4. Alternative Theoretical Model

4.1. Introduction

In Chapter 2 a number of different tests of Huston's Dynamic Equilibrium Model (DEM) are presented. For the most part, these tests suggest that the DEM fails to predict the response of species diversity to variation in productivity and disturbance in fish and benthic invertebrate communities in the North Sea. Under these circumstances, the DEM cannot provide the theoretical basis for a management protocol aimed at predicting diversity consequences resulting from specific disturbance regimes. Nevertheless, since the conservation and restoration of biodiversity is at the heart of many of the principal policy drivers facing managers today, understanding the processes that structure marine communities, and affects their species diversity, remains an essential goal for marine scientists tasked with providing the scientific advice necessary to underpin an "ecosystem approach to management" (EAM).

It is widely recognised that the EAM will be heavily reliant on the use of "indicators". Currently there is considerable emphasis on the development of frameworks wherein indicators can be employed to inform and guide management. Many of these frameworks, for example the "Pressure-State-Response" (PSR) framework, rely on the application of a suite of indicators that are theoretically mechanistically linked (Figure 4.1.1). "Pressure" indicators relate variation an anthropogenic activity, or the anthropogenic disturbance caused to the system. Such indicators might include fishing effort statistics, or the mortality indices derived from models that use these statistics to provide more biologically meaningful measures of the actual impact caused by any given activity regime (see chapter 8). "State" indicators then reflect changes in the state of the biological system. Such indicators are normally (but need not necessarily be) specific to particular components of the marine ecosystem, for example the demersal fish community or the epibenthic invertebrate community, and to particular characteristics of these components, for example species diversity or mean body size (see chapters 9, 10, and 11). In order for there to be a management issue, application of relevant "State" indicators will usually have provided evidence of a change in "State" that is deemed undesirable, for example the long-term declines in the species diversity of fish or benthic communities noted in chapter 1, and which managers will wish to rectify. To initiate the remedial process, objectives for state (Ecological Quality Objectives, {EcoQOs}) will be set and managers will then commence mitigating action, the "Response", for example reducing Total Allowable Catches (TACs), whereby the TACs themselves become the third, or "Response", indicator in the series (Figure 4.1.1).

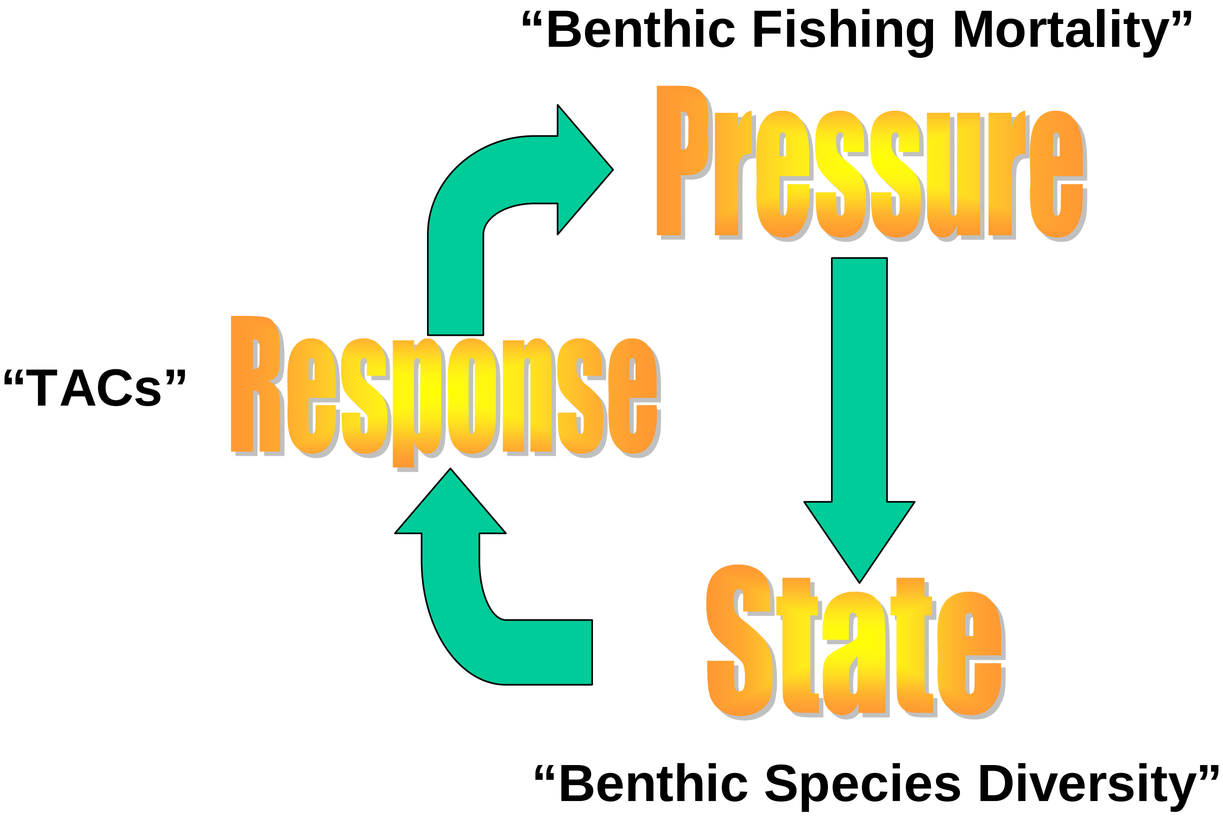

Figure 4.1.1. Representation of the "Pressure-State-Response" indicator based management framework.

For such management frameworks to be successful, appropriate indicators have to be identified, and the mechanistic linkages between these indicators have to be well understood. In the example considered in Figure 4.1.1, the relationship between TACs and fishing activity regime needs to be well defined to ensure that a specific change in the suite of single species TACs (the "Response" indicator) brings about a predictable change in benthic mortality caused by fishing (the "Pressure" indicator), for example, a particular spatial distribution of a given level of fishing effort by a specific set of fishing gears that gives rise to unique distribution of benthic mortality. Most critically of all, it is important the relationship between the "Pressure" and "State" indicators are well known. This is essential if the change in "Pressure" brought about by the" Response" is to have the desired effect on "State". Failure to properly define the relationship between "Pressure" and "State" indicators may result in fisheries being constrained more than is necessary, or insufficiently constrained, to achieve management objectives. At worst, failure to elucidate and understand this link in the PSR framework my cause fisheries to be blamed and penalised for changes in state brought about by other factors altogether.

It is clear from the above discussion that the MAFCONS project was set up with the clear intention of providing the scientific support to management frameworks such as the PSR framework. The link between "Response" and "Pressure" indicators has largely been addressed elsewhere in the report (Chapters 12 and 3). Here we devote our attention towards progressing our knowledge regarding the relationship between fishing activity ("Pressure") and the species diversity ("State") of fish and benthic invertebrate communities. In chapter 7 we provide an in depth review of the literature on the subject, and start to apply what is largely (but not entirely) a set of terrestrial paradigms to the marine situation. In chapter 7 we considered the "forces" that contribute to Huston's DEM and in chapters 1 and 2 the DEM is described in more detail with regard to the derivation of specific hypotheses from the model that were testable with the data available to the MAFCONS project. In chapter 2, where we test these hypotheses directly, we demonstrate that the DEM fails to predict variation in species diversity of fish and benthic communities in the North Sea; certainly it fails to do this with the precision required to form the basis for management decision making. However, the importance of understanding the link between ecological disturbance and species diversity with respect to the EAM remains undiminished. Here we consider why the DEM failed when applied to marine communities and we return to what was learnt by our review of theoretical community ecology so as to consider a possible alternative theoretical model.

4.2. The shortcomings of traditional community ecology theory when applied to marine fish and benthic invertebrate communities

In communities consisting of species with deterministic growth, it makes sense to consider species as the "individual units" that make up the community. Individuals of each species quickly grow through their juvenile phase and mature as fully-grown adults occupying the adult "niche". The greater part of any individual's life span is spent as the mature adult, generally eating the same type of prey and occupying the same habitat. In communities of species that for the most part display non-deterministic growth, the idea of the species as the community unit makes far less sense (Persson 1988). An archetypal demersal fish in the North Sea, for example, may start life as a pelagic or demersal egg, hatch into a pelagic larval form preying on zooplankton such as copepods. As it grows it preys increasingly on larger planktonic prey, which may include the larvae of other fish. The larva metamorphoses and often, for a short while, goes through a pelagic juvenile phase, continuing to consume planktonic prey, which at this stage can consist of adult crustaceans, as well as the larvae of fish and benthic invertebrates (Robb and Hislop 1980; Robb 1981). After several months the juvenile fish settles to the seabed, now preying on benthic invertebrates and hyper-benthic crustaceans. The young fish continues to grow, and as it does so, its diet continues to change to include larger and larger prey, which at this stage may start to include fish, either the adults of small species such as gobies, or the juveniles of larger species (Hislop et al 1991; Greenstreet 1996; Hislop 1997; Greenstreet et al 1998). Some demersal fish species may not change to a piscivorous diet, but nevertheless their diets also change so that they prey on ever larger invertebrate species, such as squat lobsters, hermit crabs, whelks and Nephrops (Daan 1973; 1989). As these fish grow, their habitat preferences may also change, for example, moving from shallow areas into deeper waters. Many marine species can increase in body mass through more than five orders of magnitude (Cushing 1975; Cohen et al. 2003) It is difficult to reconcile the changes in life-style that occur as the result of the continued growth of such non-deterministic growth species with the concept of the species niche. It would perhaps make more sense to consider particular organism size classes as the community unit, rather than maintaining the focus on species. In communities of non-deterministic growth species, differences in "ecological function" between the size classes of individuals within the community tend to be at least as great, if not greater, than the differences between species when all life-history phases of each species are considered (Werner & Gilliam 1984). Interaction strengths between different cohorts of both predators and prey will change continuously as both increase at varying rates and to different ultimate body-lengths. Different cohorts of the same species may interact, through cannibalism, or through mediation of prey responses to predators of different length for example, to alter species interactions between predators and prey and between competitors (Biro et al 2003; Rudolf 2006).

Unicellular algae are the principal primary producers in marine ecosystems (Duarte and Cebrián 1996). These support strongly size-structured food chains in which predators tend to be larger than their prey (Pope et al 1994). This, together with the transient predator-prey relationships that occur as individuals of any one species pass through so many different size-classes (eg Daan, 1973; 1989; Hislop et al 1991; Boyle and Pierce 1994; Greenstreet 1996; Hislop 1997; Greenstreet et al 1998), has led many scientists to undertake size based, rather than species oriented, analyses of food webs. Since non-deterministic growth is more prevalent in marine and aquatic environments, a high proportion of such studies have involved marine and aquatic communities (Platt and Denman 1978; Sheldon and Parsons 1967; Sheldon et al. 1972; 1973; Sprules 1980; Sprules and Goyke 1994; Sprules and Munawar 1986; see also references in Kerr and Dickie 2001). One of the principal features of many of these studies is the use of "biomass-size spectra" to describe the structure of the community in question. Such spectra have been used to describe the structure of both fish and benthic communities in the North Sea and elsewhere (Pope and Knights 1982; Pope et al 1988; Murawski and Idoine 1992; Duplisea and Kerr 1995; Rice and Gislason 1996; Duplisea et al 1997; 2002; Gislason and Rice 1998; Bianchi et al 2000; Jennings et al 2002a; 2002b; 2002c; Daan et al 2005). Because energy transfer between trophic levels is inefficient, production in lower trophic levels will always exceed production in the next higher trophic level. Consequently, and because predators tend to be larger than their prey (Warren and Lawton 1987; Cohen et al 1993), biomass-size spectra tend to demonstrate a typical form whereby biomass decreases in progressively heavier size classes (Kerr 1974, Dickie et al 1987; Boudreau et al 1991; Thiebaux and Dickie 1992, 1993; Kerr and Dickie 2001).

Long-term changes in the shape of fish and benthic community biomass spectra in the North Sea (and other seas) where fishing constitutes a major cause of mortality are often characterised by an increase in the gradient of the negative slope (Rice and Gislason 1996; Gislason and Rice 1998; Duplisea et al 2002; Jennings et al 2002a). The communities have changed such that the biomass of small organisms has increased while the biomass of large size class animals has decreased. Such changes in biomass size-spectra imply major changes in energy flow through the food webs involved. Production at higher trophic level will be reduced, whilst lower down food chains, production will be increased. The numbers of top predators in systems will be reduced, while their potential prey abundance will have increased (Pinnegar et al 2002). Because of the profound implications that these observed changes in biomass size-spectra hold for marine ecosystem function (eg Jennings et al 2002a), considerable effort has been spent confirming the relationship between biomass size-spectra and trophic structure (Fry and Quinones 1994; France et al 1998; Jennings et al 2001a; 2001b; 2002c; 2002d; 2003). In most instances, this linkage has been established, leading to the inevitable conclusion that the changes in size composition within these communities has coincided with change in their trophic structure (Pinnegar et al 2002; Jennings et al 2002a; Jennings and Warr 2003). If so, then any consideration of marine fish and benthic invertebrate community species diversity must also take account of community biomass size-spectra. The observed changes in size-spectra imply major disruption to top-down, bottom-up, and competitive processes that may be operating between and within size classes to determine the number of coexisting species within each size class. Thus models of marine community species diversity also need to be size-based, particularly where non-deterministic growth is the norm for most species in the community.

To sum up therefore, consideration of the size-based processes common in marine fish and benthic invertebrate communities consisting of species with non-deterministic growth has several implications that species-based models, such as Huston's dynamic equilibrium model, simply do not take into account. Firstly, fishing is itself a size-based activity, encouraged by the higher value attributed to larger fish and regulated through minimum legal landing sizes and minimum legal mesh sizes, so that only the larger individuals in any species suffer the highest "fishing disturbance", or mortality. Secondly, as a result of size-based trophic structuring, not all individuals in a population are competing for the same prey resource. With increase in size, individuals of each species are involved in competitive interactions with a variety of different species at different trophic levels. Thirdly, as a corollary of this, not all individuals are subjected to the same levels of predation mortality, inflicted by the same predator species. Furthermore, through varying top-down predatory processes, large individuals of a particular species have the capacity to influence the outcome of competitive interactions in their smaller sized conspecifics (eg Biro et al 2003; Svanbäck & Persson 2004). Consequently, individuals of any given species in marine fish and benthic invertebrate communities are likely to be "limited" or "controlled" to differing extents by different "top-down control" and "bottom-up limiting" processes (Rudolf 2006).

In addition, models such as the dynamic equilibrium model, and indeed much of the theory relating to the mechanisms believed to structure communities, assume Lokta-Voltera type *per capita* population growth. Population dynamics of this type infer that the potential for population growth at any particular point in time is a function of the current population size. Fish communities in particular, but also in all likelihood benthic invertebrate communities as well, are instead characterised by what has been termed "storage" and "lottery" model population growth potential (see review of community theory in Chapter 7). The "storage" model infers that future population growth potential is, for a considerable period of time, decoupled from current population size and such population dynamics seem particularly appropriate for populations of species that are characterised by non-deterministic growth, and where individual fecundity is a function of individual body mass (McLaren 1965; Griffiths 1977; Achituv & Barnes 1978; Strong & Daborn 1979; Hughes & Roberts 1981; Emerson et al 1990; Bliel & Oberst 2005). Thus, a population of fish where recruitment, immigration, and emigration rates are set to zero (ie a single annual cohort in a closed population) will decline in number at a predictable rate dependent on the rate of mortality. However, the survivors will continue to grow in body mass such that, with the passage of time, the population will consist of a dwindling number of increasingly large individuals. Since fecundity in fish is tightly linked to body mass (Hislop 1988; Emerson et al 1990; Marteinsdottir & Begg 2002; Bliel & Oberst 2005), total population fecundity may remain constant, or even increase with time, despite decreasing numbers of spawners present in the population (Figure 4.2.1). In the example illustrated in Figure 4.2.1, loosely based on cod life-history characteristics, population growth potential (gamete mass) in the population increases for the first six years and it is not until seven years have passed that a serious decline begins. By this stage, the number of individuals in the population (cohort) has been reduced by 74% by an annual mortality of 20%. By age 7 in this example, the modelled fish have reached 80% of their ultimate body length and it is only from this point on that the loss of potential gamete mass through mortality losses each year exceeds the gains achieved through growth in body size in the surviving individuals.

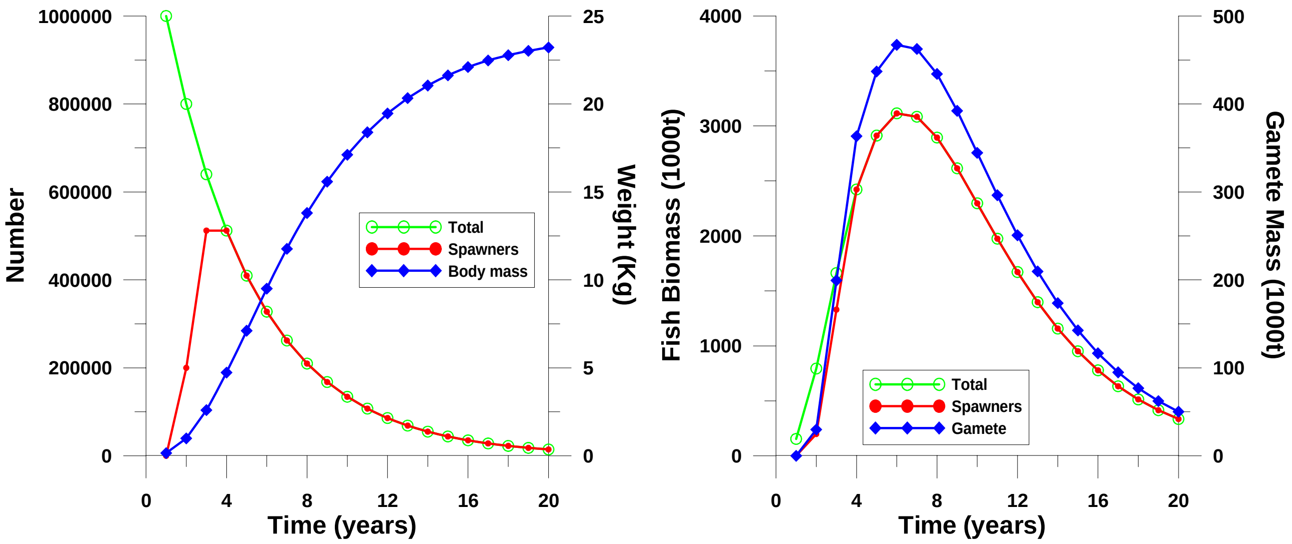

Figure 4.2.1. Illustration of the "storage" model based on life-history characteristics of a cohort of cod. Growth in length is driven by the von Bertalanffy growth function with L_∞=123.1 and K=0.230. Conversion to weight assumes values of c=0.0051 and b=3.192 in the weight at length power function. Cohort "seed" size at t=1 is 1000000. Mortality losses are assumed to be 20% per year and the proportions mature at t=1, t=2, t=3, and t=4+ are assumed to be 0%, 25%, 80% and 100% respectively. Gamete mass in a mature fish is assumed to be 15% of body mass. Left panel shows variation in total number of fish, number of spawners, and individual body mass of fish with time. Right panel shows variation in total cohort biomass, spawner biomass and gamete biomass with time.

The "lottery" model refers to the stochastic nature of recruitment that is a well known characteristic of marine fish and benthic invertebrate populations. Thus frequently, many years pass and despite high levels of gamete production, recruitment to the population may be relatively low. But on occasion, various factors combine to produce highly favourable conditions for larval/juvenile survival – the "lottery win" effect – resulting in markedly higher level of recruitment. The combination of both the "storage" and "lottery" effects means that despite declining numbers of individuals in a population due to mortality, arising through both natural processes and anthropogenic activities, relatively long periods of low recruitment rates may be sustainable due to the "storage" effect, until the "lottery" pays off and a single cohort of offspring experiences unusually high survival so that exceptionally high numbers recruit to the population and the population size recovers.

4.3. An alternative size-structured species-interactive model

Figure 4.3.1 illustrates the type of form that a size-structured species-interactive model to simulate the effects of fishing activity on species diversity at various community organisational levels might have. In this example, which we describe here as it might be applied to a fish community, 10 species are modelled, labelled A through J, with a variable number, between 5 and 11, of Log_2 body-mass classes. For each species, the number of possible Log_2 body-mass classes is dependent upon the species ultimate body size, characterised by the von Bertalanffy growth curve $\text{Length}_{\text{infinity}}$ L_∞, parameter. Logged body-mass weight classes would be used so as to produce the linear Log total biomass – log body-mass biomass spectra predicted across all taxa from metabolic theory (Kerr & Dickie 2001). By convention, Logs to the base 2 are used so that each successive body-mass class represents a doubling in body-mass over the previous class. Provided abundance in the "mature" body-mass classes of each modelled species exceeded a set limit, then annual recruitment to the smallest body-mass class would be randomly generated based on observed mean and variance in recruitment for each species concerned. Should abundance in the "mature" body-mass classes fall below the set limit, then species-specific stock-recruit relationship would be assumed. In section 9.2.5.2, we present a method by which species specific daily growth rates as a percentage of current body-mass can be determined. These growth rates would be used to progress individuals of each species through successive body-mass classes.

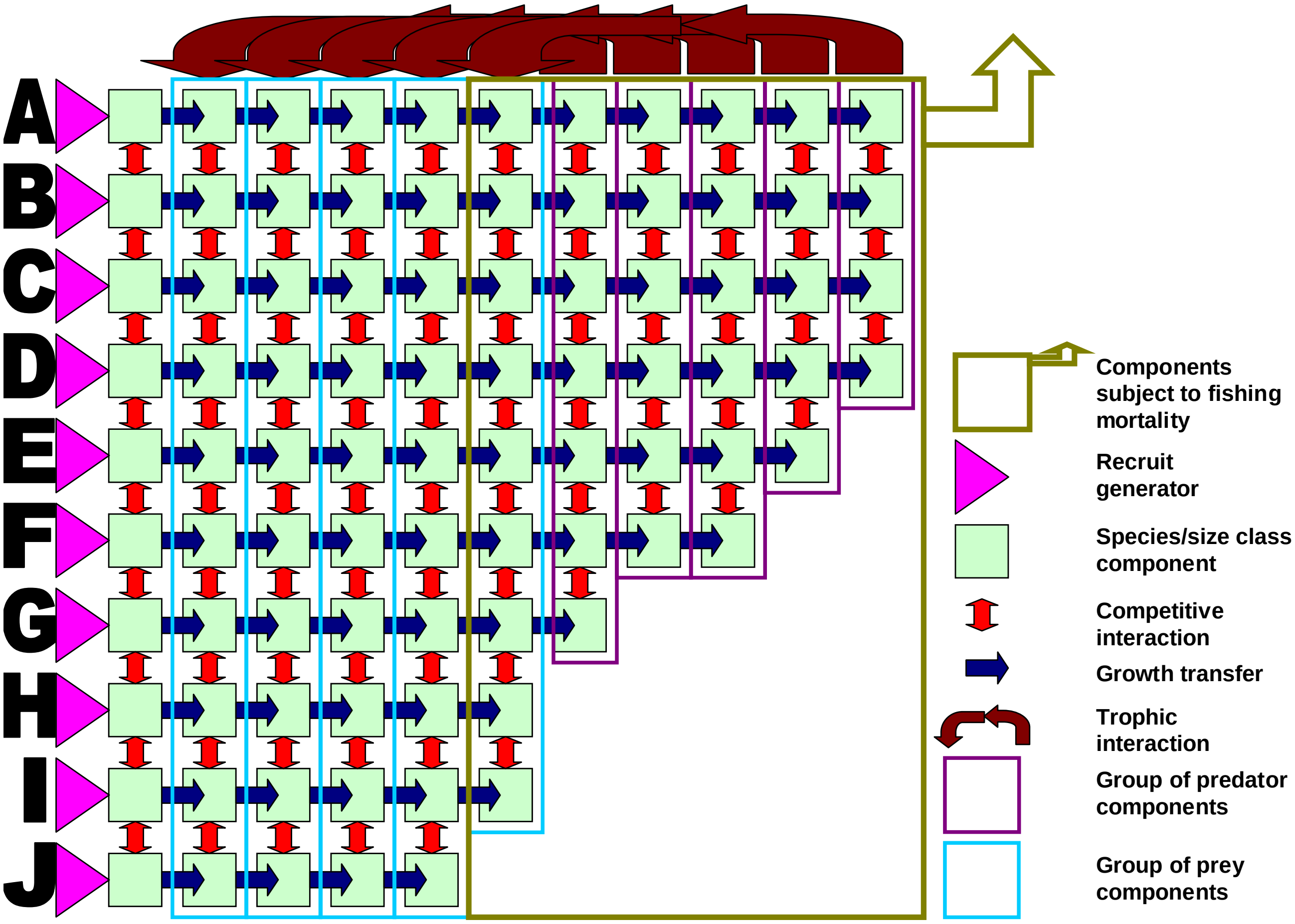

Figure 4.3.1. Proposed form for a size-structured species-interactive model to simulate the effect of fishing disturbance on the relative abundance of species with differing life-history characteristics.

To model top-down predatory forces, specific predator mass – prey mass ratios would be assumed (eg. Jennings et al 2002; Jennings & Warr 2003). These predator-prey size ratios can be parameterised through stable isotope analyses for both fish and benthic communities, but in addition a wealth of feeding ecology data are available for fish from numerous North Sea diet and food consumption studies (eg Daan 1989; Hislop et al 1997; Greenstreet 2006). These would also allow direct estimation of predator-prey size ratios for fish predators consuming fish prey. Actual predation loadings on the prey body-mass classes will depend on abundance in the predator body-mass classes. Individual predation rates can be fixed as a function of their daily specific growth rate, ie assuming set trophic transfer efficiency rates, for example of 10% to 20%. Thus if the daily specific growth rate of predators in a given body-mass class was 0.3%bw.day^{-1}, consumption rates on the prey body-mass class might need to be 1.5% to 3.0% of biomass in the predator body-mass class in order for such growth rates to be achievable with the specified trophic transfer efficiency.

Consumption rates determined in this way can be validated by the data available from diet and food consumption studies such as those cited above. Alternatively, such data can be used to parameterise consumption rates directly for predators of given body-mass.

In the absence of data to the contrary, there is no absolute imperative to model specific competition coefficients between individuals of different species within a given body-mass class. Simply, if productivity in a given prey-body mass class is insufficient to meet the consumption needs in the predator body-mass class preying on it, then growth in the predator body-mass class would be reduced across all species as a constant proportion of each individual species' daily specific growth rate. That is to say, all the daily specific growth rates of each species in the predator body-mass class would be reduced by a constant fraction. Under such circumstances, the life history characteristics of the species in the predator body-mass class will determine which species perform best under situations of strong competition and limiting prey resources. However, the model could also be structured so as to allow a variety of different competitive processes to be explored, depending upon the most likely scenarios suggested by developing theory.

Finally, to explore the effects of fishing disturbance, an additional fishing mortality can be imposed on the body-mass classes deemed to be exploitable. The effects of this on the relative abundance of individuals of different species and body-mass classes can then be followed.

This model form addresses all the short-comings in the DEM and any alternative species-centric models that might be considered instead. It takes account of variable top-down forces as total abundance in the larger piscivorous body mass classes varies. Variable bottom-up (competitive) forces are also accounted for as abundance in the prey body-mass classes varies, affecting the resources available to the predator body-mass classes, thereby influencing predator growth rates. The inclusion of biologically realistic recruitment random generators disconnects the population growth potential of each species from their standing spawning stock abundance. By summing individuals of each species across all body-mass classes, the effects of size and species selective fishing exploitation patterns on diversity at the species level can still be explored. Such output can be compared with the data available from field studies (Greensteet & Hall 1996; Greenstreet et al 1999; Piet & Jennings 2005; Greenstreet & Rogers 2006), and used to form the basis for advice to managers attempting to achieve community level EcoQOs. Size-structured modelling of fish communities so as to explore the effects of fishing on community size-structure is a new development, but one that has already started (eg Pope et al 2006). Development of such models, particularly to take account of competitive interactions, will provide powerful tools for scientists providing advice in support of the EAM.

4.4. Theoretical Size-based Maximum Species Richness Profiles

In Figure 4.3.1 illustrating the proposed form for a size-structured species-interactive community model not all species were represented by all size classes. As pointed out in the description of the proposed model, species ultimate body-lengths vary, as determined by their von Bertalanffy growth function L_∞ parameter, result in only a small proportion of species growing large enough to enter the largest Log_2 body-weight classes. If L_∞ parameter values can be determined for all species in a particular species "pool", then theoretical size based species richness profiles can be determined for the "pool".

In section 9.2.5.2 we developed a regression model to parameterise the von Bertalanffy growth function for each species sampled by the different groundfish surveys. Thus for each species the ultimate body-length of a fully grown individual, L_∞, if not available from appropriate published growth studies, could be estimated given values of L_{max}, the maximum recorded body-length from *FishBase* (Section 9.4 Appendix 2). For each species, the ultimate body-weight of a fully grown individual, W_∞, can be determined by from the weight at length relationship $W_\infty = cL_\infty{}^b$, given the species specific c and b parameter values also provided in Section 9.4 Appendix 2. Assuming that each species might be expected to be found in all Log_2 weight classes up to and including the weight class that included its calculated W_∞, then the maximum species richness at each Log_2 body-mass size-class profile for each survey data set can be determined (Figure 4.4.1). The SAGFS data set had no abundance data for individual goby species, all gobies had been given a single, unidentified goby code. Eight goby species were identified between the IBTS and DBTS surveys, six species in the former and 5 in the latter. Three species were common to both data sets; sand goby, black goby and Fries's goby. The SAGFS unidentified goby code was therefore considered to consist of these three species and these species were added to the SAGFS species list.

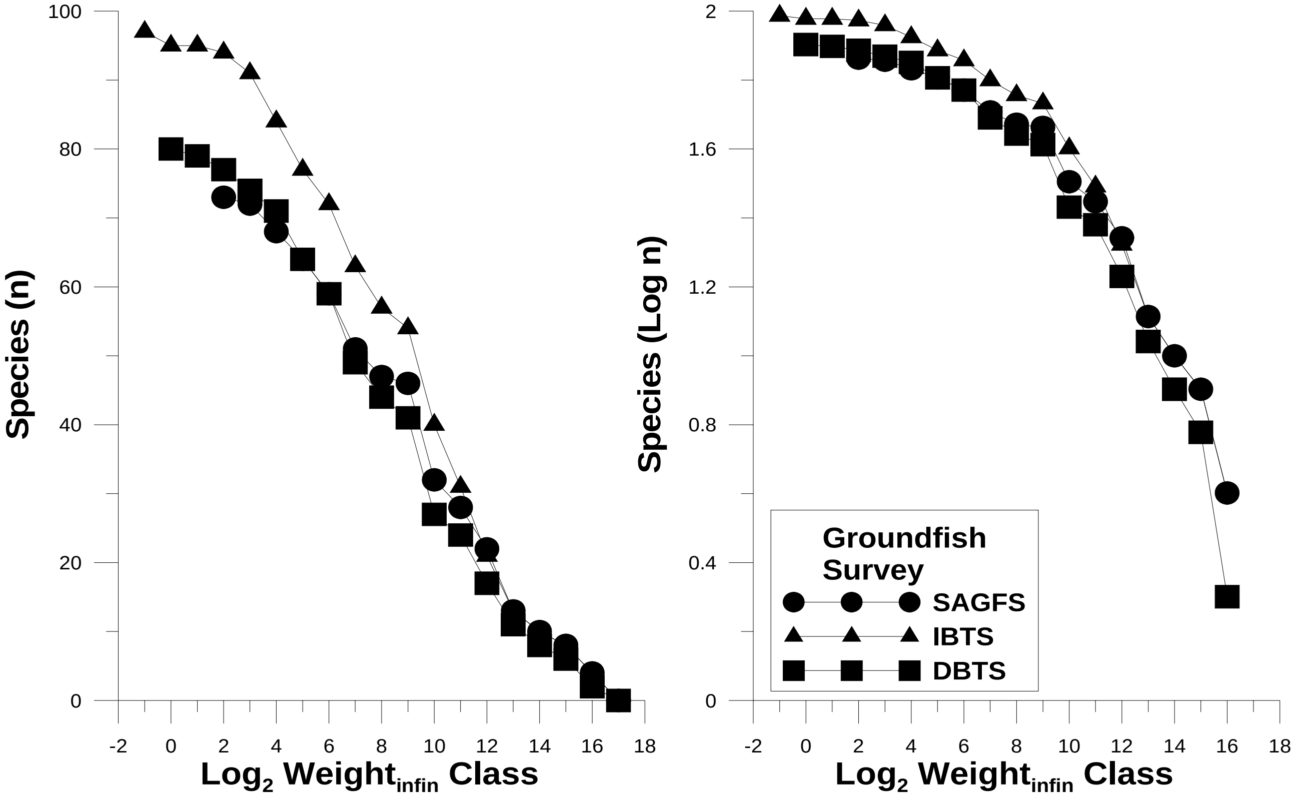

Figure 4.4.1. Relationships between maximum potential species richness in each Log_2 body-mass size class with increase in body-mass size class for the species suites sampled by each of the three main groundfish surveys for which data were available; the Scottish August Groundfish Survey (SAGFS), ICES Q3 International Bottom Trawl Survey (IBTS), and the Dutch Q3 Beam Trawl Survey (DBTS). Left panel show species richness in each body-mass class on a linear scale, while right panel shows Log_{10} of number of species.

4.5. Evidence for Size-based Diversity Processes

4.5.1. Relationships between species richness and abundance with body-mass

Many studies have demonstrated unimodal relationships between species richness and body-size class (Blackburn and Gaston 1994a; 1994b 1994c; Brown 1995; Brown, Marquet and Taper 1993; Cotgreave and Harvey 1994; Erwin and Scott 1980; May 1986; Morse, Stork and Lawton 1988; Navarrete and Menge 1997; Stanley 1973), while others have demonstrated similar unimodal relationships between abundance and body-size class (Bassett and Kitching 1991; Brown 1995; Janzen 1973; Morse et al 1985; Morse et al 1988). Few studies, however, have undertaken a detailed analysis of these relationships simultaneously. In two studies where variation in both the number of individuals and the number of species in body-mass size classes of increasing size on a log scale were examined together, remarkable similarities were observed despite one study focusing on grassland arthropod communities (Siemann, Tilman and Haarstad 1996; 1999), while the other examined a marine demersal fish assemblage (Hall and Greenstreet 1996).

Both studies demonstrated similar unimodal relationships between the number of individuals (I_m) or the number of species (S_m) and body mass size class (m). In each of the studies, S_m and I_m tended to peak at the same, or similar, body-mass class and in both cases, power functions of the form $S_m = cI_m{}^a$ were observed. Furthermore, these relationships held irrespective of whether data from only the ascending (smaller body-mass classes), descending (larger body-mass classes), or both sides of the unimodal relationships were analysed. In the arthropod study, the constant c=1.05 while the exponent a=0.51. Little variation in the values of these parameters was observed when each of the five most abundant arthropod orders was examined independently, despite the peaks of species richness and abundance occurring at different body-mass class in different taxonomic groups. In the demersal fish study, the constant c=1.72, while the exponent a=0.25. Thus while the shapes of the relationships were similar, species richness per individual in each body mass class in the demersal fish assemblage was considerably lower than in the arthropod communities.

In both studies, far from finding the descending sigmoid shaped theoretical size based species richness profiles shown in Figure 4.3.1, the observed profiles were unimodal in shape. We return to this point towards the end of section 4.5.2.

4.5.2. Fishing effects on size-based species richness and abundance profiles

Here we look at the effect of fishing on the relationships between species richness and abundance at different body-mass size classes in the demersal fish assemblage of the northwestern North Sea. Our purpose is twofold. Firstly we wish to explore the relationships to gain insight as to the processes operating to structure the fish community and the extent to which these processes might be modulated by size dependent variation in fishing mortality. Secondly we intend to explore the potential for these relationships to provide indications of a "fishing effect" that might be useful within a management context. We follow the analytical design described by Greenstreet & Rogers (2006).

Firstly, we compared the fish communities sampled in 75 ICES statistical rectangles assigned to three international otter trawl fishing effort "treatments"; "Low" (40 rectangles with an average annual otter trawl activity of 0 to 4999 h.y^{-1}), "Medium" (25 rectangles with an average annual otter trawl activity of 5000 to 19,999 h.y^{-1}), and "High" (10 rectangles with an average annual otter trawl activity of 20,000 to 65,000 h.y^{-1}). For each rectangle, 10 Scottish August Groundfish Survey

(SAGFS) trawl samples were selected from the data set for the 14 year period 1983 to 1996. To reduce the number of trawl samples to 10 per rectangle, samples collected in 1983, 1985, 1987 or 1995 were selected at random and excluded from the data set. In this way sampling effort per rectangle was as standardised as possible (for further details of the SAGFS and international fishing effort data sets see Greenstreet and Hall 1996; Greenstreet et al 1999a; 1999b; Greenstreet and Rogers 2006; Jennings et al 1999). All 10 samples in each rectangle were combined to give a single demersal fish community sample for each rectangle.

The relationships between Log$_2$ body-mass class (m) and both Log$_{10}$ of the number of species per body-mass class (S_m) and Log$_{10}$ of the number of individuals per body-mass class (I_m) were examined. For each of the 75 rectangles, unimodal relationships for both parameters were observed. The mean relationships for each effort treatment are shown in Figure 4.5.2.1, in which the mean S_m and mean I_m in each Log$_2$ body-mass class for all rectangles assigned to each effort treatment are plotted. The unimodal relationships for both are clear, however, contrary to the earlier study (Hall and Greenstreet 1996), there is some indication that the peaks in S_m and I_m do not always coincide. Divergence between the peaks was most apparent in the Low effort treatment, less so in the Medium effort treatment, while in High effort treatment rectangles, the two peaks tended to coincide. Divergence between the two distribution peaks, in terms of the mean number of Log$_2$ body-mass classes separating the peaks, was examined explicitly (Figure 4.5.2.2). Both mean maximum S_m and mean maximum I_m were significantly higher in ICES rectangles of high and medium fishing effort (One Way ANOVA, $p<0.001$ in both cases). However, this was essentially because there was a trend for the Log$_2$ body-mass class at which the peaks of the curves occurred to be smaller in rectangles assigned to the medium and high fishing effort treatments (significant in respect of Log$_2 W_{max} S_m$, One Way ANOVA, $p<0.01$) and, according to biomass spectrum theory, abundance would be expected to be inversely related to body-mass (Kerr & Dickie 2001). In rectangles of low fishing effort, divergence between the peaks of I_m and S_m was around two Log$_2$ body-mass classes, but in rectangles of medium and high fishing effort, the level of divergence was reduced to around 1.6 Log$_2$ body-mass classes (Figure 4.5.2.2).

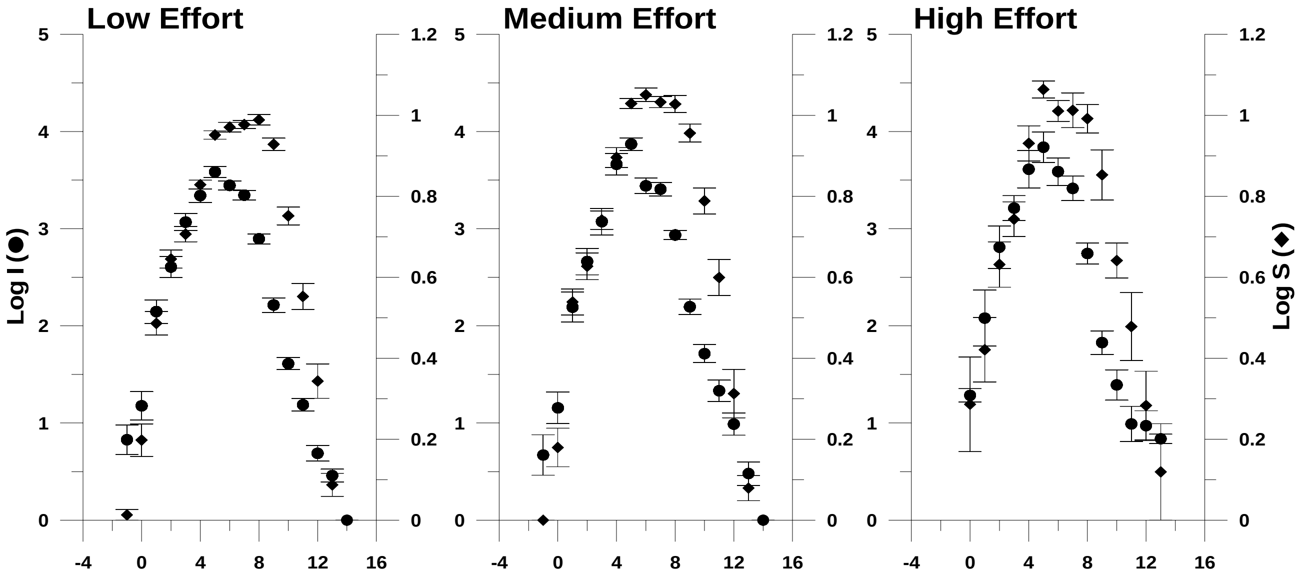

Figure 4.5.2.1. Mean (± 1 S.E.M.) of the number of individuals (I) and the number of species (S) recorded at each log$_2$ body-mass class for rectangles assigned to one of three different fishing effort treatments.

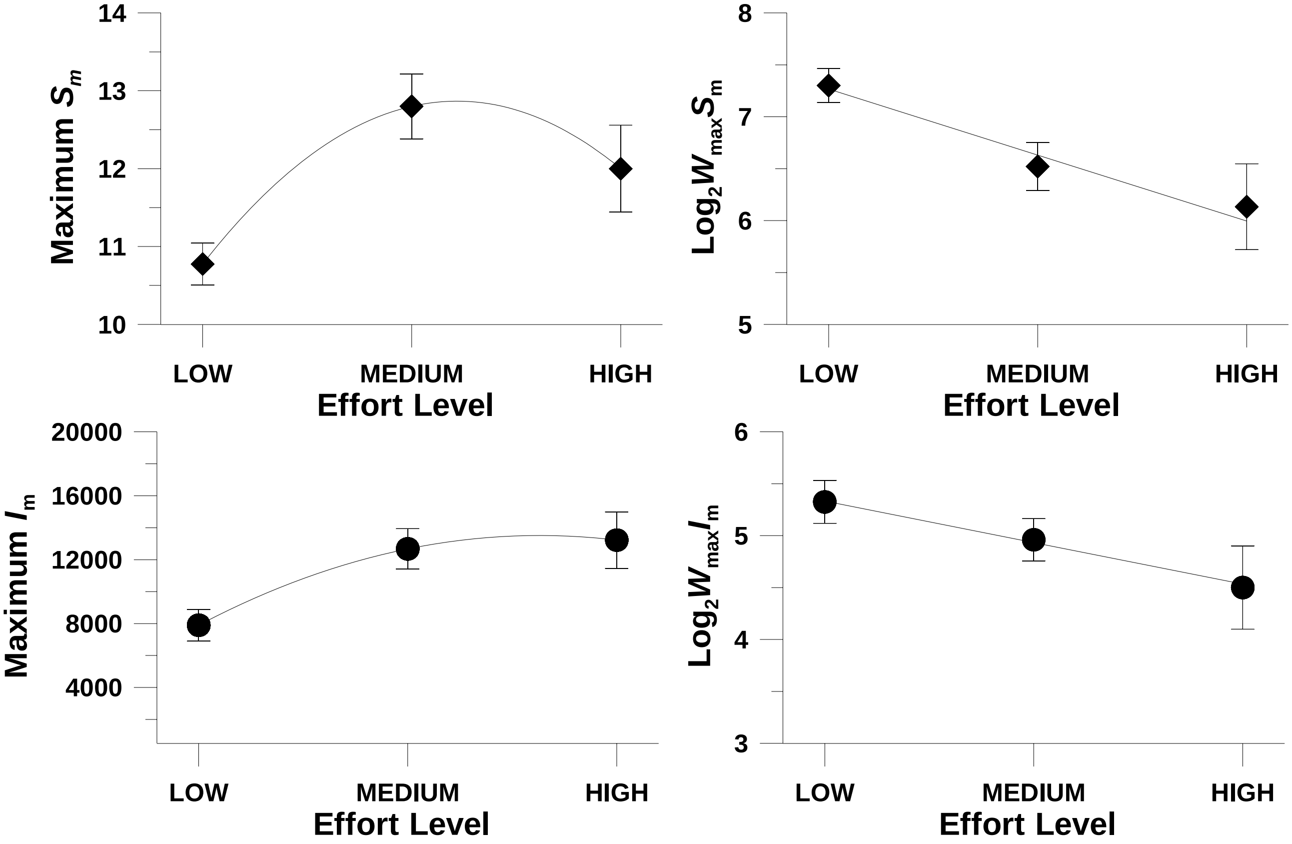

Figure 4.5.2.2. Plots showing mean (± 1 S.E.M.) maximum I_m and S_m at the peaks of the unimodal curves for I_m and S_m against Log_2 body-mass class and the mean (± 1 S.E.M.) Log2 body-mass class at which these peaks occurred in rectangles assigned to treatments of low, medium and medium fishing effort.

After first $\log_{10}$-transforming both variables, the number of individuals (I_m) per Log_2 body-mass class was regressed on the number of species (S_m) per Log_2 body-mass class to estimate the parameters c and a in the relationship $S_m = cI_m{}^a$ for each individual ICES rectangle. All 75 individual rectangle regressions were statistically significant at $P<0.05$ or less. The mean parameter values obtained for rectangles assigned to each otter trawl effort treatment were compared by ANOVA (Figure 4.5.3.3). Variation in the level of otter trawling had no significant effect on the exponent values, however the mean constant value in high otter trawl effort rectangles was significantly higher than values estimated in low otter trawl effort rectangles (ANOVA P=0.36, post-hoc Tukey comparison P=0.028).

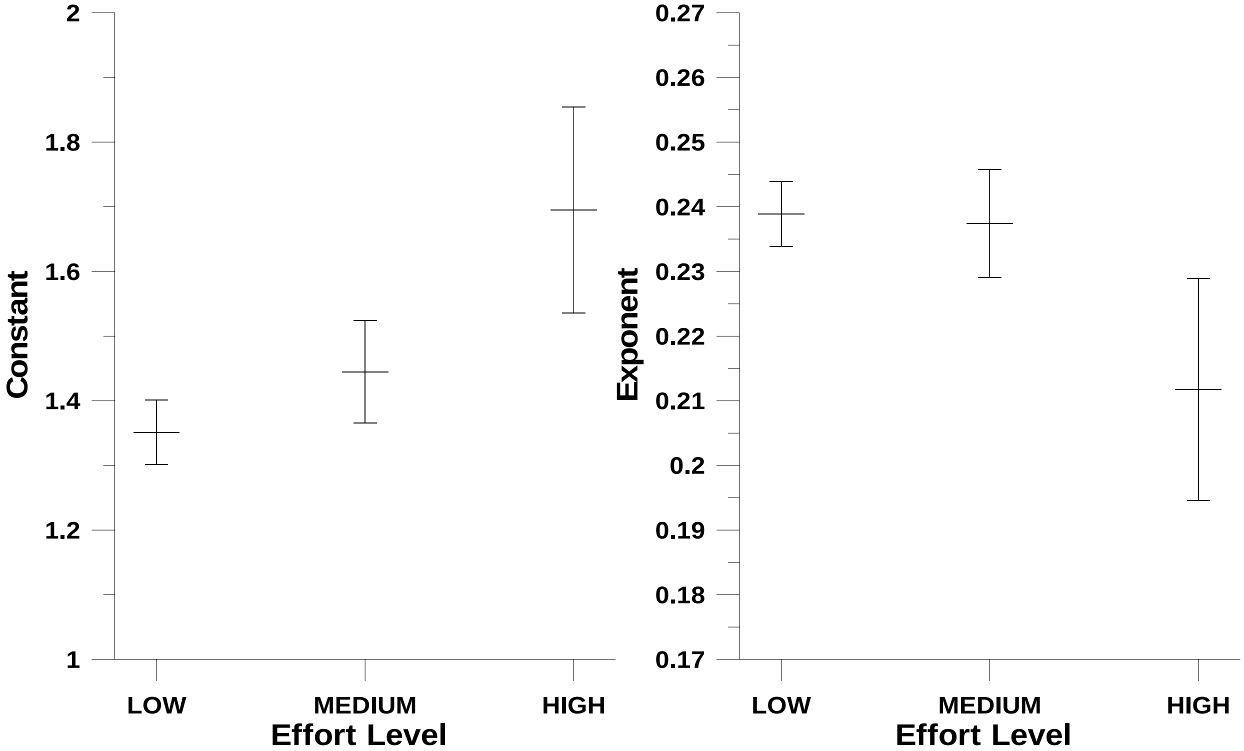

Figure 4.5.2.3. Mean (± 1 SE of Mean) constant and exponent values for the relationship $S_i = cI_i^{\,a}$ for 40 ICES rectangles with low otter trawl effort (0 to 4999h.y^{-1}), 25 rectangles with medium otter trawl effort (5000 to 19,999h.y^{-1}), and 10 rectangles with high otter trawl effort (20,000 to 65,000h.y^{-1}).

These preliminary analyses demonstrate a number of points. Firstly, the distributions of individuals and species across body-mass classes do appear to follow fairly rigidly defined general patterns, but the precise distributions are affected by fishing activity. This tends to confirm that the development of size-structured species interactive models certainly has potential to be of great values in aiding the development and implementation of an ecosystem approach to management. Secondly, the parameters obtained from the power function $S_m = cI_m^{\,a}$, particularly the constant, offer potential for use as indicators of the effects of fishing on the distributions of individual and species across body-mass classes in fish communities.

Finally we return to the discrepancy in the shapes of the expected and observed species richness – body mass profiles. Observed peaks in species richness occurred at Log_2 body-mass of around 7 (Figure 4.5.2.1 and Figure 4.5.2.2), close to the steepest part of the downward slope of the descending sigmoid curve of the theoretical species richness body-mass profile. Thus for the larger Log_2 body-mass classes, the observed and theoretical plots were similar. However, it is clear that not all species are equally likely to be represented at smaller size classes. In retrospect, the explanation for this is obvious. These smaller body mass classes consist largely of the younger individuals of larger growing species. At young age, overlap in body mass between different aged cohorts is much smaller, and may even be zero if comparing 0 group and 1 group fish of any particular species. Thus whilst fish certainly grow continuously, at any single time point, for example sampling in quarter 3, younger fish in the smaller body-mass classes of any one species will only have a very limited range of possible sizes. Thus smaller bodied fish of any given species cannot be distributed across all possible Log_2 body-mass classes at the lighter end of the range.

Biomass spectrum theory predicts a linear relationship between Log abundance and Log body-mass class, yet the observed distributions being unimodal were far from linear. A similar discrepancy to that noted above for the species v body-mass class profile. Kerr and Dickie (2001) explain such discrepancies on the basis that no one taxa can vary along the full body-mass range. In other words you can only be so small and still be a fish! In essence, according to Kerr and Dickie (2001), the complete abundance body-mass spectrum may well be linear, but that the smaller body-mass classes in Figure 4.5.2.1 are increasingly dominated by taxa other than fish.

4.6. References

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