derive a final dichotomy. The process proceeds in the same way over the two sides of this dichotomy.

The final results of TWINSPAN are displayed in a two-way table that fulfills requirements of non-exclusivity. An ubiquitous species can therefore be associated with more than one cluster of stations by simple visual inspection. Inspection of such two-way tables allowed the recognition of biological features of each of the main station clusters previously identified by cluster analysis. Such features included not only actual differential species (i.e. species having clear preference for a given cluster) but also the presence or absence of a very widespread species in a cluster, or anomalies in cluster richness (number of species present). These features were used to classify stations laid off the main clusters or to ratify the classification of those ambiguous stations usually located on geographical boundaries of the areas occupied by the main station groups.

2.3. Results

2.3.1. Fish assemblages: A global picture

Four major clusters of stations recurred consistently in the dendrograms computed for each Spring of the 16-year time series. When these clusters were mapped, they were closely associated with the bottom topography of the Grand Bank. The geographic contours of the areas comprising three of the clusters approximately followed isobaths near the edge of the Bank. These three groups were therefore named according to their most common depths: Shallow Group (stations shallower than 80 m), Intermediate Group (stations between 80 and 200 m), and Deep Group (stations deeper than 200 m). The fourth major cluster comprised stations just to the east of the Avalon Peninsula and therefore was called Avalon Group (stations between 70 and 180 m, in the Avalon Channel area). Fig. 1 shows two dendrograms (for the first and last Spring) yielded by the group average algorithm. Although the major clusters could usually be identified at the higher levels of the clustering hierarchy, their Bray-Curtis distances in the dendrogram were rather variable from year to year and no special meaning was attached to them.

Both the Intermediate Group and the Deep Group could be further subdivided on the basis of faunal differences. Stations in each of these subclusters were located in continuous strips encircling the Bank in a way that was geographically consistent from year to year. Following their geographic location, the Intermediate Group was subdivided into the NE Intermediate Sub-Group to the northeast and the SW Intermediate Sub-Group to the southwest. The Deep Group was subdivided into the NES Deep Sub-Group around the north, east, and south of the Bank slope and the W Deep Sub-Group to the west.

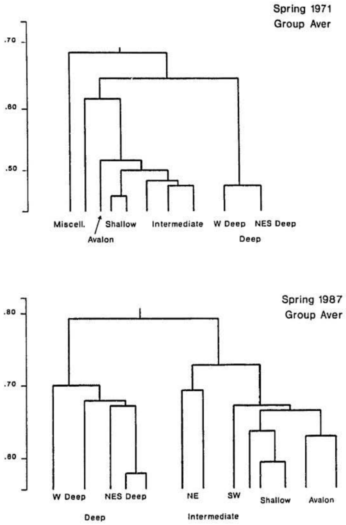

Figure 1. Results of cluster analysis with the Group Average algorithm for Spring 1971 and 1987. The dendrograms shown are cut at high hierarchical levels where it is possible to distinguish the major recurrent clusters of stations.

Fig. 2 shows the major physical features of the Grand Bank and the major NAFO (Northwest Atlantic Fisheries Organization) divisions that will be mentioned in the forthcoming text. Fig. 3 portrays an "average" picture, the most typical geographical extent of the six main clusters of stations (Avalon, Shallow, NE Intermediate, SW Intermediate, NES Deep, W Deep) identified on the Grand Bank. The area defined by each cluster has a characteristic composition of groundfish species that recurrently co-occurred therein, i.e. a fish assemblage. Table 3 lists the composition of these fish assemblages for every area, and the most abundant species in each area are shown in Fig. 4. I have ranked the species according to their relative abundance in the trawl catches, with straight lines separating groups of species that have different orders of magnitude in abundance (Table 3 and Fig. 4). This is only a rough ordering because assemblages underwent quantitative changes in their composition during the time period analyzed (see section 2.5 for details). A global description of the main characteristics of each of these zoogeographic areas follows. Section 2.3.2 presents an account of the year by year characteristics of each area.

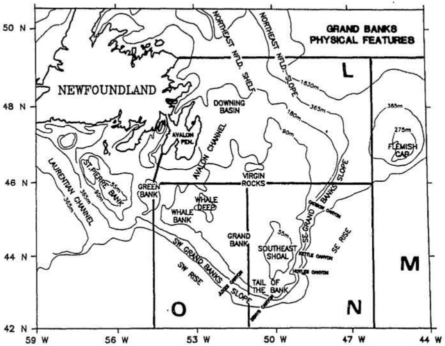

Figure 2. Bathymetry and other physical features of the Grand Bank region. The straight lines countour NAFO Divs. 3L, 3N, 3O, and 3M.

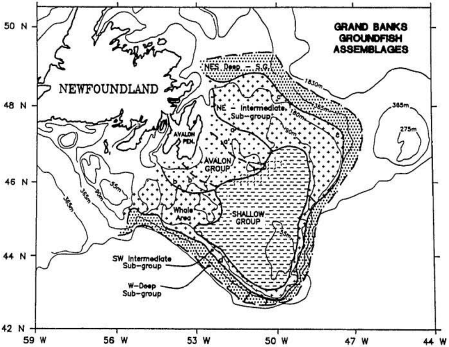

Figure 3. Geographic position of the main clusters of stations defining the fish assemblages of the Grand Bank. The contours presented were pooled out of 16 Spring situations analysed. They represent the most typical situation found, rather than any particular year. Different patterns cover areas with different fish assemblages. The Deep and Intermediate areas are subdivided in two sub-groups (see text).

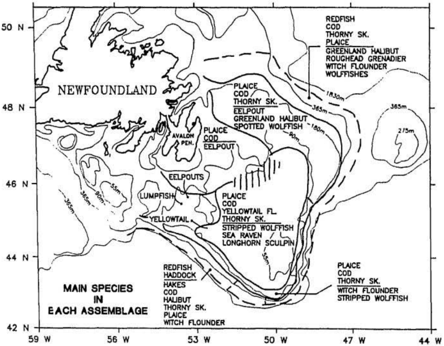

Figure 4. Main species in each of the six fish assemblages considered. Species are ranked by approximate decreasing order of abundance in the hauls. Straight horizontal lines separate groups of species having different orders of magnitude in the catches.

TABLE 3. Species composition of the goundfish assemblages on the Grand Bank. Horizontal lines separate sets of species with decreasing orders of magnitude as expressed by kg/tow in hauls. Within each order of magnitude, species were ranked by approximate decreasing order of abundance. Species without asterisks were found present throughout the area of the correspondent assemblage at least 13 out of 16 years. Species with (*) showed up in at least 13 out of 16 years, although in more or less restricted regions within the correspondent assemblage area. Species with (* *) showed up between 7 and 12 years out of 16.

Shallow Assemblage

Plaice, cod, yellowtail flounder, thorny skate
Striped wolffish (*), sea raven, longhorn sculpin

Avalon Assemblage

Plaice, cod
Arctic eelpout

Intermediate Assemblage

NE Intermediate Assemblage

Plaice, cod, thorny skate
Arctic eelpout, Greenland halibut, spotted wolffish

SW Intermediate Assemblage

Plaice, cod, thorny skate
Witch flounder, striped wolffish, arctic eelpout (*)

Deep Assemblage

NES Deep Assemblage

Redfish, cod, thorny skate, plaice
Greenland halibut, roughhead grenadier, witch flounder, striped wolffish
Vahl's eelpout (* *), spotted wolffish (* *), broadhead wolffish (* *)

W Deep Assemblage

Redfish, haddock (* *)
White hake, cod, halibut, thorny skate, plaice
Witch flounder, silver hake, longfin hake, argentine, angler, marlin-spike

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Shallow Group

The Shallow Group occupies a major shallow area on the southeast Grand Bank (Fig. 3). Its species composition was remarkably constant over the time period analyzed (section 2.5). The eastern, southern and western borders of the Shallow Group lie near the 90-m isobath. The group extends to the Whale Bank in the west and meets the Avalon Group to the north. Stations in the Shallow Group had depths ranging from 40 to 100 m, with average values around 70 m and standard deviations of 12 m or less. Bottom temperatures were usually between -1 and $+2°$ C.

Four species dominate this group: American plaice, cod, yellowtail flounder, and thorny skate. Yellowtail flounder was the key species used to identify stations belonging to this group. Three other species also recur in the Shallow Group, but in much lower abundance: striped wolffish, sea raven, and longhorn sculpin. Striped wolffish was usually restricted to samples taken south of 45° N latitude.

Avalon Group

The Avalon Group occupies the zone around the Virgin Rocks, most of the Avalon Channel, and the southern Downing Basin (Figs. 2 and 3), with boundaries that changed position considerably from year to year. They can be expected to lie between lines *a* and *a'* of Fig. 3 to the east, and lines *b* and *b'* of the same figure to the west. Station depths varied between 70 and 180 m with average values around 120 m and standard deviations between 25 and 40 m. Bottom temperatures were usually between -1.5 and $0°$ C.

The Avalon Group has two strong dominants: American plaice and cod. The third characteristic species is the Arctic eelpout, almost always present although in very low amounts. The group is remarkably poor in regard to number of species relative to the other areas of the Bank. Stations of this group were distinguished from Shallow Group stations to the south by the disappearance of two important species: thorny skate and yellowtail flounder. These two species were not usually found north of a line between Whale Bank and Virgin Rocks. Yellowtail was often caught further north than was thorny skate, mainly in the Virgin Rocks area. The differential distribution of these two species suggested the existence of an intermittent narrow transition zone between the Avalon Group and the Shallow Group, indicated in Fig. 3 with a different shadowing pattern, where typical dominants are cod, plaice and yellowtail with eelpouts in very low abundance. The Avalon Group was distinguished from the Intermediate Group by the absence of thorny skate and lower species richness.

Intermediate Group

This group occupies a transition zone between the two shallow water groups (Shallow and Avalon) and the Deep Group. Three species dominate: American plaice, cod and thorny skate. Other species, much lower in abundance though constant in their presence, provided a basis upon which to subdivide the Intermediate Group into a NE Intermediate Sub-Group and a SW Intermediate Sub-Group.

NE Intermediate Sub-Group

The NE Intermediate Sub-Group occupies a vast area comprising the Downing Basin and much of the northeast Grand Bank (Fig. 3). Its southwest limit extends to near Carson Canyon. The deeper boundaries of this Sub-Group lie between the 200 m and 280 m isobaths. These boundaries were relatively variable in depth from one year to another (section 2.3.2), their exact placement depending on the upper distribution limit of redfish, the dominant species in the NES Deep Sub-Group (see below). The shallower limits of the NE Intermediate Sub-Group were near the 90 m isobath, with average depths around 150 m and standard deviations close to 50 m. Bottom temperatures were usually between -1.2 and 2.3° C.

The NE Intermediate Sub-Group includes American plaice, cod and thorny skate. Other species usually present in relatively low abundance were Arctic eelpout, Greenland halibut and wolffishes (especially spotted wolffish). Arctic eelpout was usually the more abundant of these lesser species, with a distribution mainly to the north and northeast of Carson Canyon but also often found in the Hoyles and Kettle Canyon region.

SW Intermediate Sub-Group

The SW Intermediate Sub-Group occurs along a narrow strip on the southern and western upper continental slope (Fig. 3). Typical depths of stations belonging to this Sub-Group were between 90 and 200 m, with average values around 110 m. In the Whale Bank area, some included stations were shallower than 90 m. Difficulties arose for almost every year in determining the deeper boundary of this Sub-Group, not only due to yearly changes in the actual depth of the boundary but also because of imprecision in depth determination arising from the steep slope in the area. As with the previous Sub-Group, the position of the deeper boundary was set depending on the upper limits of typical species in the Deep Group (see below). Throughout the year-by-year analysis hakes and redfish from the W Deep Sub-Group appeared more prone to move above the 150-200 m depth zone in the southwest than to the north and east of the Bank.

The SW Intermediate Sub-Group comprises American plaice, thorny skate and cod. Species recurring in much smaller amounts are witch flounder and striped wolffish. Localized invasion by species from deeper waters, especially redfish and hakes, was a frequent phenomenon. The SW Intermediate Sub-Group includes the Whale Bank and the Whale Deep to the west of the Grand Bank (Fig. 2). This region is relatively unstable in species composition, compared to the rest of the area occupied by the Sub-Group and might justify separate treatment. The core of the Whale Bank and Deep region seems to be fairly constant in regard to the dominating presence of cod, thorny skate and American plaice. Most of the area, however, is prone to invasion by species typical of other assemblages. Stations to the north often resemble typical stations from the Avalon Group in that they lack thorny skate and/or may include Arctic eelpout, which has extended its distribution all along the

Avalon Channel. Yellowtail flounder, a typical representative of the Shallow Group, is often found to the south in the Whale region but shallower than 90 m. Lumpfish, whose main distribution is further to the north on the St. Pierre and Green Banks, is also sometimes found in significant amounts on Whale Bank. One other species occasionally found in the Whale region as well as the rest of the SW Intermediate Sub-Group is the witch flounder.

Deep Group

The Deep Group encircles the Grand Bank below 200 m (Fig. 3). The upper depth limit is rather variable. Boundaries between the Deep and the Intermediate Groups tend to become shallower as one moves south and west along the upper continental slope. To the west of the Grand Bank the boundary frequently lies shallower than 150 m. The absence of deeper samples precludes a full assessment of the Deep Group distribution limits. The outside depth limits are expressed by a dashed line in Fig. 3 which is drawn to include all samples taken on the upper slope by the groundfish surveys analyzed. The Deep Group is dominated by redfish, but is also distinguished in being the richer group in terms of number of different species. Differences in the relative importance of species other than redfish lead to a subdivision of the group into a NES Deep Sub-Group and a W Deep Sub-Group.

NES Deep Sub-Group

This Sub-Group occurs along the northern, eastern and southern borders of the Grand Bank. Its boundary with the W Deep Sub-Group is in the Tail of the Bank region, lying in a relatively unstable position between Denys and Jukes Canyons. The shallow limit of the NES Deep Sub-Group to the north and east of the Grand Bank ranged between 180 and 280 m from year to year. These variations were mostly caused by irregular invasions of shallower waters by redfish. In some years a transition strip between the NES Deep Sub-Group and the NE Intermediate Sub-Group was identified, with redfish, Arctic eelpout, cod, thorny skate and plaice the important species. To the southwest, the upper limit of the NES Deep Sub-Group becomes progressively more indeterminate, but it seems to become somewhat shallower. Stations in the NES Sub-Group had average depths around 280 m and standard deviations around 50 m. Bottom temperatures were warmer than in most other groups, ranging from 0 to 4° C.

Three species dominated the NES Deep Sub-Group by abundance and constant presence: redfish, cod and thorny skate. Five other species and species-groups were found on a regular basis; in approximate rank order they were American plaice, wolffishes (striped, spotted and broadhead), Greenland halibut, witch flounder and roughhead grenadier. Vahl's eelpout was often present, although its abundance was always very low.

W Deep Sub-Group

The W Deep Sub-Group occurs along the western slope of the Grand Bank (Fig. 3). As mentioned, its boundary with the NES Deep Sub-Group lies between Jukes and Denys Canyons. The upper depth limit of this Sub-Group can be as shallow as 100 m, somewhat shallower than the upper limit of the NES Deep Sub-Group. Variability in that limit is mostly due to occasional invasions of shallower waters by redfish and hakes. Average depth of stations was around 250 m and there were high annual standard deviations, ranging from 60 to 90 m. Bottom temperatures were almost always greater than 0 and could reach +9° C, the highest temperature recorded at the bottom during the surveys analyzed.

One species dominated the W Deep Sub-Group – redfish. Haddock (since 1983), halibut (since 1978), cod, white hake and thorny skate followed in importance. Nevertheless the abundance of these species in relation to redfish was much lower than in the NES Deep Sub-Group. Other species usually present in low abundance were American plaice, other hakes (silver and longfin) and argentine. Angler and marlin-spike were almost always present though in very low abundance.

2.3.2. Fish assemblages year by year

This section is an account of apparent anomalies in the year-by-year distribution and temperature conditions of the fish assemblage areas on the Grand Bank (Figs. 5 to 20). This information is included for completeness, but the matter of annual variation here described will not be an issue in the chapters which follow. Those readers wishing to pursue the central themes of the thesis can skip to the discussion of the overall coherence of the fish assemblages identified (section 2.4).

The situation described for each year should be compared with the "average" pictured portrayed in Fig. 3. The hatching patterns representing each major fish assemblage in Figs. 5 to 20 (the same used in Fig. 3) cover only areas that were sampled, leaving blank those that were unsampled. The assemblages are separated by a continuous thick line that is not to be confused with the isobaths of the Grand Bank (Fig. 2); in some areas this line is dashed due to uncertainties about its location. The line is not drawn when the limits of a given area are unknown due to lack of sampling stations; a typical example was the outward limit of the Deep Group, always unknown because sampling stations seldom went beyond the 400 m isobath. Figs. 5 to 20 also show the number of sampling stations on which the hatching of each area is based. Surface and bottom temperature anomalies will sometimes be mentioned for specific areas in specific years. For every area, the anomalies refer to major deviations from the mean of the 16-year time series in the area.

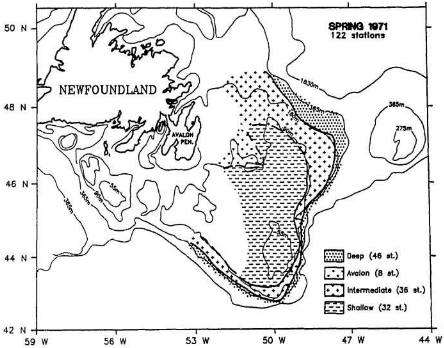


Figure 5. Areas covered by each major cluster of stations in Spring 1971.

Spring 1971

The number of sampling stations was relatively low in the first half of the 1970's, usually not covering the west of the Bank and the Avalon Channel area. In Spring 1971 yellowtail flounder (and therefore the Shallow Group) appeared to extend unusually far to the north, along the 90 m isobath, entering an area that is usually Intermediate. The Intermediate Group appeared to extend deeper than usual to the north, almost reaching the 365 m isobath, basically meaning that the northern limit of redfish distribution (the main indicator of the Deep Group) was deeper than usual there. Average surface temperatures were abnormally high in the

Shallow Group (6.95° C), in the Avalon Group (6.81° C), in the NES Deep Group (4.64° C), and in the NE Intermediate Group (5.73° C). There were no such anomalies in bottom temperatures.

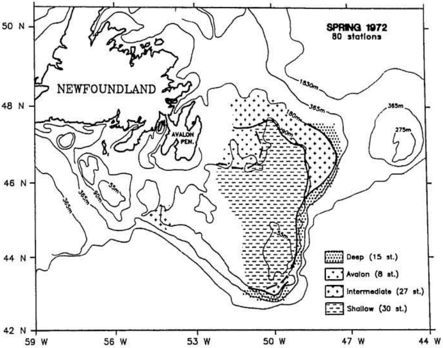


Figure 6. Areas covered by each major cluster of stations in Spring 1972.

Spring 1972

This is the year with the smallest total number of sampling stations (only 80). As in 1971, yellowtail flounder (and the Shallow Group) appears to extend up to the north into an area that in most of the years was NE Intermediate.

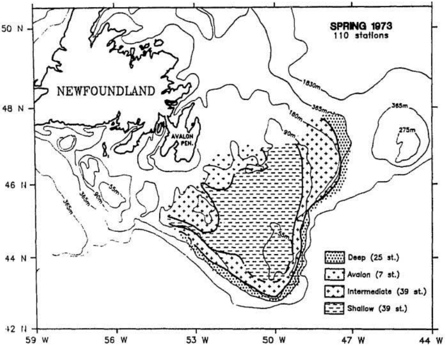


Figure 7. Areas covered by each major cluster of stations in Spring 1973.

Spring 1973

The major anomaly in 1973 seems to be an unusual extension of the SW Intermediate Sub-Group to shallow waters around 52° W on the SW shelfbreak of the Bank, which could have been caused by an intrusion of warm waters from the south. Bottom temperatures of five stations in the area averaged 3.06° C (st. dev. = 0.8), which is warm relative to the −0.16° C (st. dev. = 1.08) average for water close to the bottom in the Shallow Group as a whole. Witch flounder was particularly abundant in the SW Intermediate Sub-Group this Spring, more abundant than thorny skate and cod. Overall 1973 appeared to be a very cold year. The average surface (0.55° C) and bottom temperatures (−0.16° C) in the Shallow Group were the coldest in the 16-year time-series of this Group. The same applies to the average surface (−0.33° C) and bottom (−1.37° C) temperatures in the Avalon Group, and for the bottom temperature (−0.99° C) in the NE Intermediate Sub-Group. The SW Intermediate Sub-Group was not particularly cold near the bottom (average of 0.14° C), but had the third coldest average surface temperature (1.11° C) in this Sub-Group.

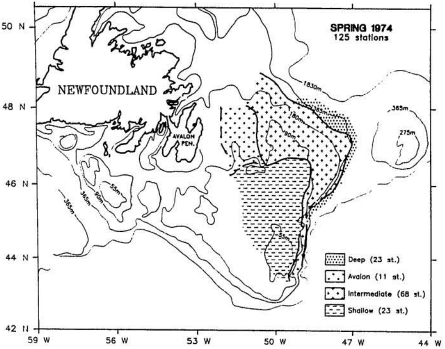


Figure 8. Areas covered by each major cluster of stations in Spring 1974.

Spring 1974

The sampling plan in 1974 was geographically restricted but still revealed what appears to be an anomalous situation. The Avalon Group was unusually extended to the NE, entering an area of the Downing Basin that in other years is typically part of the NE Intermediate Sub-Group. This means that thorny skate was not abundant in this area and that the distribution of eelpouts extended NE along the Avalon Channel. Unusually low temperatures are a possible explanation for this observation. The average bottom temperature of 11 stations there was −1.28° C (st. dev. = 0.16) which is relatively cold if compared with typical bottom temperatures of the NE Intermediate Group this Spring (average of −0.08° C, st. dev. = 1.24), but not so different from typical bottom temperatures of the Avalon Group (usually below 0° C). Along the NE slope, the deeper limit of the Intermediate Group stays close to the 365 m isobath, suggesting that the upper limit of the redfish distribution (Deep Group) was deeper than usual this Spring. This year appears to be relatively cold on the Grand Bank, but apparently not as cold as 1973. Average temperatures in the Avalon Group were −1.25° C at the bottom and 0.65° C close to the surface. In both cases these were the third coldest averages in the time series of this Group. Surface temperatures were also relatively low in the Shallow (1.68° C) and in the NE Intermediate Sub-Group (0.55° C).

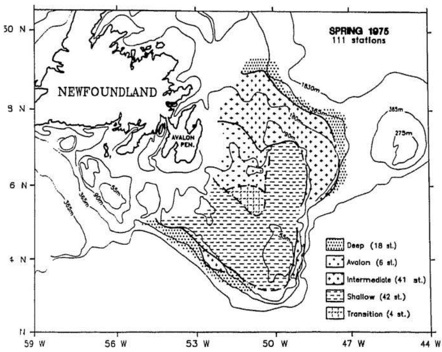


Figure 9. Areas covered by each major cluster of stations in Spring 1975.

Spring 1975

The distribution of yellowtail flounder appears to have extended a little more than usual onto the Whale area and the western Avalon Channel in 1975. Another distinctive feature is the appearance of a transition area to the south of the Virgin Rocks, intruding onto the central Grand Bank. This area has the characteristics of the Avalon Group (low species richness, absence of thorny skate, eelpouts present) mixed with the major characteristic of the Shallow Group (i.e. high catches of yellowtail).

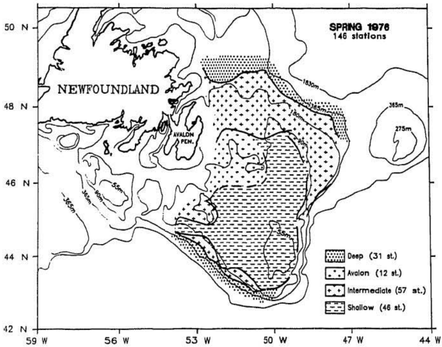


Figure 10. Areas covered by each major cluster of stations in Spring 1976.

Spring 1976

The Spring of 1976 appeared to have rather "average" conditions insofar as the distribution of fish assemblages is concerned.

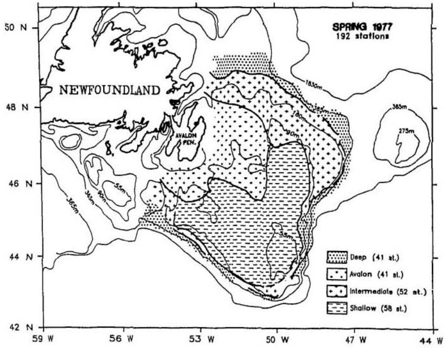


Figure 11. Areas covered by each major cluster of stations in Spring 1977.

Spring 1977

The Avalon Group covered an unusually large area this Spring. Basically this means that thorny skate was uncommon in the area extending from the NE of the Avalon Channel up to the Downing Basin and there were few yellowtail on the Virgin Rocks. The average bottom temperature of four stations at the NE limit of the Avalon Group was -0.74° C (st. dev. = 0.19) which might not be cold enough to explain the absence of thorny skate to the north. The average bottom temperature of six stations at the SW limit of the Avalon Group (close to the Whale Deep, but within the Avalon Group) was -0.8° C (st. dev. = 0.61) which is relatively cold in that area and suggests an intrusion of cold water along the Avalon Channel. Average temperatures were relatively high at the surface in some of the areas (5.88° C in the Shallow, 4.74° C in the Avalon, 5.08° C in the SW Intermediate, and 3.34° C in the NES Deep), but not so at the bottom.

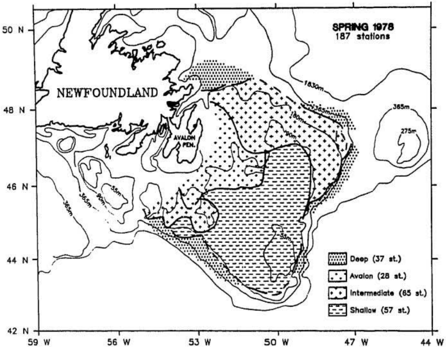


Figure 12. Areas covered by each major cluster of stations in Spring 1978.

Spring 1978

Perhaps the most unusual feature of this year was the apparent intrusion of redfish onto the SW shelfbreak of the Grand Bank. White hake followed redfish in abundance in that area, although one or two orders of magnitude lower. Bottom temperatures of seven stations located in that particular area averaged 7.9° C (st.

dev. = 1.43), which suggests an intrusion of warm water onto the shelf. In the Shallow Group as a whole, average bottom temperature was the highest of the time series in that Group (1.58° C, along with 1979); it was also the highest in the Avalon Group (0.47° C) and in the NE Intermediate Sub-Group (0.77° C). Average bottom temperature was the second highest of the series in the W Deep Sub-Group (8.26° C).

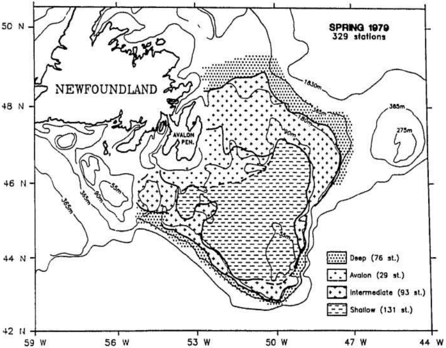


Figure 13. Areas covered by each major cluster of stations in Spring 1979.

Spring 1979

This year had the best sampling coverage of the 1970's and early 1980's. The fish assemblages appear to have an "average" distribution with the only characteristic feature being perhaps the intrusion of yellowtail onto the north of the Whale Deep. The Spring of 1979 was warm. Both bottom and surface average temperatures hit high values, relative to the 16-year time series, within all Groups and Sub-Groups of stations over the Bank.

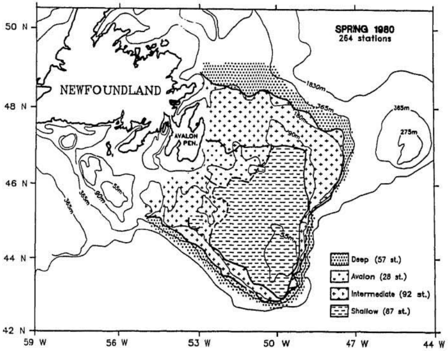


Figure 14. Areas covered by each major cluster of stations in Spring 1980.

Spring 1980

This Spring thorny skate was relatively abundant to the NE of the Avalon Channel, apparently spreading from the Downing Basin area. Redfish appears to have intruded onto areas shallower than usual at the north of the Bank, reaching the 180 m isobath at the northern outskirts of the Downing Basin. There were no major temperature anomalies.

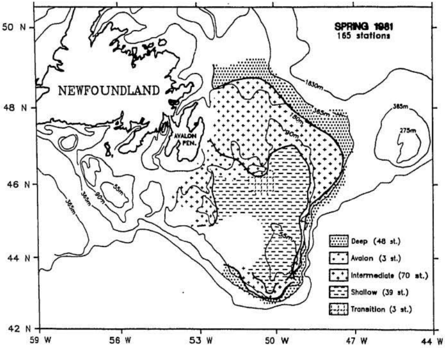


Figure 15. Areas covered by each major cluster of stations in Spring 1981.

Spring 1981

The NE Intermediate Sub-Group exhibited an unusually wide distribution this year, intruding into the Avalon Channel and the Virgin Rocks. This was due to an apparent southward extension of the distribution of thorny skate. Species richness in those areas was also more characteristic of the Intermediate Group. It was possible to distinguish a transition area to the south of the Virgin Rocks (with yellowtail, cod, plaice, and no skate). As in 1975, the sample size is too small (3 and 4 stations) in this transition area. In the Shallow Group, average bottom water temperature was the highest of the time series (1.73° C), and it was also relatively high at the surface (5.5° C).

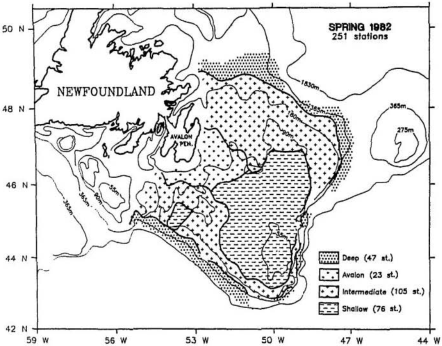


Figure 16. Areas covered by each major cluster of stations in Spring 1982.

Spring 1982

Perhaps the main anomaly in 1982 was the apparent retreat of yellowtail flounder from the area to the south and SW of the Whale area, along the SW shelfbreak of the Bank. The area was nevertheless relatively well sampled (about 17 stations), but yellowtail was caught only in a small area inside the Whale area (Shallow Group hatching inside the Whale area). The average bottom temperature of 9 stations located along the SW of the Bank, close to the break but above 90 m, was 0.79° C (st. dev. = 1.02), which does not appear unusual for Shallow Group stations, although yellowtail was not caught there. Thorny skate appeared to be relatively abundant to the NE of the Avalon Channel, and therefore the Avalon Group is relatively restricted. Bottom temperatures of five stations at the border between the Avalon and the NE Intermediate Sub-Group (but inside the latter) averaged −0.44° C which seems to be a transition temperature between the NE Intermediate (with average 0.19° C) and the Avalon (average −0.59° C).

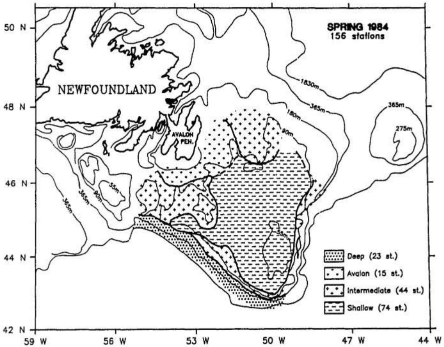


Figure 17. Areas covered by each major cluster of stations in Spring 1984.

Spring 1984

The distribution of fish assemblages on the Grand Bank in 1984 did not exhibit any major anomalies.

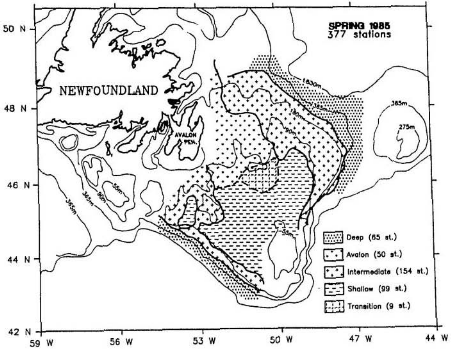


Figure 18. Areas covered by each major cluster of stations in Spring 1985.

Spring 1985

The Avalon Group appeared to have shifted its usual center of gravity to the NE, basically because thorny skate was fairly abundant to the SW of the Avalon Channel. However, bottom temperatures in 5 stations located inside the SW of Avalon Channel, where thorny skate was caught, averaged −1.46° C (st. dev. = 0.11) which is cold even for the Avalon Channel. A transition area was apparently present to the south of the Virgin Rocks, with cod, plaice, yellowtail, and very few thorny skate. The Spring of 1985 was cold. There were some particularly low temperatures close to the bottom (averages of −0.02° C in the Shallow Group, −0.81° C in the NE

Intermediate, −0.61° C in the SW Intermediate) and at the surface (averages of 0.67° C in the Shallow Group, −0.15° C in the Avalon, −0.4 ° C in the NE Intermediate, 0.29 ° C in the SW Intermediate, −0.52° C in the NES Deep, and 1.95° C in the W Deep).

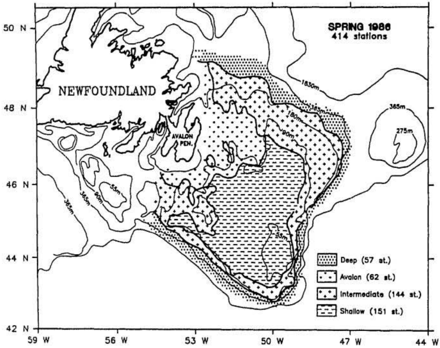


Figure 19. Areas covered by each major cluster of stations in Spring 1986.

Spring 1986

Spring of 1986 was a well-sampled year with conditions that appear close to the "average".

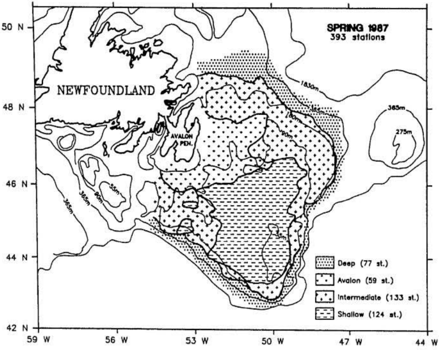


Figure 20. Areas covered by each major cluster of stations in Spring 1987.

Spring 1987

The Avalon Group in 1987 intruded eastward into the NE Intermediate Sub-Group, mostly due to the absence of thorny skate in the area. I have averaged the bottom temperatures of 6 stations located in the area of the intrusion (around 47.5° N, 50.5° W) but the value appears too high to be reliable (4.3° C, st. dev. = 1.29). Practically no thorny skate was caught along the Avalon Channel this year. Yellowtail flounder appeared to be less abundant than usual close to the shelfbreak of the Bank in the Carson Canyon and Kettle Canyon areas.

2.4. Biological Coherence of Assemblages

Multivariate techniques are useful tools for taking a first exploratory step towards defining faunal assemblages. The next step is to identify those that are biologically coherent. A biologically coherent assemblage is one in which the component fish stocks are totally enclosed within it, as opposed, for example, to an assemblage whose area encompasses only an ontogenic phase of a given stock with the other ontogenetic phases in areas of other contiguous assemblages. A coherent assemblage is most easily recognized when its species are exclusively found in that assemblage. For example, yellowtail flounder seems exclusive to the Shallow Assemblage of the Grand Bank. Regardless of whether it is composed of one or several stocks, the Shallow Assemblage is coherent with respect to yellowtail. The same is not true with regard to the cod, a species that was important in all assemblages identified.

Where ubiquitous recurrent species are responsible for a part of the overlap between assemblages, further investigation is required to judge how coherent and natural are the assemblages yielded by the multivariate analysis. One might end up fusing areas belonging to initially separated assemblages if they share stocks comprising an important proportion of the total biomass. A brief literature review was carried out for the dominant groundfish species in order to confront the assemblages herein presented with biological information on their populations.

Atlantic cod

Cod populations in NAFO div. 3L have been integrated in the 2J 3KL northern stock complex for management purposes, whereas cod in 3NO have been managed on its own as a single southern stock. There are, however, differences in the characteristics of cod in div. 3L (Lear 1986). There is evidence that deep-dwelling cod (350-450 m) in div. 3L (my NES Deep Sub-Group) are more similar to those from 2J 3K divisions in vertebral numbers and allele frequency at a studied locus than cod caught in shallower depths (180 m) of div. 3L. The latter are more similar to cod in div. 3NO. Analysis of tag data, studies of growth rates and parasitic infection rates (Templeman 1974; Lear 1985, 1986) suggest the possible existence of a northern Grand Bank stock comprising the area of the "nose of the Bank" (inside my NE Intermediate area), the Virgin Rocks area and the Avalon Channel area, separated from a Labrador-East Newfoundland complex (div. 2J 3K and deep 3L) and from the 3NO cod to the south. This hypothetical cod stock overwinters on the northern Grand Bank, is basically limited to div. 3L, and contributes to inshore fisheries from Trinity Bay south to St. Mary's Bay in summer (Lear 1986). Templeman (1974) called this group the Virgin Rocks population or stock. A great deal of cod in my NE Intermediate Assemblage, as well as in the northern part of the Shallow Assemblage, would belong to this stock. Cod from the NES Deep Assemblage would be part of the northern complex (2J 3K). In the area of the Avalon Assemblage is the Avalon-Burin stock complex (Templeman 1962, 1974), localized close to the Avalon Peninsula. The area is also visited in summer by individuals from the Labrador-Newfoundland complex and from the Virgin Rocks group. It is also especially visited by migrants from the 3NO area (Templeman 1974, Lear 1986). Overall, it is obvious that there is little sense in keeping the Avalon Assemblage distinct from a "cod's point of view", but it is not so clear with which other group it should be merged. In keeping with current practice, I will assume that this group has more association with the NE Intermediate Assemblage (NAFO div. 3L) than with the Shallow Assemblage, but I acknowledge that a case could be made for doing the opposite.

Yellowtail flounder

The Shallow Assemblage encompasses the bulk of the yellowtail distribution on the Grand Bank. This species is found in all shallow waters of NAFO div. 3LNO, although the majority of the commercial catch comes from 3N (Brodie and Walsh 1988). Yellowtail was also found in small amounts on St. Pierre Bank and in inshore areas around the Avalon Peninsula (Pitt 1970). Yellowtail is a shallow water species with relatively restricted movements as shown by tagging experiments (Lux 1963, Walsh 1987). Stock delimitation within the Shallow Assemblage area, if any, is not known. Yellowtail has been managed as a single stock in NAFO div. 3LNO and there seems to be no good reason to join the Shallow Assemblage with any other assemblage based on this species.

American plaice

American Plaice has been managed as a single stock on the Grand Bank (NAFO div. 3LNO). Its distribution on the Bank is fairly wide, ranging from deep water concentrations (520 m) in the northern part of our NES Deep Assemblage to a juvenile nursery in shallow waters of the Tail of the Bank (Walsh and Brodie 1988). The majority of the plaice biomass is in the shallow-intermediate waters (55-183 m) of 3L and 3N (Walsh and Brodie 1987). Fish appear to move little once settled, and little intermingling is expected among adults. The strongest suggestion for merging assemblages from a "plaice's point of view" is between the Shallow and NE Intermediate Assemblages, but existing evidence was not considered strong enough to take this action.

Redfish

There are three redfish species on the Grand Bank, the abundant beaked redfishes (*Sebastes mentella* and *Sebastes fasciatus*) and the more sporadic golden redfish (*Sebastes marinus*). Ni (1981a,b) presents evidence that *S. fasciatus* is dominant in the shallower range of redfish distribution (200-400 m in 3LN, 200-500 m in 3O) and *S. mentella* is dominant in the deeper parts, with transition zones at 400-500 m in 3LN and more than 500 m in 3O. Sampling stations during the surveys analyzed in this work seldom went deeper than 500 m and in most cases were shallower than 400 m. The redfish in my Deep Group is therefore assumed to be mostly *S. fasciatus*. The usual NAFO practice of separating redfish in 3O from 3NL for management purposes will be followed here.

2.4.1. Merging fish assemblages

There is evidence that some of the groundfish stocks which make up an important percentage of the biomass in the Grand Bank assemblages extend their geographic distribution over more than one assemblage. For example, the cod in the Shallow Assemblage probably belong to the same stock as the cod in another contiguous assemblage and therefore it makes little sense to consider the Shallow Assemblage as a relatively independent compartment in the Grand Bank ecosystem. This rationale underlines the need for reformulating assemblages when certain sorts of ecological investigation are intended, namely to analyze groundfish biomass trends in biologically coherent areas or to conduct ecological modelling.

The Deep Group is dominated by beaked redfish, a deep-water species caught in very small amounts in all the Intermediate Assemblage area. Cod in the NES Deep Sub-Group area may belong to the northern complex while in the W Deep Sub-Group cod biomass is relatively low. Cod does not seem to offer any good reason for merging any Deep and Intermediate sub-groups. The same is true of plaice. The Deep Sub-Groups will therefore be kept separate.

The Avalon Group and NE Intermediate Sub-Group were merged as were the Shallow Group and SW Intermediate Sub-Groups. These decisions were made in keeping with current evidence and practice regarding the structure of the cod stocks, with cod taken south of 46° N latitude associated with the 3NO stock, and other cod, particularly those from the northern Grand Bank and Avalon Channel, treated separately. Hereafter I will use the term Northeastern Region (or Northeastern Grand Bank) to refer to the area that encompasses the Avalon Group plus the NE Intermediate Sub-Group (see Fig. 3), a large area under the influence of the inshore and offshore branches of the Labrador Current (see section 2.6). I will use the term Southern Region (or Southern Grand Bank) to refer to the area that encompasses the Shallow Group plus the SW Intermediate Sub-Group (see Fig. 3), a shallow area that comprises all the Bank proper and extends onto the Whale Bank area.

Having gone through this reformulation of geographic areas, we end up with *four groups of stations that encompass areas with biologically coherent fish* assemblages on the Grand Bank: NES Deep, W Deep, Northeastern, and Southern. The next section presents trends in biomass and species composition over time for the entire Grand Bank as well as for each of these four zoogeographic regions.

2.5. Abundance Trends in Fish Assemblages

Catch per unit effort (Kg/tow) from the groundfish surveys was used as an index of biomass abundance within every biologically coherent fish assemblage for the period 1971-82, 1984-87. The same data were used to build cumulative percentage graphs illustrating the evolution of species proportions in the trawl catches (Figs 21 to 25). Reliability of each data point in the graphs (each year in each assemblage) depends upon the number of stations used to derive that data point (Table 4). Special care should also be taken when analyzing catch rates of merged assemblages in regard to species that are present in only one of a pair of merged regions (section 2.4.1). Examples are yellowtail in the Southern Region (present in the Shallow Group, absent in the SW Intermediate) and thorny skate in the Northeastern Region (present in the NE Intermediate Sub-Group, absent in the Avalon). The catch rates of these species are affected by the number of stations in the region where they are not present. Catch rates of such species in years of particularly anomalous ratios between the number of stations in each merged area should be regarded with care. Next I summarize the trends in the relative proportion of species in each assemblage and for the Grand Bank as a whole.

Southern Assemblage. Cod, plaice, yellowtail and thorny skate dominate the biomass of demersal catches in this assemblage (Fig. 21) which extends over almost all the shallow Bank. The index of total abundance fluctuated around 150 Kg/tow since 1973 but rose to over 200 Kg/tow since 1984. This peak followed a rising trend in the biomass of cod. Cod more than doubled its relative proportion in survey catches during 1984-87 compared to the 1970's (Fig. 21). Baird and Bishop (1988) analyse this increase presenting also 1988 data. Analysis of catch at age data of combined Canadian and Soviet surveys, as well as cohort analysis (VPA) results, present evidence for an increase in the 6+ age group of cod in NAFO div. 3NO relative to the late 1970's. A decline was observed in 1988, but cod biomass nevertheless remained at a level above that of the early 1980's.

TABLE 4. Number of stations in each assemblage area used to calculate abundance indices and species proportions. All stations were done during Spring trawl surveys of period 1971-82, 1984-87. The Southern and Northeastern Regions are broken down by the original assemblage areas that comprise them.

	Years															
Assemblages	71	72	73	74	75	76	77	78	79	80	81	82	84	85	86	87
Southern	49	33	65	37	50	63	68	75	164	123	62	129	101	158	199	213
Shallow	32	30	39	23	42	46	58	57	131	87	39	76	74	108	151	124
SW Intermdt	17	3	26	14	8	17	10	18	33	36	23	53	27	50	48	89
Northeastern	27	32	20	65	43	52	83	75	89	84	52	75	32	154	158	143
Avalon	8	8	7	11	10	12	41	28	29	28	3	23	15	50	62	59
NE Intermdt	19	24	13	54	33	40	42	47	60	56	49	52	17	104	96	84
NES Deep	34	11	13	15	10	17	31	23	50	41	41	28	5	52	40	55
W Deep	12	4	12	8	8	14	10	14	26	16	7	19	18	13	17	22

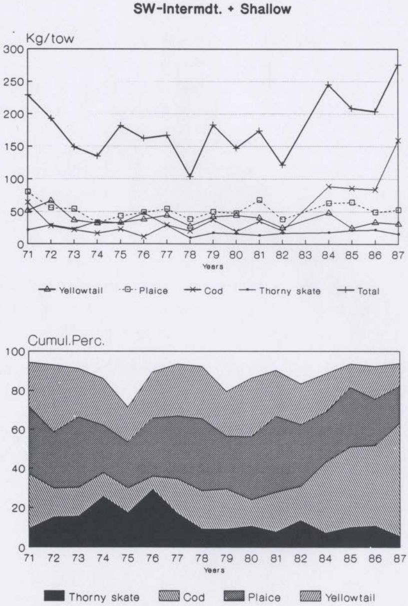


Figure 21. Trends of species abundance in the Southern Region. The line graph presents trends in Kg/tow of Spring trawl surveys. The shadowed graph presents relative proportion (cumulative percentage) of main species in the hauls.

Northeastern Assemblage. The broad area comprised by this assemblage is dominated by only two species – plaice and cod (Fig. 22). Total catch per unit effort has been stable at over 150 Kg/tow since 1976, but there has been a shift in relative abundance of cod and plaice in the catches since 1982. An increase in the catch rates for cod since that date has been matched by a decrease for plaice.

NES Deep Assemblage. Total catch rates in the area comprised by this assemblage exhibit strong fluctuations (Fig. 23), reflecting the variability in the two dominant species of the assemblage – cod and redfish. Redfish attains catch rates well over 100 Kg/tow, a value that stands near the top for all species in any assemblage studied. The fluctuations in redfish are likely not to be real, but rather a consequence of the patchy distribution of this species. Catch rates for cod are also rather unstable when compared with the same index in shallower assemblages. The awkward value for cod in 1984 should be regarded with caution due to the low sampling rate in this assemblage area in that year (Table 4).

W Deep Assemblage. Sampling rates in this assemblage are the lowest ones recorded (Table 4) and the values for years like 1972 and 1981 are particularly unreliable. Catch rates for total biomass in the area of the Bank comprised by this assemblage exhibit strong fluctuations (Fig. 24) caused by high variability in redfish, the dominant species in the assemblage. Some of the catch rates observed here for redfish are the highest for any species on the Bank. As in the NES Deep Assemblage, the fluctuations of redfish are likely to be a consequence of changes in the coefficient of catchability of this species rather than real fluctuations in species abundance.

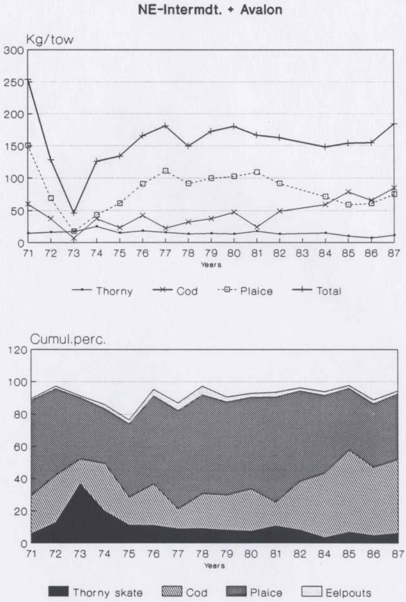


Figure 22. Trends in species abundance in the Northeastern Region. The line graph presents trends in Kg/tow of Spring trawl surveys. The shadowed graph presents relative proportion (cumulative percentage) of the main species in hauls.

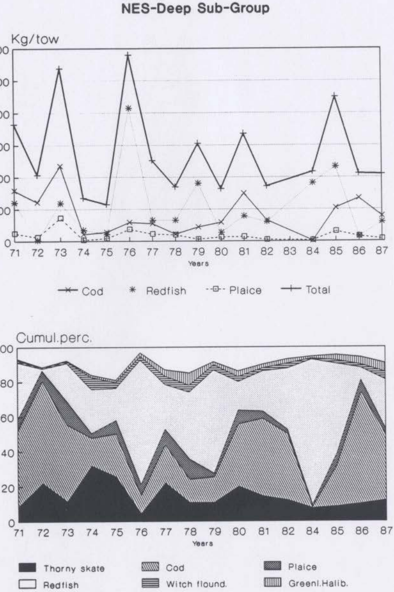


Figure 23. Trends in species abundance in the NES Deep Region. The line graph presents trends in Kg/tow of Spring trawl surveys. The shadowed graph presents relative proportion (cumulative percentage) of the main species in hauls.

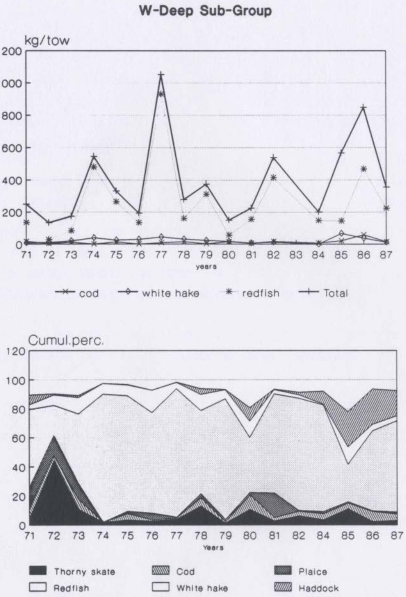


Figure 24. Trends in species abundance in the W Deep Region. The line graph presents trends in Kg/tow of Spring trawl surveys. The shadowed graph presents relative proportion (cumulative percentage) of the main species in hauls.

Entire Grand Bank. The biomass of demersal groundfish catches on the Grand Bank during the time period analyzed was dominated by a small number of species (Fig. 25). The index of total abundance has fluctuated around 200 Kg/tow with relatively higher values since 1984. This high is apparently due to an increasing trend in the catch rate of cod observed in all assemblages except the deep ones. Other species, like yellowtail or plaice, remained relatively stable or, like redfish, did not exhibit any clear trends.

A species which deserves mention is the thorny skate. Usually making up a significant proportion of the catch (Fig. 21, 22, 25), thorny skate is not a target species in the fisheries and has often been neglected as an important component of the Grand Bank ecosystem. Apparently this species underwent a shift from a catch rate level of 25-30 Kg/tow in the 1970's to 15-20 Kg/tow in the 80's (Fig. 26). This shift closely follows trends in the Southern assemblage for this species.

Fig. 27 compares total catch rates in each of the various assemblages considered and for the entire Grand Bank. The highest fluctuations are found in the two deep assemblages, but with no apparent match in their peaks and valleys. The other two assemblages, which occur over large areas of the Bank, are comparatively much more stable over time, and the same is true for the entire Grand Bank.

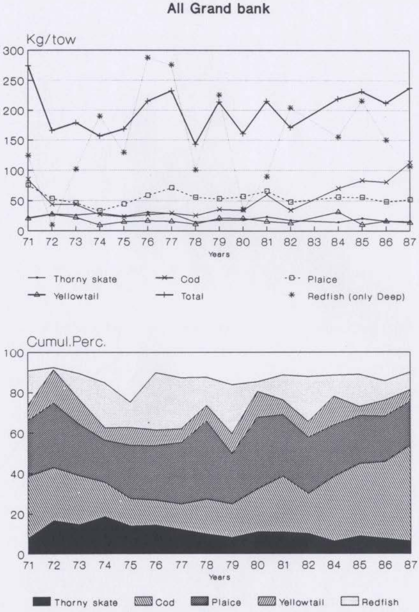


Figure 25. Trends in species abundance in the entire Grand Bank. The line graph presents trends in Kg/tow of Spring trawl surveys. The shadowed graph presents relative proportion (cumulative percentage) of main species in hauls.

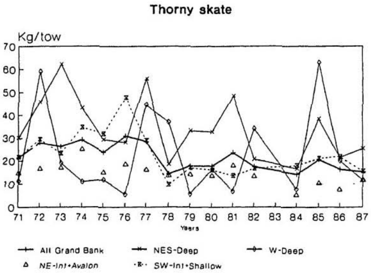


Figure 26. Trends in Kg/tow of thorny skate in the major assemblage regions and in the entire Grand Bank.

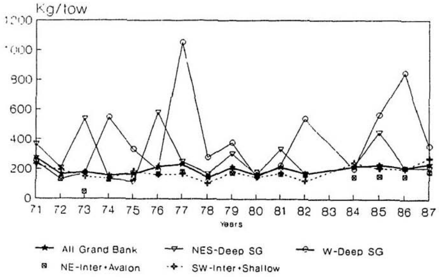


Figure 27. Trends in Kg/tow of all species in the major assemblage regions and in the entire Grand Bank.

2.6. Oceanographic Framework

Ocean circulation on the Grand Bank is dominated by the cold southward-flowing Labrador Current. This Current originates near the entrance of Davis Strait by the juncture of the West Greenland Current and the Baffin Island Current (Smith et al. 1937, Lazier 1982, Petrie and Anderson 1983). The union of these two water types is not complete so two streams can roughly be identified along the Labrador shelf. Most of the volume transport of the Labrador Current occurs in a high velocity offshore core (temperature +3 to 4° C, salinity around 34.9 ppt) centred over the 600-800 m isobath of the continental slope off Labrador (Lazier 1982). An inshore portion of the Current contains the greatest volume of cold water (temperature −1 to +2° C, salinity 32.5 to 33.5 ppt) and flows over the Labrador shelf or upper continental slope. Approaching the northern Grand Bank, the Labrador Current splits into three main branches – an inshore shelf stream through the Avalon Channel, a main branch along the eastern edge of the Bank and a third eastern component towards and around Flemish Cap.

Another important feature in the Grand Bank region is the presence of the North Atlantic Current. This warm current (temp. 8-10° C, salin. 34.7-35.1 ppt) enters the region off the Tail of the Bank from southwest and exits toward the northeast. An oceanic front with a wide dynamic trough of current reversal between the North Atlantic Current and the Labrador Current main branch, seems to be a permanent feature offshore to the south and west of the Tail of the Bank, with frequent and very active eddy formations (Voorheis et al. 1973, Legeckis 1978, Forrester and Benoit 1981)

There appears to be a close relationship between the major physical oceanographic features of the Grand Bank and the distribution of the groundfish assemblages identified in section 2.3.1. The Avalon Assemblage, with its low diversity, is basically under the influence of the inshore branch of the Labrador Current. This branch is the coldest and least saline one, probably accounting for the biological characteristics observed. Species richness in the Avalon Assemblage is low and all the three significant species present (cod, plaice, Arctic eelpout) tolerate very cold water (< 0° C).

The NE Intermediate Assemblage could be called the 'Labrador Current main branch assemblage', because the geographic areas covered by both roughly coincide. The main offshore branch of the Labrador Current is generally confined between 50 and 200 m along the eastern edge of the Bank. This branch contains waters of the two different types and origins present in the entire Labrador Current, and it bounds and interacts with the shelf water on the northern and eastern parts of the Bank (Buzdalin and Elizarov 1962). Bottom temperatures in the NE Intermediate area are usually higher and in a broader range than in the Avalon area. Thorny skate is absent in the Avalon Assemblage but present in the NE Intermediate area.

The NES Deep Sub-Group, basically characterized by the presence of redfish, apparently occurs underneath the Labrador Current main branch. Bottom temperatures are usually low but positive. Annual variability in the position of the upper limit of this assemblage (section 2.3.2), interpreted as shallow intrusions of redfish, may depend on the depth of the Labrador Current main branch.

Warm waters of the North Atlantic Current sometimes penetrate the southern and southwestern parts of the Grand Bank. This penetration does not have the same magnitude every year and is spatially heterogeneous in relation to the bottom topography of the area. Mixed water forms over the western, southern and southeastern slopes of the Bank from the Atlantic water, the cold water from the Labrador Current and, particularly over the western slope, the fresh run-off from the St. Lawrence River (Forrester and Benoit 1981). The SW Intermediate Sub-Group is under the influence of this mixed water, with very heterogeneous characteristics around the Bank. Bottom temperatures in the area occupied by this assemblage occur over a broad -1.5 to 9° C range.

The W Deep Sub-Group is clearly under the influence of warm slope water. Bottom temperatures in the W Deep area were seldom negative and average values during surveys fell between 3 and 8° C, with values as high as 11° C. The number of species present in hauls in the W Deep area were usually the highest recorded in all the Bank in spite of the fact that total biomass was strongly dominated by a single species, redfish (Fig. 24). Species usually found only there, with temperature range preferences suggested by Scott and Scott (1988), include common angler (6-10° C), pollack (7-15° C), marlin-spike (3-4° C), Atlantic argentine (7-10° C), haddock (1-13° C), spiny dogfish (3-15° C), silver hake (6-8° C), longfin hake (3.5-6.5° C) and white hake (5-11° C).

Shelf water on the central Grand Bank, the area of the Shallow Assemblage, is a mixture of Labrador Current water and slope water plus modifications due to local seasonal heating. There is little detailed information available on water circulation in the area. Conflicting evidence exists concerning the presence of a gyre on the central part of the Grand Bank which could be responsible for an apparent retention of water there (Smith et al. 1937, Buzdalin and Elizarov 1962, Forrester and Benoit 1981).

2.7. Discussion

Classificatory analysis of 16 years of Spring groundfish survey data indicated a high degree of spatial consistency in the clustering pattern of stations and in the species that characterize each cluster. The Grand Bank could be divided into six areas defined on the basis of their fish assemblages. These were mapped, described, and reformulated for biological coherence. The assemblages maintained their species composition over the time period analyzed and also retained the major attributes of their spatial configuration. The analysis was conducted in spite of the limitations imposed by the selectivity of the sampling gear (the demersal trawl) and the temporal restriction in the sampling plan (only Spring surveys considered). It is therefore emphasized that the assemblage areas defined on the Grand Bank are primarily representative of the species that are vulnerable to demersal trawl in that season of the year. This includes some of the most abundant and commercially important species on the Bank.

There are common methodological problems involved in the type of data analysis used (e.g. Chandon et Pinson 1981, Mahon et al. 1984, Gabriel and Murawski 1985). The intrinsic variance of ecological samples may result in the misallocation of stations by the clustering procedure selected. I have sought to overcome this by using a reallocation procedure, mapping the clusters, and by checking the agglomeratively built dendrograms against a divisive, and more robust, method. Even so, one cannot preclude misclassifications. Stations occurring near assemblage boundaries on the steep continental slope at the edge of the Bank are particularly prone to these.

Worldwide studies of demersal fish assemblages on continental shelves (section 2.1.2) have shown that it is usually possible to recognize without much trouble a characteristic group of species that dominates the shallow portion of the shelf within a restricted depth range. Easily recognizable also is a group of deep dwellers dominating portions of the continental slope, this group tends to have a much broader depth range than the shallow shelf group. Groups falling intermediate between these two extremes have been identified, but are usually more difficult to characterize. They are sometimes no more than a mix of species from the shallow and deep groups with no abundant or distinctive species of their own. The fish assemblages identified on the Grand Bank fit well into this general picture. The contours of Figure 3 are strongly aligned with depth and the general oceanographic circulation of the area. Yellowtail and redfish are the typical abundant representatives from the shallow and deep areas respectively, while cod, plaice and thorny skate are abundant and widespread enough over the whole area. This raises problems when attempting to compartmentalize the Bank.

Coincidence in the species distributions that form the bases of the assemblage definitions does not necessarily imply significant strength of interaction among the species. Multivariate techniques in and of themselves bring little insight to the question of the influence of abiotic factors versus species interactions in determining the observed distribution patterns. Further investigation concerning trophic ecology of the species involved is required to clarify connectance within assemblages. But regardless of the actual balance between biotic and abiotic factors in determining the observed patterns of Figure 3, the simple definition of relatively homogeneous areas in terms of species composition has relevance to ecological studies and to multispecies management. On the one hand, broad areas characterized by an homogeneous faunistic composition are a useful guide for the definition of a spatial scale appropriate for studies at the community level. On the other hand, catches within the area of a given assemblage offer a certain redundancy in terms of species composition and relative abundances. Such information can be of value in dealing with bycatch and providing general guidelines for overall rational planning and management.

SUMMARY OF CHAPTER 2

Delimitation of broad zoogeographic areas characterized by an homogeneous biological composition is a reasonable initial approach to the definition of a spatial scale suited for community studies. Six fish assemblage areas constitute a regular pattern on the Grand Bank and their geographic distributions are strongly aligned with bottom depth and oceanographic circulation. Consideration of overall biological coherence led to the merging and reformulation of the original six assemblages into four assemblages (Southern, Northeastern, NES Deep, and W Deep) whose species composition was found relatively predictable over the 17-year time period considered. The extent to which species within the assemblages are functionally linked remains an open question of considerable practical and theoretical interest.

Chapter 3

Feeding Interactions and Food Webs on the Grand Bank

3.1. Introduction

Chapter 2 described areas on the Grand Bank that are characterized by a relatively homogeneous groundfish species composition. The species inhabiting each area were identified simply based on the fact that every year the sampling gear collects the same groups of species in the same geographic areas. Following common practice, I have called the groups so identified species assemblages, mapped their contours, and suggested that there is a certain physical homogeneity in the areas inhabited by each assemblage. This pragmatic way of grouping species, although providing a means for defining an appropriate spatial scale for studies at the community level, offers no unequivocal explanations for the observed coincidence of species distributions, and much less so for the observed pattern of species abundances.

Ecologists usually accept that the limits to the distribution of a species are ultimately determined by the tolerance of that species to extremes of physical conditions. Most ecologists would also agree that the large-scale co-occurrence of species is usually well (but not necessarily uniquely) explained by common responses to some influential environmental factor. There is, however, plenty of disagreement as to the degree of species interdependence within a group of co-occurring species. Classical autecology holds that co-occurring species are not interdependent in any sense, viewing co-occurrence simply as a consequence of similar (but uncoordinated) responses of the individual species to gradients in the physical environment (for a critique see, for example, Levins and Lewontin 1985). Another view argues that assemblages consistently recurring in time and space imply complex and interdependent relationships among their component species (for history and the controversy see Saarinen 1982, McIntosh 1985, Underwood 1986). I suspect that most contemporary ecologists would adopt some intermediate stance between these two views, claiming that the degree of interdependence within a community is actually rather variable in time, space, and with respect to the particular pair of species under consideration. Actually, the opposition between biotic and abiotic factors in determining community patterns is most likely a wrong way to put things. As Levins and Lewontin (1985) point out, "the community view is not that other species are more important than physical factors but rather that there is a mutual interpenetration of the physical and biotic aspects". The ecological significance of physical conditions depends on a species' relations with other species and vice-versa (Levins and Lewontin 1985, p. 143).

Many contemporary ecologists (e.g. Bender et al. 1984, Kareiva 1989, Hairston 1989) favour investigating species interactions with controlled experiments and deliberate species manipulation. Sih et al. (1985), for example, report on the increased number of papers concerning predator manipulations in seven ecological journals. But controlled experiments require control sites, replications, and often the maintenance of constant environmental factors other than the ones deliberately changed. These requirements cannot be met when dealing with highly mobile animals within a geographical scope as broad as a continental shelf. Here, techniques of indirect observation have been the only resort, as illustrated by Daan (1980) and Beddington and May (1982) who attempt to detect significant changes in large marine populations as a result of hypothetical species interactions. Unfortunately, these studies have been more an illustration of how the best available data is unable to falsify hypotheses rather than a production of unequivocal answers to questions about species interdependence in the open ocean.

Chapter 3 adopts the viewpoint expressed in an influential paper by Hutchinson (1959): "In any study of evolutionary ecology, food relations appear as one of the most important aspects of the system of animate nature. There is quite obviously much more to living communities than the raw dictum 'eat or be eaten', but in order to understand the higher intricacies of any ecological system, it is most easy to start from this crudely simple point of view". Each population on the Grand Bank exists within a web of consumer/resource relationships that affects its growth rate to an extent that is poorly known but certainly not null. The consumer/resource concept appears to be a reasonable, although not unique way of initiating a global community approach. I would argue that it imposes no major restrictions to the (desirable) future incorporation of physical factors, so long as it is possible to state explicitly how they influence specific attributes of population biology, namely growth rates.

Chapter 3 begins with a literature review (section 3.2) of the main species and their feeding interactions on the Grand Bank. Whenever possible, this review is made within the context of the two major biologically coherent assemblage areas defined in section 2.4.1, the Northeastern and the Southern regions. Sections 3.3 and 3.4 summarize differences and similarities in the networks of feeding interactions in the two regions. Section 3.4, in particular, presents the information reviewed in the form of diagrams representing standardized community food webs for each region. There are a number of static features that one can evaluate in these diagrams. In section 3.5 these features are computed and compared with the same features in other marine food webs. Section 3.6 argues that when the same information on feeding interactions is displayed in the form of niche overlap graphs, body size appears to be a dominant structuring factor in the Grand Bank community. Finally, section 3.7 further simplifies the information on feeding interactions to a degree that allows the study of our ability to make certain predictions about community dynamics.

3.2. Feeding Interactions

This section is a literature review of the main species and their feeding interactions on the Southern and Northeastern regions. The sampling coverage of feeding interactions on the Grand Bank is very uneven in space, time and in respect to taxa. The sampling of invertebrates for feeding habits is poor all over the Bank, and in many cases I had to resort to information on the feeding habits of the same taxa in other world areas. Sampling has been better for some commercially important fish species, especially Atlantic cod, but uneven in space and time. Generally speaking, feeding habits of vertebrates in the Avalon, Shallow, and NE Intermediate areas (Fig. 3), are better known than in the Deep areas and in the SW Intermediate area. Feeding habits in spring and summer are better known than during the rest of the year. Whenever possible, species or at least the genus level is used. For some important groups this level of resolution is not possible, major examples being polychaetes and gammarids in the benthos or organisms in the microbial loop. Most of these taxonomic aggregations can, however, be considered trophospecies (sensu Briand and Cohen 1984), i.e. groups of species that have essentially the same prey *and* predators. The information presented here will be synthesized in the form of stereotyped food webs in section 3.4.

Zooplankton

Analyses of stomach contents of the most abundant commercial fish species on the Grand Bank provide evidence for fish feeding directly on zooplankton, at least during their early life stages. Part of the available information concerning zooplankton on the Grand Bank will be included in the appropriate fish sections whenever such information appears to be relevant. There are, however, some general aspects that deserve mention here.

Strong (1981) provides the most comprehensive account of zooplankton on the Grand Bank. He reports 86 species from 11 phyla. Three copepods dominated the holo-zooplankton: the macroplanktonic species *Calanus finmarchicus* and *Pseudocalanus minutus*, and the microplanktonic *Oithona similis*. All exhibited a strong peak of abundance in spring-summer, a period when they were widespread on the Bank. A second, weaker, peak of abundance, was also found for most copepod species in January-February. The overwhelming abundance of *C. finmarchicus* confirms previous reports by Bainbridge (1961), Vladimirskaya et al. (1976) and Akenhead (1980). Vladimirskaya et al. (1976) connected the breeding and development of *C. finmarchicus*, a heavy herbivorous grazer, with phytoplankton development in the Grand Bank - Flemish Cap - southern Labrador area.

Euphausiids are far less numerous than copepods on the Grand Bank (Vladimirskaya et al. 1976, Strong 1981). *Thysanoessa raschii* predominates on the Bank proper, exhibiting higher concentrations in August and September. *Thysanoessa longicaudata* is another abundant euphausiid (Bainbridge 1961, Lindley 1977, Strong 1981), and is particularly important on the slope beyond the 200 m isobath. Judging from their apparently lower relative abundance, Strong (1981) maintains that euphausiids play a minor role in the Grand Bank ecosystem as compared to other areas in the north Atlantic and Antarctic. But Strong's (1981) observation does not agree with information based on stomach content analysis, which indicates that euphausiids play a key role in the diet of most abundant fish and marine mammal species on the Bank. It is likely that the fish are strongly selecting for euphausiids due to their bigger size. Other very abundant zooplanktonic organisms found by Strong (1981) were the copepods *Calanus glacialis* (mainly on the slopes below 200 m), *Temora longicornis* (mainly south of 46° N), *Anomalocera patersoni* (in the neuston) and *Centropages hamatus*. Chaetognaths (*Sagitta* sp.) are very abundant from May to August and, along with the medusa *Aglantha digitale* (especially abundant in July-August), were reported by Strong (1981) as likely to be the major invertebrate predators of zooplankton. Closer attention will now be devoted to some of the groups thought to be more abundant on the Bank and important prey.

Calanus finmarchicus. This copepod is primarily herbivorous (Raymont 1963, Anraku and Omori 1963; Hargrave and Geen 1970) although it probably also feeds on microzooplankton (Turner 1984).

Oithona sp. These cyclopoid copepods are claimed to be mostly carnivorous (Parsons et al. 1983). Strong (1981) however argues that the large abundance of these organisms on the Grand Bank can hardly be accounted for by carnivory, hypothesising that *Oithona* sp. actually exploits the phytoplankton (see also Hargrave and Geen 1970). Petipa et al. (1970) have shown that in the Black Sea *O. similis* changed diet with growth. Nauplii stages 1-3 were herbivorous, copepodites in stages 4-6 were omnivorous, and adults were chiefly carnivorous and fed on young copepodite stages. It is possible that the numerous *Oithona* sp. on the Grand Bank fit better into the so-called microbial loop (Azam et al. 1983), feeding mostly on nanoplankton (2-20 μm) and on the smaller microplanktonic (20-200 μm) organisms. Major prey might then be nonpigmented flagellates and the smaller ciliates.

Thysanoessa sp. According to Mauchline and Fisher (1969) these euphausiids are omnivorous. They have been reported to feed opportunistically on phytoplankton (diatoms and dinoflagellates), copepods, particulate suspended material, bottom detritus, and individuals of their own species. I will assume that euphausiids on the Bank prey mostly on *Calanus* sp., *Oithona* sp., and phytoplankton.

Hyperiids. These amphipods are usually pelagic organisms whose feeding habits are poorly known. Bowman and Gruner (1973) reviewed most of the literature describing common parasitic associations between hyperiids and gelatinous hosts like coelenterates and thaliaceans, suggesting feeding habits based on these associations. *Parathemisto* sp. in particular, the common hyperiids of the Grand Bank, are planktonic carnivores likely to feed mostly on copepods (e.g. Dunbar 1946 for *P. libellula*, Raymont 1963).

Benthos

The general distribution and community dynamics of benthos on the Grand Bank of Newfoundland are poorly understood. The studies of Nesis (1965), Squires (1970), Hutcheson et al. (1981), and Schneider et al. (1987) cover only macro- and megabenthos, but are still the most comprehensive available. They were used here for guidance.

Nesis (1965) addresses the distribution of the biomass of benthos on the Bank, with special focus on epi-macrobenthos and epi-megabenthos. The highest biomass values (> 1 Kg/m^2) were recorded on the Southeast Shoal and along the edge of the southern-southeastern shelf, an area corresponding to the outer reaches of the Shallow Assemblage plus the eastern part of the SW-Intermediate Assemblage (see Figs. 2 and 3). On the greater part of the Bank plateau, including most of the Shallow Assemblage and all the southern NE Intermediate Assemblage, Nesis (1965) reports an intermediate level of biomass (0.1-1 Kg/m^2). The lowest levels of macrobenthic biomass were found in an area corresponding to the Avalon Assemblage, the Whale area, the northern parts of the NE Intermediate Assemblage and the Deep Assemblage. Nesis (1965) suggests that the observed biomass distribution of macrobenthos is likely to be tied to the distribution of primary production. Vladimirskaya et al. (1976) also address this subject when discussing the apparent time lag between the settling of *Calanus finmarchicus* and the bloom peak. This time lag would cause a large sinking of unutilized phytoplankton, which could support the high biomass of benthos on the shoal and on the upper slopes. Hutcheson et al. (1981) found a strong positive correlation between the standing crop of macrobenthos in their sampling locations and annual primary production measured in stations nearby, providing some support for the suggestions of the Soviet investigators. The same hypothesis is corroborated by the existence of a macrobenthic fauna that is dominated by suspension feeders and detritivores exploiting the surface deposits. Many of these animals were commonly found ingesting particles of vegetal origin (see below). Actually the high concentrations of bivalves and barnacles reported for some areas of the Bank probably can only be accounted for in terms of a tight coupling to water column production.

In terms of biomass, molluscs are the dominant benthic organisms on the Grand Bank. Also very important are crustaceans (mostly the barnacles *Balanus crenatus*) and polychaetes. In terms of numbers, polychaetes are the most abundant organisms on the Bank, and in some areas (south of Virgin Rocks, Hibernia area) their biomass was reported to be higher than that of any other group (Hutcheson et al. 1981). The most numerous single macrobenthic species on the Grand Bank is the polychaete *Exogone hebes* (220 individuals/m^2 on average). Other numerous polychaetes are *Parapionosyllis longicirrata*, *Glycera capitata*, and *Prionospio steenstrupi*. The dominance of molluscs is largely the result of an unusually high concentration (22 Kg/m^2 and 3010 to 5890 individuals/m^2) of the infaunal bivalve *Mesodesma deauratum* on the Southeast Shoal area, this high concentration may have no parallel in North American continental shelves (Hutcheson et al. 1981). The echinoderms follow the polychaetes, the barnacles, and the molluscs in numerical abundance. Most abundant are the sand dollar *Echinarachnius parma* (all over the Bank) and the brittle star *Ophiura robusta*. Other numerically abundant species are the amphipods *Priscillina armata*, *Monoculodes edwardsi*, and *Pontogeneia inermis*. Sand lance (*Ammodytes* sp.), an important prey for bottom-dwelling fishes, was reported present in association with the benthic communities in almost all areas sampled.

Nesis' (1965) description of the benthic zoogeography of the Grand Bank is valid as a general large-scale picture of an epi-macrobenthos that is not too mobile. His areas seem to fit well the zoogeographic description developed in Chapter 2 (Fig. 3). It is likely that key physical variables (depth, water masses, sediment), rather than biological links, are responsible for this coincidence. The Shallow Assemblage (dominated by plaice, cod, yellowtail and thorny skate) approximately fits the *Echinarachnius parma* - *Ammodytes americanus* biocoenosis (in Nesis' 1965 terminology), i.e. sand dollar and sand lance. The bottom in this area is mostly sandy. Most of the NE-Intermediate Assemblage (mostly plaice, cod, and thorny skate, but with eelpouts and Greenland halibut too) fits Nesis' *E. parma - Strongylocentrotus droebachiensis - Ophiura sarsi* biocoenosis, i.e. sand dollars, sea urchins and brittle stars. The bottom is still basically sandy and the depth range given by Nesis (1965) (95 - 220 m) agrees well with the NE Intermediate range (90 to 200-280 m). All the southern (and shallower) part of the Avalon Assemblage, as well as the Virgin Rocks, is covered by this biocoenosis. There are however major pitfalls in Nesis' (1965) account in respect to the infauna. It is known from the work of Hutcheson et al. (1981) that polychaetes, known to comprise a significant part of the diet of some fish (young plaice, yellowtail, young skates), are one of the most abundant groups on the Bank and still they are included by Nesis (1965) only in the slope biocoenosis. Also gammarid amphipods, important for young cod and yellowtail, were not used in the definition of Nesis' areas, and neither were shrimps or crabs.

The general picture of the bottom of the Grand Bank is one dominated by detritivores feeding on suspended particles, at the sediment-water interface, and in the sediment layers. The food of those macrobenthic organisms that comprise a significant portion in the diet of fish and marine mammals will be addressed next. The feeding classification follows Hutcheson et al. (1981).

Polychaetes. The polychaetes on the Grand Bank were reported by Nesis (1965) to be mostly detritivores, feeding either by gathering particules directly or by ingesting sediment. Nesis (1965) observations are in good agreement with the extensive review of Fauchald and Jumars (1979). These authors describe the feeding habits of about ten species present in the list of the more abundant polychaetes reported by Hutcheson et al. (1981).

Ophiura robusta. A brittle star that feeds on detrital organic material in and on the sea bottom (Nesis, 1965). Other brittle stars on the Bank are also reported by Nesis (1965) to be detritivores.

Echinarachnius parma. (Sand dollar). The feeding mechanism of *E. parma* has been described by Mooi and Telford (1982). Sand dollars feed on organic detritus at or near the sediment-water interface.

Strongylocentrotus pallidus. (Sea urchin). Gilkinson et al. (1988) analysed the gut contents of 133 sea urchins collected in 11 locations on the Bank. Urchins were found to be omnivorous, with the guts containing chiefly sand, either loose or in the form of pellets. The pellets included foraminiferan tests, diatom frustules, calcareous material attributed to coralline algae, and negligible detritus. There were also animal remains like amphipods, fish eggs, and barnacles. The authors suggest that *S. pallidus* probably feeds on animal remains and detritus found while processing sandy sediments.

Mesodesma deauratum. (Bivalve). This suspension feeder, filters water immediately above the sediment surface, probably containing resuspended material from the bottom and including particles of vegetal origin (Hutcheson et al. 1981). Nesis (1965) acknowledges that most bivalves on the Bank are suspension feeders.

Amphipods. *Amphiporeia lawrenciana, Oediceros saginatus, Syrrhoe crenulata, Monoculopsis longicornis* and others. Nesis (1965) and Hutcheson et al. (1981) found that most gammarid amphipods on the Bank feed on organic detritus at the sediment-water interface, including material of vegetal origin. Some however (*O. saginatus, M. longicornis*) are also likely to prey upon small live crustaceans. Some of the most abundant benthic amphipods on the Grand Bank belong to families described in the study of Enequist (1950) as detritives.

Shrimps. *Pandalus* sp., are the most commonly reported shrimps in cod and Greenland halibut stomachs, are very abundant on the shallow Grand Bank and upper slopes. Most *Pandalus* sp. found with food in their stomachs contained phytoplankton and/or crustacean remains (gammarids, copepods, euphausiids). Squires (1970) analysed stomach contents of *P. borealis*, and found mostly phytobenthos (greatest number of occurrences), crustaceans (e.g. gammarids), pelecypod shells and small shrimps. The shrimp also fed on copepods if available. As for *P. montagui*, which appear to be omnivorous, phytobenthos occurred in 33% of stomachs, gammarids and *Calanus* sp. in 19 %, and polychaetes in 10% (Squires 1970). *Spirontocaris spinus, S. phippsi, S. polaris* are other shrimps reported to be frequently preyed upon by cod on the Grand Bank. They appear to be bottom feeders (Squires 1970), with a high proportion of phytobenthos and foraminiferans in their stomachs. *S. polaris* is a larger shrimp (4-19 cm) reported also as the prey of seals and murres. They seem to be bottom omnivorous feeders, with phytobenthos, ostracods, and gammarid amphipods in their stomachs.

Pagurus sp.. Hermit crabs have been reported mostly in thorny skate stomachs. The common food reported by Squires (1970) in stomachs of these crabs is of both plant and animal origin. Phytobenthos was often found, and so were foraminiferans, amphipods, and other crustacean remains.

Spider and snow crabs. *Hyas araneus, H. coarctatus*, and *Chionocetes opilio* are very abundant crabs in the Newfoundland region, being often reported in cod stomachs. Food found in stomachs of these crabs is for the most part phytobenthos, crustacean remains (gammarids, ostracods etc), foraminiferans, polychaetes, and brittle stars (Squires 1970).

Capelin

Capelin (*Mallotus villosus*) is a boreo-arctic pelagic species thought to be a key prey for commercially important fish on the Grand Bank of Newfoundland. A literature review on capelin of the Newfoundland-Labrador area leads to the conclusion that very little attention has been paid to the role that this species plays as a predator. Most literature has focused on its possible role as prey for many important species of the area, including cod, plaice, skate, Greenland halibut, haddock, salmon, seabirds and marine mammals. The relationships of capelin with the most important of these predators are summarized later in this section.

Carscadden (1983a) reviews the capelin fishery and stock structure. Capelin of the Northern Grand Bank stock (NAFO div. 3L, Northeastern area) spawn on inshore Newfoundland beaches in June-July. Capelin of the South Grand Bank stock (NAFO div. 3NO, Southern area) form offshore spawning aggregations on the shallow Southeast Shoal at about the same time of the year (Templeman 1968). June is also the month when the most numerous micro-zooplanktonic species on the Bank, the copepod *Oithona similis*, begins increasing its population size (Strong 1981). It has not been investigated whether the larval stages of capelin depend on this copepod for food. Campbell and Winters (1973) note that during the spawning season capelin virtually cease feeding, although eggs can be incidentally ingested at that time. Kovalyov and Kurin (1973) report the dominant stomach contents of capelin in the second half of June as being capelin larvae (20-42 mm), eggs and *Calanus sp.*. Euphausiids and amphipods were also present though in very low abundance.

After spawning capelin has a very high mortality rate, usually greater than 80%. Survivors are believed to migrate to the northeastern Grand Bank, where feeding is intense until it ceases in late fall (Kovalyov and Kurin 1973, Campbell and Winters 1973, Carscadden, 1983a). This feeding season matches the period of greatest abundance of the copepod *Calanus finmarchicus* on the Bank. The first cohort of this species appears around April in the south, copepodites in early stages (C1-C2) become widely spread in May, and in June-July the entire Grand Bank is populated by a dense C3-C4 population (Vladimirskaya et al. 1976; Strong, 1981). Another abundant macrozooplankter, the copepod *Pseudocalanus minutus*, also has its greatest concentrations between April and September on the Bank, and would be available for capelin to feed upon. *Thysanoessa raschii*, one of the most abundant euphausiids on the Bank, exhibits dense concentrations around the Avalon Peninsula, in the Virgin Rocks area and over the northeastern slopes of the Bank during July and August (Strong 1981). The planktonic amphipod *Parathemisto gaudichaudi*, extremely abundant in the neuston, also has its highest concentrations between May and August, particularly on the Tail of the Bank, the SW slope, and in areas beyond the 200 m contour (Strong 1981).

The northern and southern Grand Bank stocks of capelin apparently mix when overwintering on the northern slopes of the Grand Bank, including along the east coast of Newfoundland. Campbell and Winters (1973) report large inactive capelin schools concentrated from January to March at 140-200 m and not feeding. Lilly (1982) associates these overwintering concentrations on the slopes of the Bank with the cold core (<0° C) of the Labrador Current and suggests their possible availability to overwintering cod in the deeper warmer waters. In early April overwintering capelin move onto the Bank and disperse for feeding, exhibiting a highly variable and poorly understood distribution (Lilly and Carscadden 1986). Immature and mature fish appear to segregate from each other but both feed intensely in May (Campbell and Winters 1973). Mature capelin decrease their feeding activity in June before spawning. Kovalyov and Kurin (1973) report stomach contents in March-June/1972 in different areas of the Bank (Virgin Rocks, SW slope, Avalon Channel, SE Grand Bank). Diet was dominated by planktonic species: *Calanus sp.*, euphausiids and amphipods. Also present in low abundance were *Sagitta sp.*, fish larvae and capelin eggs.

Sand lance

Sand lance are small semi-pelagic fishes in the genus *Ammodytes*. Two species have been reported in the NW Atlantic, *A. americanus* (= *A. hexapterus*) and *A. dubius* (Winters 1970), the latter being the one commonly reported on the outer Grand Bank. Important commercial fishes on the Bank (plaice, cod), non-commercial abundant fishes (skate), and whales depend on sand lance during certain periods of the year as an important food resource. Sand lance is therefore likely to play an important ecological role in linking planktonic production to abundant commercial species. Nevertheless its behaviour, distribution, and feeding habits on the Grand Bank remain poorly understood.

Sand lance have been reported in close association with sandy bottom areas where they can be particularly abundant. These fish feed in the water column but have the ability to burrow quickly into the sand or gravel, remaining there for a long time. Sand lance on the Grand Bank appear to be particularly important in the food chain of the southern parts of the Bank (NAFO div. 3N) where they comprise the bulk of American plaice diet, on the NE of the Shallow Assemblage (to the east of the Virgin Rocks, north of 46° N) where they are heavily preyed upon by cod in spring, and on the southern half of the NE Intermediate Assemblage where they also are heavily preyed upon by cod. These areas, reported from analysis of stomach contents (see the respective sections on the predators), are in relatively good agreement with the areas of greater abundance reported by Winters (1983). Sand lance are apparently more abundant on the eastern Grand Bank at depths shallower than 100 m (150 m during August-September) in temperatures ranging from −1° to +2° C (Winters 1983).

Studies of the food of *Ammodytes* in different areas of the NW Atlantic, North Sea, and Pacific Ocean have shown that their diets are remarkably similar (see Meyer et al. 1979 for a review). Sand lance are basically zooplankton feeders, usually selecting larger organisms, with copepods often comprising at least half of their stomach contents. The most detailed study for *A. dubius* in the NW Atlantic is Scott (1973), for the Scotian Shelf, who analysed the guts of 486 individuals ranging from 15 to 31 cm. The main prey items found (in percent volume) were copepods (65%) (especially *Calanus finmarchicus*), polychaete larvae (15%) and euphausiids (14%). Scott (1973) points out the possible ability of sand lance to feed both by filtering small prey and by chasing larger prey. It is probably safe to consider that the major prey items for sand lance on the Grand Bank are *C. finmarchicus* and euphausiids. It is possible however that the chaetognaths become important prey in periods of the year when they are abundant (summer-autumn). In fact Meyer et al. (1979) found evidence that *Sagitta* sp. could be a resource for *A. americanus* in eastern Massachusetts Bay. The copepods *Oithona* sp. are likely to be too small to be effectively exploited by sand lance on the Bank (0.05% of diet by weight in the study of Meyer et al. 1979).

Atlantic cod

Lilly and Rice (1983) list over 100 prey taxa found in cod (*Gadus morhua*) stomachs, from NAFO div. 3L (approximately the Northeastern region) during spring, illustrating how diverse the diet of cod can be. The number of taxa comprising a significant proportion by weight in the stomach contents of cod is, however, relatively small. In the Grand Bank area these are sand lance (*Ammodytes dubius*), capelin (*Mallotus villosus*), crabs (*Chionocoetes opilio, Hyas araneus, H. coarctatus*), euphausiids (mostly *Thysanoessa raschii*), amphipods (Hyperiidae, Gammaridea), shrimp (*Pandalus montagui, P. borealis*) and flatfish (Templeman 1965, Minet and Perodou 1978, Lilly and Fleming 1981, Lilly and Rice 1983, Lilly 1987). A summary of temporal and spatial patterns in feeding behaviour of cod on the Grand Bank (NAFO div. 3LNO) is presented next.

In winter cod concentrate along the northern and northeastern slopes of the Grand Bank below the cold core of the Labrador Current where they spawn and where capelin and sand lance seem to be available (Templeman 1965, Campbell and Winters 1973, Lilly 1982). Turuk (1978) asserts that a common behaviour of cod in winter on the Grand Bank is to follow daily migrations of capelin into the water column. The cod stay concentrated close to the bottom during daytime and disperse in the water column at night in pursuit of capelin, exhibiting peaks of capelin consumption at dawn and in the evening (Turuk 1978). Feeding intensity during the pre-spawning winter period is probably much lower than in spring and summer at least in NAFO div. 3L (Stanek 1975, Turuk 1978), although cod on the Grand Bank feeds on capelin throughout the winter (Carscadden 1983b). Lilly et al. (1984) analysed stomachs taken in the northern part of my NES Deep area in winter (1981, 1983). Total fullness indices were low, particularly on the offshore NE slopes of the Bank. In Bonavista Bay the main prey were capelin, small pleuronectids (Greenland halibut, American plaice) and crustaceans (hyperiid amphipods, shrimp and crab). On the NE slope capelin and shrimp were the main prey.

In spring the schools of cod migrate onto the shallower parts of the Bank and disperse, apparently following the capelin spawning migrations towards the coast of Newfoundland and to the Southeast Shoal in div. 3N. Lilly and Rice (1983) present a detailed description of the food of cod in NAFO div. 3L (Northeastern region) in spring (May-June/1979). About 95% (by weight) of the total food was accounted for by the following organisms: sand lance (28%), crab (27%), capelin (15%), unidentified and other fish (11%), euphausiids (9%), amphipods (3%) and shrimp (2%). From mid-June to July cod in NAFO div. 3L approach the coast (Avalon Assemblage area) and feed intensively on the capelin that migrate inshore to spawn. Templeman (1965) and Lilly and Botta (1984) report almost 100% capelin in cod stomachs taken inshore from mid-June to early August. Observations in Spring/1984-86 (Lilly and Meron 1986) and at various seasons in 1965-70 (Lilly 1982) suggest that sand lance is much more important for cod diet in div. 3NO (Southern region). Nevertheless cod in this area also feed on capelin (Templeman 1965, Kovalyov and Kurin 1973, Stanek 1975, Turuk 1978).

After spawning inshore, capelin die or move offshore, and cod feed much less intensively, and mainly on benthic invertebrates, in August and in the Fall. Templeman (1965) reports stomach contents made up of 44% crabs, 9% shrimp and 5% molluscs (mainly the clam *Cyrtodaria siliqua*) in stomachs in August-November. Lilly and Osborne (1984) report the possible importance of short-finned squid (*Illex illecebrosus*) for large cod in years of high summer immigration of squid, although other authors do not make reference to this prey. In October offshore movements resume towards warmer waters on the Bank slope, where the cod will overwinter, concentrate again and spawn. Stanek (1975) reports that feeding intensity of cod decreases significantly in NAFO Div. 3LNOP in autumn and winter, and Turuk (1978) suggests the same in 3NO, but the truth is that very little information is available on the feeding behaviour of cod in div. 3NO during autumn.

Investigators have devoted special attention to the interaction between cod and its particular prey capelin on the Grand Banks of Newfoundland. As Templeman (1965) points out, it is possible that cod prefer fish for food, particularly capelin and sand lance, when available. There is however no unequivocal evidence that cod and capelin are strongly linked on the Bank. In the absence of preferred prey cod seem to accept a broad range of food items, vertebrate and invertebrate, giving rise to a large year-round food spectrum. Similar observations have been made in other areas of the North Atlantic (see Klemetsen 1982 for a literature list). Strong cod-capelin interaction is, however, likely in some particular area/time-periods (see Lilly et al. 1981 for a summary). Little is known about a possible numerical response of cod to the density of its preferred prey. Lilly (1986) found a positive correlation between indices of capelin abundance in div. 2J+3K (autumn, 1978-85) and partial fullness indices of capelin in cod stomachs. In years of low capelin abundance, stomach contents suggested that cod did not compensate by feeding more intensively on other prey. Lilly (1986) points out the difficulties in drawing implications from these observations, especially in terms of the way population parameters of cod could be influenced by fluctuations in capelin abundance.

Various studies describe quantitative and qualitative changes in prey species and in prey size spectrum as cod grow (Stanek 1975, Minet et Perodou 1978, Lilly and Fleming 1981, Lilly and Rice 1983, Lilly 1987). Fig. 28 summarizes changes in cod diet with growth on the Grand Bank of Newfoundland from information in the literature. The division of the total cod length range into five discrete stages (Fig. 28) is somewhat arbitrary since changes in diet with length occur gradually. Still one can safely make some broad generalizations: small cod (<40 cm) feed basically on small crustaceans (euphausiids, amphipods) medium-sized cod (40-69 cm) are the greatest capelin and sand lance consumers, and large cod (>90 cm) are the greatest flatfish consumers. Such a pattern is in general good agreement with observations in the North Sea (Daan 1973) and in the Gulf of St. Lawrence (Waiwood and Majkowski 1984).

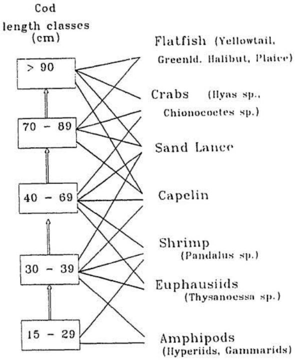


Figure 28. Changes in the diet of Atlantic cod with growth.

There is much less information on cod as a prey. On the Grand Bank of Newfoundland the main predators of small cod are probably adult cod and squid. The main predators of large cod are marine mammals and man. Daan (1973) reports years of considerable cannibalism (up to 20% of food weight) in the North Sea that followed a period of apparent absence of such behaviour. Cod prey were less than 15 cm (0-year old) and there was no strong trend in the degree of cannibalism with the predator size. Daan (1973) briefly reviews the literature concerning this subject for cod in the North Atlantic, with cases that range from 0 to 55% of stomach contents made up of small cod. Lilly (1983) reports cannibalism on 1- and 2-year old cod (10-25 cm) on the Flemish Cap. Authors have tentatively related cannibalism with strong year classes of cod and/or low abundance of other prey organisms, but the phenomenon appears to be poorly understood.

American plaice

Pitt (1973) presents the most comprehensive account of the diet of American plaice (*Hippoglossoides platessoides*) on the Grand Bank of Newfoundland, based on samples from transects along the northeastern, eastern and southern slopes of the Grand Bank, in NAFO div. 3LN, from 1964 to 1971 at different seasons. In div. 3L the transects cover a great part of the NE Intermediate area and in div. 3N they cover the southeastern slopes of the Southern region. The transects covered depths from 70 to 290 m where plaice biomass is high enough to sustain most of the fishery (Walsh and Brodie 1987, 1988).

The diet of plaice on the Grand Bank in terms of weight was dominated by fish (sand lance, capelin), echinoderms (brittle stars, sand dollars, sea urchins), crabs, shrimp, and gammarid amphipods (Pitt 1973). Molluscs and annelids were also present although in much lower amounts. American plaice has therefore a diversified diet comprising both pelagic and benthic organisms, confirming past evidence suggested about its ability to assume pelagic habits (see Pitt 1973). There are significant differences between plaice diet in divs. 3N and 3L (Pitt 1973). In div. 3L diet (in weight percentage) was composed by sand lance (29%), capelin (22%), echinoids (sand dollars, sea urchins) (18%), brittle stars (14%), pelecypod molluscs (6%), decapods (5%), and polychaetes (2%). Diet in div. 3N was less diversified comprising sand lance (76%), capelin (6%), euphausiids (5%), brittle stars (4%), and echinoids (4%). Pitt (1973) points out, however, the discrepancy between percentage by weight in stomachs and percentage by occurrence. Fish, for example, in div. 3L, accounted for 53% of total weight but occurred in only 9% of stomachs. In div. 3N fish accounted for 83% of food weight but occurred in only 30% of stomachs.

Fish, and sand lance in particular, therefore appear much more important for plaice in div. 3N than in 3L. Pitt (1973) suggests that this might be a result of the greater predator-prey (fish) probability of encounter on the steeper and narrower southeastern slope (3N) of the Grand Bank as compared with the larger slope to the north (3L). In spite of its pelagic abilities, American plaice seems to be basically a benthophagic fish (notice that sand lance has known bottom-dwelling habits) and is probably the most important one on the Grand Bank due to its abundance and widespread distribution. Konstantinov et al. (1985) analysed the diet of plaice on the Flemish Cap, confirming a similar dependence of plaice on benthos and pointing out a relatively small diet overlap of plaice with the much more planktophagic habits of cod and redfish.

Pitt (1973) also provides information on diet change of American plaice with growth. This information is summarized in Fig. 29 for NAFO div. 3L (Northeastern region) and 3N (part of the Southern region), where I have considered only two length groups (10-29 cm and 30-69 cm). Thicker arrows were used to indicate the most important prey items. Only prey believed to comprise at least 5% of plaice diet year-round were retained. In both divs. 3L and 3N it was noted that as plaice grows, there is a gradual shift in the relative importance of crustaceans relative to fish in the diet (see also Minet 1973).

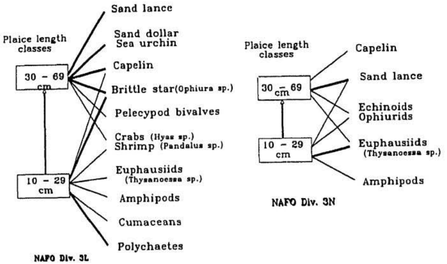


Figure 29. The diet of American plaice in NAFO divs. 3N and 3L (after Pitt 1973).

Thorny skate

The most comprehensive papers on the food of thorny skate (*Raja radiata*) in the NW Atlantic are by McEachran et al. (1976) for the U.S. coast and Scotian Shelf, and by Templeman (1982) for the Canadian coast. The results of both authors are in relatively good agreement. The differences observed are accounted for by Templeman (1982) in terms of differences in the size spectrum of the skates caught and prey availability in the areas sampled. From both papers it is clear that thorny skate is a benthophagic fish with a very diverse diet, even in comparison with other *Raja* species studied in the NW Atlantic (McEachran et al. 1976). The same general observations were made by Antipova and Nikiforova (1983) for thorny skate in the Barents Sea. Species having an important role in the diet of this skate in the Barents Sea (capelin, euphausiids, *Pandalus borealis*) were different from the ones listed below. Interestingly enough these Barents Sea prey species are nevertheless abundant on the Grand Bank.

Templeman's (1982) results are presented for the entire area studied (West Greenland down to Georges Bank) but 80% of the stomachs found with food were taken in NAFO divs. 3KLNOP. In terms of volume of contents, fish dominated (74%) with the chief species being redfish, haddock, and sand lance. Invertebrates (spider and hermit crabs, short-finned squid, polychaetes, benthic amphipods) comprised 25% of total volume of contents but were much more numerous than fish. Small skates (21-60 cm) were found to eat less fish (35% of volume), mainly sand lance, than larger (61-102 cm) skates (78% of volume). A similar result concerning differences in the diet of skates with size was reported by Tyler (1972) and McEachran et al. (1976). Invertebrates such as crabs (22%), squids (20%) and polychaetes (11%) were an important component in the diet of small skates. The same invertebrates were found in the stomachs of large skates though in much lower proportions. Fig. 30 summarizes the main items in the diet of small and large skates. Some species other than the ones present in Fig. 30 comprise a significant proportion of the diet when taken together but not separately. Examples for the small skates are several decapods, capelin, and lanternfish (Myctophidae).

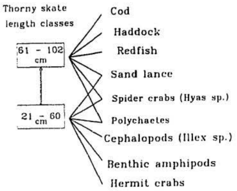


Figure 30. The diet of large and small thorny skate on the Grand Bank (after Templeman 1982).

Templeman (1982) also reports differences in the diet of thorny skate with depth. Fish were more important between 200 and 700 m (82% of volume) than above 200 m (69%). Crabs were more important between 17 and 200 m; shrimp species and octopus were found only in skates caught deeper than 400 m. Although Templeman (1982) does not provide the exact locations of skate captures, his 200-m frontier can probably be roughly matched with the border between the Intermediate and Deep assemblage areas for general purposes of analysis of the main differences in feeding habits of thorny skate between areas.

Yellowtail flounder

Pitt (1976) presents a study of the diet of the yellowtail flounder (*Limanda ferruginea*) on the Grand Bank of Newfoundland, based on 1100 stomachs collected during 1968-73. Although covering a wide range of taxa, the food of the yellowtail was found to be dominated by only two groups of organisms: amphipods (30% of stomach contents by weight) and polychaetes (38% by weight). Polichaetes included free-living, burrowing, and tube-building forms. Amphipods of the genera *Haploops* and *Caprella* could be recognized. These two groups of organisms were important for all length classes (20 to 49 cm) of yellowtail in both NAFO div. 3L and 3N. Polychaetes were significantly more abundant in stomachs from 3L than from 3N. Amphipods were significantly more abundant in 3N than 3L. The importance of these organisms for yellowtail in the NW Atlantic has been confirmed by other authors, and provides evidence for a typically benthic feeding behaviour (Efanov and Vinogradov 1973, Langton 1983). Also found by Pitt (1976) in yellowtail stomachs from the Grand Bank were echinoderms (7% of total food weight), mainly brittle stars, sand dollars, and sea urchins. Fish (capelin and sand lance) were found in very few stomachs (1.2%), although accounting for 7.5% of total food weight. Both echinoderms and fish were relatively important only for large (40-49 cm) yellowtails. Fig. 31 is based on Pitt (1976), and summarizes the role played by yellowtail as a predator on the Southern region.

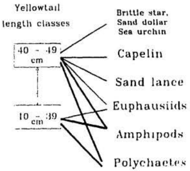


Figure 31. The diet of small and large Yellowtail flounder.

Greenland halibut

Greenland halibut (*Reinhardtius hippoglossoides*) is a bathypelagic fish that feeds mostly on pelagic organisms, primarily fish. Although the number of species that might be found in stomachs of Greenland halibut is large (Chumakov and Podrazhanskaya 1983), like so many other marine predators it tends to concentrate on a relatively small number. Small Greenland halibut (10-20 cm) feed mainly on small crustaceans and cephalopods. Lear (1970) found that euphausiids comprised as much as 90% by volume in the diet of small halibut caught in Trinity Bay (div. 3L). The proportion of euphausiids quickly decreased as the halibut grew from 21 to 30 cm, being replaced by capelin. In NAFO divs. 2J+3K, Bowering and Lilly (1985) found other crustaceans, hyperiid amphipods, dominating the diet of small halibut (<20 cm) along with cephalopods. The cephalopods remained important in the diet up until a halibut size of 30 cm.

Capelin is the major prey for Greenland halibut of intermediate size (20 cm to 70 cm). Lear (1970) found capelin made up about 90% of the volume of stomach contents of halibut larger than 20 cm in Trinity Bay. Even for predators in the 71-80 cm length class capelin was dominant in the diet. Capelin was fed upon all year' round, with lower intensity during the capelin spawning season (1 June- 15 July) and when capelin dispersed on the Bank (16 August- 30 Nov). Greenland halibut tended to prey upon shrimp (*Pandalus sp.*) and euphausiids during these periods although the relative importance of crustaceans remained low. Bowering and Lilly (1985) also found capelin dominating in stomachs of the Greenland halibut in the range 20-69 cm, but animals larger than 69 cm displayed a shift in the diet to groundfish. Large Greenland halibut prey upon groundfish larger than capelin and exhibit pronounced cannibalism. Lear (1970) found that small Greenland halibut comprised 40% by volume of the diet of animals larger than 80 cm in Trinity Bay. Capelin (30%) and Atlantic cod (10%) followed in importance. Similarly Bowering and Lilly (1985) found that the main prey of Greenland halibut larger than 69 cm in div. 2J+3K was groundfish, particularly beaked redfish and small Greenland halibut.

The stations made during the spring groundfish surveys analysed in Chapter 2 rarely went to depths beyond 500 m, therefore failing to cover the areas of densest Greenland halibut concentrations below 700 m (Chumakov and Podrazhanskaya 1983). If the Deep Assemblage is extended offshore to cover these deep areas on the slope, it will include most of the Greenland Halibut stock. It is known that the Greenland halibut change their diet with depth (Lear 1970, Bowering and Lilly 1985, Chumakov and Podrazhanskaya 1983) reflecting not only prey availability but also an increasing trend in size and age of the animals with depth. Chumakov and Podrazhanskaya (1983) found that cod and squid become an important food item (respectively 46% and 10% by weight) at 600-700 m in the NW Atlantic. The same authors report a generalized increase in feeding intensity (as assessed by stomach fullness) with depth in the Labrador-Newfoundland area.

Eelpouts

The eelpouts are bottom dwelling fishes generally found in cold waters and belonging to the family Zoarcidae. Most of the eelpouts caught during fishing stations in the the Northeastern region belonged to the species *Lycodes reticulatus*, the Arctic eelpout. There appear to be no large-scale detailed studies on the diet composition of eelpouts in the Grand Bank area and information on feeding habits of the genus *Lycodes* is rather scarce in general. Houston and Haedrich (1986) analysed stomach contents of demersal fishes caught in the Carson Canyon region of the Grand Bank (Fig. 2), including four species of Zoarcidae. They found that the eelpouts fed primarily on benthic invertebrates, namely gammarid amphipods, cumaceans, echinoderms and polychaetes.

Andriashev (1954), McAllister et al. (1981), and Scott and Scott (1988) mention benthic invertebrates, namely polychaetes, small crustaceans (amphipods, isopods, cumaceans), molluscs, and echinoderms, as the food of different species of *Lycodes*. Green (1979) reports the presence of amphipods, polychaetes, cumaceans and isopods in a small sample of stomachs of *Lycodes polaris* and *L. mucosus* taken in

Cornwallis Island, NW Territories, Canada. Nash (1986) discusses aspects of the distribution, growth, and sex ratio in *Lycodes vahlii* in southern Norway, stating that it occurs on soft sediments and feeds on polychaetes, small crustaceans and molluscs, ophiurids, and rhyzopods. It seems reasonable to conclude that eelpouts in the Northeastern region are also likely to depend mostly on benthic invertebrates, namely polychaetes, small crustaceans, bivalves and echinoderms.

Marine mammals

There are ten species of whales and three of seals usually found on the Grand Bank (Parsons and Brownlie 1981). Of these, harp seals (*Pagophilus groenlandicus*) and baleen whales (mainly humpback *Megaptera novaeangliae*, minke *Balaenoptera acutorostrata*, and fin whales *B. physalus*) seem abundant enough to deserve mention. Harp seals are migratory marine mammals inhabiting Newfoundland waters in winter and moving in spring to summer in the Arctic. In the Newfoundland area they eat mostly pelagic fish, especially capelin. Also important in their diet, especially for young seals, are benthic and pelagic crustaceans, namely shrimps *Pandalus* sp. and euphausiids *Thysanoessa* sp. (Sergeant 1973, Bowen 1981). To a lesser extent they also feed on groundfish like plaice, cod, and Greenland halibut. Feeding takes place mainly inshore and is more intensive in winter and summer (Sergeant 1973, 1976a,b). Judging from the geographic distribution of the harp seals (Sergeant 1976a) I will assume that they do not play a significant role in the fully offshore Southern region. They should, however, be taken into consideration in the Northeastern region.

There is a general lack of detailed information about the diet of whales on the Grand Bank of Newfoundland. Baleen whales have a diet that includes mostly small pelagic fish, copepods and euphausiids, depending on area and time of the year. Humpback whales are summer visitors to the Newfoundland-Labrador area and appear to play a significant role in the Southern region by feeding heavily on the South Grand Bank stock of capelin (Parsons and Brownlie 1981, Carscadden

1983b) during the capelin spawning season (June-July) on the Southeast Shoal. This situation was described by Whitehead and Glass (1985) for 1982 and 1983. These authors also spotted other marine mammals (fin and minke whales, and dolphins) apparently preying upon spawning capelin concentrations in the same area. About 900 humpbacks (15-30% of the NW Atlantic population) were estimated visiting that area, and these were suggested to be the most important marine mammals feeding on spawning southern capelin.

Whales (fin, minke, and humpbacks) also feed on the Northern Grand Bank stock of capelin in summer (in the Northeastern region). Piatt et al. (1989) found a strong correlation between capelin and baleen whale abundance during 1982-85 in the Witless Bay region (eastern coast of the Avalon Peninsula). The authors point out, however, that the impact of whale predation on capelin concentrations in the area appeared to be minimal. Although there seemed to be thousands of tons of capelin locally available during the spawning season, the whales were estimated to have taken no more than 100 tons each season (Piatt et al. 1989). Other reports point out the importance of capelin to whales on the Grand Bank. Sergeant (1963) found capelin in 85% of the stomachs of minke whales and reported that sei whales, though less abundant, also feed on capelin. Mitchell (1974) also reports capelin as being the main prey of fin whales in the Newfoundland area (up to 90% of diet). The emphasis of current literature on the whale-capelin interactions on the Grand Bank should not hide the fact that whales have a more diversified diet, including species that are abundant on the Bank like euphausiids, sand lance and copepods (Mitchell 1974). Fin whales, for example, eat mainly krill and sei whales eat copepods and euphausiids in the Nova Scotian region (Mitchell 1974). Parsons and Brownlie (1981) suggest that sand lance could have become an important prey for humpbacks offshore with the decline of capelin stocks. All this suggests a much greater versatility and ability of whales to adjust to prey availability and abundance than reports of their diet on the Bank might otherwise suggest.

Seabirds

Newfoundland seabird colonies contain two to three million breeding birds, and the number of birds that visit the Grand Banks over the course of a year has been estimated to be about 35-45 million individuals (Williams et al. 1981, Brown and Nettleship 1984, Montevecchi and Tuck 1987). The most numerous species breeding in Newfoundland is a planktivorous seabird: Leach's storm-petrel (*Oceanodroma leucorhoa*) (Cairns et al. 1986, Sklepkovych and Montevecchi 1989). The petrels feed on amphipods, euphausiids and small myctophid fish. Williams et al. (1981) suggest they might also prey upon capelin eggs and larvae when these disperse over the Banks in summer. In the summer, however, the petrels are probably outnumbered by the piscivorous shearwaters (greater, *Puffinus gravis* and sooty, *P. griseus*), Wilson's storm-petrels (*Oceanites oceanicus*), and the omnivorous northern fulmar (*Fulmarus glacialis*). In winter, there is a large contribution of migrants from the north: dovekies (*Alle alle*), a planktivorous species, and the piscivorous black-legged kittiwake (*Rissa tridactyla*) (Brown 1986, D. C. Schneider pers. comm. in Apr 1991).

On the Avalon peninsula of the Island of Newfoundland there are four major colonies of seabirds (Cape St. Mary's, Witless Bay, Baccalieu and Funk Islands) that are numerically abundant inshore (Brown and Nettleship 1984, Montevecchi and Tuck 1987). These colonies include 90% or more of the breeding seabirds of the NW Atlantic. The main piscivorous species are the gannet (*Sula bassanus*), the Atlantic puffin (*Fratercula arctica*), the common murre (*Uria aalge*), and the herring gull (*Larus argentatus*). Puffins and murres are heavy capelin consumers. Capelin in some years might comprise as much as 90% of their diet (Brown and Nettleship 1984, Piatt and Methven 1986). Piatt and Methven (1986) report that the number of capelin in stomachs of puffins and murres is significantly correlated with local capelin abundance. They found evidence for a Type III (sigmoidal) numerical response of murres and puffins to capelin density. Chicks diet was found to be almost totally dependent on capelin (on a weight basis), whereas adults also fed on small cod and on sand lance as a complement to capelin. Percent weight composition of adult diets in the three-year period of study was 83% capelin, 7% cod, 10% sand lance, in the case of murres; and 79% capelin, 2% cod, 14% sand lance, in the case of puffins (Piatt and Methven 1986).

All the dominant seabirds in Newfoundland and Labrador consume capelin. Capelin comprises around 30-40 % of the diet of kittiwakes and gulls. These birds are less specialized than murres and puffins, feeding also on crustaceans and cephalopods (Threlfall 1968). Greater shearwaters feed mostly on capelin and squid. Non-breeding shearwaters have been seen in the Southeast Shoal area in large numbers during the spawning season of capelin which they are probably exploiting. Estimations of their abundance and food consumption are not available, but they are likely to be high. All these species consume other fish, namely sand lance and small gadoids. Gulls are also known to be heavy predators of other birds like young puffins and adult Leach's storm-petrels. Brown and Nettleship (1984) estimate that the total consumption by kittiwakes, murres, and puffins in NAFO div. 3L could be around 9000 tons, about 7900 of which are capelin. The same authors estimated that the total consumption of capelin by seabirds in Newfoundland area could go up as high as 250,000 tons.

Brown and Nettleship (1984) and Carscadden (1984) discuss the ability of the seabirds of Newfoundland to adjust to low biomass levels of their preferred prey species. In spite of their apparently wide range of potential prey in the NW Atlantic (e.g. capelin, sand lance, herring, mackerel, small gadoids, squid, polychaetes, crustaceans), seabirds like murres and puffins seem to be too specialized to avoid detrimental population effects in years of low capelin availability. Brown and Nettleship (1984) claim that there might not be an acceptable substitute for capelin in the Newfoundland area from the point of view of both availability and nutritional value. These authors associated a drastic shift in diet composition of Witless Bay puffins in 1981 from capelin to sand lance, with high chick mortality and a drop in the average weight of successfully fledged youngs as a result. Carscadden (1983a, 1984) however points out that seabirds exhibit wide variations in breeding success which can be associated with weather conditions alone. When these natural variations are combined with the long life span and late maturity of seabirds, populational changes caused by changes in diet composition might be too difficult to identify.

3.3. Differences Between the Southern and the Northeastern Regions

The foregoing review of feeding interactions suggests some important differences between the two major zoogeographic regions on the Grand Bank of Newfoundland, the Southern and the Northeastern Regions. Part of these differences could be anticipated from differences in the species composition of each region (Fig. 4). The major difference is due to the yellowtail flounder, a very abundant flatfish (Fig. 21), strongly linked to the benthos of the Southern region but hardly present in the deeper Northeastern region. Other major differences in species composition concern the presence in the Northeastern region of two water column feeders that are absent to the south, the seals and the Greenland halibut. As for seabirds, the shearwaters appear to be more important in the Southern region, at least in the summer. Gannets, puffins, murres, and gulls appear to be more important inshore, in a small part of the Northeastern region. The topological position of seabird species in the food web is nevertheless very much the same in the two regions.

There are also differences between the two major zoogeographic regions that stem from the information on feeding behaviour and diet composition reviewed in section 3.2. Some of the most abundant species appear to have a different diet in different areas of the Bank. These differences in diet may translate into actual differences in the topological structure of the community food web or in the extent to which species affect each other's growth rates. The link between cod and capelin appears to be less important in the Southern region than in the Northeastern. Sand lance appears to be relatively more important for cod in the south than in the north. Another difference concerns the diet of American plaice. Pitt's (1973) study suggests that American plaice in part of the Southern region (more precisely, NAFO div. 3N) is a predominantly pelagic feeder, as compared to its more benthic role in the Northeastern region (NAFO div. 3L) (see Fig. 29). Prey groups like the polychaetes, brittle stars, and sand dollars play an important role in the diet of American plaice in the north of the Bank. The same species appear far less important for plaice in the south, where they actually comprise a significant proportion of the yellowtail diet (Fig. 31). Although there is potential for a competitive situation between plaice and yellowtail, the information available is too scarce to elaborate on this quite interesting matter.

3.4. Food Webs on the Grand Bank

One way to summarize the information reviewed in sections 3.2 and 3.3 is to build stereotyped diagrams representing community food webs (Cohen 1978, Pimm 1982) for each major region on the Grand Bank. As with most attempts to synthesize information in any scientific endeavour, there are advantages and disadvantages in doing so. An important advantage of constructing food webs is the possibility of being able to compare the net of feeding interactions in different ecosystems in a relatively easy way. The disadvantages involved have to do with the loss of information about the biological detail and the variation in time and space of those feeding interactions. There are actually a number of standard simplifying procedures, common in the food web literature, that have been followed to construct food webs. These simplifications raise a number of difficult conceptual issues (see Pimm 1982 and Yodzis 1989 for reviews) but do have the advantage of rendering the webs comparable.

Figs. 32 and 33 summarize predator-prey interactions in the Southern and in the Northeastern regions of the Grand Bank. Figs. 32A and 33A present relationships in the water column; Figs. 32B and 33B present relationships involving bottom-dwelling organisms. This is obviously an arguable division because abundant species like cod and plaice feed in both habitats and benthic species have pelagic life-stages. I will return to this point in section 3.5. Using Tyler's (1971) terminology, I have included in the food webs all the abundant "regulars" (species present all year) and abundant "seasonals" (only present in certain parts of the year), but did not include "occasionals" (species that show up irregularly). Furthermore, a number of standard simplifications were followed. Species thought to have basically the same predators *and* the same prey were lumped together into the same unit, a trophospecies (Briand and Cohen 1984). Intraspecific interactions were omitted in the diagrams, and life-stages characterized by a different diet (Figs. 28 to 31) were not distinguished.

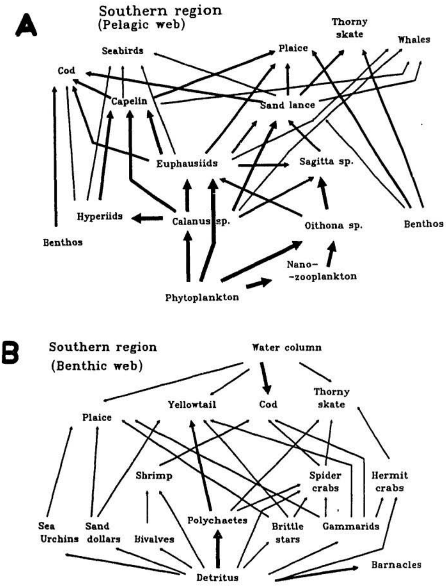


Figure 32. Main species and their trophic interactions in the Southern Grand Bank region. A. In the water column. B. Macro- and megabenthos on the bottom. The width of the arrows indicate major directions of energy flow.

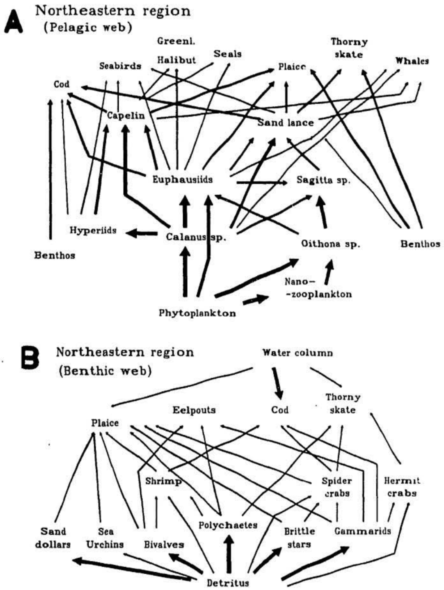


Figure 33. Main species and their trophic interactions in the Northeastern Grand Bank region. A. In the water column. B. Macro- and mega-benthos on the bottom. The width of the arrows indicate major directions of energy flow.

The feeding links in the food webs of Figs. 32 and 33 represent feeding interactions averaged over the entire year, with seasonal patterns not taken into consideration. A link is included whenever a prey is believed to comprise at least 5% of the annual diet of a predator *and* both predator and prey are fairly abundant in the respective regions. I have used links with different thicknesses, which indicate a subjective assessment of the main directions of energy flow. This assessment is based both on the proportion of prey in the diet of predators and on the relative abundance of each predator-prey pair on the Bank. It is emphasized that interaction strength, as expressed by the elements of the community matrix (i.e. the per capita effect of a species density on another species' growth rate; see section 4.2.2) is not necessarily reflected in the arrow thickness of Figs. 32 and 33.

3.5. Static Properties of Food webs

There is a major dichotomy in the food web literature of the past two decades that translates into two complementary ways of viewing an ecosystem. One view focuses on the movement of materials through ecosystem compartments. It emphasizes general system properties, such as total biomass, productivity, and nutrient cycling. Taxonomic considerations are minimized, implying that the energetic nature of the ecosystem is somehow more important than the particular biotic units performing each task. Most of this work focuses on the base of the food web, i.e. on primary production and the very lowest trophic levels. The top carnivores, like fishes, are usually left to the fisheries biologists. Despite considerable literature on models of nutrient flow in the sea, oceanographic studies either do not reach the level of fish populations (Hofmann and Ambler 1988, Anderson and Nival 1989, Roff et al. 1990) or tend to lump fish into a very small number of compartments (e.g. pelagic, demersal) (Walsh et al. 1981, Pace et al. 1984, Fasham 1984).

Another viewpoint, historically rooted in the stability-diversity controversy, centers on the network design of community food webs. This view is inextricably linked to the use of simplified mathematical models describing the dynamics of isolated and interacting populations (MacArthur 1972, May 1973). This network/population dynamics approach received a boost a decade ago with Cohen's (1978) monograph on food web static structure and Pimm's (1982) influential synthesis. From studies based on a growing collection of published food webs (Briand 1983, Briand and Cohen 1987), investigators have found that certain features of food web networks recur more often than would be expected by chance alone (see Lawton 1989 and Yodzis 1989 for reviews).

Both views on the nature of ecosystems (nutrient flow and network/population dynamics) have recognised limitations. I have chosen the tools of the network/population dynamics approach for my study on the Grand Bank of

Newfoundland. The Bank as a whole is an intensively exploited ecosystem and various components of the food web are influenced by the fishery. This being the case, community studies should be conducted at a level of taxonomic resolution at least comparable with that of the fishery. On the Grand Bank, such a level of resolution appears more readily available through application of the network/population dynamics approach. For this purpose, the simplifications adopted to construct the food webs presented in section 3.4 have an advantage. They render them comparable with other published food webs whose static features have been studied in the network/population dynamics context (Cohen 1978, Pimm 1982, Briand 1983, Briand and Cohen 1984, 1987). I will proceed with a comparative examination of the Grand Bank food webs and postpone the discussion of the dynamic aspects to Chapter 4.

3.5.1. Food chain length

A food chain is a sequence of feeding links between species (A eats B eats C...) that starts at a basal species (a species that preys on no other species) and ends at a top predator (a species that is preyed upon by no other species). The length of a chain is the number of links it comprises. The mean chain length of a food web is the arithmetic average of all chain lengths within the web. In absolute terms, food chains in real food webs are known to be short (Hutchinson 1959, Cohen 1978, Pimm 1982). The Grand Bank food webs, with mean chain lengths between 2.30 and 3.79 (calculated from Figs. 32 and 33) are no exception (Table 5).

TABLE 5. Mean and maximum chain lengths of the Grand Bank food webs.

	Southern		Northeastern	
	Pelagic	Benthic	Pelagic	Benthic
Number of species	15	15	17	14
Mean chain length	3.79	2.43	3.75	2.30
Max. chain length	6	3	6	3

The pelagic webs on the Bank are longer than the benthic webs (3.75 and 3.79 versus 2.43 and 2.30, respectively; Table 5), which is in good agreement with the results of Briand and Cohen's (1987) analysis of a collection of 113 published food webs. Briand and Cohen (1987) found that the mean length of food webs does not seem to be directly related with productivity and environmental variability. However, webs in three-dimensional environments (e.g. marine pelagic, rain forest) are longer, on average, than webs in planar environments (e.g marine benthic, intertidal). Briand and Cohen (1987) made no distinction between food webs from terrestrial, freshwater, and marine environments. I have selected (Table 6) marine food webs that were classified as being distinctly either from two- or three-dimensional environments (Briand and Cohen 1987). These webs typically have 2 to 3 links (mean = 2.5) in two-dimensional marine environments (e.g. benthic, intertidal) and 3 to 5 (mean = 4.1) in three-dimensional ones (e.g. marine pelagic). The mean lengths of the benthic and pelagic webs on the Grand Bank (Table 5) appear quite comparable with these values.

There are at least five (not exclusive) theoretical explanations for food chain shortness, mostly centered on arguments of energy constraints and dynamic stability (Pimm 1982, Schoener 1989, Lawton 1989, Yodzis 1991), but at present there is no conclusive empirical basis on which to decide what is (are) the most appropriate one(s). Schoener (1989) suggests that his Productive Space Hypothesis predicts the observed difference in length between two- and three-dimensional food webs. Productive space (PS) is the product of the spatial extent (area or volume) of the food web by the productivity of the area (or volume). Assuming that each individual has a certain requirement of PS and that a population will therefore require some multiple of this individual requirement, the PS hypothesis predicts that "maximum food-chain lengths are determined by the amount of productive space required to allow critical component species populations to persist with some high probability" (Schoener 1989, p. 1568). If one makes the controversial assumption that PS is, on average, likely to be bigger in three-dimensional environments than in two-dimensional ones, the hypothesis predicts the difference in food chain lengths reported by Briand and Cohen (1987) and observed on the Grand Bank.

TABLE 6. General descriptive characteristics of food webs in two- and three-dimensional marine environments (compiled from Briand and Cohen 1987).

TWO-DIMENSIONAL ENVIRONMENTS

Web number(•)	Mean chain length	Max. Length	nC	Habitat
10	2.00	2	2.0	Exposed rocky shore, N. Engl., USA
11	2.00	2	2.0	Protected rocky shore, N. Engl., USA
12	2.25	3	3.3	Exposed rocky shore, Washington
13	2.50	3	3.5	Protected rocky shore, Washington
50	2.44	3	3.5	Sand beach, California
52	2.08	3	3.4	Rocky shore, Torch Bay, Alaska
53	1.95	2	3.0	Rocky shore, Cape Flattery, Washington
104	3.16	5	4.8	Rocky shore, Bay of Panama
105	3.67	5	4.9	Rocky shore, Gulf of Maine, USA
106	2.41	5	4.3	Rocky shore, Monterey Bay, California
107	2.50	3	3.1	Bay pilings community, New Jersey
108	2.27	3	3.1	Rocky shore, Cabrillo Point, California
109	2.88	4	5.7	Rocky shore, central Chile
110	2.13	3	3.8	Rocky shore, Cape Ann, Mass.
Mean:	2.45	3.3	3.6	
St. dev.:	0.49	1.1	1.0	
THREE-DIMENSIONAL ENVIRONMENTS				
17	3.56	5	3.5	Coral reefs, Marshall Islands
20	3.26	5	3.3	Antarctic Pack Ice Zone
21	4.61	7	5.0	Ross Sea
29	3.14	5	2.9	Arctic Seas
30	5.02	7	4.9	Antarctic Seas
41	5.92	8	5.8	Tropical seas, epipelagic zone
43	3.13	5	4.0	Kelp bed community, South Calif.
86	4.09	6	4.9	Suruga bay, epipelagic zone, Japan
Mean:	4.09	6.0	4.3	
St. dev:	1.02	1.2	1.0	

(•) Original numbers in Briand and Cohen (1987).

A crucial point in Schoener's hypothesis is the explicit introduction of space, which suggests a tautological reasoning in this explanation. An interesting test would be to compare food webs from environments with equal PS and different dimensionality. If the PS hypothesis is correct, then dimensionality in these webs should not correlate with food chain length. But if the correlation holds, then there is something intrinsic about space, other than its obvious link to total production, that promotes longer food chains. This is easy to say, but quite difficult to investigate. One can anticipate difficulties in making comparisons of PS across very different types of environment. Schoener (1989) himself pointed out practical difficulties in testing his hypothesis.

3.5.2. Connectance

Connectance (C) is a measure of food web complexity. It is defined as the actual number of interspecific interactions in the web divided by the maximum number of binary interactions possible. Herein I adhere to the original definition of connectance (Gardner and Ashby 1970) whereby interactions in the numerator include only trophic interactions. If n is the number of species in the web and L is the number of trophic links in the food web matrix, then $C = 2L/n(n-1)$ (and C varies from 0 to 1). May (1973), on theoretical grounds, anticipated the existence of bounds to food web complexity as measured by the product nC. Simple biological assumptions are nevertheless enough to account for the relative constancy of nC (Pimm 1982). If each species interacts with an approximately constant number of species (s = 3 to 5), independently of the total number of species in the web (n), then $C \approx sn/n^2$, and $nC \approx s$. Statistical analysis of published food webs has confirmed that the nC does remain within restricted bounds (Rejmanek and Stary 1979, Yodzis 1980) and that the number of links in webs is proportional to n: $L \approx 2n$ (Cohen et al. 1986). Winemiller (1990), however, has recently argued that the values of L/n in published food webs are underestimated by idiosyncratic omissions of weak trophic links, and that they should be expected to be well above 2 (Winemiller [1990] found values of L/n that average 6.31 in his detailed tropical webs).

The values of nC in the Grand Bank food webs (Table 7) lie close to the top of the 2–5.8 range found in published marine food webs (Table 6). Thus, on average, each species in Figs. 32 and 33 interacts directly with a relatively high number of other species. It is not likely that this can be explained only by a relatively low degree of taxa lumping in the Grand Bank food webs. Sugihara et al. (1989), assessing the effect of taxa aggregation in 60 invertebrate-dominated food webs , found that the product nC tends to fall only slightly with increasing taxa lumping. Is there an unusually high proportion of any particular type of trophic link that can be related to the high values of nC ? There are links between basal and intermediate species (L_{BI}), intermediate and top species (L_{IT}), intermediate and intermediate species (L_{II}), and basal and top species (L_{BT}). Table 7 presents the proportions of each type of link relative to the total number of links ($L = L_{BI} + L_{IT} + L_{II} + L_{BT}$) in the Grand Bank food webs and the same proportions based on information pooled from a catalog of 62 published food webs (Briand and Cohen 1984). The link between intermediate species and top predators (L_{IT}) is the only type of link that shows an unusually high value in the Grand Bank webs (Table 7). The high values of L_{IT} appear to be related to a high degree of omnivory, as compared with most published food webs.

TABLE 7. Connectance and the proportion of each type of trophic link in the Grand Bank food webs. L is the total number of trophic links in the food web, L_l is the number of links of type l (see text for link types), and n is the number of species. Food web statistics of the ratios L_l/L are also presented for a sample of 62 webs from Briand and Cohen (1984).

	Southern		Northeastern		Briand & Cohen (1984)
	Pelagic	Benthic	Pelagic	Benthic	
Connectance	0.35	0.28	0.30	0.35	
nC	5.3	4.2	5.1	4.9	
L/ n	2.47	1.93	2.41	2.29	≈ 2(*)
L_{BI} /L	0.19	0.31	0.17	0.28	0.27
L_{II} /L	0.35	0.17	0.32	0.19	0.30
L_{IT} /L	0.43	0.48	0.49	0.53	0.35
L_{BT} /L	0.08	0.03	0.07	0.00	0.08

(*) From a sample of 113 food webs (Cohen et al. 1986)

3.5.3. Omnivory

I follow Sprules and Bowerman (1988) in defining an omnivore as any predator that has at least one omnivorous loop. Such a loop exists when a feeding path can be traced directly to a prey and then back to the predator through at least one other prey that occupies an intermediate position. Table 8 presents the values of two common indices of omnivory in the Grand Bank webs, in a collection of 40 food webs (Pimm 1980, Briand 1983), and in zooplankton webs in lakes (from Sprules and Bowerman 1988). The indices used are the degree of omnivory (the ratio between the number of omnivore loops and the number of top predators) and the ratio between the number of omnivore species and the number of top predators.

Omnivory in the pelagic webs of the Grand Bank appears to be unusually high (Table 8), quite comparable to the high values for glacial lakes found by Sprules and Bowerman (1988). This high degree of omnivory appears to explain the relatively

TABLE 8. Average degree of omnivory and the ratio of number of omnivores to number of top predators in the Grand Bank food webs, in a sample of 40 webs (Pimm 1980), and in samples of 246 nonglacial and 269 glacial lakes (Sprules and Bowerman 1988). Numbers in brackets are standard deviations.

	Southern		Northeastern		Pimm	Nonglacial	Glacial
	Pelagic	Benthic	Pelagic	Benthic	(1980)	lakes	lakes
Number of species	15	15	17	14	15 (5.5)	11 (2.5)	13 (2.0)
Average degree omnivory	5.6	1.4	5.0	3.0	1.5 (1.9)	0.3 (0.3)	5.5 (2.6)
# omnivores /# top predats.	2.0	1.0	2.0	1.5	0.96(*) 2.5(+)		

(*) In miscellaneous webs, (+) In insect-dominated webs

high proportion of L_{IT} links which result in high connectance values. Pimm and Lawton (1978) studied the local stability of Lotka-Volterra models of food chains with omnivore loops. They concluded that omnivory should be relatively rare in nature and that the omnivore, when present, should feed in non-adjacent trophic levels only rarely. Pimm (1980) subsequently showed that real food webs indeed appear to have less omnivory than expected by chance alone. Yodzis (1984), however, argued that the rarity of omnivory could be explained without invoking dynamical stability arguments. The argument was that it is difficult, in an evolutionary sense, to feed efficiently at different trophic levels, and these difficulties are probably enhanced when omnivory spans both plants and animals (Yodzis 1984).

But the observation that omnivory is rare may in itself be distorted by poor-quality data used to build published food webs. As Winemiller (1990) points out, from his analysis of detailed tropical webs, in aquatic environments, omnivory is likely to be far more abundant than is suggested by Pimm and Lawton (1978) and Pimm (1980). The trophic position of aquatic species depends largely on body size and, consequently, these species can exhibit dramatic ontogenic shifts in habitat and diet of a kind that are uncommon among terrestrial predators (Werner and Gilliam

1984). In the course of a lifetime, a large marine predator is likely to exploit a very wide range of prey (Figs. 28 to 31). If these feeding interactions are all included in aquatic webs where lifestages are not explicitly represented (as in Figs. 32 and 33), then omnivory can be expected to be high. There is some evidence that such "life-history omnivory" may increase the chances of stability in very simple food web models that include omnivory (Pimm and Rice 1987). Ursin (1982) suggests that omnivore loops are probably quite common in the sea, and describes how substitution of the traditional linear chain: small prey → small predator/ big prey → big predator by the triangular omnivore loop:

$$\begin{tikzcd}
\text{small predator/ big prey} \arrow[dr] & \\
\text{small prey} \arrow[u] \arrow[r] & \text{big predator}
\end{tikzcd}$$

helps to explain trends in species abundance in the North Sea ecosystem.

Notwithstanding the fact that our sample size is relatively small, the Grand Bank food webs also exhibit the association between omnivory and long food chains suggested by Sprules and Bowerman (1988). A possible explanation is that the way omnivory is being measured necessarily leads to higher values for longer food chains when predators exhibit life-history omnivory. Assume that a predator feeds upon most trophic levels below its own in the course of its ontogeny. As the number of trophic levels (t) increases linearly, omnivorous loops increase at least as t^2. Consider, for example, a linear food chain (A eats B eats C...). If it is assumed that every non-herbivorous predator feeds upon all trophic levels below it (excluding primary producers), then the number of omnivorous loops equals $(t-3)(t-2)/2$. Since the number of top predators increases linearly with the number of species in observed food webs (Briand and Cohen 1984), the average degree of omnivory (Sprules and Bowerman 1988 and Table 8) can be expected to increase with food chain length.

3.6. Food webs, Niche Space, and Body Size

One version of Gause's "competitive exclusion principle of niche separation" (Hardin 1960) states that species in a community can coexist because their niches are not coincident. Species preserve niche separation by differing in their pattern of resource utilization, and there are different ways through which they can achieve that. Investigators have often considered different categories of niche dimension to systematize the study of resource utilization. Three common categories are habitat, time, and food type (Goodall 1974, Schoener 1974). Any of these three categories may comprise more than one dimension in the (abstract) Hutchinsonian niche, but they are not meant to be exhaustive. Predator avoidance and foraging abilities are examples of other dimensions seldom reported, probably because they are so difficult to assess. Schoener (1974) conducted a review of 81 case studies on the dimensions that primarily separate species with respect to resource utilization. He found that "habitat dimensions are important more often than food-type dimensions, which are important more often than temporal dimensions" (Schoener 1974, p. 33) and that species are usually separated along two dimensions of natural resources (see also Pianka 1974).

Four years later, Cohen (1978) presented his investigation of 30 published food webs aimed, among other things, at answering a question somewhat complementary to Schoener's (1974) interests: "What is the minimum dimensionality of a niche space necessary to represent the overlap among observed [trophic] niches ?" (Cohen 1978, p. 4). Using a graphic approach at the time uncommon in ecology, Cohen (1978) found that in habitats with limited physical and temporal heterogeneity, the overlap of species along trophic dimensions can almost always be represented in a single niche dimension. Cohen's result is not to be expected by chance alone and, in spite of conceptual ambiguities and data limitations stressed by Cohen (1978), the result remained intriguingly unexplained until Sugihara's (1983) study. Sugihara (1983) demonstrated that Cohen's finding was just "the tip of the iceberg", an expression of evolutionary constraints underlying the way communities are assembled. Sugihara (1983) demonstrates that if, during the course of community assemblage by sequentially arriving colonists, every new species feeds on relatively similar resources, then, as a by-product, the resulting food web should almost always be an interval food web. Sugihara's result makes perfect sense in the marine environment, where body size is probably a major determinant of prey selection (see below). However, the evolutionary implications of his result are beyond the scope of this thesis and therefore I will mainly focus on Cohen's result in the context of the Grand Bank food webs.

The first step in the investigation of the trophic dimensions of niche space is the adoption of some habitat concept. This is an intuitive consequence of Schoener's (1974) findings. The features differentiating between habitats are probably multidimensional and different from the dominant dimensions within each habitat. If the scope of the study extends over composite habitats, one can expect an increase in niche dimensionality simply because of that. Habitat, however, is a term usually ambiguously defined, when defined at all. Cohen (1978) uses an interpretation attributed to Kohn (cit. in Cohen 1978) whereby habitat is defined as a physical space where there is some sort of uniformity in respect to a set of (biotic and/or abiotic) environmental variables. As with so many other ecological concepts, habitat is therefore highly scale dependent (O'Neill et al. 1986) and is potentially divisible into a hierarchy of nested subunits (Kolasa 1989). It is left to the investigator to solve the problem of identifying these subdivisions at the appropriate level of his/her interest. From this standpoint, the definition of fish assemblage areas presented in Chapter 2 can actually be seen as an attempt to identify, objectively, the first hierarchical division of the whole Grand Bank habitat. But should the major zoogeographic regions identified be further subdivided ? I do not have a definitive answer to this question.

Given the mobility of most pelagic species and their apparent widespread distribution on the Grand Bank, it seems unlikely that biological coherence will be preserved with further horizontal subdivisions of the zoogeographic regions defined in Chapter 2. However, examination of the food web matrices (Pimm 1982) of each region (Table 9 is an example for the Southern region) suggests the existence of species guilds (i.e. functionally linked subsets of species in a given area), that could be associated with the water column on the one side and the bottom on the other.

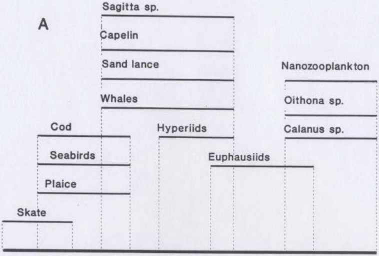
TABLE 9. Food web matrix of the Southern region (pelagic + benthic). A cross (X) indicates that a consumer (in columns) feeds on a resource (in rows). Notice the guilds formed by pelagic consumers (cloud of X's at top left) and by benthic consumers (bottom right). Plaice, skate, and cod feed in both habitats.

	2	3	4	5	6	7	8	9	10	11	12	13	14	16	17	18	19	20	21	22	23	24	25	26
1. Phytoplank	X	X		X	X																			
2. Calanus sp			X	X		X	X	X	X															
3. NanoZooplk					X																			
4. Hyperiids							X			X			X											
5. Euphausiid						X	X	X	X	X	X		X											
6. Oithona sp				X		X																		
7. Sagitta sp								X																
8. Capelin									X	X	X		X											
9. Sand lance								X		X	X	X	X											
10. Whales																								
11. Seabirds																								
12. Plaice																								
13. T. skate																								
14. Cod																								
15. Detritus														X	X	X	X	X	X	X	X	X	X	
16. Urchins											X													
17. Sand dolr											X													X
18. Bivalves																							X	
19. Polychaet												X										X		X
20. Britt star											X											X		X
21. Gammarids											X		X								X	X		X
22. Barnacles																								
23. Herm crab												X												
24. Spid crab												X	X											
25. Shrimps													X											
26. Yellowtail																								

In the water column one finds planktonic species, highly mobile piscivorous predators, and planktonic predators. On the bottom one can identify an important guild largely dominated by benthic detritivores. This pelagic versus benthic food web dichotomy, shown in Figs. 32 and 33, is obviously an oversimplification. It is better viewed as trade-off between the need for a relatively uniform habitat background for each food web, as claimed by Cohen (1978), and biological continuity. I would point out, however, that it marches in good agreement with the claims that there are basic structural differences between food webs in two- and three-dimensional environments (section 3.5).

Suppose that the information on feeding interactions in each region of the Grand Bank is summarized according to graphic rules other than the ones used in Figs. 32 and 33. We could, for example, represent every predator by a vertex and connect two predators with a link if these predators exploited a common resource. Consider for example Fig. 32A. Seabirds would be linked to whales because they both exploit sand lance, euphausiids, and capelin. *Calanus* sp. would be linked to the nano-zooplankton because they have phytoplankton as a common resource. A graph constructed according to this rule is called a niche overlap graph (NOG) (Cohen 1978), also refered to as a consumer graph (Sugihara 1983). There are disadvantages in collapsing information into NOG's, and actually they are not the only alternative to the graphic rules of Figs. 32 and 33 (Sugihara 1983). However, the NOG provides a general picture of the competitive outlines of a community and is useful to illustrate Cohen's (1978) main empirical result.

Cohen (1978) found that the NOG of almost all published food webs can be represented by a one-dimensional picture called an interval graph without loss of information. In graph theory, an interval graph is a graph whose points are represented by intervals along the real line (Harary and Palmer 1973). Figs. 34 and 35 are attempts to represent the NOG's of the Grand Bank food webs in interval graph form. Each predator is represented by an interval along a straight line, and two predators are made to overlap if they overlap in their diet (i.e. if they are connected in the NOG). Figs. 34 and 35 illustrate that in three of the Grand Bank food webs considered (Southern pelagic, Southern benthic, Northeastern pelagic) the information on the diet overlap of the predators can be collapsed into a single, yet unidentified, dimension (Figs. 34A,B and 35A). These three food webs are called interval food webs (Cohen 1978). The same was not possible for the Northeastern benthic web (Fig. 35B), for one cannot collapse all predators into a single dimension without leaving at least one out (hermit crabs in Fig. 35B).



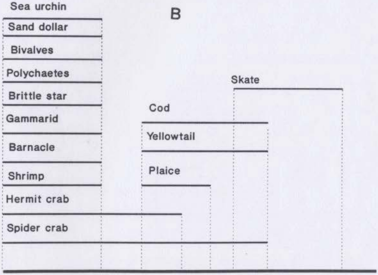


Figure 34. Interval graphs of food webs of the Southern region. Predators are represented as intervals of the line at the bottom. Intervals overlap when species overlap in diet. A. Southern pelagic web. B. Southern benthic web.

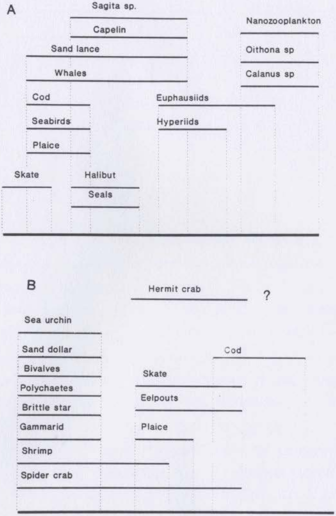


Figure 35. Food webs in the Northeastern Region (as in Fig. 34). A. Northeastern pelagic web, an interval food web. B. Northeastern benthic web. This is not an interval food web because it cannot be collapsed into one single dimension. The interval representing hermit crabs should overlap with all species but skate. It cannot be fitted into the picture unless the graph is rebuilt with two or more dimensions.

But is this important at all ? There is, of course, a fundamental intellectual curiosity that arises from the observation that the vast majority of published food webs are interval, something that is not to be expected by chance alone. There are at least two additional interests of intervality. One is that most mathematical theory on the limitations of niche overlap assumes one single dimension in niche space (e.g. May and MacArthur 1972, May 1974). For analytical convenience, theorists had assumed, without empirical evidence, "a one-dimensional spectrum of resources [...] sustaining several species, each of which has a preferred position in the spectrum" (May 1974, p. 298). Now the evidence that most food webs are interval validates the assumption (Cohen 1978). In most food webs a single dimension is enough to ordinate the information about the diet overlap of consumers in agreement with Gause's principle. Another interest of intervality is the meaning that can be attached to the species positioning along a line in each particular habitat. Before addressing this point, however, I want to stress that we are stepping on very speculative grounds since there are no reasons to believe that any real meaning can be attached to the line. As Sugihara (1983) remarks, this single dimension has a conceptual analogy with an axis of a factorial method in multivariate analysis (e.g. Principal Components), combining linearly dependent variables without always having a straightforward interpretation. Moreover, intervality does not exclude the interpretation of the community in a higher dimensional space. The single dimension refers not to the number of biologically relevant environmental factors, which may be high, but to the minimum number of factors needed to separate species.

Bearing the above warning in mind, there appears to be a general trend in increasing (or decreasing) predator body size as one moves along the single interval dimension of Figs. 34 and 35. With the exception of whales, the pelagic interval graphs range from top predators (fish and birds) to the nano-zooplankton in a relatively orderly way. The conspicuous misplacement of whales is due to their well known predation upon swarming small pelagic species. The benthic graphs split the species into two guilds: detritivore invertebrates and larger nektonic predators. It would be precipitate, however, to conclude that body size is the unique dimension sufficient to represent trophic niche space on the Grand Bank. As Schoener (1974) points out, dimensions in a habitat are seldom independent, and some other monotonic correlate of body size could probably be used to interpret Figs. 34 and 35 as well. But it is hardly surprising that body size is the organizative dimension of niche overlap on the Grand Bank. On the one hand, this finding is completely consistent with the apparent predominance of "life-history omnivory" in the sea discussed in section 3.5.3.. On the other hand, contemporary research has identified body size and energy transfer along size spectra, from plankton to fish, as a structuring mechanism in marine communities (e.g. Sheldon et al. 1972, Landry 1977, Platt and Denman 1978, Pope et al. 1987).

In the marine environment, where most plants can be easily integrated in a continuum of size spectrum, as opposed to land where there is need to consider organic structures with different eatable properties (e.g. Cousins 1980), the simple rule that "the larger eats the (some order of magnitude) smaller" is likely to be the major determinant of niche structuring. If competition in the sea exerts a dominant influence along the body size axis of the Hutchinsonian niche, the net result of the process should be a regular spacing of species along that axis and at random positions along others, as claimed by Gatz (1979) for stream fish communities. A possible test of whether body size is the determinant of niche overlap would be to consider the universe of all species arbitrarily divided into size classes, and then examine if every pair of overlapping classes also overlaps in diet. Conversely, it should also be checked if there are non-overlapping size classes that do overlap in diet.

In the absence of available data to conduct the above test, I have rebuilt the NOG of the Grand Bank food webs, this time splitting some of the top predators into size-classes and treating these as "species" in the NOG. The interval properties of the food webs remained the same, still suggesting a gradual spacing of species along the body size dimension of the trophic niche. Fig. 36 exemplifies the interval food web of the Southern pelagic region with size classes taken into consideration. In this example I have considered three classes of cod, and two of plaice and thorny skate. The diet spectra of these size classes draws upon the information of Figs. 28 to 30. Large cod (cod III) are assumed to feed on flatfish, capelin, sand lance, and benthos; medium cod (cod II) does not feed on flatfish but feeds on euphausiids; small cod (cod I) also does not feed on flatfish but feeds on euphausiids and hyperiids. Small plaice (plaice I) are assumed to feed on euphausiids, capelin, sand lance, and benthos; large plaice (plaice II) feed on the same species with the exception of euphausiids. Finally, small skates (skate I) are assumed to feed on benthos and sand lance, and large skates (skate II) also include cod in this diet.

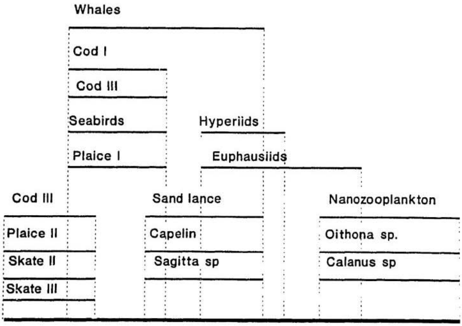


Figure 36. Interval pelagic food web of the Southern Region with cod, plaice, and thorny skate split into size classes.

3.7. Ecological Abstraction and Structure of the Southern Community

3.7.1. Ecological abstraction

The enormous complexity of real world ecological systems is the reason why "The study of population dynamics and population interactions is, of necessity, a process of ecological abstraction" (Tilman 1989, p. 89). Both field ecologists and ecological modellers acknowledge such need by carefully selecting the variables that are to be measured and incorporated into their equations. Even relatively simple boreal marine ecosystems apart from any physical variables (as epitomised in the food webs of Figs. 32 and 33) are complex enough to impose the practical need to consider less than the total number of species interactions in modelling exercises. Then it is reasonable to inquire as to what species should be selected for being incorporated into the models, and how the system properties which they predict compare with properties of an hypothetical model for the whole system.

Perhaps the most sensible approach is to begin with some intuitive criterion of species selection in the hope of arriving at testable predictions that lead to later refinements (Yodzis 1989). One such criterion is simply to select very abundant species in the area of study and infer their main interactions from the type of information presented in section 3.2 and summarized in sections 3.3 and 3.4. There are, however, theoretical insights that can help in the course of this process, mostly centered in the works of Schaffer (1981) and Bender et al. (1984). Schaffer (1981) generalized MacArthur's (1972) derivation of the Lotka-Volterra model of direct competition among consumer species, in which the dynamics of the resource is assumed to proceed much faster than that of the consumer. Bender et al. (1984) achieved one other generalization that will be summarized below.

Suppose that we represent the dynamics of the whole set of n species in the community by a system of n differential equations with very general form, as in [4.1] (section 4.2.2). Then suppose that we restrict our study to a subset of m consumer species ($m < n$) extracted ("abstracted" in Schaffer's terminology) from the entire n-dimensional system. Schaffer (1981) showed that the accuracy of the abstracted system of m equations increases the faster the rate of renewal of the omitted $(n-m)$ resource species as compared to the rate of renewal of the m abstracted consumers. One can think of this rate of renewal as expressed either by the parameter r in the Lotka-Volterra equations of the omitted species, or as the elements of a hypothetical community matrix (see section 4.2) with dimension $(n-m)\times(n-m)$ representing only the interactions among the omitted species. The intuitive idea is the same as MacArthur's (1972), i.e. the consumers' densities change but, because of their faster dynamics, the resources instantaneously adjust to the density levels appropriate to the current consumers' densities.

Bender et al. (1984) arrived at another generalization. Consider again the whole system of n species and the abstracted subset of m species. Bender et al. (1984) showed that if *either* the effect of every species in the m subset on every other $(n-m)$ species in the remaining system is sufficiently small *or* the effect of species in the $(n-m)$ remaining system on the subset of m abstracted species is sufficiently small, then we can approximate the behaviour of the subset of m species fairly well even if we ignore the remaining $(n-m)$ species. I have not defined the expression "effect of one species on another species" here because that will require the mathematics of sections 4.2 and 4.4. Loosely speaking, I am refering to the long term effects of one species on another both directly and indirectly via intermediate species (as expressed by the inverse of the community matrix; see section 4.4.1).

At least for certain purposes, including those of Chapter 4, it appears that the dynamics of certain sets of species embedded in a whole system can be reasonably well approximated when they are abstracted from the whole (see also Yodzis 1989), so long as the dynamics of the abstracted species proceed at a very different pace from the rest of the system and/or there is a loose interaction between the species abstracted and the rest of the system. As Yodzis (1989) points out, the decision to do the abstraction is a difficult one, and on the Grand Bank we do not have more than speculative considerations about how to do it. My abstraction of the Grand Bank community takes special advantage of Schaffer's (1981) findings, and is more grounded on inferences about population dynamics stemming from body size of the individual organisms (Peters 1983) than on actual measurements at the population level.

To model the trophic relationships in the marine community in the Southern region, I have abstracted a simplified system composed of only seven species out of the entire system stereotyped in Figs. 32 and 33. The species selected for my analysis are the dominant vertebrates on the southern Grand Bank: capelin, sand lance, Atlantic cod, American plaice, thorny skate, yellowtail flounder, and seabirds. This selection comprises species that accounted for 80 to 90% of the catches during 16 years of groundfish surveys on the Grand Bank (Figs. 21 and 22), as well as those very abundant vertebrates known to be less vulnerable to demersal trawling. The omitted species are the whales and, most importantly, invertebrates with very small body size (see Figs. 32 and 33). Whales are seasonal visitors whose biomass is at least one order of magnitude lower than that of the fish. They were assumed to have a minimal impact on the species selected (see also Piatt et al. 1989). Simply based on allometric relationships between body size and population parameters (Blueweiss et al. 1978, Peters 1983), I assume that all the main invertebrates omitted have both larger intrinsic population growth rates and much shorter generation times than any of the vertebrates included. The faster the turnover rate of the species omitted relative to the dominant vertebrates, the closer the predictions of my simplified models should be relative to what one would predict had all the species been considered.

3.7.2. Alternative model structures on the Southern Grand Bank

There are two main types of relationships between species in a community. *Inter*specific relationships (e.g. between prey and predator) and *intra*specific relationships (usually assumed self-damping) due to interference between individuals of the same species. Interspecific relationships, in their broader sense, can be inferred from the type of review on feeding interactions presented in section 3.2 and summarized in the food webs of section 3.4. Food webs, however, are imprecise representations of species interactions, because they provide no insight into the influence that species have on each other's dynamics. Questions such as "What are the relative consequences for the densities of cod and plaice if capelin growth rate decreases ?" cannot be answered without a more precise formulation of the system in which these species are embedded. However, even in a simplified system involving only seven species there is considerable uncertainty in regard to the structure that translates well the main features of species interactions over the full year. For example, should competition between yellowtail flounder and other fishes be taken into account ? And what about intraspecific relationships: are there significant self-damping effects for each species? I shall handle this problem by building alternative hypothetical configurations to represent the main species interactions in the Southern Grand Bank community.

Using the information reviewed in this Chapter and resorting to the digraph symbology described by Levins (1974) and Jeffries (1974), I have built five hypothesized configurations of community topology on the Southern Grand Bank (Fig. 37) which I will hereafter refer to as the basic models. Each species is represented by a vertex and two vertices are linked when an important relationship is assumed to exist between the corresponding species. Each link in Fig. 37 is identified by the corresponding element of the community matrix (see section 4.2 and Appendix 1). Links headed by an arrow indicate a positive enhancing effect of the donor on the recipient (e.g. capelin on plaice, a_{51}), whereas those headed by a circle represent a negative effect (e.g. plaice on capelin, $-a_{15}$). The main differences between the basic models in Fig. 37 concern the position of yellowtail flounder in the community. A short description of each model follows.

Basic model I. This is the basic model of which all others are extensions. Six main predator-prey interactions are hypothesized. These include the exploitation of capelin by cod, plaice, and seabirds; and the exploitation of sand lance by cod, plaice, and thorny skate. Yellowtail is not represented in model I. Pitt's (1976) study of yellowtail feeding habits suggests a greater dependence upon amphipods, euphausiids and polychaetes. The predation of large yellowtail (> 39 cm) upon capelin and sand lance is assumed not to have an importance comparable to that attributed to cod and plaice (Pitt 1973, Akenhead et al. 1982, Lilly 1987). This model also assumes that there is no significant competition between yellowtail and cod, plaice or skate.

Basic model II. Yellowtail is included in this model and is hypothesized to compete directly with plaice. Competition here is understood as purely consumptive with a collectivist utilization of space (e.g. Yodzis 1989). Following Pitt (1973, 1976), this could be due to a diet overlap that includes amphipods, euphausiids, ophiuroids, echinoids, sand lance, and capelin.

Basic model III. Yellowtail is represented preying upon a common resource with cod, plaice, and thorny skate. Although labeled sand lance in Fig. 37, this resource could include a much broader range of bottom dwelling organisms common to the diet of these species.

Basic model IV. Yellowtail is hypothesized to be in direct competition with thorny skate. This could be justified by a diet overlap on polychaetes, benthic amphipods and sand lance (Pitt 1976, Templeman 1982).

Basic model V. Combines models II and IV. Yellowtail is hypothesized to be in direct competition with plaice and thorny skate.

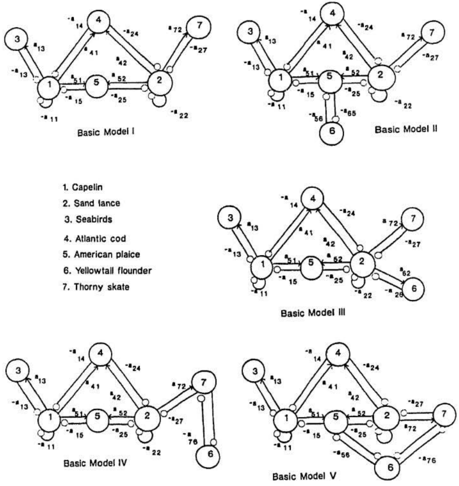


Fig. 37. Five basic models hypothesizing the predominant interactions between the dominant vertebrates in the southern Grand Bank. Arrows indicate a positive effect of the donor on the recipient, whereas links headed by a circle indicate a negative effect. Links are identified by the corresponding elements of the community matrix.

There are at least two other major sources of structural uncertainty not covered by the basic models of Fig. 37. One concerns the existence of intraspecific effects. In Fig. 37 it is assumed that species at the bottom of the structure (capelin, sand lance) are self-damped because they exploit depletable resources, not explicitly represented in the model, that are themselves limited by physical factors (Pimm 1982, Puccia and Levins 1985). It is very difficult to evaluate intraspecific effects in other than basal species (see Pimm 1982, Chap. 4 for a review of the controversy). It is possible that thorny skate, yellowtail, and seabirds should also incorporate such effects. Competition among birds for breeding sites might be among the reasons for justifying self-damping effects. For thorny skate and yellowtail, their diets may be only marginally dependent upon sand lance (Templeman 1982, Pitt 1976). Self-damping effects would therefore be justified because they exploit depletable resources not explicitly included in the model.

Self-damping effects are additional biological interactions that can be incorporated into the basic models of Fig. 37. One other potentially important interaction not yet considered is the preying of large cod (> 89 cm) on small plaice (Minet and Perodou 1978, Lilly and Rice 1983). Eight different combinations of these additional species interactions were considered. Each combination (hereafter called a model version) is labelled from *a* to *h* and is incorporated in turn with each basic model of Fig. 37, yielding a total of 40 possible topological configurations representing the main structural features of the southern Grand Bank community. These will all be considered in Chapter 4. Table 10 summarizes the topological differences among the five basic models and among the eight versions of each basic model. An additional detail, not shown in Table 10, is that I treat the two "satellite" predators (seabirds and skate) in a different way. When self-damping is introduced in seabirds I will treat them as having a donor controled (e.g. Pimm 1982, Lawton 1989) relationship with capelin i.e. (coefficient $-a_{13}$ in the community matrix is made null).

TABLE 10. Features of the 40 models to be screened. Features 1 to 5 distinguish the basic models I to V. A cross (x) indicates that the model incorporates the feature in that row. Each basic model combines with eight different model versions (a to h). Features 6 to 9 distinguish the model versions.

	Basic Models				
	I	II	III	IV	V
1. Yellowtail present		x	x	x	x
2. Yellowtail competes w/ plaice		x			
3. Yellowtail competes w/ skate				x	
4. Yell. competes w/ plaice and skate					x
5. Yellowtail feeds on sand lance			x		

	Versions of each basic model							
	a	b	c	d	e	f	g	h
6. Cod feeds on plaice					x	x	x	x
7. Self-damp. in seabirds		x	x			x		x
8. Self-damp. in skate			x	x	x	x		
9. Self-damp. in yellowtail			x	x	x	x		

All 40 models are simplistic but biologically acceptable representations of the Southern Grand Bank community. It is very difficult to discriminate among them on a biological basis. In Chapter 4 I will use a mathematical criterion to screen all models and make a selection of what I will call "viable models".

SUMMARY OF CHAPTER 3

There is a complex network of trophic interactions within the two major zoogeographic regions of the Grand Bank (the Southern and the Northeastern Regions). It is possible to depict the major features of these networks and to recognize differences between them, but the extent to which populations influence each other's growth rates as a consequence of trophic interactions is by no means clear. The most important differences between the two regions are probably related with a very abundant benthic feeder, yellowtail flounder, that is present in the Southern region but is absent in the Northeastern. On average, food chains on the Grand Bank are short, especially when involving the benthic organisms, but they involve a high degree of omnivory that is uncommon in other published food webs. An examination of the Grand Bank food webs with a focus on diet overlap of predators suggests that body size is probably the most important structuring factor of niche space. Abstraction of seven dominant vertebrates and their trophic interactions out of the entire community in the Southern Region, yields five basic digraph models with 40 possible versions. All are biologically reasonable, but there is no objective biological basis upon which to discriminate between them.

Chapter 4

Making Predictions in an Uncertain Grand Bank

4.1. Introduction

In Chapter 2 I have identified and described broad areas on the Grand Bank characterized by a relatively homogeneous groundfish composition. The species inhabiting these areas remained roughly the same over the time period surveyed and the contours of each area recurred around the same geographical positions year after year. In Chapter 3 I have reviewed available literature on the diet of the dominant species on the Grand Bank and compared the static properties of the food webs in the above areas with the properties of other published marine food webs. All the most abundant species in the two major fish assemblage regions of the Grand Bank are both directly and indirectly connected through important pathways of feeding interactions. Such connections raise the possibility that species dynamics can be treated from an integrated, multispecific perspective. This synecological view of the marine community will be present throughout Chapter 4.

In the closing section of Chapter 3, we have seen that although food webs can provide useful guidance to general outlines of community organization, they are poor sources of information when it comes to details of functional relationships among species. Even in a simplified system involving only seven species, there is considerable uncertainty in regard to which structure best represents the community. In Chapter 4 I focus on the consequences that these and other types of uncertainty have on our ability to understand community dynamics in the Southern Grand Bank. More specifically, I investigate how uncertainty hinders our ability to predict changes in species abundance provoked by certain types of environmental perturbations that marine communities are known to endure. The matter is of direct importance to discuss if there are limits to our knowledge about the long term behaviour of biological communities. To what extent can we determine community dynamics, given the pervasive character of uncertainty in the real world and in our models ?

Chapter 4 begins with a brief summary of the familiar mathematical background that characterized most theoretical community ecology in the 60's and 70's. In section 4.3 I introduce press perturbations, a convenient way of describing certain types of environmental impacts (Bender et al. 1984). The mathematical protocol of this technique is presented in section 4.4. Since my purpose is to investigate how uncertainty hinders our predictive abilities on the Grand Bank, it is convenient to systematize the types of uncertainty that one may expect to find (section 4.5), as well as their possible consequences. Section 4.6 is a statement of the methods used based on the foregoing exposition. The results are organized by topics in section 4.7 and discussed in section 4.8.

4.2. Mathematical Background

4.2.1. The community matrix approach

Throughout Chapter 4 I assume that, at the spatial scale defined by the contours of the major assemblage regions on the Grand Bank, the growth rates of the most abundant long-lived species are *not* simply uncoordinated responses to the physical environment. If this is true, one should be able to write some sort of relationship between the growth rate of each species and the abundance of all species in the system. I impose practically no restrictions on the form of this relationship or on the time scale to which it applies. There is, however, a price to pay for these generalities, as one might anticipate from Godfray and Blythe's (1990) recent assertion that "The question of the actual complexity of the dynamics of natural communities is one of the major problems of contemporary population biology".

It is out of the question to study the global dynamics of a realistic set of species within the full range of values that their densities can take. In the first place, the mathematics of single species and two-species models are not readily extended to more complex and realistic multispecies systems, even with the simplifying assumptions of the logistic equation (May 1973, 1976). Actually, the step from two to three species is enough to introduce qualitative changes that make the dynamics exceedingly complicated (May and Leonard 1975, Gilpin 1979, Hastings and Powell 1991). In the second place, the global analysis of multispecies models imposes a strict mathematical definition of functional relationships among species about which we are uncertain and, with it, a proliferation of relevant parameters that we ignore.

The most common alternative to studies of the global dynamics of communities has been the local specification of species growth rates near a point of phase space (i.e. the multidimensional space defined by axes that represent species densities) around which the community is assumed to fluctuate (Levins 1968, May 1973, Pimm

1982, Yodzis 1989). The community is then represented by the community matrix (Levins 1968) whose elements, a_{ij}, are the per capita influence of species j on species i at the equilibrium point. Despite the controversial assumption of a point equilibrium that is inherent in the community matrix approach (Yodzis 1988b), it is still quite reasonable to use it as a simplified way of addressing certain questions that would otherwise require an intractable mathematical formulation. It is usually impossible to establish global stability existence or non-existence around the equilibrium point in biologically realistic models, whereas the establishment of local stability is a relatively simple matter that I summarize next.

4.2.2. Basic definitions

Assume the rate of change in abundance of any of the n species abstracted in the Southern Grand Bank is some function of the abundance of all species in the system. Then the rate can be represented by an expression with general form

$$[4.1] \qquad \frac{\partial X_i}{\partial t} = f_i\,(X_1, X_2, \ldots, X_n), \qquad i = 1, \ldots, n$$

where X_i is the abundance of species i and f_i is any continuously differentiable function of the state variables X_i. Assume system [4.1] has a non-trivial equilibrium point, $\mathbf{X}^*$ (with all $X_i^* > 0$). At $\mathbf{X}^*$, all rates of change will be null:

$$[4.2] \qquad 0 = f_i\,(X_1^*, X_2^*, \ldots, X_n^*), \qquad i = 1, \ldots, n$$

One can evaluate the effect of one species' density upon another species' growth rate when the system is at $\mathbf{X}^*$ by calculating the partial derivatives of [4.1] at equilibrium:

[4.3] $$a_{ij} = \frac{\partial f_i}{\partial X_j^*}$$

The Jacobian matrix, **A** , formed by the n^2 partial derivatives a_{ij} for all pairs *(i, j)*, is commonly called the <u>community matrix</u> (Levins 1968) in the ecological literature.

The a_{ij}'s have a particularly important biological meaning. They are the *per capita* effect of the density of species *j* on the growth rate of species *i* in a sufficiently small neighborhood of the equilibrium point. Their exact form depends on the form of functions f_i in [4.1], and even if the f_i's are not known, one can do qualitative predictions concerning at least some of the a_{ij}'s. Their *sign* and relative magnitude are immediately determined from the biological nature of the interaction between species *i* and *j*. For example, if *j* is a prey and *i* is a predator, then a_{ij} should be positive, whereas a_{ji} should be either negative (if the predator affects the prey growth rate) or null (if it does not – a situation called *donor control* dynamics – see DeAngelis 1975 and Lawton 1989). As illustrated in section 4.6.1, one can even go further, stating relative orders of magnitude for the a_{ij}'s. For example, because the per capita impact of a predator on the prey population is likely to be much stronger than the reverse impact, then a_{ji} is likely to be at least one order of magnitude larger than a_{ij}.

Suppose system [4.1] is allowed to attain its point attractor $\mathbf{X}^*$. It is relevant to know how [4.1] behaves if displaced away from $\mathbf{X}^*$, for example by a change in the density of the component species *i*. Does the new vector of population densities **X** tend to return to $\mathbf{X}^*$? If yes, how fast ? In a sufficiently small neighborhood of $\mathbf{X}^*$, the behaviour of [4.1] can be analysed through a procedure familiar to community ecologists. The system is approximated by the first-order expansion of Taylor's series around the equilibrium. The behaviour of such approximation depends on *n* constants, λ_i, which are the eigenvalues of the community matrix **A**. It can be shown that once perturbed, system [4.1] will return to equilibrium with time if, and only if, all eigenvalues of **A** have negative real parts (e.g. Lewontin 1969, May 1973 Chap. 2, Pimm 1982 Chap. 2, Yodzis 1989 Chap. 5). Such equilibrium is then said to be asymptotically stable. Because the return to equilibrium is guaranteed only within a (usually unknown) domain of attraction around $\mathbf{X}^*$, where the Taylor first-order approximation does not deviate too much from system [4.1], it is called a locally stable equilibrium. Local stability of system [4.1] can therefore be ascertained based on the correspondent community matrix **A**. This is an important result that allows the study of system [4.1] so long as the populations remain close enough to equilibrium and the elements a_{ij} of **A** can be estimated.

The speed of decay of a deviation of system [4.1] away from $\mathbf{X}^*$ turns out to be relevant. One can argue that species densities may be expected to exhibit less fluctuation in a system whose return to equilibrium is rapid, following a perturbation, as compared to species densities in a system whose return is slow (May 1973, Pimm 1982). An intuitive viewpoint is that smaller population fluctuations, characteristic of the former type of systems, are associated with a greater likelihood of population persistence (Levins 1968, Beddington et al. 1976, Pimm and Lawton 1977). The speed of decay of any system deviation away from the equilibrium is usually faster the more negative the real part of the smaller eigenvalue (λ_{min}) of **A**. A possible measure of how fast this return to equilibrium occurs is the return time: $-1/\text{Re}(\lambda_{min})$, where $\text{Re}(\lambda_{min})$ is the real part of λ_{min} (May 1973, Pimm and Lawton 1977).

Consider a community matrix **A**, based on some given system [4.1]. Suppose the signs of the non-zero elements a_{ij} are kept unchanged, but their magnitudes are arbitrarily altered. If every new system so obtained is never locally stable, then the original matrix is said to be qualitatively unstable. This definition is simply the mirror image of the definition of qualitative stability commonly found in the ecological literature (May 1973, Jeffries 1974, Pimm 1982). Qualitative instability therefore depends only on the qualitative nature (i.e. the signs) of the non-zero elements of **A**. It is a consequence of the biological nature of the interactions linking the species in the community, irrespectively of the strength of these links. For a system of type [4.1] which is not qualitatively unstable, one may then associate some non-null probability that the system is locally stable. I will say that a system of type [4.1] is a viable system (or a viable model) if it is not qualitatively unstable and it has a likelihood greater than 1% of being locally stable.

4.3. Environmental Perturbations and Press Perturbations

Certain categories of environmental perturbations are characterized by having a unidirectional and persistent effect upon marine populations. Examples are human activities, such as fisheries and polluting industries, that introduce persistent mortality factors and therefore affect population growth rates. Climatic parameters that change unidirectionally through time and produce responses at the population level (Davis 1986) also fall into this category. A simple way of conceiving the effect of these perturbations is to think of a continuous removal (or, more rarely, addition) of a certain number of individuals per unit area per unit time to the population. Bender, Case, and Gilpin (1984) developed the mathematical protocol of a certain type of ecological experiment that fits well into this description of unidirectional and persistent environmental perturbations. They have described experimental manipulations of biological communities that consist of a sustained alteration of species densities (usually by removing individuals) maintained until the unperturbed species reach a new equilibrium density. Bender et al (1984) dubbed these experiments press perturbations. I will use press perturbations in the context of the Southern Grand Bank community as a way of simulating a broad range of environmental perturbations that fulfill the requirements of persistence and unidirectionality described above.

A relevant question concerning the outcome of press perturbations is "Once the experiment is initiated, how do species densities in the community compare with the original densities ?". To answer this question it is crucial to make a distinction between short and long term outcomes of press perturbations (Yodzis 1989). Short term outcomes of press perturbations are very much what one would intuitively predict from a basic knowledge of "who eats who" in the food web (Yodzis 1989, Chap. 7). Short term effects are basically the result of direct effects between species. For example, if species *j* eats species *i*, then a continuous removal of species *j* prompts an immediate increase in the density of species *i*. This immediate response, however, is the beginning of a transient move of species densities in the whole community to a new situation. The final, long term, consequences of press perturbations in complex systems are by no means obvious (see section 4.4). It is well known that indirect effects, whereby species A affects species C through a chain of intermediate species (B_1, B_2, ...), may sometimes nullify or even reverse intuitively expected outcomes (Levins 1975, Holt 1977, Lawlor 1979, Kerfoot and Sih 1987).

Both short and long term outcomes of press perturbations are potentially predictable (section 4.4), so long as we are able to adequately describe the functional relationships between species in the community and so long as the description remains valid for a reasonable period of time. The problem arises because we are not able to do so. Our ecological models are usually plagued with uncertainties of various types. We are uncertain about what biological interactions significantly influence population growth rates, and we are uncertain about the values that we should attribute to all sorts of population parameters. In the following sections I present the mathematical framework of press perturbations and then proceed to examine the extent to which the outcomes of press perturbations can be determined in the face of these various sources of uncertainty.

4.4. Theory of Press Perturbations

The mathematical protocol of community perturbation experiments has been developed by Bender et al. (1984) (see also Yodzis 1989). Suppose that system [4.1] has some point in phase space, $\mathbf{X}^*$, such that [4.2] is true. We conduct a press perturbation on the community represented by system [4.1] by continuously removing individuals of species *k* from the community at rate I_k. System [4.1] will then be written:

[4.4]

$$\partial X_i / \partial t = f_i(X_1, \dots, X_n) \qquad i \neq k$$

$$\partial X_k / \partial t = f_k(X_1, \dots, X_n) - I_k$$

As pointed out in section 4.3, there is a critical distinction between what happens to species densities at once and a long time after the perturbation is initiated. I will begin by addressing the long term behaviour of [4.4].

4.4.1. Long term: The importance of indirect effects

Assume that I_k is small enough not to drive any of the species to extinction. Given time, the community will move to a new (or return to the same) point attractor where all species have non-null equilibrium densities and system [4.4] is null. The new equilibrium densities will depend on I_k. If we represent them by $X_i^*(I_k)$, system [4.4] can then be written:

[4.5]

$$f_i[X_1^*(I_k), \dots, X_n^*(I_k)] = 0 \qquad i \neq k$$

$$f_k[X_1^*(I_k), \dots, X_n^*(I_k)] - I_k = 0$$

To evaluate the change of $X_i^*(I_k)$ in the neighborhood of the equilibrium point, we differentiate equations [4.5] with respect to I_k. Using the chain rule,

$$\sum_j \frac{\partial f_i}{\partial X_j^*} \frac{\partial X_j^*}{\partial I_k} + \frac{\partial f_i}{\partial I_k} = 0 \qquad i = 1, \ldots, n$$

notice however, from [4.3] and [4.4], that

$$\frac{\partial f_i}{\partial X_j^*} = a_{ij} \; , \qquad \frac{\partial f_i}{\partial I_k} = \begin{cases} 0 & \text{if } i \neq k \\ -1 & \text{if } i = k \end{cases}$$

hence,

$$\sum_j a_{ij} \frac{\partial X_j^*}{\partial I_k} = 0 \qquad i \neq k$$

$$\sum_j a_{kj} \frac{\partial X_j^*}{\partial I_k} = 1$$

in matrix terms, assuming non-singularity of **A**,

$$\frac{\partial \mathbf{X}^*}{\partial I_k} = \mathbf{A}^{-1} \; [0, \ldots, 1, \ldots, 0]^T$$

where $[0, \ldots, 1, \ldots, 0]^T$ *is the transpose of the* n*-column vector whose only non-null* element is in row k. It is then clear that the rate of change of the equilibrium density of species i, in respect to the rate of removal of individuals from species k, simply equals $a_{ik}^{(-1)}$,i.e. the element (i, k) of the matrix that is the inverse of the community matrix:

$$\frac{\partial X_i^*}{\partial I_k} = a_{ik}^{(-1)} \qquad [4.6]$$

Expression [4.6] is crucial because it illustrates why the long term consequences of press perturbations are not obvious. All the elements of an inverse matrix are linear combinations of the elements of the matrix from which it originates. Each $a_{ik}^{(-1)}$ is therefore a function of the elements of **A**, and includes both the direct effect of population k on i (defined in [4.3]) and the effects mediated by intermediate species that are found in all possible paths between i and k, that is the indirect effects between i and k. As an example, consider model I in Fig. 37. A press perturbation that removes capelin continuously has a direct negative effect on cod density through a_{41}. However it also has indirect effects mediated by plaice and sand lance, and these must be taken into account. In the long run, the global effect of a perturbation of capelin on cod may turn out to be rather counter-intuitive.

4.4.2. Short term

Yodzis (1989) showed that the transient behaviour of the density of species i, in response to a sufficiently small perturbation of the density of species k, ΔI_k, is given by

$$X_i(t) = X_i^* + \sum_{m=1}^{\infty} (t^m / m!)\, a_{ik}^{(m-1)}\, \Delta I_k \qquad [4.7]$$

where $X_i(t)$ is the density of species i at time t, X_i^* is the density before the perturbation, and $a_{ik}^{(m-1)}$ is element (i, k) of the community matrix raised to the power (m-1). The magnitude of the change observed in any species i at time t (time in the same units used in eqs. [4.1]) is therefore a sum of products involving the elements a_{ik} of the matrices A^{m-1} ($m = 1, + \infty$). The successive terms in the sum are weighted by terms of the series (t^m / m !). For small values of t (t = 1, 2) these weightings rapidly become negligible as m increases:

t	t^1	$t^2/2$	$t^3/6$	$t^4/24$	$t^5/120$	$t^6/720$
1	1.00	0.50	0.17	0.04	0.01	0.00
2	2.00	2.00	1.33	0.67	0.27	0.09
3	3.00	4.50	4.50	3.38	2.03	1.01
...	...	...	...	...	...	...

meaning that the change in the density of species i is dominated by the elements a_{ik} of matrices **A** and $\mathbf{A}^2$. These elements express the direct effect of species k on species i (the elements of **A**), and the indirect effect via paths having only one intermediate species between k and i (the elements of $\mathbf{A}^2$). As time goes by, the importance of weighting terms with larger m's increases, therefore increasing the role of elements of matrices $\mathbf{A}^3$, $\mathbf{A}^4$, etc.. The indirect effects of species k on species i, involving progressively more intermediate species, are then brought into play. During the transient period, the density of species i may change in a direction that is contrary to the final density that the species will achieve.

Clearly, qualitative predictions about the short term effect of press perturbations are only affected by uncertainty concerning model structure (uncertainty of type (1) – see section 4.5). Once a model structure is selected (and therefore the *sign* of all a_{ij}'s), short term predictions are automatically determined. Uncertainty about the absolute values of parameters a_{ij} will not change short term qualitative predictions. For this reason, and because resource managers are usually concerned with the long term consequences of sustainable perturbations on marine populations, I will not devote further attention to short term effects.

4.4.3. Loop Analysis

We have seen that the long term outcome of press perturbations can be studied using the inverse of the community matrix (equation [4.6]). When **A** is unknown, one way to investigate press perturbations is to simulate "plausible" **A** matrices through Monte Carlo methods (see section 4.6.1). Another method is the one described by

Levins (1974, 1975) and Puccia and Levins (1985) under the name of "loop analysis" (see Appendix 1). Levins (1975) derived a relationship between [4.6] and an important expression of loop analysis:

$$[4.8] \qquad \mathbf{A}^{-1} = -\frac{\sum P_{ij}^{(r)} F_{n-k} (Comp\, P_{ij}^{(r)})}{F_n}$$

where F_n is called the feedback at level n in the community and n is the total number of species. In general, feedback is the effect that a species has on itself by way of a number of intervening species (see Appendix 1 for full explanation of eq. [4.8]).

There are two points to take note of in regard to expression [4.8]. One is that the denominator is always negative in locally stable systems of type [4.1]. The other is that the numerator can be expanded in terms of sums of products of the (unknown) a_{ij}'s. These sums can be extremely long for systems with many species, but can be dealt with in simpler ones. Consider for example our model *If* (section 3.7.2, Appendix 1). Suppose we want to know the effect of a negative press perturbation upon capelin on the equilibrium density of cod. The numerator of [4.8] can be written (Appendix 1):

$$[4.9] \qquad -a_{41}a_{25}a_{52}a_{56} - a_{51}a_{45}a_{26}a_{62} - a_{51}a_{45}a_{22}a_{66} + a_{51}a_{25}a_{42}a_{66}$$

We can make an educated guess on the *sign* that [4.9] would have were the real values for the a_{ij}'s known. It seems likely that it would be negative, which implies that [4.8] will be negative too (remember that F_n is negative). In other words, in the context of model *If*, a sustained removal of capelin will affect cod density negatively, or, even more simply stated, "the less capelin, the less cod in the long run". In section 4.6.2 I present a more rigorous criterion used to decide on the sign of expressions like [4.9].

4.5. Uncertainty and Indeterminacy

In section 4.4 we have seen that a critical antecedent of predicting the outcome of press perturbations is a basic knowledge of community structure, as expressed by the community matrix. But we are usually very uncertain about **A**: what are the non-null elements of **A** and what values should they take ? When uncertainty is so pervasive it becomes a topic in itself, and it is convenient to start by systematizing it according to the criterion that better fits our purposes (Hilborn 1987, Rice 1990). I stay close to Rice's (1990) classification by considering two major types of uncertainty:

(1) Uncertainty about the way species affect each other's growth rates and, therefore, about correct model structure.

(2) Uncertainty about model parameters.

Both types of uncertainty have consequences for our ability to make predictions about community dynamics. I will examine the combined effect of the two types of uncertainty and the effect of uncertainty of type (2) alone.

4.5.1. Uncertainty and structural indeterminacy

Section 3.7.2 provides a typical example of uncertainty of type (1). Ignorance about the extent to which species affect each other's dynamics leads to uncertainty about the model structure that best describes year-round species interactions. I have handled uncertainty of type (1) by building 40 alternative model configurations that, although far from comprehensive, cover a fair range of structural possibilities. The models stay within the boundaries of what is biologically acceptable, judging from the literature review conducted in Chapter 3. They were presented in section 3.7. The methodology used (loop analysis), however, will not allow to isolate the consequences of uncertainty of type (1) alone.

Suppose we explore the qualitative behaviour of a set of structurally different models in regard to the long term outcome of press perturbations in a predator-prey relationship. For each model we simulate the sustained removal of individuals of prey *i*, and predict what will happen in the long run to the density of the predator *j*. At one extreme, all our models will yield exactly the same answer (for example: the density of predator *j* will decrease). The long term outcome of the press perturbation for the pair (*i*, *j*) is then said to be completely determined. In this case uncertainty did not hinder our ability to predict the outcome of the perturbation. At the other extreme, 50% of the models will predict a decrease of *j* whereas the other 50% will predict an increase. In most cases, however, we will have some intermediate situation, with different proportions of models predicting the three qualitative possibilities (increase, no change, decrease) of change in the density of *j*. We can then establish a criterion to decide when the outcome of the perturbation is determined or not. We can, for example, establish that if a minimum of 90% of the models make predictions that are not contradictory, we still say that the outcome is determined. Otherwise we say that it is undetermined. Indeterminacy originated in this way (by uncertainty of type 1 and 2 combined) will be called structural indeterminacy.

4.5.2. Uncertainty of type (2) and directional indeterminacy

Uncertainty of type (2) concerns the correct values that the parameters of our models should take. The parameters in this study are the community matrix elements a_{ij} . As Rice (1990) points out, statisticians deal with uncertainty of type (2) by building confidence intervals for the parameters. Food web theory has also handled uncertainty of type (2) in community matrices by resorting to a very simplified version of this approach (Pimm and Lawton 1977, 1978; Cohen 1978, Yodzis 1980, 1981, 1988a; Pimm 1980, 1982). Neither the appropriate limits for the intervals around the a_{ij}'s nor the underlying statistical distributions are known. Still it is possible to use some biological reasoning to establish tentative orders of magnitude for the bounds and size of those intervals (see section 4.6.1).

Suppose that we want to investigate how uncertainty of type (2) affects our ability to predict the long term outcome of press perturbations. We pick a given model structure (thereby eliminating uncertainty of type (1)) and randomly draw a set of parameter values from their confidence intervals to fill in our model. A press perturbation is then simulated upon species *i* and we take note of the long term direction of change in the density of species *j*, as expressed by the sign of element (*i*, *j*) of $\mathbf{A}^{-1}$. This process is then repeated a large number of times, thereby originating a certain amount of random variation in $\mathbf{A}^{-1}$. Notice that the model structure remains the same, only the set of values taken by the parameters varies. In an extreme situation, our prediction about direction of change of the density of species *j* will always be the same no matter what set of parameter values was used. As in section 4.5.1, I will then say that the outcome of the press perturbation for the pair (*i*, *j*) is completely determined. Most likely, however, some sets of values will lead to a given prediction (increase, no change, decrease) and other sets will lead to other predictions. Yodzis used the term directionally determined to refer to the long term effect of species *i* upon species *j* when at least 95% of the sets of parametric values lead to the same qualitative prediction about the direction of change of species *f*. Otherwise, Yodzis (1988a) calls the outcome directionally undetermined. Hereafter I employ Yodzis' terminology to avoid unnecessary proliferation of terms. Although directional indeterminacy can be caused by both types of uncertainty, in this study I always associate it with uncertainty of type (2), and reserve the term structural indeterminacy (defined in section 4.5.1) to refer to directional indeterminacy that is caused by uncertainty of type (1) and (2) combined.

4.5.3. Topological indeterminacy

Up until now I have only referred to the consequences of uncertainty in respect to our ability to make qualitative predictions. But we can also think in terms of "rank predictions". We can ask, for example, "Which species has a greater effect upon species *i* once that species is perturbed ?" or: "Which species is the most affected when species *i* is perturbed ?" Answers to these questions are likely to be of major relevance for biological resource management. Managers may be interested to know which species will be more strongly affected by some sort of environmental impact that is acting directly upon some other species in the system. Both uncertainty of type (1) and uncertainty of type (2) can be expected to hinder our ability to answer this sort of question. Yodzis (1988a) has examined this problem in model food webs of real communities and henceforth I follow his *modus operandi* and terminology.

Consider $\mathbf{A}^{-1}$, the inverse of the community matrix of a given model structure. As we have seen, the element $a_{ij}^{(-1)}$ encapsulates the long term effect on species i of a press perturbation on species j. Let $|a_{ij}^{(-1)}|$ be the absolute value of this effect. If, for every k,

$$\text{magnitude of } |a_{ij}^{(-1)}| \geq \text{ magnitude of } |a_{ik}^{(-1)}|$$

the effect of species j on species i is called a major effect on i. And if for every k,

$$\text{magnitude of } |a_{ij}^{(-1)}| \geq \text{ magnitude of } |a_{kj}^{(-1)}|$$

then the effect is called a major effect of j. If either of these two conditions is satisfied the effect of species j on i is called a major effect (Yodzis 1988a). Magnitude of a number in the above inequalities is simply the common "order of magnitude", i.e. magnitude of x is M, if $10^{M} \leq x < 10^{M+1}$.

Suppose that we simulate uncertainty of type (2) in the way described in section 4.5.2. For every community matrix $\mathbf{A}$ that we build, there is a corresponding inverse $\mathbf{A}^{-1}$ where we can identify the major species effects. Does the inherent variation in $\mathbf{A}^{-1}$ affect our ability to identify the major effects in the community represented by $\mathbf{A}$? Yodzis (1988a) found the answer to be yes. Uncertainty of type (2) is sufficient to cause a high degree of indeterminacy in regard to which interaction effects (i, j) are major effects in a given community. He called this type of indeterminacy topological indeterminacy.

4.6. Methods

4.6.1. The Monte Carlo method

In sections 4.2 and 4.4 we have seen that the community matrix, **A**, plays a key role both in establishing local stability of systems of type [4.1] and in investigating the long term outcome of press perturbations. The signs of the elements (a_{ij}'s) of **A** can be deduced from the biological nature of the interaction between species *i* and *j*, but the absolute values of the a_{ij} coefficients are unknown. I will resort to a Monte Carlo method commonly used in food web theory, whereby a_{ij} values are drawn from likely intervals of real numbers where they can be expected to vary (Pimm and Lawton 1977, 1978; Cohen 1978; Rejmanek and Stary 1979; Yodzis 1980, 1981, 1988a; Pimm 1980, 1982).

The most appropriate limits for the intervals of variation of the a_{ij}'s are unknown, but using simple biological reasoning it is possible to establish relative orders of magnitude for the bounds and size of each interval. Once such intervals are established, I simulate a <u>plausible community matrix</u> (in Yodzis' 1981 terminology) by drawing the a_{ij}'s at random from a uniform distribution truncated at the limits of each interval. The process was conducted using RANDOM, a portable pseudo-random generator presented by Wichmann and Hill (1982). Appendix 2 touches upon some technical problems involved in the use of random generators and briefly describes the properties of RANDOM. This generator was tested using a small battery of empirical tests that differs from the original battery reported by the authors. Overall, RANDOM's behaviour appeared to be quite acceptable.

There are two major lines of argument in defense of the use of the Monte Carlo method in theoretical community ecology (May 1975, Pimm 1982, Yodzis 1989). I rephrase these arguments in the Grand Bank context:

a) To measure all the a_{ij}'s in the open ocean is an immense and difficult task. Experimental approaches are not on the horizon and our data bases for commercial species leave much to be desired, let alone those for non-commercial species. We could consider ourselves lucky to achieve even the accuracy of the intervals used in the simulations presented here.

b) Independent of our ability to measure interaction coefficients, the many sources of variability in the ocean will likely render the assignment of exact values to the a_{ij}'s meaningless. Even if integrated over a period of time or a broad area, parameters of species interactions would be best described in probabilistic terms. As May (1975) puts it, "in the real world, we do not deal with fixed parameter values, but rather with parameter spaces".

The intervals of variation adopted for the a_{ij} coefficients take into consideration their biological meaning (see section 4.2.2) and are in basic agreement with established practice in the literature (e.g. Pimm 1982, sec. 7.1.1):

1. *Intraspecific coefficients.* These are the diagonal elements a_{ii} of the community matrix. If non-null, they should be negative, therefore self-damping the population and not allowing it to grow indefinitely. These coefficients are known to have a critical influence on model stability and their values are usually the most controversial. The argument is usually about whether nonbasal species should be self-damped or not (see Yodzis 1981, 1989; Pimm 1982 for the controversy). I have partially handled this by considering alternative model structures (section 3.7.2) with and without intraspecific coefficients in some of the nonbasal species. When present, intraspecific coefficients are assumed uniformly distributed in the interval $[-1, 0]$. This order of magnitude scales the system. My general conclusions concerning ecological indeterminacy were found not to be biased by this option. I did tentative runs with alternative intervals, mostly $[-0.1, 0]$, and found that they led to similar conclusions.

These self-damping, intraspecific coefficients are *direct* effects of a species density upon its own growth rate. They should not be confused with what herein is sometimes refered to as "self-effects", the long term effect that changes in one species's growth rate will have on that same species's density via a_{ii} *and/or* looping paths that involve other species.

2. *The direct effect of predator on prey.* Vertebrate predators in the sea are usually much larger than their prey. I will assume that their feeding requirements impose a relatively strong negative impact on the main prey populations. Because the a_{ij}'s represent *per capita* effects, I will assume a greater order of magnitude for these effects by making them vary uniformly over the interval $[-10, 0]$. There will be two exceptions however: the influence of seabirds on capelin and the influence of cod on plaice. I assume that only part of the capelin population is accessible to seabirds, and that only the smaller size classes of the plaice population are exploited by cod. The interaction coefficients in these two cases are randomly chosen over the interval $[-1, 0]$.

3. *The direct effect of prey on predator.* Prey have a positive effect on predator growth rate, but the number of predators produced per prey eaten is small. I will assume that it is two orders of magnitude lower than the converse effect of predator on prey. Values are taken from a uniform distribution in the interval $[0, +0.1]$.

4. *Interspecific competition.* This is assumed to be consumptive competition (Schoener 1983) between species, i.e. pure exploitation of resources with a collectivist utilization of space. Interspecific competition will be assumed to be negative and weaker than intraspecific competition and therefore distributed over the uniform interval $[-0.1, 0]$.

4.6.2. Loop Analysis

Loop analysis is used with the primary goal of investigating the consequences of uncertainty of type (1). It was also used to check Monte Carlo results concerning uncertainty of type (2) within each viable model. A rule used in evaluating the sign of the numerator of expressions [4.8] for every (i, j) pair (of which expression [4.9] is an example) is described next. Suppose the numerator has N negative and M positive terms. If $2 \leq N+M < 6$ then I make a decision (negative or positive) if either N or M equals 2 (for $N+M = 2$ or 3), 3 (for $N+M = 4$), or 4 (for $N+M= 5$). In the case where $N+M \geq 6$, a decision is made (negative or positive) if either N or M is greater than about 2/3 of N+M. This rule is a subjective assessment of the likelihood of the numerator of [4.8] to have a given sign, based on the signs of the terms that compose the numerator.

4.6.3. Viable models of community structure

The 40 model structures of the Southern Grand Bank community presented in section 3.7.2 were scrutinized for local stability and viability. For each of the 40 models, the following operations were performed using the Monte Carlo method:

1. Simulate 1000 plausible community matrices. Each set of matrix elements a_{ij} is randomly drawn from uniform distributions over their respective intervals of variation.
2. The real part of the largest eigenvalue of each plausible matrix is computed. If negative then that matrix is locally stable. I take note of the proportion of simulated community matrices that are stable and decide whether the model under scrutiny is viable.

It is well known (Saunders 1978, Pimm 1980, 1982; Yodzis 1981) that self-damping favours local stability. Yodzis (1981) illustrated how this remains true regardless of whether intraspecific interference is increased by lowering the bottom limit of the interval from whence the a_{ii}'s assume their values, or by increasing the proportion of species for which the a_{ii} is negative. In both cases the trace (i.e. the sum of the diagonal elements) of the community matrix is rendered greater in absolute value (i.e. more negative). The eight versions of each basic model (Table 10) incorporate a different number of species with self-damping effects. Versions c and *f* incorporate self-damping in five species: seabirds, skate, yellowtail, capelin, and sand lance. The lower limit for the trace of simulated community matrices of these two versions is -5, which is as negative as a trace can be in these cases. Since the sum of the eigenvalues of a matrix equals the trace of the matrix, it is of interest to investigate whether a greater stability of versions *c* and *f* could be simply a result of making the lower limit of the trace more negative. All the 40 model configurations were again simulated 1000 times each, but this time the interval of variation for the intraspecific coefficients, a_{ii}, was adjusted in such a way that the lower limit of the matrix trace remained constant throughout the 40 model simulation. This lower limit was set at -2. The intervals of variation for the a_{ii}'s were then changed accordingly in the following way:

Model versions	Number of a_{ii}'s	Interval for a_{ii}
a, g	2	$[-1.00, 0]$
b, h	3	$[-0.67, 0]$
d, e	4	$[-0.50, 0]$
c, f	5	$[-0.40, 0]$

4.6.4. Species interaction strength

Consider the models found to be viable. Does strengthening (or weakening) of particular combinations of a_{ij}'s increase the likelihood of local stability in these models ? The number of possible combinations of a_{ij}'s whose effects of change in strength one can investigate is very high (the magnitude is 2^m, m = number of interactions in the model). A model as simple as Ie (Table 10) has over 130,000 possible combinations and therefore it is out of the question to attempt an exhaustive analysis of this subject. I shall illustrate, however, how local stability is affected by changes in the strength of a very restricted selection of combinations of species interactions. These combinations are labeled C1 to C6 and will be described next, as well as the method used to simulate a change in their strength:

C1. *Direct effect of prey on cod.* Refers to the positive direct effect of capelin and sand lance upon cod, represented by coefficients a_{41} and a_{42} in the viable models.

C2. *Direct effect of prey on plaice.* Refers to the positive direct effect of capelin and sand lance upon plaice, represented by the coefficients a_{51} and a_{52}.

C3. *Direct effect of cod on prey.* Refers to the negative direct effect of cod upon capelin and sand lance, represented by coefficients $-a_{14}$ and $-a_{24}$.

C4. *Direct effect of plaice on prey.* Refers to the negative direct effect of plaice upon capelin and sand lance, represented by coefficients $-a_{15}$ and $-a_{25}$.

C5. *Satellite predators.* Refers to the interaction between seabirds and capelin and between thorny skate and sand lance. Altogether this comprises four interaction coefficients: a_{31}, $-a_{13}$, a_{72}, and $-a_{27}$.

C6. *Competition.* Refers to all the direct competition interactions present in each model (Fig. 37). In the versions of the basic models I and III there are none (Table 10); in the versions of the basic model II there are two coefficients ($-a_{56}$, $-a_{65}$), representing direct competition between yellowtail flounder and American plaice; in the versions of the basic model IV there are two coefficients representing competition between yellowtail and skate; and in the versions of basic model V there are four competition coefficients, representing direct competition between yellowtail flounder, thorny skate and American plaice.

The simulation proceeds as follows. All coefficients are drawn from exactly the same intervals of variation as described in section 4.6.1, except for the coefficients belonging to the combination (C1 to C6) selected to change. These changes can be either an increase or a decrease in interaction strength. An increase in strength is simulated by fixing the value of the coefficient at the upper absolute limit of the interval of variation. A decrease is simulated by dividing the upper absolute limit of the interval by ten. Consider for example a coefficient varying in the interval $[-10, 0]$. An increase in strength is simulated by fixing the coefficient at -10. A decrease is simulated by making the coefficient vary in the interval $[-1, 0]$. Notice that after the change, a given interaction still remains within the boundaries of its former interval of variation. For every viable model, I have systematically investigated the effect of increasing and decreasing each of the combinations of coefficients C1 to C6. In every case (i.e. a given change in a given combination, in a given model), 1000 community matrices are simulated and the proportion of stable models registered.

4.6.5. Uncertainty

In the following presentation I use the term "effect of species *j* on *i* " to mean the long term effect on species *i* of a removal of species *j* in a press perturbation experiment. It should not be confused with the "direct effect" represented by coefficient a_{ij} of the community matrix. Hereafter, and unless preceded by the word "direct", an "effect of *j* on *i*" is the element (*i*, *j*) of the inverse of the community matrix: $a_{ij}^{(-1)}$ (section 4.4.1).

The following two steps were taken in order to investigate the combined consequences of uncertainty of type (1) and (2) upon our ability to predict the effect of species *j* on species *i* for every pair (*i*, *j*):

1. For each viable model, loop analysis is used to determine the sign of the effect of species *j* on *i*, using the criterion defined in section 4.6.2. If differences in model structure are not to affect our predictions about the effect of *j* on *i*, then all the viable models should predict the same effect.

2. The effect of species *j* on *i* is called structurally determined at level Q % if at least Q % of the total number of viable models predicts the same direction of change (+, 0, or –). Otherwise, it is called structurally undetermined. The quantiles Q used are 71% and 82% (respectively 12 and 14 of the 17 viable models (see section 4.7.1)) for all interactions not involving yellowtail flounder. Since there will be only 12 viable models with yellowtail, in interactions involving this species the above ratios 12/17 and 14/17 are changed to, respectively, 8/12 and 10/12.

The following three steps were taken in order to investigate the consequences of uncertainty of type (2) alone on our ability to predict the effect of species *j* on *i* and the relative importance of this effect (as explained in sections 4.5.2 and 4.5.3):

3. For each viable model, the Monte Carlo method is used to simulate 1000 locally stable plausible community matrices, **A**. The inverse, $\mathbf{A}^{-1}$, is computed for every matrix.

4. The effect of species *j* on *i* is called directionally determined at level P % if at least P % of inverse matrices have the same sign in element (*i, j*). Otherwise it is called directionally undetermined. The quantiles P used are 90% and 95% (i.e. 900 and 950 matrices, respectively, out of the 1000 simulated matrices).

5. The effect of species *j* on *i* is called unimportant if in the sample of 1000 matrices the probability that it is a major effect (section 4.5.3) is less than 0.05. It is called most important if the probability that it is a major effect is greater than 0.95. Effects that are neither unimportant nor most important are deemed topologically undetermined. The terminology used in this paragraph follows that established by Yodzis(1988a).

4.7. Results

4.7.1. Viable models

The Monte Carlo method was used to investigate the local stability of the 40 possible model structures of the Southern Grand Bank. The results are summarized in Table 11. Twenty-one models have a probability greater than 0 of being locally stable (second column, Table 11). Of these, 17 models (marked with an asterisk) were found to be stable in more than at least 1% of the cases; these are the ones considered to be viable models. They include five versions of model I, and three versions of each of the other basic models (II to V). Fifteen of the viable models belong to either versions *c*, *e*, or *f* of the basic models. Table 11 also presents the number of cases in four return time intervals (columns 4–7). Shorter return times mean a faster return of the community to its point attractor after being perturbed. None of the five initial basic model configurations of Fig. 37 appears to be any more stable than the others, but there are two particular versions of these models (*c* and *f*) that consistently appear to have a greater chance of stability and shorter return times.

The third column of Table 11 and columns 8 to 11 present the results of the simulations with the adjusted intervals of intraspecific interaction. The major conclusions in regard to which model versions are more stable do not change. Again, these are versions *c* and *f* of every basic model I to V. Therefore one cannot attribute the greater stability of versions *c* and *f* to more negative matrix traces, but rather to the high proportion of species exhibiting intraspecific effects in each model (see also Yodzis 1981).

TABLE 11. Proportion of the 1000 simulated plausible matrices of each model configuration of the Southern Grand Bank community that was found to be locally stable. Each configuration is identified by the same code as in Table 10. Results in the second column are from matrices having non-null diagonal elements varying between -1 and 0 ($a_{ii} \in [-1, 0]$). Results in the third column are from matrices whose diagonal elements were adjusted to keep the lower limit of their sum constant (a_{ii} adjusted). Also shown is the number of cases in four different return time intervals for the two instances. Models with (*) are considered viable models.

		Percentage stable		Return times (upper limits)							
		a_{ii} $\in [-1,0]$	a_{ii} adjusted	$a_{ii} \in [-1,0]$				a_{ii} adjusted			
Model version				0-10	-50	-100	-150	0-20	-50	-100	-150
Ia		0.0	0.0	0	0	0	0	0	0	0	0
Ib		0.0	0.0	0	0	0	0	0	0	0	0
Ic	*	42.9	41.2	93	213	75	23	52	228	92	21
Id		0.0	0.0	0	0	0	0	0	0	0	0
Ie	*	6.7	6.8	0	25	25	7	0	24	21	15
If	*	20.2	20.3	53	118	18	13	33	123	30	11
Ig	*	4.3	4.3	0	11	17	11	0	11	17	11
Ih	*	11.6	10.0	6	70	27	8	4	61	25	6
IIa		0.0	0.0	0	0	0	0	0	0	0	0
IIb		0.0	0.0	0	0	0	0	0	0	0	0
IIc	*	40.1	34.1	89	204	36	33	18	216	66	23
IId		0.0	0.0	0	0	0	0	0	0	0	0
IIe	*	5.9	5.1	0	23	13	13	0	18	19	11
IIf	*	19.1	16.7	46	122	16	3	12	108	31	9
IIg		0.0	0.0	0	0	0	0	0	0	0	0
IIh		0.0	0.0	0	0	0	0	0	0	0	0
IIIa		0.0	0.0	0	0	0	0	0	0	0	0
IIIb		0.0	0.0	0	0	0	0	0	0	0	0
IIIc	*	39.0	34.1	64	189	71	43	9	178	82	41
IIId		0.0	0.0	0	0	0	0	0	0	0	0
IIIe	*	7.4	7.6	0	25	25	15	0	18	34	19
IIIf	*	16.2	14.2	32	96	23	10	8	90	22	16
IIIg		0.0	0.0	0	0	0	0	0	0	0	0
IIIh		0.0	0.0	0	0	0	0	0	0	0	0
IVa		0.0	0.0	0	0	0	0	0	0	0	0
IVb		0.0	0.0	0	0	0	0	0	0	0	0
IVc	*	42.1	36.7	94	211	64	28	24	227	64	30
IVd		0.0	0.0	0	0	0	0	0	0	0	0
IVe	*	6.8	6.4	0	21	17	18	0	21	20	17
IVf	*	20.1	17.4	48	120	18	11	9	127	31	3
IVg		0.6	0.6	0	0	1	1	0	0	1	1
IVh		0.9	1.0	0	0	7	5	0	2	4	6
Va		0.0	0.0	0	0	0	0	0	0	0	0
Vb		0.0	0.1	0	0	0	0	0	0	0	0
Vc	*	36.8	31.9	85	181	56	30	22	193	68	22
Vd		0.0	0.0	0	0	0	0	0	0	0	0
Ve	*	7.2	5.4	0	34	24	11	1	20	20	7
Vf	*	19.3	16.9	56	103	21	11	7	117	31	6
Vg		0.4	0.4	0	0	1	1	0	0	1	1
Vh		1.0	1.1	0	1	3	3	0	1	4	4

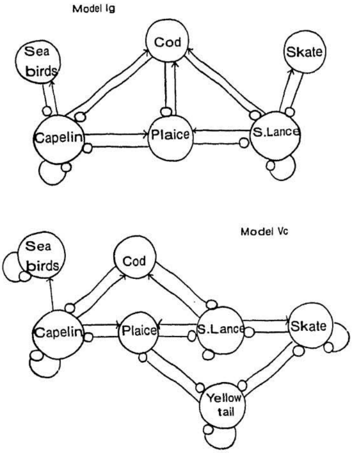


Figure 38. Two viable models. Note self-damping indicated for capelin and sand lance (model *Ig*) and seabirds, capelin, yellowtail, and skate (model *Vc*).

Fig. 38 illustrates two of the viable models found in Table 11. Insofar as mathematical modeling is concerned, two features common to all the viable models (compare Tables 10 and 11) promote stability in the Grand Bank: abundant self-damping effects and the existence of a triangular configuration in model topology (caused by cod predation on American plaice; see model *Ig* in Fig. 38). Neither of these features comes as a surprise. Several authors have pointed out that strong self-damping effects favour stability in model ecosystems (see section 4.6.3) and the possible importance of triangulated structures has also drawn previous comment. Ursin (1982) stressed the possible stabilizing effect of triangulated food webs in the sea, providing examples that constitute interesting empirical evidence (section 3.5.3). Simple computer models also point to the stabilizing effect of triangularity (Giavelli et al. 1988).

4.7.2. Interaction strength

Table 12 summarizes the results of changes in the interaction strength of combinations of coefficients C1 to C6 (section 4.6.4) for all the 17 viable models of the Southern Grand Bank community (in rows). Changes always refer to departures from the initial intervals of variation as explained in section 4.6.4. A change can be either an increase or a decrease in all the interactions included in the combination considered. Entries in Table 12 are the proportion of simulated models found to be stable after the change was imposed. Consider, for example, the direct effect of prey on cod (combination C1). Table 12 shows that the likelihood of model *If* to be locally stable is 0.202 (20.2% of 1000 simulations - see Table 11) with the conventional intervals of variation for interaction coefficients (section 4.6.1). However, when the direct effects of cod's prey on cod are made relatively strong, that likelihood drops to 0.113 (i.e. 11.3%). When those effects are made weak, the likelihood of stability increases to 0.612.

TABLE 12. When there are changes (Incr = increase, Decr = decrease) in the strength of certain coefficients of interspecific interaction, the percentage of each model version that is locally stable also changes. Entries in the table are the percentages of stable models when the changes indicated in the columns (incr, decr) took place. They should be compared with the percentages before the change (third column from the left). C1 to C6 are different combinations of coefficients of species interactions (see text).

Basic		Without	C1		C2		C3		C4		C5		C6	
Mod	Vers	change	Incr	Decr	Incr	Decr	Incr	Decr	Incr	Decr	Incr	Decr	Incr	Decr
I	c	42.9	43.5	29.4	41.5	29.3	42.6	29.4	43.8	29.2	37.0	46.5		
	e	6.7	1.5	48.3	10.1	2.2	12.1	1.9	1.7	48.1	15.3	0.0		
	f	20.2	11.3	61.2	25.7	3.6	27.6	3.7	9.4	61.1	19.0	20.9		
	g	4.3	1.7	38.6	7.5	2.1	8.5	2.0	0.8	38.0	9.5	0.0		
	h	11.6	4.3	57.1	18.1	4.0	18.4	4.0	3.0	55.6	17.8	1.0		
II	c	40.1	39.1	27.9	39.0	22.0	39.4	27.9	39.4	22.0	32.2	43.3	33.2	42.4
	e	5.9	0.9	46.1	9.5	2.1	9.0	1.9	1.4	40.8	11.9	0.0	4.8	6.8
	f	19.1	8.8	59.0	25.6	4.1	25.7	5.5	9.2	53.3	17.5	19.4	17.5	20.1
III	c	39.0	36.4	22.9	38.3	23.9	41.1	22.9	36.8	23.9	33.5	42.0		
	e	7.4	1.8	45.0	11.1	2.9	11.7	3.5	2.3	47.0	14.3	0.0		
	f	16.2	8.3	61.6	24.3	4.0	22.8	4.1	7.1	62.7	17.1	16.1		
IV	c	42.1	42.2	28.4	39.4	29.6	42.6	28.4	40.1	29.6	35.5	44.8	23.3	42.5
	e	6.8	1.3	46.5	10.0	2.7	10.3	2.6	1.5	46.1	13.3	0.0	6.1	6.7
	f	20.1	10.4	59.4	26.9	5.0	26.9	5.5	9.3	59.1	18.6	19.9	11.4	20.1
V	c	36.8	36.7	24.5	38.3	21.3	37.5	24.4	38.0	20.5	29.6	40.6	29.3	39.6
	e	7.2	1.0	46.3	9.7	2.3	9.8	2.4	1.8	41.0	12.9	0.0	5.8	7.9
	f	19.3	9.1	61.4	26.5	4.5	25.8	4.3	8.8	55.1	17.5	18.9	17.2	20.7

The results of Table 12 can be summarized by each interaction combination:

C1. *Direct effect of prey on cod.* Model versions with a triangulated structure caused by the incorporation of cod predation upon plaice (versions *e, f, g, h*) indicate that a decrease in the per capita direct effect of capelin and sand lance on cod growth rate is highly stabilizing. The model version without triangularity (version *c*) indicates the opposite. The improvement in model stability is much more pronounced in models *e, f, g, h*.

C2. *Direct effect of prey on plaice.* All model versions are concordant in that an increase in the per capita direct effect of capelin and sand lance on the growth rate of plaice has a stabilizing effect on community dynamics.

C3. *Direct effect of cod on prey.* All model versions are concordant in that an increase in the per capita direct effect of cod on the growth rate of its prey also has a stabilizing effect.

C4. *Direct effect of plaice on prey.* Model versions with a triangulated structure caused by the incorporation of cod predation upon plaice (versions *e, f, g, h*) indicate that a decrease in the per capita direct effect of plaice on the growth rate of its prey is highly stabilizing for community dynamics. The model version without triangularity (version c) indicates the opposite.

C5. *Satellite predators.* Results are somewhat more controversial in regard to satellite predators. Model versions *c* (no triangularity) suggest an increase in the likelihood of stability with a decrease in the strength of interaction links between satellite predators and their prey. Model versions *e* indicate the opposite. Model versions *f* exhibit little change in the likelihood of stability.

C6. *Competition.* All model versions are concordant in that decreasing the strength of competitive interactions promotes stability in community dynamics.

4.7.3. Structural indeterminacy

We have seen that only 17 of the initial 40 configurations hypothesized for the Southern Grand Bank turn out to be viable. Perhaps it is sensible to start by examining how these 17 models differ in respect to predicting the long term response of the community to press perturbations. I have screened every possible (*i*, *j*) interaction in the 17 viable models using loop analysis and counted the number of models that predicted each type of outcome. Tables 13 and 14 present the results according to the criterion defined in section 4.6.5.

TABLE 13. Results of the simulation of press perturbations in the 17 viable models as assessed by loop analysis. Species in columns suffered a constant rate of removal of individuals. Species in rows had consequent long term changes in their equilibrium densities. These changes were either non-existent (0), an increase (+), or a decrease (–). When at least 12 out of 17 models indicate non-contradictory directions of change (0 and either – *or* +) these directions are displayed as entries in the table. Otherwise the changes were considered structurally undetermined (Und).

	Capelin	S.Lance	Seabirds	Cod	Plaice	Yeilt	Skate
Capelin	Und	0 –	0 +	Und	Und	0	0 +
S. Lance	0 –	Und	0	Und	Und	Und	0 +
Seabirds	0 –	Und	–	Und	Und	Und	Und
Cod	Und	Und	0 +	–	+	Und	+
Plaice	Und	Und	0	+	–	Und	Und
Yellowt	0	Und	0	Und	Und	–	Und
Skate	0	0 –	0	Und	Und	Und	–

TABLE 14. Same as Table 13, but here it is required that at least 14 out of 17 models indicate non-contradictory directions of change.

	Capelin	S.Lance	Seabirds	Cod	Plaice	Yellt	Skate
Capelin	Und	Und	0 +	Und	Und	Und	Und
S. Lance	Und	Und	0	Und	Und	Und	Und
Seabirds	Und	Und	–	Und	Und	Und	Und
Cod	Und	Und	0 +	–	Und	Und	Und
Plaice	Und	Und	Und	+	–	Und	Und
Yellowt	Und	Und	Und	Und	Und	Und	Und
Skate	Und	Und	Und	Und	Und	Und	–

Scanning down the columns of Tables 13 and 14 gives an idea of our ability to predict the long-term consequences on the community of a press perturbation that affected a species in the column; for example, if cod is continuously removed, in both tables we are able to predict only two of the long term effects of such perturbation: cod equilibrium density decreases and plaice equilibrium density increases. Scanning across the rows indicates how well we can predict the consequences for a given species of press perturbations on the whole community; for example, in Table 13 we are able to predict the effect of removing four species (S. Lance, seabirds, yellowtail, skate) upon the equilibrium density of capelin, but with the more strict demands of Table 14 we are only able to predict the effect of removing seabirds. Overall, the results indicate that the outcome of press perturbations is highly sensitive to model structure: 53% of the species interactions are structurally undetermined when 12 of 17 models (71 %) are non-contradictory (Table 13) and 84% of the cells are structurally undetermined when 14 of 17 models (82%) are non-contradictory (Table 14).

The long term effect of removing individuals of a given species on the density of that same species, i.e. self-effects, and the effects on the community caused by perturbations in satellite predators (seabirds and the thorny skate) appear to be the less sensitive to changes in model structure. These effects are usually, but not always, the ones we would intuitively expect. For example, in 5 cases our species models are concordant in predicting that removing individuals of a given species leads to a long term decrease in the abundance of that same species (see diagonals of Table 13). However, removing individuals of a top predator does not necessarily lead to a long term increase in the density of their prey (e.g. thorny skate preying on capelin).

4.7.4. Directional indeterminacy

I have investigated the direction of change of the density of species *i* due to a persistent removal of individuals of species *j*, for every pair (*i*, *j*) in every viable model. The results are summarized in Table 15 for the two levels of confidence in direction of change established in section 4.6.5. Long term changes that fail to be determined are signaled by *u* (undetermined) in Table 15. Throughout this section it is important to recall that what is here called "effect", as well as the resultant "change in species density", is actually a net effect that combines a direct and an indirect component, as explained in sections 4.3 and 4.4.1. Table 15 illustrates that indirect interactions within the community will sometimes nullify or even reverse the intuitively expected consequences of direct interactions. In model Ic, for example, a continuous removal of thorny skate does not lead to any long term change in the equilibrium density of its prey sand lance. In model Ie, a sustained removal of cod leads to a (intuitively unexpected) long term decrease of the density of sand lance.

TABLE 15. Results of the Monte Carlo simulation of press perturbations. For each viable model, 1000 community matrices were simulated. For each matrix, species in columns suffered a constant rate of removal of individuals. Species in rows had consequent long term changes in their equilibrium densities. These changes were either a decrease (–), an increase (+), or non-existent (0). When at least 900 of the 1000 matrices predict the same direction of change, this direction is displayed as an entry in the table on the left. Tables on the right require that at least 950 matrices predicted the same change. When these requirements are not fulfilled, the prediction is said to be directionally undetermined and is signaled *u*. Abbreviations: Cp = capelin, Ln = sand lance, Sb = seabirds, Pla = American plaice, Ska = thorny skate, Yel = yellowtail flounder.

Model Ic

	Determinacy at 90%						Determinacy at 95%					
	Cp	Ln	Sb	Cod	Pla	Ska	Cp	Ln	Sb	Cod	Pla	Ska
Capelin	0	0	0	u	u	0	0	0	0	u	u	0
S.Lance	0	0	0	u	u	0	0	0	0	u	u	0
Seabird	0	0	–	u	u	0	0	0	–	u	u	0
Cod	u	u	0	–	+	u	u	u	0	–	+	u
Place	u	u	0	+	–	u	u	u	0	+	–	u
Skate	0	0	0	u	u	–	0	0	0	u	u	–

Model Ie

	Determinacy at 90%						Determinacy at 95%					
	Cp	Ln	Sb	Cod	Pla	Ska	Cp	Ln	Sb	Cod	Pla	Ska
Capelin	0	0	+	0	0	0	0	0	+	0	0	0
S.Lance	0	–	u	–	+	+	0	–	u	–	+	+
Seabird	–	u	–	u	u	u	–	u	u	u	u	u
Cod	0	–	u	–	u	+	0	–	u	–	u	+
Plaice	0	+	u	+	–	–	0	+	u	+	–	–
Skate	0	–	u	–	+	u	0	–	u	–	+	u

Model If

	Determinacy at 90%						Determinacy at 95%					
	Cp	Ln	Sb	Cod	Pla	Ska	Cp	Ln	Sb	Cod	Pla	Ska
Capelin	u	u	0	u	u	u	u	u	0	u	u	u
S.Lance	u	u	0	u	u	u	u	u	0	u	u	u
Seabird	u	u	–	u	u	u	u	u	–	u	u	u
Cod	u	u	0	–	+	u	u	u	0	–	u	u
Plaice	u	u	0	+	–	u	u	u	0	+	–	u
Skate	u	u	0	u	u	–	u	u	0	u	u	u

Model Ig

	Determinacy at 90%						Determinacy at 95%					
	Cp	Ln	Sb	Cod	Pla	Ska	Cp	Ln	Sb	Cod	Pla	Ska
Capelin	0	0	+	0	0	0	0	0	+	0	0	0
S.Lance	0	0	0	0	0	+	0	0	0	0	0	+
Seabird	–	0	–	–	+	u	–	0	–	–	+	u
Cod	0	0	+	0	–	+	0	0	+	0	–	+
Plaice	0	0	–	+	0	–	0	0	–	+	0	–
Skate	0	–	u	–	+	u	0	–	u	–	+	u

Model Ih

	Determinacy at 90%						Determinacy at 95%					
	Cp	Ln	Sb	Cod	Pla	Ska	Cp	Ln	Sb	Cod	Pla	Ska
Capelin	–	0	0	–	+	u	–	0	0	–	+	u
S.Lance	0	0	0	0	0	+	0	0	0	u	0	+
Seabird	–	0	–	–	+	u	–	0	–	–	+	u
Cod	–	0	0	–	u	u	–	0	0	–	u	u
Plaice	+	0	0	+	–	u	+	0	0	+	–	u
Skate	u	–	0	u	u	u	u	–	0	u	u	u

Model IIc

	Determinacy at 90%							Determinacy at 95%						
	Cp	Ln	Sb	Cod	Pla	Yel	Ska	Cp	Ln	Sb	Cod	Pla	Yel	Ska
Capel	+	−	0	u	u	u	+	+	−	0	u	u	u	+
Lance	−	+	0	u	u	u	−	−	+	0	u	u	u	−
Birds	u	u	−	u	u	u	+	u	u	−	u	u	u	u
Cod	u	u	0	−	+	−	u	u	u	0	−	+	−	u
Place	u	u	0	+	−	+	u	u	u	0	+	−	+	u
Yellt	u	u	0	−	+	−	u	u	u	0	−	+	−	u
Skate	u	u	0	u	u	u	−	u	u	0	u	u	u	−

Model IIe

	Determinacy at 90%							Determinacy at 95%						
	Cp	Ln	Sb	Cod	Pla	Yel	Ska	Cp	Ln	Sb	Cod	Pla	Yel	Ska
Capelin	0	0	+	0	0	0	0	0	0	+	0	0	0	0
S.Lance	0	−	u	−	+	−	+	0	−	u	−	+	−	+
Seabird	−	u	−	u	u	u	u	−	u	u	u	u	u	u
Cod	0	−	u	−	u	u	+	0	−	u	u	u	u	+
Plaice	0	+	u	+	−	+	−	0	+	u	+	−	+	−
Yellowt	0	−	u	−	+	−	+	0	−	u	−	+	−	+
Skate	0	−	u	−	+	−	u	0	−	u	−	+	−	u

Model IIf

	Determinacy at 90%							Determinacy at 95%						
	Cp	Ln	Sb	Cod	Pla	Yel	Ska	Cp	Ln	Sb	Cod	Pla	Yel	Ska
Capelin	u	u	0	u	u	u	u	u	u	0	u	u	u	u
S.Lance	u	u	0	u	u	u	u	u	u	0	u	u	u	u
Seabird	u	u	−	u	u	u	u	u	u	−	u	u	u	u
Cod	u	u	0	−	+	−	u	u	u	0	−	u	u	u
Plaice	u	u	0	+	−	+	u	u	u	0	+	−	+	u
Yellowt	u	u	0	−	+	−	u	u	u	0	−	+	−	u
Skate	u	u	0	u	u	u	−	u	u	0	u	u	u	u

Model IIIc

	Determinacy at 90%							Determinacy at 95%						
	Cp	Ln	Sb	Cod	Pla	Yel	Ska	Cp	Ln	Sb	Cod	Pla	Yel	Ska
Capelin	0	0	0	u	u	0	0	0	0	0	u	u	0	0
S.Lance	0	0	0	u	u	0	0	0	0	0	u	u	0	0
Seabird	0	0	–	u	u	0	0	0	0	–	u	u	0	0
Cod	u	u	0	–	+	u	u	u	u	0	–	+	u	u
Plaice	u	u	0	+	–	u	u	u	u	0	+	–	u	u
Yellowt	0	0	0	u	u	–	0	0	0	0	u	u	–	0
Skate	0	0	0	u	u	0	–	0	0	0	u	u	0	–

Model IIIe

	Determinacy at 90%							Determinacy at 95%						
	Cp	Ln	Sb	Cod	Pla	Yel	Ska	Cp	Ln	Sb	Cod	Pla	Yel	Ska
Capelin	0	0	+	0	0	0	0	0	0	+	0	0	0	0
S.Lance	0	–	u	–	+	+	+	0	–	u	–	+	+	+
Seabird	–	u	–	u	+	u	u	–	u	u	u	u	u	u
Cod	0	–	+	–	u	+	+	0	–	u	–	u	+	+
Plaice	0	+	u	+	–	–	–	0	+	u	+	–	–	–
Yellowt	0	–	u	–	+	u	+	0	–	u	–	+	u	+
Skate	0	–	u	–	+	+	u	0	–	u	–	+	+	u

Model IIIf

	Determinacy at 90%							Determinacy at 95%						
	Cp	Ln	Sb	Cod	Pla	Yel	Ska	Cp	Ln	Sb	Cod	Pla	Yel	Ska
Capelin	u	u	0	u	u	u	u	u	u	0	u	u	u	u
S.Lance	u	u	0	u	u	u	u	u	u	0	u	u	u	u
Seabird	u	u	–	u	u	u	u	u	u	–	u	u	u	u
Cod	u	u	0	–	u	u	u	u	u	0	–	u	u	u
Plaice	u	u	0	+	–	u	u	u	u	0	+	–	u	u
Yellowt	u	u	0	u	u	–	u	u	u	0	u	u	u	u
Skate	u	u	0	u	u	u	–	u	u	0	u	u	u	u

Model IVc

	Determinacy at 90%							Determinacy at 95%						
	Cp	Ln	Sb	Cod	Pla	Yel	Ska	Cp	Ln	Sb	Cod	Pla	Yel	Ska
Capelin	0	0	0	u	u	0	0	0	0	0	u	u	0	0
S.Lance	0	0	0	u	u	0	0	0	0	0	u	u	0	0
Seabird	0	0	–	u	u	0	0	0	0	–	u	u	0	0
Cod	u	u	0	–	+	u	u	u	u	0	–	+	u	u
Plaice	u	u	0	+	–	u	u	u	u	0	+	–	u	u
Yellowt	0	0	0	u	u	–	+	0	0	0	u	u	–	+
Skate	0	0	0	u	u	+	–	0	0	0	u	u	+	–

Model IVe

	Determinacy at 90%							Determinacy at 95%						
	Cp	Ln	Sb	Cod	Pla	Yel	Ska	Cp	Ln	Sb	Cod	Pla	Yel	Ska
Capelin	0	0	+	0	0	0	0	0	0	+	0	0	0	0
S.Lance	0	–	u	–	+	–	+	0	–	u	–	+	–	+
Seabird	–	u	–	u	u	u	u	–	u	u	u	u	u	u
Cod	0	–	u	–	u	–	+	0	–	u	–	u	–	+
Plaice	0	+	u	+	–	+	–	0	+	u	+	–	+	–
Yellowt	0	+	u	+	–	–	u	0	+	u	+	–	–	u
Skate	0	–	u	–	+	u	u	0	–	u	–	+	u	u

Model IVf

	Determinacy at 90%							Determinacy at 95%						
	Cp	Ln	Sb	Cod	Pla	Yel	Ska	Cp	Ln	Sb	Cod	Pla	Yel	Ska
Capelin	u	u	0	u	u	u	u	u	u	0	u	u	u	u
S.Lance	u	u	0	u	u	u	u	u	u	0	u	u	u	u
Seabird	u	u	–	u	u	u	u	u	u	–	u	u	u	u
Cod	u	u	0	–	+	u	u	u	u	0	–	u	u	u
Plaice	u	u	0	+	–	u	u	u	u	0	+	–	u	u
Yellowt	u	u	0	u	u	–	+	u	u	0	u	u	–	u
Skate	u	u	0	u	u	+	–	u	u	0	u	u	u	u

Model Vc

	Determinacy at 90%							Determinacy at 95%						
	Cp	Ln	Sb	Cod	Pla	Yel	Ska	Cp	Ln	Sb	Cod	Pla	Yel	Ska
Capelin	+	−	0	u	u	u	u	+	−	0	u	u	u	u
S.Lance	−	+	0	u	u	u	u	−	+	0	u	u	u	u
Seabird	u	u	−	u	u	u	u	u	u	−	u	u	u	u
Cod	u	u	0	−	+	−	u	u	u	0	−	+	u	u
Plaice	u	u	0	+	−	u	u	u	u	0	+	−	u	u
Yellowt	u	u	0	−	u	−	u	u	u	0	u	u	−	u
Skate	u	u	0	u	u	u	−	u	u	0	u	u	u	−

Model Ve

	Determinacy at 90%							Determinacy at 95%						
	Cp	Ln	Sb	Cod	Pla	Yel	Ska	Cp	Ln	Sb	Cod	Pla	Yel	Ska
Capelin	0	0	+	0	0	0	0	0	0	+	0	0	0	0
S.Lance	0	−	u	−	+	−	+	0	−	u	−	+	−	+
Seabird	−	u	−	u	u	u	u	−	u	u	u	u	u	u
Cod	0	−	u	−	u	u	+	0	−	u	−	u	u	+
Plaice	0	+	u	+	−	+	−	0	+	u	+	−	+	−
Yellowt	0	u	u	u	u	−	+	0	u	u	u	u	−	+
Skate	0	−	u	−	+	u	u	0	−	u	u	+	u	u

Model Vf

	Determinacy at 90%							Determinacy at 95%						
	Cp	Ln	Sb	Cod	Pla	Yel	Ska	Cp	Ln	Sb	Cod	Pla	Yel	Ska
Capelin	u	u	0	u	u	u	u	u	u	0	u	u	u	u
S.Lance	u	u	0	u	u	u	u	u	u	0	u	u	u	u
Seabird	u	u	−	u	u	u	u	u	u	−	u	u	u	u
Cod	u	u	0	−	u	u	u	u	u	0	−	u	u	u
Plaice	u	u	0	+	−	u	u	u	u	0	+	−	u	u
Yellowt	u	u	0	u	u	−	u	u	u	0	u	u	−	u
Skate	u	u	0	u	u	u	−	u	u	0	u	u	u	u

On average, the proportion of directionally undetermined entries in the cases of Table 15 is 0.44 (std. dev. = 0.21) at the 90% level of confidence and 0.48 (st. dev. = 0.22) at the 95% level. Table 16 shows the proportion of directionally undetermined entries of Table 15 broken down by basic model and by model version.

TABLE 16. Proportion of directionally undetermined cells by basic model (in rows) and by model version (in columns) for the two levels of confidence considered. Average indeterminacy is 0.44 (at 90%) and 0.48 (at 95%).

	Directional indeterminacy by model type and version									
	90% level					95% level				
	Model version					Model version				
	c	e	f	g	h	c	e	f	g	h
I	0.39	0.28	0.69	0.08	0.25	0.39	0.31	0.75	0.08	0.28
II	0.51	0.27	0.65			0.53	0.31	0.71		
III	0.37	0.22	0.76			0.37	0.29	0.80		
IV	0.37	0.29	0.69			0.37	0.31	0.78		
V	0.61	0.35	0.76			0.65	0.39	0.78		

Version *f* of the basic models consistently exhibited the higher degree of indeterminacy among all model versions. Tables of this version always had 69 to 80% of their cells undetermined. Version *f* is the one that incorporates a higher degree of complexity as evaluated by the number of intra- and interspecific interactions (see Table 10). There is an association between model complexity and indeterminacy in Table 16. In Fig. 39 I have plotted directional indeterminacy at the 90% level (from Table 16) against the number of non-null elements in the community matrix that correspond to each model (diagonal elements included). There is a weak positive correlation ($r^2 = 0.20$, significant only at $\alpha = 0.1$) between the two variables.

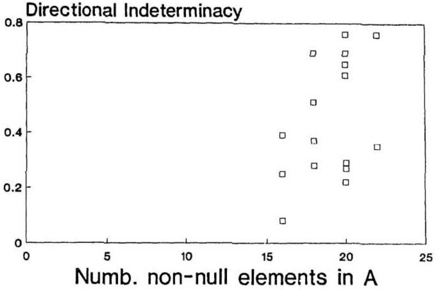


Figure 39. Directional indeterminacy (90% level) against number of non-null elements in the community matrix for the 17 viable models.

I have pooled the results of Table 15 for the 90% level of confidence in Table 17 which presents the most common predictions stemming from Table 15 for every pair (*i, j*). To include predictions in Table 17, however, I require that they contain no contradictions (a contradiction being a + and a −) and that they stem from a minimum of 12 models (8 models if either *i* or *j* is yellowtail). Information in Table 17 is therefore very much the same presented in Table 13, although this time *obtained by a different method. The two tables were thus used to cross-check the* results of loop analysis and the Monte Carlo method and, where cells are determined, they were very concordant. Table 17 combines indeterminacy originated by uncertainty of types (1) and (2). About 80% of its entries are undetermined. The most predictable effects seem to be intraspecific effects (diagonal of the table) and the effects caused by removing seabirds (a satellite predator for which donor control was assumed).

TABLE 17. Most common predictions with Monte Carlo simulations (from Table 15 at level 90%) concerning the effect on species in rows of a press perturbation in species in columns. It is required that at least 12 models show non-contradictory results or else the effect is considered undetermined (Und).

	Capelin	S.Lance	Seabirds	Cod	Plaice	Yellt	Skate
Capelin	Und	0 –	0 +	Und	Und	Und	Und
S. Lance	0 –	Und	0	Und	Und	Und	Und
Seabirds	Und	Und	–	Und	Und	Und	Und
Cod	Und	Und	0 +	0 –	Und	Und	Und
Plaice	Und	Und	0 –	+	–	Und	Und
Yellowt	Und	Und	Und	Und	Und	Und	Und
Skate	Und	Und	Und	Und	Und	Und	Und

Table 18 summarizes the results at the 90% level of confidence by type of effect. A self-effect refers to the long term effect of removing individuals of a given species on the density of that same species. One expects these effects to be negative, but Table 18 shows that only 67% of the 114 self-effects were consistent with the expectations, whereas 16% were directionally undetermined and 3% pointed in the opposite direction of change. As for the predator-prey effects, both the effect of the predator on its prey and the reverse effect have to be considered. The number of predator on prey effects in Table 18 is smaller than the number of reverse effects (105 versus 116) because in model versions *c*, *h* and *f*, seabirds were assumed to have a donor control relationship with capelin (section 3.7.2). Removing predator individuals might be expected to have a positive effect on prey population density, but 45% of these effects were found undetermined and 7% were the opposite of what was expected (Table 18). As for the effect of removing prey on the predator density (expected negative), 53% of the cases were directionally undetermined and 8% showed effects in the opposite direction.

TABLE 18. Changes in population density and directional indeterminacy categorized by type of effect. Entries in the table are proportions of the effects in rows that originated the type of changes signaled in columns. Asterisks signal the type of change intuitively expected for a given effect.

Type of effect	Number of effects	Proportion negative	Proportion null	Proportion positive	Proportion undetermined
Self-effect	114	0.67 (*)	0.14	0.03	0.16
Predator on prey	105	0.07	0.19	0.29 (*)	0.45
Prey on predator	116	0.19 (*)	0.20	0.08	0.53
Indirect competition	165	0.10	0.15	0.19 (*)	0.56
Direct competition	24	0.00	0.00	0.50 (*)	0.50

Table 18 also considers two types of competitive effects. Direct competition refers to pairs of species whose mutual direct effects were assumed to be negative (i.e. both a_{ij} and a_{ji} negative). Examples are yellowtail flounder and plaice in Basic Model II (see Fig. 37), or yellowtail flounder and skate *or* plaice in Basic Model V. Indirect competition refers to pairs of species that share the same prey. Examples are cod and skate sharing sand lance in all models, or cod and yellowtail sharing sand lance in all versions of Basic Model III. In both cases one expects the removal of one of the competitors to have a positive effect on the density of the other competitor, but in both cases about half of all competition interactions were found directionally undetermined (Table 18). The other half was a positive effect, as expected in direct competition, but in only 19% of the cases the removal of one competitor had a positive effect on the other competitor when indirect competition is considered (Table 18).

4.7.5. Topological indeterminacy

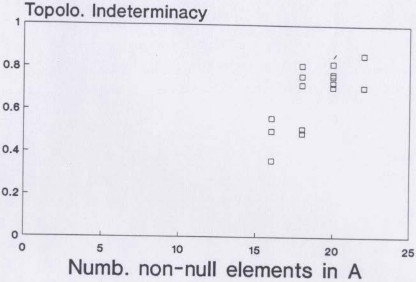
For every possible effect *(i, j)*, in every viable model, I have counted the number of times that *(i, j)* was a major effect (as defined in section 4.5.3) and decided whether *(i, j)* is unimportant, most important, or topologically undetermined (as defined in section 4.6.5). On average, 68% (st. dev. = 14) of all possible *(i, j)* effects were topologically undetermined in the 17 viable models. Table 19 shows the proportion of topological indeterminacy by basic model and by model version. Version *f* of the basic models consistently showed a higher degree of topological indeterminacy; 77 to 85% of all possible effects were undetermined in this version.

TABLE 19. Proportion of effects that were found topologically undetermined broken down by basic model and by model version.

Topological Indeterminacy by model type and version

	Model version				
Basic Model	c	e	f	g	h
I	0.56	0.72	0.81	0.36	0.50
II	0.76	0.71	0.82		
III	0.49	0.73	0.82		
IV	0.51	0.71	0.77		
V	0.76	0.71	0.86		

The same type of association suggested in section 4.7.4, between model version complexity and directional indeterminacy, is much stronger for topological indeterminacy. Fig. 40 (top) plots topological indeterminacy (from Table 19) against number of non-null elements in the community matrix of each model (diagonal elements included). There is a significant positive correlation between the two variables (r^2 = 0.53, significant at α = 0.01). On the other hand, there is no association between topological indeterminacy and measures of model complexity based on the idea of connectance. Fig. 40 (bottom) illustrates a typical plot, where connectance was computed as the total number of non-null elements in the community matrix (diagonal elements included) divided by the total possible number of elements (n^2). The coefficient of determination is $r^2 = 0.03$.



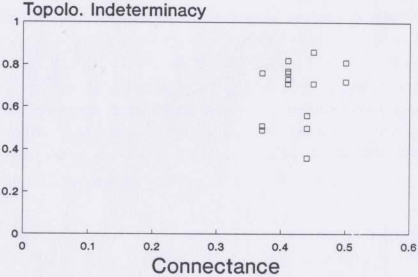


Figure 40. Topological indeterminacy versus number of non-null elements in the community matrix (top) and versus connectance (bottom).

Table 20 presents the proportion of viable models in which effect (i, j) was considered unimportant (NI), most important (MI), and topologically undetermined (TU). For example, the long term effect of seabirds on capelin was unimportant in 0.65 of the 17 viable models (11 out of 17), it was most important in 0.35 of the models (6 out of 17), and was never topologically undetermined. In another example, the effect of thorny skate on cod was never found either unimportant or most important, meaning that there is 100% of topological indeterminacy in this interaction.

There is a restricted number of species interactions that registered most important effects, and it is instructive to more closely inspect these particular effects. This is done case by case in the next few pages. Because of the recognized economic importance of cod and capelin, I also examine the mutual long term effect of interactions of these two species.

1. *Seabirds on capelin.* This effect was most important in 6 of the 17 models. All 6 models were either versions *g* or *e*, where seabirds are represented feeding on capelin as satellite predators that are not self-damped ($a_{33} = 0$) and with no donor control ($a_{13} < 0$). In all cases the effects were considered most important for being a major effect on capelin (as opposed to a major effect of seabirds; see definitions in section 4.5.3). The effects were directionally determined (at 95% level) and happened in the direction intuitively expected, i.e. a removal of seabirds prompts an increase in the density of capelin. It is worth noting that these major effects were registered in spite of the fact that the interval of variation for coefficient $-a_{13}$ was set one order of magnitude lower than other coefficients representing the direct effect of predator on prey (see section 4.6.1).

TABLE 20. Proportion of viable models in which the effect of species in columns on species in rows was found unimportant (NI), most important (MI), or topologically undetermined (TU).

		Capelin	S.Lance	Seabirds	Cod	Plaice	Yellt	Skate
Capelin	NI	0.53	0.59	0.65	0.35	0.35	0.50	0.47
	MI	0.00	0.00	0.35	0.00	0.06	0.00	0.00
	TU	0.47	0.41	0.00	0.65	0.59	0.50	0.53
S.Lance	NI	0.59	0.29	0.71	0.12	0.12	0.17	0.25
	MI	0.00	0.00	0.00	0.00	0.00	0.00	0.17
	TU	0.41	0.71	0.29	0.88	0.88	0.83	0.58
Seabird	NI	0.29	0.41	0.00	0.00	0.00	0.17	0.24
	MI	0.35	0.00	0.65	0.00	0.06	0.00	0.00
	TU	0.36	0.59	0.35	1.00	0.94	0.83	0.76
Cod	NI	0.35	0.12	0.65	0.06	0.00	0.00	0.00
	MI	0.00	0.00	0.00	0.24	0.00	0.00	0.00
	TU	0.65	0.88	0.35	0.70	1.00	1.00	1.00
Plaice	NI	0.35	0.12	0.65	0.12	0.06	0.00	0.00
	MI	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	TU	0.65	0.88	0.35	0.88	0.94	1.00	1.00
Yellowt	NI	0.58	0.42	0.58	0.00	0.00	0.00	0.08
	MI	0.00	0.00	0.00	0.00	0.00	0.25	0.00
	TU	0.42	0.58	0.42	1.00	1.00	0.75	0.92
Skate	NI	0.65	0.41	0.65	0.00	0.00	0.06	0.00
	MI	0.00	0.12	0.00	0.00	0.00	0.00	0.00
	TU	0.35	0.47	0.35	1.00	1.00	0.94	1.00

2. *Capelin on seabirds*. The models where the effect of capelin on seabirds was most important (a major effect on capelin), were also the models where the reverse effect was most important (see paragraph above). The models therefore suggest that in predator-prey relationships where the predator is sattelite and not self-damped, the two species are likely to have a mutual strong effect on each other's growth rate (see also paragraph 3.). The long term outcome of this effect was always found to be directionally determined (95% level of confidence) and in the direction intuitively

expected, i.e. a removal of capelin prompts a decrease in seabird density and a removal of the seabirds increases capelin density in the long run.

3. *Thorny skate on sand lance* and *sand lance on thorny skate*. This is another example of a satellite predator and its prey. Unlike seabirds, however, there are only two models where thorny skate is not self-damped ($a_{77} = 0$): models Ig and Ih. These are the ones where the effect of skate on sand lance and the reverse effect was found to be a major effect. As in the seabirds-capelin interaction, the long term consequences of these effects were always directionally determined and occurred as intuitively expected, i.e. a removal of the sand lance prompts a decrease in the density of thorny skate and a removal of the skate prompts an increase in sand lance.

4. *Self-effects.* Cod, yellowtail flounder, and especially seabirds, exhibited major self-effects in some of the models (Table 20). Self-effects were always directionally determined (95% level of confidence) and occurring in the direction expected (removal of species i prompts a long term decrease of i density). Remember that "self-effects" should not be confused with "self-damping". The latter refers only to the coefficients a_{ii}, expressing intraspecific direct effects. The former refers to the long term effect that changes in one species' growth rate will have on that same species' density, via a_{ii} *and/or* looping paths that involve other species in the community. Cod, for example, was never assumed to have a non-null a_{ii} coefficient, and yet the effect of removing cod was found to be a major self-effect in the four model versions *f*. The seabirds had major self-effects in all models where the coefficient $-a_{33}$ was set non-null (versions *c, f, h*). Finally, yellowtail flounder was found to have major self-effects in all versions of basic model IV where $-a_{66}$ is non-null.

5. *Cod and capelin.* The six models where the long term effect of cod and capelin on each other's densities was found to be unimportant are the ones where cod is represented sharing capelin with seabirds (versions *e, g*; see also paragraph 1. above). In these model versions cod is also represented feeding on plaice. The long

term effect of removing cod on capelin's density (and vice-versa) was always found to be null in these particular models (Table 15). The reason is probably because the models also predict that removing cod causes a long term increase in plaice density which, in turn, also feeds on capelin. Almost all other models (versions *c* and *f*) are directionally undetermined in respect to the long term effect of cod and capelin on each other's densities.

4.8. Discussion

Uncertainty about functional relationships is a serious hindrance to our ability to predict the long term behaviour of a biological community. This is the major message stemming from Chapter 4. The models used to represent the marine community on the Southern Grand Bank were all relatively simple and biologically acceptable. The parameters of these models took values within relatively short intervals of variation, differing overall by no more than two orders of magnitude. But even with these simplifications there is a very high degree of indeterminacy when it comes to predicting the long term outcomes of press perturbations on the community. Additional complexity aimed at introducing more realism into the models is likely only to increase rather than decrease doubts about correct model structure, and would therefore be unlikely to improve the situation. In what follows I will revisit the major assumptions of Chapter 4, compare my results with those of other authors, attempt some generalizations, and finally consider how the techniques developed in Chapter 4 may fit into the broad context of the management of natural resources.

At the outset of almost any community study, one stumbles into one of the major historical debates among ecologists: What is the actual unit of study ? The integrated versus the individualistic view of the community has been the subject of extended debates to which I will not add (see Saarinen 1982 and McIntosh 1985 for the general controversy). The synecological viewpoint adopted here is to a large extent a consequence of the predominant adherence of mathematical theory in community ecology to the concept of the community as a well-defined and integrated set of populations (exemplified by system [4.1]) rather than as a loose set of non-interacting populations that happen to be together simply due to common responses to physical factors. In accordance with this view I have assumed, following Underwood (1986), that the assemblages of species inhabiting the Grand Bank *(i)* consistently recur in time and space, and *(ii)* show complex but interdependent interactions. Chapter 2 provides good support for assertion *(i)*, stemming not only from the 16-year time series analysed but also from our current knowledge about species assemblages on world continental shelves (section 2.1.2). Chapter 3 provides very limited support for assertion *(ii)* and I suspect that firm support for this assertion can only derive from controlled large-scale experiments that do not seem to be a likely prospect in the near future.

The second assumption of Chapter 4 concerns stability. There are actually two assumptions here. One is that it is reasonable to assume stability in the Grand Bank community, in the sense that there is at least one bounded region of phase space that attracts initial community conditions (Lewontin 1969, Yodzis 1989). In other words, the community tends to maintain the same species composition and the relative proportions of these species remain within given boundaries. If the community is disturbed, the species relative proportions are assumed to return to within the original boundaries. The other assumption is that such bounded region is a point attractor (Yodzis 1988b), i.e., the relative proportion of each species is assumed constant. Although important these assumptions may appear, they are unlikely to jeopardize the main conclusions regarding the sensitivity of long term predictions to uncertainty in initial conditions (model structure and parameter values). The relaxation of these assumptions could be achieved in different ways, for example allowing the community to move along an unbounded trajectory (an example would be allowing processes of extinction and colonization), permitting the community to have a limit cyle (with species abundance exhibiting a cyclical behaviour), or permitting a complex attractor (with species abundance exhibiting a chaotic behaviour). None of these relaxations is likely to decrease sensitivity to initial conditions, quite the contrary. In this sense, the assumptions about local stability are simplifications that make the results in section 4.7 look conservative.

The existence of stable communities is a matter of major controversy. Connell and Sousa (1983) questioned whether any ecological community yet studied has conclusively been shown to be stable and dismissed much of the evidence for the existence of multiple stable points in natural communities. However, Sutherland

(1981) and Silvertown (1987) arrived at contrasting views, and Sutherland (1990) later suggested that Connell and Sousa's criterion for stability was too strict. Pimm (1982) reviewed the evidence for stability in individual populations (mostly terrestrial) concluding that nearly all populations keep their abundance within bounds, which suggests the existence of regulatory mechanisms and lends credibility to equilibrium assumptions. Other authors have claimed evidence for complex types of attractors in which a community can be in perpetual change and yet be stable. Examples are the limit cycles claimed by Nisbet and Gurney (1982) and the chaotic attractors recently reviewed by Godfray and Blythe (1990). The evidence for regulatory mechanisms in marine fish populations is especially conflicting (Sissenwine 1984, Shepherd and Cushing 1990). The persistence of exploited fish populations, despite high levels of fishing mortality and the fact that the populations do not boom when exploitation is relaxed, suggest some sort of population regulation. However, if regulation exists, the high variance of stock-recruitment plots has concealed its *modus operandi* from fisheries biologists for a long time (see however Shepherd and Cushing 1990). Insofar as the Southern Grand Bank community is concerned, Fig. 21 is not a demonstration of community stability, perhaps not even in the restricted sense of community persistence (i.e. the assemblage maintains its composition without any species going extinct), but Fig. 21 cannot be used to dismiss persistence either. As Underwood (1986) points out, the problem of establishing persistence is basically one of temporal scale. "Some communities will appear to have consistent structure [...] simply because the organisms are long-lived relative to the length of study" (Underwood 1986, p. 358). If one is concerned with establishing stability, rather than persistence, a strict interpretation of the definition of stability (e.g. Lewontin 1969) actually would require two complete community turnovers, the first to establish equilibrium and the second to evaluate the return to equilibrium following a perturbation (Connell and Sousa 1983, Sutherland 1990). The time series used in Chapter 2, although unusually long for such a large-scale study, measures up poorly against these conservative requirements.

It is quite possible, however, that the most dangerous assumptions of Chapter 4 are not that species influence each other's growth rates or local stability, but lie rather in the choice of state variables in system [4.1]. It is true that system [4.1] does not impose unrealistic restrictions on the form that the functional relationships between species should take, but the possibility remains that the choice of state variables was inappropriate. Suppose, for example, that the influence exerted by a predator on its prey is a function of the probability of predator-prey encounters. Suppose that for a fair range of prey densities this probability is mostly *not* a function of prey density, but rather of some other factor, such as the pattern of prey distribution, environmental influence on prey vulnerability, or some other reasons that are not linearly related with prey density. It is then clear that the growth rate of the predator will not be adequately described by its equation in [4.1] because this equation assumes that species density is the major determinant of predator-prey encounters. An appropriate choice for a state variable representing the effect of prey on predator would not be prey density, but rather the factor influencing the likelihood of predator-prey encounters. It would probably make sense to treat the prey density as a parameter for a fair range of prey density.

Although the above hypothetical example might be an accurate description of some predator-prey interactions, I am not aware of clear evidence for such phenomena on the Grand Bank or on any other continental shelf. There are, however, well known examples of marine fish populations, namely clupeoids, that exhibit substantial changes in distribution pattern with changes in stock abundance and oceanographic conditions (e.g. Zuta et al. 1983, Murphy 1977, MacCall 1990). Sharp (1981) has even suggested that one of the best indicators of stock abundance is given by its distribution range and the size of its aggregations within this range. Zuta et al. (1983) suggest that fish species that are able to retain a greater spatial dispersion over time, namely because of a greater capacity to tolerate extreme environmental conditions, might be less prone to depletion by predation, as opposed to those that shrink their distribution range with decreasing stock abundance

(Murphy 1977, MacCall 1990). But there is very little information to judge how spatial contractions and expansions of marine populations affect interactions with natural enemies. The question of evaluating interactions at the population level on continental shelves is simply one of the most difficult problems that marine scientists and resource managers have to face.

The results about species interaction strength presented in section 4.7.2 are probably the only ones whose implications are strongly restricted by the assumption that stability is an important prerequisite. Considerations about which species interactions should be stronger or weaker only make sense within a framework of optimization of some quantity (local stability likelihood in this case). Another point to keep in mind about the results in section 4.7.2 is that conclusions must be stated in comparative terms. It makes little sense, for instance, to state that the results indicate weak per capita effects of capelin on cod. Rather, the results indicate that a weak per capita effect of capelin and sand lance on cod *as compared* to the same effect on plaice (results of C1 and C2) has a stabilizing effect in community models. In the same way, the negative per capita effect of cod on its prey (C3) is suggested to be much stronger than the per capita effect of plaice on the same prey (C4). The results also suggest that direct competitive interactions (C6) are destabilizing in community models of type [4.3], as compared to predator-prey interactions. This finding was also reported by Giavelli et al. (1988), who found that pure predation models are relatively easy to stabilize, but they tend to become unstable when direct competition is incorporated. The biological interpretation is that the per capita direct effect of one species' density on a competitor's growth rate should be relatively weak when compared with the same effect in predator-prey relationships. Considerable controversy exists, however, as to whether interspecific competition between fishes is important in large marine systems (see Branch 1984 for a review).

The results in sections 4.7.3, 4.7.4, and 4.7.5 are the most general ones, and confirm Yodzis (1988a,b) suggestion that there is a great deal of indeterminacy in the long term outcome of species interactions, at least as expressed by deterministic models of form [4.1]. The proportion of species interactions that are undetermined is naturally dependent on the degree of confidence that one wants to put on long term predictions. However, even working at levels of confidence that are less demanding than the usual (i.e. 12/17 = 71% and 14/17 = 82%, versus 95% and 99%), Table 14 indicates that uncertainty about model structure still results in a very high degree of structural indeterminacy (84% at the 14/17 level of confidence). Globally, the consequences of uncertainty about model parameters (type (2) only) are apparently milder (44% and 48% of directional indeterminacy at 90% and 95% levels of confidence; see Table 16). A great deal of directionally determined effects are, however, self-effects rather than interspecific effects (see Table 18). The similarity with Yodzis' (1988a,b) results are striking. Yodzis analyzed only the consequences of uncertainty of type (2) (at the 95% level of confidence) in 16 models of published food webs from a wide variety of habitats, and found that 27% of self-effects and 50 to 58% of interspecific effects are directionally undetermined. The consequences of uncertainty of type (2) for our ability to predict which species have important effects on another species' dynamics are also severe (Tables 19 and 20), and the combination of the consequences of uncertainty of type (1) and (2) on our ability to make predictions is devastating (Table 17).

What promotes indeterminacy in community models ? Yodzis (1988a,b) plotted topological indeterminacy against species richness in his 16 food webs and found that there was a trend for topological indeterminacy to be less pronounced as the number of trophospecies in food webs increases. Since variation in number of trophospecies is due primarily to differing degrees of aggregation of species in published food webs, Yodzis (1988a,b) suggested that topological indeterminacy might be a pathology of highly aggregated models. However, the 17 viable models of the Grand Bank have little aggregation but high levels of indeterminacy. There is very little variation in species numbers in the 17 models, so I have not attempted to correlate indeterminacy with number of species. Within the restricted bounds of 6 and 7 species, Figs. 39 and 40 suggest that indeterminacy in the models is associated with the number of non-null elements in the community matrix, i.e. the total number of links in a digraph representation of the community.

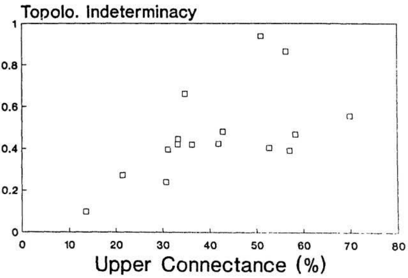


Figure 41. Topological indeterminacy against upper connectance for Yodzis' (1988a,b) 16 food webs.

Since connectance and species number are negatively correlated in food webs (section 3.5.2), it is possible that Yodzis' negative correlation between indeterminacy and species richness is also a result of a positive correlation between indeterminacy and some measure of connectance. In Fig. 41 I have plotted topological indeterminacy in Yodzis' 16 food webs (data from Yodzis 1988b) against upper connectance (data from Briand 1983). There is a positive significant correlation ($r^2 = 0.35$, significant at $\alpha = 0.05$). Variance in indeterminacy increases with the mean, especially for values of connectance above 0.4. This might be the reason why I have not been able to find a significant correlation between indeterminacy and connectance in the 17 models of the Grand Bank (Fig. 40). The factors that promote indeterminacy in community models deserve further investigation but, if any generalization is justified at the moment, it is probably that for a fixed number of species in a community model the more links we construct between and within species the more thwarted are our abilities to make predictions about that community. For relatively high values of connectance, however, we may expect a large variance in the proportion of undetermined cases.

Anderson and Lilly (1985) reviewed past attempts to understand species interactions on the Grand Bank of Newfoundland. Some of these studies were concerned with the direct effect of the abundance of one population on the growth parameters of another population (e.g. Akenhead et al. 1982; Fahrig et al. 1990). These studies had a common approach based on the search for statistically significant pairwise coupling among populations. Fahrig et al. (1990) suggested that the existence of such relationships might then be invoked to establish links between populations in multispecies modeling. But these types of approaches do not take into account that species correlations in multispecies systems may turn out to be rather counter-intuitive. My results confirm previous theoretical (Levins 1975, Holt 1977, Lawlor 1979, Yodzis 1988a) and experimental studies (several papers in Kerfoot and Sih 1987) suggesting that in the long run, indirect effects between species may "swamp" direct effects and yield "surprising" results. When the long term effects in the Grand Bank are determined, they are not necessarily what one would intuitively expect. Table 18 shows that overall the proportion of unexpected results can be surprisingly high. For example, in 7% of 105 cases of predator-prey interactions, the continuous removal of the predator resulted in a long term decrease of prey density (Table 18) and in 19% of the cases prey density did not change (see also Table 15 for details of particular models). Overall, pairwise correlation analysis does not appear to be an adequate basis from which to draw conclusions about the long term behaviour of the system.

In the face of uncertainty, aware of its hindering consequences, and in prospect of counter-intuitive community responses, is there a best strategy to design management programs for natural resources ? The host of controversial issues raised by this question goes far beyond the scope of this thesis. I can do little more than to convey my own viewpoint, biased of course by my own results but also reflecting other authors' thoughts on management under uncertainty.

The dominant practice in fisheries management has been the development of deterministic predictive models based on the best available population parameters (estimated from historical data). Protection against uncertainty then involves recommending an exploitation pattern somewhat more conservative than the models predict to be the optimal. Some parameters are revised annually and, available information permiting, there is usually a small set of models used to cross-check results. Walters and Hilborn (1978) and Walters (1986) have called this strategy passive adaptive management and pointed out its potential pitfalls. An alternative is active adaptive management, whose basic premise is that knowledge of the system will always be incomplete and therefore we should expose our doubts at the very beginning (Walters and Hilborn 1978). Active adaptive management starts by revealing uncertainties in the form of alternative working hypotheses, followed by an assessment of risks and gains involved in the baseline (current) management policy and in the experimentation of the alternatives. A decision should then be taken on whether deliberate experimentation is worth pursuing or if it is better to keep the more conservative baseline policy currently in effect (Walters 1986, Walters and Holling 1990).

What is common to both types of adaptive management is the recognition that the best action cannot be established *a priori* but must be repeatedly reassessed through a process of "learning by doing" (thus the word *adaptive*). The issue then is to know how to optimize the adaptive process: "Should resource management attempt to stabilize stock sizes and/or production rates at safe and reasonably productive levels, or should management instead deliberately permit or actively induce informative variation in stock sizes through variable harvest regulations ?" (Walters 1985 p. 90). Actually, there is no indisputable evidence that passive active management is not preferable to deliberate experimentation. Uncontrollable natural factors for example, by driving the system across a wide range of states, may sometimes provide ground for "natural experiments" (Diamond 1986). There is, however, some computational evidence that natural variation might not provide the range of population sizes needed for an optimal adaptive management, but rather would lead to systematically erroneous estimates of production rates (Walters 1985).

In the situation that is most familiar to fisheries ecologists, where functional relationships and error probability distributions are very difficult to specify, Walters and Hilborn (1978) recognize that it might be impossible to conduct optimal adaptive management. There are however suboptimal active adaptive policies, where techniques such as those presented in Chapter 4 (namely model building and press perturbations) might find their place. They include the erection of structurally different models, where the state variables are not necessarily only species (e.g. Puccia and Levins 1985), accompanied by alternative management policies including deliberate experiments that would help to discriminate among the hypotheses (Walters and Hilborn 1978).

In this context, perhaps the only encouraging result of section 4.7 is that our uncertainty about parameter values appears to have milder consequences than when we are also uncertain about model structure. There is theoretical ground (e.g. Bender et al. 1984) on which to base a program of research aimed at clarifying which species interactions are important and which are not, therefore diminishing uncertainty of type 1 (regardless of whether the full implementation of such a program is practicable or not). Uncertainty of type 2, however, is apparently beyond control. Given complete biological understanding, we would still be faced with the action of unpredictable environmental agents on population parameters. As May (1975) points out, parameters in the real world are better described in probabilistic terms, maybe even varying to within an order of magnitude greater than the one used in the simulations presented here. It would be still more disturbing if the sensitivity of long term predictions could not be significantly reduced by ecological research.

SUMMARY OF CHAPTER 4

We have mathematical tools to make both short and long term predictions about the behaviour of complex systems given certain simplifying assumptions. In community ecology, however, long term predictions are very difficult because we are usually uncertain about what are the major determinants of species growth rates and because of natural variation in population parameters. Chapter 4 investigates the limits to our knowledge about the dynamics of the marine community on the Southern Grand Bank due to these types of uncertainty. Uncertainty about the "best" model structure of this community kept me from predicting the outcome of 84% of all possible species interactions (at the 82% level of confidence). The consequences of uncertainty about the value of population parameters appear to be associated with model complexity (as measured by connectance). In models with low connectance I was able to predict the outcome of as much as 92% of all possible species interactions (at the 95% level of confidence) but when models were complex I could not predict the outcome of about 80% of all the interactions. Unfortunately, long term predictions of community behaviour are therefore highly sensitive to initial conditions in our models, rendering the behaviour of the community to a large extent indeterminate.

Chapter 5

Conclusions

Broad geographic areas on the Grand Bank are characterized by a relatively persistent (i.e. constant in time) and homogeneous (i.e. constant in space) species composition. Classificatory analysis of biological data from a 16-year time series of Spring groundfish surveys identified six such areas (Shallow, Avalon, NE Intermediate, SW Intermediate, NES Deep, and W Deep; see Fig. 3) whose contours recur at approximately the same geographic positions year after year. These areas are strongly aligned with bottom depth and are roughly coincident with major water types on the Grand Bank. American plaice, Atlantic cod, yellowtail flounder, and thorny skate are the dominant species in the areas of shallow and intermediate depth, whereas redfish dominates in the deep areas (see Table 3 and Fig. 4 for details of species composition). Since some of the dominant species are present in more than one area, it is possible that some populations may be distributed across the boundaries between different areas. These considerations about biological coherence led me to merge the Shallow with the SW Intermediate area (originating the Southern Region) and the Avalon with the NE Intermediate area (originating the Northeastern Region). These two major zoogeographic regions of the Grand Bank encompass the year-round movements of very abundant, commercially important fish species, and define an appropriate spatial scale for studies at the community level.

Food web graphs, epitomizing the major year-round trophic relationships within the two major zoogeographic regions (Southern and Northeastern), indicate a complex network of species interactions that suggest a synecological approach to community dynamics. When the static properties of the food web graphs are compared with those of other marine food webs, food chains on the Grand Bank appear to be as short as other marine chains (typically 2 to 3 links in benthic webs and 3 to 5 links in pelagic webs) but there is an unusually high proportion of links between top predators and intermediate species (i.e. species having both predators and prey). This is a consequence of a relatively high degree of omnivory in the Grand Bank which, in turn, is a consequence of ontogenetic changes in the diet of the top predators. Changes in diet were taken into consideration when building the food webs, but separate life stages were not represented. Another static property present in most published food webs, the interval graph property, was found to characterize three of the four Grand Bank webs. One can collapse the information concerning the diet overlap of the Grand Bank consumers into a single (abstract) dimension. This dimension was interpreted as representing consumer body size, which marches in good agreement with the importance usually attributed to body size in determining resource/consumer interactions in the sea.

It is not possible to infer community dynamics from static food web representations alone. One has to resort to assumptions about the major factors determining population growth rates and the way these factors interact. When it is assumed that species growth rates are mostly determined by biotic interactions (predator/prey, competition), the Grand Bank community can be represented by biologically acceptable models involving only six or seven species. But even in these simple models there is considerable uncertainty concerning the major outlines of species interactions. This type of uncertainty about model structure (uncertainty of type 1) adds to uncertainty about the values that population parameters should take in community models (uncertainty of type 2), and both types of uncertainty impose limitations on our ability to predict the community dynamics.

One way to investigate the extent to which uncertainties of type 1 and 2 limit our knowledge about community dynamics is to simulate persistent environmental (natural or man-made) perturbations and then examine how uncertainty hampers our ability to predict the consequences for the community. The perturbations are simulated by means of a continuous removal of individuals of a given species in the community. The consequences of this type of experiments (dubbed press perturbations) for the density of every species in the community, depends on the structural details of the models representing the community (which are affected by uncertainty of type 1) and on the values that population parameters take (which are affected by uncertainty of type 2). In the models of the Grand Bank community, uncertainty of type 1 and 2 combined, was highly damaging for long term predictions of community dynamics. I could not predict the outcome of 84% of all possible species interactions (at the 82% level of confidence) because of my inability to decide what was the "best" model structure of the Grand Bank community. Uncertainty of type 2, when isolated, was found to be little damaging when the models had a relatively low proportion of links between species (92% of the interactions could be predicted at the 95% level of confidence) but became increasingly damaging as complexity in the models increased by incorporating more links between species. In the most complex models only 20% of the interactions could be predicted at the 95% level of confidence.

The inclusion of an indiscriminate number of species interactions in community models (keeping the number of species constant) has an inflating effect on the indeterminacy of community dynamics, i.e., connectance promotes indeterminacy. Ecologists are usually uncertain about the importance that interactions observed at the individual level have at the level of population dynamics. As a matter of completeness, they sometimes include a link in a food web whenever there is some evidence for a predator/prey interaction between the species, even if there is no reason to believe that such interaction has any major significance at the population level. If such interactions are included in community models, side-by-side with those interactions that really do have profound population effects, the result is an undesirably high degree of indeterminacy in the long term behaviour of community models. My results therefore suggest the need for being very selective when using information on feeding interactions to predict community dynamics. Ideally, some measure of interaction strength should be attached to each link included in the models. More research is needed, however, concerning the factors that promote indeterminacy in community models.

All biological communities are likely to have a certain degree of indeterminacy in their long term behaviour. This is probably an inescapable fact because even if uncertainty of type 1 can (at least theoretically) be diminished through ecological research, uncertainty of type 2 is promoted by environmental factors largely beyond any control. Building complexity into community models (e.g., adding more variables, adding non-linear relationships between variables) is not always likely to improve our ability to predict community dynamics because of its inflating effect on uncertainty. The choice of the right state variables in models of type [4.1] (p. 138), although very important for accurate predictions, is also not a guarantee against indeterminacy. The substitution of a biotic variable by an abiotic one, for example, does not necessarily decrease either type of uncertainty. Ecologists and managers of natural resources are therefore condemned to live with uncertainty and, as a consequence, with indeterminacy in community behaviour. It is crucial that they address the wide array of ecological, social, and political questions concerning the best strategy to limit uncertainty in the management of natural resources, even if this implies a need to consider deliberate experimentation in the wild.

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APPENDIX 1

A Brief Summary of Digraph Models and Loop Analysis

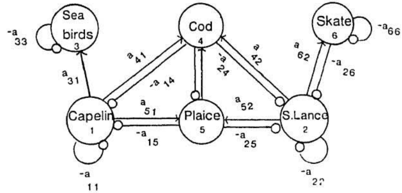
Consider a community formed by the following six species: (1) Capelin, (2) Sand lance, (3) Seabirds, (4) Cod, (5) American plaice, and (6) Thorny skate. Assume that the growth rate of every species can be represented as in equation [4.1],

$$\frac{\partial X_i}{\partial t} = f_i\,(X_1, X_2, \ldots, X_n), \qquad i = 1, \ldots, n$$

If the density of species j has any direct effect on the growth rate of species i, then the element a_{ij} of the community matrix **A**, defined by $a_{ij} = \partial f_i / \partial X_j^*$ (equation [4.3]), is non-null. The sign of a_{ij} is the sign of that effect. For example, it is positive if j is a prey and i is a predator, or it is negative if i and j compete. In the particular case where $i = j$, the i-th diagonal element of **A** is non-null. It is usually assumed that when non-null, the diagonal elements a_{ii} are negative, expressing interactions among individuals of species i. Suppose that the direct interactions between the above six species can be described by the following community matrix, which corresponds to my model If (section 3.7.2):

$$\begin{array}{lcccccc}
 & \text{Capel} & \text{Lance} & \text{Sbird} & \text{Cod} & \text{Plaic} & \text{Skate} \\
\text{Capelin} & -a_{11} & 0 & 0 & -a_{14} & -a_{15} & 0 \\
\text{S. Lance} & 0 & -a_{22} & 0 & -a_{24} & -a_{25} & -a_{26} \\
\text{Seabirds} & a_{31} & 0 & -a_{33} & 0 & 0 & 0 \\
\text{Cod} & a_{41} & a_{42} & 0 & 0 & a_{45} & 0 \\
\text{Plaice} & a_{51} & a_{52} & 0 & -a_{54} & 0 & 0 \\
\text{Skate} & 0 & -a_{62} & 0 & 0 & 0 & -a_{66}
\end{array}$$

All the information contained in the community matrix can be displayed in a digraph (Jeffries 1974, Levins 1974), where species are represented by vertices and every non-null a_{ij} is represented by a link. A link headed by a circle means that the donor has a negative effect on the recipient and an arrow means a positive effect. The following digraph represents model If and summarizes all the information in the community matrix:



A path (i.e. a series of links) that leaves one species and returns to that same species in the digraph, is called a <u>loop</u>. The number of links of that path is called the <u>loop length</u>. Consider for example the following loop of length two that leaves and returns to capelin going through plaice: a_{51}, $-a_{15}$. Other examples are $-a_{11}$, a loop of length one (self-loop); or a_{51}, $-a_{25}$, a_{42}, $-a_{14}$, a loop of length four involving capelin, plaice, lance, and cod. When two loops share no vertex in common they are called <u>disjunct</u>. Levins (1974, 1975) defined a function expressing the effect that a species has on itself by way of k intervening species in the system, the <u>feedback at level k</u>, represented by F_k, in the following way:

$$F_k = \sum (-1)^{m+1} L(m, k)$$

where L (m, k) is a product of k links and m is the number of disjunct loops involved in that product. The sum is over all possible products of k links for each m ($m = 1, \ldots, k$). By definition $F_0 = -1$. As an illustration, let us compute feedback at the first two levels for model If. At level k = 1, there are four loops each involving just one vertex, therefore:

$$F_1 = -a_{11} - a_{22} - a_{33} - a_{66}$$

At level k = 2, all possible products involving two vertices (for m = 2 and m = 1) are added up as follows:

$$-a_{11}a_{22} - a_{11}a_{33} - a_{11}a_{66} - a_{22}a_{33} - a_{22}a_{66} - a_{33}a_{66} - a_{14}a_{41}$$

$$- a_{15}a_{51} - a_{24}a_{42} - a_{25}a_{52} - a_{45}a_{54} - a_{26}a_{62}$$

Levins (1975) demonstrated that when matrix **A** is locally stable, the feedbacks of the digraph corresponding to **A** are negative at all levels. The demonstration takes advantage of the fact that the successive feedbacks *(k = 1, ..., n)* of the digraph representation of **A** turn out to equal the n coefficients of the characteristic polynomial of **A**. Levins (1975) then applies the Routh-Hurwitz theorem, which imposes conditions for the roots of the characteristic polynomial of matrix **A** to have only negative real parts (see Chen 1970 for technical exposition of the conditions and proof).

Loop analysis, the technique introduced in ecology by Levins (1974, 1975), allows one not only to determine if matrix **A** is locally stable by inspection of the feedbacks at all levels, but also to address the long term effects of press perturbations. Levins (1975) has shown that the inverse of the community matrix (whose element *(i, j)* is given by eq. [4.6]) can be written:

[A1.1]

$$A^{-1} = - \frac{\sum P_{ij}^{(r)} F_{n-k} (Comp\ P_{ij}^{(r)})}{F_n}$$

where F_n is the feedback at level n (n is the total number of species) and is negative if matrix **A** is stable. $P_{ij}^{(r)}$ is the product of the a_{ij} coefficients in a non-looping path involving r species and linking species i and j in the digraph representation of the community. The righthand factor in the numerator is the feedback of the complementary subsystem to the open path (i.e. the subsystem including the $n-r$ species not in path $P_{ij}^{(r)}$). The sum in the numerator is over all possible paths from species i to j.

Let me illustrate the use of expression [A1.1], in the context of model If, to investigate the long term effect on the density of cod of a negative press perturbation on capelin. Notice that the denominator of [A1.1] is negative because model If is locally stable (section 4.7.1), and therefore [A1.1] has the same sign as the numerator. There are three possible open paths (i.e. $P_{41}^{(r)}$) leading from capelin to cod. These are the lefthand side of the terms in the numerator of [A1.1]:

1) $P_{14}^{2} = +a_{41}$

2) $P_{14}^{3} = +a_{51}\,a_{45}$

3) $P_{14}^{4} = -a_{51}\,a_{25}\,a_{42}$

The first path goes through vertices 1 and 4; the second through vertices 1, 5, 4; and the third path through 1, 5, 2, 4. Each of the paths defines a complementary subsystem that is formed by the vertices that are not touched by the path. The complementary subsystem to the first path is the set of vertices 3, 5, 2, 6; the complement of the second path is 3, 2, 6; and the complement of the third path is 3, 6. The righthand terms in the numerator of [A1.1] are the feedbacks of these complementary subsystems:

1) $-a_{25}\, a_{33}\, a_{52}\, a_{56}$
2) $-a_{26}\, a_{33}\, a_{62} - a_{22}\, a_{33}\, a_{66}$
3) $-a_{33}\, a_{66}$

To compute the terms in the numerator of [A1.1] we multiply the paths by their corresponding complementary feedbacks. Adding up these three products and simplifying, we get:

$$-a_{41}a_{25}a_{52}a_{56} - a_{51}a_{45}a_{26}a_{62} - a_{51}a_{45}a_{22}a_{66} + a_{51}a_{25}a_{42}a_{66}$$

It is very likely that the sign of the numerator of [A1.1] will be negative. Following the criterion and symbolism defined in section 4.6.2, the number of negative terms (N) is 3 and there is only one positive term (M = 1). Since N+M = 4, and N = 3, I decide that the sign of the numerator of [A1.1] is negative. In other words, in the context of model If, a sustained removal of capelin has a negative long term effect on the density of cod.

APPENDIX 2

A Note on the Application of Monte Carlo Methods

Monte Carlo simulations are the basis of a considerable body of food web theory developed in the past dozen years (see refs. in section 4.6.1). This is justified both by the mathematical intractability of the underlying food web models and because ecologists are usually more interested in finding stable regions of the parameter space than sets of constant values unlikely to exist in the real world (section 4.6.1). A review of food web literature suggests, however, that recommendations conspicuously flagged in text books of simulation techniques have often been ignored. The random generators used and the corresponding statistical tests that they have undergone have rarely been reported. Cohen's (1978 Chap. 5, sec. 5.3) bad experience is nevertheless a warning. Even widely distributed random generators have sometimes been found to be seriously flawed. The multiplicative generator RANDU provided by IBM for system/360 is one well known example (Forsythe et al. 1977, Kennedy and Gentle 1980).

Most algorithms generating pseudo-random numbers make some essential use of hardware and/or software characteristics, such as word size and overflow handling. Use of system peculiarities may increase computational efficiency but simultaneously reduces portability, the ability of the software to run on a different system and yield similar results. It is unlikely that we will see a decline of the role played by Monte Carlo methodology as a way of coping with uncertainty of type (2) (section 4.5) in ecological models. As in any scientific endeavour, however, reproducibility of results is desirable and portable software makes this more easily achievable.

The most common random generators are probably the multiplicative congruential ones, expressed by the recurrent formula: $X_{i+1} = a\,X_i\ modulus\,(m)$, where X_i is the pseudo-random number generated in passage i. There is a considerable body of knowledge about the appropriate choices for the constants a and m (e.g. Marsaglia 1972, Knuth 1981). These generators satisfy desired statistical properties while retaining long period lengths (Knuth 1981), but the sequences produced are not truly random. In some simulations the failure of randomness in some sense may lead to erroneous conclusions. Marsaglia (1968) showed that if a succession of overlapping n-tuples $(u_1, u_2, ..., u_n)$, $(u_2, u_3, ..., u_{n+1})$ of uniform variates produced by these generators are viewed as points in a unit cube of n dimensions, then all the points will lie on less than $(n\,!\,m)^{1/n}$ parallel hyperplanes intersecting the n-cube. For example, consider a community matrix with, say, 20 non-null a_{ij}'s. Marsaglia's rule indicates that every overlapping set of 20 a_{ij}'s stemming from a multiplicative generator in a binary computer with 32-bit words ($m=2^{32}$) will lie on less than approximately 25 hyperplanes in the 20-dimensional space. This number of hyperplanes is many orders of magnitude less than the theoretical bound, were the numbers truly random. The generation of a large number of such matrices will give the misleading impression of an appropriate sampling in the parameter space.

RANDOM

There are no perfect pseudo-random generators. Probably the best way to reduce non-randomness is to combine two or more individual generators in a way that makes up for the imperfections of each generator taken individually (Marsaglia 1985). Bearing portability in mind, I have selected the generator RANDOM for the simulation of the Southern Grand Bank community matrices. RANDOM is a combination of three multiplicative generators presented by Wichmann and Hill (1982). It is practically machine-independent and can be easily converted to different programming codes.

Tests of random generators are usually divided into theoretical and empirical (or statistical) tests (Knuth 1981). Well known theoretical tests such as the lattice and spectral tests have been shown to apply only to generators of certain types (Atkinson 1980). I have applied only empirical tests to RANDOM. Although less stringent than theoretical tests, empirical tests have broader applicability and measure a type of randomness that is intuitively more clear. In empirical tests, a sample of pseudo-random numbers is taken and statistically assessed with no regard to how the numbers were generated.

The cycle length of RANDOM exceeds 2.78 x 10^{13} (Wichmann and Hill, 1982). I have tested only part of this long sequence by means of a small battery of tests of uniformity and independence. Wichmann and Hill (1982) report very satisfactory results from another test battery. All tests were initiated with the same arbitrary triplet seed ($ix = 25691$, $iy = 13427$, $iz = 233$) later used to initiate community matrix simulations throughout section 4.6.

Kolmogorov test. 100,000 sequences with 155 pseudo-random numbers each were generated by RANDOM and tested to detect departures from the null hypothesis of being drawn from a uniform distribution function. The Kolmogorov statistic (e.g. Conover 1980 Chap. 6) was computed for each sequence and checked in a two-sided test at the level of significance $\alpha = 0.05$. The null hypothesis of uniformity was rejected for only 3.7% of the sequences. When the size of each single sequence was increased from 155 to 250 numbers, the null hypothesis was rejected in 3.9% cases.

Digit Frequencies Test. This test compares the frequency of each digit (0 to 9) in any fixed position to the right of the decimal point with the expected number under the null hypothesis of uniformity. The test was used for the first, second, and third decimal position, in sequences of pseudo-random numbers from RANDOM. In each case 500,000 sequences with 155 pseudo-random numbers each were tested by means of the chi-square statistic at the level of significance $\alpha = 0.05$. The null hypothesis of uniformity was rejected in 6.1%, 6.2%, and 6.1% of the sequences, respectively for the first, second, and third decimal position. When the size of each sequence was increased from 155 to 250 numbers, the performance improved to 4.9%, 5.0% and 4.9%.

Runs Test. This test detects propensity for the occurrence of monotonic subsequences longer than expected in a sequence of pseudo-random numbers. Under the hypothesis of independence and identical distribution (i.i.d.) of the elements in the sequence, the test statistic V has an approximate chi-square distribution with 6 d.f. (assuming a sequence longer than 4,000 numbers) (see Knuth 1981). The test was done for both ascending ("runs up") and descending ("runs down") subsequences. The version of the test used was the one of Levene and Wolfowitz (1944) incorporating the matrix of covariances between numbers of runs of a given length (e.g. Morgan 1984 p. 144). Overall RANDOM performed better in the test for runs up than for runs down, meaning a slight propensity for descending monotonic sequences. In both cases the results were found dependent of the total length of the sequence tested. Table 21 summarizes the results for different sequence lengths. Values of V above 12.59 are significant at the 5% level. Table 22 presents two examples of the most significant deviations from the expected number of monotonic runs of lengths 1 to 6 (6 includes runs ≥ 6) found in Table 21.

TABLE 21. Summary of the application of the test of runs to RANDOM. Sequences of pseudo-random numbers with different lengths (1st column) were generated with the same initial seeds. The values of V shown are a measure of discrepancy between observed and expected number of monotonic runs of different sizes. Under the null hypothesis of i.i.d., V is chi-square distributed with 6 d.f. (Chi-sq. w/ 6 d.f. at $\alpha=0.05$ is 12.59).

	V - Statistic	
Run length	Runs up	Runs down
4,000	15.83	39.21
5,000	11.25	29.50
7,500	13.81	24.97
10,000	18.01	10.24
15,000	17.61	15.17
20,000	19.04	16.72
30,000	12.59	12.76
40,000	7.24	10.81
60,000	3.31	11.64
80,000	3.18	10.93
100,000	8.48	16.43
200,000	11.04	20.53
400,000	7.37	14.08
600,000	8.65	9.77
800,000	7.36	10.89
1,000,000	5.68	9.42

TABLE 22. Details of two examples taken from Table 21 (above) with significant departures from the null hypothesis of i.i.d..

Test for Runs Up of a sequence w/ length 20,000

Length of monotonic (ascending) run

	1	2	3	4	5	≥6
Observed	3419	4062	1912	530	102	15
Expected	3333	4166	1833	528	115	24

V = 19.04, significant at $\alpha = 0.005$

Test for Runs Down of a sequence w/ length 5,000

Length of monotonic (descending) run

	1	2	3	4	5	≥6
Observed	848	1027	465	122	36	6
Expected	833	1041	458	132	29	6

V = 29.50, significant at $\alpha = 0.001$

Table 21 and various tables like Table 22, built for all sequence lengths analysed, suggested no systematic departures from the null hypothesis of independence. Overall the generator displayed a very satisfactory behaviour.