SIZE-BASED DYNAMICS OF A DEMERSAL FISH COMMUNITY: MODELING FISH-FISHERIES INTERACTIONS

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Your file Votre référence
ISBN: 0-612-99038-9
Our file Notre référence
ISBN: 0-612-99038-9

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by

©María de las Nieves Martínez Murillo, M.Sc.

A thesis submitted to the School of Graduate Studies in partial fulfilment of the requirements for the degree of Doctor of Philosophy

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December 2003

St. John's Newfoundland

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Abstract

This thesis defends a holistic approach to fish dynamics, supports size as a factor determining functional groups in a community, and presents a model that can serve as a framework for the integration of biological knowledge of fish communities with decision-making about resource exploitation.

We discuss the aspects that should be considered to approach the study of fish species dynamics. In their natural environment fish species dynamics are influenced by the presence of other species. Interacting species form a community that lies at the core of this thesis. Fishery and survey data show drastic changes in the Newfoundland demersal fish community during the period from the late 70s to the early 90s.

We use these changes to analyse size as an indicator of species response to fisheries. We find that size at the community level can substitute for species to determine functional groups that direct community dynamics.

This size-based approach shows properties of the community that cannot be explained by looking at each single species one at a time. Thus, a size-based simulation model is built to analyse long-term community dynamics and its response to fisheries. The model has only three simple assumptions: (1) fish pass through a series of age-determined size classes through their life history, (2) big fish eat little fish, and (3) predation cannot drive species to extinction. The model is stable over runs of centuries, and from a stabilized state can be used to explore several scenarios involving environmental and fishery disturbances.

Acknowledgments

Without my parents and their tireless efforts to make me into a well-accomplished person I would not be here today and this thesis would have never seen the light. They and my brothers and sisters have supported me in many ways all through the process leading to the completion of this thesis.

Richard Haedrich gave me the opportunity to undertake a Ph.D. He opened for me the door to the world of practising science, and I will never forget that. More, Richard's always-constructive criticism and supervising skills have taught me in fact more than science and have made my learning process very enjoyable. As has done also David Schneider to whom I see as a reference of excellence in science, and I am very thankful for his comments on, and corrections to, my thesis.

At times, during the preparation of this thesis I had doubts. At times, a word from Javi, would have been enough for me to give up. However, he not only did not mutter that word but also encouraged me always to go on and dismissed any doubt, whether personal or academic, which I may have had.

David Methven was always willing to help me with the thesis and other university related matters. Also many other people I met while at MUN have directly or indirectly helped me during my thesis. Without the computer team at MUN and Marcos, in Spain, the computer technical problems would have been impossible to overcome.

Finally, I also want to thank Roy Knoechel for his valuable review of my thesis.

The work was made possible with support provided by the Social Sciences and Humanities Research Council (SSHRC) and the Natural Sciences and Engineering Research Council (NSERC) for the "Coast Under Stress" Project under the SSHRC Major Collaborative Research Initiatives (MCRI) Program, and NSERC operating grant to R. Haedrich, and a U.S. National Science Foundation (NSF) Arctic Science and Arctic Social Sciences programs grant to the North Atlantic Arc (NAArc) program (University of New Hampshire)

Stylistic note: The reason I use "we" throughout the thesis is because I follow the Spanish rule of the *Plural de modestia* whereby "we" is used as a polite form for "I".

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Chapter 1

On the Matter of Fish-fisheries Interactions

1.1. INTRODUCTION

This work emerges from an interest in fish interactions and dynamics. Understanding how fish communities operate is crucial for fisheries management. In this introductory chapter we present the fish-fisheries system, addressing the uncertainties and boundaries of fish dynamics. All considered, size is identified as a possible tracer to follow the fish community dynamics and its interaction with fisheries. Convenient temporal and spatial scales are defined for the study.

No ecosystem in the world escapes human action (Vitousek et al., 1997). Humans, to some extent, influence all earth's ecosystems directly or indirectly. In many cases, this action means direct exploitation of the ecosystem to obtain some natural resource. Such is the case of fishing, which represents an important source of protein for developed and developing countries (FAO, 1995; Idyll, 1978). When the ecosystem has the capacity to regenerate resources cyclically, these resources are known as renewable resources. Fisheries resources belong to this group.

However, the status of renewability is not always maintained. It can change in ecosystems under intense or prolonged stress (Odum, 1985; Rapport et al., 1985; Rapport and Whitford, 1999). Depletion of resources can occur when the rate at which a resource is taken exceeds the rate at which that resource is naturally produced, or when the activity of taking has a negative indirect effect in the natural production of the resource.

Normally, the rate at which resources are exploited increases in response to social development (Deimling and Liss, 1994; Ommer, 2002). The process of resource exploitation involves the creation of jobs and the attainment of economic profits. If the activity can support many social and economic activities, the exploitation also becomes important for the governments involved as a political and economic tool. The goal moves from obtaining resources to making profits and the measurement unit is no longer the resources themselves but the money obtained from their exploitation. With the short-term view to maximize benefits and profits, more effort and more people enter the business of exploitation not considering or unaware of the risk of overexploiting the resource. This risk is even greater when there is a competition for the resources and everyone wants to make the most of them, i.e. the tragedy of the commons (Hardin, 1968), as is the case in many fisheries. Regulations for exploitation cannot be imposed when several countries are involved and agreement on these regulations is difficult to reach. What usually happens is that sooner or later exploitation exhausts the ecosystem's productive capacity, at which point the system cannot respond to human demand any longer. This triggers chaos at natural, social, economic and political levels (Harris, 1998; Haedrich and Hamilton, 2000; Sherman, 1994). On the one hand, economic profits stop or become losses that cause social turmoil. The immediate consequence is that people working in activities related to the resource lose their jobs; they need an immediate solution because they need to make a living in the near future. On the other hand, resources may have disappeared for good or may need a long time to recover. From the moment the depletion becomes serious the only choice humans have is to either permit the resources to recover (if it is still possible) or to keep exploiting whatever is still left. The conclusion is that humans have power over resources, but the resources ultimately set the limits for their own exploitation (Daily, 1997; Folke et al., 1993), and hence the importance of understanding the natural dynamics of the resources in order to avoid the serious social consequences of their depletion.

The future of fisheries resources is no longer the exclusive concern of fish biologists. Sustainability is now the focus of ecosystem management (Olver et al., 1995; Sherman, 1994; Garcia, 1997; ICES, 1999; Zabel et al., 2003). There is need for a clear definition of this term (Phillis, 2001; Ayres, 2001; Hueting and Reijndiers, 1998; Pendry, 1998; Svirezhev, 1998) and for consensus among all social sectors about sustainability of what, for whom and for how long. Sustainability at economic levels may be incompatible with sustainability at ecological levels (i.e., for the resources and their habitat) unless an objective measure to weight resources versus profits is used. Constanza et al. (1997) estimated the economic value of the resources provided free by nature to be something like US $33 trillion per year, contrasting with the global gross national product of US $18 trillion per year. The inclusion of humans as part of the ecosystem (Coward et al., 2000, Newell and Ommer, 1999; Stephenson and Lane, 1995; Barrett, 1985) is another step towards the unification of the term sustainability, and probably the most convincing argument for ecosystem conservation. Nonetheless, it seems as though the resources instead of the humans have been neglected in ecosystem management over a long period, judging the perilious situation of many ecosystems as a result of human decision-making. It is now clear that future fisheries management will require putting sustainability, ecosystem health and human welfare in the same context, as the US National Research Council recently stated (NRC, 1999).

1.2. HISTORY REPEATS ITSELF IN FISHERIES

The general pattern of the interaction between fish and fisheries can be described as an action-reaction feedback loop (Fig. 1.1), with a unidirectional flux of biomass towards the fishery (Regier and Loftus, 1972; Jackson et al., 2001, Pauly and Palomares, 2001). Within this framework, humans, acting as a selective predator, target one or a few demersal species. They proceed intensely and persistently until the community balance breaks down and the system's structure changes. This change becomes evident when the target species becomes scarce. This response of the fish community reflects back to the fishery, which diversifies and chooses new target species mainly as a function of species availability, abundance and economic value. This causes a new perturbation and the process repeats itself.

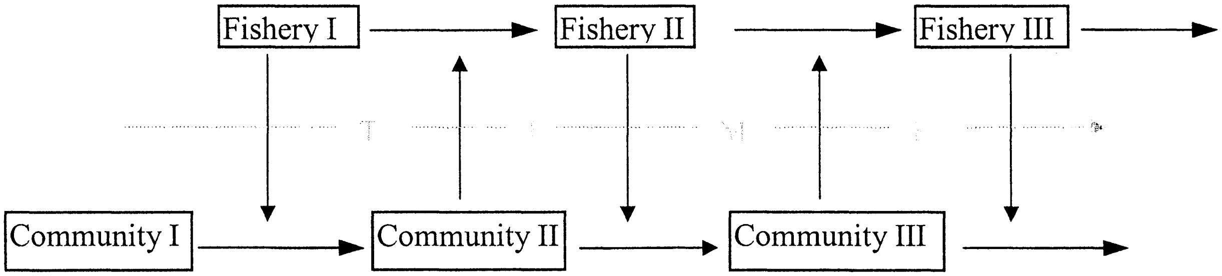


Fig. 1.1. Fisheries - fish community dynamics over time.

It is important to note in Fig. 1.1, that the starting point is the fish community in an unexploited state (Community I). Any fishery has to act on some existing resources. Identification of this community can indicate the kind of fishery it may support and the probable resultant trend of that fishery over time.

The long-term direction of this interaction loop is alarming (FAO, 1994; FAO, 2000; Buckworth, 1998; Smith, 1994; Weber, 1994; Ludwig et al., 1993; Safina, 1995). Fisheries all over the world are characterised by an initially prosperous and fast development followed by fishery collapse (Hilborn and Walters, 1992). The main long-term changes in the fish community are: (1) the age composition of target species changes towards younger, smaller-sized, individuals (North Sea Task Force, 1993; Large et al., 1998; Bianchi et al., 2000) and (2) catch composition shifts from larger, long-lived, top predators down to smaller, short-lived, lower trophic level species (Pauly et al., 2001; Caddy and Rodhouse, 1998; Merrett and Haedrich, 1997).

Figure 1.2 shows the world marine production since 1950 (FAO database "FISHSTAT+"). Over 40 years, production by developed countries has exceeded by far that of developing countries. The difference in production is especially remarkable during the 1950s, a time in which fisheries production in developing countries was very low and suggesting that large-scale fisheries in developed countries started sooner than in developing countries. The peak and then decline in the 1990s corresponds to the collapse of resources followed by the application of more strict rules concerning resource exploitation. Meanwhile, production in developing countries increased rapidly, probably due to economic needs, but which resulted in more relaxed management rules towards sustainability. The curve of fish production in developing countries since 1990 shows a steeper increase than ever followed previously either by developing or developed countries. It is thus likely that developing countries will reach their peak production in a shorter time than was experienced by the developed countries. It is also worth noting that the exploitation of marine resources other than fish is accelerating in developing countries, suggesting that full ecosystem effects are almost certainly taking place.

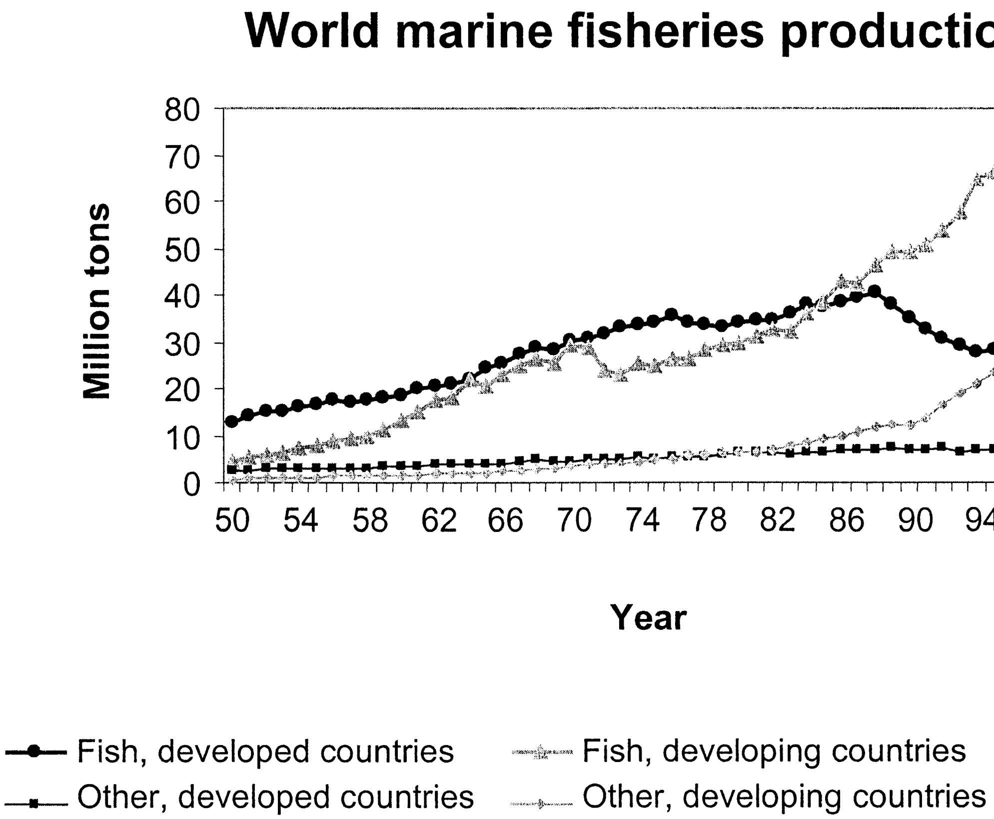


Fig 1.2. World production of marine fish, invertebrates and plants. Marine invertebrates and plants are grouped in the category "others".

Other features related to fishing activity can also show the trend of the world fishery. According to FAO the number of fisheries has doubled since 1970. In 1990, 28.5 million people were involved in fisheries. The increase is uneven, taking place mainly in Asian countries while the number of fishers decreases in industrialized countries. The same tendency shows up in the number of vessels. The fishing fleet is decreasing in developed countries and increasing in developing countries. It seems that the same scenario leading to a fish collapse and fishery overcapacity in developed countries is now being replayed in the developing counties.

The history of fisheries for the Northwest Atlantic dates back to before the official discovery of North America by the Europeans, and has been reported recently (Hutchings and Myers, 1994; Lear, 1998; Kurlansky, 1997). The following summary draws on these publications.

Right after 1497 the Portuguese, French and Spanish started fisheries in Newfoundland waters for their abundant resources, most especially cod. They were followed by the English in the mid 16th century. All these countries supplied mainly salted dry cod to European markets. The initially seasonal fishery with boats sailing from Europe in the spring-summer time expanded with the settlement of the territories by the end of the 16th century. There were signs of overexploitation of the inshore fishery as early as 1713, when declining catch rates prompted the expansion of the offshore banks fishery. At that time a small fish could weigh 60 pounds and a large one 100 pounds, much larger than any seen today. During the 18th century fish processing became the industry and way of life for the settlers of the Northwest Atlantic coast. With fluctuations in the cod fishery other species became important during the 19th century, including Atlantic halibut, haddock, flounder and redfish. Drastic changes in the fishing methods appeared in the 20th century. Inshore fishery boats started to use gasoline engines, draggers and otter trawlers were introduced in the offshore fishery, and refrigeration became available. Fish could be captured more rapidly and vessels could spend longer periods at sea. Catches of groundfish rapidly increased and fish products were used both for food and industrial purposes. Groundfish catches peaked in the 1960s and have decreased significantly since then. In 1992 a moratorium on cod fishing was established and to date it is effectively still in place with no sign of recovery.

The second half of the 20th century has seen the collapse of the centuries old groundfish fishery off Newfoundland. Crucial for this situation has been the fisheries intensification of the 1960s and the lack of strong recovery afterwards (Murawski et al., 1997; Hutchings and Myers, 1994). The total groundfish landings went from 1 million tons in the 1950s to 2 million tons in 1965. Cod catches more than doubled, reaching a maximum of 810,000 tons in 1968. In 1977 Canada and the United States extended their fisheries jurisdiction to 200 miles. This stopped the foreign fishing, but expansion of the domestic fishery quickly filled the gap left by the foreign fleets and resources were driven to collapse by 1990.

Studies on fisheries resources, which started more than a century ago (Megrey and Wespestad, 1988; Smith, 1994), have not succeeded in preventing the collapse of fisheries (Longhurst, 1999; Sutton, 1998; Botsford et al., 1997). The faster development of fisheries in comparison to scientific understanding of their basis (Haedrich et al., 2001), contributes to this failure. In addition, the constant adaptation of research to fisheries development demand favours a short-term view for the consideration of the problem and its solution, which is a major handicap in regard to the sustainability of resources. Furthermore, our control of the dynamics of fish resources is limited. Interacting forces and time lags influence marine fish community dynamics to the point that the word that best reflects fisheries in the long-term is "uncertainty". Does it make management or sustainability a utopia (Ludwig et al., 1993)? As a part of ecosystems, humans are at most times a dominant player and the one capable of more flexible and purpose-oriented actions (Kormondy, 1976; Gislason et al., 2000). If fisheries are no exception, it should be possible to regulate the state of natural fish communities to a great extent by regulating human activities. There are uncertainties concerning fish community dynamics that humans cannot control. Therefore, it seems sensible to talk about management and sustainability in terms of the way humans interact with the ecosystem.

1.3. UNCERTAINTY IN THE DYNAMICS OF FISH COMMUNITIES

There are three sources of uncertainty in the study of fish dynamics. Environmental, social and biological forces act and interact in the dynamics of fish communities. Within the model represented in Fig. 1.1 social forces would be at the top part driving changes in the fishery, at the bottom would be the environmental forces directing changes in the fish community, and biological forces would act within the community to determine relations among individuals.

The environment sets the conditions for the wax and wane of natural populations. The range of these environments is almost infinite due to the large number of environmental factors and their possible combinations. Environmentally driven fish population fluctuations have been described previous to fisheries development (MacCall, 1985). Today, there is also strong evidence that fisheries may cause the collapse of fish populations (Myers et al., 1996; Hutchings and Myers, 1994; Walters and Maguire, 1996). Government policies and the economic market are a second source of uncertainty because they change the way fish resources are exploited thereby adding variability to the dynamics of fish communities. Finally, incomplete knowledge of the structure and interactions within the fish community also creates indeterminacy (Gomes, 1993).

While environmental uncertainty is uncontrollable, human activities can be regulated, making them a source of variability rather than uncertainty. The situation of biological uncertainty would be intermediate. It can be set within certain limits since it is constrained by the life history parameters of the species. Biological uncertainty is reduced if we consider the structure and interactions in the community (Ulltang, 1996). In addition, the relative importance of environmental, human and biological factors is not always equal. In stressed ecosystems the importance of biological processes is heightened. While fish have adapted to environmental variability by mechanisms such as having a long larval stage duration, fisheries development has been so fast that fish have not been able to adapt and their abundance has decreased drastically. At this point, density-dependent biological processes become predominant forces in the dynamics of the fish community.

Most commercially important fish species spawn as r-strategists and survival of the eggs and larvae is highly dependent upon the environment in which they develop. Environmental stochasticity makes recruitment a hazardous process. However, since all larval stages are highly dependent on the environment an evolutionary adaptation to accommodate natural environmental changes has certainly occurred in all species. Recruitment is also a density dependent process (Bjorkstedt, 2000; Myers, 2001), influenced by spawning stock size and predation. At high fish abundance the effect of density dependent processes is less noticeable than environmental effects. However, at low levels of abundance these density dependent processes may have a greater effect than does recruitment. Hence, community structure and interactions, involved in density-dependent processes, are important factors to consider in the study of demersal fish community dynamics.

Predation, human activities and environmental factors are the main cause of mortality in fish species. As a biological factor, predation is intrinsic to the community and acts regardless of the presence of the other external environmental or human factors, which henceforth and throughout this thesis we will call **externalities**. Moreover, predation is the link among individuals in the community determining the indirect effects of externalities on the whole community. Defining the structure and interactions in a fish community will assist in the study of the effects of externalities on the dynamics of the fish community. As we discuss next, body size appears to be a good tracer of the structure and interactions of fish communities. Limitation of human control due to environmental uncertainty is the bottom line to consider in the study of the dynamics of fish communities.

1.4. THE IMPORTANCE OF SIZE

Fisheries research and management would profit from the refreshing view of biology expressed by J. T. Bonner (1965). In the two first chapters of his book " Size & Cycle" he challenges the reader to think of organisms as life cycles and to use size, as a characteristic of this life cycle, to make comparisons among organisms. In the marine environment, juveniles of different fish species are more similar to each other than are juveniles and adults of the same species. Habitat and diet, for example, are usually shared by individuals of different species when in the same ontogenetic stage, but not by individuals of the same species in different ontogenetic stages. If we consider characteristics such as food requirements and behaviour, which are shared by individuals, it would be possible to group fish individuals according to their life cycle stage regardless of the species to which they belong. Hastings (1988) presents some cases regarding the necessary use of age or size structure when studying population dynamics. These include competition in juvenile and/or mature stages, cannibalism, dispersion and predation, all of which are matters of concern for fish populations.

The importance of size at the different levels of organization, from individual to ecosystem, was recognized early in the history of modern ecology (Elton, 1927). Treatises on size and allometric rules concentrate in the mid 1980's (Schmidt-Nielsen, 1984; Peters, 1983; Calder, 1984; McMahon and Bonner, 1983). In biology exceptions are the rule, which make it difficult to find general laws valid for all ecosystems and organisms. However, constraints that the marine environment imposes on marine organisms make it likely that allometric rules apply for most organisms and levels of organization. Therefore studies on the implication of size in marine environments can help to further illustrate and develop allometric theory.

Many biological and ecological characteristics of species are related to size (Peters, 1983; Calder, 1984). Allometric rules generally govern physiological processes at the individual level. At the species and population level, allometric rules applied to life-history strategies allocate species along the r-K spectrum. At the community and ecosystem level, allometric rules explain the way the species utilize their environment, for example in regard to geographical distribution, prey selectivity and trophic relationships.

The size factor that underlies allometric rules is of special relevance among fish species. Most fish start their lives as very small organisms and grow over their entire lifespan (Woodhead, 1979) which makes for a strong correspondence between size and age. The energetic requirements of an individual are in accordance with this ontogenic change in size (Peters, 1983). Maximum size of individuals in a population is related to lifespan (Calder, 1984), and lifespan determines the time a population needs to adjust to local disturbances. Fecundity is also related to size (Wootton, 1979). At the community level, interaction takes place among individuals rather than among species. Community trophic interaction is also based on size. "Big eats small" (Hahm and Langton, 1984; Lundvall et al., 1999) is the norm, with fish being mostly opportunistic feeders (Lilly, 1987, 1991, 1994). From this perspective, allometry plays a significant role from the individual through to the ecosystem level. Even the spatial distribution of individual fish changes over their lifespan in relation to their size.

Most allometric characteristics relate to size in a curvilinear form:

$$V = a\,S^b$$

where V is the allometric characteristic, a and b are specific coefficients and S is the size of the individual. The same equation can be converted to a linear form using logarithms:

$$\mathrm{Log}\,V = \mathrm{Log}\,a + b\,\mathrm{Log}\,S.$$

The general rule that big eats small, the reality of trophic interactions as the main links among species, the fact that predation constitutes the main cause of fish natural mortality, and the dominance of opportunism within the feeding habits of fish species support the idea that size is a key factor in determining the structure of the community.

The hypothesis of size structuring the fish community is central in this thesis and the basis upon which we propose to study fish community dynamics. Due to fish characteristics, allometry in fish transcends the individual level to the population and community levels. Size is related to species life cycle and species interactions, which determine the structure of a fish community and drive its dynamics. In addition, fisheries usually act on size by targeting the larger individuals. Therefore, size structure is very likely to reflect fish-fisheries interactions (Dickie et al., 1987; Pauly et al., 2001). Hereafter, unless explicitly indicated, the weight of individual fish will be used as our metric of size.

1.5. TEMPORAL AND SPATIAL SCALE

A glance at any historical data set of landings or survey data on fish species shows that the answer to the question "how is the fishery doing?" depends on the point at which we ask the question and how wide a scope we want to examine (Post et al., 2002; Haury, 1978). A continuous increase in abundance over a decade may be of little importance to temporal pattern on the scale of a century. Similarly, an increase at a certain location may be insignificant when a bigger area is considered. Scale must be in accordance with the problem we want to address. It will not be possible to evaluate the state of salmon in North America if the study is limited to one river. Neither will research conducted for a period much shorter than the generation time, or covering only a spawning hot spot, inform much about the state of a fish population.

The immediate effect of a fishery on a fish community is the reduction of abundance of one or several species. This impact is effectively instantaneous, however it is only after a longer time that the full impact of the fishery shows up; there is a time lag until inter- and intra-specific interactions take place. The community reaction depends on species generation times and on individual interactions. Thus, the immediate fishery impact can be amplified or buffered by relationships within the community. Amplification can occur, for example, when fisheries removal of one species favours a competitor. In contrast, a buffer effect can lead to a reduction in predation on young individuals when cannibalistic species are fished. Many of the long-term effects of fisheries spread through the community as a result of trophic interactions (Parsons, 1992; Vanni et al., 1990).

A good criterion to use when choosing an appropriate scale is to make it big enough so as to allow the observation of the full range of variation in what is being studied (Powell, 1989). Nonetheless, the longer the time period we consider, the better we can interpret changes in a fish community (Jackson et al., 2001). Due to the long lifespan of many demersal species, a long-term period is required to assess the trend of how a species reacts to a fishery (Connell and Sousa, 1983), particularly when fisheries target a certain stage (size) of the species, most usually the large individuals. Removal of large mature individuals will reduce the number of offspring in future generations. However, the already existing younger cohorts of the species may not be affected or may even be increased by reduction of cannibalism. These already existing cohorts will replace the removed individuals and cover the effect of their removal for a certain time, until newborn generations reach adulthood. A longer time than a generation may be required considering inter-specific interactions.

Focusing on single species populations, traditional fisheries research has considered the spatial scale of the stock with the implicit difficulty of defining the stock. There are changes in the horizontal and vertical distribution of a species during its lifespan. The appropriate spatial scale to look at the dynamics of fish communities should account for these changes in distribution as well as for the geographic range in which species co-occur. In many cases the spatial distribution of species is related to the presence of other species, as in the case of a predator having a similar distribution than its prey. Therefore, consideration of species occurring together helps to find an optimum spatial scale to study species interactions, and thus community structure and dynamics. The spatial scale of fish assemblages or communities is of the magnitude of hundreds of kilometres (Gomes, 1993). In the last decades, fishery research tends towards an ecosystem scale approach. This scale is likely to include representatives of most species and most life stages. At this scale of community consideration general patterns, which would not be observed when considering single populations, can emerge (Maurer, 1999). In addition, environmental and fishery processes operate on this scale and therefore allow an ecosystem perspective (Sherman, 1994; Mann and Lazier, 1996; Haedrich, 1997).

1.6. THESIS OBJECTIVES AND OUTLINE

For a long time demersal fish species were considered inexhaustible (Smith 1994) or treated as though they were by newly developing or expanding fisheries (Merrett and Haedrich, 1997). However, demersal fish communities are suffering drastic changes. "Why are they changing?" or "How are they changing?" are questions still in debate, and now another one has been added: "Will they recover?" The answer to these questions starts with the consideration of the fish community. Using the demersal community off Newfoundland, we study the implication of size at the different levels of organization and analyse how the size structured community changes under fishery disturbance. In this thesis we study the size factor as a key in the structure of the community and its dynamics, and attempt a size based approach to simulate the natural dynamics of a fish community and how they might respond to stress from externalities.

In the current chapter we located the fish community in the global picture of fisheries. Chapter 2 introduces the demersal community used in this thesis and analyses the possible methods to approach the study of fish dynamics.

The next three chapters (3,4,5) will describe the changes in the Newfoundland demersal fish community in the last decades with special attention to the influence of size at the different levels of organization as a means to understand these changes. Then, in Chapter 6, a simulation model based on size will be applied to the community to study its structure and interactions. Next, Chapter 7 will address the long-term effects of externalities and the limits to fish community exploitation. A concluding chapter will summarize the results obtained during the course of the thesis.

Chapter 2
Approaching fish community dynamics

2.1. INTRODUCTION

Chapter 1 has considered the context in which fish-fisheries interactions take place. Within that context, attention has been directed towards the fish community for two reasons: (1) the resource must be able to sustain exploitation, (2) environmental and human disturbances can be considered externalities whose final effect depends on resource dynamics. Let us now explicitly define the fish community under consideration in this thesis. Once this is done, we proceed to address the methodology to approach its dynamics and the results that can be expected from them.

The continental shelf off the coast of Newfoundland and Labrador has attracted attention due to its important cod fishery. Using Tansley's ecosystem concept (Smith and Smith, 1998; p.315) we refer to the organisms and their habitat in this area as the continental shelf fishing ecosystem. The largest source of data available to us from this ecosystem corresponds to the demersal fish. Hence, we will focus on this component of the ecosystem. Demersal fish can be considered as an assemblage, a contemporary term used to indicate a group of species found in the same place at the same time. However, we define them as a community to emphasize the existence of interactions among this group of species (Paine, 1994; Gomes, 1993). Based on these interactions we will treat them as a unit. Doing so has a twofold implication that must be supported.

On the one hand, treating the demersal fish as a unit means adopting a synecological approach. It is not strange that fisheries research neglected biological interactions for a long time and focused on single species populations. The primary reason was to eliminate the effect of movement in order to estimate recruitment and loss (Hjort, 1914 in Kenneth and Leggett, 1994). Other uncertainties affecting the estimation of species abundance were presented in Chapter 1. Furthermore, the conduct of fisheries research itself presents additional difficulties (Smith 1994; Mitchell, 1982; Paine, 1984; Steele, 1984): the habitat does not allow direct observation, surveys are expensive, and reliability of data obtained from fisheries is questionable (by-catch, discards, unreported catches, etc) Nonetheless, even now, most approaches consider only single populations despite the fact that biological knowledge of species is currently broad, that fisheries have diversified extensively, and that the decrease of stock abundance has emphasized the importance of species interactions (Pauly, 1988; Dugan and Davis, 1993; Orensanz et al., 1998). An autecological approach has proven to be limited (Beddington, 1984; Beverton et al., 1984; Larkin, 1996; Botsford, et al., 1997), especially for looking at the long-term effect of externalities. As early as the end of the 19th century, Lankester (in Smith, 1994) pointed out the importance of species interactions in fish stock changes. The strong suggestion was that other species should at least be considered.

An individual's life is constrained into a certain time period, the time between birth and death. Life span is determined genetically and can be modified by the environment, but it is time limited. Only at the next level of organization, the population level, is there the possibility of continuity over time. Whether a population persists over time or not depends on the relation among birth and death rates. A population will have continuity over time as long as birth rate is equal to or exceeds death rate. Fecundity becomes important. But also important are the interactions between species. Therefore the permanency of a species has to be considered at the community level. If the aforementioned interactions are trophic interactions that take place between organisms of different size rather than between specific species, then we can talk about continuity of the community regardless of the permanency of a certain species. Thus all species form a unit, the community.

On the other hand, if we only consider a certain number of species as components of the community, this group of species should present some features which differentiate them from the rest of the components of the ecosystem, apart from the practical reason of data availability. In the marine environment, plankton, invertebrates, fish, marine mammals, birds and humans are linked by trophic interactions. However, there are some facts that allow us to both differentiate demersal fish species from other taxa and to treat them as a unit. The temporal and spatial scales at which demersal fish live their lives (Steele, 1978), as well their physiological and behavioural characteristics distinguish them from other taxa; e.g. generally in temperate waters, fish have a more extended migratory pattern than invertebrates or a reproductive strategy distinct from that of mammals or birds. Size implications inherent in these characteristics create a common ground for their study as a community. Using size, individuals can be classified regardless of the species they belong to, allowing treatment of the community as a whole instead of as a cluster of separate species. Strong interactions among demersal species in comparison to trophic links with other species of the ecosystem serve to justify our focus only on this group. Bax (1991) showed that predation of fish by fish is a far more important cause of mortality than is predation by mammals, birds or humans, and Jennings et al. (2002) observed that competition for food with invertebrates is low. In addition, since predation is the most important link among fish individuals, to deal only with fish reduces the importance of other non-trophic interactions which can therefore, for the purpose of this thesis, be neglected.

2.2. DATA

Lack of long-term scientific data is one of the main difficulties in studying fish community structure over time and space. This work focuses on the continental self within the 200-mile limit and the latitudes corresponding to NAFO subdivisions 2J3K, a deep shelf area of around 233,000 Km^2 (Fig. 2.1). We consider two kinds of data to study the demersal fish community in this area: fisheries landing data from 1960 to 1994, and scientific survey data from 1978 to 1993. Defining the information that can be extracted from each data source, fisheries and scientific survey data complement each other in the study of the demersal fish community.

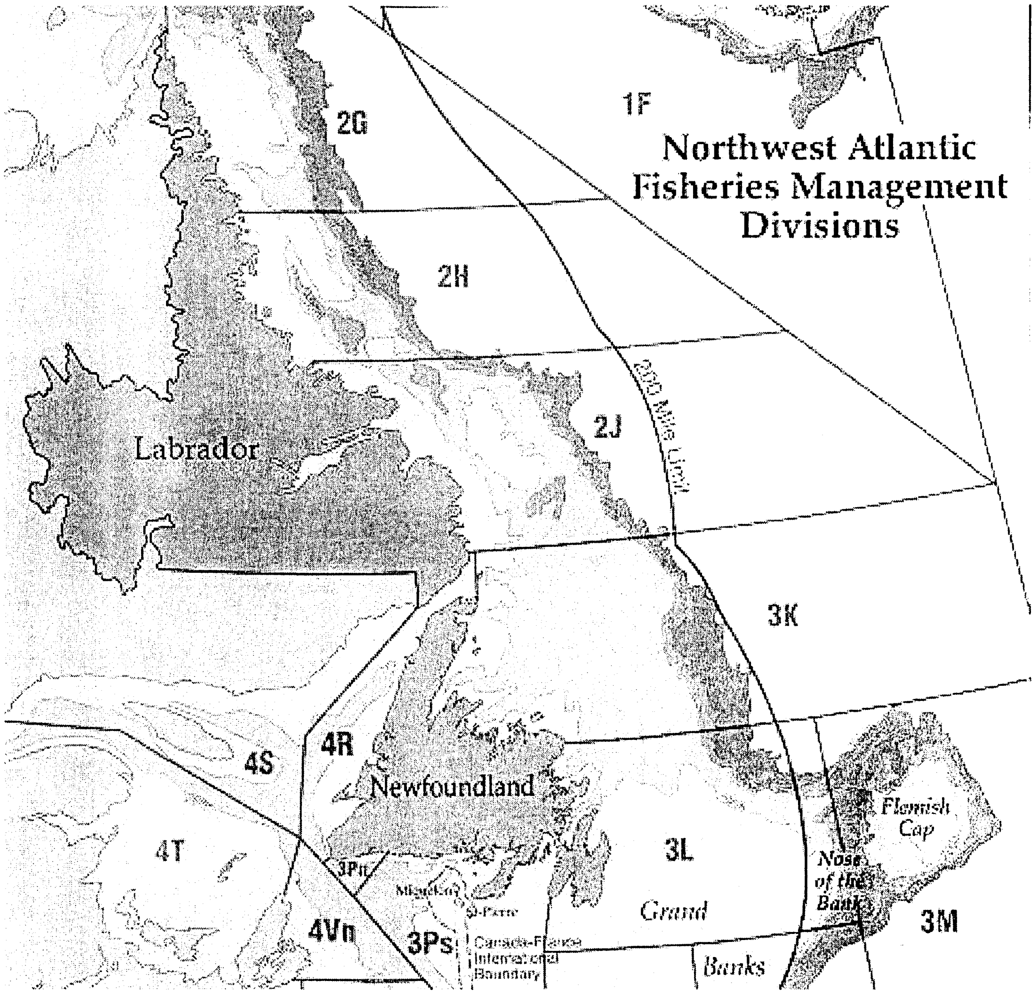


Fig. 2.1: Study area. It corresponds to NAFO areas 2J3K inside the 200-mile limit in the centre of the chart.

2.2.1. FISHERY DATA

Fishery data do not pretend to reflect the state of an entire fish community. If anything, fishery data reflect trends rather than accurate estimations of fish abundance in fishing area. Next we address their limitations for this purpose and select the fishery data corresponding to the demersal community off Newfoundland.

The use of fishery data in the study of demersal ecosystems has, to some extent, been achieved in freshwater environments of the Great Lakes (Keleher, 1972; Regier and Loftus, 1972; Regier, 1973) and in some marine environments (Deimling and Liss, 1994; Pauly, et al., 1998). Landings are usually the only available data that go far enough back in time to cover the generation time of large species. Landings may indicate the intensity of direct human disturbance on the community, although discards and bycatch are usually not reported. Fisheries catches usually indicate which are the most abundant species, since often these species are the most commercially valuable, and therefore are the ones that are targeted. They can also show shifts in the relative abundance of species. Despite the fact that politicians, fishermen, economists and scientists agree on the unreliability of fisheries statistics, all of them at least agree that qualitative changes in target species are usually the consequence of the collapse in abundance of some fish stock.

Fisheries information is a reflection not only of the state of the stocks, but also of human decision-making. Fisheries effort intensifies when the abundance of species decreases in order to maintain the same level of catches over time, and fisheries technology enables the effective targeting of areas in which there are high levels of fish abundance remaining. As a result, fisheries data do not represent the real abundance of fish species. The index CPUE (catch per unit effort) homogenizes fishery data in order to compare the state of the fish species over time. However, the difficulty in calculating effort effectively produces a high error probability for the index value, which has discouraged its use in quantitative analysis of stock abundance (Hall, 1999). In addition, fishery data sometimes may not permit resolution to the species level in the classification of captured individuals. This is the case of the 2J3K fishery data, in which some landing groups refer to a single species while some others can be very broad, for example simply as finfish or flatfish. However, the classification used here has been consistent through time, thus allowing comparison between years.

For the analysis carried out in this thesis we have defined our fish community as those demersal species commonly occurring in the Newfoundland continental shelf ecosystem, plus those species that might not be demersal but are of primary importance as prey species. The classification groups are presented in Table 2.1. This table does not contain as separate classification groups 8 demersal species that are present in the NAFO classification of landings. These species are silver hake, red hake, blue ling (rare but reported), lumpfish, eelpouts, sculpins, argentines and spiny dogfish. Since individuals of these 8 species appear in less than 3 non-consecutive years in the catches, each of those species was included in their correspondent indeterminate group: Groundfish or Finfishes. The pelagic species capelin and Arctic cod were also included in Table 2.1 because of their trophic importance in the fish community.

Table 2.1: List of demersal groups (plus pelagic species capelin and Arctic cod) that make up the commercial catches off Newfoundland (NAFO areas 2J 3K) during the years from 1960 to 1994. NS in the table means that the groups they refer to are not resolved to the species level.

Species name	**Species NAFO code**
Atlantic cod	101
Haddock	102
Atlantic redfishes	103
Pollock (saithe)	106
American plaice	112
Witch flounder	114
Yellowtail flounder	116
Greenland halibut	118
Atlantic halibut	120
Winter flounder	122
Flatfishes (NS)	129
Amer, angler (goosefish)	132
Cusk (tusk)	144
Greenland cod	148
Roundnose grenadier	168
Roughhead grenadier	169
White hake	186
Wolffishes (catfishes)	188
Groundfish (NS)	199
American eel (reported)	308
Bairds slickhead	326
Capelin	340
Dogfishes (NS)	459
Large sharks (NS)	469
Skates	479
Finfishes (NS)	499

2.2.2. SCIENTIFIC SURVEY DATA

Autumn surveys (mainly from October to December), conducted by Canada's Department of Fisheries and Oceans (DFO), collected the data used in this thesis (as reported by Villagarcía, 1995). Sampling of groundfish was performed using a stratified random method with stratification by latitude, longitude and depth in a range of 100 to 1300 metres. Each stratum contained at least 2 sampling stations in each year. For each station sampling usually corresponded to a 30-minute tow at 2.5 knots with a codend mesh of 29-mm. Details of the survey procedure can be found in Atkinson (1993). Survey data are intended to provide information on species abundance. Samples are distributed orderly in time and randomly in space to allow statistical analysis to determine the state of the fish community.

Unless explicitly indicated in further chapters, the way species are selected for inclusion in the analysis is explained here and the resulting fish community is shown in Table 2.2. From the data of the annual surveys, the number of individuals and total weight of each species were recorded. Data were standardised for duration of the tow and for number of stations surveyed each year. Thus, row data correspond to abundance as number or biomass per 30-minute tow and per year.

In order to eliminate sporadic or uncommon species whose presence will not significantly affect the analysis of interactions in the demersal community, species were excluded from the analysis if: (1) individuals were not identified to the species level, (2) they were pelagic (with the exception of capelin and Arctic cod), (3) they were present in only one year, or if (4) in half of the years in which the species occurred their abundance was less than 5 individuals, and their abundance in those years never comprised more than 0.05% of the total catch in that year.

As indicated before, despite the fact that capelin and Arctic cod are not demersal species, they were included in the study due to their importance in the demersal trophic web. In scientific surveys, the total number of fish by tow is recorded and individuals are identified to the level of species whenever possible. Nonetheless, having different lifestyles, each species shows a different response to the sampling method. Capelin and Arctic cod are two species underrepresented in the data because they are pelagic species taken in a groundfish survey. That results in a certain bias in the representation of species in the sample that should be taken into account for future discussion of results.

Table 2.2: List of the 33 species selected as components of the demersal community from scientific survey data off Newfoundland (NAFO areas 2J 3K) during the 1978 to 1993 period. Scientific code corresponds to that used by Northwest Atlantic Fisheries Centre (Akenhead and LeGrow, 1981)

Species scientific name	**Canadian (English) name**	**Abbrev.**	**Scientific code**
Agonus decagonus	Northern Alligatorfish	Ago-dec	836
Anarhichas denticulatus	Broadhead Wolffish	Ana-den	699
Anarhichas lupus	Sriped Wolffish	Ana-lup	700
Anarhichas minor	Spotted Wolffish	Ana-min	701
Antimora rostrata	Blue Hake	Ant-ros	432
Aspidophoroides monopterygius	Common Alligatorfish	Asi-mon	838
Bathyraja spinicauda	Spinytail Skate	Bat-spi	102
Boreogadus saida	Arctic Cod	Bor-sai	451
Centroscyllium fabricii	Black Dogfish	Cen-fab	27
Coryphaenoides rupestris	Roundnose Grenadier	Cor-rup	481
Cottunculus microps	Arctic Deepsea Sculpin	Cot-mic	829
Cyclopterus lumpus	Common Lumpfish	Cyc-lum	849
Eumicrotremus spinosus	Spiny Lumpfish	Eum-spi	843
Gadus morhua	Atlantic Cod	Gad-mor	438
Gadus ogac	Greenland Cod	Gad-oga	439
Glyptocephalus cynoglossus	Witch Flounder	Gly-cyn	890
Hippoglossoides platessoides	American Plaice	Hip-pla	889
Hippoglossus hippoglossus	Atlantic Halibut	Hip-hip	893
Lycodes esmarki	Esmark's Eelpout	Lyc-esm	727
Lycodes reticulatus	Arctic Eelpout	Lyc-ret	729
Lycodes vahlii	Vahl's Eelpout	Lyc-vah	730
Macrourus berglax	Roughhead Grenadier	Mac-ber	474
Mallotus villosus	Capelin	Mall-vill	187
Myoxocephalus scorpius	Shorthorn Sculpin	Myo-sco	819
Nezumia bairdii	Common Marlin Spike	Nez-bar	478
Notacanthus nasus	Large Scale Tapirfish	Not-nas	386
Raja radiata	Thorny Skate	Raj-rad	90
Raja senta	Smooth Skate	Raj-sen	91
Reinhardtius hippoglossoides	Greenland Halibut	Rei-hip	892
Sebastes marinus	Golden Redfish	Seb-mar	793
Sebastes mentella	Deep Water Redfish	Seb-men	794
Synaphobranchus kaupi	Longnose Eel	Syn-Kau	372
Trachyrhynchus murrayi	Roughnose Grenadier	Tra-mur	483

2.3. METHODOLOGY

There are many approaches to the study of fish community dynamics. As Rice (2000) points out, single indices, multivariate analysis, descriptive curves and models can complement each other in obtaining a global picture when applied together to fish-fisheries interaction studies. In order to choose the study methods and get them working synergistically, it has to be understood that the aim here is to show the changes in community structure over time and how these changes are affected by externalities. From that perspective we can discuss next the applicability of each approach.

A combination of abundance and biomass indices to yield the average size of individuals in a population gives more information about its real state, and this information is especially relevant to fisheries. Abundance and biomass are traditional measures that summarise the state of fish populations for fishery purposes. They are complemented with length at age, length frequency, fecundity at age or sex ratio data. Despite their use to show changes over time in marine populations, these indices do not explain whether the observed changes came along with changes in age structure or even if age structure changes are taking place regardless of a constant value for these indices over time. Thus, abundance and biomass indices by themselves do not show the real state of populations. For example, a population can keep a constant abundance, despite the fact that it may be losing its oldest and largest individuals and decreasing in average size of individuals, as long as recruitment is enough to balance the loss of large individuals. Changes of average weight over time for a population and its relation to changes in abundance can indicate whether the adult individuals of the population are decreasing or increasing in number. This is important information when considering the capacity of the population to produce new individuals or to recover from a disturbance.

When applied to individuals instead of populations, size allows as well a synecological approach to the fish community because size groups can be considered regardless of the species that individuals belong to. In addition, as will be explained later, size can be used to build biomass and abundance spectra of the community as a whole.

At the community level, there are other indices used to represent the state of the community. The most popular of those indices is diversity. However, the use of these indices as indicators of the community state is debatable, and controversy concerning theory and practice is extensive (see Pimm and Hyman, 1987). In an open environment, changes in diversity can be due to the migration of species. That means that a change in abundance can be compensated for by migration of new individuals into the community yielding no change in diversity despite a serious change in the community structure. Spatial density-dependent aggregation of individuals, which may mislead in the interpretation of diversity values, is also likely to occur in demersal environments. An additional drawback in the use of community diversity indices is that they can be misleading in the same way as happens with abundance and biomass indices. The same value of any of these indices can correspond to very different structural states of the fish community.

The search for an holistic approach to the fish community has popularised the application of multivariate analyses, which operate by considering all the species of the community simultaneously. Three different multivariate analysis are applied herein to the demersal fish community data from 2J3K: cluster analysis, multidimensional scaling

(MDS) and principal components analysis (PCA) Cluster analysis groups years or species that are more similar in some respect. MDS not only groups, but also orders the variables. PCA allows us to find important factors that underlie the behaviour of species over time. All these analyses reveal changes in the community structure. However, they are exploratory analyses, which means that they identify patterns but cannot confirm the reasons for them. Therefore, the outcomes from these methods should be complemented by confirmatory analysis (regression, rank correlation….) to determine whether they might help to explain the changes observed in the community.

Size spectra analysis goes beyond the population to the community as a unit, by considering individual characteristics of the organisms. A size spectrum is the distribution of an attribute of a community as a function of size. Hence, individuals are grouped together according to the size stage they are in and regardless of the species to which they belong. The shape of the size spectrum and its change over time can give information about the ecological state of the community.

The more complex a system is, the more difficult it is to apply experimental tests to it. Indirect effects and time lag effects among variables are difficult to find using statistical models (Akenhead et al., 1982; Henderson, 1987). Experimental tests assume an understanding of the system in order to be able to set the experiment and to give cause-and-effect results. Many ecological phenomena are complex, include many variables, and are not completely understood. In these cases a model is useful to put the pieces together and show the possible expected outcomes. Simulation models are appropriate for dynamic studies in which the processes themselves are equally as important as the final outcomes. Furthermore, a model can cover temporal scales that other methods do not and can be very valuable when studying a large spatial scale, where experimental replications are not possible (Carpenter et al., 1995). In particular the dynamics of species with a long lifespan and a wide habitat range are difficult to deal with experimentally. In those cases, models are very helpful to complement experimental studies and to identify possible important processes or factors that should be looked at more closely. In addition, a model allows the incorporation of new information about the system that may not have been considered or not have been available in the first instance. Although these reasons support a simulation exercise, it is worth discussing to what extent a model will give us useful information.

2.4. EXPECTATIONS FROM A MODEL

Most methods mentioned in the last section give a representation of the community; thus they can be considered as models. Nonetheless, they are static and none of them can test the long-term dynamics of the fish community under different scenarios. A simulation model will not only attain these objectives, but also will permit integration of all levels of organization, from individual to community and, without losing resolution at these levels, observe the emergent properties that come from their integration. The model used in this thesis is based on the interactions of the individuals of the community. Because the abundance of offspring will influence the future abundance of large adult individuals, and at the same time the abundance of large adult individuals will influence that of offspring, a continuous cycle is established with no specific bottom-up or top-down structure which could influence the results.

A simulation model for the Newfoundland demersal fish community is intended to serve as a tool to: (1) study the importance of size in the structure of a fish community and (2) quantify sensitivity to externalities in the fish community.

The difficulty of obtaining accurate quantitative results already mentioned in the introduction stems from: (1) background noise, as for example environmental uncertainty, which creates constant uncertainty (Beddington et al., 1984; Larkin 1996), (2) the absence of universal laws in ecology and the uniqueness of each ecological situation (Roughgarden, 1998), (3) past scenarios may be completely different from future ones, i.e. it will not work to model the asymptotic part of a sigmoidal curve using the equation created to model the exponential growth of that same curve, and (4) data may be insufficient to give exact outcomes, e.g., many survey data do not cover the lifetime of species. Nonetheless, a model may still be useful even when it is not completely accurate. As Roughgarden (1998: ix) points out:

> *"Think of cooking. In most dishes the ingredients don't have to be measured to a milligram, nor the baking timed to the millisecond. A model too doesn't have to get everything exactly right, because it may still account for what is going on pretty well."*

Trends, magnitude and relative abundance are more robust measures for a model result than absolute abundance of the variables for a model result. Therefore, it may be better to look for significant changes in these measures rather than at exact abundance values when interpreting the results from a demersal fish community simulation model.

The analysis of these measures can reveal: (1) emergent properties at the community level induced by the size factor, (2) indirect effects, i.e., the links between elements are as important as the elements themselves, (3) possible drastic change in the dynamics of the system, and (4) a framework for fisheries management, i.e., a general approach to consider fisheries resources and the effect of fisheries.

General modelling problems of balancing complexity with prediction error as well as generality with accuracy (Clark, 1984; Puccia and Levins, 1985; Sugihara, 1984) are easier to deal with when the modelling process is viewed as an approach to ecological phenomena. Again Roughgarden (1998: xi):

> *'Think of building a bridge at the mouth of a river. There's no universal bridge – one size doesn't fit all, but civil engineering offers a general approach to building bridges. Similarly, no two lakes are the same……. Through modelling one can present the information about different systems in a common format, and see general features emerge."*

The most important factors for the outcome of a model are the variables selected and assumptions considered in the construction of the model (McAllister and Kirkwood, 1998; Lai and Gallucci, 1988). The underlying assumptions in the simulation of the fish community under study here are that predation is the main interaction within the individuals and that it is both density and size-dependent. These assumptions are well recognized in the literature (Bax, 1991; 1998; Yodzis and Innes, 1992; Dunn, 1972). In its basic form the model is deterministic, but it can incorporate internal or external stochasticity.

2.5.CONCLUSION

The fish community defined by its populations of interacting species sets the biological limits within which any disturbance must take place. The practical importance for fisheries demands more than a description of the fish community; it requires an ability to quantitatively measure the standing stock and, furthermore, quantification of changes over time. Uncertainties discussed in Chapter 1 limit the accuracy of quantitative measures. The reality of uncertainty is a compelling reason to look for overall trends instead of quantitative accuracy in fish-fisheries interactions. For this reason, many international organizations are adopting a precautionary approach to fisheries management (NAFO working paper 97/15, MS 1997). This precautionary approach looks for limits and target reference points. Multivariate methods and size spectra analysis, reflecting changes occurring at the whole community, may indicate whether these reference points need to be defined at the community level. Based on the structure and links among individuals within the community, a simulation model can serve as a framework to observe the trends followed by the community under different management scenarios. We will build the case for a new size-based simulation model (introduced explicitly in Chapter 6) in the next few descriptive and analytical chapters.

Chapter 3

From landings to fish community

3.1. INTRODUCTION

Species characteristics are expected to influence the long-term changes of a fish community structure when it suffers a continuous fishery pressure. We describe and analyse the changes undergone by the demersal fish community off Newfoundland using the two sources of data introduced in the previous chapter: fisheries landings and survey data. Despite the fact that landings data are easier to obtain, more common and cover a longer time period, they do not directly reflect the state of the fish community. Comparison of the two kinds of data help to determine the extent to which fishery data can provide information about the state and change of the fish community.

The collapse of the Newfoundland groundfish fishery has followed a familiar pattern observed in other fisheries around the globe (Sinclair and Murawski, 1997; Johnson et al., 2001; Deimling and Liss, 1994): increasing catches, diversification of target species and then collapse. The timing of this overall process is related to the structure of the fish community. Each species' life history parameters have implications for the response of fish to fisheries (Regier and Loftus, 1972).

As an economy of scale, the fishery usually targets a species because of its abundance in terms of biomass. For the biomass of a population to be high, there must be many individuals or/and the individuals must be of big size.

The basic equation for population dynamics is of the form:

$$N_t = N_0 e^{(b-m)t}$$

where N_0 and N_t represent the number of individuals in the population at the initial time, 0, and after a certain time, t, respectively, b is the reproductive rate of the population and m is the death rate (mortality). When b and m cancel each other, the population is in equilibrium, i.e. it remains constant over time. Regardless of equilibrium conditions, the actual values of b and m are important (Margalef, 1978). The magnitude of b and m reflects the fluctuation range for a population. The greater the fecundity the larger the fluctuations a population can cope with, because the range within which b and m can adjust to each other is larger. In many animals, greater fecundity is observed in small, short lifespan species (Pimm, 1991, Margalef, 1978). However, most fish species, despite different size and lifespan, behave as r-strategists with respect to offspring production. Small fish species are reported to undergo more frequent fluctuations than larger ones (May, 1984). Since b and m are both average measures for all cohorts in the population, their value is smaller in large, long lifespan species. For each individual cohort, b (as recruitment to the next age) and m decrease with age. Therefore, the age (size) structure of the community influences the values of b and m, especially in species with a long generation time. Furthermore, the age (size) structure of the population will greatly influence its biomass, a fact that is not explicit in the basic equation given above.

Life history parameters have implications with respect to population stability, i.e. the time for a species to recover after a disturbance (resilience) and the time it remains unchanged under a perturbation (resistance). According to life history parameters, small short-lived species should have low resistance but high resilience due to their short generation time. On the contrary, large long-lived species will have greater resistance because they have more biomass accumulated in older individuals. At the same time, because longer time is needed to replace lost older individuals, large species will have lower resilience.

3.2. DATA AND METHODS

Fishery data that are used here correspond to landing catches, measured by weight, from the NAFO areas 2J and 3K in the years 1960 to 1994. The way the species are classified by NAFO is shown in Chapter 2 (Table 2.1). As was already explained, in some cases several species are lumped together. For clarity, hereafter we will refer to these classification groups as species, even though some of them include several species in the reported landings data. Scientific survey data available for the same area only cover the period 1978 to 1993. The selection procedure and list of demersal species from survey data have also been explained in Chapter 2 (Table 2.2).

Several analytical methods are applied to the data in order to obtain a complete picture of the fish community change in species composition and to evaluate the fishery data. First, descriptive analyses show the trend of the fishery over time and help to identify the structure of the exploited community regarding species abundance, dominance and life history. Second, community indices are calculated and discussed. Finally, cluster analysis is performed with the purposes of: (1) observing changes in the species composition of catches over time, (2) showing which species follow the same trend over time, and (3) describing any possible relationship between each group of species that might follow a similar trend and the overall trend of the community over time.

Description of total landings as well as landings of the most abundant species are presented. Descriptive analyses are also performed using survey data. Comparisons of the results obtained from landings and survey data help to determine whether fishery landings really reflect the state of the fish community. In comparing graphics, attention should be paid to the fact that the time period covered is different for survey than for landings data. The Shannon diversity index (Stiling, 1996) and richness (as number of species in landings data) are calculated, and the relative importance of each species in the total yearly catches is discussed.

Time series of landings data are further analysed using a cluster technique, the so-called Sequential Agglomerative, Hierarchic Non-overlapping Cluster methods (Sneath and Sokal, 1973; see also Legendre and Legendre, 1983) performed using the software package NTSYS (Rohlf, 1995). Analyses are carried out in two ways, first to group years and then to group species. Both cluster analyses stem from the same data matrix. The input matrix is that of the weight of each species in each year. In a first step the input data matrix values are transformed to $\log_{10}(x+1)$ in order to minimize the importance of the most abundant species and stress the relative change rather than the absolute value of change. The addition of 1 to the variable value previous to the log transformation is to deal with 0 values, for which the logarithm cannot be taken.

From the resulting matrix, the Bray-Curtis distance metric is chosen as a dissimilarity index for the temporal analysis, because it reduces the weight of the most abundant species in the results and better accounts for the change in magnitude of species groups over the time series. Thus, in the resulting cluster plot, years with the same or similar species composition of catches will be close together, and the existence of continuity over time in catches can be determined. When a second cluster analysis is performed on the species (as opposed to years), Pearson correlation is used as the similarity index. The reason is to centre attention on species with similar fluctuations (as directions of change in abundance rather than the abundance value itself) over time. Thus, species that increase or decrease in the same years are going to be more similar than species with opposite changes in abundance, and therefore they are grouped together.

The equation to calculate Bray-Curtis distance is:

$$d_{ij} = \sum_k \left| x_{ki} - x_{kj} \right| / \sum_k \left(x_{ki} + x_{kj} \right)$$

where d_{ij} is the distance between two observations, and x_{ki} and x_{kj} are the values of the variable k in observation i and j respectively.

The equation to calculate Pearson correlation is:

$$r_{ki} = s_{ki} / \sqrt{s_k^2 \bullet s_i^2}$$

where r_{ki} is the Pearson correlation coefficient (varies from -1 to +1), s_{ki} is the covariance of variables k and i, and s_k and s_i are the standard deviations of variable k and variable i respectively.

3.3. RESULTS AND DISCUSSION

3.3.1 DESCRIPTIVE ANALYSES AND COMMUNITY INDICES

Fishery landings (Fig. 3.1) indicate an overall decrease over time. This trend matches most of the time the trend of cod, because cod accounts for most of the weight of total landings. Capelin is the other species that in the 70s and a little bit in the late 80s has a significant weight in total fishery landings. Survey data (Fig. 3.2) cover only the period from 1978 to 1993. They indicate a decline in overall community biomass, but cod does not account for most of the community weight. A significant weight in the community is accounted for by other species, and their proportion is reduced over time. Capelin does not seem to have a significant weight in the community. However, it should be remembered that this species is under-represented in bottom trawl surveys. The picture of the fish community as reflected by survey data (Fig. 3.2) is different from that seen in the catches. Survey data show that even though cod is the most abundant species in the community, it does not account for most of the community biomass.

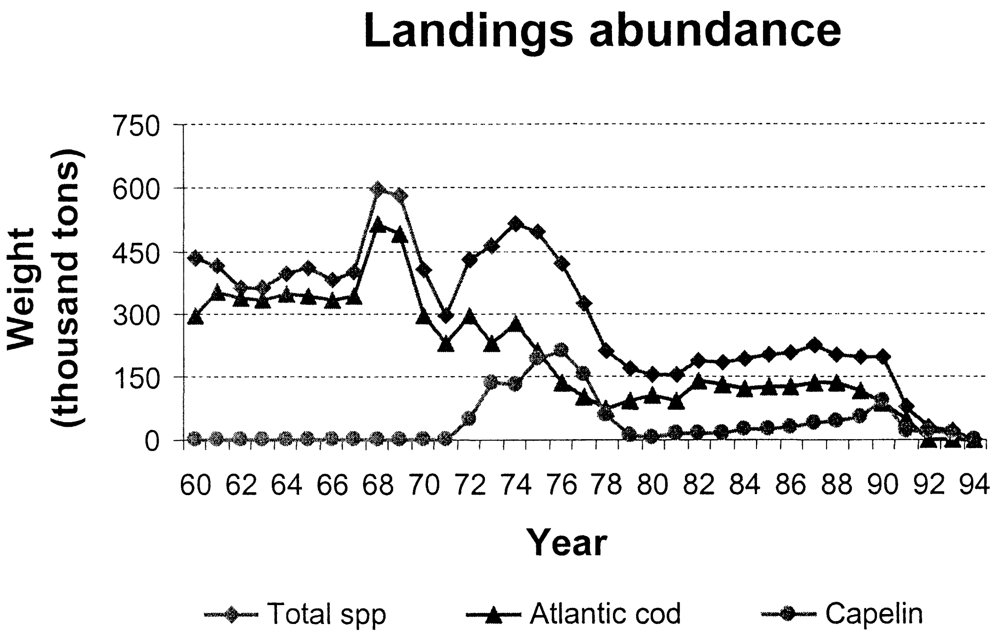


Fig. 3.1: Comparison of total landings with cod and capelin catches

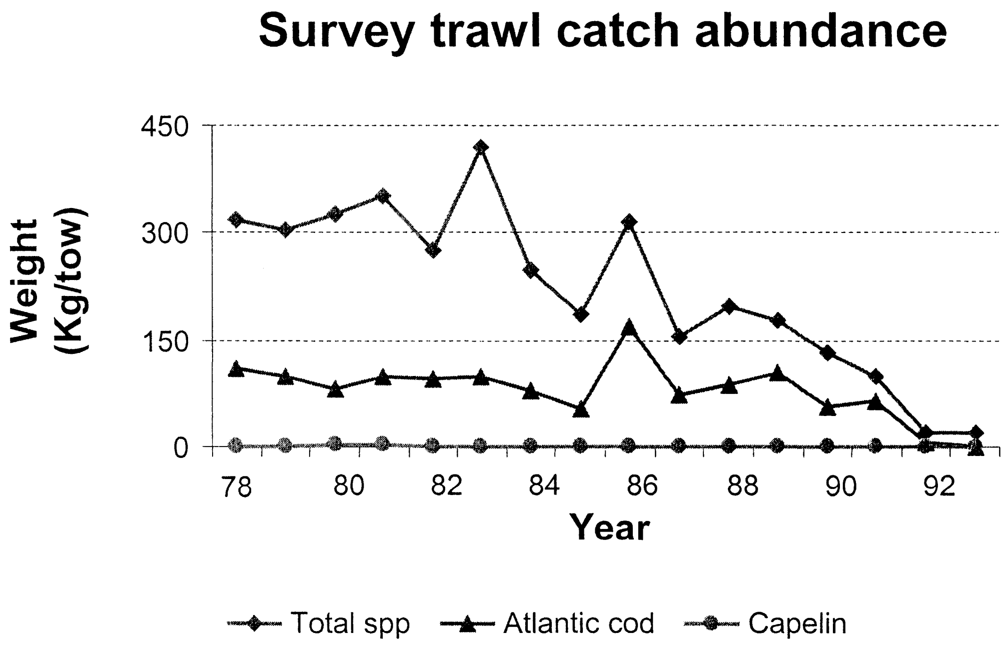


Fig. 3.2: Total community abundance change over time and change of cod and capelin.

Cod has historically been the principal commercial species in the Newfoundland area, accounting for most of the yearly catch in the fishery. Only the catches of capelin are comparable during the 1970s. The only time when total catches do not follow cod trend is when capelin captures increase. Nonetheless, decline of cod catches is only temporarily buffered by catches of capelin and no other species can replace the loss of cod, which remains the principal fishery species even when its catch declines. Capelin, a short-lived small species, can only cope with fishery stress for a short time, less than a decade. It is in the early 80s, when the decrease in cod catches is no longer compensated for by capelin catches, that total catches begin to reflect the overall lack of resources and this situation is not compensated for by any other additional species in the following years.

Figure 3.3 describes the biomass change over time of some species (other than cod or capelin) relevant to the fishery at one time or another. None of these groups ever reach an abundance comparable to that of cod or capelin. These species cannot support the fishery over either as long a time or as high in abundance as cod did, even though their relative abundance in the catches may increase over time. An increase of relative abundance of some species in total catch can mislead fisheries managers to believe that there are prospects for a new fishery. To avoid that, changes in relative abundance of species should be considered in relation to the relative abundance of the rest of the species and to the total amount of catches. The percentage comprised by each group in each year's catch is not by itself an adequate index to compare landings in different years. The abundance of a certain group, for example, may decrease over time yet its percentage may increase due to a reduction in the overall abundance.

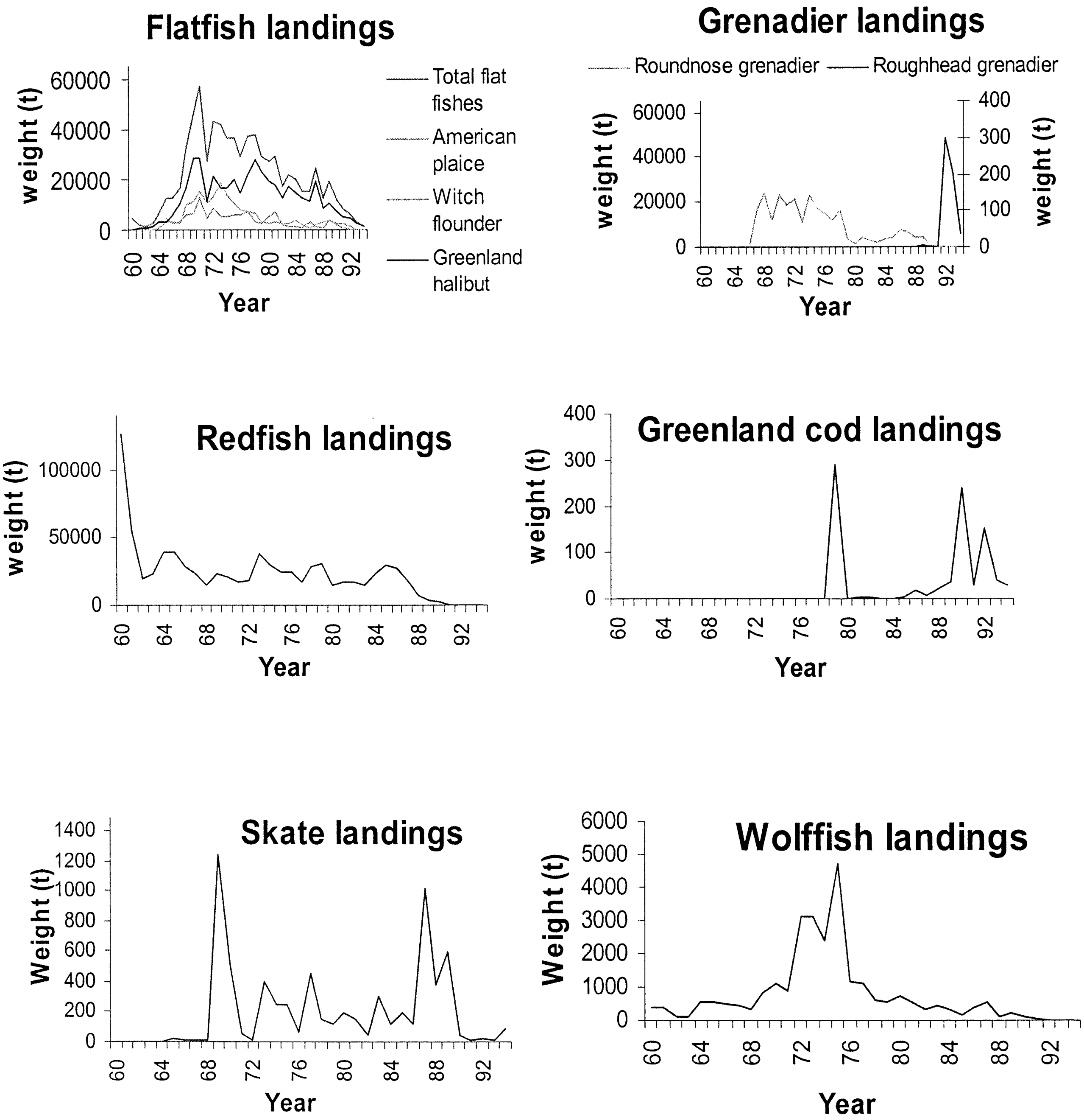


Fig.3.3: Trend in landings of: flatfishes, grenadiers, redfishes, Greenland cod, skates and wolffishes.

The catches for many of the non-dominant species peak at a similar moment in time (around 1970). Several causes might explain this observation. It may be due to an intensification of fishing. That would explain why for many groups the increase starts around 1968, the year corresponding to the maximum capture of cod. That might be the case for some flatfishes and grenadiers (Fig. 3.3). The time match for the peak of catches could also correspond with an especially favourable time for the fish community. Non-dominant species might also increase in abundance as a result of indirect effects caused by the decrease of competitors or predators. That would be the case of substituting one species for another related one, e.g. catching Winter flounder when other flatfishes decline or in the shift from Roundnose grenadier to Roughhead grenadier. Yet, the increase in catches of these newly fished species does not correspond to any real increase in nature. Often, the catches decline observed in these species is faster and even anticipates the decline of cod.

Changes of diversity and richness for fishery and survey data are shown in Figures 3.4 and 3.5 respectively. Fishery landings data show a trend of increasing species richness from 1960 to 1988. Diversity also increases from 1960 to peak in 1978. Survey data, covering from 1978 to 1993, do not show any change over that period either for the diversity or for species richness. The dominance of cod in total landings weight until 1971 suggest that during this time the increasing diversity is likely due to the variation in the number of species entering the fishery. From 1971 to 1978 (the year of maximum diversity) change in relative abundance of species may as well contribute to diversity increase, since capelin catches increase and cod catches decrease. Species richness increases during all this time and until 1988 does not indicate that new species appear in the area, but rather that more species are targeted. Supporting this idea is the fact that survey trawl data show always a higher species richness than does fishery landing data. Increasing number of target species is probably due to intensification of the fishery, as supported by the correspondence in time between catch peaks of other species and the decline of cod. Diversity obtained from fishery data do not reflect the real state of the community. Diversity or richness from survey data do not show any clear trend over time (3.5) despite the drastic changes in community abundance (Fig. 3.2). Thus, neither gives much information about the changes of the fish community.

Despite the fact that fisheries abundance does not necessarily correspond to natural abundance of species, life history parameters of individual species seem to influence the behaviour of the fishery. Cod, a long-lived top predator, dominated the fishery even during its decline. Capelin, although it seems to have been favoured by the removal of its most important predator, cod, has neither approached the maximum catches of cod nor has sustained large catches for as long a time as cod. Capelin, with a short generation time and fewer cohorts, is able to sustain overfishing but not for very long, because its biomass does not become accumulated in large old individuals as is the case for cod. Redfish species, also important in fisheries, do not reach the level of capture of cod but remain in the fishery for a long time. Redfishes are also long-lived species but are smaller than cod and are ovoviviparous.

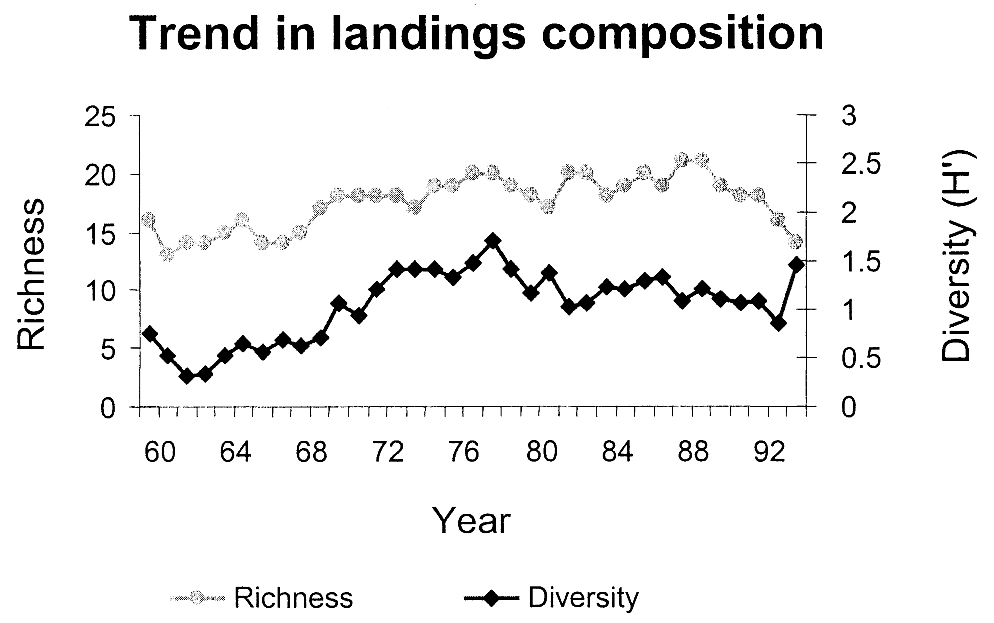


Fig. 3.4: Fishery diversity and richness over time.

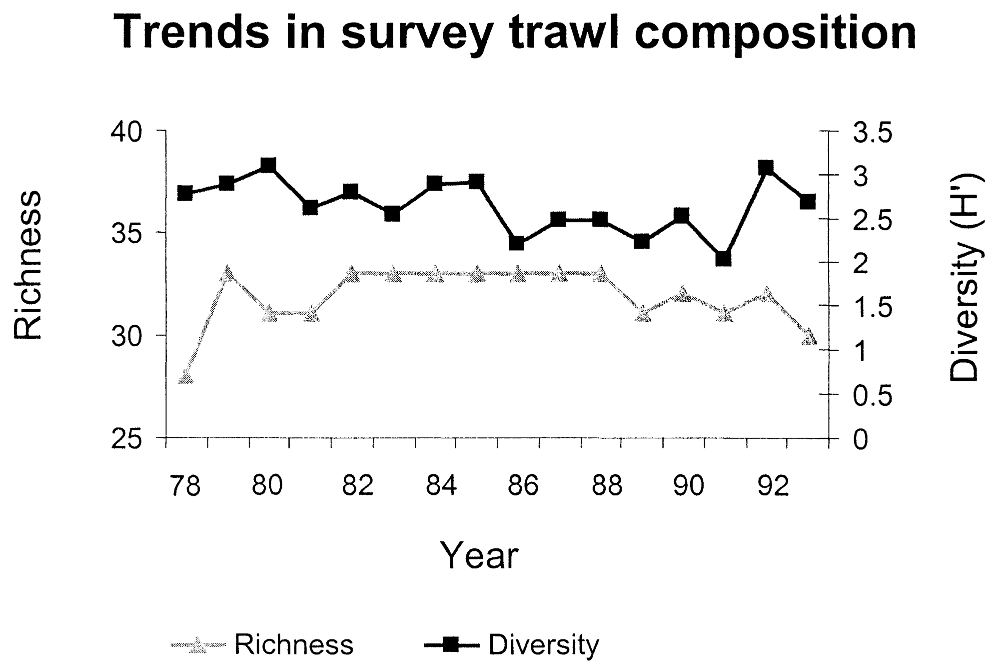


Fig. 3.5: Fish community diversity and richness over time.

3.3.2 CLUSTER ANALYSES

Further insight into changes followed by the fishery comes from the application of cluster analysis to landing data. Grouping of years according to their fishery landing composition is shown in Figure 3.6. A constant tendency towards more dissimilar catches over time results. Four periods are clearly distinguished, limited by approximately 22% of Bray-Curtis dissimilarity. A first period corresponds to the years 1960 to 1966; catches are high and diversity is more or less constant. A second period of diversification begins with a peak in catches in 1967, and the end of this period corresponds to the dramatic reduction of cod in 1978. The period of the 1980s corresponds to the maintenance of moderate levels of catches, but the number of target species continues growing. Finally, 1992 to 1994 is the period of fisheries collapse.

When cluster analysis is based on the species (Figure 3.7), species that follow a similar trend over the study period are gathered together. Three main groups are differentiated: species that are present at the beginning but disappear in the last years, species that appear only in the last years, and species that are present in the intermediate period. The results of this analysis help to explain that the structure observed in Fig. 3.6, where the fishery follows a continuous orderly change over time, is the result of a progressive decrease in abundance of target species and the addition of new ones.

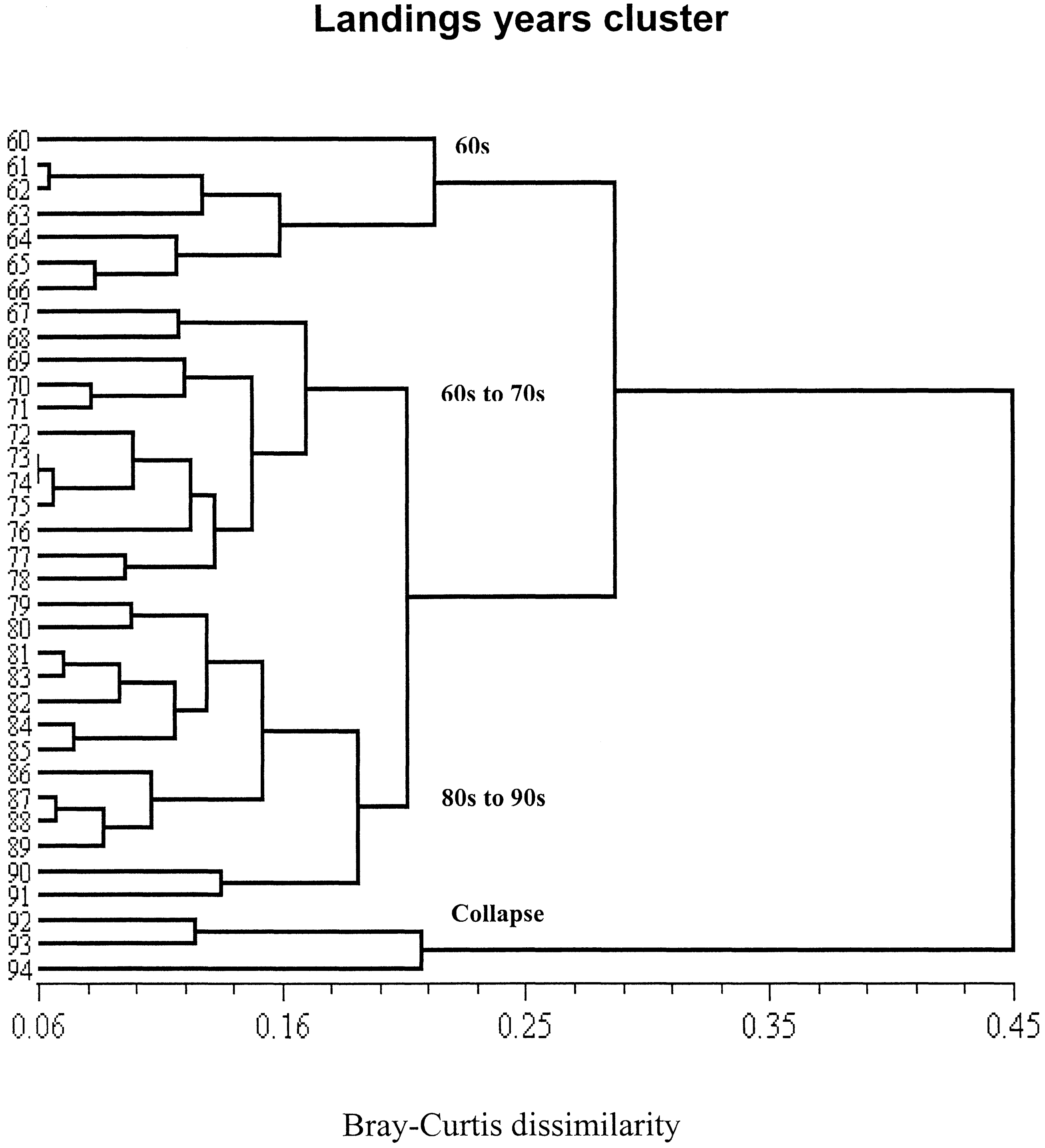


Fig. 3.6: Change over time of catch composition. NAFO ladings data

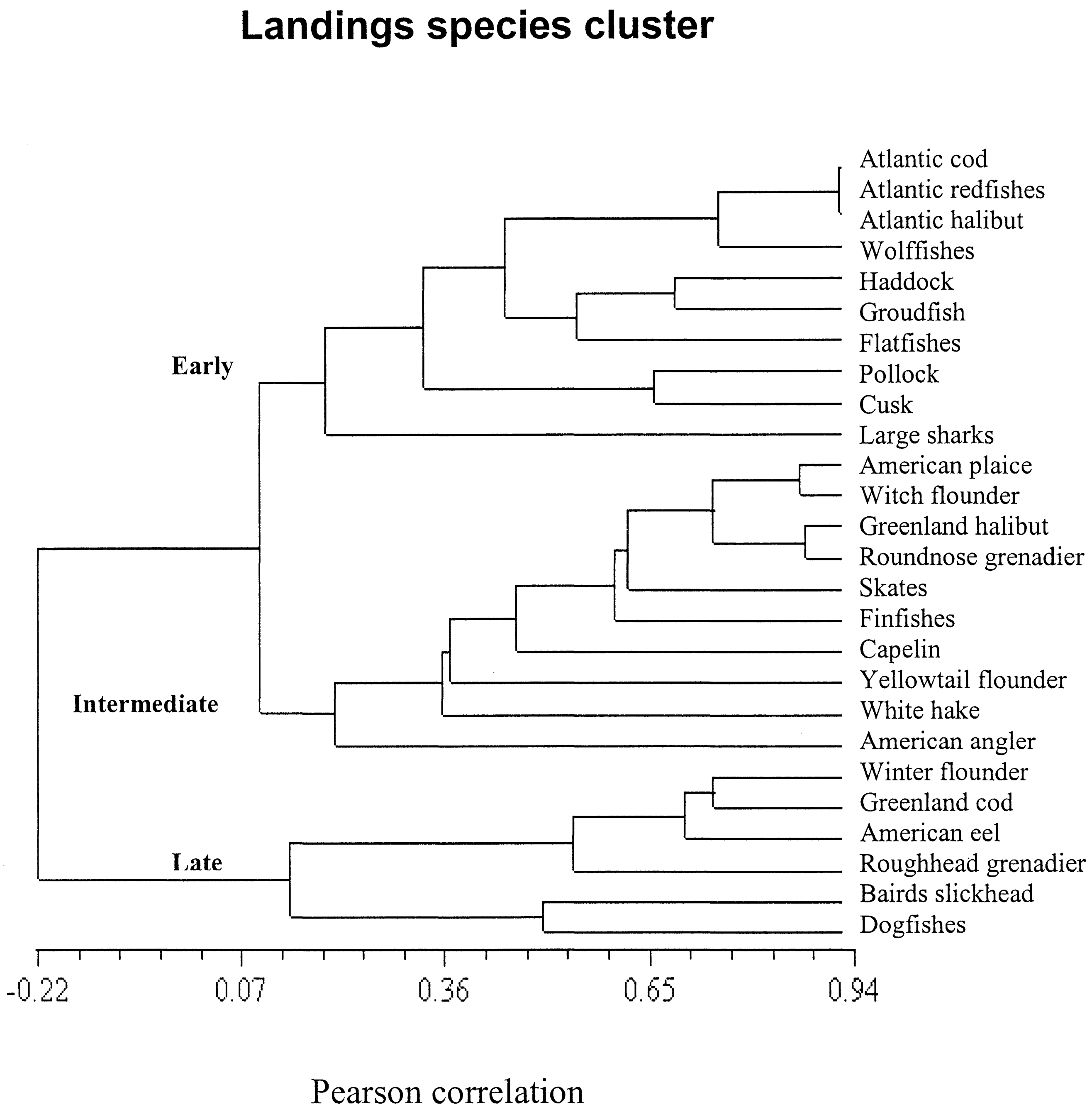
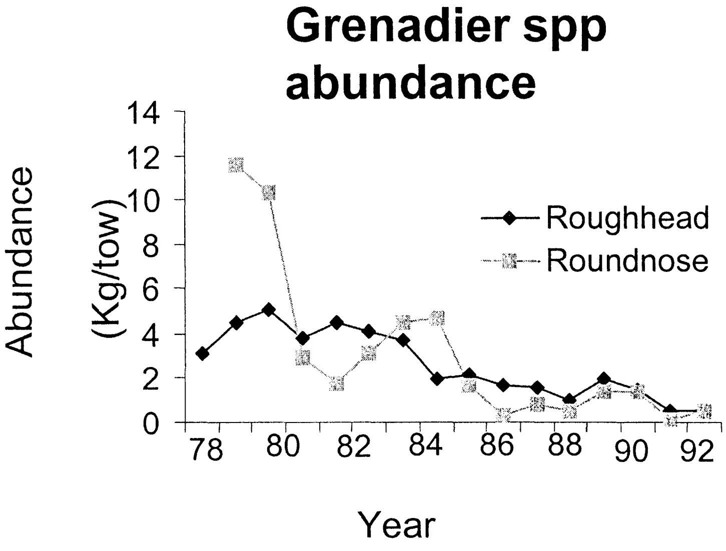


Fig. 3.7: Species groups cluster according to their similar trend over time. Index = correlation coefficient. NAFO landings data.

The first species group identified in the cluster analysis, for which the overall trend is a decrease over time, corresponds mostly to the abundant large top predators (Atlantic cod, Atlantic halibut, redfish). This group is related most closely in the dendrogram (Fig. 3.7) to the group where the abundance peak occurs in the mid-years, suggesting an intensification of captures that aims to maintain total landings. This second group is dominated by flat, deeper-living or smaller species (plaice, Witch flounder, Roundnose grenadier, capelin). Both groups differ strongly from the final group comprised of species that appear only in the last years. These species are smaller in size with respect to the other groups and less abundant (Winter flounder, Greenland cod, Roughhead grenadier, etc). This shift in effective target species (perhaps landed as bycatch) suggests an overall restructuring of the community. Since most of the species of the last cluster are not present at all in earlier years, their appearance is likely in response to the suppression of other species and an attempt to diversify in the market.

Those species that only appear in landings in the last years are covered completely in all years by survey data. Thus, we can examine whether the real trend of these species is reflected by fishery landing data. Species such as Greenland cod or Roughhead grenadier that are present in landings only in the last years (later than 1978), can be observed in all years as recorded in survey data (Fig. 3.8). Survey data show that these species are not exclusively present in only the last years of the fishery and even that their abundance has been decreasing over time. Furthermore, the time of their appearance in the fishery does not correspond to their period of greatest abundance in the survey data.



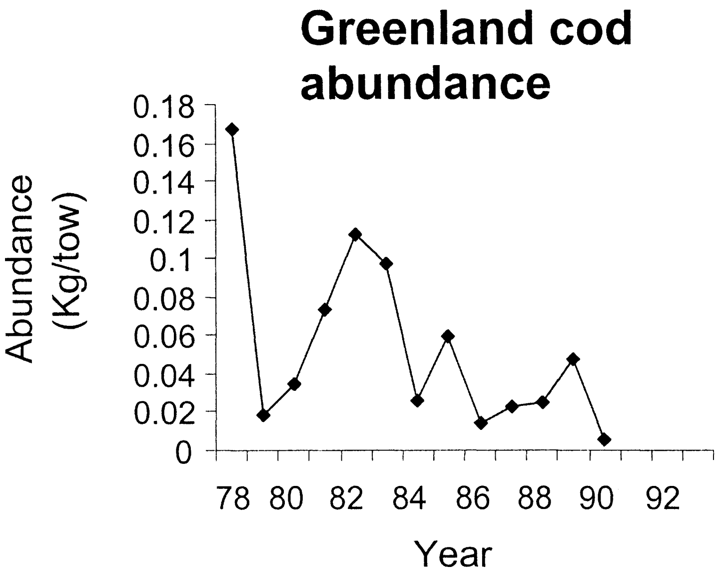


Fig. 3.8: Biomass change over time of grenadier species and Greenland cod. From survey data.

Socio-economic factors influence fishery data, which cannot be treated as scientific data. Fishery development has been the joint result of economic impositions and ecosystem restrictions. If fishery landings reflect in any way the state of the fish community, they will pertain mostly to the past. Nonetheless, the long-term trend observed in fishery data for each fish species, once it becomes targeted, is useful to bring a focus on the life history and ecology of the species as a factor to consider in the sustainability of future fisheries. Life history parameters of each species group seem to play a major role in determining how long each species group can sustain the fishery and the abundance of the catches that can be expected. Species life span, size and reproductive capacity determine the potential of any species to accumulate biomass and to renew itself.

Commercial species usually have a long life cycle. This makes it more difficult to stop their collapse once a downward trend becomes obvious, and more difficult for the stock to recover if it indeed is possible at all. In addition, the fact that commercial species occur over wide areas enlarges the impact of their removal. As they are normally top predators, the top-down effect through the food web of their removal is more dramatic. Finally, the high level of adaptation shown by these species to their habitat is also an important factor determining the possibility of recovery of the functional capacity of the ecosystem, since ecologically equivalent substitute species may not exist. The characteristics of commercial species influence the amplitude of the action-reaction cycles represented by the conceptual model of Fig. 1.1 (Chapter 1: page 4).

3.4. SUMMARY AND CONCLUSIONS

The Newfoundland demersal fish community is characterized by a marked dominance by cod. This large top predator has dominated both the groundfish community and the fishery. The high abundance of biomass accumulated in the older, large-sized individuals has sustained fishery catches over a long time. But the natural process of producing biomass is slow, especially in a long-lived species like this one, and a long time is also expected to be required to recover lost biomass. The decline of cod has unveiled important changes taking place in the fish community. Other species that are less productive or have shorter generation times have been unable to compensate for the reduction in cod catches and have themselves suffered a rapid decline once they become exploited. Even non-target species have suffered changes in abundance, indicating that disturbance of one species can spread throughout the whole community (directly as bycatch and indirectly through fish interactions), which can have implications for the future composition and structure, and ultimately the overall productivity of the fish community.

The data on total landings and diversification of captures contribute to cover up signs of perturbations in the fish community. When a perturbation occurs in a long-lived species, the time lag between the perturbation and its effect is still longer, although more dramatic. High diversity of many natural communities is usually interpreted as an indication of mature unstressed ecosystems (Müller, 1996). Landings diversity does not reflect the natural community diversity. For the Newfoundland demersal fish community diversification of fisheries more likely indicates instability of the system. For a fishery directed towards a dominant species like cod, the fishery diversifies when capture of individuals of this target species decreases, and what becomes apparent is that the fish community is being disturbed. The next chapter will consider this idea in more detail using multivariate techniques and introducing size as a relevant indicator.

Chapter 4:

Species size in relation to changes in the community

4.1. INTRODUCTION

The life cycle of a species has implications for the dynamics of that species (Chapter 3). In a first section of this chapter attention is paid to trends in the community as a whole and identification of the species that contribute mostly to these trends. Nonetheless, the dynamics of single species are influenced by their inter-specific interactions, and the community structure and dynamics represent the sum of all these interacting species. Size is a possible quantitative measure of the characteristic life cycle of each species (Bonner, 1965). Size-dependent predation is the major link among species. The hypothesis follows that size is an underlying factor accounting for the abundance of species in a community. A second section of this chapter studies the relevance of size as an indicator of the change in the relative abundance of species within the community. If the size individuals attain is an underlying factor determining the trends of species abundance, a step further will be the consideration of size groups instead of species as functional groups within the community. Chapter 5 will continue this line of inquiry with a consideration of the community size spectrum.

4.2. DATA AND METHODS

In this chapter we use scientific survey trawl data for the demersal fish community off Newfoundland as presented in Chapter 2 (Table 2.2). These data are analysed using two multivariate techniques, Multidimensional Scaling (MDS) and Principal Components Analysis (PCA). These multivariate analyses are performed using the computer package Numerical Taxonomy and Systematics (NTSYS) version 2.0. The initial row data matrix contains the standardized biomass (by tow duration) of each species at each station and for each year of the study. To track the dynamics of populations, biomass and abundance alone give little idea of changes in age structure over time. However, biomass is a better indicator when the data used come from consecutive years, because biomass is less affected than abundance by recruitment variability. Another concern would be that the use of biomass data could induce a spurious importance of size in the results of the analyses. This is not the case because at the community level it is the pattern of change instead of the biomass that is considered in the analyses. Prior to MDS analysis, data on species biomass were log-transformed to reduce the effects of wide variation in the values of the variables. The log-transformation applied was $\log_{10}$ (weight +1). For the PCA the row matrix is standardized with respect to both the total biomass of each species and the total biomass of each year. The first standardisation, by species, is done to focus attention on the relative change of species biomass rather than on absolute change, which is influenced by the difference in magnitude of the species biomass. The second standardization, by years, eliminates the influence of a possible overall continuous tendency of the community over time.

To observe the changes in the community, we applied MDS to order the survey years in a two-dimensional space based on the distances (similarity) among survey years. A distance obtained expresses the differences in species composition of the community in each year with respect to each of the rest of the survey years. The index used to estimate the distance (similarity) between any two survey years was the Bray-Curtis dissimilarity index. The reason this index was chosen is because it takes the relative change in abundance (as measured by biomass) of species into account, and those have more ecological significance than does a change simply in absolute biomass. If variation in absolute biomass is considered, changes in very abundant (as biomass) species will have more weight in the analysis than changes in less abundant (as biomass) species, even for small percentage variations of the very abundant species. As an example, a change of an abundant species from 100 to 90 in biomass is a less drastic change than a change of another species from 10 to 5 in biomass, even though in absolute terms the decrease of the latter species is half the decrease of the former one.

To analyse the contribution of each species to the changes in the community we complete the MDS analysis with a biplot in the same scale of the species that form the community following the method indicated by Legendre and Gallagher (2001). As they indicate: "To obtain biplots of species and sites [years in our analysis] from PcoA or NMDS, one can (1) compute correlations between the original species vectors….and the site [year] scores along the PcoA or NMDS ordination axes and scale these correlations as described in Eq. 14….." The Eq. 14 they refer to is:

$$\text{Species Score}_{jk} = r_{jk}\, s_j / s_k$$

where r_{jk} is the correlation between species j and year k, s_j is the standard deviation of species j, and s_k is the standard deviation of the year score vector k.

In a second section of this chapter PCA is used to explore the possibility of a link among species in the community. This exploratory analysis is intended to reveal any underlying patterns in the change of the species as a group. This analysis was followed by a correlation analysis in a confirmatory mode to identify whether the observed underlying pattern had anything to do with size. If size is an indicator of the relative abundance of species within the community, it should correlate well with the score of the species along one of the principal axes and thereby explaining much of the variance of the species dispersion in the PCA result.

The mathematical objective of PCA is to find linear combinations of the variables that best fit the data. These linear combinations (i.e. Principal Components) are selected in order according to a maximisation of the variance explained by the component. When a few Principal Components (PCs) account for most of the variance, they not only indicate interrelationship among the variables, but also continue to represent the original variables, facilitating their representation and manipulation. The matrix from which PCs are obtained is the correlation matrix of the double standardized biomass matrix of the species.

For the correlation analysis to identify size with the first Principal Component, the species size used corresponds to the usual maximum size (as length) attained by each species according to Scott and Scott (1988). Weight would be the most desirable measure of size, but available information is complete only for length. Therefore, length is the measure of size used here. This measure is allometrically related to weight (especially at maximum size), and has the advantage of not suffering variation due to food intake; i.e., once a length is attained it is assumed that the fish is not likely to shrink in length when food intake is reduced.

The correlation analysis is performed using Spearman rank correlation. For the Spearman rank correlation coefficient (r_s) we use the formula:

$$r_s = 1 - (6 \bullet \sum d^2/(N \bullet (N^2 - 1)))$$

where N is the number of pairs of ranks and d is the difference in the ranks between the two variables.

This method measures the association among variables considering their rank in the data list. Thus, we are concerned with whether or not a larger size in a species corresponds to a higher coordinate score for the species in the PC obtained from PCA. The two reasons for the use of correlation instead of regression analysis are: (1) the regression looks for a specific function to relate two variables, but the changes in the variables, although related, may not fit a specific equation, and (2) the possibility to rotate the PCs in a PCA implies a change in the value of the variable coordinates, but the order (rank) of the variable coordinates remains unchanged. Other reasons for choosing the Spearman rank correlation method are that it requires neither normality in the variables nor that any of the variables be known without error. Finally, imperfect knowledge of the maximum adult size a species can attain does not interfere with the analysis as long as the ranking of species according to size remains constant.

4.3. RESULTS AND DISCUSSION

4.3.1 MULTIDIMENSIONAL SCALING ANALYSIS

Figure 4.1 shows the two-dimensional plot from the MDS analysis. Arrows have been used to join consecutive years in order to better appreciate the trend in community change. In addition, a vector is drawn in the graph indicating the overall trend of the community during the study period. The location of each year in Fig. 4.1 corresponds to the community structure of that year, according to species composition and abundance (as biomass), in relation to the structure in the rest of the years. The community follows a continuous departure from its initial situation, entering a period of substantial yearly changes in the 90s. Superimposed on this overall diverging trend are two cyclic changes, one from 1979 to 1983 and the other from 1987 to 1990. The years of the survey data coincide with the time leading up to the fishery collapse in 1992, when drastic changes in the community structure could be expected and appear to be reflected in the MDS plot. The community seems to be changing at a rate that increases over time. The random stratified survey was initiated in 1978, and thus most probably the earlier survey data reflect learning and adjustment to methodology. If the point corresponding to 1978 in the MDS plot is considered an outlier, the community can be considered in a more-or-less stable state in the initial years of the analysis. From those initial conditions the community appears to change and move away at an ever-increasing rate.

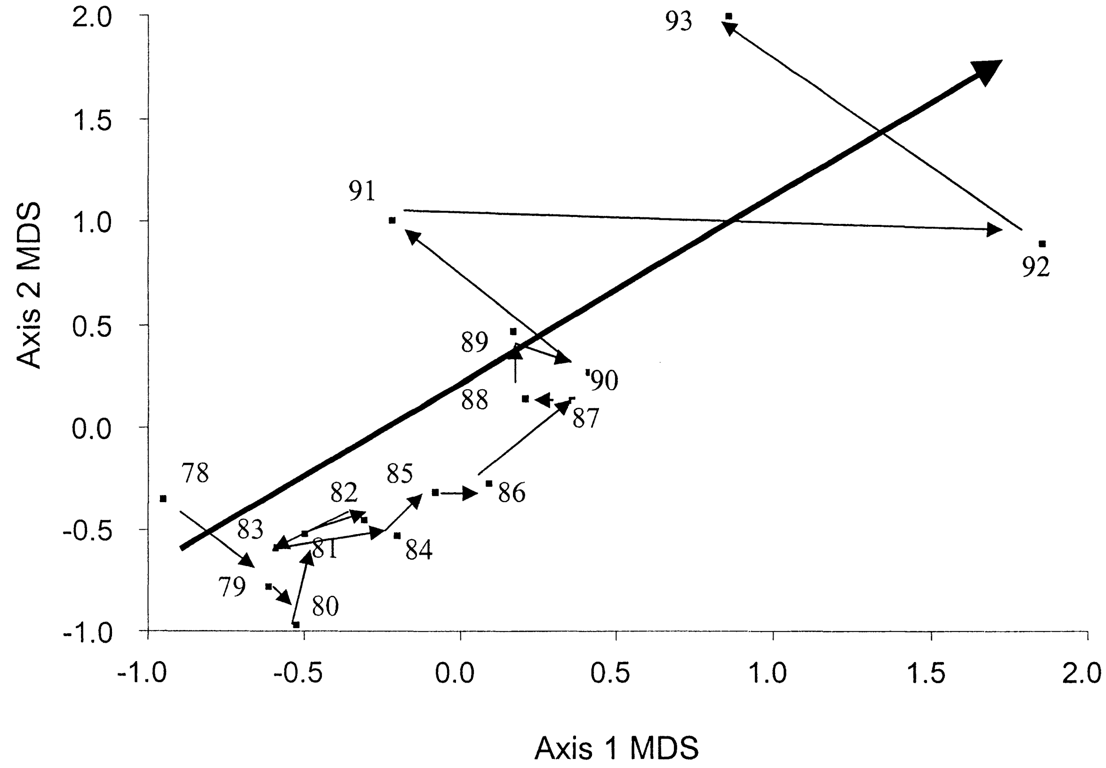


Fig. 4.1: Two-dimensional MDS plot representing demersal fish community dynamics from 1978 to 1993. Small arrows show the annual trend and the heavier arrow show the overall trend.

The causes of the pattern observed in Figure 4.1 can possibly be explained by the plot axes. The first MDS plot axis can be considered a "size factor", i.e. it reflects a continuous decline over time of community biomass, especially tracking the cod decline. The second axis appears to discern between target species, with the highest negative loading for target species and a positive loading for non-target species (Table 4.1). The two axes are highly correlated as shown by the similar loading values for each species on both axes. This high correlation responds to the fact that target species are also the ones that drive the community biomass decline. To confirm this interpretation the contribution of each species to the community change is graphically represented in another MDS plot (Fig. 4.2).

Table 4.1 Species coordinates (equivalent to loadings) in the MDS plot.

Species common name	Axis 1 loading	Axis 2 loading
Deep Water Redfish	-0.72478	-0.69363
Atlantic Cod	-0.54037	-0.49016
Broadhead Wolffish	-0.49527	-0.48600
Atlantic Halibut	-0.45446	-0.43256
Golden Redfish	-0.39395	-0.38184
Witch Flounder	-0.38837	-0.38373
Spotted Wolffish	-0.29796	-0.24012
Greenland Halibut	-0.28142	-0.28308
Arctic Deepsea Sculpin	-0.25552	-0.28292
Striped Wolffish	-0.24581	-0.23207
Roughhead Grenadier	-0.24296	-0.23120
Thorny Skate	-0.18244	-0.16682
Spinytail Skate	-0.16791	-0.17265
Vahl's Eelpout	-0.16339	-0.11772
Smooth Skate	-0.12487	-0.10747
Black Dogfish	-0.08534	-0.12277
Arctic Eelpout	-0.07966	-0.02790
American Plaice	-0.05023	-0.05781
Common Lumpfish	-0.04756	-0.04362
Blue Hake	-0.03626	-0.04565
Capelin	-0.03523	-0.04925
Large Scale Tapirfish	-0.02026	-0.03318
Greenland Cod	-0.01785	-0.01211
Esmark's Eelpout	-0.01356	-0.01123
Shorthorn Sculpin	-0.00646	-0.00179
Common Marlin Spike	-0.00438	-0.00700
Longnose Eel	-0.00088	-0.00192
Common Alligatorfish	-0.00061	-0.00017
Roughnose Grenadier	-0.00055	-0.00083
Northern Alligatorfish	0.00044	0.00226
Roundnose Grenadier	0.0191	0.0799
Spiny Lumpfish	0.0359	0.0400
Arctic Cod	0.5864	0.4857

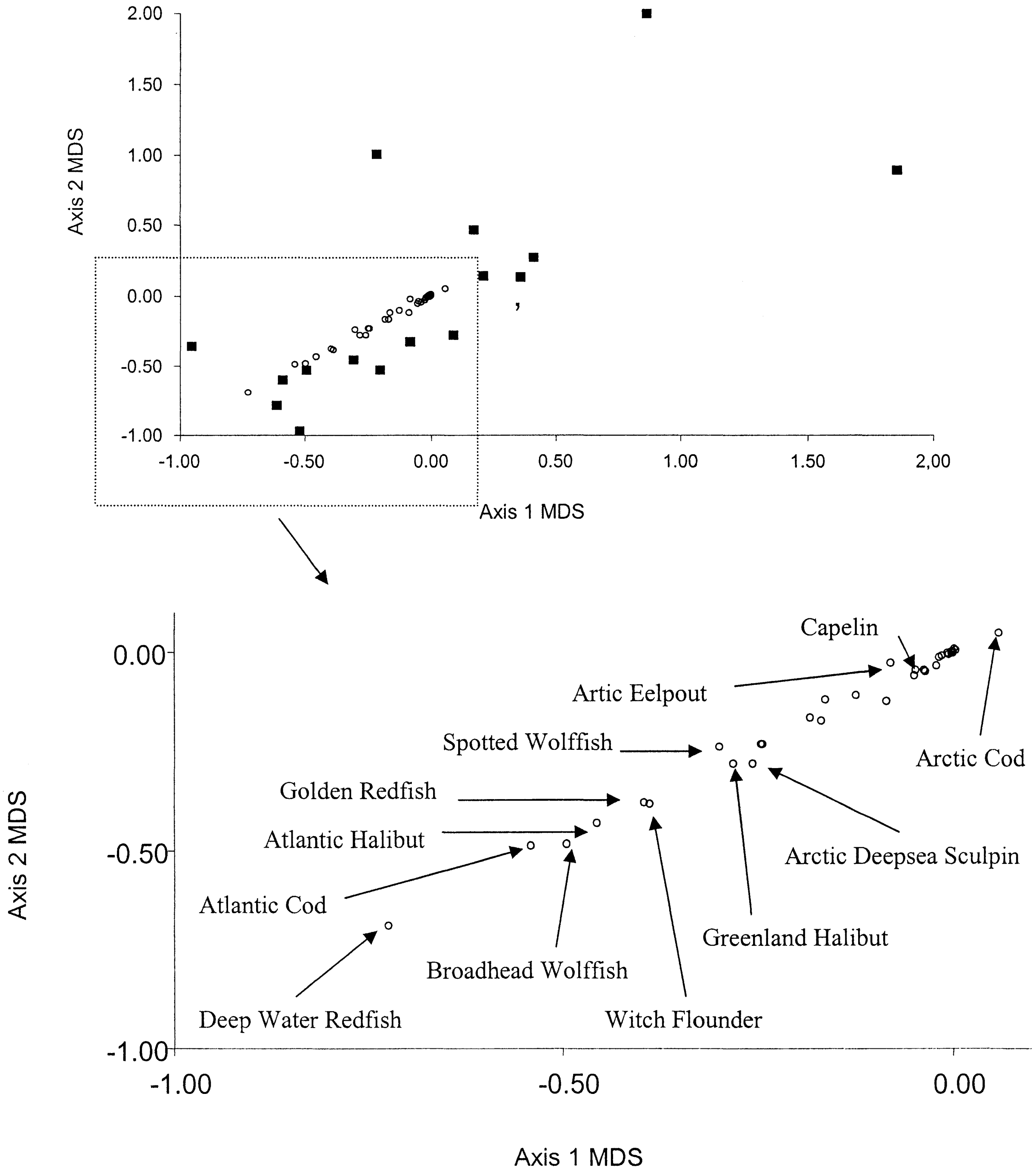
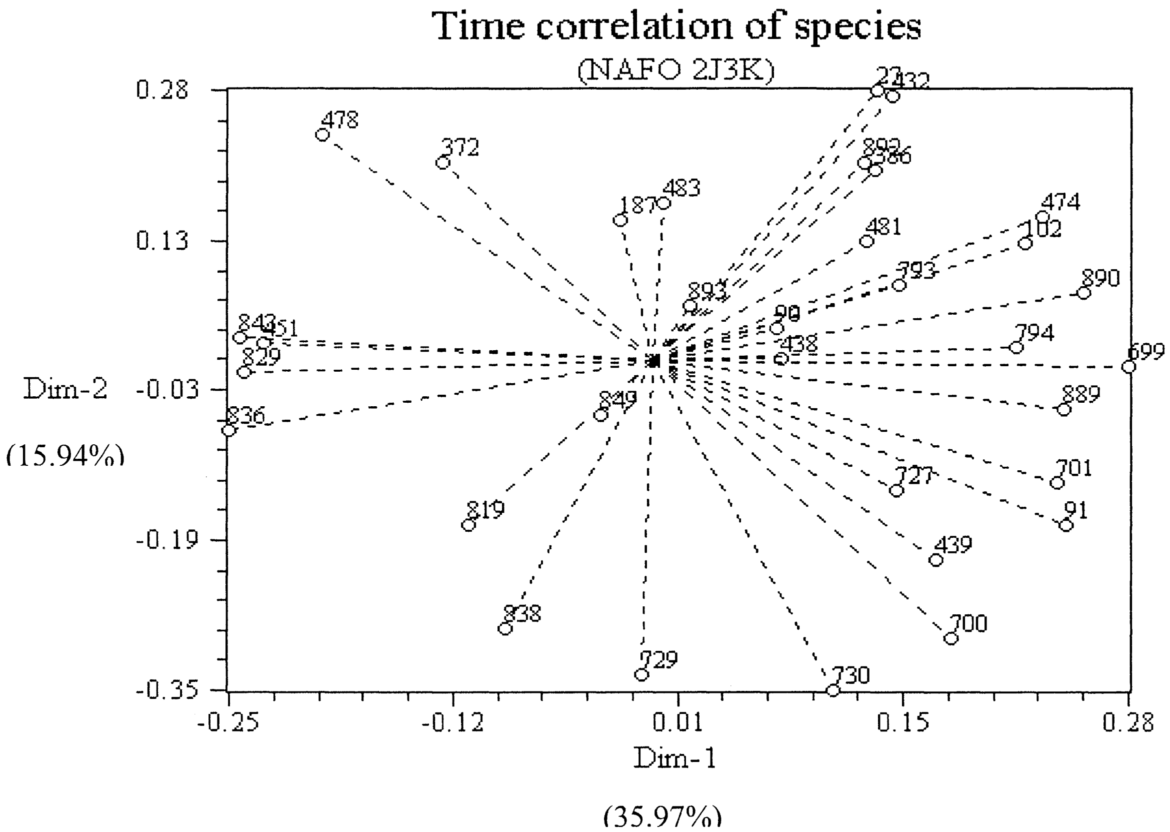


Fig. 4.2. Species representation in the MDS space. Upper: MDS plot with open circles representing species and solid squares the years as in Fig. 4.1. Lower: Detail of the section containing the species. Only species, not the years, are represented and the common name for some is indicated.

The plot of species along the same axes obtained for the years by MDS gives an idea of the species that contribute most to the community in one year or another. Fishery-targeted (Atlantic cod), large (Broadhead wolffish) or long lived (Deep water redfish) species were characteristic of the community in the first years of the analysis. Biomass reduction of these species directs the trend of the community over time. The fact that most species cluster in the mid years of the analysis and no species appear related to the last years indicates that no species compensates for the decline of large species. In an exploited fish community where the fishery is size selective, as is the case for the demersal fish community off Newfoundland, it is not surprising to find large fishery species implicated in the community changes. However, abundance and size changes are observed in both fishery target and non-target species (Haedrich and Barnes, 1997).

4.3.2 PRINCIPAL COMPONENTS ANALYSIS

In order to detect whether there is a structure underlying the species changes over time, PCA was applied. The results of this analysis gave two main factors that explain 35.9% and 15.9% of the variation in the species over time. The plot of the coordinates (factor scores) of the species on the axes defined by these two factors is shown in Figure 4.3.



	Eigenvector 1	Eigenvector 2
Eigenvalue	11.87	5.26
% of Variance explained by eigenvalue	35.97	15.94
Cumulative % of total variation	35.97	51.92
Variance expected with broken-stick method	12.39	9.36

Fig. 4.3. Two-dimensional plot of the results of PCA and a table of the variation explained by each PC. For the clarity in the graph, scientific code (Table 2.2, Ch 2: pg 28) has been used to identify the species location instead of species name.

NTSYS performs a significance test for the equality of all roots or the equality of all but the first root, which will indicate absence or homogeneous correlation among variables. However, this significance test produced results not applicable in our study due to the sample size. Since the analysis begins with only 16 observations (years), this limits the maximum number of dimensions, i.e., principal components, to 16. This implies that 17 of the 33 variables (species) we have are indeed linear combinations of the others. Therefore the total variance of the data must be contained in no more than 16 dimensions. Nonetheless, it is still remarkable in our demersal community that the two first PCs alone explain 51.9% of the total variance in the data, and both explain greater variance than would be expected by chance alone, according to the broken-stick method (Fig. 4.3). The idea of this test (Legendre and Legendre, 1983) is to consider a stick formed from all the PCs and to randomly break this stick into as many PCs as were considered in the PCA and to compare whether their variance is greater than that of the observed PCs. In addition, the small sample size only limits the generality of the analysis (Jolliffe, 1986), but not the description (visualisation) of the samples. Nonetheless, generalizations from these results should be stated with caution because of the sample size involved.

Why are the species distributed the way they are in the PCA (Fig. 4.3)? The first PC accounts for 35.9% of the variance. This indicates the presence of a factor that may relate all species (variables) and therefore may underlie the trend of changes over time. The loading of some species on this first PC suggests that the underlying factor may be the size that the species can attain during their full life span. Small species (Northern alligatorfish, Spiny lumpfish, Arctic cod) tend to have high negative loadings and large species (Broadhead wolfish, Spinytail skate) have some of the highest positive loadings (Table 4.2).

Table 4.2: Coordinate and loading of each species on the first two PCs obtained by PCA. Species ordered by their loading on the first PC.

Species common name	PC axis 1	PC axis 2	Load PC1	Load PC2
Northern Alligatorfish	-0.253	-0.074	-0.873	-0.169
Spiny Lumpfish	-0.247	0.023	-0.852	0.052
Roundnose Grenadier	-0.245	-0.014	-0.842	-0.031
Arctic cod	-0.233	0.018	-0.802	0.042
Common Marlin Spike	-0.198	0.238	-0.681	0.545
Longnose Eel	-0.125	0.209	-0.431	0.480
Shorthorn Sculpin	-0.109	-0.171	-0.377	-0.393
Common Alligatorfish	-0.088	-0.280	-0.303	-0.642
Common Lumpfish	-0.031	-0.058	-0.106	-0.133
Capelin	-0.019	0.148	-0.065	0.340
Arctic Eelpout	-0.007	-0.329	-0.024	-0.753
Roughnose Grenadier	0.006	0.166	0.021	0.382
American Plaice	0.023	0.057	0.078	0.130
Thorny Skate	0.073	0.034	0.253	0.078
Atlantic Cod	0.077	0.002	0.264	0.004
Vahl's Eelpout	0.108	-0.345	0.372	-0.791
Spotted Wolffish	0.125	0.209	0.432	0.479
Arctic Deepsea Sculpin	0.127	0.126	0.437	0.288
Large Scale Tapirfish	0.133	0.200	0.457	0.459
Black Dogfish	0.133	0.283	0.459	0.650
Blue Hake	0.142	0.277	0.490	0.635
Esmark's Eelpout	0.145	-0.135	0.501	-0.311
Deep Water Redfish	0.146	0.080	0.503	0.184
Greenland Cod	0.168	-0.209	0.578	-0.479
Greenland Halibut	0.177	-0.291	0.610	-0.666
Golden Redfish	0.216	0.014	0.744	0.031
Spinytail Skate	0.221	0.124	0.760	0.284
Roughhead Grenadier	0.231	0.153	0.796	0.350
Striped Wolffish	0.240	-0.127	0.828	-0.291
Atlantic Halibut	0.244	-0.050	0.841	-0.116
Smooth Skate	0.246	-0.171	0.849	-0.392
Witch Flounder	0.256	0.072	0.881	0.164
Broadhead Wolffish	0.283	-0.006	0.976	-0.014

At this stage, two points should be clarified to be sure that the relation among PC results and species size is not an artefact: (1) the use of biomass data, and (2) the possibility of the PC being a “size factor" (following the terminology of Principal Components Analysis).

In respect to point 1.- We have performed PCA starting with a row matrix of biomass data. Therefore, it could be thought that these data force the results to be related somehow to species size. However, the result of PCA and the position of each species along the PCs is not the result of species biomass, but the result of how that biomass changes over time. That change is independent of the actual amount of the biomass. Two species of very different absolute biomass can follow the same trend over time and so will appear together in the PCA.

In respect to point 2.- When the overall (summed values of all) value of variables changes in a continuous way (increasing or decreasing) across the observations, the first PC collects this overall trend and do not differentiate between variables (species in our case). An overall decrease in biomass over the observed period has occurred in the demersal fish community of Newfoundland (see Fig. 3.2) . One of the standardizations mentioned in Section 4.2 is performed to eliminate this trend which could influence PCA results. By standardizing the original matrix of species biomass by the total biomass of the community each year, the sum of species biomass adds up to 1 for all years. Thus, the overall trend over time is eliminated. However, the relationship among species regarding their tendency of change over time is maintained.

In order to test the hypothesis that species size is the underlying factor for the observed species trend, we apply the Spearman rank correlation analysis between species size and the first PC scores. The maximum length each species can attain enters the variable ‘species size’, and the coordinates of each species from PCA enter the variable ‘1^{st} PC’. The result of the correlation is $r_S = 0.58$. This result is contrasted with the significance test that assumes as a null hypothesis that the correlation between species size (length in this case) and 1^{st} PC is zero. To do this it is considered that the random variable $r_s\sqrt{(N-2)/(1-r_s^2)}$ follows a t distribution with N-2 degrees of freedom. In this study the value of $r_s\sqrt{(N-2)/(1-r_s^2)}$ is 4.01, greater than $t_{31,0.05}$ (=2.03). Therefore, the null hypothesis can be rejected with 95% confidence, and the premise that the first PC reflects species size is accepted. Ranks and distances of species size and the first PC are shown in Table 4.3.

The Spearman rank correlation coefficient (r_S) for these data indicates a significant correlation of size with the first PC. This result supports the implication of size as an underlying factor in the species interrelations and community change over time. The structure of the community is based on species interrelations, which are known to be based on size trough the food web. Therefore, a constant perturbation limiting the maximum size a species can reach will induce changes in species links and relationships. Functional groups based on size rather than taxonomic species might then usefully represent and reconstruct the structure and dynamics of the community.

Table 4.3: Species size, species rank according to size and to 1st PC co-ordiante, and the distance (d) and squared distances (d^2) used in the Rank correlation analysis. Size data from Scott and Scott (1988).

Species common name	Sp size (cm)	Rank of size	Rank of species on first PC	d	d^2
American Plaice	155	33	13	20	400
Arctic Cod	25	4	4	0	0
Arctic Deepsea Sculpin	100	26	18	8	64
Arctic Eelpout	75	20	11	9	81
Atlantic Cod	120	30	15	15	225
Atlantic Halibut	81	22	30	-8	64
Black Dogfish	84	23	20	3	9
Blue Hake	65	17	21	-4	16
Broadhead Wolffish	143	31	33	-2	4
Capelin	25	5	10	-5	25
Common Alligatorfish	18	2	8	-6	36
Common Lumpfish	50	12	9	3	9
Common Marlin Spike	40	9	5	4	16
Deep Water Redfish	46	11	23	-12	144
Esmark's Eelpout	63	16	22	-6	36
Golden Redfish	46	10	26	-16	256
Greenland Cod	70	18	24	-6	36
Greenland Halibut	90	25	25	0	0
Large Scale Tapirfish	25	6	19	-13	169
Longnose Eel	74	19	6	13	169
Northern Alligatorfish	23	3	1	2	4
Roughhead Grenadier	100	27	28	-1	1
Roughnose Grenadier	38	8	12	-4	16
Roundnose Grenadier	30	7	3	4	16
Shorthorn Sculpin	50	13	7	6	36
Smooth Skate	61	15	31	-16	256
Spiny Lumpfish	12	1	2	-1	1
Spinytail Skate	152	32	27	5	25
Spotted Wolffish	90	24	17	7	49
Striped Wolffish	107	29	29	0	0
Thorny Skate	102	28	14	14	196
Vahl's Eelpout	51	14	16	-2	4
Witch Flounder	78	21	32	-11	121
					2484

The tendency for species to be distributed along the first PC according to their body size (length) can be visualised by a scatter plot of the species using the rank of species by size *vs.* the rank of species by loading (score) on the first PC (Fig. 4.4). Despite the tendency observed, the correlation is not perfect, and that is in addition to the the only partial explanation (35.9%) of the changes observed by the first PC. However, the difficulty of obtaining unambiguously clear results in ecological studies must also be borne in mind (Chapter 1). When dealing with ecosystems many interacting factors are involved, resulting in a great deal of noise when trying to isolate any one of them. Furthermore, when species are under fishery and large individuals are continuously removed the maximum size of the individuals present is being changed. This supports the idea of looking at the community as integrated by size-based functional groups instead of as species-based functional groups, an idea that will be developed in the next chapter.

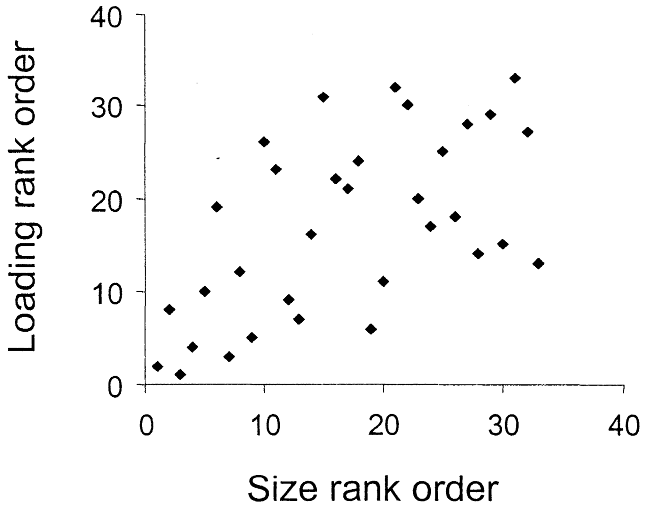


Fig. 4.4: Scatter plot of species considering their size (length) and their location along the first PC. There is a rough tendency of the species to fall along the first PC according to their size (larger species - larger loadings). Data in Table 4.3.

4.4. CONCLUSION

The demersal fish community off Newfoundland has changed from 1978 to 1993. Targeted, large-sized species seem to drive the dynamics of a disturbed community by changes in their biomass abundance over time. Other more conventional studies of the same community showed that both target and non-target species have undergone change. The present study reveals the importance of a common factor that is related to the changes of species over time. This factor is identified with species size, supporting the idea that size is involved in species interrelationships as well as in their changes in response to disturbance. Thus, the size attained by individual component species is related to structure at the community level. If sizes of individuals are changed the whole structure and interactions of the community will be changed. With this in mind, we can now move to consider size as a simplifying factor to analyse community dynamics.

Chapter 5:

Fish community size spectrum change over time

5.1. INTRODUCTION

Allometric processes at the individual and population levels make body size a good indicator of species dynamics (previous chapters). Due to the ontogenetic change in size and diet in fish, when species form a community the trophic interactions might be better regarded as interactions between different size groups of individuals rather than as interactions between different species (Dickie et al., 1987; Jennings et al., 2002). When thought of in this way, the classical representation of a food web as linkages between many species becomes a simpler diagram of linkages between size classes. When individuals are associated according to size instead of by species to form functional groups, then the size structure can be considered an emergent property of the fish community (Salt, 1979; Thiebaux and Dickie, 1993).

The first observation of a biomass size-spectrum in the marine environment is attributed to Sheldon et al. (1972). They observed the distribution of particle sizes ranging from 1 to 100 μ and found that biomass presented roughly the same concentration across logarithmically equal size intervals. They then extrapolated this idea to include all sizes, including fish and whales. Their observation implies a decrease in the number of particles with increasing size. Since this observation, many authors have tried to explain the reason for that pattern (Platt, 1985; Marquet et al., 1990, 1995; Lawton, 1990;

Blackburn and Gaston, 1994). Sheldon et al. (1972) had already mentioned the implication of the size distribution for the food chain and many authors have looked into energetic requirements and trophic processes within the community to explain the cause of the size-spectrum general pattern (Kerr, 1974; Boudreau et al., 1991; Thiebaux and Dickie, 1993; Cohen et al., 1993). However, the causes suggested have been debated (Marquet et al., 1990, 1995; Blackburn et al., 1993). Theoretically grounded or just empirical, the negative relation between density and size have proven useful to compare different communities (Leaper and Raffaelli, 1999; Haedrich, 1997, MacPherson and Duarte, 1994), the same community over time (Pope et al., 1994) or the effects of disturbance on a community (Gislason and Lassen, 1997; Rice and Gislason, 1996; Bianchi et al., 2000). Later in this thesis, in Chapter 7, size spectra will be proposed as a means to verify and validate the size-based modeling of the dynamics of a fish community that will be presented in Chapter 6.

Size dependency is the main characteristic governing predator/prey relationships in a demersal fish community. Thus, continuous growth that begins from a generally similar larval size but reaches very different adult sizes changes the trophic interactions between species over time, and makes it a process that takes place among size groups within the community rather than strictly among species of the community. The importance of size-dependent predation in fish communities is twofold. Predation is the main cause of mortality in fish and, at the same time, the main link among fish individuals. As a result of this size-dependent interaction the community is size-structured and this size structure reflects the organization of individuals in successive trophic levels.

If the trophic chain of the community is represented by its size spectrum, the different density of individuals between two consecutive size groups indicates the transfer of biomass (and therefore energy) between trophic levels. At the same time, the magnitude of abundance of the smallest size groups indicates the potential productive capacity of the community (Rice and Gislasson, 1996; Bianchi et al., 2000).

Next we use survey data to describe the size spectrum change over time of the demersal fish community off Newfoundland and discuss the future implication of these changes for the fish community and the fisheries. The terms size group and size class have the same meaning and are used interchangeably here.

5.2. DATA AND METHODS

A size spectrum is the distribution of a community attribute as a function of body size. The attribute we focus on is the density in number of individuals. As for size, it is measured as weight. It is important to make it clear that the community is considered as a whole unit in which individuals are not further subdivided into species. Thus, individuals will be grouped together when they share the same size (weight) at the moment of data collection and regardless of the species they belong to.

However, in doing this we face a problem: the data available to us do not allow that fine a resolution. Species data used for the analysis are those first introduced and explained in Chapter 2 (Fig. 2.2). The row data matrix for each survey year presents the number of individuals and their added biomass for each species in each station sampled. The biomass of each single individual (i.e. size frequencies) within a certain species is not at our disposal.

We approximate using mean size. A rough estimation of size as weight for the individuals of each species in each station is obtained by dividing the biomass of the species by the number of individuals in each station. This average size is biased towards the smallest sizes due to the inverse relation between density and size of individuals. A sample is more likely to have a larger number of individuals of small sizes than of large ones. Despite this bias, the results comparing the fish community size spectra from several years is not going to be affected because the same bias applies to the way we obtain the size spectrum in all years.

For each one of the 16 survey years (from 1978 to 1993) the number of stations sampled was between 125 and 353. The steps towards obtaining the size spectrum of a certain year start with the estimation of average size of the individuals of each species in each station as mentioned above. This measure is then used to distribute the individuals of all stations into size classes. At this step no consideration of species is taken. Therefore, the number of individuals in each final size class is the sum of all individuals of all stations for which the calculated average size (as weight) falls within the corresponding size class. The total biomass in that size class will be the addition of the biomass of all individuals of all species in that size class. Once individuals are distributed among size classes, individuals of the same species may appear in several size classes and individuals of different species are present in the same size class.

The graphical representation of a size spectrum varies depending on the scale in which the axes are expressed and the scale at which size classes are defined. In this chapter equal width size classes of 500 g each over a range from 0 to 12000 g are considered, i.e. there are 24 size classes. The results are plotted on a logarithmic scale for both abundance (y-axis) and size class (x-axis). The width of size classes has been choosen to avoid as much as possible the presence of densities equal to zero (explained below). Nonetheless, this value is present on several occasions and presents a problem for logarithmic transformation. To deal with this problem the logarithm is referred to the density +1. Another problem then appears when the density has values between 0 and 1 (very frequent in our data), since the addition of 1 would change the distance among them in the logarithmic scale. To solve this problem we determine the density as the number of individuals per 1000 tows. Thus, all densities are either 0 or greater than 1 before the unit is added and the $\log_{10}$ calculated.

A regression line can be associated with each size spectrum. This linear size spectrum regression has the advantage of providing two parameters, the slope and the intercept, that can be used to compare the changes over time of the community size spectrum. In addition, these parameters have a biological meaning as indicators of the mortality (slope) and production (intercept) of the community (Rice and Gislasson, 1996). If the community were at equilibrium, the slope that indicates mortality in passing from one size group to the next would be as well an indicator of the energy transfer efficiency, since the biomass lost in a level can be thought of as maintaining the biomass in the next higher level. Many ecology texts refer to this value as "ecological efficiency". Furthermore, linear size spectra allow statistical tests to resolve whether changes observed in the size spectrum of the community over time are significant or might be produced simply by sample variability.

The intercept is taken because it represents the abundance for the smallest possible size, i.e. when the size is the unit. The smallest size class for us is that of individuals between 0 and 500 g, which has a mean of 250g. Therefore, the value of our regression line for the size spectrum at 250g will be considered as the intercept. Otherwise the value will be well outside our data range.

Data manipulation may influence the results of the size spectrum analysis (Blanco et al., 1994; Vidondo et al., 1997). One of the factors that has an effect on the resultant linear regression of the size spectrum is the presence of size classes with 0 density. Sizes larger than 12000g are rare in the demersal community off Newfoundland during the time frame in which the community data were recorded. This is the reason why individuals with an estimated weight greater than 12000 g were not included in the analysis. This avoided possible distortion in the shape of the spectrum and in the values of the regression parameters.

To describe the changes in the community we first construct the size spectrum for each survey year and then analyze the changes observed over time. Changes in each size group alone and the relative importance of each size group in each year considered are also developed, and are used to explain the trend of the community and its implications.

5.3. RESULTS AND DISCUSSION

Figure 5.1 shows the size spectrum of the community for each of the 16 years of the survey. The magnitude of the left-hand side of the spectrum (smallest size classes) tends to decrease somewhat over time. Even more dramatic is the decrease suffered by the largest size classes at the right-hand side of the spectrum. Linear regression of $\log_{10}$ density+1 *vs.* $\log_{10}$ weigth+1 facilitates the comparison between years as shown for 4 of the 16 size spectra presented again in Figure 5.2. These four years separated by a 5-year time lag from one another are representative of the community changes over the entire study period. Table 5.1 shows the parameters and regression coefficient for the regression line of the community size spectrum in each one of the 16 years of the survey. A statistical test (ANOVA test for differences among slopes) to determine whether the slope of the size spectrum is significantly different over time shows a significant difference among slopes of the community size spectrum during the study period (Table 5.2).

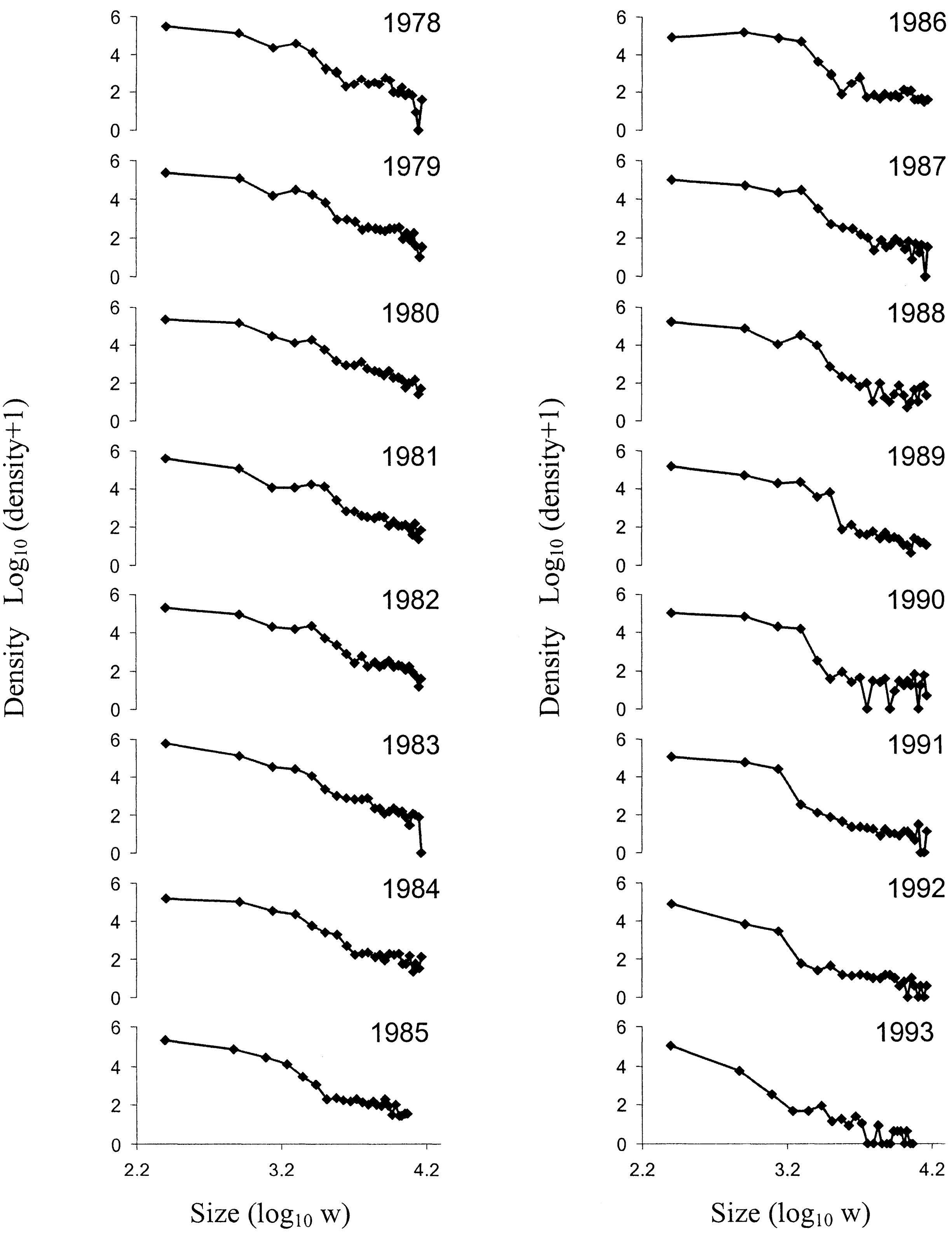


Fig. 5.1. Size spectrum of the demersal fish community during the 16 years of survey. Density = No of individuals/1000 tows, w = average weight of size group.

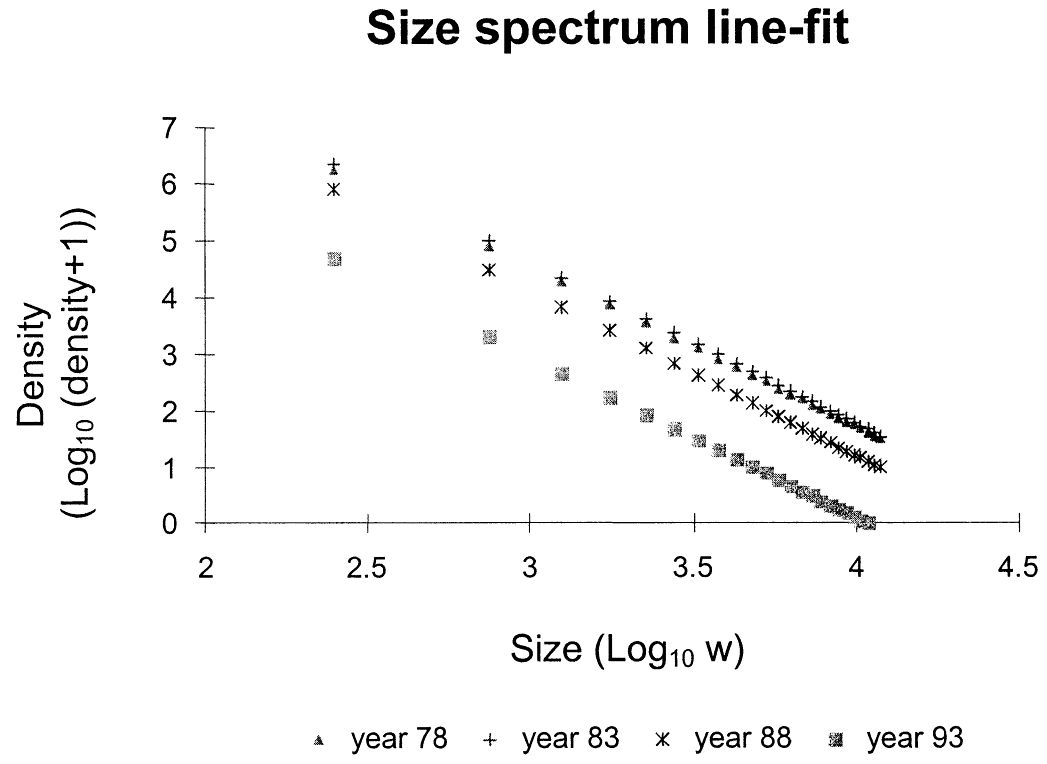


Fig. 5.2. Linear regression of the community size spectrum for years separated in 5-year time intervals.

Table 5.1. Size spectrum regression fit parameters for each survey year.

Year	Slope	Intercept y(x=250)	R2
78	-2.82	6.23	0.84
79	-2.56	6.07	0.9
80	-2.5	6.06	0.93
81	-2.59	6.12	0.93
82	-2.5	5.98	0.91
83	-2.86	6.38	0.88
84	-2.52	5.89	0.9
85	-2.54	5.72	0.92
86	-2.64	5.83	0.82
87	-2.82	5.81	0.85
88	-2.93	5.89	0.82
89	-3.05	6.00	0.87
90	-2.86	5.44	0.71
91	-2.97	5.37	0.86
92	-2.69	4.68	0.89
93	-2.87	4.67	0.89

Table 5.2. Statistical test for difference among slopes. The size spectrum slope varies significantly over time.

source of variation	df	SS	MS	Fs	p
among b's	15	463.0476	30.86984	100.2517	0.0000
weighted avg deviations	352	108.389	0.307923		

As mentioned above, the intercept of the size spectrum regression line is an indicator of the production of the system. This is so because the intercept value corresponds to the abundance of individuals in their first life stages. For the purposes of this chapter the intercept is taken to be the y-axis value for the smallest size group, i.e., intercept = y value when x = 250g. Loss in abundance from one size to another forms the slope of the spectrum and corresponds to fish mortality (=slope of the regression) that in an equilibrium community reflects the energy transfer efficiency through the food chain and in a community under fishery is an index of fishing exploitation rate. Considering these two parameters of the size spectrum, the community overall trend over time is towards a lower productivity and greater fishing stress over time (Fig. 5.3).

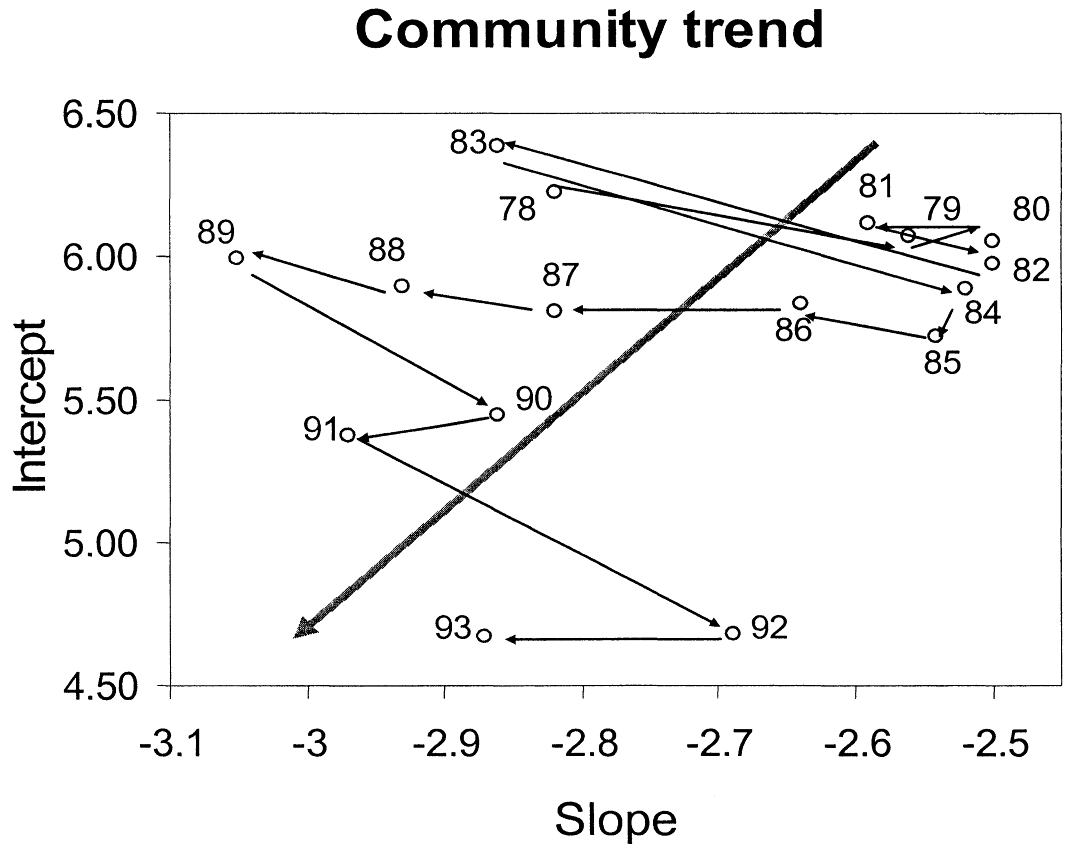


Fig. 5.3. Plot of the distribution of years according to intercept (y-axis) and slope (x-axis) of their corresponding linear size spectrum. The arrow indicates the overall trend of the community over time with respect to those two parameters. The ecological meaning is that the community is becoming less productive and less efficient or more exploited over time.

Rice and Gislasson (1996) argued that the removal of the largest individuals by a fishery is expected to result in a more negative slope of the size spectrum regression line, which becomes steeper and consequently raises the intersection intercept point. Similar changes could be hypothesized for the Newfoundland demersal community, since the period in which survey data for that community are recorded correspond to a time during which the fish community has been under strong fishery pressure and eventually leading to a collapse. Instead, the empirical data from the Newfoundland fish community shows a slight increase over time in the steepness of the size spectrum slope (i.e. the slope becomes more negative in value), and also shows a high variability for the intercept but with an overall decreasing trend (Figure 5.4). It is only during the period from 1985 to 1989 that the trend for the slope and intercept match the expected pattern under fishing pressure as suggested by Rice and Gislasson (1996). For the whole study period, the observations are not conclusive regarding the effect of fishing pressure. A reason for the fluctuations of the intercept can be that recruitment is not constant over time because reduction in the number of the largest-sized individuals will reduce the number of recruits. In any case, the test determining whether the slope of the community size spectrum varies over time (Table 5.2) indicates that the community is in fact changing in respect to size-spectrum parameters.

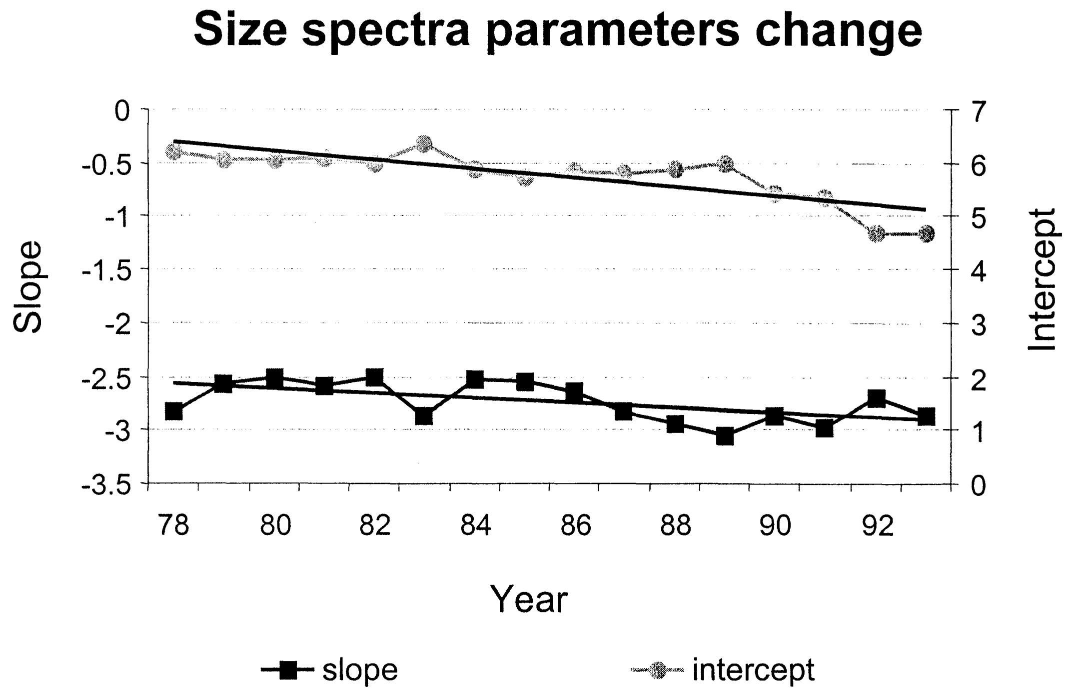


Fig. 5.4 Trend followed by the size spectrum parameters of the fish community. The intercept represents the productivity of the community. The slope may reflect fishing pressure. Despite the fact that there is no clear trend, the intercept follows an overall decline as the slope steepness over time.

It can be argued that these results indicate the independence between fisheries and the drastic changes affecting the fish community or that the complexity of fish-fisheries interactions prevents fishing pressure from being clearly reflected by size spectra analysis. Nonetheless, before rushing to these conclusions it is worth taking a closer look at the size spectra obtained from survey data.

The hypothesis that under fishery pressure the size spectrum parameters (slope and intercept) increase in absolute value over time as stated by Rice and Gislason (1996) may well correspond to the changes over time of the community from 1985 to 1989, when removal of large individuals becomes noticeable. Continuation of the fishing pressure affects offspring production and a decrease in the intercept of the size spectrum may therefore be expected, as is the case observed in our Newfoundland demersal fish community since 1989. Thus, our observations can be interpreted as being in accord with the hypothesized effects of fishing pressure.

If attention is paid to the changes of each single size class (Figure 5.5), we see that the density of individuals in every size group is decreasing over time. The larger size groups are the ones that disappear first from the community since the fishery targets them. The sporadic peaks in density that appear in a size group during the course of an overall density decrease may be explained by the high recruitment of individuals from smaller size groups in the years corresponding to the peak. As an example, in Figure 5.5 this argument can be used to relate the peak in density observed in 1983 for size class 1 (250g) with that observed in 1986 in size groups 3 and 4 (1250g and 1750g respectively). The strong cohorts that produced the high density of size class 1 in 1983 would have grown to give the 1986 peaks for size classes 3 and 4. The reason why the peak does not appear in size class 2, might be interpreted as a consequence of the variation in the residence time of individuals in each size group, which depends on the growth rate of each species involved.

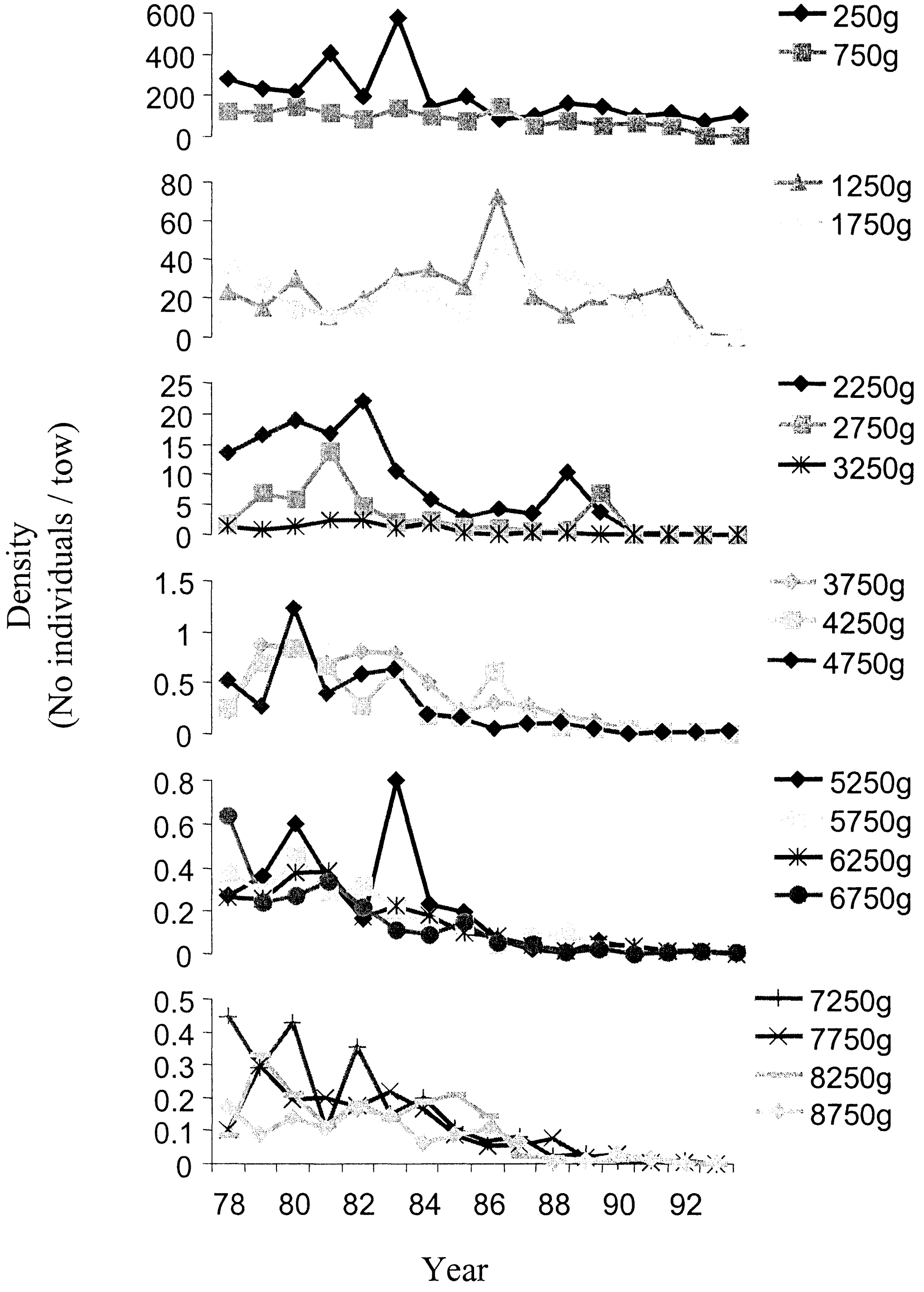


Fig. 5.5. Change over time of the first 17 size groups of the community. Groups are arranged from the smallest at the top to the largest at the bottom. Different y axis scales are used to take into account the different magnitude of density in the different groups.

As larger individuals disappear from the community and the fishery continues to target the largest remaining sizes, the community becomes re-structured into fewer size groups. To see this effect we plot the number of size groups, starting from the smallest one, which accounts for most of the abundance of the community (i.e. 99% of the density) against time (Figure 5.6). Over time, the individuals are concentrated towards the smallest sizes. In 1979, 99% of the individuals of the community were distributed through 8 size groups, whereas in 1992 the three first size groups comprised 99% of the individuals in the community. Therefore, the size range of the community as calculated here has decreased by a factor of approximately 2.5 in only 14 years.

Fig. 5.6 Number of size groups representing 99% of the community abundance over time.

5.4. CONCLUSIONS

After describing the size spectrum of the community over time and undertaking a detailed analysis of its changes some facts about the fish community situation can be stated: (1) density of individuals is decreasing over time in all size groups, (2) density of individuals in the largest size groups become so low over time that these size groups disappear from the community, (3) as a result of (1) and (2) individuals become concentrated in the smallest size groups, and (4) size spectra intercept and slope change over time with a long term trend of decrease in absolute value for both.

The density decrease over time observed in all size groups and the associated compression of the number of trophic levels help to explain the changes and ecological significance of the size spectrum parameters. The continuous selective fishery in Newfoundland is decreasing the productivity of the demersal fish community and fish biomass is lost to the fishery instead of passing to the next size group (trophic level), especially in the largest sizes. Thus, the fish community retains less energy with an overall higher turnover rate, and which over time is likely to make the community more unstable in respect to perturbations (Chapter 3).

A consequence of these changes in the community is that the biomass available to the fishery decreases. The result will be negative social consequences for the fishery. Therefore, our empirical analysis of size spectra in the Newfoundland demersal fish community tells us that the whole fish-fishery system is deteriorating.

Chapter 6:
Size-based simulation of community dynamics

6.1. INTRODUCTION

From a holistic point of view a fish community can be depicted as a food web based on sizes (Chapter 5). From this perspective, individuals of equal size occupy the same trophic level regardless of the species they belong to, and individuals different in size of the same species occupy different levels. In most predator-prey models, each species is considered as the simplest unit within the trophic web (Link, 2002). However, when trophic levels are determined by size, and this size varies through the species' lifespan, the predator-prey-relationship between two species can be reversed within that lifetime. The same species passes from being potential prey to predator over time. Cannibalistic species such as cod, are both predator and prey at the same time. Sizes, not species, constitute functional groups in the community food web. Yet, the time spent in a trophic (size) level as well as the reproductive capacity varies among species. Thus, both species and body size of the individuals should be considered in order to describe the community as a food web.

Individual sizes and species life history parameters are assumed to determine the community structure (Chapters 3 and 4). In the present chapter a simulation model is built to test the dynamics of the fish community under these assumptions. This model will show the consequences of size-dependent predation and life history parameters on the relative abundance of species in the Newfoundland demersal fish community. It is a discrete time model showing the yearly changes of a demersal fish community with focus on the abundance in number of individuals. The model replaces the classical autoecological and species-based view of the ecosystem with a synecological and size-based view. The abundance of a group of individuals (of similar size) depends on the abundance of their predators (individuals big enough to prey on them) rather than on the overall abundance of any particular predator species. Models considering size groups rather than species have been developed for plankton communities (Koslow, 1983), but not completely for fish communities. The static size structure model of ecosystems has proven acceptable and useful (Chapter 5). The closest dynamic approaches include especially MSVPA (Sparre, 1991) that takes into account shifts in diet of each individual species during their life. Also some applications of the ECOSIM model (Walters et al., 1997) separate individuals of certain species into different size units according to their size-related diet. There are also the works of Silvert and Platt (1981), and Duplisea and Bravington (1999) that present dynamic models of fish communities considering trophic interactions strictly between size groups instead of between species.

The abundance of the model populations will result only from a combination of species life history characteristics (growth, maturity, fecundity, lifespan) and species interactions through predation. The production and structure of the community is first considered in the absence of externalities (i.e. environment and fishing influences, Chapter 1). Under these conditions, presumably, the community will reach its maximum production capacity. This maximum places a limit on the conditions within which any external disturbance can operate, and also provides a reference point against which to determine the impact of external disturbances. The influence of externalities on the fish community will be considered in Chapter 7.

6.2. TROPHIC INTERACTIONS

Trophic relations are described using a variation of the Lotka-Volterra equations in order to more accurately reflect natural communities (Berryman, 1992; Ginzburg and Akçakaya, 1992) and systems with a spatially heterogeneous distribution of prey and predator (Ardity and Saïah, 1992), which is the case in respect to demersal fish communities.

The number of mature individuals will determine the number of offspring in each species population. Mortality in fishes, which determines the number of individuals that reach maturity, is mainly dependent on predation. Rates and linkages of this predation are reflected in the community food web.

Usually, trophic web models are based on classic predator-prey equations:

$$dN/dt = aN - bNP \qquad (1a)$$

$$dP/dt = cNP - eP \qquad (1b)$$

where a is the per capita rate of increase of the predator ($\text{time}^{-1} = \#/(\#*\text{time})$), e is the per capita mortality rate of the predator (time^{-1}), b is the predation efficiency as the per capita rate of prey consumed per predator ($\text{predator}^{-1} * \text{time}^{-1}$), c is the conversion efficiency as the per capita rate of predator produced per prey consumed ($\text{prey}^{-1} * \text{time}^{-1}$), and N and P are the number of prey and predators respectively (# for both).

Berryman (1992) follows the evolution of predator-prey theory and shows how the representation of predator-prey dynamics has been improved by considerations of:

1. *The logistic equation in the population rate of birth.* The application of the logistic equation to equation (1) will change the per capita rate of increase of the prey (represented by a in equation (1)) from being a constant to being a function of the number of prey individuals (=a (N)).

   The logistic equation represents the change in numbers of prey per unit time in the absence of the predator:

   $$dN/dt = aN(1 - (N/K)) \qquad (2)$$

   where a is the per capita rate of increase of the prey (time^{-1}) as in equation 1a. N is the number of prey individuals (#) and K is the carrying capacity of the ecosystem, the maximum number of individuals the ecosystem can support (#).

   The function a(N) in equation 3a is equal to $a(1 - (N/K))$ in equation 2, and its dimensions are time^{-1}.

2. *The functional response in the predator's feeding behaviour.* The consideration of predator satiation prompts the change of the representation of prey decrease and predator increase due to species interactions (bNP and cNP, respectively, in equations

1a and 1b). In equation 1a, the prey decrease due to interaction among species is based on the mass action law. Thus, the parameter b is a constant representing the per capita rate of prey consumed per predator. Consideration of predator satiety implies that b becomes a function of the number of prey (=b(N)), which represents the rate of prey consumed per predator as a function of prey abundance. In equation 1a the parameter b had to be multiplied by N and P to obtain the total number of prey consumed per unit time. However, the new parameter, b(N), is not a per capita rate but a rate (number of prey individuals eaten per predator); therefore, it only needs to be multiplied by P to obtain the total number of prey consumed per unit time. Similarly, predator increase, cNP, in equation 1b becomes c(N)P.

3. *The density-dependent mortality of prey and production of predators*. Density of prey will influence predator interaction; it will make the rate of prey consumed by a predator not just dependent on prey density, but also on the relative density of predator with respect to prey. Therefore, the rates of change due to interaction (i.e. b(N) for the prey and c(N) for the predator) will now be represented as b(N,P) and c(N,P) respectively.

Once points 1, 2 and 3 are considered, the predator prey equations become:

$$dN/dt = a(N)N - b(N,P)P \qquad (3a)$$

$$dP/dt = c(N,P)P - eP \quad (3b)$$

N and P are numbers of prey and predator. a(N) is the per capita rate of change of the prey in the absence of interaction, and is dependent on the number of prey individuals according to the logistic equation. b(N,P) and c(N,P) are the predation and conversion efficiencies respectively, as a function of the relative abundance of prey to predator and predator satiation (which includes functional response and density dependence). e is the per capita mortality rate of the predator as in the equation system (1). The parameter and variable dimensions are as in equation 1 except for b(N,P) and c(N,P) which have the dimension time^{-1}.

6.3. YET ANOTHER FISHERY MODEL

In Chapter 2 we discussed why to use a model and what to expect from it. It would have been possible to choose some already existing model that best matched our purpose, yet we decided to create a new one. The main reason was to escape from the idea of a species-based community in favour of the idea of a size-based community. Another important reason was to follow the idea of reversing the usual treatment of species as dependent variables and processes as independent variables (Lawton, 2000). We focus on interactions as much as on individuals in the community, and both variables depend on one another. Not only do biological interactions influence the number of individuals in the community, the number of individuals influences as well the interactions.

Megrey and Wespestad (1988) give an excellent review and explanation of the models applied by fishery scientists since the early days of fishery studies up to recent times, and Megrey (1989) completed this review focusing on age-structured models. Fisheries models range from the simplest one-species models to the most complicated ecosystem or bio-economic models. MSVPA (Pope and Knight, 1992; Magnusson, 1995; Helgason and Gislason, 1979; Pope, 1979) and Ecopath with its dynamic form Ecosym (Walters et al., 1997) are the most widespread and accepted multispecies models. We disagree with the former because of its most common assumption, when used for forecasting (MSFOR), of a constant production over time in the community, and because it relies on fishery data to solve the model equations despite a recognized unreliability concerning the value that should be used for fishery mortality. Our disagreement with the latter stems from its assumption of equilibrium between production and loss of fish biomass for each trophic level or the constant and arbitrary accumulation of biomass in each trophic level. We propose a model in which production and equilibrium are not a prerequisite characteristic of the system. But the main difference from other models is the use of functional groups based on size and the interactions that occur among these size groups. In its basic form, our model is not a fishery prediction model; it is an ecological model of the fish community.

The model presented here uses biological features known about the fish community to simulate the community dynamics and abundance. We have done our best to follow the parsimony principle and maintain the maximum simplicity possible while admitting the complexity of the community, and furthermore to keep the model as transparent as possible. In doing so, we have ignored interactions other than predation among individuals, mortality other than that caused by predation or end of lifespan, and the influence of morphological (mouth gape) or behavioural constraints, in addition to size, in prey selection. It can be argued that the model is an oversimplification, and we agree that it is. However, the factors accounted for in the model are important enough so as to generate some emergent patterns in the community. As Bonner (1965: 15) states: *"It is, after all, quite accepted that in a quantitative experiment, a statistical significance is sufficient to show a correlation. The fact that there are a few points that are off the curve, even though the majority are on it, does not impel one to disregard the whole experiment. Yet when we make generalizations about trends among animals and plants, such as changes in size, it is almost automatic to point out the exceptions and throw out the baby with the bath."*

Therefore, we argue that our decision to create a new model is the best compromise between complexity and generality (Lawton, 2000). In addition this new model can accommodate exceptions to the assumed characteristics, e.g. the presence of non-piscivorous species.

6.4. BUILDING THE MODEL

Matlab® computer software (Kernan, 1997) allows construction of the model, the ability to run scenarios, and the presentation of results as graphics. It is worth pointing out some technicalities about the model. It runs on a personal computer (PC). The computer memory required for the model file is around 10 KB and its performance takes no more than a couple of minutes to generate around 500 annual iterations. The input data required to run the model are an initial number of individuals by species and size group, the time period (number of iterations) for the simulation and a factor that identifies whether the simulation starts afresh or follows from the output of a previous run. The model in its computational form is presented in Appendix A (p. 185) and is available on disk upon request. In this appendix the reader will find a full explanation of equations and notations as they have been programmed in Matlab, the procedure to run the model and the changes that need to be made in order to consider new starting points or scenarios. Special attention should be paid to make sure the appropriate changes are made in all the model sections where the changed terms occur in order to ensure the running and proper performance of the model. Finally, Table 6.5 at the end of this chapter contains the list of variables and parameters used in the model and mentioned in this chapter.

6.4.1. MODEL ASSUMPTIONS

1. All individuals die after the end of the assumed life span for the species.
2. Mortality is caused by predation and is density dependent (on both prey and predator abundance) except for that at the end of life span.
3. Predation depends on size and is independent of the individual species.
4. Offspring production is density dependent. There is a limit for each species in the number of offspring. This limit ($K=10^{10}$) is applied to the number of mature individuals that are going to reproduce; therefore the maximum offspring production varies among species.
5. Egg production capacity increases with size of mature individuals and varies among species.
6. Food intake is a function of individual size according to the allometric equation:

$$z=3.504\ w^{0.82} \qquad \text{(Peters, 1984)}$$

where z = Kg of prey eaten by a single fish in a year and w = mass in Kilograms of the predator fish.

7. Individual classification into size groups is Size 1=[0g-9g] (avg. 5g), Size 2= [10g-99g] (avg. 50g), Size 3 = [100g-999g] (avg. 500g), Size 4 = [1000g-9999g] (avg. 5000g) and Size 5= more than 10000g (avg. 15000g). Based on the predator/prey weight ratio observed by Hahm and Langton (1984), it is assumed that Size 1 is prey of Sizes 2 and 3, Size 2 is prey of Size 4 and Size 3 is prey of Size 5. Sizes 4 and 5 do not have predators within the community. Size 2 is assumed to feed on larval stages of Size 1.
8. The time an individual remains in a size group will depend on the species to which it belongs. This time has been determined based mainly on growth rate information about the species given by Scott and Scott (1988)
9. The model is dynamic (i.e. variables change through time). The number of individuals of a certain size group at time (t+1) is going to be the number of survivors of the preceding size group in the time (t). In the 0-1 age class, the number of individuals at time (t+1) is going to be the number produced by the individuals in the mature sizes at time (t) which have survived predation.
10. Since annual periodicity tends to be dominant in the marine environment (Bakun, 1985), a year will be the time unit in the model (i.e. this is a discrete time model) and all rate parameters will be related to this unit time.
11. Extinction of species is not possible. Since predation is dependent on the predator/prey ratio, a proportion of the prey will always survive. However, this

fractional quantity may get to very close to zero, which makes no sense, as the minimum number of individuals can only be an integer, 1 or 0. To avoid as much as possible the complications that arise with these small values (<1), offspring production is always rounded to the next upper whole number. Therefore, at least one individual is always present for each species in the model. Also in order to avoid indeterminacy in the equations, whenever a fraction is present a unity is added to the denominator. This does not have a significant effect for the computations and its effect decreases when the values of the variables increase. We find this convention helps to avoid the crashes that characterized the early stages of model development.

6.4.2. THE SIZE STRUCTURE OF THE FISH COMMUNITY

Predator-prey relations and food intake in fish are a function of body size (Yodzis and Innes, 1992; Peters, 1983; Bax, 1998). Trophic relations among individuals in demersal fish communities are based on individual size, so size-based models of the community dynamics have been encouraged (Boudreau et al., 1991). The fundamental role is that big eats small, but size varies during a life span and hence trophic relations will change as well. As a result, we propose a novel representation of the community dynamics based on size (Fig. 6.1).

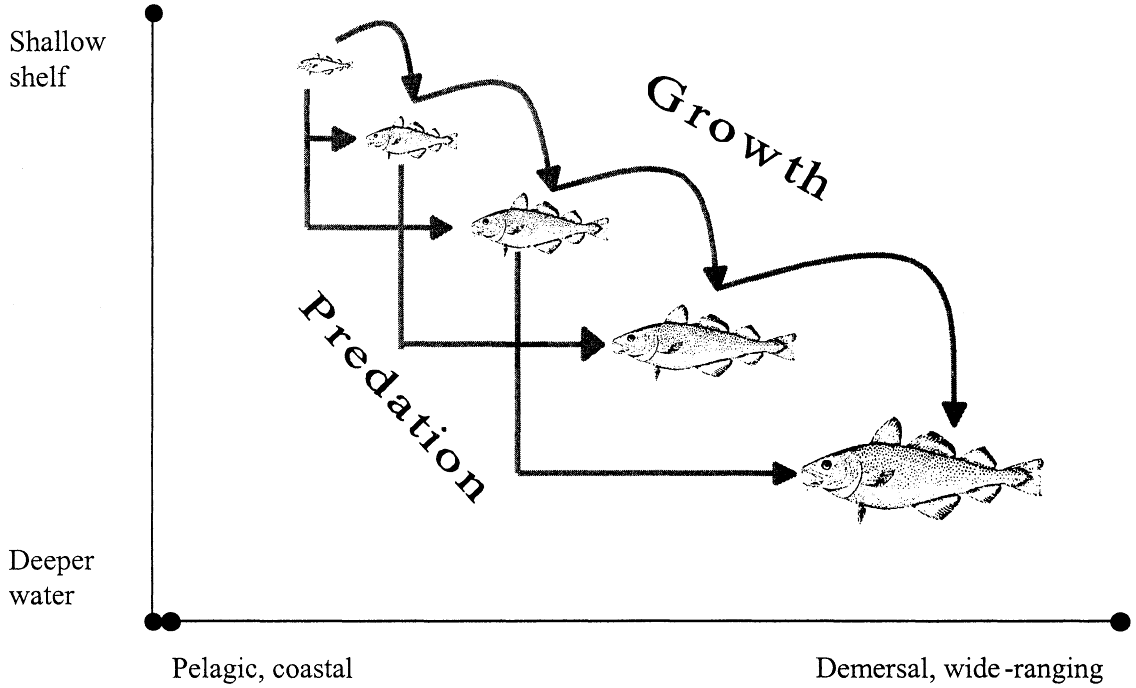


Fig. 6.1: Graphic representation of trophic relations and habitat location changes during a fish's lifespan.

Individuals are positioned in a trophic level according to their size. Trophic interactions will take place between sizes, regardless of the age or species of the individuals in each size group. Predator-prey interactions will be considered at the size level. The selection of size groups forming the community and their trophic interaction (see model assumptions pp. 96-97) is based on published information. Hahm and Langton (1984) find that fish prey on food that is between two to three orders of magnitude smaller (by weight) than their own size. Paradis et al. (1996)

indicate that the maximum vulnerability of prey to predator is when prey is 10% of predator weight regardless of prey item.

In contrast with other food web models in which amount of prey is key to determining predator abundance, in our size-based model food is taken for granted (i. e. predators are never considered to be food-limited). However, this fact does not imply an exclusive predator-to-prey control, i.e. "top-down". There are three main reasons to neglect food dependency: (1) the ability of fish to fast during long periods of time, which will diminish the effect of a temporary lack of prey; (2) that invertebrate species, not a part of the model, are nonetheless considered to be a non-decreasing constant in the ecosystem and therefore fish can shift to them if necessary; and (3) in most piscivorous species cannibalism is the norm, inducing an indirect "bottom-up" control of predator abundance. For example, a decrease of individuals in prey stages (i.e. small size) of a species due to cannibalism will result in a decrease of individuals in the predator stages (i.e. larger sizes) over time. Usually the predator stages of a species correspond to mature stages, and therefore a high abundance of predator stages will induce a high abundance of larvae and juveniles through reproduction. However, since the intensity of the trophic interactions is density dependent, predation on those abundant young stages is also going to be more dramatic. Thus, species composition and density dependent interactions within the community induce multiple indirect effects that can result in both depensation and compensation.

Size and density dependent predation, combined with recruitment, define the links among individuals in the food web model. Although survival rate during the first life stages is known to be highly influenced by environmental factors, there is a positive relationship between spawner abundance and subsequent recruitment (Myers and Barrowman, 1996) and density dependent mortality due to predation on juvenile stages attenuates density independent variability in abundance (Myers and Cadigan, 1993). In addition, drastic changes in fish abundance (as is happening in the area under study) make it likely that density dependent processes overcome other factors in respect to the influence they have on the community (Levin, 1988).

From the demersal fish community off Newfoundland (see Table 2.2 in Chapter 2), the most abundant species have been selected to enter the model, i.e. those with a number of individuals comprising more than 1% of the total number of individuals in the community. The scientific and common names of these species are presented in Table 6.1. Within each species, age determines size, and within the community model, size will also determine trophic level. A double entry matrix can then represent the community, with columns being the species and rows being the sizes. Each cell of the matrix is filled with the average number of years individuals of any species remain in that particular size group. Life-history parameters of the species have been used to determine the structure of the community on a realistic basis (Table 6.2); an estimation of the fecundity (number of eggs released from each mature female) is presented in Table 6.3.

Table 6.1. Scientific and common name of the ten most abundant demersal fish species (abundance >1% of individuals in the community) off northeast Newfoundland (NAFO areas 2J 3K). The third column contains the species abbreviation used in the model.

SCIENTIFIC NAME	COMMON NAME	Abbr.
Boreogadus saida	Arctic Cod	Bs
Coryphaenoides rupestris	Roundnose Grenadier	Cr
Gadus morhua	Atlantic Cod	Gm
Glyptocephalus cynoglossus	Witch Flounder	Gc
Hippoglossoides platessoides	American Plaice	Hp
Mallotus villosus	Capelin	Mv
Raja radiata	Thorny Skate	Rr
Reinhardtius hippoglossoides	Greenland Halibut	Rh
Sebastes marinus	Golden Redfish	Sma
Sebastes mentella	Deep Water Redfish	Sme

Table 6.2. Age distribution of species in the different community size groups. There are five size groups: Size 1 corresponds to individual weights between 0 and 10 g, Size 2 weights between 11-100 g, Size 3 101-1000 g, Size 4 1001-10000 g and Size 5 more than 10001 g. Ages with mature individuals are indicated in bold characters. Data mainly from Scott and Scott (1988).

		Species									
		Bs	Cr	Gm	Gc	Hp	Mv	Rh	Rr	Sma	Sme
Size	1	1~2	1~2	1	1~2	1~2	1~2	1~2	1	1	1
	2	**3~5**	3~9	2	3~4	3~4	**3~5**	3~4	2	2~4	2~4
	3	**6~8**	**10~25**	**3~5**	5~**6~10**	5~**6~10**		**5~10**	3~4	5~**8~10**	5~**8~10**
	4		**26~40**	**6~15**	**11~30**	**11~25**		**11~15**	**5~20**	**11~40**	**11~40**
	5			**16~20**				**16~20**			

Table 6.3. Offspring production from mature-sized individuals of each species. The matrix shows the average number of eggs released per year by a mature female of the species and size indicated. Data mainly from Scott and Scott (1988).

		Species									
		Bs	Cr	Gm	Gc	Hp	Mv	Rh	Rr	Sma	Sme
Size	1										
	2	10^{4}					$4*10^{4}$				
	3	$2*10^{4}$	$2*10^{4}$	$2*10^{5}$	$3*10^{5}$	$3*10^{5}$		$3*10^{4}$		$1.5*10^{4}$	$1.5*10^{4}$
	4		$6*10^{4}$	$3*10^{6}$	$6*10^{5}$	$1.5*10^{6}$		$2*10^{5}$	20	$2.5*10^{4}$	$2.5*10^{4}$
	5			$1.2*10^{7}$				$4*10^{5}$			

6.4.3. INTERACTIONS WITHIN THE COMMUNITY

Growth, predation and reproduction parameters translate into numbers of individuals that pass to the next age-class, that are preyed upon and that are born. Growth reduces the number of individuals in a size group and increases the number of individuals in the next size group. Predation reduces the number of individuals in a size group and, therefore, the number of individuals that can pass to the next superior size group. Finally, through reproduction the number of individuals of size group 1 increases in accordance to the abundance of mature individuals in the larger mature size classes of each species in the community.

Growth rate and maximum size are characteristic of each individual species. How long an individual remains in a certain size group varies from one species to another;

therefore an age-division of individuals within species is also necessary. In spite of the allometric relation of offspring production with size, offspring production should be considered at the species level because maturation age and fecundity vary greatly among species. Similarly, growth rates also vary among species and therefore also should be considered at the species level.

No matter how complex the system becomes it can be well-represented by the aforementioned interactions which we now go on to address in detail, explaining how they are mathematically expressed in the model.

6.4.3.1. Predator-prey interactions

Predation is determined by prey size, therefore trophic interactions are considered according to size regardless of the individual species or age within each size group. Prey death due to predation will depend on predator-prey density, satiation of the predator, and the concentration of prey in different species. To define the percent of survivors from predation we will consider each factor affecting predation one at a time.

Let us first consider relative abundance of predator and prey alone. If there are two size groups (e.g. s_i and s_j, where s_i is the prey group and s_j is the predator group), the ratio of predator to total number of predator and prey will be:

$$p_{Si} = s_i/(s_i + s_j) \tag{4}$$

where p_{si} = ratio of individuals of the group size i (prey, in this case) in relation to the total number of individuals in group size i and group size j (predator) (dimensionless = #/#), s_i =number of individuals in group size i in a certain year (#), s_j = number of individuals in group size j in a certain year (#).

Under the basic assumptions that all encounters result in successful predation and that encounter probability depends on relative abundance of predator and prey in such a way that the ratio $p_{si} = 0.5$ when the number of prey equals the number of predators and p_{si} increases with increasing number of predators relative to prey, p_{si} represents the per capita rate of prey (individuals of size group i) survival from predation in a year. In other words, when the number of prey equals the number of predators, half of the prey will survive. In the absence of predators, all prey survive, and when the number of predators tends to ∞, the number of prey that survive tends to 0. These relationships are shown graphically in Figure 6.2.

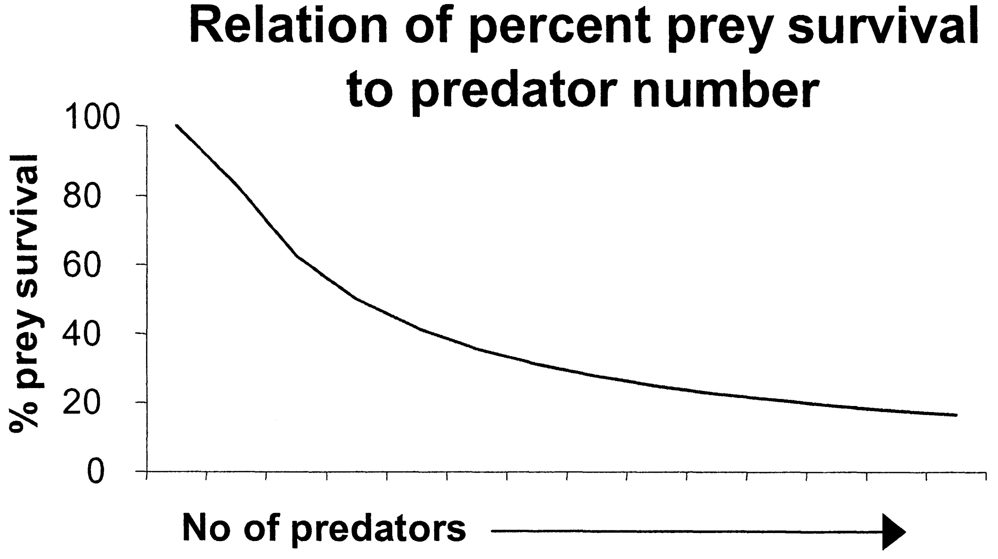


Fig. 6.2. Percent of prey surviving predation (p_{si}) under different pressure (as abundance) from a predator (s_j) when the prey number remains constant.

Let us now consider satiation of the predator. Capture and intake as a consequence of a predator-prey encounter will be influenced by the satiation of the predator. The amount of food intake for a single predator when there is no shortage of food is an allometric characteristic of the predatory fish (i.e. it will depend on the size (mass) of the individual). Following the previous example, we will call g_{Sj} the food intake in grams of a single predator of size j per year when there is no shortage of food (i.e. individuals of size 1). Therefore the number of prey individuals eaten by a predator when it reaches satiation will be g_{S2} divided by the average weight of its prey (individuals of size i). Taking into account predator satiation, equation 4 will become:

$$p_{Si} = s_i/(s_i + (s_j \bullet (g_{Si}/w_{Si}) \bullet y)) \qquad (5)$$

where p_{si}= ratio of individuals of the group size i (prey, in this case) that survive predation in a certain year (dimensionless), s_i =number of individuals in group size i in a certain year (#), s_j =number of individuals in group size j in a certain year (#), g_{Sj}= food intake of a predator (of size group j) individual at satiation (g/#*year), w_{Si} = average weight of a prey (of size group i) individual (g/#), y = time period considered (years). We said above that this model would consider that change occurs on a yearly basis; thus, y is unity and does not affect the computations (it will not be included in nest equations).

If we define $$l_{Sj,Si} = (g_{Sj}/w_{Si}) \quad (6)$$

then equation (5) can be expressed more easily as:

$$p_{Si} = s_i/(s_i + (s_j \bullet l_{Sj,Si})) \quad (7)$$

Graphic representation of equation (7) will have the same shape as the representation of psi in Figure 6.2.

Finally, whether the prey individuals are concentrated in only one species or dispersed among many prey species is likely to influence predation. For example shifting and searching for different preys is time and energy consuming for the predator or bigger patches of prey may be easier to find. At the same time, large schools may present a better defence against a predator or less abundant species may find refuge in more inaccessible habitats or simply in their rarity. To determine how prey mortality is distributed among prey species we define the term "exposure to predation" (Ep) as the proportion of the predator intake corresponding to a certain prey species considering the number of individuals of other potential prey species in the same size group. To quantify Ep we consider first the relative abundance of each prey species with respect to the rest of the potential prey that belongs to other species. Then we define Ep as the ratio of that relative abundance in relation to the relative abundance of prey. Therefore, the equation of Ep for the individuals in size 1 of a certain species, A, is:

$$Ep_{Ai} = (x_{Ai} /(t_i - x_{Ai}))/\sum_{h=A}^{Z}(x_{hi} / t_i - x_{hi}) \qquad (8)$$

Ep_{Ai} = proportion of predation directed to prey Ai (dimensionless), $x_{A,i}$ = number of individuals of size i in species A (#), t_i = total number of individuals in size group i, $t_i - x_{A,i}$ = Number of individuals of size group i which do not belong to species A (#), and $\sum_{h=A}^{Z}(x_{h,i} / t_i - x_{h,i})$ = sum of the relative abundance of each prey species with respect to the rest of prey species. h being from the first, A, to the last, Z, potential prey species. (dimensionless)

The final equation that determines the proportion of each prey species that survives predation is a variant of equation 7 of the form:

$$p_{Ai} = s_i/(s_i + (Ep_{Ai} \bullet s_j \bullet l_{Sj,Si})) \qquad (9)$$

p_{Ai} = proportion of individuals of species A and size group i surviving predation (dimensionless), s_i = number of prey individuals from all species (#), Ep_{Ai} = Proportion of predation directed to prey A_i (dimensionless), and $s_j * l_{Sj,Si}$, as in equation 7, = the number of prey that would be eaten by size group j if they reached satiation (#)

6.4.3.2. Offspring production

In determining offspring production three main factors are considered:

1. Offspring production is characteristic of each individual species.
2. There is an allometric relation between the number of offspring an individual produces, and the size of that individual (for all fish species, the number of eggs released increases the increasing in size of the mature female).
3. Offspring production is density dependent, but the form of this dependency does not follow a straight line (the number of eggs will increase with the number of mature individuals until a limit is reached when the spawning individuals interfere with each other and production does not increase any more).

An expression similar to the Beverton-Holt stock recruitment curve (Beverton and Holt, 1993) determines the offspring production for each species. The difference here lies in the regulation of maximum offspring production. In order to account for the differences in reproductive capacity between species, we set a limit, N_{max}, to the number of mature individuals that will produce offspring. Thus, maximum number of offspring will vary among species as will the carrying capacity (K). Equation 10, below, indicates how the offspring production for a certain size of a certain species is calculated. The total number of offspring produced by the species will be the sum of the offspring produced by all the individuals of each mature size. The graphic representation of offspring production *vs.* number of mature individuals is shown in Figure 6.3. The actual number of offspring will depend on the size of the mature individuals; if larger sizes are more abundant then the overall number of offspring will be larger. There is also an overall limit corresponding to the offspring production that will be achieved if there were N_{max} individuals all belonging to the largest size group in the population.

$$O_S = N_{max}/M_S + N_{max} \bullet \sum_{j=i}^{h} \left|F_{Sj} \bullet M_{Sj}\right| \tag{10}$$

where O_S = Offspring production of mature individuals of species s (#), M_S = Number of mature individuals of species s (#), F_{Sj} = Fecundity, as average number of eggs released, of a mature individual of species s and size j. j evaluated from size at maturity, i, to the largest size, h, that the species attains (#), M_{Sj} = Number of mature individuals of species s size j (#), $\left|F_{Sj} \bullet M_{Sj}\right|$ indicates that the value assumed is the rounded up absolute value of the multiplication result, and N_{max} = maximum number of mature individuals that will spawn in the absence of interference (i.e. no limit to the production of offspring). In the model N_{max} is arbitrarily set at 10^{10} individuals (#).

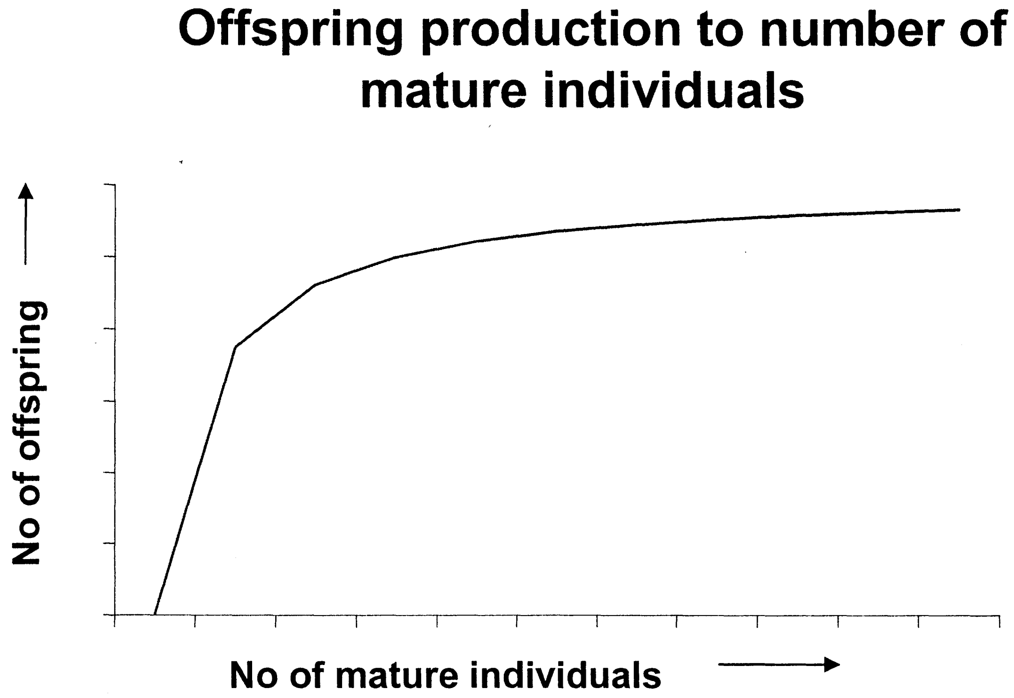


Fig. 6.3. Form of the relationship of number of offspring produced as a function of the number of mature individuals in the population. This is the sort of curve that will be obtained from equation (10).

At the offspring production level, taking the absolute value of O_S (rounded up) imposes a minimum (limit) to the number of individuals in a population. In this way the number of individuals in a species is at least 1 and does not fall between 1 and 0 for the species as a whole despite the fact that computationally this can be the case for a size group within the community.

6.4.3.3. Passing from one size group to the next

Within a species, it is assumed that all individuals of the same size group will have the same probability of surviving predation or of being eaten. That probability will be the same regardless of the age of the individuals within the size group. As indicated in Table 6.2, the time a species remains in a size group ranges from 1 to 30 years. Therefore, the individuals from a size group that pass to the next size group will be the number of individuals in the oldest age of the size group times the survival probability of the individuals of that species and size group.

6.4.4. SOME COMMENTS ON VERIFICATION, CALIBRATION AND VALIDATION

Verification and validation of the model are processes that continue during the whole life of any model (Haddon, 2001; Banks, 1998). Verification deals with the rationale for the processes simulated, i.e. whether they qualitatively reflect nature (or more exactly the way we think nature works), while validation examines how accurately reality is simulated. A major pitfall to verification and validation is that even in cases where there are enough data from the real system to be able to carry out these assessments, i.e. the data are sufficiently accurate and representative of the real community so that one can confidently contrast the outputs of the model against them, validation is always challenged by new data. The reality of a changing community creates the necessity to adjust this process over time. Fitting the model to past situations does not guarantee it will fit future situations. In changing ecosystems, the calibration of parameters to verify and then validate the model does not necessarily mean that we are improving the model. It may rather mean that the model is changed into a new version that matches very well the actual present situation but meanwhile looses track of past situations. In addition, comparison of a model with reality must, in principle, be inexact, since we know that no model is perfect and that most commonly the simulation is of systems where not all variables and interactions are included in the model.

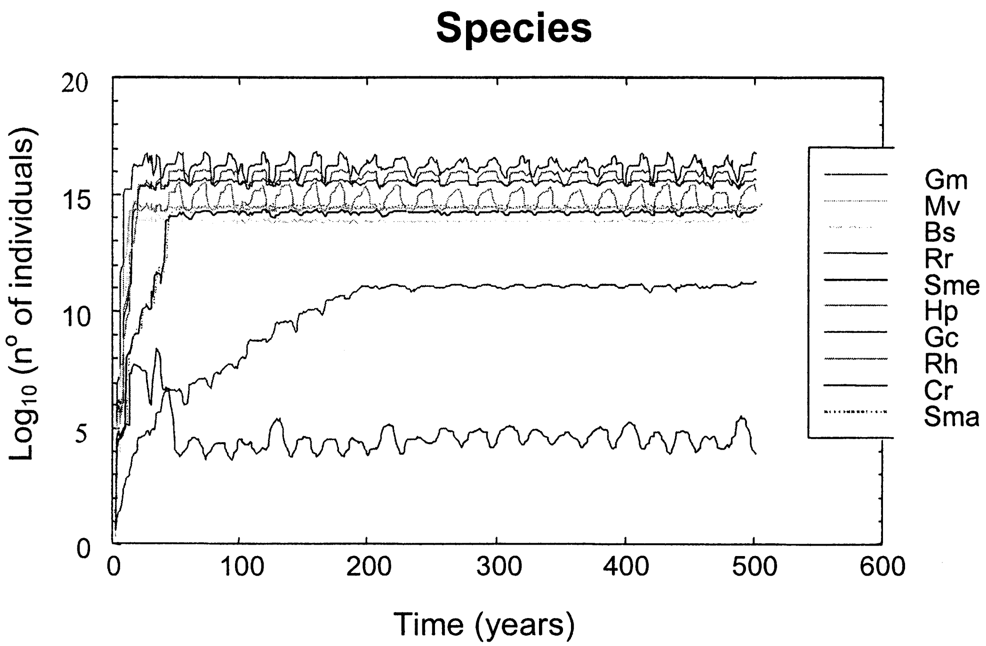
Because we are interested in dynamics at the community level, we pay more attention to global trends and relations among variables than to quantitative accuracy. Setting the right time frame for looking at the model outputs may be a key to making the model valid. Life history and trophic parameters determined the accuracy of the outcome. In the case of low parametric error, quantitative results for short-term predictions may be valid, but the error in the results is likely to increase when the time frame is extended. In the medium/long-term, the trends of the variables give insight into the system and adjustment of parameters is not so essential. In the very long-term, genetics and adaptation induce evolutionary changes and probably the model needs to be accommodated with new sorts of information.

Because the model parameters are taken from the literature, calibration is not used. Sensitivity analysis gives an idea of how important some parameters are for the output of the model. It is clear in our model that life history parameters of the species are the important factors that can change the abundance and production of each species and, therefore, the relationships among functional groups. The model is most sensitive to the time each species remains in each size group. The longer the time spent in prey size groups the greater the probability of being preyed upon, and the longer the time spent in larger sizes the more offspring production there will be. The model is also sensitive to the values of fecundity for each species, since the maximum number of individuals for each species depends on how many can be produced. Validation of the overall structure of the community can be approached using size spectra analysis from real data. The size spectrum shows a general pattern at the level of community. By integrating all individuals of the community, the size spectrum is more robust to errors in life history parameters of species than is the index of abundance of each species separately. A size spectrum analysis for the model introduced here appears in Chapter 7, section 7.4.

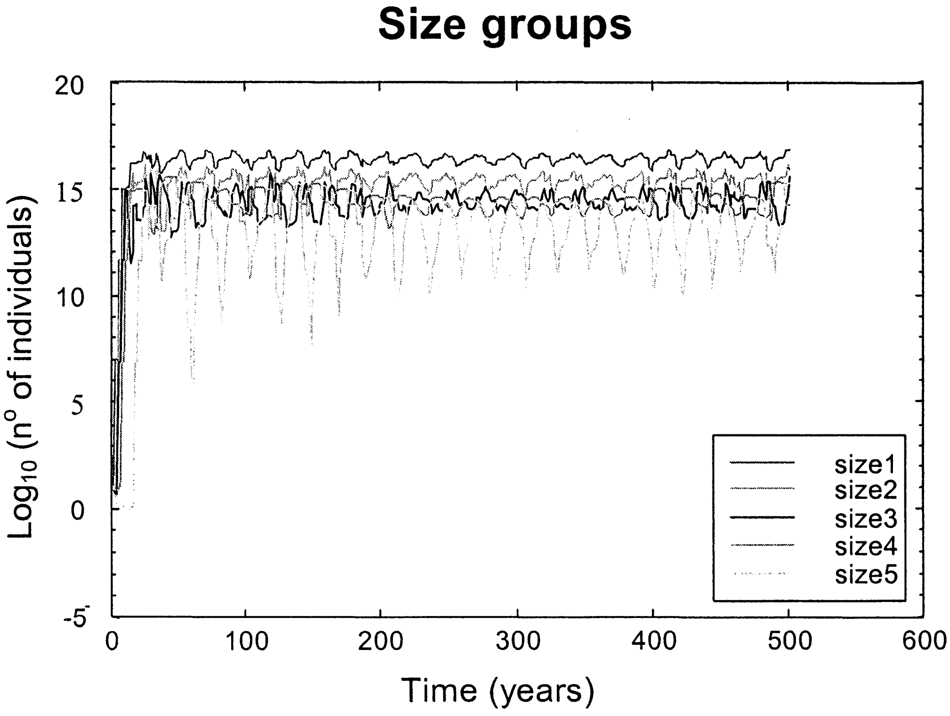
6.5. DYNAMICS OF THE NEWFOUNDLAND DEMERSAL FISH COMMUNITY

6.5.1. MODEL OUTCOMES

Figure 6.4 shows the dynamics of the Newfoundland demersal fish community over a long enough period of time (500 years) for the community to stabilize. The model was initiated starting in year 1 from an arbitrary point of 1 individual in each age for each species. The number of individuals is presented on a logarithmic scale. This scale is preferred because it emphasizes the magnitude of change of abundance in species or size groups, and furthermore facilitates the representation of all species or sizes in one or a few graphics without distorting the information. In addition, the arbitrarily chosen N_{max} and the lack of calibration do make the values of the model outcomes inaccurate, and therefore probably unreal. In fact, though, it is the relative abundances of species and size groups that we want to consider rather than absolute values. The time required for the model to "crank up" to a more-or-less stable situation depends on the generation time of the most long-lived members of the community. That is at least 40 years for *Coryphaenoides rupestris*, *Sebastes marinus*, and *Sebastes mentella* (Table 6.2)



(a)



(b)

Fig. 6.4. Community dynamics. Change over time of each species (a) and of each size group (b). Size 1 is the smallest ($\overline{w} = 5g$) and size 5 the largest ($\overline{w} = 15Kg$).

Once the community stabilizes, after about 200 years in the species plot, we observe repeated periodic cycles over time of the order of 4-5 per century (Fig. 6.4). The cycles are not all exactly equal, but their amplitude (or structure) is similar with certain regular periods of ups and downs. That periodicity resembles the curious cycles observed by Russell in the English Channel ("Russell Cycle": Cushing, 1982). Despite the fact that the Russell cycle refers mainly to zooplankton, changes in stock densities in demersal fishes were also observed during the cycle (Southward, 1963 *in* Cushing, 1982). Environmental changes appear to be the driving forces for this cycle, and might also explain other fish stock fluctuations, e.g. Steele and Henderson (1984) were able to simulate the medium-to-large time scale fluctuations of pelagic species in the marine environment when environmental variability was considered.

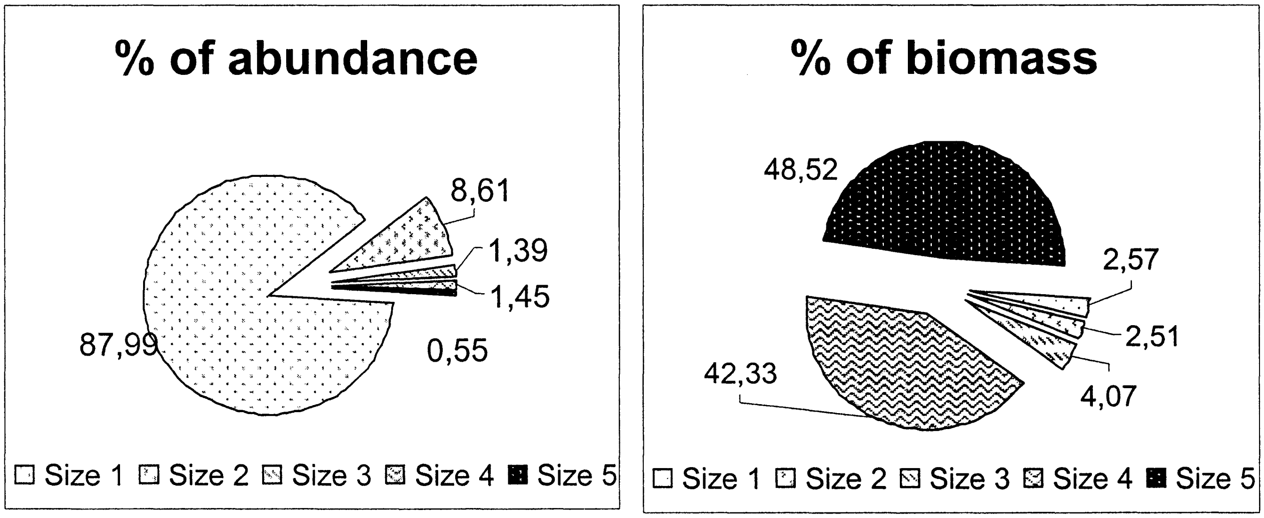
Environmental variability, however, has nothing to do with the cycles that appear in our model's output. Life history and predation are the only factors that enter in our simulation thus suggesting a biological alternative to the environmental one as the cause of the fluctuations (see Chitty, 1967; Krebs, 1979). In our model cycles occur in response to trophic interactions that result in more offspring production during some years than in others, and their amplitude is related to the life spans of individual species, which produce a time lag between consecutive years of abundant offspring production. The presence of various peaks reflects survival of offspring production as the fish pass through the consecutive size groups. That survival depends on the dynamics of trophic interactions among size groups.

An example of how trophic interactions induce cycles follows. At some particular time, t, size group 5 can be very abundant, producing many offspring and preying on many individuals from size group 3 (their prey). By time t+x the fish of size group 3 from time t (with low abundance due to predation) enter size group 5, which will therefore then become relatively low in abundance. Meanwhile, offspring from time t may have reached size group 3, and, since they will not then suffer high predation (because of the low abundance of size group 5 at time t+x), they will reach size group 5 at time t+x+y in abundance, and the cycle will start all over again. The timing of these steps is different for each species depending on how long individuals remain in a size group (Table 6.2) and the abundance of the other species in the same and in the other size groups. When the species are considered all together (i.e. as a community), the drastic changes observed at each size level become reduced and the maximum abundance variation may be around an order of magnitude (10 times), which reflects to some degree the kind of instability observed in nature.

To summarise and analyse the dynamics of species and size groups, we calculate the mean, maximum and minimum abundance of species and size groups once the community has reached a certain stability (which occurs in the time period of years 500 to 1000). Table 6.4 shows the mean relative abundance and biomass of species within the community at that time. Figure 6.5 shows the mean relative abundance and biomass of the community by size groups. The mean value and range of variation for the abundance of both size groups and species in the community is presented in Figure. 6.6. Finally, Figure 6.7 presents, for two important representative species, a bar chart showing the magnitude and variability of abundance for each size group within each species (cod and capelin).

Table 6.4. Percentage comprised within the model community of the mean abundance and biomass of species during the years 501 to 1000 of the simulation. The + sign indicates that the value is greater than zero.

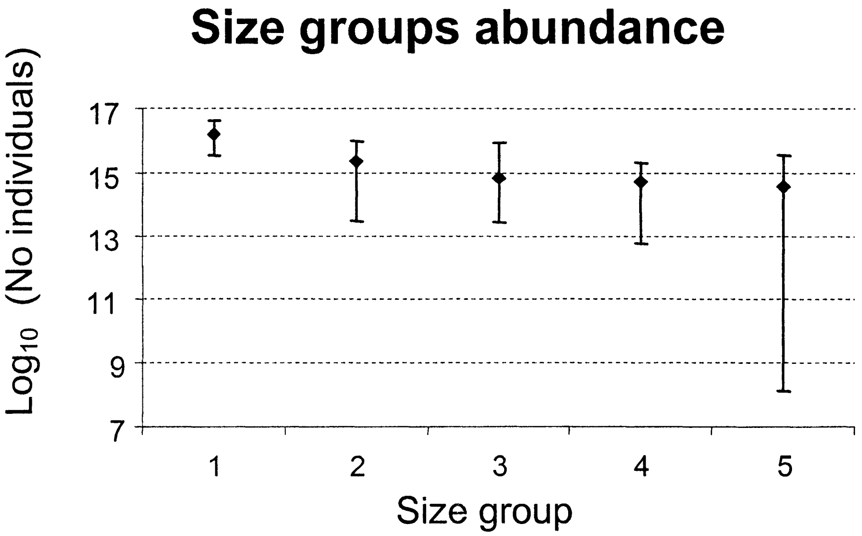
Abbrev.	Species	% mean abundance	% mean biomass
Hp	American Plaice	20,02	5,85
Bs	Arctic Cod	0,21	0,01
Mv	Capelin	0,77	0,04
Gm	Cod	65,01	87,17
Sme	Deep Water Redfish	0,49	0,69
Sma	Golden Redfish	0,49	0,69
Rh	Greenland Halibut	2,95	1,12
Cr	Roundnose Grenadier	+0,00	+0,00
Rr	Thorny Skate	+0,00	+0,00
Gc	Witch Flounder	10,06	4,43



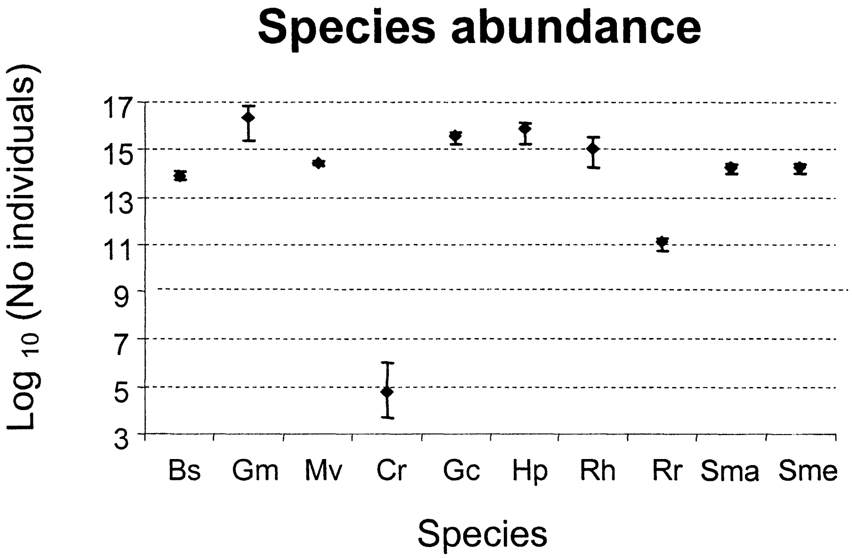
(a)

(b)

Fig. 6.5: Relative percentage of each size group in the community. (a) Abundance (b) Biomass.



(a)



(b)

Fig. 6.6: Mean abundance and range of variation for the size groups (a) and species (b) of the community during the period from year 501 to 1000. Bars correspond to minimum and maximum abundance of the size group within that time period.

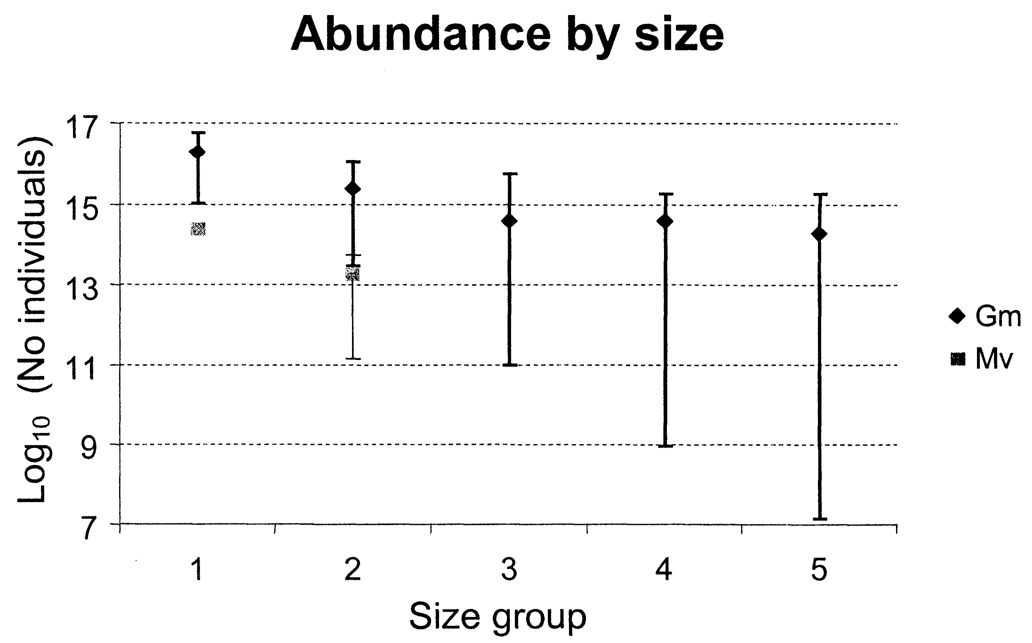


Fig. 6.7: Mean abundance of size groups for cod and capelin during the period between year 501 and 1000 once the community is stable (Fig. 6.5). Bars correspond to minimum and maximum abundance of the size group within that time period.

Cod is the dominant species in the Newfoundland demersal fish community. This is due to the synergy of high fecundity, long life span and relatively quick growth, with a dominance of fish in the older ages (larger sizes). These characteristics make it difficult for other species to overtake the dominant position of cod unless cod abundance is constantly and strongly suppressed; even then, how dominant any other species can be depends on its individual productive capacity. The model result, with cod in a dominant position within the community, is in accordance with the real data. In NAFO areas 2J3K (northeast Newfoundland), cod was by far the most abundant species before its collapse, and since then no other species has taken the dominant lead in the demersal fish community there.

A result of the model that may look suspicious is the relative abundance of the predator, cod, and its commonly associated prey, capelin. We would expect the prey to outnumber the predators that it supports and in fact that is the case if we consider that the turnover and P/B ratio of each species is very much influenced by the accumulation of biomass of cod in large size classes during their long lifespan. In addition, we must remember that in this model interactions take place among sizes, and therefore cod, while in size group 1, is prey of bigger sizes among which capelin is included. It will be more appropriate to construct and analyse the biomass pyramid based on sizes rather than on species.

There are, however, other species whose model abundance differs from that found in nature, as is the case of the two species of *Sebastes*. Since in the model it is assumed that both species have the same life history parameters, life span and growth, the final abundance for both species is the same according to the model, whereas in nature *S. mentella* is far more abundant than *S. marinus*. Lack of knowledge concerning the biological differences between these species or a tendency to capture one in greater proportion due to survey procedures could account for the disagreement between the model results and real data.

When sizes in the entire community are considered (Fig. 6.5a), there is a logical decrease in abundance from that in small size groups (i.e. the lower trophic levels which support the food web) to that in large size groups (i.e. higher trophic levels). Bax (1991) observed that fish predation by fish was more important than predation by birds, mammals or a fishery, especially at larval and early juvenile stages. The larval to juvenile stage corresponds to the model size group 1. Loss to predation is reflected in the model by the difference in abundance between size groups 1 and 2; the result indicates that 79% of the individuals are lost before they reach size group 2. The small proportion of individuals in the larger size groups indicates the high level of resources necessary to sustain those size groups. However the biomass pyramid shows an increase along with size (Fig. 6.5b). Biomass is accumulated in large individuals and the time period individuals remain in large size groups is longer than that spent in small size groups (Table 6.2).

The considerable time needed to replenish populations in the larger sizes as well as the indirect effect of these size groups on abundance in smaller size groups must also be taken into account. The magnitude of variation in abundance is more pronounced in the larger size groups of each species (Fig. 6.7). Species in the large size groups are commonly the target of fisheries, and fisheries can often reduce the variability in abundance of these size groups through intensifying their catches. This, in turn, can significantly influence the impact that these size groups have on the abundance in smaller size groups. This matter will be taken up in Chapter 7.

6.5.2. COMMENTS ON MODEL PERFORMANCE

The time required by the model community to reach stability depends on the initial conditions (i.e. on the starting abundance of each species and its distribution among the different size groups). However, in the absence of externalities, the final state does not change significantly (i.e. it is stable). The maximum abundance of individuals in the community depends on the carrying capacity of the system for each species. A limiting number (in the model $K=10^{10}$) is applied to the number of mature individuals that produce offspring. However, since fecundity varies among species, the maximum number of individuals varies for each species. The relative abundance of species remains constant when K is changed; slight variations are due to model constraints. Thus, in the graphic representation of the community dynamics, the shape and relative positions of variables assume a greater importance than do the exact values in the two dimensions time (x-axis) and abundance (y-axis). The reader is cautioned not to take the abundance results too literally.

The final range of abundances within which the species oscillate over time is constrained by species life history characteristics, as well as by the presence of other species in the community. In the long-term these characteristics guide the community composition and abundance in the absence of external perturbations (externalities).

Each age in the life span of a species is treated separately. Inter- and intra-specific interactions control the abundance of the individuals of a species within a certain age. In the same species, there can be both the long-term effect of offspring production and the short-term effect of survival from the previous year. As for the effects that result from the presence of all the other species, these are modulated by the abundance of the different predator sizes (which can include as well individuals from the same species, i.e. cannibalism is allowed), and the abundance of individuals from the other species in the same prey size group. If size groups instead of age are considered, the number of ages that are lumped together can be another factor controlling abundance.

To achieve equilibrium, all age groups of a species would have to contain a constant number of individuals. Furthermore, this simple statement would require further conditions in the model that are:

1. The number of individuals passing from the immediately inferior age group has to be constant over time.
2. If a constant number of individuals passes from one size group of a species to the next, mortality and offspring production of that species have to be constant over time.
3. Constant mortality requires equilibrium in all the species (i.e. each age group in the rest of the species should also contain a constant number of individuals over time).
4. In order to remain constant over time, the constant values required in all the ages of all the species should be understood as interrelated; they cannot be arbitrarily chosen.

Taken together, these conditions help to explain why a constant equilibrium is rarely found in nature and it does not apply in the model either (i.e. the line is not flat).

Reproductive capacity, density-dependent predation, and growth influence the dynamics of each size group. Certain factors are more influential in some size groups than in others. Thus, in size group 1 there is an important species differentiation in abundance dynamics due to the different reproductive capacity of each species. In size groups 2 and 3 predation affects the abundance trend of species and, because predation does not discriminate among species, all species follow a similar trend although at different abundance levels. Growth, related to the time individuals remain in each size group, influences mainly size groups 4 and 5. This is due not only to an accumulation of differences in residence time from sizes 1 to 4 for different species, but also because size groups 4 and 5 are those where individuals of most species remain the longest. Therefore, the differences observed at these higher levels are the most obvious.

According to model computations, species abundance can be expressed as a fractional amount. This representation of abundance has no biological sense; individuals can only be present in whole numbers. Often, fractions may simply be ignored but, for some species (e.g. Roundnose grenadier, Thorny skate), there are times when the abundance falls between 0 and 1. In order to calculate offspring production this amount is rounded up to 1, placing a limit on how small the fraction can be in the next size groups (i.e. ages). This rounding up is not performed for the remaining size groups because doing so would mask differences in relative abundance among species, and the number of species with longer life spans would be artificially increased. Treating abundances between 0 and 1 in this way allows all species to survive in the model (assumption 11, section 6.4.1).

Since life history characteristics determine the ultimate abundance of a species in relation to all the other species, the model is sensitive to variations in the life history characteristics of single species. However, errors due to inaccuracy of parameter values are unlikely to change the overall structure of the community. In order to do this, the errors should be big enough to overcome the basic differences between species, which are usually greater than the possible differences between real and estimated parameters within the same species. The model is, nonetheless, flexible enough to allow incorporation of new knowledge about parameter values. "Top-down" and "Bottom-up" disturbances can also be incorporated in the model and, as the next step in model development, will be treated in the next chapter.

The complexity of the model is a consequence of its ambitious goal, which is to consider the naturally occurring shifts in trophic levels and relationships that a species undergoes due to changes in its size over time, and the influence that each species has on all the other species present, i.e. a synecological view. Doing this, however, does seem to offer a realistic insight into the structure of the community and its dynamics. The distribution of the total biomass of a species among its various size groups gives a realistic view of the state of the species, and from this perspective its response to perturbation by externalities can be better studied. The idea of a static community gives way to one of a community in constant dynamic change. Questions of interest in the biological arena, for example the consequences of invasion by a new alien species or the study of human and environmental disturbances, can be studied from this new and informative perspective. Externalities like this are the subject of the next chapter.

Modern fisheries research and management require a sound understanding of community dynamics. Species interactions, life-history parameters, and time influence the dynamics. When the various factors are considered in the way presented here, a community appears in which size groups are the functional groups that determine the community structure and dynamics. This view lends itself to the development of a dynamic model.

Our model of a fish community based on size-groups shows a community in constant change, though there is a certain stability attained around which the abundances of individual species fluctuate in a regular way. Species interactions over time and life-history characteristics determine those abundances.

We built the model for the demersal fish community on the continental shelf off Newfoundland in the northwest Atlantic. Nonetheless, the approach can be generalized and should be applicable to other real fish communities. It is especially suitable for fish communities where biological information is less comprehensive, for example the recently developed deep-sea fisheries.

Table 6.5: Variables and parameters mentioned in this chapter.

Symbol	**Name**	**Units**	**Defined in Eq**
N	Preys' number	#	1
P	Predators' number	#	1
a,b,c,e	Per capita rates of change	t^{-1} or $\#^{-1}$ t^{-1}	1
K	Carrying capacity of the system. Maximum number of individuals that can coexist	#	2
p_{Si}	Per capita rate of prey (size group i) survival to predation in a certain year	ratio	4
s_i, s_j...	Number of individuals in size group i, j…..	#	4
g_{Sj}	Food intake of an individual of size group j	g/(# year)	5
w_{Si}	Average weight of an individuals of size groupi (prey)	g/#r	5
y	Time considered	year	5
l_{SjSi}	Number of prey of size j eaten by a predator of size j in a year if satiated	ratio	6
Ep_{Ai}	Percent of predation directed to prey Ai	ratio	8
x_{Ai}	Number of individuals of size group i in species A	#	8
t_i - x_{Ai}	Number of individuals in size group i except for those of species A	#	8
p_{Ai}	Percentage of A_i surviving predation	ratio	9
O_S	Offsring production of species s	#	10
N_{max}	Cte=Maximum number of individuals that can spanw without interfering each other	#	10
M_S	Number of mature individuals of species s	#	10
F_{Sj}	Average number of eggs released by individuals of species s and size j	#	10
M_{Sj}	Number of individuals of species s in size j	#	10

Chapter 7:

Dynamics of the community under the effect of external influences

7.1. INTRODUCTION

In the last chapter we developed and applied our size-based model to simulate the Newfoundland demersal fish community considering only biological factors to show the structure and dynamics of the community in the absence of externalities (environmental factors and fisheries) that might possibly alter the community. That situation can be identified with what we called "Community I" in Chapter 1 (Fig. 1.1). In doing so, it is possible to go back to that global picture and study the dynamics of the community considering the broader system in which it functions.

Both environmental factors and fisheries act on the real demersal fish community (Fig. 1.1, Chapter 1). These externalities present differences in the way they impact the fish community (Table 7.1). Environmental disturbances are ever present in the ecosystem and fish species have adapted to them in an evolutionary sense over time. Contrary to the environment, intensive fisheries act over a much shorter period of time, years and decades as opposed to millennia (Apollonio, 1994). Environmental conditions are considered to have a bottom-up effect on the community because their immediate effect is on the first stages of the fish's life – eggs, larvae and juveniles. Conversely, fisheries have a top-down effect because they selectively target large adults. Furthermore, fisheries target only a few select species out of many, whereas the exposure to environmental disturbances is in principle equal for all species. As Begon (1986) points out: "*A condition may be modified by the presence or absence of other organisms, but unlike resources, is not consumed by an organism or made invariable or less available to others.*" Finally, fisheries usually act as an incremental and continuous disturbance, whereas environmental disturbances are more commonly punctual and intermittent, lasting for a relatively short time and affecting mainly one or a few generations.

Table 7.1: Contrast between fisheries and environmental disturbances.

Fisheries	**Environmental disturbances**
Predictable	Stochastic
Directed to specific target	No target
Continuous	Intermittent
Top-down	Bottom-up
Intensifying over time	Variable over time

In their evolution, fisheries have passed from acting as a casual, uncommon, selective predator (with little effect on the entire fish community) to play the role of dominant, omnivorous, top predator. However, as elements of the community humans display three main differences in respect to the rest of the fish species: (1) they only "take" from the system, (2) their adaptation is very quick and occurs by giant steps compared with the evolutionary adaptation of other species in the community (Apollonio, 1994), and (3) economic and social factors promote change in fisheries, whereas physical and biological factors lead to fish species adaptation and evolution.

In this chapter we introduce externalities to our simulation model of the Newfoundland demersal fish community (Chapter 6). We first consider the action of stochastic environmental variability and after that consider the action of a size-oriented fishery. The purpose is to observe and compare the response of the community and its long-term resultant dynamics and structure under these two different kinds of disturbances.

7.2 SCENARIOS

Simulation of the community dynamics under environmental and/or fisheries perturbation is carried out by including these externalities in the basic model presented in Chapter 6. Three different scenarios are considered:

1. In the first scenario, environmental variability is introduced into the community at the level of offspring production, and acts only to reduce the number. Each year offspring production is reduced by a stochastically varying annual percentage. This random variability is applied to all species, and therefore, production of each species varies independently from all the others.
2. In a second scenario fishery pressure through its action on a single species is applied to the community. This fishery acts on cod and is constant over time (10^{14} individuals/year are removed), and progresses from the largest to smaller individuals depending on availability.
3. A third, more realistic, scenario simulates fish-fisheries interactions (Fig. 1.1) considering both environmental variability (as in scenario 1) and fisheries acting

together on the community. Initially, the fishery targets cod at a rate of 10^{14} individuals/year, progressing from the largest to the smaller individuals. Later a new fishery starts and capelin is exploited at a rate of 10^{12} individuals/year. Finally, the fishery for cod stops but the fishery for capelin continues.

It should be clarified that the fishery in all cases is only applied to the adult size individuals of each species, and a minimum of 1 individual in the smaller mature size group is always kept to avoid extinction. Nonetheless, we have chosen an extreme situation in which the fishery is intense enough so as to provoke drastic changes in the target species.

In order to be able to compare the different scenarios, we must apply the influence of externalities to a community in the same initial state. To begin, the model is run considering only biological interactions until the community has stabilized (arbitrarily a period of 500 years). This provides the starting point (initial conditions) from which the study of the different situations begins, and it is from that point that we run the model under the different scenarios. To begin with, we again assess the community considering only biological interactions so as to stabilize the model. In this way we obtain the reference scenario that will serve as the basis to compare the effects of externalities to that of the community dynamics in isolation, i.e. considering only internal biological factors (Chapter 6). For the scenarios including externalities, an adaptation period of the same number of years as run the reference scenario is allowed before running the model. We can then follow the model run by removing the externality or we can start again with another simulation applying a new externality. Various indices (explained below) of the community situation under different scenarios are obtained over the same time period (500 years) to allow comparison. That time is recorded after an adaptation period to the externalities that is common for all simulations (100 years). Figure 7.1 shows how the model runs for the different scenarios.

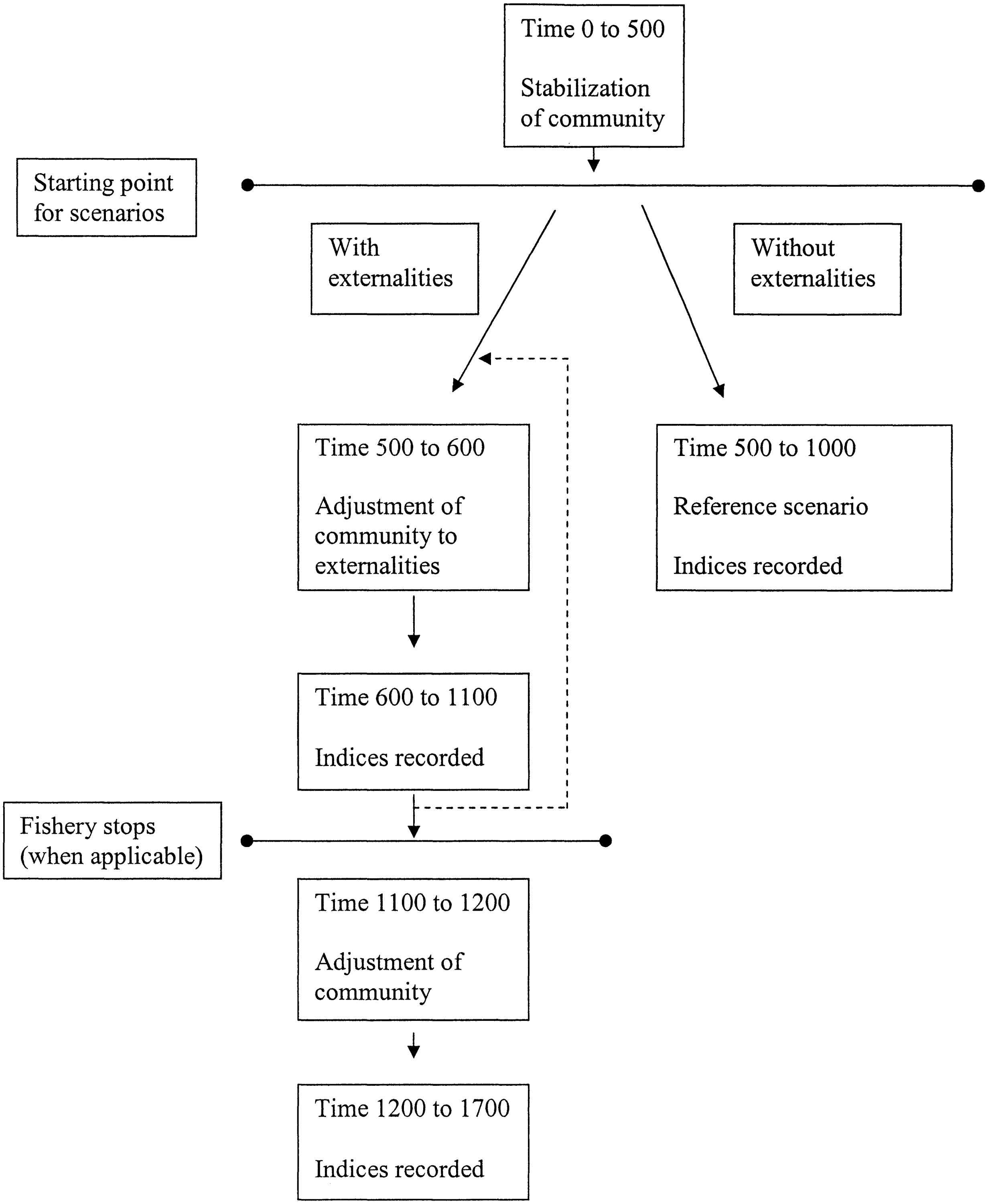


Figure 7.1: Steps to simulate community dynamics under different situations. The initial points for each situation and the periods for which indices are recorded are indicated.

The indices that are used to facilitate comparison of the structure of the community under different scenarios are the maximum, minimum, mean, range of variation (as maximum – minimum) and magnitude of variation (as the ratio range / minimum) of the abundance and biomass of the whole community, of each species, and of each size group within the community. When size groups or single species are considered, the maximum, minimum and mean values for each group usually correspond to a different moment in time, whereas for the community values all size groups and species are considered at the same time. For example, the value of the maximum abundance of size group 2 can correspond to the year x and value of the maximum abundance of size group 5 can correspond to the year y, however when considering the value for the maximum abundance of size group 2 + size group 5 together, both size groups must be from the same year. That is why the abundance or biomass for the whole community does not correspond to the sum of the abundance or biomass of each size group or of each species. That is also why the biomass value is proportional to that of the abundance for those measures that specify size groups, but they are not necessarily proportional for measures of each species as a unity or of the whole community.

Comparison of each scenario to the reference scenario (biological interactions alone) is performed by describing each index of each scenario as a percentage of the corresponding index in the reference scenario. Within the scenarios two situations are considered: (1) under the disturbance, i.e. externality applies, and (2) when the disturbance ceases. In this way, it is possible to analyse the recovery time of the community from the disturbance resulting from environmental variability, and from a fishery with and without the presence of environmental variability. Because the model does not allow extinction, the community recovers from all scenarios but it can reach alternative final stable states. These recovery processes are not deeply analyzed because for their interest they would require further work beyond the scope of this thesis. The primary goal here has been to develop and prove the value of the size-based model, but our plan is to focus on alternative stable states as a next step.

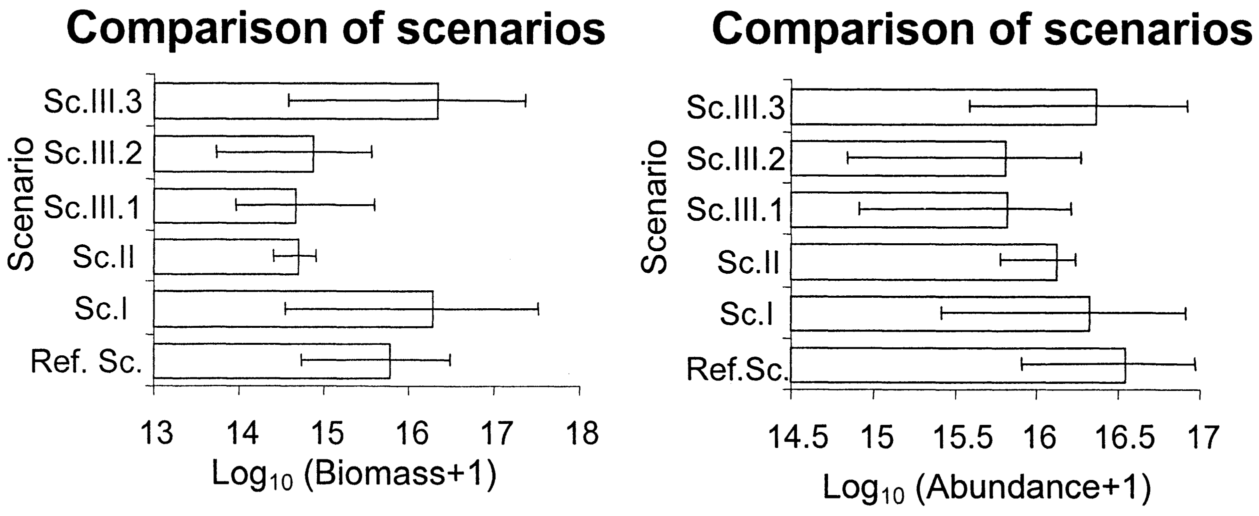
7.3. COMMUNITY RESPONSE

Table 7.2 presents the features of the community under the different scenarios. Comparison of the changes in the community induced by the different scenarios is summarized graphically by plotting the abundance and biomass of the community for each scenario (Fig. 7.2). The change in the community structure is observed by plotting the mean abundance and biomass for each single size group (Fig. 7.3). The abundance and biomass of the community and its species and size groups under the different scenarios appears in a series of tables (Tables from 7.3a to 7.8b). The tables record whether the index is equal (0), less than 10% (-/+ 1), between 10% and 50% (-/+ 2) or more than 50% (-/+ 3) above or below the same index value for the community in the reference scenario. All externalities decrease the mean abundance of individuals in the community, but their effect on community mean biomass and the range of variation for both abundance and biomass varies. Another way of representing the data on Tables 7.3a to 7.8b would be to use the logarithmic values of abundance and biomass instead of the absolute values, an approach that would reduce the percentage range of the indices. This representation, however, is left for future work.

		Scenario				
Feature		*Scenario I Environment (stochastic)*	*Scenario II Fishery (focussed)*	*Scenario III: Environment and fishery*		
				Step 1 Cod fishery alone	*Step 2 Cod+capelin fishery*	*Step 3 Capelin fishery alone*
Main effect of disturbance on		Smallest stages All species	Largest stages One species	Smallest stages of all species Largest stages of one/few species		
Community biomass	*mean*	306%	8.1%	7.6%	12.1%	364%
	Fluctuations	1660%	3.9 %	78.1%	115%	1110%
Community abundance	*mean*	60.5%	37.9%	18.7%	18.6%	65.7%
	fluctuations	288%	17.4%	176%	235%	1.91%
Size groups change	*S1*	52.4%	40.2%	19.5%	19.1%	55.9%
	S2	68.5%	27%	14.5%	14.8%	74.3%
	S3	162%	6.8%	6.59%	10.6%	192%
	S4	292%	11.4%	12.7%	21.5%	348%
	S5	357%	2.75%	62.42%	3.5%	424%
Diversity Ref. Scenario = 1.5		1.3	1.65	1.67	1.54	1.25
Time to recover		≈ 5 years	≈ 20 years	≈ 20 years		≈ 10 years
Recovery state		To initial stable state	To alternative stable state			

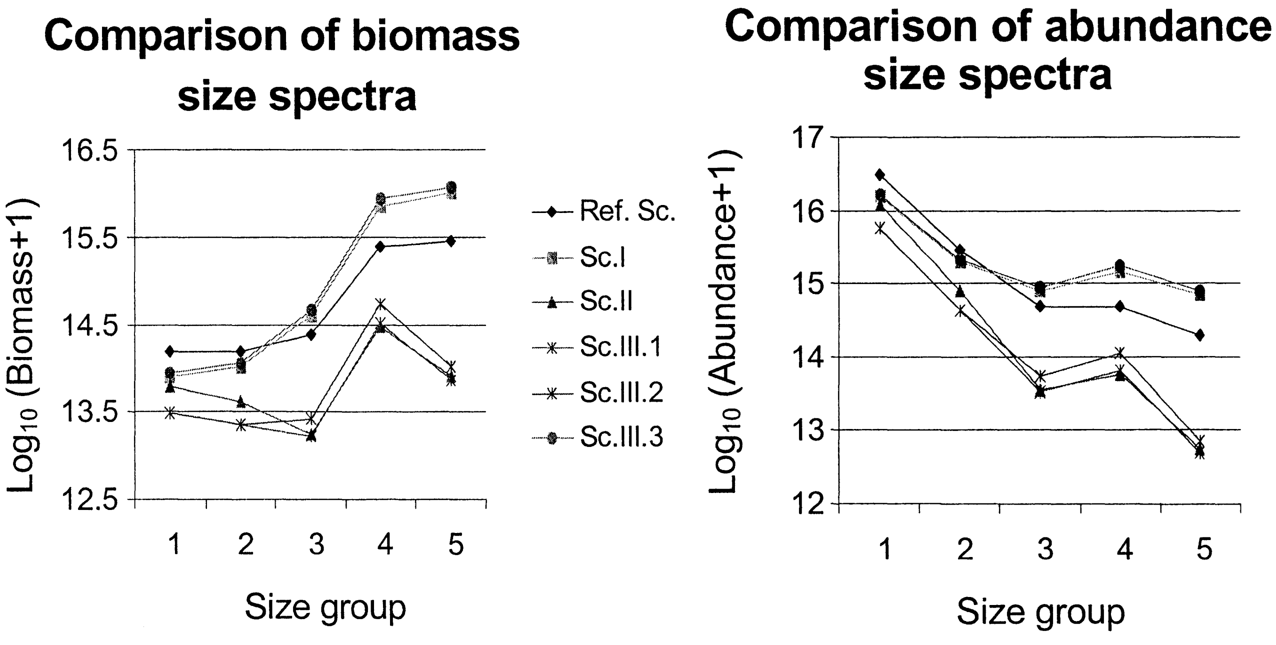
* Fluctuations are as the ratio (maximum – minimum) / minimum.

Table 7.2: Community outcomes under different scenarios, relative to the reference scenario (no externalities, Chapter 6).



(a) (b)

Fig. 7.2: Biomass (a) and Abundance (b) of the community under different scenarios. Ref.: Reference scenario, I: First scenario, II: Second scenario, III.1: Step 1 of the third scenario, III.2: Step 2 of the third scenario and III.3:Step 3 of the third scenario



(a) (b)

Fig. 7.3: Size spectra change under different scenarios (a) biomass (b) abundance. See Fig. 7.2 for abbreviations.

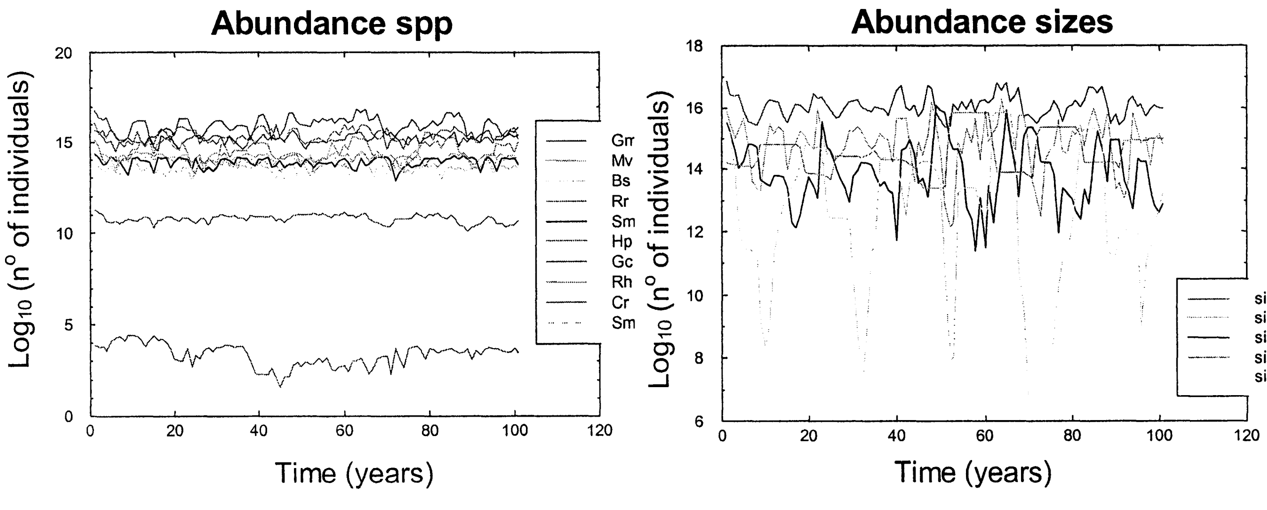
Environmental variability (Scenario I) has a direct bottom-up effect on the community due to: the reduction of offspring production. Interactions within the community lead to indirect effects as well. The result is an increase in the mean biomass of the community due to an increase in abundance of large individuals. Environmental variability slightly decreases the range of variation of abundance and greatly increases the range of variation in biomass. When environmental variability is removed, the community recovers to the initial state in a short time (around 5 years for most species).

On the other hand, the direct effect of the cod fishery (Scenario II) on the community is top-down. The cod fishery drastically decreases both community biomass and abundance. In addition, the fishery results in a decrease in the range of variation for these indices. When the fishery stops the community never recovers to the reference scenario, but instead reaches an alternative stable state in which the largest size groups are less abundant.

The combined effect of environmental variability and fisheries (Scenario III) reveals that the target species determine the effect on size structure of the community as well as the time to revert back to the reference scenario. When the fishery acts on the large top predators (Scenario III, Steps 1 and 2), the community structure shifts towards the smallest sizes and the effect is similar to that of Scenario II. However, when the fishery only targets small species (Scenario III, Step 3) the effect is more similar to Scenario I when only environmental variability acts on the community. Contrary to the top-down effect of the cod fishery, the capelin fishery acts on size group 2 and the overall result is therefore a bottom-up effect similar to that of Scenario I (Fig. 7.3). In any case, the fishery always reduces the final abundance and biomass of the community (Fig. 7.2), and the recovery time to a stable state is at least equal to the generation time of the target species. Each one of these scenarios will be treated in greater detail in the following sections (7.3.1 to 7.3.3).

7.3.1. SCENARIO I: THE EFFECT OF ENVIRONMENTAL VARIABILITY

Figure 7.4 shows how the community first reacts to the introduction of environmental variability in the model. The initial conditions are those established from a run of the reference scenario over 500 years (the starting point indicated in Fig. 7.1). A slight initial decrease in abundance is observed, and then the community starts to fluctuate in a more chaotic way than that observed in the absence of externalities (Chapter 6, Fig. 6.4 reference scenario).



(a) (b)

Fig. 7.4. Scenario I: Changes due to environmental variability. (a) change in species abundance, (b) change in size groups abundance. See Chapter 6, Table 6 for species abbreviations.

After that initial 100-year period of transition, the model is run over 500 years to obtain the final community indices (Tables 7.3a and 7.3b). The action of environmental variability in reducing the number of offspring lowers the community minimum abundance and, to a lesser extent, the maximum also. The result is a reduction of the mean community abundance and a slight (less than 10%) reduction of the community abundance range of variation. Regarding the biomass, there is a reduction of the community minimum and a great increase of the maximum to yield a larger community mean biomass than in the reference scenario and a higher range of variation for community biomass.

The different direction of change for the community mean abundance and biomass is an indication of the higher contribution of small size groups to the overall community abundance. Model results for the size groups (Fig. 7.4b) indicate that the abundance and biomass is reduced in the smaller sizes and increased in the large ones. The resulting community has a lower number of individuals but they are of larger size. Thus, the biomass tends to be higher under the externality of environmental variability.

If environmental variability is eliminated, the community reverts back to a state similar to the reference scenario (Tables 7.4a and 7.4b). The mean community biomass and abundance vary less than 10% of the standard set in the reference scenario. Mean abundance and biomass for each size group separately also remain around the 10% of the reference scenario, despite the fact that greater changes may occur for the minimum and maximum limits of each size group.

Table 7.3a: Abundance comparison of Scenario I (environmental variability). For explanation see text page number 139.

Scenario I Environmental variability		Trend of variation with respect to reference scenario				
group		% min	% max	% mean	% range (max-min)	% magnitude range (range/min)
Abundance of size groups within the community	Size1	-3	-1	-2	-1	3
	Size2	-3	3	-2	3	3
	Size3	-3	3	3	3	3
	Size4	-3	3	3	3	3
	Size5	-3	3	3	3	3
Abundance of species	Bs	-3	-1	-3	3	3
	Gm	-3	1	-2	1	3
	Mv	-3	-1	-3	3	3
	Cr	-3	-2	-3	-2	3
	Gc	-3	-1	-3	2	3
	Hp	-3	-1	-3	2	3
	Rh	-3	-2	-3	-2	3
	Rr	-3	-1	-2	2	3
	Sma	-3	-1	-2	3	3
	Sme	-3	1	-2	3	3
Community Abundance	Community	-3	-2	-2	-1	3

Table 7.3b: Biomass comparison of Scenario I (environmental variability). For explanation see text page number 139.

Sceanrio I Environmental variability		Trend of variation with respect to reference scenario				
group		% min	% max	% mean	% range (max-min)	% magnitude range (range/min)
Biomass of size groups within the community	Size1	-3	-1	-2	-1	3
	Size2	-3	3	-2	3	3
	Size3	-3	3	3	3	3
	Size4	-3	3	3	3	3
	Size5	-3	3	3	3	3
Biomass of species	Bs	-3	-1	-2	1	3
	Gm	-2	3	3	3	3
	Mv	-3	2	-2	3	3
	Cr	-3	1	-3	1	3
	Gc	-3	2	-2	2	3
	Hp	-3	3	-2	3	3
	Rh	-3	3	2	3	3
	Rr	-3	2	-2	3	3
	Sma	-3	3	2	3	3
	Sme	-3	2	2	2	3
Community Biomass	Community	-2	3	3	3	3

Table 7.4a: Abundance comparison of the recovery from Scenario I (environmental variability). For explanation see text page number 139.

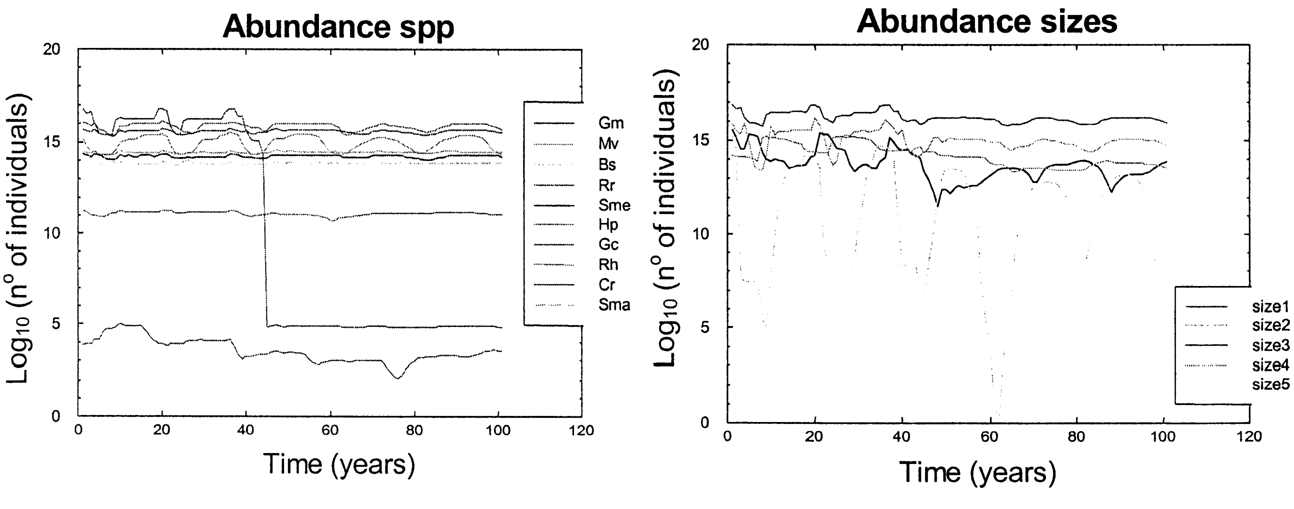
Recovery from environmental variability		Trend of variation with respect to reference scenario				
group		% min	% max	% mean	% range (max-min)	% magnitude range (range/min)
Abundance of size groups within the community	Size1	-1	1	1	1	1
	Size2	-3	1	1	1	3
	Size3	-2	-2	-1	-2	2
	Size4	3	2	-1	2	-2
	Size5	-3	2	-1	2	3
Abundance of species	Bs	1	-1	-1	-1	-1
	Gm	1	1	1	1	-1
	Mv	-1	1	-1	1	2
	Cr	-1	-3	-2	-3	-3
	Gc	-1	1	1	1	1
	Hp	-1	1	1	1	1
	Rh	1	1	1	-1	-1
	Rr	1	-1	1	-1	-2
	Sma	1	-1	-1	-2	-2
	Sme	1	-1	-1	-2	-2
Community Abundance	Community	-1	1	1	1	1

Table 7.4b: Biomass comparison of the recovery from Scenario I (environmental variability). For explanation see text page number 139.

Recovery from environmental variability		Trend of variation with respect to reference scenario				
group		% min	% max	% mean	% range (max-min)	% magnitude range (range/min)
Biomass of size groups within the community	Size1	-1	1	1	1	1
	Size2	-3	1	1	1	3
	Size3	-2	-2	-1	-2	2
	Size4	3	2	-1	2	-2
	Size5	-3	2	-1	2	3
Biomass of species	Bs	1	-2	-1	-2	-2
	Gm	3	2	-1	2	-2
	Mv	-1	-1	-1	-1	-1
	Cr	-1	-3	-2	-3	-3
	Gc	3	-2	-1	-2	-3
	Hp	-2	-2	-1	-2	1
	Rh	2	1	-1	1	-2
	Rr	-2	-1	-1	-1	2
	Sma	2	-2	-2	-2	-2
	Sme	2	-2	-2	-2	-2
Community Biomass	Community	-1	2	-1	2	2

7.3.2. SCENARIO II: THE EFFECT OF A COD FISHERY

The adaptation period and the dynamics of the community under a fishery are shown in Figure 7.5. The cod fishery decreases the abundance of all size groups and smoothes the fluctuations of all size groups but size 5, which correspond only to Greenland halibut because cod size 5 is removed by exploitation in the fishery. The continuous removal of a constant number of individuals (10^{14} individuals/year) in the large sizes eventually eliminates these size groups from the cod population and finally results in the drastic decline (i.e. a "collapse") observed for cod around year 43 after the fishery starts, when all cod individuals in size group 3 are also eliminated. Figure 7.6 shows that the change in abundance of cod individuals is not in all size groups. Since there is no fishery on immature individuals, cod size groups 1 and 2 are the only ones that remain in the long term.



(a) (b)

Fig. 7.5. Scenario II: Changes due to cod fishery. (a) change in species abundance, (b) change in size groups abundance.

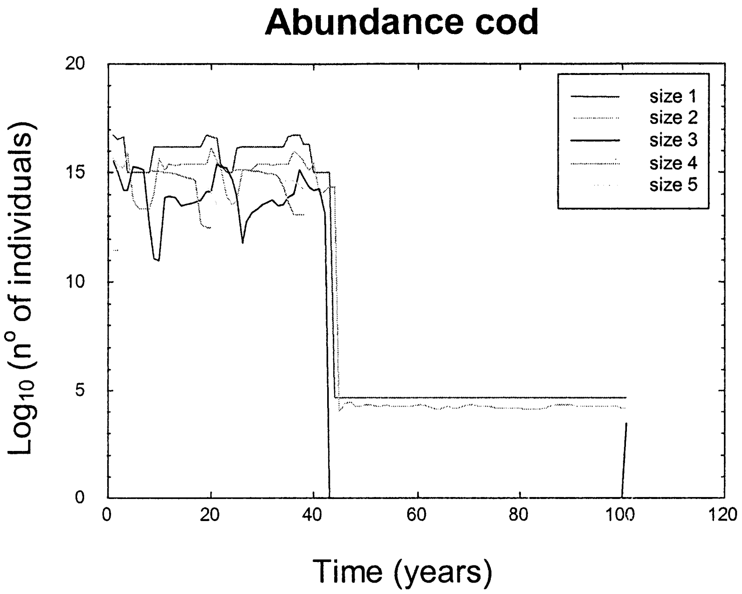


Figure 7.6. Adaptation period for cod size groups. A constant rate of intense fishing drastically reduced the largest sizes of the species.

Index values comparing this fishery scenario to the reference scenarios are presented in (Tables 7.5a and 7.5b).The community range of variation under a cod fishery highly decreases with respect to the reference scenario for both abundance and biomass of the community as a whole. The mean abundance and biomass of the community are much reduced. The same trend is observed for each size group separately. However, when species are considered separately, the mean abundance of some of them is increased under a cod fishery. The mean abundance of all species, except that of cod and Roundnose grenadier, increases slightly (less than 10%) or moderately (between 10 and 50%). This mean value is due to a higher minimum abundance limit for these species, because their maximum abundance limit decreases therefore not contributing to the mean increase. Yet, the mean biomass is only increased for short-lived species (capelin and Arctic cod) and the only other species that reaches size 5 (Greenland halibut).

Table 7.5a: Abundance comparison of Scenario II (cod fishery). For explanation see text page number 139.

Scenario II Cod fishery		Trend of variation with respect to reference scenario				
group		% min	% max	% mean	% range (max-min)	% magnitude range (range/min)
Abundance of size groups within the community	Size1	-2	-3	-3	-3	-3
	Size2	3	-3	-3	-3	-3
	Size3	-3	-3	-3	-3	-3
	Size4	3	-3	-3	-3	-3
	Size5	-3	-3	-3	-3	3
Abundance of species	Bs	2	-2	1	-3	-3
	Gm	-3	-3	-3	-3	-3
	Mv	2	-1	2	-3	-3
	Cr	-3	-3	-3	-3	-3
	Gc	3	-2	1	-2	-3
	Hp	2	-2	1	-2	-3
	Rh	2	-2	2	-2	-2
	Rr	3	-2	1	-3	-3
	Sma	2	-2	1	-3	-3
	Sme	2	-2	1	-3	-3
Community Abundance	Community	-2	-3	-3	-3	-3

Table 7.5b: Biomass comparison of Scenario II (cod fishery). For explanation see text page number 139.

Scenario II Cod fishery		Trend of variation with respect to reference scenario				
group		% min	% max	% mean	% range (max-min)	% magnitude range (range/min)
Biomass of size groups within the community	Size1	-2	-3	-3	-3	-3
	Size2	3	-3	-3	-3	-3
	Size3	-3	-3	-3	-3	-3
	Size4	3	-3	-3	-3	-3
	Size5	-3	-3	-3	-3	3
Biomass of species	Bs	3	-3	2	-3	-3
	Gm	-3	-3	-3	-3	-3
	Mv	3	-2	2	-2	-3
	Cr	-3	-3	-3	-3	-3
	Gc	3	-3	-2	-3	-3
	Hp	3	-3	-3	-3	-3
	Rh	3	-1	3	-1	-3
	Rr	3	-2	-1	-3	-3
	Sma	3	-3	-3	-3	-3
	Sme	3	-3	-3	-3	-3
Community Biomass	Community	-3	-3	-3	-3	-3

Contrary to the first scenario (under environmental variability), the community does not return to the reference scenario situation when the cod fishery stops, but seems to reach an alternative stable state (Tables 7.6a and 7.6b). The mean abundance is reduced to less than 10% of that of the reference scenario, but both its minimum and maximum decrease to between 10 and 50%. The differences are more noticeable when community biomass is considered, with a mean reduced more than 50% with respect to the reference scenario. There is an important change in the community size structure, with greatest variations in the largest sizes. The maximum abundance limit for the two species that reach size 5 (cod and Greenland halibut) is reduced to between 10 and 50% from that from the reference scenario.

Table 7.6a: Abundance comparison of the recovery from Scenario II (cod fishery). For explanation see text page number 139.

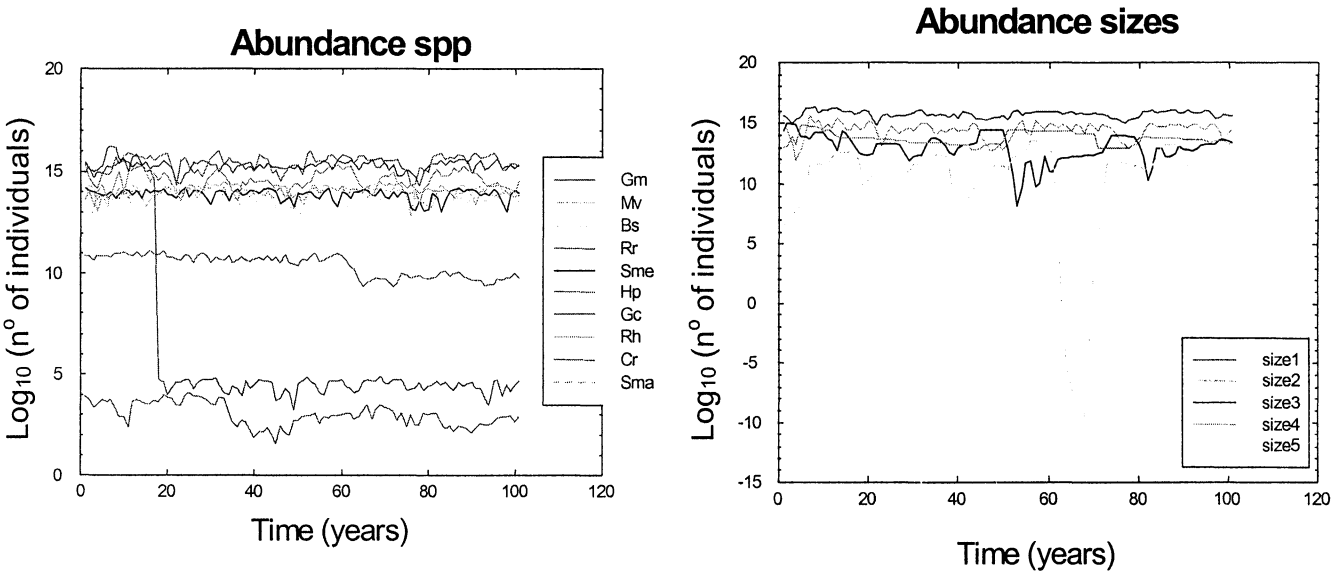
Recovery from cod fishery		Trend of variation with respect to reference scenario				
group		% min	% max	% mean	% range (max-min)	% magnitude range (range/min)
Abundance of size groups within the community	Size1	-1	-1	-1	-1	-1
	Size2	3	-2	-2	-2	-3
	Size3	3	-3	-2	-3	-3
	Size4	3	-3	-3	-3	-3
	Size5	3	-3	-3	-3	-3
Abundance of species	Bs	1	-1	-1	-2	-2
	Gm	1	-2	-2	-2	-2
	Mv	1	-1	-1	-2	-2
	Cr	2	-3	-2	-3	-3
	Gc	1	-1	-1	-1	-2
	Hp	1	-1	-1	-1	-2
	Rh	1	-2	-2	-2	-2
	Rr	3	-1	-1	-2	-3
	Sma	2	-1	-1	-2	-2
	Sme	2	-1	-1	-2	-2
Community Abundance	Community	-2	-2	-1	-2	-1

Table 7.6b: Biomass comparison of the recovery from Scenario II (cod fishery). For explanation see text page number 139.

Recovery from cod fishery		Trend of variation with respect to reference scenario				
group		% min	% max	% mean	% range (max-min)	% magnitude range (range/min)
Biomass of size groups within the community	Size1	-1	-1	-1	-1	-1
	Size2	3	-2	-2	-2	-3
	Size3	3	-3	-2	-3	-3
	Size4	3	-3	-3	-3	-3
	Size5	3	-3	-3	-3	-3
Biomass of species	Bs	1	-2	-1	-3	-3
	Gm	2	-3	-3	-3	-3
	Mv	1	-2	-1	-2	-2
	Cr	2	-3	-2	-3	-3
	Gc	2	-2	-2	-2	-2
	Hp	2	-2	-2	-2	-2
	Rh	1	-3	-2	-3	-3
	Rr	3	-2	-1	-2	-3
	Sma	3	-2	-2	-2	-3
	Sme	3	-2	-2	-2	-3
Community Biomass	Community	-2	-3	-3	-3	-3

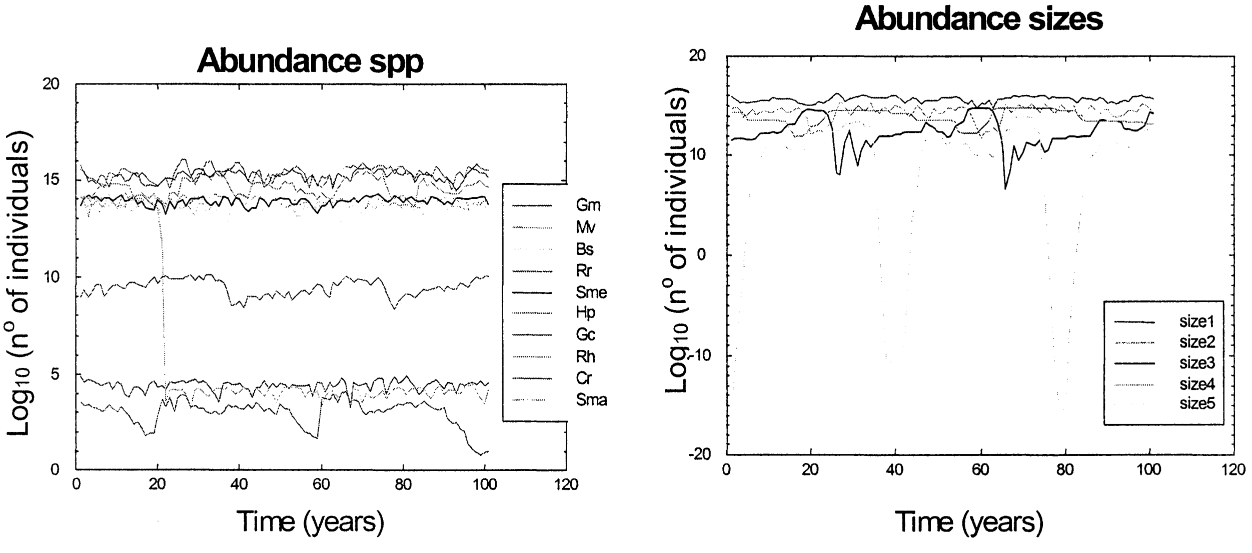
7.3.3. SCENARIO III: FISHERIES AND THE ENVIRONMENT ACTING TOGETHER

This scenario represents a progressive fishery and can be divided into three steps: (1) fishery for cod, (2) fishery for cod and capelin and (3) the fishery for cod stops but the fishery for capelin continues. The community adaptation to these three steps is shown in Figure 7.7. Combination of cod fishery and environmental variability (Step 1 in Fig. 7.7) is observed in the more frequent but less dramatic fluctuations of the size groups (except for size group 5). Environmental variability induces the cod (species) to collapse in a shorter time than was observed in Scenario II. Because the species is less abundant and heavily fished, capelin removal is drastic from the moment its fishery begins (Fig. 7.7, Step 2). When (Fig. 7.7) the cod fishery stops in step 3, this species recovers to reach a high abundance. At the same time fluctuations of size group 5 are reduced in range. But the real recovery of size groups, hence biomass, of cod appears in Figure 7.8, which shows the size groups recovery of cod when its fishery stops (Step 2 to 3) and the recovery of capelin at the end of Step 3 (assuming the fishery stops for all species). Because of its longer life span the recovery of cod takes longer, e.g. no individuals of size group 5 appear before around 16 years after the fishery stops because that is the time for an individual cod to grow to that size.



Step 1 (a)

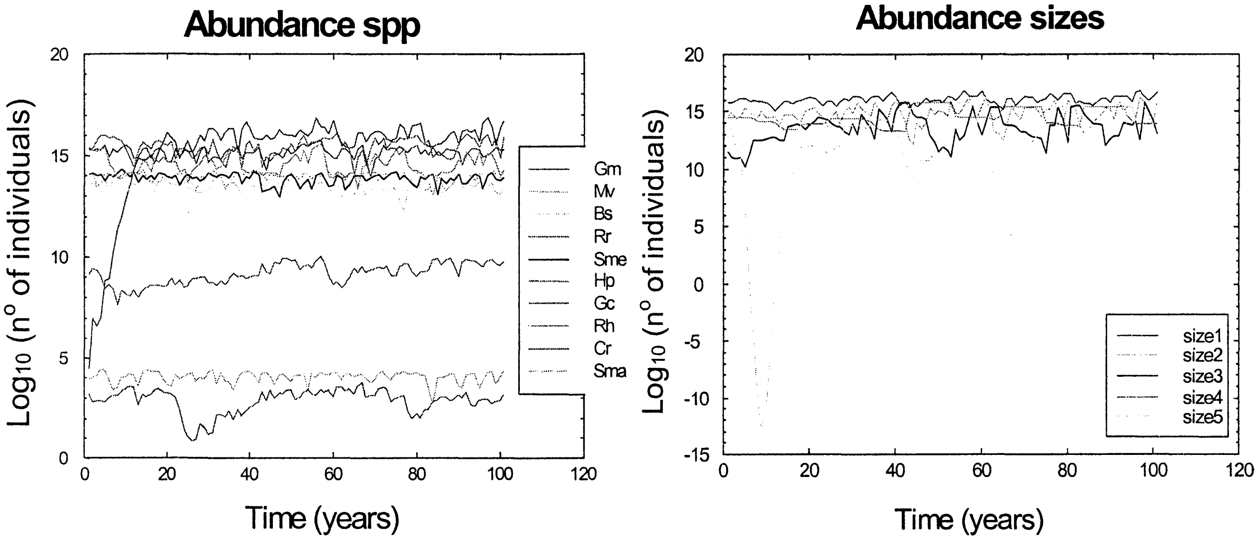
Step 1 (b)



Step 2 (a)

Step 2 (b)

Fig. 7.7. Scenario III: Changes due to progressive fishery and environmental variability. (a) change in species abundance, (b) change in size groups abundance.



Step 3 (a)

Step 3 (b)

Fig. 7.7. Continued. Changes caused by a progressive fishery and environmental variability acting together. (a) change in species abundance, (b) change in size groups abundance.

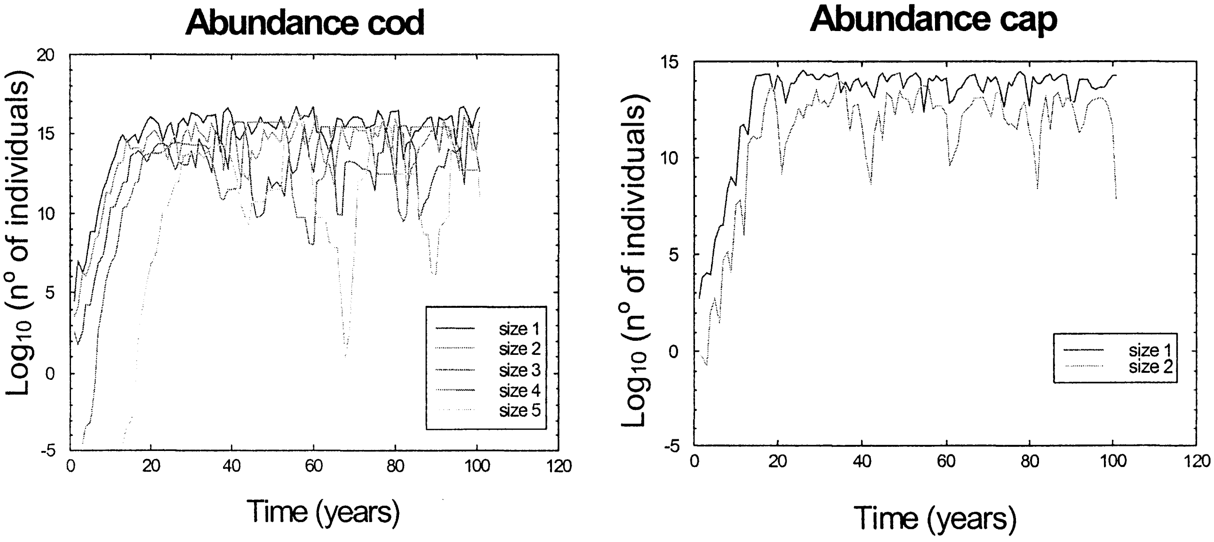


Fig. 7.8. Cod and capelin size groups recovery from their respective targeted fisheries.

The three steps of this scenario can be analysed considering the index values recorded in Tables 7.7a to 7.10b. In Step 1, the community suffers a similar effect to that seen under a cod fishery (Scenario II), only that in this case, because environmental variability also affects the community, the minimum limit for abundance changes more than under a cod fishery alone. This minimum limit is less than 50% of the reference scenario. A drastic decrease of minimum limit is also observed when size groups and species are considered separately. Fishery expansion to capture capelin in addition to cod does not seem to have a significant effect on the community with respect to the situation in Step 1. However, at the level of species, even more species amplify their variation range as a result of an increase in their maximum limit. When the fishery for cod stops (Step 3) the mean abundance remains low because the fishery for capelin continues, but the mean biomass increases. The range of variation of community biomass, which had decreased drastically in Steps 1 and 2, now displays a significant increase because the upper and lower limits are extended.

Table 7.7a: Abundance comparison of Scenario III step 1 (fishery of cod and environmental variability). For explanation see text page number 139.

Scenario III (step 1)		Trend of variation with respect to reference scenario				
group		% min	% max	% mean	% range (max-min)	% magnitude range (range/min)
Abundance of size groups within the community	Size1	-3	-3	-3	-3	3
	Size2	-3	-3	-3	-3	3
	Size3	-3	-3	-3	-3	3
	Size4	-2	-3	-3	-3	-3
	Size5	-3	-3	-3	-3	3
Abundance of species	Bs	-3	-2	-2	2	3
	Gm	-3	-3	-3	-3	2
	Mv	-3	1	-2	3	3
	Cr	-3	-3	-3	-3	3
	Gc	-3	-1	-2	2	3
	Hp	-3	-2	-2	-1	3
	Rh	-3	-2	-2	-2	3
	Rr	-3	-2	-3	-2	3
	Sma	-3	-2	-2	2	3
	Sme	-3	-2	-2	2	3
Community Abundance	Community	-3	-3	-3	-3	3

Table 7.7b: Biomass comparison of Scenario III step 1 (fishery of cod and environmental variability). For explanation see text page number 139.

Sceanrio III (step 1)		Trend of variation with respect to reference scenario				
group		% min	% max	% mean	% range (max-min)	% magnitude range (range/min)
Biomass of size groups within the community	Size1	-3	-3	-3	-3	3
	Size2	-3	-3	-3	-3	3
	Size3	-3	-3	-3	-3	3
	Size4	-2	-3	-3	-3	-3
	Size5	-3	-3	-3	-3	3
Biomass of species	Bs	-3	-3	-2	-3	3
	Gm	-3	-3	-3	-3	-3
	Mv	-3	2	-2	3	3
	Cr	-3	-3	-3	-3	2
	Gc	-2	3	-2	3	3
	Hp	-3	2	-3	2	3
	Rh	-3	3	3	3	3
	Rr	-3	-3	-3	-3	3
	Sma	-3	-2	-3	-2	3
	Sme	-3	-3	-3	-3	3
Community Biomass	Community	-3	-3	-3	-3	-2

Table 7.8a: Abundance comparison of Scenario III step 2 (fishery of cod and capelin and environmental variability). For explanation see text page number 139.

Sceanrio III (step 2)		Trend of variation with respect to reference scenario				
group		% min	% max	% mean	% range (max-min)	% magnitude range (range/min)
Abundance of size groups within the community	Size1	-3	-3	-3	-3	3
	Size2	-3	-3	-3	-3	3
	Size3	-3	-3	-3	-3	3
	Size4	-3	-3	-3	-3	-1
	Size5	-3	-3	-3	-3	3
Abundance of species	Bs	-3	-2	-2	2	3
	Gm	-3	-3	-3	-3	3
	Mv	-3	-3	-3	-3	3
	Cr	-3	-3	-3	-3	3
	Gc	-3	-1	-2	2	3
	Hp	-3	-1	-2	1	3
	Rh	-3	-2	-2	-2	3
	Rr	-3	-2	-3	-2	3
	Sma	-3	-2	-2	2	3
	Sme	-3	-2	-2	2	3
Community Abundance	Community	-3	-3	-3	-3	3

Table 7.8b: Biomass comparison of Scenario III step 2 (fishery of cod and capelin and environmental variability). For explanation see text page number 139.

Scenario III (step 2)		Trend of variation with respect to reference scenario				
group		% min	% max	% mean	% range (max-min)	% magnitude range (range/min)
Biomass of size groups within the community	Size1	-3	-3	-3	-3	3
	Size2	-3	-3	-3	-3	3
	Size3	-3	-3	-3	-3	3
	Size4	-3	-3	-3	-3	-1
	Size5	-3	-3	-3	-3	3
Biomass of species	Bs	-3	-2	-2	-1	3
	Gm	-3	-3	-3	-3	-2
	Mv	-3	-3	-3	-3	3
	Cr	-3	-3	-3	-3	3
	Gc	-3	3	1	3	3
	Hp	-3	3	-2	3	3
	Rh	-3	3	3	3	3
	Rr	-3	-3	-3	-3	3
	Sma	-3	-2	-2	-2	3
	Sme	-3	-1	-2	1	3
Community Biomass	Community	-3	-3	-3	-3	2

Table 7.9a: Abundance comparison of Scenario III step 3 (fishery of capelin and environmental variability). For explanation see text page number 139.

Sceanrio III (step 3)		Trend of variation with respect to reference scenario				
group		% min	% max	% mean	% range (max-min)	% magnitude range (range/min)
Abundance of size groups within the community	Size1	-3	-2	-2	-2	3
	Size2	-3	3	-2	3	3
	Size3	-3	3	3	3	3
	Size4	-3	3	3	3	3
	Size5	-3	3	3	3	3
Abundance of species	Bs	-3	1	-2	3	3
	Gm	-3	1	-2	1	3
	Mv	-3	-3	-3	-3	3
	Cr	-3	-2	-3	-2	3
	Gc	-3	-2	-2	2	3
	Hp	-3	1	-2	2	3
	Rh	-3	-2	-2	-1	3
	Rr	-3	1	-2	2	3
	Sma	-3	2	-2	3	3
	Sme	-3	1	-2	3	3
Community Abundance	Community	-3	-2	-2	-1	3

Table 7.9b: Biomass comparison of Scenario III step 3 (fishery of capelin and environmental variability). For explanation see text page number 139.

Sceanrio III (step 3)		Trend of variation with respect to reference scenario				
group		% min	% max	% mean	% range (max-min)	% magnitude range (range/min)
Biomass of size groups within the community	Size1	-3	-2	-2	-2	3
	Size2	-3	3	-2	3	3
	Size3	-3	3	3	3	3
	Size4	-3	3	3	3	3
	Size5	-3	3	3	3	3
Biomass of species	Bs	-3	3	-2	3	3
	Gm	-2	3	3	3	3
	Mv	-3	-3	-3	-3	3
	Cr	-3	-2	-3	-2	3
	Gc	-3	3	-1	3	3
	Hp	-3	3	-1	3	3
	Rh	-3	3	-2	3	3
	Rr	-3	3	-2	3	3
	Sma	-3	3	2	3	3
	Sme	-3	3	2	3	3
Community Biomass	Community	-2	3	3	3	3

Table 7.10a: Abundance comparison of the recovery from Scenario III (fishery and environmental variability). For explanation see text page number 139.

Recovery from Fishery and environmental variability		Trend of variation with respect to reference scenario				
group		% min	% max	% mean	% range (max-min)	% magnitude range (range/min)
Abundance of size groups within the community	Size1	-3	-2	-2	-1	3
	Size2	-3	3	-2	3	3
	Size3	-3	3	3	3	3
	Size4	-3	3	3	3	3
	Size5	-3	3	3	3	3
Abundance of species	Bs	-3	-2	-2	3	3
	Gm	-3	2	-2	2	3
	Mv	-3	-1	-3	3	3
	Cr	-3	3	3	3	3
	Gc	-3	2	-2	3	3
	Hp	-3	-1	-2	1	3
	Rh	-3	-2	-2	-2	3
	Rr	-3	2	-2	3	3
	Sma	-3	-1	-2	3	3
	Sme	-3	2	-2	3	3
Community Abundance	Community	-3	1	-2	2	3

Table 7.10b: Biomass comparison of the recovery from Scenario III (fishery and environmental variability). For explanation see text page number 139.

Recovery of Fishery and environmental variability		Trend of variation with respect to reference scenario				
group		% min	% max	% mean	% range (max-min)	% magnitude range (range/min)
Biomass of size groups within the community	Size1	-3	-2	-2	-1	3
	Size2	-3	3	-2	3	3
	Size3	-3	3	3	3	3
	Size4	-3	3	3	3	3
	Size5	-3	3	3	3	3
Biomass of species	Bs	-3	3	-2	3	3
	Gm	-3	3	3	3	3
	Mv	-3	3	-2	3	3
	Cr	-3	3	2	3	3
	Gc	-3	3	3	3	3
	Hp	-3	3	3	3	3
	Rh	-3	3	2	3	3
	Rr	-3	2	-1	3	3
	Sma	-3	3	3	3	3
	Sme	-3	3	3	3	3
Community Biomass	Community	-2	3	3	3	3

7.4. COMPARISON OF SCENARIOS AND EXPERIMENTAL DATA

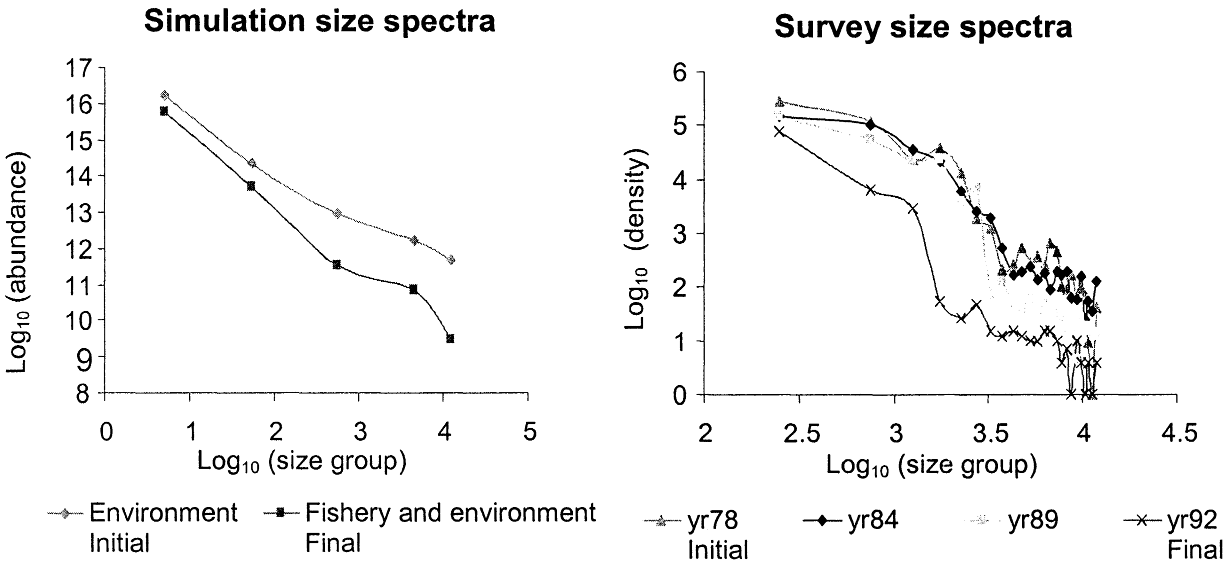
Only a rough comparison can be made between the simulation results and empirical data. There are several results. First, in the empirical data, size group 1 (and probably 2) is certainly underrepresented. This stage corresponds to individuals living in pelagic and nearshore habitats, and therefore they are generally not recorded in the bottom trawl surveys. Another problem concerns the simulation assumptions. The model considers that only one or two species are removed by a fishery and at a constant rate over time. In addition, in the model no species is allowed to go extinct because the fishery is applied to mature sizes and stops when only one mature individual remains. The fishery in the real community is of course much more diverse and complex. In a real fishery many species are captured and the fishery usually intensifies over time. Most size classes are captured, and are effectively removed from the community either as bycatch or dead discards. Not all species present in the community are considered in the model, though the 10 species considered in the model do account for more than 99% of the community abundance. Finally, the empirical data cover a period of 16 years and the comparison must be of this short-time trend with the long-term trend (100^+ years) that results from the simulation. Recognizing these pitfalls, we go on to compare the changes in the community observed in nature with the response of the community in the simulation exercise.

The changes in the Newfoundland demersal community are the result of heavy fishery exploitation (Myers et al., 1996; Walters and Maguire, 1996). Therefore, the community should have passed from a situation similar to the environmental variability scenario (Scenario I) to a situation similar to the fishery and environmental variability combined scenario (Scenario III, step 1). The fact that our empirical data concerning the community corresponds to a period of drastic changes in the demersal fish community allows us to compare the change of the size spectrum of the community during the survey period (see Chapter 5) with the changes in size spectrum of the community when simulated under Scenarios I and III, Step 1.

Nonetheless, comparison cannot be done directly between apparently similar scenarios in the real and in the simulated community. The reason is that we cannot determine equal size group intervals for the empirical data directly equivalent to the size groups present in the simulation model. As mentioned before, the two smallest size groups considered in the model (from 0 to 10 g and from 10 to 100 g) are underrepresented in the survey data of the Newfoundland fish community. Their use will change the shape of the size spectrum, which will appear to have a dome shape. Therefore, what is compared here is whether the real and simulated community follow a similar trend when passing from one scenario to another. The size spectrum is used to study these changes.

In order to build the size spectrum for a simulated community we consider size intervals of width equal to that of the first size group, i.e. of 10g. But size groups in the model are on a logarithmic scale. Thus, to obtain a representative 10g interval for each size we divide the abundance in the size intervals of the model to make groups of 10g. We then select the central group of each size group to construct the size spectrum of the community, i.e. for size group 1 there is only one group so all individuals of this size group are considered, for size group 2 there are 9 intervals of 10g, so we select the central interval, 50-60g, and consider that the number of individuals in this interval is equal to the number of individuals in size group 2 divided by 9, and for the rest of the size groups we proceed similarly depending on the number of 10g intervals each contains.

The change of the simulated community size spectrum is represented in Fig. 7.9 (a) by curves at the beginning and at the end of the period of perturbation and can be compared with the changes observed in the real community (Chapter 5, Fig 5.2) included here in Fig. 7.9 (b). The changes in both cases follow a similar trend. The simulation of a fishery targeting large top predators induces an overall reduction of the community abundance, and a decrease in all size groups that is also seen in the real Newfoundland community size spectrum. In both the real and the simulated community, this reduction increases across size classes. Thus, there is only a slight reduction (in logarithmic scale) in the smallest sizes compared to a drastic reduction in the largest sizes of the community. The changes predicted by the model resemble the changes observed in the real community under heavy size selective exploitation of cod.



(a)

(b)

Fig. 7.9: Comparison of community size spectrum change over time between the simulated community (a) and the real community (b).

7.5. CONCLUSIONS

At first sight the model simulating the dynamics of Newfoundland demersal fish community might seem to give contrived and/or self-evident results. We set the premises and we observe the consequent results under those premises. As with any model, the results respond to and depend a great deal on the construction and assumptions made during the process of building the model. However, the model also shows community characteristics that are not easily observed without simulation. Outcomes indicate the relative abundance and biomass of species and size group structure in the community, as well as indicators concerning the long-term indirect effect of different kinds of disturbances on the community. The simulation exercise allows testing whether the community is going to become more or less variable under different scenarios, and which size groups and species are prone to change more under a specific disturbance. Of course, how well we simulate the disturbing process will influence how well we can simulate its effect. That constitutes a future task; here the purpose was to formulate a dynamic model reflecting the size structure of the fish community and see it at work.

As can be concluded from the simulation of the three scenarios presented in this chapter, the fish community fluctuates strongly due to environmental variability. When size selective fishing pressure is added, the community as a whole is reduced more than 50% in both abundance and biomass. All size groups in the community suffer this reduction, but not all species do so when considered separately. However, the punctuated increases in abundance and/or biomass of some species do not compensate for the total net loss in the community. Thus, evaluation of single stocks may be misleading in regard to conclusions about the whole community. In the fishery simulation a constant fishery was assumed and the output of that model can be identified with Community II in Chapter 1 (Fig. 1.1), with the figure redrawn here as Fig. 7.10 to show the scenarios.

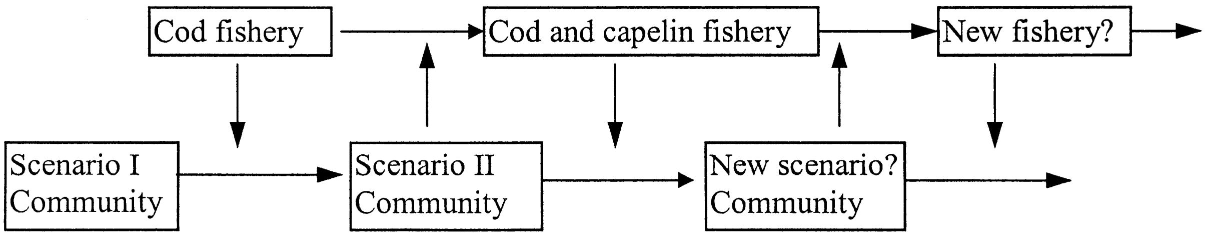


Fig. 7.10 Simulation of fish-fisheries dynamics with the model scenarios indicated.6

If the fishery intensifies or shifts its target to those species where mean abundance or biomass has increased, then the fishery will change the community again from an already decimated one (more than 50% decrease in biomass and abundance) to a new state (Community III in Chapter 1, Fig. 1.1) which is likely to be even poorer. At this stage the community should be compared to the first reference point of the community stage (Community I) instead of to Community II. This is important in order to conclude the true state of the community, i.e. Community III may appear in a better condition (as more abundant and with a greater presence of large size groups) than Community II, but may still be very far from the standard of Community I. Short-term management of fisheries tends to focus alone on the period in which initial conditions from the previous few years influence community dynamics, neglecting the importance of life history characteristics in the long run. In the model, which does not contemplate extinction of species, the community may recover to the initial or an alternative stable state, but only if given enough time. A conclusion from the model is that knowing about the fluctuations of the community is at least as important as knowledge of abundance or biomass. For the fish community, large fluctuations represent a wider range in which the community may exist, whereas for the fishery greater fluctuations in the fish community means more variability of captures, which reduces the ability to manage the fishery.

Chapter 8:
Epilogue

St. John's, 2 July 2002, the 10th anniversary of the cod moratorium in Newfoundland: Just as in those days 10 years ago, scientists still struggle to predict the abundance trend of the fish stock, governments struggle to manage the fishery, fishermen struggle to make a living, fishing villages struggle to keep their culture, and the fish struggle to survive. After 10 years, I think it can be said that this is not a short-term problem, and thus a long-term approach to addressing fish community dynamics must be adopted.

This thesis started by defining the fish-fishery interaction system and considering its unfortunate history. Through the first chapter we argued that the fishery is the only variable that can be manipulated but that the fish community must be the ultimate focus of study and that its dynamics set the limits of the system. Despite the fact that our main interest is in the ecology of a demersal fish community, the drastic changes that fishing communities are suffering led us to pursue the study within a framework that hopefully can be useful for the long-term management of the resources.

The composition of the demersal fish community off Newfoundland has changed over time in what seems to be a trend towards a different structure. The life history characteristics of each component species influence the species dynamics. The length of life stages for a certain species will influence the species survival rate in respect to environmental variability and predation, the therefore percentage of individuals that reach maturity and contribute to the production of new generations. The combination of these processes results in the different species reactions, in time and abundance, to perturbations. Allometry of life history parameters makes size a good indicator of species response to perturbations. Size consideration improves the usual species-by-species approach to study the response of fish to perturbation. Predation not only occurs within the same species, it links species together making the dynamics of a species dependent on what happens with the rest of the species in the community. Furthermore, trophic interactions structure the community as a whole and determine its dynamics. Based on the importance of size dependent predation as a link among individuals in the community, we study size as an indicator of structure and dynamics at the community level. We propose the idea of size groups as functional groups of the community as others has also suggested.

A size-based approach seems most adequate considering that under the size selective pressure a fishery exerts, the structure of populations of many fish is shifted towards smaller sizes and these changes must affect trophic interactions. Therefore, the whole community structure will change. Size spectra analysis, in which size groups are considered the functional groups within the community, reflects the trophic structure of the community.

The construction of a size-based model permits simulation of the fish community dynamics, and achieves a three-fold objective: (1) explain how interactions among species result in the structure and dynamics of the fish community overall, (2) test how external disturbances influence the community structure and dynamics, and (3) provide a tool for management decisions by allowing the consideration of possible long-term effects of different fishing strategies.

Biological interactions maintain the abundance of species and size functional groups in a stable state within which species and size groups fluctuate within certain limits. Environmental variability decreases the mean abundance of the community but greatly increases the mean biomass. The biomass fluctuations are amplified and only the high number of small individuals reverts this tendency in the abundance fluctuations. Thus, abundance fluctuations of the whole community are reduced, despite they are amplified in most size groups. A continuous cod fishery has a drastic effect on the relative abundance of size groups decreasing the abundance and biomass of the community and reducing the limits between which the community may vary. Despite changes in the relative abundance of species, in no case is there any indication of replacement in absolute abundance of one species by another. If environmental variability ceases the community recovers to a stable state similar to the original situation without disturbances. The recovery process from a fishery, however, may take the community to an alternative stable state and the time to reach that state will take longer than the life span of the species of the community. For long-lived species this time is longer than 30 years.

The results here are only some of the many scenarios that can be considered. Better knowledge about species biology and the better data on size will significantly improve the performance of the model. However, conservative estimation of species parameters may be used as a precautionary approach to test the behaviour of species, size groups and the whole community under possible management scenarios.

We find that a size-based approach to the study of fish communities is necessary to deal with properties of the community that cannot be explained by looking at each single species one at a time, especially over the long term. In the future, size-based functional group dynamics in time and space can help to define the spatial and temporal frameworks within which to consider the community. Future challenges for the model are its adaptation to deal with the spatial variability of interactions and to include new taxa in order to observe whole ecosystem dynamics. Reference to recent work with stable isotopes (e.g. δ^{15} N) to determine trophic levels can be especially important to improve the model, as well as a collaboration among single-species fishery experts to determine the community matrix with the highest possible quality.

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Appendix A

Computer form of size-based community model

Matlab is the software program in which the model is built as an M-file and run in the Matlab workspace. The symbol % preceding a sentence indicates that the sentence is only an explanation or notation for the author or users and do not form part of the model. In those sentences the reader will find the explanation to understand and run the model.

% S, is the arbitrary name given to the model of the community considering only biological interactions (the one presented in this appendix). Under this name (S) is saved the file that contains the model. This name also identifies the model (in the command "function" below), and indicates to the workspace the model that should be run.

% **Section 1: Input data**

% To initialize the model it is necessary to state in the Matlab workspace:

% 1.- The initial value of the variables:

% The model variables are the individuals of each size group and species. Thus the variables are named by the letter n followed by 2 or 3 letters identifying the species plus a number identifying the corresponding size group.

% The letters Gme for the species identification is: Bs for Arctic Gm, Cr for Roundnose grenadier, Gm for Atlantic Gm, Gc for Witch flounder, Hp for American plaice, Mv for capelin, Rr for Thorny skate, Rh for Greenland halibut, Sma for Golden redfish, and Sme for Deep water redfish. The size group number can go from 1 to 5.

% To refer to the initial value of the variables, a 0 is added after the size group number. Thus for the variable nGm1 (Gm individuals in size group 1), the initial value is named nGm10. To initialize the model we gave the value of 1 to each size group of each species as follows:

```
% nGm10=1; nGm20=1; nGm30=1; nGm40=1; nGm50=1; nMv10=1; nMv20=1;
nBs10=1; nBs20=1; nBs30=1; nSme10=1; nSme20=1; nSme30=1; nSme40=1;
nHp10=1; nHp20=1; nHp30=1; nHp40=1; nRh10=1; nRh20=1; nRh30=1;
nRh40=1; nRh50=1; nCr10=1; nCr20=1; nCr30=1; nCr40=1; nGc10=1;
nGc20=1; nGc30=1; nGc40=1; nSma10=1; nSma20=1; nSma30=1; nSma40=1;
nRr10=1; nRr20=1; nRr30=1; nRr40=1;
```

% 2.- The number of iterations, i.e. the time period for which we run the model: For the first time we selected a 500 years time period as follows:

```
% runlen =500;
```

% 3.- The order to start to run the model that correspond to the order "function" in the model but removing the word "function". Thus it will be the expression:

```
%[nGm1,nGm2,nGm3,nGm4,nGm5,nMv1,nMv2,nBs1,nBs2,nBs3,nHp1,nHp2,n
Hp3,nHp4,nRh1,nRh2,nRh3,nRh4,nRh5,nSme1,nSme2,nSme3,nSme4,nCr1,nCr2
,nCr3,nCr4,nGc1,nGc2,nGc3,nGc4,nSma1,nSma2,nSma3,nSma4,nRr1,nRr2,nRr3
,nRr4]=S(nGm10,nGm20,nGm30,nGm40,nGm50,nMv10,nMv20,nBs10,nBs20,n
Bs30,nHp10,nHp20,nHp30,nHp40,nRh10,nRh20,nRh30,nRh40,nRh50,nSme10,n
Sme20,nSme30,nSme40,nCr10,nCr20,nCr30,nCr40,nGc10,nGc20,nGc30,nGc40,
nSma10,nSma20,nSma30,nSma40,nRr10,nRr20,nRr30,nRr40,runlen)
```

% The key “enter” is pressed after each input data. The model will star to run when this key is pressed after writing the order to start the model run and will end when all iterations requested have been done. Once all iterations finish it will appear in the screen the initial model output corresponding to the value of the variables in each iteration performed.

% **Section 2: Model set up**

% The function statement below indicates to the computer the model we are going to run. This function indicates that the model variables (in the first term) are going to be obtained by the model (indicated by its name) using the initial variables values (in the second term) and considering the number of iterations (runlen command).

```
function[nGm1,nGm2,nGm3,nGm4,nGm5,nMv1,nMv2,nBs1,nBs2,nBs3,nHp1,nH
        p2,nHp3,nHp4,nRh1,nRh2,nRh3,nRh4,nRh5,nSme1,nSme2,nSme3,nSme
        4,nCr1,nCr2,nCr3,nCr4,nGc1,nGc2,nGc3,nGc4,nSma1,nSma2,nSma3,nS
        ma4,nRr1,nRr2,nRr3,nRr4]=S(nGm10,nGm20,nGm30,nGm40,nGm50,nM
        v10,nMv20,nBs10,nBs20,nBs30,nHp10,nHp20,nHp30,nHp40,nRh10,nRh2
        0,nRh30,nRh40,nRh50,nSme10,nSme20,nSme30,nSme40,nCr10,nCr20,n
        Cr30,nCr40,nGc10,nGc20,nGc30,nGc40,nSma10,nSma20,nSma30,nSma
        40,nRr10,nRr20,nRr30,nRr40,runlen)
```

% The next line means that the variables initial values are going to be named by means of adding a 0 at the end of the model variables' name.

```
nGm1=[nGm10];nGm2=[nGm20];nGm3=[nGm30];nGm4=[nGm40];nGm5=[nGm5
        0];nMv1=[nMv10];nMv2=[nMv20];nBs1=[nBs10];nBs2=[nBs20];nBs3=[nBs
        30];nHp1=[nHp10];nHp2=[nHp20];nHp3=[nHp30];nHp4=[nHp40];nRh1=[n
        Rh10];nRh2=[nRh20];nRh3=[nRh30];nRh4=[nRh40];nRh5=[nRh50];nSme1
        =[nSme10];nSme2=[nSme20];nSme3=[nSme30];nSme4=[nSme40];nCr1=[
        nCr10];nCr2=[nCr20];nCr3=[nCr30];nCr4=[nCr40];nGc1=[nGc10];nGc2=[n
        Gc20];nGc3=[nGc30];nGc4=[nGc40];nSma1=[nSma10];nSma2=[nSma20];
```

```
nSma3=[nSma30];nSma4=[nSma40];nRr1=[nRr10];nRr2=[nRr20];nRr3=[n
Rr30];nRr4=[nRr40];
```

% **Section 3: The model**

% The next line indicates that the model should run the same number of iterations indicated in the input data.

```
for t=1:runlen
```

% **Subsection 1: Distribution among ages**

% The following subsection is only used in the first iteration in the first running of the model, i.e. only for time =1. This section indicates the initial age distribution of species. It is necessary because although the model variables are species size groups, it considers the age distribution of individuals.

% The input values are for each species in each size group, but a size group can account for several ages of the species. In this section the number of individuals of each species size group is equally distributed in the corresponding ages of that species size. The equal distribution could be changed if there were a case where the real age distribution of individuals of a species was known.

% New variables corresponding to the individuals of a species in a size group and in a certain age are Created and named using the same notation as for the variables of species size groups adding a number at the end corresponding to the age of the individuals, e.g. a new variable will be nGm11, which refers to the individuals of species Gm in size group 1 and age 1.

% Further in the model other variables are created and in all of them the reference to the species, size group and age will be done as indicated in the previous line for the new variable.

```
%       The letter t in brackets identifies the iteration for which the value is considered: (t)
        for the actual iteration or (t-1) for the previous iteration.
%       It can be considered that the model really starts in the year 2, since the output for
        year 1 will be the same as the input.

if t<=1

nGm11(t)=nGm1(t);
nGm22(t)=nGm2(t);
nGm33(t)=nGm3(t)/3;
nGm34(t)=nGm3(t)/3;
nGm35(t)=nGm3(t)/3;
nGm46(t)=nGm4(t)/10;
nGm47(t)=nGm4(t)/10;
nGm48(t)=nGm4(t)/10;
nGm49(t)=nGm4(t)/10;
nGm410(t)=nGm4(t)/10;
nGm411(t)=nGm4(t)/10;
nGm412(t)=nGm4(t)/10;
nGm413(t)=nGm4(t)/10;
nGm414(t)=nGm4(t)/10;
nGm415(t)=nGm4(t)/10;
nGm516(t)=nGm5(t)/5;
nGm517(t)=nGm5(t)/5;
nGm518(t)=nGm5(t)/5;
nGm519(t)=nGm5(t)/5;
nGm520(t)=nGm5(t)/5;
nMv11(t)=nMv1(t)/2;
nMv12(t)=nMv1(t)/2;
nMv23(t)=nMv2(t)/3;
```

```
nMv24(t)=nMv2(t)/3;
nMv25(t)=nMv2(t)/3;
nBs11(t)=nBs1(t)/2;
nBs12(t)=nBs1(t)/2;
nBs23(t)=nBs2(t)/3;
nBs24(t)=nBs2(t)/3;
nBs25(t)=nBs2(t)/3;
nBs36(t)=nBs3(t)/3;
nBs37(t)=nBs3(t)/3;
nBs38(t)=nBs3(t)/3;
nSme11(t)=nSme1(t);
nSme22(t)=nSme2(t)/3;
nSme23(t)=nSme2(t)/3;
nSme24(t)=nSme2(t)/3;
nSme35(t)=nSme3(t)/6;
nSme36(t)=nSme3(t)/6;
nSme37(t)=nSme3(t)/6;
nSme38(t)=nSme3(t)/6;
nSme39(t)=nSme3(t)/6;
nSme310(t)=nSme3(t)/6;
nSme411(t)=nSme4(t)/30;
nSme412(t)=nSme4(t)/30;
nSme413(t)=nSme4(t)/30;
nSme414(t)=nSme4(t)/30;
nSme415(t)=nSme4(t)/30;
nSme416(t)=nSme4(t)/30;
nSme417(t)=nSme4(t)/30;
nSme418(t)=nSme4(t)/30;
nSme419(t)=nSme4(t)/30;
nSme420(t)=nSme4(t)/30;
```

```
nSme421(t)=nSme4(t)/30;
nSme422(t)=nSme4(t)/30;
nSme423(t)=nSme4(t)/30;
nSme424(t)=nSme4(t)/30;
nSme425(t)=nSme4(t)/30;
nSme426(t)=nSme4(t)/30;
nSme427(t)=nSme4(t)/30;
nSme428(t)=nSme4(t)/30;
nSme429(t)=nSme4(t)/30;
nSme430(t)=nSme4(t)/30;
nSme431(t)=nSme4(t)/30;
nSme432(t)=nSme4(t)/30;
nSme433(t)=nSme4(t)/30;
nSme434(t)=nSme4(t)/30;
nSme435(t)=nSme4(t)/30;
nSme436(t)=nSme4(t)/30;
nSme437(t)=nSme4(t)/30;
nSme438(t)=nSme4(t)/30;
nSme439(t)=nSme4(t)/30;
nSme440(t)=nSme4(t)/30;
nHp11(t)=nHp1(t)/2;
nHp12(t)=nHp1(t)/2;
nHp23(t)=nHp2(t)/2;
nHp24(t)=nHp2(t)/2;
nHp35(t)=nHp3(t)/6;
nHp36(t)=nHp3(t)/6;
nHp37(t)=nHp3(t)/6;
nHp38(t)=nHp3(t)/6;
nHp39(t)=nHp3(t)/6;
nHp310(t)=nHp3(t)/6;
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```
nHp411(t)=nHp4(t)/15;
nHp412(t)=nHp4(t)/15;
nHp413(t)=nHp4(t)/15;
nHp414(t)=nHp4(t)/15;
nHp415(t)=nHp4(t)/15;
nHp416(t)=nHp4(t)/15;
nHp417(t)=nHp4(t)/15;
nHp418(t)=nHp4(t)/15;
nHp419(t)=nHp4(t)/15;
nHp420(t)=nHp4(t)/15;
nHp421(t)=nHp4(t)/15;
nHp422(t)=nHp4(t)/15;
nHp423(t)=nHp4(t)/15;
nHp424(t)=nHp4(t)/15;
nHp425(t)=nHp4(t)/15;
nRh11(t)=nRh1(t)/2;
nRh12(t)=nRh1(t)/2;
nRh23(t)=nRh2(t)/2;
nRh24(t)=nRh2(t)/2;
nRh35(t)=nRh3(t)/6;
nRh36(t)=nRh3(t)/6;
nRh37(t)=nRh3(t)/6;
nRh38(t)=nRh3(t)/6;
nRh39(t)=nRh3(t)/6;
nRh310(t)=nRh3(t)/6;
nRh411(t)=nRh4(t)/5;
nRh412(t)=nRh4(t)/5;
nRh413(t)=nRh4(t)/5;
nRh414(t)=nRh4(t)/5;
nRh415(t)=nRh4(t)/5;
```

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nRh516(t)=nRh5(t)/5;
nRh517(t)=nRh5(t)/5;
nRh518(t)=nRh5(t)/5;
nRh519(t)=nRh5(t)/5;
nRh520(t)=nRh5(t)/5;
nCr11(t)=nCr1(t)/2;
nCr12(t)=nCr1(t)/2;
nCr23(t)=nCr2(t)/7;
nCr24(t)=nCr2(t)/7;
nCr25(t)=nCr2(t)/7;
nCr26(t)=nCr2(t)/7;
nCr27(t)=nCr2(t)/7;
nCr28(t)=nCr2(t)/7;
nCr29(t)=nCr2(t)/7;
nCr310(t)=nCr3(t)/16;
nCr311(t)=nCr3(t)/16;
nCr312(t)=nCr3(t)/16;
nCr313(t)=nCr3(t)/16;
nCr314(t)=nCr3(t)/16;
nCr315(t)=nCr3(t)/16;
nCr316(t)=nCr3(t)/16;
nCr317(t)=nCr3(t)/16;
nCr318(t)=nCr3(t)/16;
nCr319(t)=nCr3(t)/16;
nCr320(t)=nCr3(t)/16;
nCr321(t)=nCr3(t)/16;
nCr322(t)=nCr3(t)/16;
nCr323(t)=nCr3(t)/16;
nCr324(t)=nCr3(t)/16;
nCr325(t)=nCr3(t)/16;
```

```
nCr426(t)=nCr4(t)/15;
nCr427(t)=nCr4(t)/15;
nCr428(t)=nCr4(t)/15;
nCr429(t)=nCr4(t)/15;
nCr430(t)=nCr4(t)/15;
nCr431(t)=nCr4(t)/15;
nCr432(t)=nCr4(t)/15;
nCr433(t)=nCr4(t)/15;
nCr434(t)=nCr4(t)/15;
nCr435(t)=nCr4(t)/15;
nCr436(t)=nCr4(t)/15;
nCr437(t)=nCr4(t)/15;
nCr438(t)=nCr4(t)/15;
nCr439(t)=nCr4(t)/15;
nCr440(t)=nCr4(t)/15;
nGc11(t)=nGc1(t)/2;
nGc12(t)=nGc1(t)/2;
nGc23(t)=nGc2(t)/2;
nGc24(t)=nGc2(t)/2;
nGc35(t)=nGc3(t)/6;
nGc36(t)=nGc3(t)/6;
nGc37(t)=nGc3(t)/6;
nGc38(t)=nGc3(t)/6;
nGc39(t)=nGc3(t)/6;
nGc310(t)=nGc3(t)/6;
nGc411(t)=nGc4(t)/20;
nGc412(t)=nGc4(t)/20;
nGc413(t)=nGc4(t)/20;
nGc414(t)=nGc4(t)/20;
nGc415(t)=nGc4(t)/20;
```

```
nGc416(t)=nGc4(t)/20;
nGc417(t)=nGc4(t)/20;
nGc418(t)=nGc4(t)/20;
nGc419(t)=nGc4(t)/20;
nGc420(t)=nGc4(t)/20;
nGc421(t)=nGc4(t)/20;
nGc422(t)=nGc4(t)/20;
nGc423(t)=nGc4(t)/20;
nGc424(t)=nGc4(t)/20;
nGc425(t)=nGc4(t)/20;
nGc426(t)=nGc4(t)/20;
nGc427(t)=nGc4(t)/20;
nGc428(t)=nGc4(t)/20;
nGc429(t)=nGc4(t)/20;
nGc430(t)=nGc4(t)/20;
nSma11(t)=nSma1(t);
nSma22(t)=nSma2(t)/3;
nSma23(t)=nSma2(t)/3;
nSma24(t)=nSma2(t)/3;
nSma35(t)=nSma3(t)/6;
nSma36(t)=nSma3(t)/6;
nSma37(t)=nSma3(t)/6;
nSma38(t)=nSma3(t)/6;
nSma39(t)=nSma3(t)/6;
nSma310(t)=nSma3(t)/6;
nSma411(t)=nSma4(t)/30;
nSma412(t)=nSma4(t)/30;
nSma413(t)=nSma4(t)/30;
nSma414(t)=nSma4(t)/30;
nSma415(t)=nSma4(t)/30;
```

```
nSma416(t)=nSma4(t)/30;
nSma417(t)=nSma4(t)/30;
nSma418(t)=nSma4(t)/30;
nSma419(t)=nSma4(t)/30;
nSma420(t)=nSma4(t)/30;
nSma421(t)=nSma4(t)/30;
nSma422(t)=nSma4(t)/30;
nSma423(t)=nSma4(t)/30;
nSma424(t)=nSma4(t)/30;
nSma425(t)=nSma4(t)/30;
nSma426(t)=nSma4(t)/30;
nSma427(t)=nSma4(t)/30;
nSma428(t)=nSma4(t)/30;
nSma429(t)=nSma4(t)/30;
nSma430(t)=nSma4(t)/30;
nSma431(t)=nSma4(t)/30;
nSma432(t)=nSma4(t)/30;
nSma433(t)=nSma4(t)/30;
nSma434(t)=nSma4(t)/30;
nSma435(t)=nSma4(t)/30;
nSma436(t)=nSma4(t)/30;
nSma437(t)=nSma4(t)/30;
nSma438(t)=nSma4(t)/30;
nSma439(t)=nSma4(t)/30;
nSma440(t)=nSma4(t)/30;
nRr11(t)=nRr1(t);
nRr22(t)=nRr2(t);
nRr33(t)=nRr3(t)/2;
nRr34(t)=nRr3(t)/2;
nRr45(t)=nRr4(t)/16;
```

```
nRr46(t)=nRr4(t)/16;
nRr47(t)=nRr4(t)/16;
nRr48(t)=nRr4(t)/16;
nRr49(t)=nRr4(t)/16;
nRr410(t)=nRr4(t)/16;
nRr411(t)=nRr4(t)/16;
nRr412(t)=nRr4(t)/16;
nRr413(t)=nRr4(t)/16;
nRr414(t)=nRr4(t)/16;
nRr415(t)=nRr4(t)/16;
nRr416(t)=nRr4(t)/16;
nRr417(t)=nRr4(t)/16;
nRr418(t)=nRr4(t)/16;
nRr419(t)=nRr4(t)/16;
nRr420(t)=nRr4(t)/16;
```

% The model will start at this point in the second iteration. Further runs of the model when starting with the final output of previous runs will also start at this point.

```
else
```

% **Subsection 2:Calculation of predation mortality**

% First the number of individuals in each size group is calculated. All individuals of the community are considered regardless of the species they belong to.

% s1, s2, s3, s4, s5 = number of individuals in size group 1, 2, 3, 4 and 5 respectively. The only reason why s4 is calculated by partial sums of individuals (s41, s42, s43) is for a limitation in the string longitude in the student edition of Matlab.

```
s1=nGm11(t-1)+nMv11(t-1)+nMv12(t-1)+nBs11(t-1)+nBs12(t-1)+nRr11(t-
        1)+nSme11(t-1)+nHp11(t-1)+nHp12(t-1)+nGc11(t-1)+nGc12(t-1)+nRh11(t-
        1)+nRh12(t-1)+nCr11(t-1)+nCr12(t-1)+nSma11(t-1);
s2=nGm22(t-1)+nMv23(t-1)+nMv24(t-1)+nMv25(t-1)+nBs23(t-1)+nBs24(t-
        1)+nBs25(t-1)+nRr22(t-1)+nSme22(t-1)+nSme23(t-1)+nSme24(t-
        1)+nHp23(t-1)+nHp24(t-1)+nGc23(t-1)+nGc24(t-1)+nRh23(t-1)+nRh24(t-
        1)+nCr23(t-1)+nCr24(t-1)+nCr25(t-1)+nCr26(t-1)+nCr27(t-1)+nCr28(t-
        1)+nCr29(t-1)+nSma22(t-1)+nSma23(t-1)+nSma24(t-1);
s3=nGm33(t-1)+nGm34(t-1)+nGm35(t-1)+nBs36(t-1)+nBs37(t-1)+nBs38(t-
        1)+nRr33(t-1)+nRr34(t-1)+nSme35(t-1)+nSme36(t-1)+nSme37(t-
        1)+nSme38(t-1)+nSme39(t-1)+nSme310(t-1)+nHp35(t-1)+nHp36(t-
        1)+nHp37(t-1)+nHp38(t-1)+nHp39(t-1)+nHp310(t-1)+nGc35(t-1)+nGc36(t-
        1)+nGc37(t-1)+nGc38(t-1)+nGc39(t-1)+nGc310(t-1)+nRh35(t-1)+nRh36(t-
        1)+nRh37(t-1)+nRh38(t-1)+nRh39(t-1)+nRh310(t-1)+nCr310(t-
        1)+nCr311(t-1)+nCr312(t-1)+nCr313(t-1)+nCr314(t-1)+nCr315(t-
        1)+nCr316(t-1)+nCr317(t-1)+nCr318(t-1)+nCr319(t-1)+nCr320(t-
        1)+nCr321(t-1)+nCr322(t-1)+nCr323(t-1)+nCr324(t-1)+nCr325(t-
        1)+nSma35(t-1)+nSma36(t-1)+nSma37(t-1)+nSma38(t-1)+nSma39(t-
        1)+nSma310(t-1);
s41=nGm46(t-1)+nGm47(t-1)+nGm48(t-1)+nGm49(t-1)+nGm410(t-1)+nGm411(t-
        1)+nGm412(t-1)+nGm413(t-1)+nGm414(t-1)+nGm415(t-1)+nRr45(t-
        1)+nRr46(t-1)+nRr47(t-1)+nRr48(t-1)+nRr49(t-1)+nRr410(t-1)+nRr411(t-
        1)+nRr412(t-1)+nRr413(t-1)+nRr414(t-1)+nRr415(t-1)+nRr416(t-
        1)+nRr417(t-1)+nRr418(t-1)+nRr419(t-1)+nRr420(t-1)+nSme411(t-
        1)+nSme412(t-1)+nSme413(t-1)+nSme414(t-1)+nSme415(t-
        1)+nSme416(t-1)+nSme417(t-1)+nSme418(t-1)+nSme419(t-
        1)+nSme420(t-1)+nSme421(t-1)+nSme422(t-1)+nSme423(t-
```

```
        1)+nSme424(t-1)+nSme425(t-1)+nSme426(t-1)+nSme427(t-
        1)+nSme428(t-1)+nSme429(t-1)+nSme430(t-1)+nHp411(t-1)+nHp412(t-
        1)+nHp413(t-1)+nHp414(t-1)+nHp415(t-1)+nHp416(t-1)+nHp417(t-
        1)+nHp418(t-1)+nHp419(t-1)+nHp420(t-1)+nHp421(t-1)+nHp422(t-
        1)+nHp423(t-1)+nHp424(t-1)+nHp425(t-1)+nGc411(t-1)+nGc412(t-
        1)+nGc413(t-1)+nGc414(t-1)+nGc415(t-1)+nGc416(t-1)+nGc417(t-
        1)+nGc418(t-1)+nGc419(t-1)+nGc420(t-1)+nGc421(t-1)+nGc422(t-
        1)+nGc423(t-1)+nGc424(t-1)+nGc425(t-1)+nGc426(t-1);
s42=nCr426(t-1)+nCr427(t-1)+nCr428(t-1)+nCr429(t-1)+nCr430(t-1)+nCr431(t-
        1)+nCr432(t-1)+nCr433(t-1)+nCr434(t-1)+nCr435(t-1)+nCr436(t-
        1)+nCr437(t-1)+nCr438(t-1)+nCr439(t-1)+nCr440(t-1)+nGc427(t-
        1)+nGc428(t-1)+nGc429(t-1)+nGc430(t-1)+nRh411(t-1)+nRh412(t-
        1)+nRh413(t-1)+nRh414(t-1)+nRh415(t-1)+nSma411(t-1)+nSma412(t-
        1)+nSma413(t-1)+nSma414(t-1)+nSma415(t-1)+nSma416(t-
        1)+nSma417(t-1)+nSma418(t-1)+nSma419(t-1)+nSma420(t-
        1)+nSma421(t-1)+nSma422(t-1)+nSma423(t-1)+nSma424(t-
        1)+nSma425(t-1)+nSma426(t-1)+nSma427(t-1)+nSma428(t-
        1)+nSma429(t-1)+nSma430(t-1);
s43=nSme431(t-1)+nSme432(t-1)+nSme433(t-1)+nSme434(t-1)+nSme435(t-
        1)+nSme436(t-1)+nSme437(t-1)+nSme438(t-1)+nSme439(t-
        1)+nSme440(t-1)+nSma431(t-1)+nSma432(t-1)+nSma433(t-
        1)+nSma434(t-1)+nSma435(t-1)+nSma436(t-1)+nSma437(t-
        1)+nSma438(t-1)+nSma439(t-1)+nSma440(t-1);
s4=s41+s42+s43;
s5=nGm516(t-1)+nGm517(t-1)+nGm518(t-1)+nGm519(t-1)+nGm520(t-
        1)+nRh516(t-1)+nRh517(t-1)+nRh518(t-1)+nRh519(t-1)+nRh520(t-1);
```

% Predation by size groups: These equations calculate the number of prey individuals that would be eaten by each size group if all predators could get satiation.

% Is21 and Is31 are optimum predation of size group 2 and 3 respectively on size group 1. Is42 is the optimum predation of size group 4 on size group 2, and Is53 is the optimum predation of size group 5 on size group 3.

% Similarly: Is3, Is2 and Is1 are the number of individuals in size group 3, 2 or 1 respectively that would be eaten in optimum conditions for the predator.

```
Is21=60.08*s2;
Is31=396.96*s3;
Is42=262.27*s4;
Is53=64.56*s5;
Is3=Is53;
Is2=Is42;
Is1=Is21+Is31;
```

% But predation is density dependent, therefore this is not the final real predation of each size group. It depends on the relative density of the prey size group to the predator size group and within each species prey the relative density of each prey species with respect to the rest of prey species.

% First we calculate the relative abundance of each prey species size group with respect to the rest of individuals in the same prey size group.

% For example, Gm1 is the relative abundance of size group 1 of Gm divided by the rest of the individuals present in size group 1 in the community.

% For prey size group 1 the calculation is:

```
Gm1=nGm1(t)/(s1-nGm1(t)+1);
```

```
Mv1=nMv1(t)/(s1-nMv1(t)+1);
Bs1=nBs1(t)/(s1-nBs1(t)+1);
Rr1=nRr1(t)/(s1-nRr1(t)+1);
Sme1=nSme1(t)/(s1-nSme1(t)+1);
Hp1=nHp1(t)/(s1-nHp1(t)+1);
Gc1=nGc1(t)/(s1-nGc1(t)+1);
Rh1=nRh1(t)/(s1-nRh1(t)+1);
Cr1=nCr1(t)/(s1-nCr1(t)+1);
Sma1=nSma1(t)/(s1-nSma1(t)+1);

%       Then we calculate the addition of the values just calculated.

ss1=Gm1+Mv1+Bs1+Rr1+Sme1+Hp1+Gc1+Rh1+Cr1+Sma1;

%       Finally we estimate the predation mortality for each prey species size group by
        considering that the proportion of the optimum predation corresponding to each
        species is determined by multiplying this optimum by the relative value of that
        prey species with respect to all prey species. Then the final predation of each prey
        species of a size group is calculated means of the multiplication divided by the
        addition of that percentage of the optimum value and the number of individuals in
        the prey species size group.
%       For example pGm1 is the number of individuals of species Gm and size 1 that die
        due to predation that year.

pGm1=((Gm1/(ss1+1))*Is1*nGm1(t))/((Gm1/(ss1+1))*Is1+nGm1(t)+1);
pMv1=((Mv1/(ss1+1))*Is1*nMv1(t))/((Mv1/(ss1+1))*Is1+nMv1(t)+1);
pBs1=((Bs1/(ss1+1))*Is1*nBs1(t))/((Bs1/(ss1+1))*Is1+nBs1(t)+1);
pRr1=((Rr1/(ss1+1))*Is1*nRr1(t))/((Rr1/(ss1+1))*Is1+nRr1(t)+1);
pSme1=((Sme1/(ss1+1))*Is1*nSme1(t))/((Sme1/(ss1+1))*Is1+nSme1(t)+1);
pHp1=((Hp1/(ss1+1))*Is1*nHp1(t))/((Hp1/(ss1+1))*Is1+nHp1(t)+1);
```

```
pGc1=((Gc1/(ss1+1))*Is1*nGc1(t))/((Gc1/(ss1+1))*Is1+nGc1(t)+1);
pRh1=((Rh1/(ss1+1))*Is1*nRh1(t))/((Rh1/(ss1+1))*Is1+nRh1(t)+1);
pCr1=((Cr1/(ss1+1))*Is1*nCr1(t))/((Cr1/(ss1+1))*Is1+nCr1(t)+1);
pSma1=((Sma1/(ss1+1))*Is1*nSma1(t))/((Sma1/(ss1+1))*Is1+nSma1(t)+1);

%       The same is done for the species of prey size group 2

Gm2=nGm2(t)/(s2-nGm2(t)+1);
Mv2=nMv2(t)/(s2-nMv2(t)+1);
Bs2=nBs2(t)/(s2-nBs2(t)+1);
Rr2=nRr2(t)/(s2-nRr2(t)+1);
Sme2=nSme2(t)/(s2-nSme2(t)+1);
Hp2=nHp2(t)/(s2-nHp2(t)+1);
Gc2=nGc2(t)/(s2-nGc2(t)+1);
Rh2=nRh2(t)/(s2-nRh2(t)+1);
Cr2=nCr2(t)/(s2-nCr2(t)+1);
Sma2=nSma2(t)/(s2-nSma2(t)+1);
ss2=Gm2+Mv2+Bs2+Rr2+Sme2+Hp2+Gc2+Rh2+Cr2+Sma2;
pGm2=((Gm2/(ss2+2))*Is2*nGm2(t))/((Gm2/(ss2+2))*Is2+nGm2(t)+1);
pMv2=((Mv2/(ss2+2))*Is2*nMv2(t))/((Mv2/(ss2+2))*Is2+nMv2(t)+1);
pBs2=((Bs2/(ss2+2))*Is2*nBs2(t))/((Bs2/(ss2+2))*Is2+nBs2(t)+1);
pRr2=((Rr2/(ss2+2))*Is2*nRr2(t))/((Rr2/(ss2+2))*Is2+nRr2(t)+1);
pSme2=((Sme2/(ss2+2))*Is2*nSme2(t))/((Sme2/(ss2+2))*Is2+nSme2(t)+1);
pHp2=((Hp2/(ss2+2))*Is2*nHp2(t))/((Hp2/(ss2+2))*Is2+nHp2(t)+1);
pGc2=((Gc2/(ss2+2))*Is2*nGc2(t))/((Gc2/(ss2+2))*Is2+nGc2(t)+1);
pRh2=((Rh2/(ss2+2))*Is2*nRh2(t))/((Rh2/(ss2+2))*Is2+nRh2(t)+1);
pCr2=((Cr2/(ss2+2))*Is2*nCr2(t))/((Cr2/(ss2+2))*Is2+nCr2(t)+1);
pSma2=((Sma2/(ss2+2))*Is2*nSma2(t))/((Sma2/(ss2+2))*Is2+nSma2(t)+1);

%       and for species of prey size group 3
```

```
Gm3=nGm3(t)/(s3-nGm3(t)+1);
Bs3=nBs3(t)/(s3-nBs3(t)+1);
Rr3=nRr3(t)/(s3-nRr3(t)+1);
Sme3=nSme3(t)/(s3-nSme3(t)+1);
Hp3=nHp3(t)/(s3-nHp3(t)+1);
Gc3=nGc3(t)/(s3-nGc3(t)+1);
Rh3=nRh3(t)/(s3-nRh3(t)+1);
Cr3=nCr3(t)/(s3-nCr3(t)+1);
Sma3=nSma3(t)/(s3-nSma3(t)+1);
ss3=Gm3+Bs3+Rr3+Sme3+Hp3+Gc3+Rh3+Cr3+Sma3;
pGm3=((Gm3/(ss3+3))*ls3*nGm3(t))/((Gm3/(ss3+3))*ls3+nGm3(t)+1);
pBs3=((Bs3/(ss3+3))*ls3*nBs3(t))/((Bs3/(ss3+3))*ls3+nBs3(t)+1);
pRr3=((Rr3/(ss3+3))*ls3*nRr3(t))/((Rr3/(ss3+3))*ls3+nRr3(t)+1);
pSme3=((Sme3/(ss3+3))*ls3*nSme3(t))/((Sme3/(ss3+3))*ls3+nSme3(t)+1);
pHp3=((Hp3/(ss3+3))*ls3*nHp3(t))/((Hp3/(ss3+3))*ls3+nHp3(t)+1);
pGc3=((Gc3/(ss3+3))*ls3*nGc3(t))/((Gc3/(ss3+3))*ls3+nGc3(t)+1);
pRh3=((Rh3/(ss3+3))*ls3*nRh3(t))/((Rh3/(ss3+3))*ls3+nRh3(t)+1);
pCr3=((Cr3/(ss3+3))*ls3*nCr3(t))/((Cr3/(ss3+3))*ls3+nCr3(t)+1);
pSma3=((Sma3/(ss3+3))*ls3*nSma3(t))/((Sma3/(ss3+3))*ls3+nSma3(t)+1);
```

% **Subsection 3: Calculation of offspring production**

% First, the number of offspring that each species would produce if there were no limitations is determined according to the individuals size groups and the species fecundity.

% For example, MGm is the potential offspring production of Gm species.

% It is assumed that 50% of mature individuals are females.

```
MGm=2*10^5*nGm3(t)/4+3*10^6*nGm4(t)/2+1.2*10^7*nGm5(t)/2;
```

```
MMv=4*10^4*nMv2(t)/2;
MBs=10^4*nBs2(t)/2+2*10^4*nBs3(t)/2;
MSme=1.5*10^4*(nSme38(t-1)+nSme39(t-1)+nSme310(t-
        1))/2+2.5*10^4*nSme4(t)/2;
MHp=3.5*10^5*(nHp36(t-1)+nHp37(t-1)+nHp38(t-1)+nHp39(t-1)+nHp310(t-
        1))/2+1.5*10^6*nHp4(t)/2;
MRh=3*10^4*(nRh35(t-1)+nRh36(t-1)+nRh37(t-1)+nRh38(t-1)+nRh39(t-
        1)+nRh310(t-1))/2+2*10^5*nRh4(t) /2+4*10^5*nRh5(t)/2;
MRr=20*nRr4(t)/2;
MGc=3*10^5*(nGc36(t-1)+nGc37(t-1)+nGc38(t-1)+nGc39(t-1)+nGc310(t-
        1))/2+6*10^5*nGc4(t)/2;
MCr=2*10^4*(nCr3(t)/2)+6*10^4*(nCr4(t)/2);
MSma=1.5*10^4*(nSma38(t-1)+nSma39(t-1)+nSma310(t-
        1))/2+2.5*10^4*nSma4(t)/2;
```

% The real offspring production is calculated considering a limitation (Nmax= 10^{10}) for the number of mature individuals that can reproduce and a minimum of 1 individual that is produced (ceil ()).

% For example, MmGm is the offspring production of Gm species that year.

```
MmGm=ceil((10^10/((nGm3(t)/2)+nGm4(t)+nGm5(t)+10^10))*MGm);
MmMv=ceil(10^10*MMv/(nMv2(t)+10^10));
MmBs=ceil((10^10/(nBs2(t)+nBs3(t)+10^10))*MBs);
MmSme=ceil((10^10/(nSme38(t-1)+nSme39(t-1)+nSme310(t-
        1)+nSme4(t)+10^10))*MSme);
MmHp=ceil((10^10/(nHp36(t-1)+nHp37(t-1)+nHp38(t-1)+nHp39(t-1)+nHp310(t-
        1)+nHp4(t)+10^10))*MHp);
MmRh=ceil((10^10/(nRh35(t-1)+nRh36(t-1)+nRh37(t-1)+nRh38(t-1)+nRh39(t-
        1)+nRh310(t-1)+nRh4(t)+nRh5(t)+10^10))*MRh);
MmRr=ceil((10^10/(nRr4(t)+10^10))*MRr);
```

```
MmGc=ceil((10^10/(nGc36(t-1)+nGc37(t-1)+nGc38(t-1)+nGc39(t-1)+nGc310(t-
        1)+nGc4(t)+10^10))*MGc);
MmCr=ceil((10^10/(nCr3(t)+nCr4(t)+10^10))*MCr);
MmSma=ceil((10^10/(nSma38(t-1)+nSma39(t-1)+nSma310(t-
        1)+nSma4(t)+10^10))*MSma);
```

% **Subsection 4: Calculation of next year abundance**

% This calculation is done at the level of each age of each species, assuming that predation mortality is distributed within each size group of each species proportionally to the relative abundance of individuals in each age of that species and size group.

% The offspring production of the previous year will pass to the age 1 of each species in the following.

% All individuals in a certain age pass to the next age or die by predation or end of lifespan in the following year. However, it should be noticed that this does not mean that all individuals in a certain size group pass to the next size group or die in the following year.

% For example, nGm22(t) is the number of individuals for the next year of species Gm in size group 2 and age 2.

```
nGm22(t)=nGm11(t-1)-pGm1;
nMv12(t)=nMv11(t-1)-(pMv1*nMv11(t-1)/(nMv1(t)+1));
nMv23(t)=nMv12(t-1)-(pMv1*nMv12(t-1)/(nMv1(t)+1));
nBs12(t)=nBs11(t-1)-(pBs1*nBs11(t-1)/(nBs1(t)+1));
nBs23(t)=nBs12(t-1)-(pBs1*nBs12(t-1)/(nBs1(t)+1));
nRr22(t)=nRr11(t-1)- pRr1;
nSme22(t)=nSme11(t-1)-pSme1;
nHp12(t)=nHp11(t-1)-(pHp1*nHp11(t-1)/(nHp1(t)+1));
nHp23(t)=nHp12(t-1)-(pHp1*nHp12(t-1)/(nHp1(t)+1));
```

```
nGc12(t)=nGc11(t-1)-(pGc1*nGc11(t-1)/(nGc1(t)+1));
nGc23(t)=nGc12(t-1)-(pGc1*nGc12(t-1)/(nGc1(t)+1));
nRh12(t)=nRh11(t-1)-(pRh1*nRh11(t-1)/(nRh1(t)+1));
nRh23(t)=nRh12(t-1)-(pRh1*nRh12(t-1)/(nRh1(t)+1));
nCr12(t)=nCr11(t-1)-(pCr1*nCr11(t-1)/(nCr1(t)+1));
nCr23(t)=nCr12(t-1)-(pCr1*nCr12(t-1)/(nCr1(t)+1));
nSma22(t)=nSma11(t-1)-pSma1;
nGm33(t)=nGm22(t-1)-pGm2;
nMv24(t)=nMv23(t-1)-(pMv2*nMv23(t-1)/(nMv2(t)+1));
nMv25(t)=nMv24(t-1)-(pMv2*nMv24(t-1)/(nMv2(t)+1));
nBs24(t)=nBs23(t-1)-(pBs2*nBs23(t-1)/(nBs2(t)+1));
nBs25(t)=nBs24(t-1)-(pBs2*nBs24(t-1)/(nBs2(t)+1));
nBs36(t)=nBs25(t-1)-(pBs2*nBs25(t-1)/(nBs2(t)+1));
nRr33(t)=nRr22(t-1)-pRr2;
nSme23(t)=nSme22(t-1)-(pSme2*nSme22(t-1)/(nSme2(t)+1));
nSme24(t)=nSme23(t-1)-(pSme2*nSme23(t-1)/(nSme2(t)+1));
nSme35(t)=nSme24(t-1)-(pSme2*nSme24(t-1)/(nSme2(t)+1));
nHp24(t)=nHp23(t-1)-(pHp2*nHp23(t-1)/(nHp2(t)+1));
nHp35(t)=nHp24(t-1)-(pHp2*nHp24(t-1)/(nHp2(t)+1));
nGc24(t)=nGc23(t-1)-(pGc2*nGc23(t-1)/(nGc2(t)+1));
nGc35(t)=nGc24(t-1)-(pGc2*nGc24(t-1)/(nGc2(t)+1));
nRh24(t)=nRh23(t-1)-(pRh2*nRh23(t-1)/(nRh2(t)+1));
nRh35(t)=nRh24(t-1)-(pRh2*nRh24(t-1)/(nRh2(t)+1));
nCr24(t)=nCr23(t-1)-(pCr2*nCr23(t-1)/(nCr2(t)+1));
nCr25(t)=nCr24(t-1)-(pCr2*nCr24(t-1)/(nCr2(t)+1));
nCr26(t)=nCr25(t-1)-(pCr2*nCr25(t-1)/(nCr2(t)+1));
nCr27(t)=nCr26(t-1)-(pCr2*nCr26(t-1)/(nCr2(t)+1));
nCr28(t)=nCr27(t-1)-(pCr2*nCr27(t-1)/(nCr2(t)+1));
nCr29(t)=nCr28(t-1)-(pCr2*nCr28(t-1)/(nCr2(t)+1));
nCr310(t)=nCr29(t-1)-(pCr2*nCr29(t-1)/(nCr2(t)+1));
```

```
nSma23(t)=nSma22(t-1)-(pSma2*nSma22(t-1)/(nSma2(t)+1));
nSma24(t)=nSma23(t-1)-(pSma2*nSma23(t-1)/(nSma2(t)+1));
nSma35(t)=nSma24(t-1)-(pSma2*nSma24(t-1)/(nSma2(t)+1));
nGm34(t)=nGm33(t-1)-(pGm3*nGm33(t-1)/(nGm3(t)+1));
nGm35(t)=nGm34(t-1)-(pGm3*nGm34(t-1)/(nGm3(t)+1));
nGm46(t)=nGm35(t-1)-(pGm3*nGm35(t-1)/(nGm3(t)+1));
nBs37(t)=nBs36(t-1)-(pBs3*nBs36(t-1)/(nBs3(t)+1));
nBs38(t)=nBs37(t-1)-(pBs3*nBs37(t-1)/(nBs3(t)+1));
nRr34(t)=nRr33(t-1)-(pRr3*nRr33(t-1)/(nRr3(t)+1));
nRr45(t)=nRr34(t-1)-(pRr3*nRr34(t-1)/(nRr3(t)+1));
nSme36(t)=nSme35(t-1)-(pSme3*nSme35(t-1)/(nSme3(t)+1));
nSme37(t)=nSme36(t-1)-(pSme3*nSme36(t-1)/(nSme3(t)+1));
nSme38(t)=nSme37(t-1)-(pSme3*nSme37(t-1)/(nSme3(t)+1));
nSme39(t)=nSme38(t-1)-(pSme3*nSme38(t-1)/(nSme3(t)+1));
nSme310(t)=nSme39(t-1)-(pSme3*nSme39(t-1)/(nSme3(t)+1));
nSme411(t)=nSme310(t-1)-(pSme3*nSme310(t-1)/(nSme3(t)+1));
nHp36(t)=nHp35(t-1)-(pHp3*nHp35(t-1)/(nHp3(t)+1));
nHp37(t)=nHp36(t-1)-(pHp3*nHp36(t-1)/(nHp3(t)+1));
nHp38(t)=nHp37(t-1)-(pHp3*nHp37(t-1)/(nHp3(t)+1));
nHp39(t)=nHp38(t-1)-(pHp3*nHp38(t-1)/(nHp3(t)+1));
nHp310(t)=nHp39(t-1)-(pHp3*nHp39(t-1)/(nHp3(t)+1));
nHp411(t)=nHp310(t-1)-(pHp3*nHp310(t-1)/(nHp3(t)+1));
nGc36(t)=nGc35(t-1)-(pGc3*nGc35(t-1)/(nGc3(t)+1));
nGc37(t)=nGc36(t-1)-(pGc3*nGc36(t-1)/(nGc3(t)+1));
nGc38(t)=nGc37(t-1)-(pGc3*nGc37(t-1)/(nGc3(t)+1));
nGc39(t)=nGc38(t-1)-(pGc3*nGc38(t-1)/(nGc3(t)+1));
nGc310(t)=nGc39(t-1)-(pGc3*nGc39(t-1)/(nGc3(t)+1));
nGc411(t)=nGc310(t-1)-(pGc3*nGc310(t-1)/(nGc3(t)+1));
nRh36(t)=nRh35(t-1)-(pRh3*nRh35(t-1)/(nRh3(t)+1));
nRh37(t)=nRh36(t-1)-(pRh3*nRh36(t-1)/(nRh3(t)+1));
```

```
nRh38(t)=nRh37(t-1)-(pRh3*nRh37(t-1)/(nRh3(t)+1));
nRh39(t)=nRh38(t-1)-(pRh3*nRh38(t-1)/(nRh3(t)+1));
nRh310(t)=nRh39(t-1)-(pRh3*nRh39(t-1)/(nRh3(t)+1));
nRh411(t)=nRh310(t-1)-(pRh3*nRh310(t-1)/(nRh3(t)+1));
nCr311(t)=nCr310(t-1)-(pCr3*nCr310(t-1)/(nCr3(t)+1));
nCr312(t)=nCr311(t-1)-(pCr3*nCr311(t-1)/(nCr3(t)+1));
nCr313(t)=nCr312(t-1)-(pCr3*nCr312(t-1)/(nCr3(t)+1));
nCr314(t)=nCr313(t-1)-(pCr3*nCr313(t-1)/(nCr3(t)+1));
nCr315(t)=nCr314(t-1)-(pCr3*nCr314(t-1)/(nCr3(t)+1));
nCr316(t)=nCr315(t-1)-(pCr3*nCr315(t-1)/(nCr3(t)+1));
nCr317(t)=nCr316(t-1)-(pCr3*nCr316(t-1)/(nCr3(t)+1));
nCr318(t)=nCr317(t-1)-(pCr3*nCr317(t-1)/(nCr3(t)+1));
nCr319(t)=nCr318(t-1)-(pCr3*nCr318(t-1)/(nCr3(t)+1));
nCr320(t)=nCr319(t-1)-(pCr3*nCr319(t-1)/(nCr3(t)+1));
nCr321(t)=nCr320(t-1)-(pCr3*nCr320(t-1)/(nCr3(t)+1));
nCr322(t)=nCr321(t-1)-(pCr3*nCr321(t-1)/(nCr3(t)+1));
nCr323(t)=nCr322(t-1)-(pCr3*nCr322(t-1)/(nCr3(t)+1));
nCr324(t)=nCr323(t-1)-(pCr3*nCr323(t-1)/(nCr3(t)+1));
nCr325(t)=nCr324(t-1)-(pCr3*nCr324(t-1)/(nCr3(t)+1));
nCr426(t)=nCr325(t-1)-(pCr3*nCr325(t-1)/(nCr3(t)+1));
nSma36(t)=nSma35(t-1)-(pSma3*nSma35(t-1)/(nSma3(t)+1));
nSma37(t)=nSma36(t-1)-(pSma3*nSma36(t-1)/(nSma3(t)+1));
nSma38(t)=nSma37(t-1)-(pSma3*nSma37(t-1)/(nSma3(t)+1));
nSma39(t)=nSma38(t-1)-(pSma3*nSma38(t-1)/(nSma3(t)+1));
nSma310(t)=nSma39(t-1)-(pSma3*nSma39(t-1)/(nSma3(t)+1));
nSma411(t)=nSma310(t-1)-(pSma3*nSma310(t-1)/(nSma3(t)+1));
nGm11(t)=MmGm;
nGm47(t)=nGm46(t-1);
nGm48(t)=nGm47(t-1);
nGm49(t)=nGm48(t-1);
```

```
nGm410(t)=nGm49(t-1);
nGm411(t)=nGm410(t-1);
nGm412(t)=nGm411(t-1);
nGm413(t)=nGm412(t-1);
nGm414(t)=nGm413(t-1);
nGm415(t)=nGm414(t-1);
nGm516(t)=nGm415(t-1);
nGm517(t)=nGm516(t-1);
nGm518(t)=nGm517(t-1);
nGm519(t)=nGm518(t-1);
nGm520(t)=nGm519(t-1);
nMv11(t)=MmMv;
nBs11(t)=MmBs;
nRr11(t)=MmRr;
nRr46(t)=nRr45(t-1);
nRr47(t)=nRr46(t-1);
nRr48(t)=nRr47(t-1);
nRr49(t)=nRr48(t-1);
nRr410(t)=nRr49(t-1);
nRr411(t)=nRr410(t-1);
nRr412(t)=nRr411(t-1);
nRr413(t)=nRr412(t-1);
nRr414(t)=nRr413(t-1);
nRr415(t)=nRr414(t-1);
nRr416(t)=nRr415(t-1);
nRr417(t)=nRr416(t-1);
nRr418(t)=nRr417(t-1);
nRr419(t)=nRr418(t-1);
nRr420(t)=nRr419(t-1);
nSme11(t)=MmSme;
```

```
nSme412(t)=nSme411(t-1);
nSme413(t)=nSme412(t-1);
nSme414(t)=nSme413(t-1);
nSme415(t)=nSme414(t-1);
nSme416(t)=nSme415(t-1);
nSme417(t)=nSme416(t-1);
nSme418(t)=nSme417(t-1);
nSme419(t)=nSme418(t-1);
nSme420(t)=nSme419(t-1);
nSme421(t)=nSme420(t-1);
nSme422(t)=nSme421(t-1);
nSme423(t)=nSme422(t-1);
nSme424(t)=nSme423(t-1);
nSme425(t)=nSme424(t-1);
nSme426(t)=nSme425(t-1);
nSme427(t)=nSme426(t-1);
nSme428(t)=nSme427(t-1);
nSme429(t)=nSme428(t-1);
nSme430(t)=nSme429(t-1);
nSme431(t)=nSme430(t-1);
nSme432(t)=nSme431(t-1);
nSme433(t)=nSme432(t-1);
nSme434(t)=nSme433(t-1);
nSme435(t)=nSme434(t-1);
nSme436(t)=nSme435(t-1);
nSme437(t)=nSme436(t-1);
nSme438(t)=nSme437(t-1);
nSme439(t)=nSme438(t-1);
nSme440(t)=nSme439(t-1);
nHp11(t)=MmHp;
```

```
nHp412(t)=nHp411(t-1);
nHp413(t)=nHp412(t-1);
nHp414(t)=nHp413(t-1);
nHp415(t)=nHp414(t-1);
nHp416(t)=nHp415(t-1);
nHp417(t)=nHp416(t-1);
nHp418(t)=nHp417(t-1);
nHp419(t)=nHp418(t-1);
nHp420(t)=nHp419(t-1);
nHp421(t)=nHp420(t-1);
nHp422(t)=nHp421(t-1);
nHp423(t)=nHp422(t-1);
nHp424(t)=nHp423(t-1);
nHp425(t)=nHp424(t-1);
nGc11(t)=MmGc;
nGc412(t)=nGc411(t-1);
nGc413(t)=nGc412(t-1);
nGc414(t)=nGc413(t-1);
nGc415(t)=nGc414(t-1);
nGc416(t)=nGc415(t-1);
nGc417(t)=nGc416(t-1);
nGc418(t)=nGc417(t-1);
nGc419(t)=nGc418(t-1);
nGc420(t)=nGc419(t-1);
nGc421(t)=nGc420(t-1);
nGc422(t)=nGc421(t-1);
nGc423(t)=nGc422(t-1);
nGc424(t)=nGc423(t-1);
nGc425(t)=nGc424(t-1);
nGc426(t)=nGc425(t-1);
```

```
nGc427(t)=nGc426(t-1);
nGc428(t)=nGc427(t-1);
nGc429(t)=nGc428(t-1);
nGc430(t)=nGc429(t-1);
nRh11(t)=MmRh;
nRh412(t)=nRh411(t-1);
nRh413(t)=nRh412(t-1);
nRh414(t)=nRh413(t-1);
nRh415(t)=nRh414(t-1);
nRh516(t)=nRh415(t-1);
nRh517(t)=nRh516(t-1);
nRh518(t)=nRh517(t-1);
nRh519(t)=nRh518(t-1);
nRh520(t)=nRh519(t-1);
nCr11(t)=MmCr;
nCr427(t)=nCr426(t-1);
nCr428(t)=nCr427(t-1);
nCr429(t)=nCr428(t-1);
nCr430(t)=nCr429(t-1);
nCr431(t)=nCr430(t-1);
nCr432(t)=nCr431(t-1);
nCr433(t)=nCr432(t-1);
nCr434(t)=nCr433(t-1);
nCr435(t)=nCr434(t-1);
nCr436(t)=nCr435(t-1);
nCr437(t)=nCr436(t-1);
nCr438(t)=nCr437(t-1);
nCr439(t)=nCr438(t-1);
nCr440(t)=nCr439(t-1);
nSma11(t)=MmSma;
```

```
nSma412(t)=nSma411(t-1);
nSma413(t)=nSma412(t-1);
nSma414(t)=nSma413(t-1);
nSma415(t)=nSma414(t-1);
nSma416(t)=nSma415(t-1);
nSma417(t)=nSma416(t-1);
nSma418(t)=nSma417(t-1);
nSma419(t)=nSma418(t-1);
nSma420(t)=nSma419(t-1);
nSma421(t)=nSma420(t-1);
nSma422(t)=nSma421(t-1);
nSma423(t)=nSma422(t-1);
nSma424(t)=nSma423(t-1);
nSma425(t)=nSma424(t-1);
nSma426(t)=nSma425(t-1);
nSma427(t)=nSma426(t-1);
Sma428(t)=nSma427(t-1);
nSma429(t)=nSma428(t-1);
nSma430(t)=nSma429(t-1);
nSma431(t)=nSma430(t-1);
nSma432(t)=nSma431(t-1);
nSma433(t)=nSma432(t-1);
nSma434(t)=nSma433(t-1);
nSma435(t)=nSma434(t-1);
nSma436(t)=nSma435(t-1);
nSma437(t)=nSma436(t-1);
nSma438(t)=nSma437(t-1);
nSma439(t)=nSma438(t-1);
nSma440(t)=nSma439(t-1);
end
```

% **Subsection 5: Model outputs**

% The following lines contain the model outputs, i.e. the values of the variables (species size groups) in the successive iterations.

% For example nGm1 is the value of nGm1 in the corresponding year or iteration.

```
nGm1=[nGm1(nGm11(t))];
nGm2=[nGm2(nGm22(t))];
nGm3=[nGm3(nGm33(t)+nGm34(t)+nGm35(t))];
nGm4=[nGm4(nGm46(t)+nGm47(t)+nGm48(t)+nGm49(t)+nGm410(t)+nGm411(t)
        +nGm412(t)+nGm413(t)+nGm414(t)+nGm415(t))];
nGm5=[nGm5(nGm516(t)+nGm517(t)+nGm518(t)+nGm519(t)+nGm520(t))];
nMv1=[nMv1(nMv11(t)+nMv12(t))];
nMv2=[nMv2(nMv23(t)+nMv24(t)+nMv25(t))];
nBs1=[nBs1(nBs11(t)+nBs12(t))];
nBs2=[nBs2(nBs23(t)+nBs24(t)+nBs25(t))];
nBs3=[nBs3(nBs36(t)+nBs37(t)+nBs38(t))];
nRr1=[nRr1(nRr11(t))];
nRr2=[nRr2(nRr22(t))];
nRr3=[nRr3(nRr33(t)+nRr34(t))];
nRr4=[nRr4(nRr45(t)+nRr46(t)+nRr47(t)+nRr48(t)+nRr49(t)+nRr410(t)+nRr411(t)
        +nRr412(t)+nRr413(t)+nRr414(t)+nRr415(t)+nRr416(t)+nRr417(t)+nRr418(
        t)+nRr419(t)+nRr420(t))];
nSme1=[nSme1(nSme11(t))];
nSme2=[nSme2(nSme22(t)+nSme23(t)+nSme24(t))];
nSme3=[nSme3(nSme35(t)+nSme36(t)+nSme37(t)+nSme38(t)+nSme39(t)+nSm
        e310(t))];
nSme4=[nSme4(nSme411(t)+nSme412(t)+nSme413(t)+nSme414(t)+nSme415(t)
        +nSme416(t)+nSme417(t)+nSme418(t)+nSme419(t)+nSme420(t)+nSme4
```

```
        21(t)+nSme422(t)+nSme423(t)+nSme424(t)+nSme425(t)+nSme426(t)+nS
        me427(t)+nSme428(t)+nSme429(t)+nSme430(t)+nSme431(t)+nSme432(t)
        +nSme433(t)+nSme434(t)+nSme435(t)+nSme436(t)+nSme437(t)+nSme4
        38(t)+nSme439(t)+nSme440(t))];
nHp1=[nHp1(nHp11(t)+nHp12(t))];
nHp2=[nHp2(nHp23(t)+nHp24(t))];
nHp3=[nHp3(nHp35(t)+nHp36(t)+nHp37(t)+nHp38(t)+nHp39(t)+nHp310(t))];
nHp4=[nHp4(nHp411(t)+nHp412(t)+nHp413(t)+nHp414(t)+nHp415(t)+nHp416(t)
        +nHp417(t)+nHp418(t)+nHp419(t)+nHp420(t)+nHp421(t)+nHp422(t)+nHp
        423(t)+nHp424(t)+nHp425(t))];
nGc1=[nGc1(nGc11(t)+nGc12(t))];
nGc2=[nGc2(nGc23(t)+nGc24(t))];
nGc3=[nGc3(nGc35(t)+nGc36(t)+nGc37(t)+nGc38(t)+nGc39(t)+nGc310(t))];
nGc4=[nGc4(nGc411(t)+nGc412(t)+nGc413(t)+nGc414(t)+nGc415(t)+nGc416(t)
        +nGc417(t)+nGc418(t)+nGc419(t)+nGc420(t)+nGc421(t)+nGc422(t)+nGc4
        23(t)+nGc424(t)+nGc425(t)+nGc426(t)+nGc427(t)+nGc428(t)+nGc429(t)+
        nGc430(t))];
nRh1=[nRh1 (nRh11(t)+nRh12(t))];
nRh2=[nRh2 (nRh23(t)+nRh24(t))];
nRh3=[nRh3 (nRh35(t)+nRh36(t)+nRh37(t)+nRh38(t)+nRh39(t)+nRh310(t))];
nRh4=[nRh4 (nRh411(t)+nRh412(t)+nRh413(t)+nRh414(t)+nRh415(t))];
nRh5=[nRh5 (nRh516(t)+nRh517(t)+nRh518(t)+nRh519(t)+nRh520(t))];
nCr1=[nCr1(nCr11(t)+nCr12(t))];
nCr2=[nCr2(nCr23(t)+nCr24(t)+nCr25(t)+nCr26(t)+nCr27(t)+nCr28(t)+nCr29(t))];
nCr3=[nCr3(nCr310(t)+nCr311(t)+nCr312(t)+nCr313(t)+nCr314(t)+nCr315(t)+nCr
        316(t)+nCr317(t)+nCr318(t)+nCr319(t)+nCr320(t)+nCr321(t)+nCr322(t)+n
        Cr323(t)+nCr324(t)+nCr325(t))];
nCr4=[nCr4(nCr426(t)+nCr427(t)+nCr428(t)+nCr429(t)+nCr430(t)+nCr431(t)+nCr
        432(t)+nCr433(t)+nCr434(t)+nCr435(t)+nCr436(t)+nCr437(t)+nCr438(t)+n
        Cr439(t)+nCr440(t))];
```

```
nSma1=[nSma1 (nSma11(t))];
nSma2=[nSma2 (nSma22(t)+nSma23(t)+nSma24(t))];
nSma3=[nSma3(nSma35(t)+nSma36(t)+nSma37(t)+nSma38(t)+nSma39(t)+nSm
        a310(t))];
nSma4=[nSma4(nSma411(t)+nSma412(t)+nSma413(t)+nSma414(t)+nSma415(t)
        +nSma416(t)+nSma417(t)+nSma418(t)+nSma419(t)+nSma420(t)+nSma4
        21(t)+nSma422(t)+nSma423(t)+nSma424(t)+nSma425(t)+nSma426(t)+nS
        ma427(t)+nSma428(t)+nSma429(t)+nSma430(t)+nSma431(t)+nSma432(t)
        +nSma433(t)+nSma434(t)+nSma435(t)+nSma436(t)+nSma437(t)+nSma4
        38(t)+nSma439(t)+nSma440(t))];
end;
```