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Size Structure and Production in a Demersal Fish Community

by

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Abstract:

Environmental factors, human activities and predation are the main causes of mortality for fish species. Predation is, at the same time, the link between species in the community. Predation also modulates the other two causes of mortality, which therefore can be considered externalities to the community. Size-dependency is the rule and the main characteristic governing predator/prey relationships in a demersal fish community. However, continuous growth that begins from a generally similar larval size but reaches very different adult sizes changes the trophic interactions between species over time through each individual life span. The life history of the individual species determines at what sizes these changes occur, including particularly the sizes at which a species matures and dies.

A dynamic model simulates the consequences of size-dependent predation and life history parameters on the relative abundance of species in a demersal fish community. The model shows the production and structure of the community in the absence of external influences (e.g. environment and fishing), and how a classical autoecological and species-based view of the ecosystem is changed by a synecological and size-based view.

INTRODUCTION

The difficulty of achieving successful fisheries management becomes apparent when one considers all the forces affecting fish populations. These range from environmental factors directed by physical laws to fishing practices influenced by socio-economic laws, and include species interactions and intrinsic population variability within the fish community that are influenced by laws of probability. With all these forces interacting, the word that best reflects fisheries management is "uncertainty". Even proving that there is a cause-effect interaction between fisheries and/or environmental factors and fish populations (Myers et al., 1996) has been a major advance. Interacting forces and time lags, among other things, will influence the final effect of any disturbance on a marine fish community.

The reality of uncertainty is a compelling reason to look for overall trends instead of quantitative accuracy in fisheries data. Many international organizations are adopting a precautionary approach to fisheries management (NAFO working paper 97/15, MS 1997). This precautionary approach recognises the necessity of limits and target reference points. The fish community defined by its populations of interacting species sets the biological limits within which any disturbances must take place. Environmental and fishing disturbances can be considered externalities. Through understanding the dynamics of the fish community in an undisturbed state it is possible to study the dimensions and directions and impacts of external disturbances.

Commonly, a single species is the sole focus of study, or else is treated as an indivisible unit (a "black box") when more than one species is studied. Both assumptions represent significant drawbacks if the importance of interactions for dynamic studies is considered. How will the community behave if we change the common assumptions about its structure? Adopting a wider and more holistic approach that considers the several and differing life stages of individuals within a species can offer a new perspective.

In this paper, the structure of a demersal community is presented, based on individual sizes and species life history parameters. A model is used to show the dynamics and productive capacity of the community in the absence of externalities. As an example, we have used the species that occur together as a part of a real ecosystem, the demersal fish community on the continental shelf off Newfoundland in the northwest Atlantic. The approach, however, is a generalised one and should be applicable to the new deep-sea fisheries where biological information is less comprehensive.

Size and allometric characteristics are of special relevance among fish species. At the population level, size influences number of offspring (Blueweiss et al., 1978, Cardinale and Arrheinius, 2000). At the community level, size influences predation (Yodzis and Innes, 1992; Bax, 1998; Dunn, 1979). The implications of size composition in fish community dynamics have been stressed during recent decades (Dickie et al, 1987), and the influence of fisheries as a continuous disturbance on the size of species in a demersal community has been reported (Haedrich and Barnes, 1997).

Considering the fish community without externalities, the number of mature individuals will determine the number of offspring in each species population. But mortality in fishes, which determines the number of individuals that reach maturity, is, as mentioned above, mainly dependent on predation. Rates and linkages of this predation are reflected in the community food web.

Sizes, not species, constitute functional groups in the food web. The same species passes from being potential prey to predator during its full life span. Therefore, individuals of equal size can be considered to 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 the trophic chain. 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 overall abundance of their particular predator species. As explained below, the demersal fish community can be depicted as a food web based on sizes.

As a first step, we are assuming an absence of any externalities. The abundance of the populations, then, will be the result only of a combination of species life history characteristics and species interactions. 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.

A COMMUNITY AND THE SIZE FACTOR

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. The fundamental role is that big eats small, but size varies along a life span; and, hence, trophic relations will change as well. The dynamics of the community are depicted here by a novel representation of the community structure in which trophic levels are size levels (Fig. 1).

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. To define the sizes that structure the community, it is assumed that fish prey on food that is between two to three orders of magnitude smaller than their own size (Hahm and Langton, 1984). In the model presented here, five possible sizes are considered: size1=(0g–9g], size2=[10g-99g], size3=[100g-999g], size4=[1000g-9999g], and size5= ≥10000g. The trophic relations are established between trophic levels. Sizes 2 and 3 feed on size 1. Size 4 feeds on size 2, and size 5 feeds on size 3. Size 2 is considered to prey on larval stages of individuals of size group 1.

Size has often been implicated as an important factor to consider when dealing with marine food webs, including those involving fish. Prey-predator interactions in the model here use the logistic equation to describe each population's birth rate, the functional response in the predator's feeding behaviour and the density dependent mortality of prey. These considerations reflect natural communities more accurately (Berryman, 1992; Ginzburg and Akçakaya, 1992) as well as systems with spatially heterogeneous distribution of prey and predator (Arditi and Saïah, 1992), which is certainly the case in demersal fish communities. Species habitats also change with size (i.e. during a life span) since older individuals tend to occupy deeper and more offshore waters.

Contrary to other food webs where prey is the key that determines predator abundance, here food is taken for granted (i. e., predators are not considered to be food limited), which 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 temporal 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, an increase in the abundance of a predator will intensify a decrease in its prey. Therefore the decrease of individuals in prey stages (i.e. small size) of the same species due to cannibalism will result in a decrease of individuals in the predator stages (i.e. larger sizes) over time. Usually predator stages of a species correspond to mature stages, and therefore a high abundance of predator stages will induce a high abundance of larval and juveniles. 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 of the community induce multiple indirect effects that can result in both depensation and compensation processes.

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).

We are going to apply these considerations of size factors to a real case: the demersal fish community off Newfoundland. This important marine region has suffered drastic changes during the last decades, which ended in the collapse of the cod fishery in the beginning of the 90s and the imposition of a fishing moratorium that is still in place. The abundance not only of cod, but also of many other species declined and no species so far seems to have filled the ecological gap left by the removal of cod. From a 16-year survey of NAFO areas 2J and 3K (northeast Newfoundland shelf), data for the most abundant species have been selected. The scientific and common names of these species are presented in Table. 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: columns being the species and rows being the sizes. Each cell of the matrix is filled with the average number of years individuals remain in that particular size group. Life-history parameters of the species (Scott and Scott, 1988) have been used to determine the structure of the community on a realistic basis (Table 2); an estimation of the number of eggs released from each mature female is presented in Table 3.

Growth rate and maximum size are characteristic of each individual species. How long an individual remains at a certain size 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.

MODELLING THE COMMUNITY

Matlab® computer software (Kernan, 1997) allows construction of the model, the ability to run scenarios, and the presentation of results as graphics. The iterative procedure that takes place to construct the community dynamics, and the interactions and assumptions in the model, are explained below.

Model steps

1. Input of individuals at time t=0 classified by species and age.
2. Determine the number of individuals in each species size-group that survive predation.
3. Determine the number of offspring for each species.
4. Output as individuals at time t=1

Model assumptions

- All individuals die after the end of their assumed life span
- Mortality is caused by predation and is density dependent except for that at the end of life span
- Predation depends on size and is independent of the individual species. Exceptions can be taken into account, i.e. non-piscivorous species, if required.
- Offspring production is density dependent. There is a limit for each species in the number of offspring.
- Egg production capacity increases with size of mature individuals
- Food intake is a function of individual size according to the equation:

$$z = 3.504 \bullet w^{0.82}.$$ (Peters, 1984)

z = Kg of food eaten by a single fish in a year
w = mass in grams of the predator

- The food of a predator (the prey) should be around 1/1000 the size of the predator (Hahm and Langton, 1984). Individual classification in 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). There may be biological reasons, such as mouth gape, why the inclusion of a certain individual of a species in a size group may not correspond to its size.
- The time an individual remains in a size group will depend on the species to which it belongs.
- The model is dynamic (i.e. 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.
- Since one year is the minimum age division considered, 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. The process of passing from one size to another will depend on the average number of years each species stays in the same size group, which depends upon the biology of each individual species. Once the individuals reach the end of their maximum life span they die.
- Extinction of species is not possible. Since predation is density dependent, a proportion of the prey will always survive. However, this 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, offspring production is always rounded to the upper next whole number. Therefore, at least one individual is always present for each species in the model.

Interactions that lead the community dynamics

Three linked processes (fig.2) define community dynamics. They are offspring production, growth and predation. 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 of 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 each species of the community.

The case represented in Fig. 2 is a very simple one. In the real world, a greater number of years in the life spans of species, more size groups and the presence of more species complicate this picture. Nonetheless, no matter how complex the system becomes it can be well represented by the interactions shown here. Now we go on to address the nature of these interactions in detail and how are they are mathematically expressed in the model:

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 number of predators (from large size groups) that the predator size group contains. In addition, large-sized individuals can be preying upon mid-sized individuals at the same time the mid-sized individuals are preying upon small-sized individuals. Thus, big-size individuals can indirectly affect predation of the small-size individuals. 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. s1 and s2, where s1 is the prey group and s2 is the predator group), the percent of prey surviving predation will be:

$$ps1 = \frac{s1}{s1 + s2} \tag{1}$$

where ps1= percent of individuals of the group size 1 (prey, in this case) that survive predation in a certain year (units = %)
s1 =number of individuals in group size 1 in a certain year (units = individuals)
s2 =number of individuals in group size 2 in a certain year (units = individuals)

The basic assumption, according to this equation, is that the probability of a predator-prey encounter is 0.5, and that all encounters result in predation. Yet, these probabilities will change with the relative abundance of the predator in relation to the prey (ratio prey/predator). Thus, 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 in Figure 3.

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(s2) the food intake in grams of a single predator of size 2 per year when there is no shortage of food (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 1). Taking into account predator satiation, equation 1 will became:

$$ps1 = \frac{s1}{s1 + s2 \bullet \dfrac{g(s2)}{w(s1)} \bullet y} \tag{2}$$

where ps1= percent of individuals of the group size 1 (prey, in this case) that survive predation in a certain year (units = %)

s1 =number of individuals in group size 1 in a certain year (units = individuals)
s2 =number of individuals in group size 2 in a certain year (units = individuals)
g(s2)= food intake of a predator (of size group 2) individual at satiation (units = g•individual^{-1}•year^{-1})
w(s1)= average weight of a prey (of size group 1) individual (units = g•individual^{-1})
y = time period considered (units = years). We said above that this model will consider that change occurs on a yearly basis; thus, y is unity and does not affect the computations.

$$\text{If we define } \quad l(s2, s1) = \frac{g(s2)}{w(s1)} \bullet y \tag{3}$$

then equation (2) can be expressed more easily as:

$$ps1 = \frac{s1}{s1 + s2 \bullet l(s2, s1)} \tag{4}$$

Graphic representation of equation (4) will have the same shape as the representation of ps1 in Figure 3.

Still, the presence of predators in the even larger size group will influence (by means of decreasing the number of mid-sized predators) the predator-prey relation between s2 and s1. s4 is the size group whose individuals prey on the individuals of size group 2 (s2). The presence of this size group (s4) and the per capita prey intake of its individuals will affect the relation between s2 and s1 in the following way:

$$ps1 = \frac{s1}{s1 + s2 \bullet l(s2, s1) \bullet \dfrac{s2}{s2 + s4 \bullet l(s4, s2)}} \tag{5}$$

where   ps1= percent of individuals of the group size 1 (prey, in this case) that survive predation in a certain year (units = %)
s1 =number of individuals in group size in a certain year (units = individuals)
s2 =number of individuals in group size 2 in a certain year (units = individuals)
s4= number of individuals in group size 4 in a certain year (units = individuals)
l(s2,s1)=number of prey individuals eaten by a single satiated predator of size group 2 (units = individuals (prey)/individual (predator))
l(s4,s2)=number of prey individuals eaten by a single satiated predator of size group 4 (units = individuals (prey)/individual (predator))

The presence of individuals of size group 4 will increase the chances that individuals of size group 1 can survive predation.

So far, we have obtained the number of individuals that survive predation in a size group or, conversely, the number that die due to predation, d1. To know how many of them will represent a certain species we define the term "exposure to predation (Ep)" as the number of individuals of a certain species that could be preyed upon considering the number of individuals of other potential prey species in the same size group. To quantify Ep we consider that more abundant species within a prey size group will be under more predation pressure. Predators will more easily find bigger patches of prey and they will tend to stick to them. At the same time, less abundant prey will find refuge in more inaccessible habitats or simply in their rarity. Therefore, the equation of Ep for the individuals in size 1 of a certain species, A, is:

$$EpA1 = \frac{I * A1}{I + A1^c} \tag{6}$$

where   EpA1 = Exposure to predation of individuals size group 1 of species A.
A1 = number of individuals of size 1 in species A.
$A1^c$ = Number of individuals of size group 1 which not belong to species A.

$I = s2 \bullet l(s2, s1) \bullet \dfrac{s2}{s2 + s4 \bullet l(s4, s2)}$ as in equation 4; it is the number of prey that would be eaten by size group 2 if they reached satiation.

From the amount of individuals which die by predation in size 1 (d1), the proportion belonging to species A will be the same as the proportion of EpA1 to the sum of Ep for all species present in size group 1.

Offspring production

In determining offspring production three main factors are considered:

- Offspring production is characteristic of each individual species.
- 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 with the increase in size of the mature female.
- 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.

To construct the offspring-number of mature individuals relationship, we need to set a carrying capacity, Nmax, for the number of mature individuals that will produce offspring. Thus, the offspring production for a certain size of a certain species will be determined by equation 7, below. The total number of offspring produced by the species will be the sum of the offspring produced by the individuals of each mature size. The graphic representation of offspring production vs. number of mature individuals was shown in Figure 4. 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 Nmax individuals, all belonging to the bigger size group in the population.

$$O_S = \frac{Nmax}{M_S + Nmax} * \sum_{j=i}^{h}(F_{Sj} * M_{Sj}) \qquad \text{(absolute value, rounded up)} \qquad (7)$$

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 being 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
   Nmax = maximum number of mature individuals that will spawn in the absence of individual interference (i.e. no limit to the production of offspring)

At the offspring production level a minimum limit for the number of individuals of a species is imposed by taking the absolute value of O_S (rounded up). 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 this can be the case for a size group within the community.

Passing from one size 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. Therefore, the individuals from that 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.

In the following section we will apply the model to the demersal fish community off Newfoundland. The structure of this community has been defined in Tables 2 and 3, and includes only the more abundant species (whose number comprised more than 1% of the total).

DISCUSSION: SIZE STRUCTURE AND PRODUCTION IN THE NEWFOUNDLAND DEMERSAL FISH COMMUNITY

Figures 5 shows the dynamics of the Newfoundland demersal community starting 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. Furthermore, the logarithmic scale facilitates the representation of all species or sizes in one or a few graphics without distorting the information.

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 in the different size groups). However, in the absence of externalities, the final state does not change (i.e. it is stable). The value the abundance of each species can reach depends on the carrying capacity of the system (which is represented in the model by $k=10^{10}$ for the offspring of each species). The relative abundance of species remains constant when k is changed, although with negligible variations due to model constraints. Therefore, the two dimensions that represent the community dynamics graphically are time on the x-axis and abundance on the y-axis, but without necessarily specifying exact values.

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. However, short-term management of fisheries tends to focus alone on the period in which initial conditions influence community dynamics, neglecting the importance in the long run of life history characteristics.

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), 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 is another factor controlling abundance.

To achieve equilibrium, all age groups of a species must contain a constant number of individuals. This simple statement has further implications, which help explain why equilibrium is rarely found in nature. These implications are:

- The number of individuals passing from the immediately inferior age group has to be constant over time.
- 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.
- 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).
- 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.

We observe repeated periodic cycles over time (Fig. 5). They are not all exactly equal, however, but their amplitude (or structure) is similar with certain regular periods of ups and downs. Those periodic cycles resemble the curious 17-year cycles observed by Russell in the English Channel ("Russell Cycles", Cushing, 1982), an observation that invites more scrutiny. In our model they occur in response to trophic interactions that result in some years with more offspring production 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 is dependent on the dynamics of trophic interactions among size groups.

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 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 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.

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, since 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 longer. Therefore, the differences observed at these higher levels are the most obvious.

To summarise and analyse the dynamics of species (fig. 5) and size groups discussed above, 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 years 100 to 450). Table 4 shows the mean relative abundance of species within the community. Figure 6 shows the mean relative abundance by size groups. Figure 7 presents, for two representative species of the community, a bar chart showing the magnitude and variability of abundance for each size group and a pie chart showing the relative abundance of size groups within a species.

Cod is the dominant species in the Newfoundland demersal fish community. This is so due to the synergy of high fecundity, long life span and 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 was constantly and strongly suppressed; even then, how dominant any other species can be depends on its individual production 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 the collapse, and since then no other species have taken the dominant lead in the demersal fish community there.

There are, however, other species whose model abundance differs from that found in nature, as 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 (see Fig. 6), there is a logical decrease in absolute 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. high 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 fish predation is reflected in the model by the difference in abundance between size groups 1 and 2; the result indicates that 74% 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.

The considerable time needed to replenish populations in the larger sizes as well as the indirect effect of these size groups on the abundance of smaller sizes 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. 7). Species in the large size groups are commonly the target of fisheries, and these can often reduce the variability in abundance of these size groups through intensifying the catches. This, in turn, can significantly influence the impact that these size groups have on the abundance of smaller size groups.

According to the model, species abundance can be expressed as a fractional amount. This representation of abundance has no biological sense; individuals can only be present in round numbers. Most of the time 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.

Since life history characteristics determine the final abundance of a species in relation to the all 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. We are in the process of doing this as the next step in model development.

The complexity of the model is a consequence of its ambitious goal, which is to consider the naturally occurring shifts in trophic levels 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. 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 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.

Modern fisheries research and management require a sound understanding of community dynamics. Species interactions, life-history parameters, and time influence the dynamics. When these 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.

Acknowledgement

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Table 1. Scientific and common name of the ten most abundant species off northeastern Newfoundland (NAFO areas 2J 3K). The third column contains the species abbreviation used in this paper.

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 2. Community structure considering size and life history parameters. 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. The matrix contains the individual ages of each species spent in each size group up until the end of the life span. The mature ages are indicated in **bold** characters.

Age		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**	3~7	2	3~4	3~4	**3~5**	3~4	2	2~4	2~4
	3	**6~8**	**8~13**	3~4	**5~6~10**	**5~6~10**		**5~10**	3~4	**5~9~10**	**5~9~10**
	4		**14**	**5~14**	**11~30**	**11~25**		**11~15**	**5~20**	**11~40**	**11~40**
	5			**15~19**				**16~20**			

Table 3. Offspring production from mature-sized individuals of each species. The matrix shows the average number of eggs released by a mature female of the species and size indicated.

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

Table 4. Percentage comprised within the model community of the mean abundance of the species from the years 99 to 450; see Fig.5.

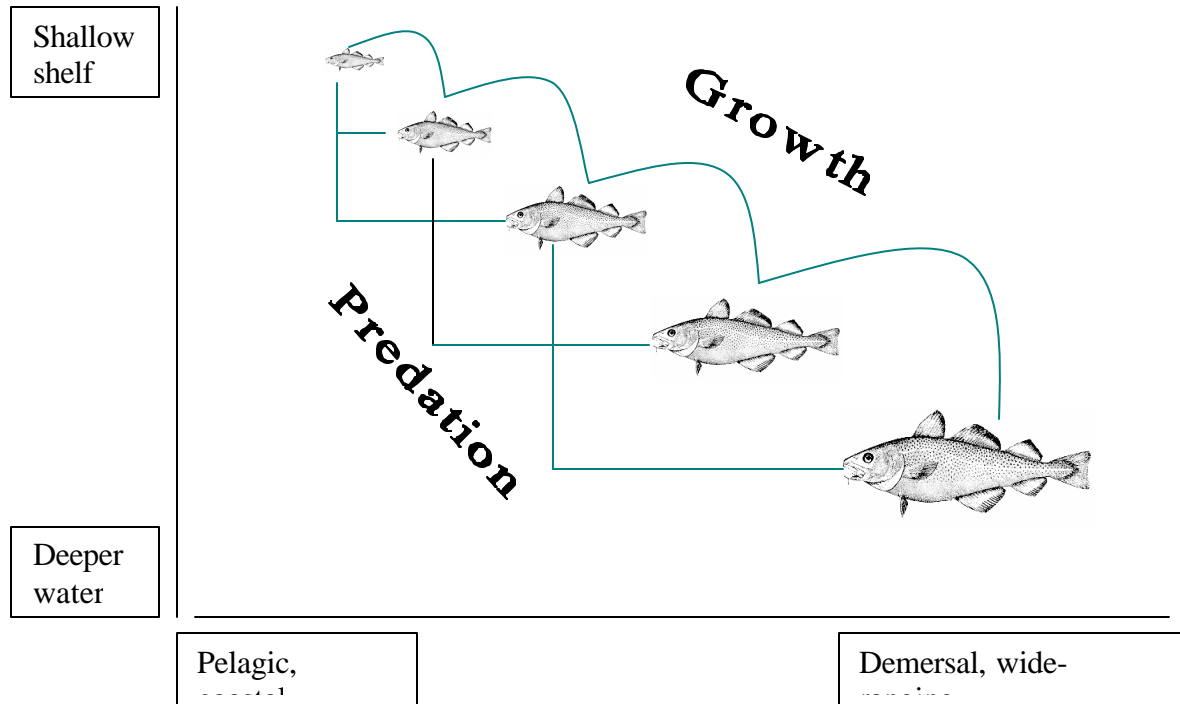| Spp	%
Bs	0.18
Cr	$0.292*10^{-13}$
Gm	70.9
Gc	8.65
Hp	16.62
Mv	0.66
Rr	$0.9*10^{-9}$
Rh	2.23
Sma	0.36
Sme	0.36

Fig. 1. Graphic representation of the trophic relations and habitat location changes during a fish's life span.
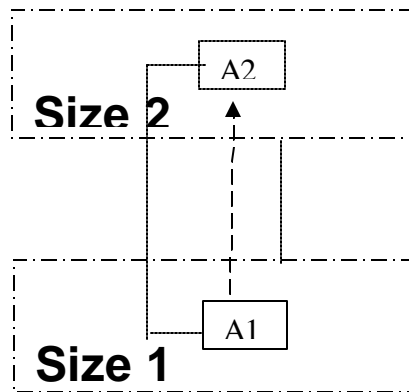

Fig. 2.   Structure and interactions of population A during a life span of 2 years. Individuals in their first year of life (A1) belong to size group 1, and in their second year of life (A2) pass into size group 2 and mature. Dashed arrow indicates the passage of individuals from size 1 to size group 2 due to growth. Continuous arrow indicates predation of individuals of size group 1 (prey group) by individuals in size group 2 (predators). Dotted arrows indicate offspring production from mature individuals.

Relation of percent prey survival to predator number
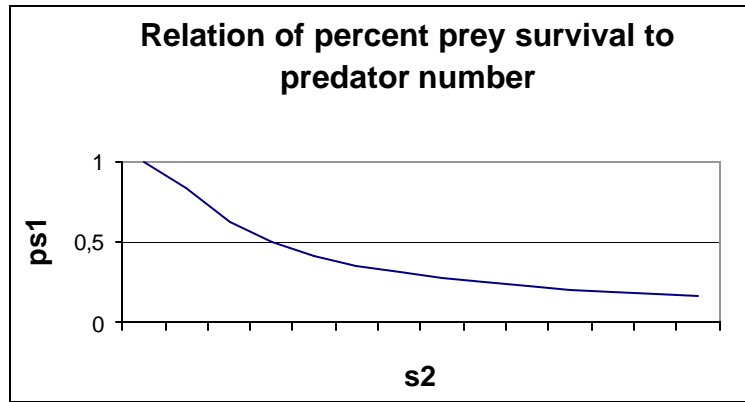
Fig. 3.   Percent of prey surviving predation (ps1) under different pressure (as abundance) from a predator (s2) when the prey number remains constant.

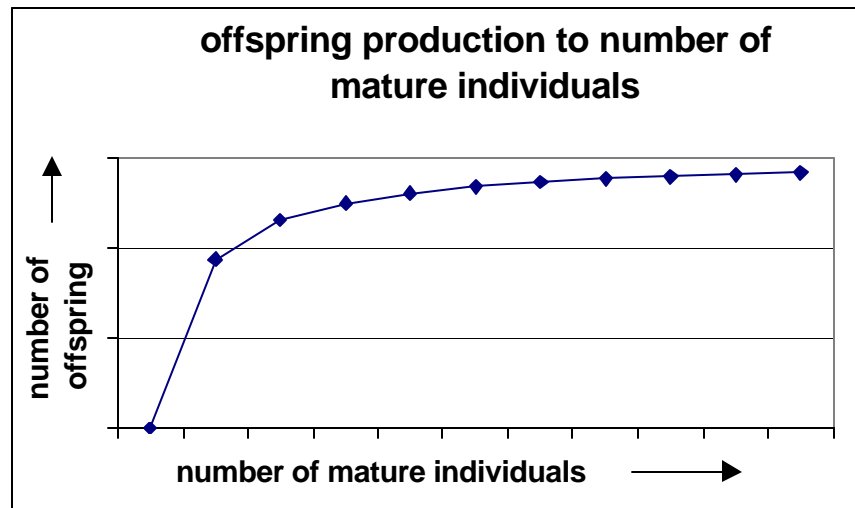**offspring production to number of mature individuals**

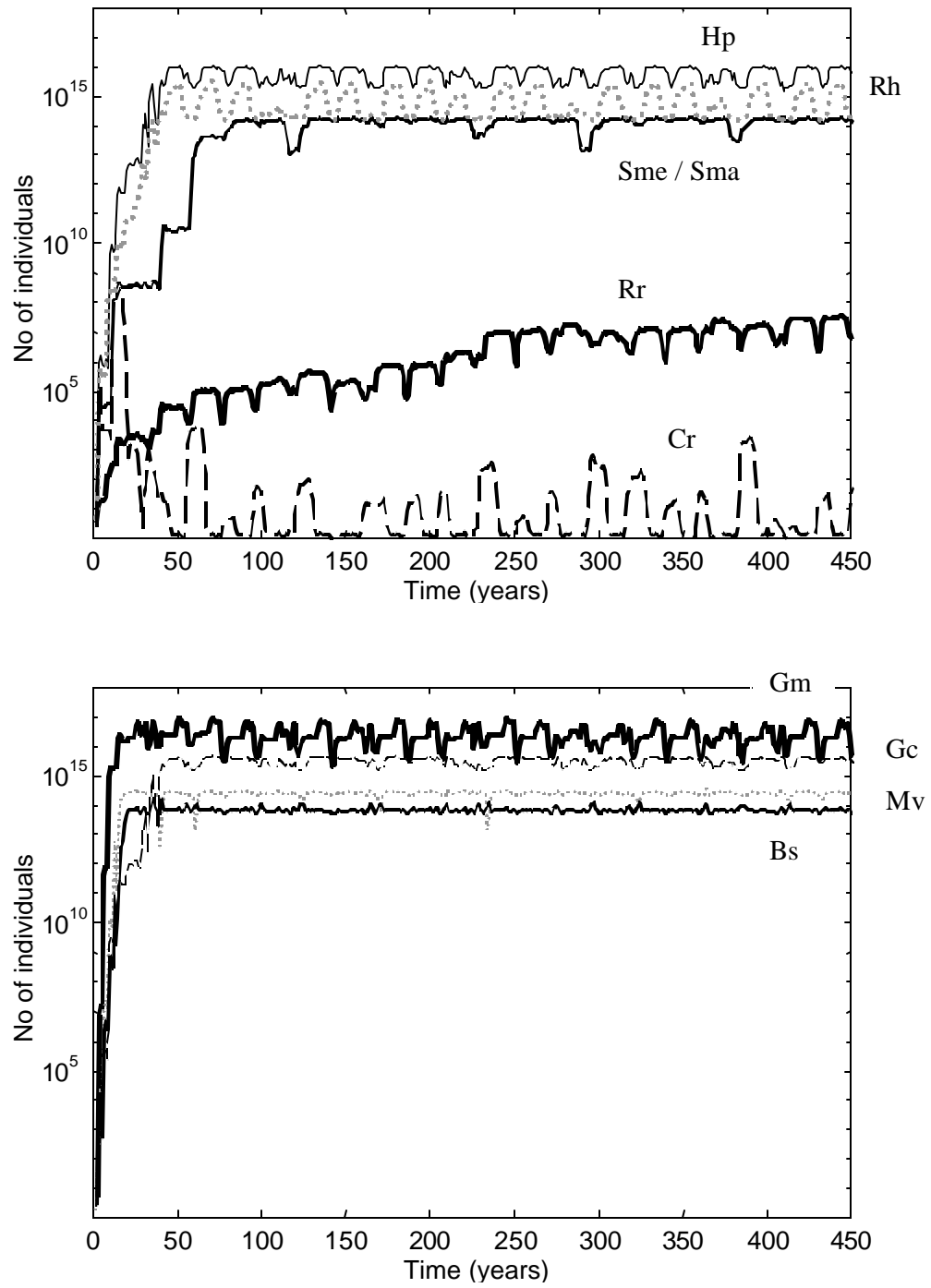Fig. 4. Number of offspring produced as a function of the number of mature individuals in the population.

Fig. 5. Community dynamics. Change over time of each species.

% of size groups in the community
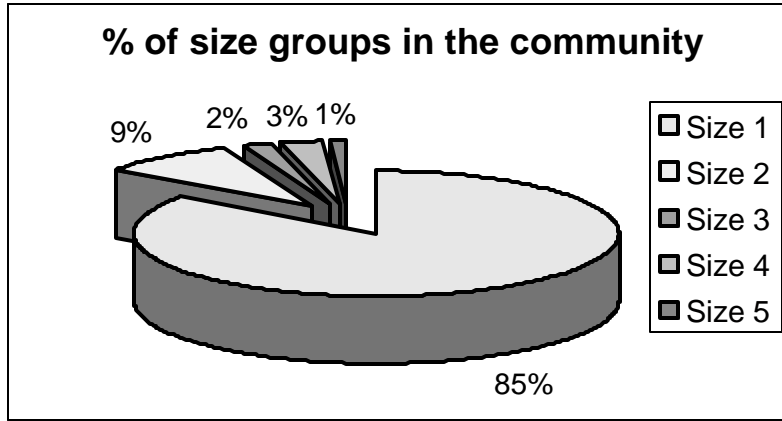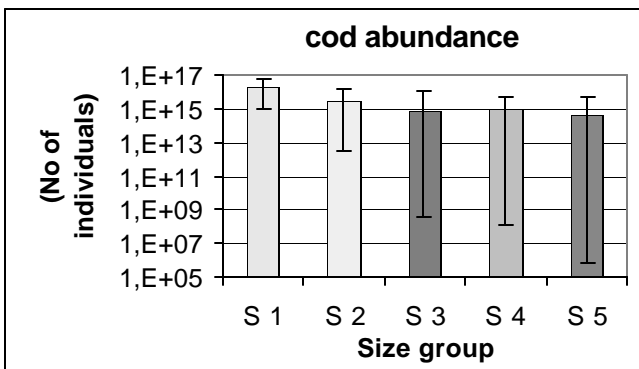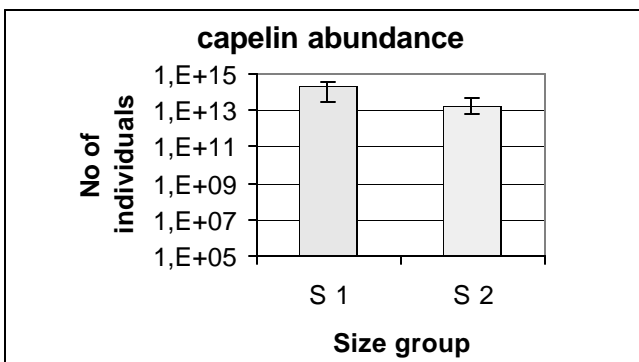
9% 2% 3% 1%

Size 1
Size 2
Size 3
Size 4
Size 5
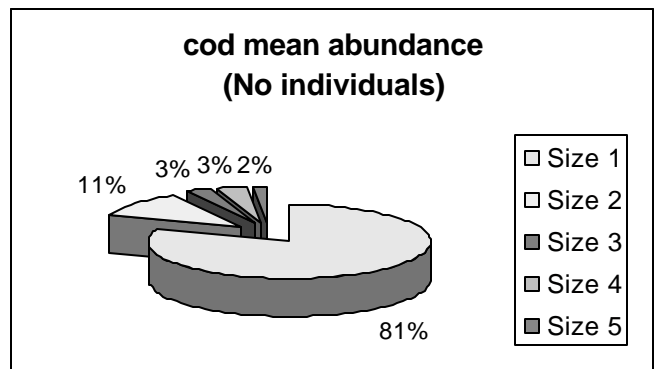
85%

Fig. 6. Relative percentage of each size group in the community.

(A)

(a)

cod abundance

(No of individuals)

1,E+17
1,E+15
1,E+13
1,E+11
1,E+09
1,E+07
1,E+05

S 1   S 2   S 3   S 4   S 5

Size group

cod mean abundance
(No individuals)

11%   3% 3% 2%

Size 1
Size 2
Size 3
Size 4
Size 5

81%

(B)

(b)

capelin abundance

No of individuals

1,E+15
1,E+13
1,E+11
1,E+09
1,E+07
1,E+05

S 1   S 2

Size group

capelin mean abundance   (No of individuals)
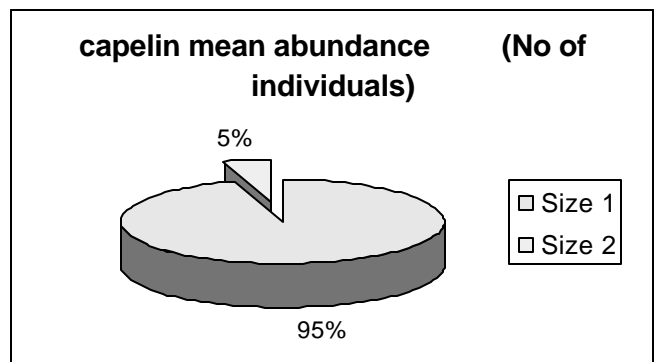
5%

Size 1
Size 2

95%

Fig. 7.   Abundance of size groups for Cod and Capelin. Bar charts A-I show the mean abundance of size groups for each species during the period between year 99 to year 450 (Fig. 5). Error bars correspond to minimum and maximum abundance of the size group within that time period. Pie charts a-i show the relative abundance of each size group in each species.