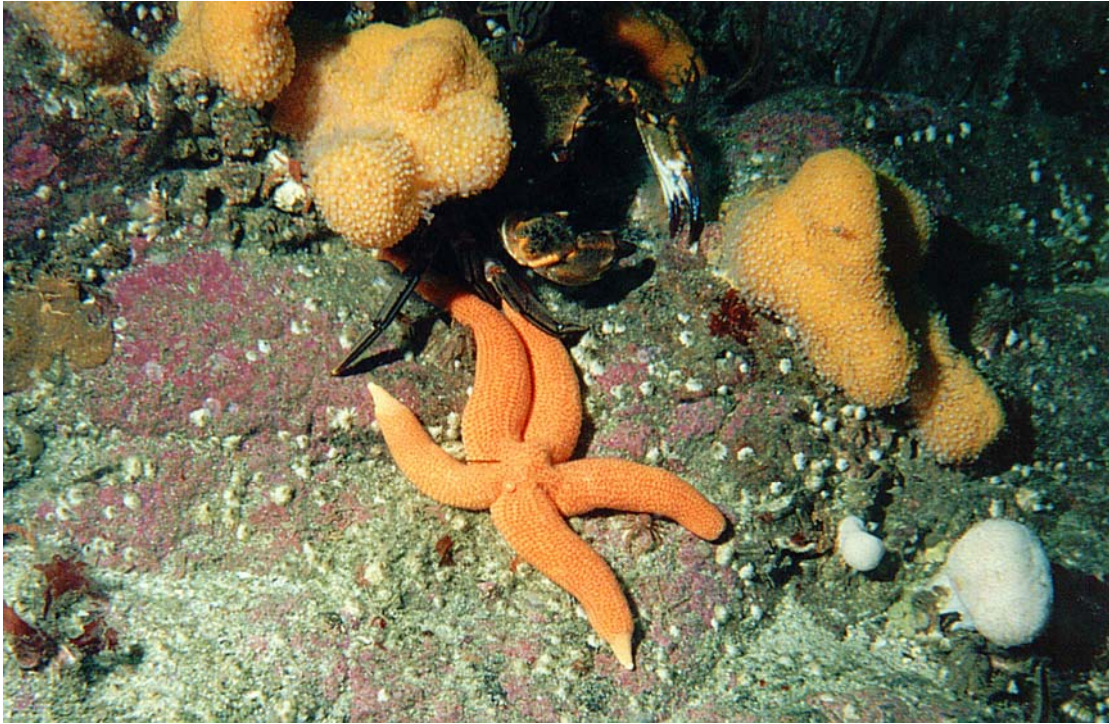


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Review of Theoretical Community Ecology: Implications for Marine Communities

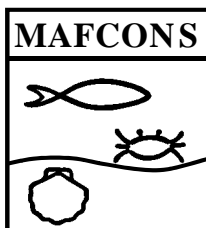


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**REVIEW OF THEORETICAL COMMUNITY ECOLOGY:
IMPLICATIONS FOR MARINE COMMUNITIES**

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1. SUMMARY

The mechanistic link between variation in fishing pressure and changes in species diversity is unclear with respect to marine fish and benthic invertebrate communities. If an EAM is to successfully address biodiversity issues then the mechanisms relating diversity and fishing activity need to be clearly understood. This requires an understanding of the processes that structure and organise marine communities. Understanding how communities are structured has been the subject of considerable research over five decades or longer. However, much of this research activity has been directed at terrestrial communities and systems. Accordingly, it is a pertinent question as to whether the huge body of theoretical community ecology literature that has emerged as a result of this research activity is at all relevant to marine communities? This literature is therefore reviewed in an effort to gain insight into how marine communities are structured.

Patterns in community structure, i.e. distributions of species relative abundance, are described. Generally, the presence of consistent patterns is taken to imply that particular forces or processes are in operation to impart the structure observed. Within trophic levels, competition provides the structuring force that limits each species to their own “niche-space” and governs the numbers and composition of species that can co-exist at any one location. However, trophic interactions between species in adjacent trophic levels can serve to alter the outcome of competition within trophic levels. Essentially predation mortality can prevent dominant competitors from reaching their carrying capacity, thereby leaving spare resource available that allows the co-existence of subordinate competitors. Disturbance can also operate to maintain diversity by increasing the mortality rates of dominant competitors, again preventing them from reaching their carrying capacity and excluding subordinate competitors. It is now widely accepted that diversity is related to both productivity and disturbance by unimodal relationships. Huston’s dynamic equilibrium model (DEM), developed through the combination of these two unimodal relationships to produce a three dimensional model linking diversity simultaneously to both disturbance and productivity, predicts that the relationship between diversity and disturbance should be positive in high productivity regions and negative in regions of low productivity.

The species-area relationship is one of the longest recognised patterns of species diversity – as the area (A) considered increases the number of species (S) present also rises. The relationship generally follows a widely recognised power function; $S=cA^z$. One of the major implications of this relationship for studies of species diversity is that estimates of species diversity are bound to be sample size dependent. Species-area relationships can be explained on the basis of competition theory in that larger areas tend to incorporate a greater variety of habitats, thus providing greater niche-space and allowing higher diversity. Island Biogeography theory also provides an explanation for species-area relationships, however this theory does not in any way rely on competitive processes providing a limit to the number of coexisting species. Instead Island Biogeography theory suggests that local species richness is the equilibrium outcome of four rate processes; speciation, extinction, immigration and emigration. However, it is also apparent that competition, predation and disturbance can all serve to vary extinction, immigration and emigration rates.

The theory of meta-population dynamics is in essence an extension of island biogeography theory in that it treats any contiguous area as a series of patches. Individuals of each species found in the entire area are distributed in sub-populations occupying different patches. No single species is represented in all patches. Sub-populations on different patches are linked by immigration and emigration processes operating between patches and subject to mortality (e.g. competition, predation, and disturbance) and birth processes within patches. Meta-population dynamics theory

predicts that at the regional scale communities may be structured by competition, but that at the local scale, competition is avoided because close competitors cannot co-exist on that same patch at the same time.

Having reviewed patterns in community structure and considered the processes (e.g. competition, predation, disturbance, top-down, bottom-up) that give rise to these patterns mainly in terrestrial systems, examples are then examined from marine communities. Marine communities have also been fitted by mathematical distributions and display latitudinal and depth gradients. There is certainly some evidence to suggest that competition plays a role in structuring marine communities and, as with terrestrial systems, diversity has been shown to be positively, negatively and unimodally related to productivity. Most examples of top-down or predation driven control of community structure have been derived from marine communities, so much so that marine communities might appear to be more often controlled by top-down processes than their terrestrial counterparts. However, top-down control does not predominate in all marine systems. Once again predation has been shown to both enhance and impair species diversity. As with terrestrial systems, habitat complexity plays a major role in determining species diversity. However in marine systems, fauna actually contribute the major part of such complexity, the presence of certain animals providing the niche space for other species. In terrestrial systems, this role is primarily played by plants.

A table of 44 differences between marine and terrestrial communities is presented. Some of these differences are profound and suggest that the theoretical community ecology developed to explain variation in the structure of terrestrial communities may be irrelevant when applied to marine systems. Terrestrial communities consist generally of species characterised by deterministic growth. In such circumstances species are likely to be the ecological functional units; species diversity is therefore a useful concept with respect to such communities. Marine communities consist largely of species characterised by non-deterministic growth, with considerable variation in resource use and ecological role occurring during ontogenetic development. Under such circumstances there is considerable variation in niche use between different sized individuals of the same species. Within species variation between size classes may indeed exceed between species variation within size classes. For marine systems therefore it makes sense to consider particular size classes of organisms as the basic ecological functional unit, not species.

Biomass-size spectra have been widely applied to marine and aquatic systems and have been shown to be influenced by fishing disturbance. The shape of such size spectra have been shown to be linked to community trophic structure. Disruption of size-spectra by fishing activity therefore implies changes in the top-down and bottom-up control processes of the communities affected. The implication here is that studies of the species diversity of marine fish and benthic invertebrate communities must take account of the size structure of the organisms concerned. Species-based models, such as the DEM, do not take account of size and are therefore unlikely to predict the impacts of fishing on marine communities.

Much community ecology theory assumes that species display Lotke-Volterra type population dynamics; that is annual *per capita* birth rates are constant, so population birth rates are directly proportional to the abundance of mature individuals in the population. But in many fish and benthic species, fecundity is proportional to body-mass, and since body-mass continues to increase in species with non-deterministic growth, *per capita* fecundity also increases. Thus the potential for population growth is much better described by the "storage model". Although mortality might reduce population abundance, the continued increase in body-mass of the survivors maintains or even increases the potential for population growth. Furthermore, recruitment survival varies considerably from year to year so that the "lottery model" further compounds the population dynamics of these species. Thus the largest recruit cohorts can potentially be produced by very

low spawning stock abundance. Such population dynamics are alien to models such as the DEM, and further explain why such models cannot predict the response of fish and benthic invertebrate communities to variation in fishing disturbance.

To counter these problems with the DEM, an alternative size-structured species-interactive model is proposed. This alternative model could form the theoretical basis for predicting the effect of fishing on fish and benthic invertebrate species diversity, both overall and within specified size classes.

2. INTRODUCTION

Recent years have witnessed a shift in emphasis in the underlying objectives of fisheries management in the North Sea. Whilst the need to conserve individual stocks at sustainable and economically viable levels is still clearly a major priority, managers are now being asked to adopt a broader ecosystem approach to managing fisheries. The political impetus behind this change in attitude has largely been provided by the “North Sea Ministerial Conferences”, five of which, along with a further two “Intermediate Ministerial Meetings”, have occurred over the period 1982 to 2002. These ministerial conferences were in turn influenced by the political commitments made to conventions such as the “Convention on Biological Diversity” (CBD) and the “Convention for the Protection of the Marine Environment of the North-East Atlantic” (OSPAR, because it combined two the two earlier Oslo and Paris Commissions). With the inclusion of Annex V in the OSPAR Convention, OSPAR was considered by ministers attending the fourth North Sea Ministerial Conference at Esbjerg in 1995 to be the competent authority with primary responsibility for the development of the ecosystem approach to management. At a workshop at Scheveningen in September 1999, a basic template for an ecosystem approach to management was proposed. Ten “issues” were identified for which Ecological Quality Objectives (EcoQOs) would be set (figure 2.1). Ecological Quality (EcoQ) was defined as the “Ecological quality of ecosystems is an overall expression of the structure and function of the aquatic systems, taking into account the biological community and natural physiographic, geographic and climatic factors as well as physical and chemical conditions including those resulting from human activities”. EcoQOs were defined as “the desired level of EcoQ relative to a reference level” where reference levels were defined as “the level of the EcoQ where the anthropogenic influence on the ecological system is minimal” (Skjoldal et al. 1999). Issues 1 to 4 were intended primarily to involve EcoQOs based at the level of individual species. Thus conservation objectives currently used in the single species assessments and management of commercial fish stocks could be carried over as EcoQOs for Issue 1. When addressing Issues 5 to 7, however, the situation becomes more complicated. For these issues, it was anticipated that EcoQOs would be directed towards multi-species, community, or assemblage attributes and this has initiated a “hunt” for appropriate indicators of community or assemblage health (Frid 2003).

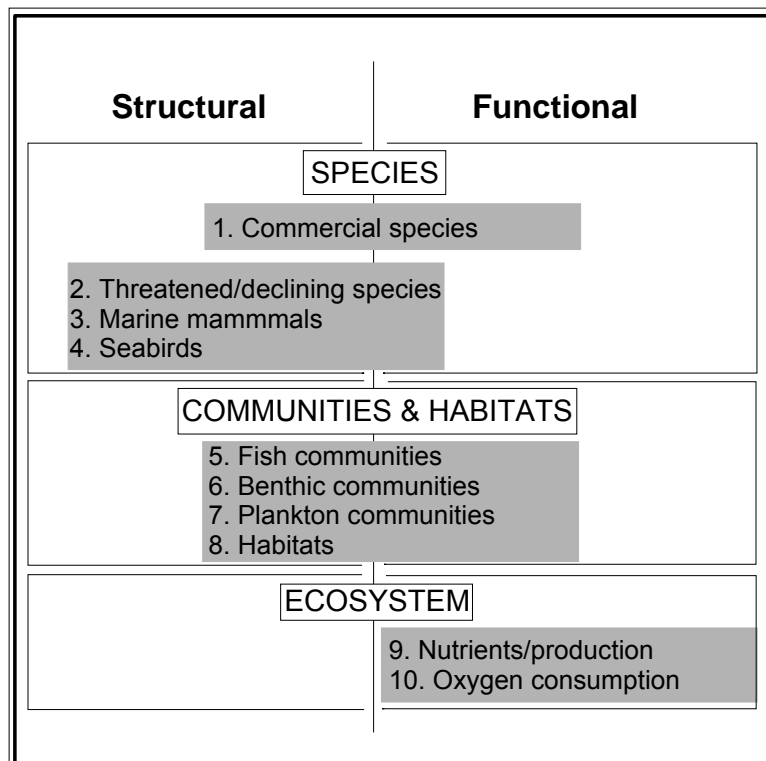


Figure 2.1. Ten OSPAR Ecological Quality Issues for each of which Ecological Quality Objectives will be set. The diagram indicates the level at which objectives are intended to be set, ie at species level or at community level, and the extent to which these objectives will address structural or functional attributes of the marine ecosystem.

Numerous different metrics or indices that numerically describe multi-species aspects of community composition and structure have been proposed and applied to biological data (Southwood 1978; Washington 1984; Magurran 1988). Many have been applied to marine community data (Clarke & Warwick 1994), including data gathered in the North Sea (Jennings & Reynolds 2000). These include variation in populations of indicator species (Bustos-Baez & Frid 2003), change in species composition, species diversity indices (Greenstreet & Hall 1996; Greenstreet *et al.* 1999), taxonomic diversity (Clarke & Warwick 1998; Hall & Greenstreet 1998; Rogers *et al.* 1999), calculation of community averaged life history traits (Jennings *et al.* 1998; Jennings *et al.* 1999), determination of community size-spectra or size composition (Rice & Gislason 1996; Hall & Greenstreet 1996), estimation of community trophic structure (Jennings *et al.* 2002), and so on. In 2001, the ICES Working Group on “The Ecosystem Effects of Fishing Activities” (WGECO) proposed a set of criterion by which to judge these various indicators (Table 2.1). After evaluation according to these criteria, ICES considered metrics based on the mean size of fish, the proportion of large fish, and the ultimate body size of fish in the community, to be the most appropriate indicators of the impact of fishing on fish communities, number 5 on the list of 10 Ecological Quality Issues. For benthic communities, number 6 in the list of EcoQ Issues, changes in the abundance of sensitive and opportunistic species were considered to be the most reliable indicators of a fishing effect. This was the advice put forward by the Advisory Committee on Ecosystems (ICES 2001), and to date, these are the only elements of Ecological Quality for fish and benthic assemblages listed in Bergen Ministerial Declaration at the 5th North Sea Ministerial Meeting.

Criterion	Property
a	Relatively easy to understand by non-scientists and those who will decide on their use
b	Sensitive to a manageable human activity
c	Relatively tightly linked in time to that activity
d	Easily and accurately measured, with a low error rate
e	Responsive primarily to a human activity, with low responsiveness to other causes of change
f	Measurable over a large proportion of the area to which the EcoQ metric is to apply
g	Based on an existing body or time-series of data to allow a realistic setting of objectives

Table 2.1. ICES criteria for a “good” Ecological Quality Objective metric.

The approach of applying these criteria to the various metrics, in order to identify the most appropriate to use as ecological indicators, puts great emphasis on identifying metrics that are easy to understand and use, and which have a tight functional relationship with the activity of concern. Metrics selected in this way instill confidence that the activity of concern has actually caused observed changes in the metric, and that reduction in activity levels will bring about a change in the metric towards some desired value – the EcoQO. From a management perspective, such tight linkage between the activity and metric performance is highly advantageous. To demonstrate this approach, consider the choice of a size-based metric as an indicator of the impact of fishing on the “health” of the broader fish community. Because fishing is so size selective on both the targeted and non-targeted fish species, mesh size being controlled by regulation, size based metrics are likely to be extremely tightly linked to the activity. Increasing mortality rates on the largest individuals (the older cohorts) in a population inevitably means that the abundance of these large individuals will decline relative to the abundance of smaller individuals (younger cohorts) not experiencing such high rates of fishing mortality. Thus there is a tight conceptual, and easily comprehensible, link between the performance of the indicators and variation in the level of fishing. Using mean fish size and the proportion of large fish in the fish community as indicators of the impact of fishing on the fish assemblage thus clearly scores highly with regard to criteria b, c, and e (Table 2.1). Furthermore, both scientist and layman alike easily understand the concept of “size”. Fish length is something that is easily and accurately measured and recorded, with no particular necessity for specialist knowledge or training, and thus these indicators also score highly against criteria a and d (Table 2.1). Finally, internationally coordinated groundfish surveys covering the entire North Sea have been routinely carried out over several decades. Estimation of the numbers of individuals in given size categories (i.e. per half-centimeter or per centimeter) of all species in each catch constitutes the basic data recorded on these surveys. Thus the use of size based metrics as community indicators clearly also scores highly on the remaining two criteria, f and g (Table 2.1). Clearly size based metrics score well on all seven criteria, suggesting that they would therefore make ideal indicators of the impact of fishing on the “health” of the fish community. Application of such indices certainly seems to confirm that fishing has had a detrimental impact on the broader fish community (Gislason & Rice 1998).

The problem with applying a set of criteria to identify the most “useful” ecological indicators in this way is that, whilst it almost certainly identifies indicators that reflect an unequivocal effect of an activity, it tends to ignore the type of effect that the activity might have. It does not necessarily identify indices that permit any judgement as to whether the effect is important, requiring mitigation, or whether it is relatively trivial and can be ignored. Reduction in the mean size of fish in the fish assemblage of the North Sea may very well be an issue of concern, particularly with respect to the long term economic sustainability of the fishing industry and the apparent limitation of opportunities

regarding alternative commercially viable species for human consumption. However, it is not one of the issues that has encouraged ministers to advocate the application of a broader, ecosystem wide, approach to fisheries management. As we have seen above, concern over biodiversity loss, and the commitments made to the CBD and Agenda 21, have provided much of the impetus behind the political desire for the development of an ecosystem approach to management. That this is the case is clearly reflected in the more recent drafting of Annex V of the OSPAR convention.

Knowing that the mean size of fish in the assemblage has decreased provides little or no information about changes in the biodiversity of the fish assemblage; neither does it help managers to set biodiversity objectives or identify appropriate measures to achieve these. In order to address questions regarding the impact of fishing on marine biodiversity, we need to apply biodiversity indicators. However, biodiversity is a far more complex concept than fish length, or vulnerable species abundance. There are numerous definitions of biodiversity in the literature, but it is generally assumed to be synonymous with the “variety of life” and to consider such variety at several levels: variety within a species, variety between species and variety between communities of organisms in different habitats or ecosystems (Gaston 1996). In fact it is hard to conceive of a single metric that could adequately convey information regarding the “variety of life” across these various levels simultaneously (Gaston 1996), consequently any suggestion for such an index is bound to fail several of the criteria listed in Table 2.1.

Since the early 1980s the number of “biodiversity” publications has increased massively (Haila & Kouki 1994; Harper & Hawksworth 1994), and invariably these studies have quantified only a single dimension of biodiversity, i.e. genetic diversity within species (Mallet 1996), or species diversity within communities (Gaston 1996). The variety of life among species is the aspect of biodiversity that has received the most attention to date: species diversity research has a history that long predates the coining of the term biodiversity (see references in this review). However, the concept of species diversity is itself also not a simple one (Hurlbert 1971), since it consists of two aspects, the number of species in a community, and the evenness of the distribution of all the individuals in the community between its constituent species. A variety of different indices of species diversity have been proposed and used (Magurran 1988), and these all tend to lie along a continuum from indices of purely species richness to indices of purely species evenness (Hill 1973). Thus no one index conveys all the information that might be required, and the majority of indices, those that lie between the extremes of this continuum, convey some information about both aspects of species diversity. However, the degree of sensitivity of each particular index to either species richness or to species evenness is often ill defined (but see Hill 1973). Species diversity indices therefore score very poorly with respect to criterion a (Table 2.1).

The calculation of indices of species diversity requires that the numbers of individuals belonging to different species be recorded. Such information is routinely recorded on groundfish surveys with respect to the fish caught. As mentioned before, these surveys, covering the whole North Sea, and other marine regions, have been carried out for many years now. Thus with respect to fish communities, species diversity indices score well under criteria f and g (Table 2.1), but similar data, collected over similar spatial and temporal scales, are simply not available for benthic communities, and are relatively scarce for plankton communities. So, with regard to these latter communities, species diversity indices score rather poorly when criteria f and g are applied (Table 2.1). Furthermore, the application of species diversity indices to sample data requires taxonomic expertise: individuals have to be identified to species. Diversity indices are therefore less easily measured and prone to error, and therefore do not score well with respect to criterion d (Table 2.1).

Given the focus of the CBD and OSPAR Annex V on biological diversity, much of the earliest work examining long-term changes in the fish community of the North Sea concentrated on changes in fish species diversity (Greenstreet & Hall 1996; Rogers *et al.* 1998; Greenstreet *et al.* 1999; Rogers

et al. 1999; Rogers & Ellis 2000). Several of these studies attempted to relate the observed trends in fish species diversity to trends in fishing effort in an attempt to implicate increased fishing disturbance as the cause of these changes. However, all such attempts were correlative in nature, the comparison of two trends, and as such they failed to unequivocally link changes in diversity to changes in fishing effort, and so confirm cause and effect. The use of species diversity indices in this way therefore scores poorly under criteria b, c, and e (Table 2.1). A later study helped to redress these failings to some extent. Jennings *et al.* (1998) hypothesised that species with k-strategist type life-history characteristics, i.e. slow growth rates, large ultimate body-size, large size and late age at maturity, would be less capable of sustaining the additional mortality inflicted by fishing than species with the opposite, r-strategist type, life-history characteristics. In a reanalysis of some of the data presented in Greenstreet *et al.* (1999), Jennings *et al.* (1999) demonstrated that in an area of the northern North Sea where fishing had steadily increased in intensity, the groundfish assemblage had indeed become increasingly dominated by fish with r-strategist type life-history characteristics. This supported the earlier contention that the changes in the species composition of the groundfish assemblage in this part of the North Sea, which resulted in the reduction in species diversity reported by Greenstreet *et al.* (1999), had indeed been caused by the increase in fishing disturbance in the area. This has since been confirmed through the combination of spatial and time series analyses that demonstrated that temporal trends in indicator values were more extreme in areas of greatest impact from fishing, and least or non-existent in areas with little fishing activity (Greenstreet & Rogers 2006).

Even though there is now some evidence to confirm that increased fishing disturbance was indeed the cause of the observed decline in groundfish species diversity in the northern North Sea (Jennings *et al.* 1999; Greenstreet & Rogers 2006), the precise functional relationship between fishing disturbance and species diversity still remains unclear. Fishing activity over recent decades in the southern North Sea, and around the southern coasts of England, has also increased, but here the species diversity of coastal demersal fish assemblages has increased (Rogers & Ellis 2000). It would seem that fishing disturbance can result in both increased and decreased species diversity. Huston's (1994) Dynamic Equilibrium Model predicts exactly this. The model suggests that in areas of high productivity the relationship between diversity and disturbance should be a positive one, while in areas of low productivity, increased disturbance should bring about a reduction in species diversity. Primary productivity in the central and southern North Sea tends to be higher than in more northern areas (Reid *et al.* 1990; Joint & Pomroy 1993), so these two opposing sets of results tend to support Huston's model. However, it is clear that, if the application of species diversity metrics as indicators of the health of marine communities is ever to be of real practical use to managers, then a much more comprehensive understanding of the mechanisms involved is required. It is widely acknowledged that the ecosystem approach to management will be heavily dependent on indicators, and operated through frameworks such as the Pressure-State-Response (PSR) framework (Figure 2.2). For such frameworks to work effectively, the mechanistic links between the three state variables (arrows in the diagram) need to be thoroughly understood, so that the response by any of the variable to variation in the downstream parameter is predictable on a theoretical, rather than a statistical basis.

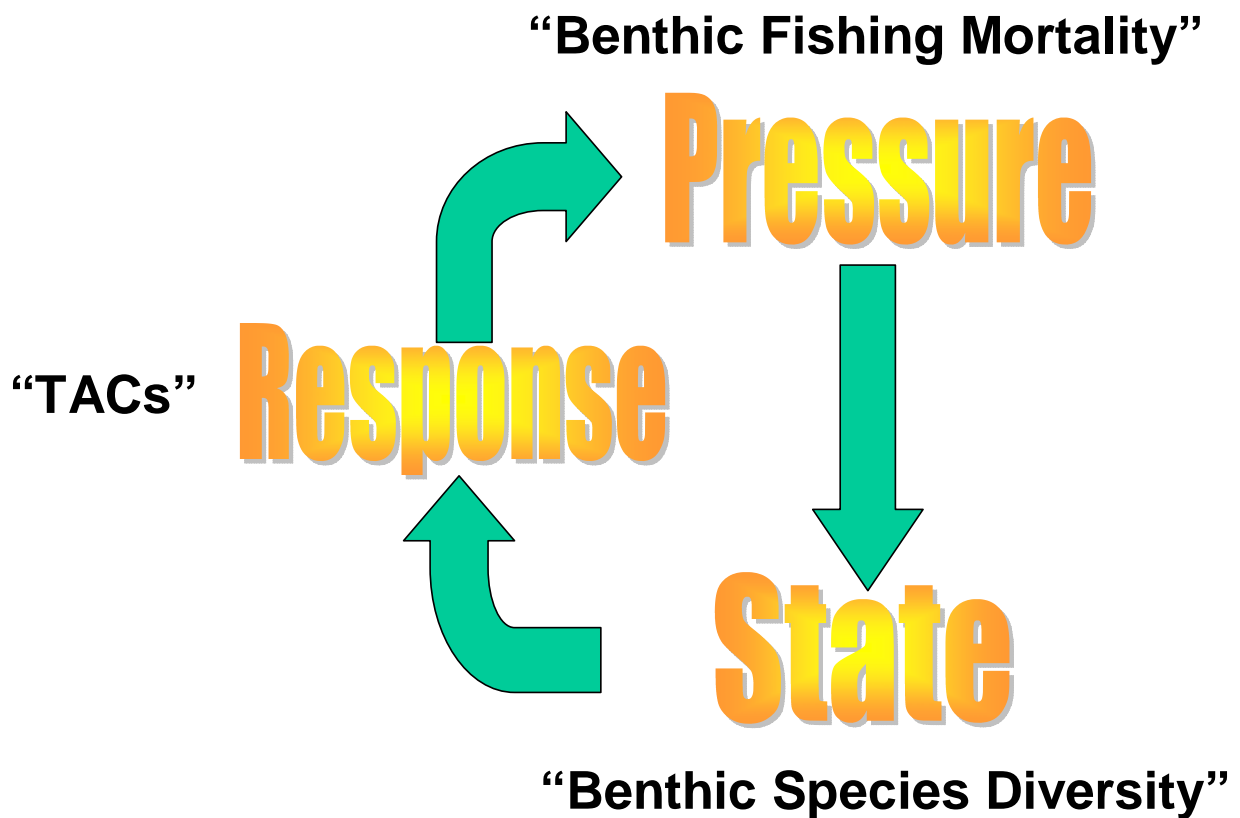


Figure 2.2. Representation of the “Pressure-State-Response” indicator based management framework.

Diversity indices may never score as highly as metrics based on body-size against the criteria for a good indicator listed in Table 2.1, but if biodiversity is a major issue for society, then some indicator of change in the biodiversity of marine systems is necessary. If scientists are to provide unambiguous advice to managers then they need to understand precisely what variation in their chosen diversity index is telling them. They need to understand how this index has been altered by changes in fishing activity in the past if they are to assess reasonable reference levels. They also need to have a clear understanding of the functional relationship between fishing disturbance and variation in their chosen index if they are to advise manager of exactly what is required, in terms of modifying fishing practice, to achieve specific target EcoQOs. If this can be realised, then diversity indices will start to score more highly against criteria b, c, and e (Table 2.1) than is currently the case. Diversity indices may never score well against criteria a, in that they will always be more difficult to understand than body-size based metrics, but it is critical that scientists fully understand them. Under these circumstances, the resulting inevitable improvement in communication between scientists and managers can only contribute positively to greater comprehension on the part of the latter. As understanding of the value of diversity metrics as indicators of change in marine biodiversity increases, so will the incentive to develop the knowledge and expertise to extend their use to more difficult taxa, such as benthic invertebrates, and to provide the resources necessary to collect the data. This review seeks to make progress towards this objective: to increase our understanding of the processes involved in structuring marine communities and controlling their biodiversity, and how these processes are modified or interrupted by man’s exploitation of marine natural resources.

This review therefore examines the theoretical community ecology literature. Various processes have been proposed as the “driving force” imparting structure to the different biological communities that inhabit the earth, and each one has their ardent followers. Here each process is examined in detail and an attempt is made to link them into a single “whole” theory, whereby the circumstances underwhich each type of structuring process will come to the fore is clearly defined. Much of the research to discover and analyse the mechanisms that determine which and how many species can coexist in one place at one time, and which determines their relative abundance, has focused on terrestrial organisms occupying terrestrial habitats. In this review many fundamental differences between the marine and terrestrial realms are identified. It is highly pertinent therefore to question whether ecological theory developed on the basis of observation of, and experimentation with, terrestrial systems is relevant to, and can be applied to, marine ecosystems? To address this, the marine literature is examined to look for examples of, or circumstances whereby, each of the structuring processes discussed in this review might operate. The ultimate objective of the review is to present a “theoretical model” for the structuring of marine communities.

3. PATTERNS IN COMMUNITY STRUCTURE - EVIDENCE OF STRUCTURING PROCESSES?

3.1. Assembly Rules

Similar types of community frequently display considerable consistency in the numbers of species, the distribution of individuals between species, and the functional role of the species present. For example, the recolonisation of mangrove islets in the Florida Keys was monitored following the experimental elimination of their fauna. In all cases, the eventual number of species on each islet returned to its original number (Simberloff & Wilson 1969). In most cases the suite of species present on an islet following recolonisation differed markedly from the original species composition, however, the trophic roles of species in the replacement communities was similar to those of the species in the original communities (Heatwole & Levins 1972). Thus although the exact taxonomic composition of the communities on the different islets differed, the trophic structures of the communities was remarkably consistent following recolonisation (May 1976). This study is far from unique. After a recovery phase following catastrophic disturbance in sub-tropical dune forests, community composition and structure closely resembled the pre-disturbance community (Wassenaar *et al* 2005). Invertebrate communities on pro-glacial chronosequences follow similar succession trajectories (Hodkinson *et al* 2004). Such studies imply a degree of determinism in community composition and structure, suggesting that underlying “assembly rules” dictate the make up of biological communities. Even in situations where a high degree of stochasticity was suspected in determining the structure of communities, determinism has in fact been observed. Thus in mussel bed and algal canopies on Gulf of Maine rocky shores, where the current driven supply of potential colonists was thought to dictate community structure, communities were found to be deterministic. Following experimental clearance of mussel and algal cover, in almost every case, the site recovered with the same community present as was removed; communities recovered to their formal state no matter what the supply of potential recruits colonists was (Bertness *et al* 2004). Assembly pathways have been examined in laboratory studies. A complex range of assembly behaviours was observed in a small pool of protist species. A variety of different assembly pathways was observed, but all pathways tended to lead to a single stable assemblage state (Warren *et al* 2003). In some instances, however, assembly history may affect the eventual outcome of the assembly process (eg Fukami 2004). If the structure and composition of biological communities is subject to the control of assembly rules, then certain combinations of species should coexist together (permitted combinations), giving rise to positive correlations in the abundance of pairs of species in assemblages at different locations, while other combinations should never coexist (prohibited combinations), resulting in negative correlations in paired

abundances. Such situations have been observed (Bell 2005) tending to confirm the presence of community assembly rules.

These species abundance patterns, and the underlying premise that communities are structured by assembly rules, give rise to the concept of convergent evolution of communities. In spatially separate and isolated regions, which are similar in terms of habitat, climate and perhaps productivity, the structure of resident communities appears to have evolved so that, in modern times, they are extremely similar. Examination of the way in which ten grassland bird communities on the American continent were organised with respect to horizontal habitat selection, vertical habitat selection, and diet, revealed that eight of the communities were clustered within a small zone in the 3-dimensional space. This was considered to be indicative of a highly ordered and repeatable structure among communities despite their having very different taxonomic composition, to the extent that the avifaunas of North and South America have different phylogenetic ancestry (Cody 1968). Despite having no species in common, the numbers, physical appearance, and the behaviour of the different species present in insectivorous bird communities found in Californian chaparral, Chilean matorral and South African macchia regions are almost identical. These similarities stem from the underlying similarities of resource portioning between members of the guilds in the three different regions (Cody 1974; 1975). The regional species richness (β diversity) of desert rodents in several desert regions across the globe was relatively high and variable, ranging from 10 to 42. There was no relationship between regional diversity and precipitation levels, an index of seed productivity in deserts. Local species richness within specific deserts (α diversity) was, however, considerably lower, unrelated to regional diversity, often correlated with local precipitation rates, and remarkably similar in deserts from around the world. Despite the quite different taxonomic origins of the desert small mammal fauna, and the differing sizes of the available species pools to “seed” communities, it would appear that the local communities were structured and organised along similar lines across the world (Kelt *et al.* 1996).

Despite a considerable body of evidence suggesting the presence of underlying rules dictating the structure of communities, not everyone is convinced. Exceptions to these rules certainly exist. For example a number of different stable states may be possible. The ultimate state that a community takes on may be dependent on the order of incorporation (timing of arrival of colonists) into the community of the different constituent species. Once incorporated, different processes, competition or predation, or a combination of both, may be involved in maintaining structure and imparting stability (Price & Morin 2004). Following catastrophic disturbance from a hurricane, recovery of tropical rainforests was best described by a “non-equilibrium model with multiple basins of attraction”. Communities tended to recover to a number of different alternative states (Vandeemeer *et al* 2004). The topic of “assembly rules” has been the subject of fierce debate, and the different sides of the argument are clearly presented and discussed in the proceedings of a conference convened to allow the debaters free rein (Weiher & Keddy, 1999).

3.2. Distributions of Species Abundance

The distribution of individuals between species is one of the most fundamental ways of describing communities. Frequently plots are produced showing abundance (often logged) on the ordinate axis and species rank along the abscissa. The general shapes of these curves are often very similar. For example, ranked abundance curves derived from open-ocean planktonic copepod, tropical bat, rainforest tree, abandoned southern Illinois old-fields, vascular plants in a deciduous cove forest in the Great Smoky Mountains of Tennessee, plants during forest succession at Brook Haven, New York, breeding birds in West Virginia deciduous forests, and British breeding birds, whilst varying in many ways, such as species richness, the level of dominance by the most common species, and the numbers of rare species, all have a very similar shape. Some are

steeper, others shallower, but all exhibit an S-shaped form turned up at the left (abundant species) and down at the right (rare species) (Bazzaz 1975; Whittaker 1975; Hubbell 2001). This has been considered to be indicative of underlying processes determining how individuals in a community are distributed between its constituent species.

Species abundance data have been fitted to theoretical distributions, such as the log-series and log-normal distributions. The fact that so many different data sets have been successfully fitted by these theoretical distributions has again been interpreted as evidence supporting the existence of underlying community assembly rules. When abundance data for over 600 butterfly species sampled in Malaya, and similar data for moths collected over a four year period at Rothamstead, were tallied into abundance classes (ie. the number of species represented by a single individual, the number by two individuals, the number by three and so on), the series was found to be a smooth hyperbolic progression, with many rare species and few common ones. The gamma distribution was considered to be the most plausible representation of the actual relative abundance of species in nature. However, this distribution would then be subjected to the stochastic processes involved in sampling, thus the number of individuals of a given species would be Poisson distributed, since most species were rare and represented by few individuals. The combination of the two distributions was a negative binomial, truncated to eliminate the zero class to take account of species belonging to the zero abundance class (too rare to be included in the sample). Because the number of species belonging to the zero abundance class could not be estimated, the number of species in the community was assumed to be infinite. The resulting one-parameter distribution was termed the log-series distribution. The log-series distribution suggests that the number of species in a collection of n individuals is given by $\alpha\chi^n/n$ where χ is a positive constant $0 < \chi < 1$ and α is a measure of diversity. In the series the number of species represented by 1, 2, 3, n individuals is given by $\alpha\chi$, $\alpha\chi^2/2$, $\alpha\chi^3/3$, $\alpha\chi^n/n$ (Fisher *et al.* 1943). Subsequently, many data sets have been fitted to log-series distributions, including ground flora in an Irish conifer plantation (Magurran 1988), stream benthic invertebrates (Shepard 1984), Bees in Mediterranean landscapes (Pottes *et al.* 2003) and lepidoptera in stable environments (Kempton & Taylor 1974). One of the advantages of the log-series distribution is the apparent sample size independence of α , the derived index of species diversity (Taylor 1978). Theoretical reasons as to why species abundance data might fit a log-series distribution have been proposed. Gamma models tend to arise through compound processes. If a geometric series type of Niche-pre-emption is postulated, but where the fractions of niche pre-empted have arisen through the arrival of species at random time intervals, rather than uniform intervals, then a log-series distribution results (Boswell & Patil 1971; May 1975; 1976; Kempton & Taylor 1976).

The log-series is not, however, the only theoretical distribution to have been applied to species abundance data. The observed distribution of species relative abundance in communities consisting of relatively large numbers of heterogeneous species is often log-normal. Log-normal distributions have successfully been fitted to Panamanian snake Communities and British bird communities (Williams 1964), bird, moth, gastropod, plant and diatom communities (Sugihara 1980), and stream diatom communities (Patrick 1973). Such distributions also have a theoretical foundation. Assuming that in a large number of species whose relative abundances are controlled through a combination of largely independent variables then, given the nature of the equations that describe population dynamics, these factors should compound multiplicatively. The Central Limit theorem applied to such a product of factors implies a log-normal distribution (May 1975; 1976). Following convention the parameter R is used to express the abundance of species as a logarithm to the base 2 so that, in a species abundance plot, successive intervals along the abscissa (by convention, termed octaves) correspond to population “doublings”. Thus, $R = \log_2(N/N_0)$ where N_0 is the abundance of species at the mode of the distribution. S_0 , the number of species at the mode of the distribution, is one of two parameters that uniquely specify the distribution. The other, α , an inverse measure of the width of the distribution, is determined as $(2\sigma^2)^{1/2}$. The log-normal

distribution is then given by: $S(R) = S_0 \exp(-\alpha^2 R^2)$. As biologists we are interested in species richness, S , the total number of species in the community – including the species too rare to be sampled, ie. those species to the left of the ordinate axis (often referred to as the “veil line”), with negative R values. This is approximated by $S \approx \sqrt{\pi} S_0 / \alpha$. Preston (1962) examined a considerable body of species relative abundance and demonstrated that in almost all instances the modal octave for the individuals curve, R_N , where the number of individuals at each octave is given by $N(R) \times S(R)$, coincided with R_{\max} which is the octave containing the most abundant species, ie. the right-hand boundary of the distribution. Such distributions have been termed canonical distributions, and the fact that natural communities tend to have such distributions, Preston’s canonical hypothesis. The relationship between R_N / R_{\max} provides a third parameter, γ . Preston’s canonical hypothesis contends that in natural communities $\gamma \approx 1$.

May has argued that non-biological data also often have canonical log-normal distributions, and that the canonical distribution arises as an artefact of the mathematical properties of the log-normal distribution. However, Sugihara (1980) has countered this, suggesting that natural communities fit the canonical log-normal distribution too well, and this is particularly so for extremely species rich communities where $S > 200$ (Ugland & Gray 1982). Sugihara’s (1980) explanation as to why biological communities should fit log-normal distributions envisaged the communal niche space being sequentially split such that the niche space occupied by each species was proportional to its relative abundance, and the probability of any niche being sub-divided was independent of size. This latter aspect separates the biological explanations underlying the log-normal and log-series distributions. The explanation for the latter distribution assumes that in the sequential niche-splitting exercise, it is always the smaller fragment that is divided (Magurran 1988). Sugihara’s explanation for the log-normal distribution allows for multi-dimensional niche space. De Angelis & Huston (1987) suggest that log-normal distributions may arise through the combined interactions of deterministic and stochastic processes, such as growth rates, where growth is dependent on current size, and prey capture by predators. Similar criticisms have also be levelled at the log-series distribution. Patil (1962), for example, points out that the distribution of 2379 publications in the journal *Review of Applied Entomology* by 1534 biologists follows a log-series distribution. The fitting of log-normal distributions has also been challenged on the grounds that they arise as a result of sampling artefacts through the amalgamation of non-replicate samples and species misidentification (Lambhead & Platt 1985; Hughes 1986). However, Magurran (1988) counters this, maintaining that there are too many cases of rigorous sampling yielding log-normal distributions, concluding that it is likely that the log-normal will remain an important tool in diversity studies. Despite this, however, a recent study has challenged the way that the lognormal distribution is fitted to species abundance data. The study concluded that the lognormal distribution does not actually provide a very good fit to the distribution of species relative abundance data, generally really abundant species tend to be under-represented, and that other distributions such as the logit-normal perform better. Consequently, the authors suggest that the log-normal distribution is not an appropriate null hypothesis for the species abundance distribution (Williamson & Gaston 2005).

MacArthur’s (1957) broken stick model considers a relatively small number of homogeneous species utilizing resources along a single dimension: in effect, a resource spectrum. He proposed the analogy of a stick broken randomly and simultaneously into S different pieces, where each piece represents the amount of niche space occupied by each of the S species in the community. The broken stick model suggest a much more even distribution of resources between species than either the log-normal or the log-series distributions. The distribution is characterised by a single parameter, S , the number of species in the community. If a broken stick distribution of species relative abundance is observed, it could be taken as an indication that a single important ecological factor is being shared more or less evenly between the species (May 1975; Magurran 1988). The broken stick distribution is routinely presented in terms of rank order abundance, where the number

of individuals, N_i , in the i th most abundant of S_T species is obtained from the term:

$$N_i = N_T / S_T \sum_{n=i}^{S_T} 1/n \text{ where } N_T \text{ is the total number of individuals and } S_T \text{ the total number of species.}$$

May (1975) also expresses this in the form of a standard species abundance distribution:

$S(N) = [S_T(S_T - 1) / N_T](1 - N / N_T)^{S_T-2}$ where $S(N)$ is the number of species in the abundance class of N individuals. The broken stick distribution of species relative abundance has been successfully fitted to a number of species abundance data sets involving passerine birds (MacArthur 1960), minnows and gastropods (King 1964), and snails (Kohn 1959).

MacArthur (1969) after consideration of Niche theory, and the body of literature supporting this concept, considered that there should be fewer dominant species in species-rich communities; that there should be a negative relationship between species richness and dominance. Species abundance data for Tasmanian phytal communities support this contention (Edgar 1983). Since the bulk of the studies supporting such a contention concerned terrestrial systems, this could be considered to be the terrestrial pattern. Birch (1981) analysed species relative abundance data for many marine communities and found the opposite relationship. As species richness increased, so did dominance.

3.3. Latitudinal Gradients

Another much-quoted pattern of species diversity is the “Latitudinal Gradient”: species richness is greatest in the tropics and decreases with distance in both directions from the equator, north and south. This pattern has been demonstrated in a wide variety of taxa and areas. It has been found in plants (Gentry 1988; Parsons & Cameron 1974). Tree diversity, for example, increases from the almost mono-specific boreal forests near the poles, to forests of enormous species richness in the tropics. This pattern has been observed in North America (Monk 1967; Glen-Lewin 1971; Currie & Paquin 1987) and Europe (Silvertown 1985). Neither is this pattern restricted to trees, other plant groups show similar latitudinal trends in diversity (Dressler 1981). Latitudinal trends in species richness have been demonstrated in mammals (Simpson 1964; Wilson 1974; Flemming 1973; McCoy & Connor 1980), including bats and marsupials (Lyons & Willig 2002). Huston (1994) suggests that much of the mammalian pattern could result from the diversification of just a few groups in the tropics: for example; bats in North and Central America (Flemming 1973; Rosenzweig 1992), quadrupedal mammals in North and Central America (Rosenzweig 1995). Similar gradients have been found in reptiles (Kiestler 1971; Arnold 1972; Duellman 1990), for example, lizards in North America (Schall & Pianka 1978). They have also been noted in bird communities (Cody 1975; Diamond 1975). The pattern is particularly strong in non-oceanic birds, especially during the breeding season when the complicating factor of migration is eliminated (Dobzhansky 1950; MacArthur 1969; Cook 1969; Tramer 1974; Karr 1971; Karr & Roth 1971). Latitudinal diversity gradients have also been observed in fishes (Barbour & Brown 1974; Rohde 1992), as well as in numerous invertebrate taxa: for example, termites (Collins 1989), litter mites (Stanton 1979), Polychaetes (Sanders 1968). The latitudinal gradient in species richness appears to be an ancient pattern in the structure of communities. The same trends can be found in the fossil records for Foraminifera (Stehli *et al.* 1969), Angiosperms (Crane & Lidgard 1989) and woody plants (Silvertown 1985). In New World Bats, the relationships between regional and local diversity were examined. Regional diversity, reflecting increases in available species pools, increased faster than local diversity as latitude decreased (Stevens & Willig 2002).

There are, however, exceptions to the normal negative latitudinal gradient of decreasing diversity with increasing latitude. Lichens thrive in the cold dry areas that higher plants cannot tolerate, and their species diversity is highest in such areas (Ahti 1977; Lindsay 1977; Rogers 1977), thus their

diversity tends to be higher near the poles and lower in the tropics (Pickard & Seppelt 1984). Other examples include bees (Michener 1979), Ichneumonid parasitoids (Owen & Owen 1974; Janzen 1981), and Collembola (Rappoport 1982). Some data suggest that the latitudinal gradients are not always monotonic, initially showing an increase in diversity as one moves away from the equator, before the anticipated decline in diversity is observed at higher latitudes. Such patterns have been demonstrated for birds, mammals and amphibians (Currie 1991).

Many explanations for the latitudinal gradient have been suggested, most infer that latitude is simply a proxy for some other causative factor. For example, it has been suggested that environmental conditions vary with increasing latitude in a way that influences speciation and extinction rates. Latitudinal bias in the discrepancy between speciation and extinction rates, giving rise to higher diversification rates (speciation – extinction) closer to the equator, appears to underpin negative latitudinal diversity gradients in New World bats (Cardillo *et al* 2005), Swallowtail butterflies (Cardillo 1999), and angiosperms (Davies *et al* 2004a; 2004b). On land, negative latitudinal diversity gradients have been linked to latitudinal variation in energy dynamics. Hawkins *et al* (2003) propose two mechanisms whereby energy limits diversity, thereby giving rise to negative latitudinal diversity gradients. Firstly, higher solar radiation close to the equator raises metabolic biochemical kinetics, thereby generally stimulating population dynamics rates, and consequently, evolutionary rates (speciation) (Allen *et al* 2002; Vereij 2005). This hypothesis therefore anticipates that diversity should be positively related to temperature, and indeed such relationships are frequently observed (Waide *et al* 1999; Mittelbach *et al* 2001; Hawkins *et al* 2003). However, the causal mechanism for such relationships is not well established (Evans, Warren & Gaston 2005). It has been suggested, for example, that colonisation rates may be greater in high energy regions, serving to maintain high levels of local species diversity (Ricklefs 1987; Srivastava 1999). The second mechanism links diversity to productivity, a relationship that is the focus of more detailed examination further on. For now though, greater sunlight levels closer to the equator stimulates primary productivity, increasing resources levels for organisms at all trophic levels. Increased growth rates associated with this are again assumed to cause a general increase in population dynamics and evolutionary rates (Huston 1994; Rosenzweig 1995). How this latter model accords with the more recent view that the relationship between species diversity and productivity is more often than not unimodal rather than linear in nature is unclear (Mittelbach *et al* 2001). Some explanations for the positive relationship between species diversity and temperature tend to blur the distinction between the energy and productivity mechanisms. For example, the “more individuals hypothesis” proposes that resource availability is raised in high energy regions. Thus, such areas are capable of supporting larger population sizes of individual species, and as a consequence of this, extinction rates are reduced (Wright 1983; Kaspari, Yuan & Alonso 2003; Hurlbert 2004). Extinction rates in British birds are lower in high energy areas, particularly among the more abundant species and common species drive much of the spatial variation in species diversity (Evans, Greenwood & Gaston 2005). Despite its appeal, the “more individuals hypothesis” does not receive unanimous support (e.g. Srivastava & Lawton 1998).

More recent embellishments of the energy dynamics – latitudinal diversity gradient hypothesis take account of the potential importance of water dynamics. Water is the only substance that, at the earth’s surface, is fully dynamic, being found in solid, liquid and gaseous states. Liquid water is essential to life and essentially drives all biological functions and processes (Franks 2000). Since the state of water is dependent upon ambient energy conditions, biological dynamics are of necessity restricted to optimal energy conditions, where water is liquid and energy is still available for work. Outside this range, biological dynamics cease, while within this range, the capacity for biological dynamics varies as a function of both energy and water availability. Over time a close correlation between rates of biological dynamics and levels of species richness is expected to develop (O’Brien 1993; 1998). Whilst the biological dynamics and species richness of plants are immediately influenced by climate induced variability in water-energy dynamics, a close secondary

relationship between climate and animal species richness also occurs as a result of tight trophic linkages between plants and animals (Andrews & O'Brien 2000). Hawkins' *et al* (2003) meta-analysis tends to suggest that water related variables provide the strongest predictor of diversity in the tropics, while at higher latitudes energy related variables best explain diversity in animal taxa, and a combination of water and energy predict plant diversity. For animals there is a latitudinal shift in the relative importance of water vs ambient energy as the drivers of latitudinal variation in diversity.

Explanations for the negative latitudinal gradient that rely on variation in speciation and extinction rates implicitly assume that processes that drive these rates, also act to modify species life-histories. Under such circumstances, latitudinal gradients in species diversity must be underpinned by latitudinal variation in species life-history attributes (Rohde 1992; 1999; Gaston 2000). For example, reducing species' latitudinal ranges towards the equator (Rapoport's rule) allows more species into a given latitudinal extent and encourages inflation of species richness estimates nearer the equator due to the occasional overspill of species beyond their normal (smaller) range (Stevens 1989). Decrease in body size towards the equator (Bergmann's rule) can cause increased rates of cladogenesis if small body size is associated with higher rates of speciation and lower extinction rates (James 1970; Blackburn & Gaston 1996; Gaston & Blackburn 2000). Also smaller body size may reduce population energy demands, allowing closer niche-packing (see below). Similarly, smaller clutch size in the tropics (Lack 1954; Yom-Tov 1994) may also reduce population energy requirements, allowing greater levels of co-existence and reducing extinction rates (MacArthur 1965). Parasite mediated sexual selection is stronger in the tropics because of increased impact of parasites on host fitness. This can lead to higher rates of speciation (Lande 1981; Barraclough *et al.* 1998; Owens *et al.* 1999). Cardillo (2002) provides evidence that in bird communities, reducing latitudinal range, reducing clutch size and increasing ecological specificity closer to the equator all contribute to the observed negative latitudinal gradients in bird species richness.

Recently, the possibility that negative latitudinal diversity gradients may be derived through non-biological causes has been suggested. The "mid-domain effect" suggests that when a series of species of variable latitudinal ranges sizes are distributed randomly between two bounds, 0° and 180°, the locations of the North and South Poles respectively, the number of overlapping ranges is highest at the mid-point between these bounds, ie at 90° or the equator (Colwell & Hurtt 1994; Colwell & Lees 2000; Colwell, Rahbek & Gotelli 2004). Rapoport's rule, which states that species latitudinal ranges are greater with increased distance from the equator (Stevens 1989), would tend to enhance this effect as greater numbers of species with smaller ranges would tend to cluster at the mid point of the latitudinal range. However, Zapata, Gaston & Chown (2003) maintain that, whilst the "mid-domain effect" hypothesis provides a useful null-model against which to test observed data, the hypothesis fails to adequately explain most empirical studies of latitudinal variation in species diversity.

3.4. Altitudinal Gradients

Another well-documented pattern of community species richness/diversity is the "altitudinal or elevational pattern": community species richness decreases with increasing altitude. Bird diversity in New Guinea, for example, decreases significantly along an altitudinal gradient of over 4000m (Kikkawa & Williams 1971). Increasing altitude by 1000m results in a decrease in temperature of approximately 6°C, equivalent to an increase in latitude of between 500 and 700km linear distance (Terborgh 1971; Huston 1994). Seasonal variability also varies along both latitudinal and elevational gradients (Huston 1994). It is not surprising therefore that altitudinal gradients in species richness and diversity have also been reported. In the southern Sierra Nevada, total plant species richness and the species richness of alien invasives both declined at higher elevation at

scales of 1 to 1000m² (Keeley *et al* 2003). However, once again this pattern is not completely consistent. In the Catalina mountains of Arizona Whittaker & Niering (1975) studied an elevational gradient from 750m to over 2500m over which the amount of water present in the habitat increased with increasing height, from creosote bush desert, through grasslands and deciduous forest, up to coniferous fir forests. They observed the highest plant species diversity at intermediate elevations. Many other studies have subsequently noted unimodal diversity patterns along elevational gradients, and such patterns are now considered to be the norm (Goodman & Carlton 1996; 1998; Goodman *et al* 1996; 1999; Goodman and Rasolonandrasana 2001; Heaney 2001; McCain 2004; Richart 2001; Sanchez-Cordero 2001). Oommen & Shanks (2005) demonstrated a unimodal distribution in woody plant species richness in the western Himalaya. They showed that models with varying assumptions, whilst leading to monotonic, unimodal, or multimodal patterns at local scale, all tended towards a unimodal distribution at regional scale when the multiple local replicates were aggregated. These results suggested that multiple mechanisms gave rise to the regional scale elevational pattern in species richness. Other studies have also demonstrated unimodal patterns of community structure along elevational gradients, for example in small mammals globally, and concluded that these arise through the interaction of several different driving factors (McCain 2005).

3.5. Trophic Level Gradients

Other patterns in community structure include the decrease in metazoan species diversity at higher trophic levels (Rosenzweig 1995). Data collected from 61 insect food webs indicated a decline in species diversity as maximum trophic level (see Yodzis 1989 for definitions) increased (Schoenly *et al.* 1991). There is also considered to be a relationship between victim diversity and predator diversity: predators follow their victims' lead so that predator diversity is proportional to prey diversity (Arnold 1992; Cohen 1977; Schoener 1989; Rosenzweig 1995). Rosenzweig (1995) combined Arnold's (1972) and Duellman's (1990) data to show that the ratio of snake species richness and frog and lizard species richness lay between 1:1 and 1:3. Arthropod predator-prey diversity ratios in south-eastern Wyoming sagebrush habitats were more or less constant across taxonomic groups (insects, arachnids and all arthropods), in both disturbed and undisturbed habitats. In undisturbed habitats predator-prey species richness ratios were generally stable both temporally and spatially. Disturbance in the form of herbicide application significantly increased predator-prey species richness ratios whilst decreasing density ratios (Lockwood *et al.* 1990). In freshwater invertebrate communities the ratio of predator species to prey species averaged around 1:3, with all the data falling between the range of 1:5 and 2:3 (Jeffries & Lawton 1985). Jeffries and Lawton (1985) actually suggest that the ratio between predators and prey is itself a function of diversity, the ratio being lower in species rich food webs and higher in species poor food webs. Aquatic communities may have lower predator to prey species diversity ratios than terrestrial communities (Van Valen 1982; Briand 1983).

4. COMPETITION AND NICHE THEORY (BOTTOM UP CONTROL)

*And NUH is the letter I use to spell Nutches
Who live in small caves, known as Nitches, for hutches.
These Nutches have troubles, the biggest of which is
The fact that there are many more Nutches than Nitches.
Each Nutch in a Nitch knows that some other Nutch
Would like to move into his Nitch very much.
So each Nutch in a Nitch has to watch that small Nitch
Or Nutches who havn't got Nitches will Snitch.*

(Geisel 1955)

If biological communities are organised, if they are assembled, and thus subjected to processes that impart their observed structure, then an understanding of what these processes are, and the way in which they operate to structure communities, is critical if we are to understand how anthropogenic activities affect communities and how managers can best mitigate against these changes. For a long time competition between species was considered to provide the mechanism that structured communities. Competition occurs when populations of two (or more) species, both jointly attempting to utilise a common resource of limiting supply, interfere with one another such that the scope for population growth of one, or both species, is reduced. Such competition has been termed *exploitation competition* and is “indirect”. Direct competition also occurs, exemplified by interspecific territoriality, and this has been termed *interference competition* (Pianka 1976). Tilman (1982) suggests that for a species to exist at a constant, or equilibrium, population size, the amount of a limiting resource available must be sufficient to support a population growth rate (birth rate) that is equal to the population *per capita* mortality rate. He calls this the equilibrium resource requirement. If resource levels exceed the equilibrium resource requirement, then the population will increase in size; if lower, the population will decrease. Tilman maintains that the outcome of competition by two or more species for a single limiting resource is predictable on the basis of the equilibrium resource requirements of each species. The species with the lowest equilibrium resource requirement will win, and the other species will go extinct. It is advantageous for species which compete to avoid one another whenever possible. This can be achieved through the use of alternative resources. Thus competition promotes the use of different resources by different species. The partitioning of resources between species in a community shapes community structure and influences species diversity (Schoener 1974). In southwestern USA deserts, where the size of seed selected was strongly positively related to ant body-size, two harvester ant species of similar body-size, *Pogonomyrmex rugosus* and *P. barbatus*, both group foragers, never co-existed. Similarly, only one of the four individual foragers within the body size range 5.8 to 7.0mm, *P. californicus*, *P. Maricopa*, *P. magnacanthus* and *P. desertorum*, was present in significant numbers at any particular site (Davidson 1977).

The term *Niche*, first used by Grinnell (1917), was initially viewed as a distributional unit, thus stressing its spatial context. Elton (1927), however, took a more ethological view and considered the *ecological niche* to be the functional role and position of the organism in its community. Over time the concept of the niche has become linked with competition following the frequently observed phenomenon that ecologically similar species were seldom able to coexist in time and/or space. The one species per niche “rule” became widely accepted (Pianka 1976). Classical competition theory thus requires that, for n species to coexist at equilibrium in a community, at least n separate limiting resources are required (Armstrong & McGehee 1980). In contravention of this “rule”, Vance (1984; 1985) developed a mathematical model to demonstrate that two competing exploiters of a single resource could co-exist at equilibrium, but this would only occur under certain specific conditions. Intra-specific interference had to exceed inter-specific interference, with respect to such parameters as resource search rates, or encounter rates, and it was necessary for the more subordinate competitor to be the more efficient resource consumer. Other special cases have also been described (eg. Edmunds *et al* 2003).

A central tenet of Niche Theory focuses on the amount of tolerable niche overlap – the degree of resource sharing – that can be permitted. There is considered to be an upper limit to the similarity of the resource requirements of two species that still allows both species to co-exist (Hutchinson 1959). This viewpoint has given rise to the “principle of competitive exclusion”. Much of the evidence supporting the principle of competitive exclusion has been derived from laboratory studies, although some removal experiments have been carried out in the field. When cultured together, *Paramecium aurelia* competitively excluded the ecologically similar species, *P. caudatum*. When cultured with a more dissimilar species, *P. bursaria*, both coexisted, albeit at lower population

densities than when each species was grown alone (Gause 1934). Similarly, when two species of flour beetle, *Tribolium castaneum* and *T. confusum*, were grown together, one always out-competed and excluded the other. The outcome of the competitive interaction was never absolute; the winner under particular circumstances could not always be predicted precisely, but probable outcomes could be expected, dependent upon the conditions of each particular experiment (Park 1948; 1953). Temperature affected the outcome of competition between two species of grain beetles, *Calandra oryzae* and *Rhizopertha dominica*. At lower temperatures *C. oryzae* always won, while at higher temperatures, *R. dominica* was the winner. The outcome of this competitive interaction was entirely predictable given the innate population growth rate capabilities of the two species at different temperatures (Birch 1953). The lizards *Lacerta sicula* and *L. Melisellensis* exist only in allopatry on islands in the Adriatic. Small populations of each species were introduced to islands where only the other species was present. In two islands the introduced population was soon lost, while on a third island, the introduced species out-competed and excluded the original occupants (Nevo *et al.* 1972).

The concept of character displacement provides further evidence of limitation in resource requirement similarity and competitive exclusion. Character displacement involves niche shifts with the result that two ecologically similar species when existing alone in allopatry, alter their resource requirements to avoid competition when in the presence of one another in areas of sympatry. The skink *Typhlosaurus lineatus* occurs in allopatry in sandveld areas in the southern Kalahari desert. In the adjacent sandridge regions it co-occurs with a smaller congener, *T. gariepensis*, but in these areas of sympatry, the mean body size and head proportions are larger, and this is associated with a dietary shift towards larger species of termite (Huey *et al.* 1974; Huey & Pianka 1974). Interference competition was shown to be the direct cause of variation in the head morphology of two species of Appalachian salamanders when they competed with one another when in sympatry, compared with living alone in allopatry (Adams 2004). Two body morphologies are possible in the spadefoot toads, *Spea bombifrons* and *S. multiplicata*, a small round body with normal sized jaw muscles for feeding on detritus (omnivore morph) and large flat-headed body with large jaw muscles for feeding on crustaceans (carnivore morph). When in allopatry, both species display both morphs and feed on both detritus and crustacea. But in sympatry, *S. multiplicata* adopts the omnivore morph only and feeds only on detritus, while *S. bombifrons* takes on the carnivore morph and feeds on crustaceans (Pfennig & Murphy 2003).

More recently, the niche has become increasingly associated with resource utilization spectra (Pianka 1976). Such emphasis largely neglects the role of reproductive success where earlier consideration of the niche relied on fitness to define niche boundaries (eg. Hutchinson 1957). However, the close ties between optimal foraging theory and reproductive fitness suggest that this view of the niche implicitly, if not explicitly, takes account of the role of reproductive success in defining the boundaries of niches (Krebs 1978; Krebs & McCleery 1984; Perrins & Birkhead 1983). For example, by modifying their foraging behaviour, effectively “prey-switching”, by switching to host species specialising on progressively older sandeels (*Ammodytes marinus*), Arctic skuas (*Stercorarius parasiticus*) in the Shetland Islands in the early 1980s managed to maintain their breeding success when other seabird species, notably Arctic terns (*Sterna paradisaea*), were experiencing total breeding failure due to exceptionally low sandeel recruitment (Phillips *et al.* 1996). Increased foraging efficiency in Arctic terns, at times when, and in areas where, prey are more available, is associated with improved breeding success (Monaghan *et al.* 1989). Variation in food availability and food acquisition rates by breeding cactus wrens *Campylorhynchus brunneicapillus* affected nestling growth and subsequent survival rates as well as the probability multiple breeding attempts within a single season by adult birds (Simons & Martin 1990).

Interspecific competition, and the limitation of niche similarity of coexisting species should cause niches to be over-dispersed; that is niches should be regularly spaced along a resource spectrum,

rather than randomly dispersed (Schoener 1974). Similar patterns of desert rodent species diversity in relation to productivity have been observed in the Great Basin, Mojave and Sonoran deserts, despite the fact that the rodent fauna of the Sonoran desert is quite distinct from that of the other two deserts. Despite this, the functional structures of the different communities show remarkable similarity. Body size differences between the component species display extremely regular increments between the smallest and the largest species present in all three communities. Rodent body size and the size of seed in the diet are highly positively correlated. This is indicative of highly structured communities of coexisting species, each occupying their particular niche along a spectrum of variation in seed size. Further evidence of this was provided by the observation that in rodent communities occupying different dunes in the Mojave and Great Basin deserts, particular species were replaced by others of similar size, suggesting local competitive exclusion (Brown 1973; 1975). The regularity of the interval in body size between adjacent species along the size spectrum was testament to the fact that the niches occupied by each rodent species were evenly distributed along the seed resource spectrum.

De Vita (1979) proposed a quantitative technique, a revised version of MacArthur's (1957) broken-stick model, to examine the hypothesis that distances between the means of species utilization spectra along a single resource continuum were more uniform than would be expected from random placement. Data for stem-boring insects, tropical hummingbirds, cone snails and flowering phenologies all supported the null hypothesis of random placement, tending to argue against the importance of competition as a structuring force in these communities (De Vita 1979; Poole & Rathke 1980). However, Pielou (1981) identified a problem with this analysis, in that all ranked inter-mean distance lists should be equally probable, making the null-hypothesis generated by the model difficult to falsify (high probabilities of Type II errors). It may also be misleading to focus attention on the means of species utilisation spectra, which could easily be arranged along a resource continuum such that the distances between them fit the broken-stick model, but with no over-lap in resource utilisation at all, a strong case in support of competitive structuring! Sugihara (1986) suggested that the extent of overlap in species resource spectra, rather than the distances between the means, should be the focus of attention. He presented a technique to test the hypothesis that the amount of overlap observed is less than expected if the utilisation spectra were randomly placed on the resource continuum. This shuffled-stick model effectively places a number of "sticks" of given length, representing the individual species resource spectra, at random along a distance of given length, representing the resource continuum, and then determines the expected amount of overlap between the different sticks. Sugihara likens this to tipping a number of pencils of different size into a large pencil box and determining the amount of overlap between the pencils. The flower phenology data of Poole and Rathke (1981), which when previously analysed using De Vita's (1979) equivalent to the broken-stick model refuted the importance of competition, when reanalysed using the shuffled-stick model now indicated that competition played a role in determining flowering times (Cole 1981).

MacArthur (1972) suggested that, unless niche widths are simultaneously reduced, individual species should invariably be disadvantaged by increases in the number of co-existing species. However, empirical studies have revealed that individual species can be either restricted (Terborgh 1971; Pianka 1974) or facilitated (Lawlor 1979; Davidson 1980) by diffuse competition, "competition by a constellation of species" (MacArthur 1972). In an experimental study, for example, Davidson (1985) demonstrated that populations of a smaller bodied harvester ant *Pheidole xerophila* were facilitated in the presence of a large bodied ant *Pogonomyrmex rugosus* as a result of the depressor effect of this large ant on an intermediate sized competitor *P. desertorum*. On sandstone outcrops in southeast Australia, removal or addition experiments involving the dominant ant competitor, *Idromyrmex purpureus*, only affected its immediate close relatives and competitors, not the entire community (Gibb & Hochuli 2004).

Most treatments of Niche Theory tend to consider resource utilisation by coexisting species along a single resource spectrum. While this may be convenient, frequently represents conditions in laboratory experiments, and is certainly an aid to comprehension, this situation is rarely encountered in the natural world. Sets of species may show considerable overlap in resource use over several resource spectra when each resource is considered in isolation, but when all the resources are considered simultaneously, the species separate in multidimensional resource space (Pianka 1976). Thus, in the Sonoran Desert, the seed eating rodents *Dipodomys merriami* and *Perognathus penicillatus* coexist, despite the fact that they feed on similar sized seeds, because they obtain them from different microhabitats. Similarly, the rodents *D. merriami* and *Dipodomys deserti* both feed in the open, but they are able to coexist through their selection of different sized seeds (Brown 1975). In the dessert habitats of southwestern USA, seed size selection was positively correlated with ant body size. Similarly sized ant species selecting similar sized seed, such as *Novomessor cockerelli* and *Pogonomyrmex rugosus*, were able to coexist because they differed in their foraging strategies (Davidson 1977). At least three distinct niche dimensions have been identified in grassland bird communities. Species that consume similar food resources separate in either their horizontal habitat or vertical habitat use (Cody 1968). Nine species of surface-gleaning bats coexist as a guild in the forests of Barro Colorado and the adjacent Panamanian mainland by partitioning resources along at least 8 niche axes. These included: variation in diet, principally differences in the proportions of Diptera, Coleoptera and Homoptera; the size of prey taken, which was related to variation in feeding apparatus; and the type of micro-habitat in which foraging occurred, which was related to variation in wing structure and echolocation apparatus. Species with similar diet either fed on different sized prey, or in different micro-habitats. Species feeding in similar micro-habitats differed in their diets or in the size of prey consumed (Humphrey *et al.* 1983).

By in effect increasing the number of dimensions in n -dimensional niche space, increased resource heterogeneity can provide additional niche space, resulting in increased species diversity. Fish species diversity in northern Ontario lakes was positively correlated with the diversity of their benthic and zooplankton invertebrate prey, but not with measures of the physical complexity of the habitat. Conversely, in southern Ontario lakes variation in fish species diversity was most closely predicted by substrate diversity and vegetation vertical complexity (Eadie & Keast 1984). Bird species diversity in deciduous forests in the USA was correlated with the height profile of foliage density. Except for its influence of this profile, plant species diversity had no influence on bird diversity. Bird diversity was controlled by the vertical structural heterogeneity of the local environment (MacArthur & MacArthur 1961). Subsequently, a near identical relationship between bird diversity and foliage height diversity was detected in Australian birds (Recher 1969). In Mediterranean landscapes, species diversity of Bee pollinators was directly proportional to the diversity of the floral resource (Potts *et al* 2003). In the Mojave Dessert, Nevada, USA, bird species richness was determined by plant volume, the total amount and range of resources, rather than vegetation structure per se. Species composition was similar in regions with similar vegetation (Fleishman *et al* 2003). Longitudinal trends in the diversity of the fish community in the Owego Creek were best explained by variation in depth. This was interpreted as indicating that structural complexity of the habitat played an important role in determining species diversity (Sheldon 1968). Lizard diversity in the south-western United States showed little relation to plant species diversity, but was strongly positively correlated with an index of vegetation structural complexity (Pianka 1966; 1967). Desert rodent communities were also more diverse in areas of greater habitat complexity or environmental heterogeneity (Rosenzweig & Winakur 1969; Kotler & Brown 1988). Higher habitat heterogeneity in three soil sub-divisions supported more diverse woodland mite communities (Anderson 1978). Aquatic mollusc community species diversity was greater in freshwater habitats with a greater variety in substrate type (Harman 1972). However, as always there seem to be exceptions to the rule! Bulldozer grazers (all or nothing) in streams generate high heterogeneity in algal resources at intermediate grazer density. But this resource heterogeneity

had little or no effect on benthic invertebrate diversity. The diversity of the benthic invertebrate community was highest at high grazer densities, when the algal resource was almost cleared and at its most homogeneous (Flecker & Taylor 2004).

Habitat heterogeneity maintains the coexistence of competing species if the competitive ranking of the species differs in the two habitats, such that species *a* out-competes species *b* in one habitat, while in the alternative habitat species *b* is the more dominant of the two species (Schreiber & Kenton 2005). A spatial mosaic of habitats of differing quality is generated by the activity of termites, and this affects the outcome of competition within a guild of four acacia ants on host trees *Acacia drepanolobium*. Close to termite mounds, new shoot formation and the densities of litter-dwelling invertebrates, important food resources for the ants, were higher. In host trees close to termite mounds a dominant ant species tended to supplant the subordinate species. However, as distance from termite mounds increased, subordinate ants tended to exclude the dominant species. Increased tolerance to lower productivity afforded the subordinate species greater persistence. As a result, termite induced habitat heterogeneity contributed to species coexistence in what is an intensively competitive community (Palmer 2003). Within heterogeneous habitats, intra-specific aggregation can enhance coexistence and increase species diversity (eg. Atkinson & Shorrocks 1981; Hanski 1981). By aggregating on specific habitat patches, species avoid competition with other species that tend to aggregate on alternative habitat patches. A meta-analysis of 76 arthropod data sets supported this hypothesis (Veech *et al* 2003), and further support has been gained from the study of plant communities (Stoll & Pratti 2001). In considering these arguments, clearly the definition of the community is critical, as is consideration of the type of diversity under investigation. When considering the effect of habitat heterogeneity, we are no longer examining local diversity – the diversity of a community at a point in space that consist really of only one habitat. Thus, such communities include a number of different habitats, and the diversity that is increasing is the diversity across habitats, ie β diversity. The aggregation of species on one particular habitat, such that subordinate species are excluded from the habitat, leads to a reduction in local diversity on the habitat in question, ie α diversity declines. But the coexistence of different species on adjacent different habitat type patches leads to enhanced β diversity.

In most species, birth and death rates vary spatially. For each species that can lead to a geographic mosaic of “source” and “sink” populations. In some locations, birth and emigration rates exceed death and immigration rates so that individuals are “exported” from such regions, and the sub-populations living there constitute “source” populations. At other localities the reverse occurs, death rates and immigration rates exceed birth and emigration rates, so that the sub-populations occupying such areas act as “sink” populations. “Sink” populations cannot persist without the immigration provided by “source” populations (Pulliam 1998; 1996; Pulliam & Daniels 1991; Holt 1985; 1997). Under such circumstances, habitat heterogeneity can allow competing species to coexist, providing the source habitats for one of the competitors are the sink habitats for the other, and *vice versa* (Schreiber & Kelton 2005).

Species utilize a broader range of habitats in areas of lower species diversity, than in areas of higher diversity. In effect where species diversity is low, the “habitat niche” is broader (Rosenzweig 1995). One species alone utilises a wide range of habitats (Fretwell & Lucas 1970; Partridge 1978), but with the addition of coexisting competitors for some or all of these habitats, then some or all of the coexisting species will utilise a smaller range of habitats (Rosenzweig 1987; 1991). This is, in effect, the equivalent to the reduction in niche width along a food resource spectrum, which permits increased niche-packing and allows greater numbers of species to coexist, however, in this case, alternative dimensions in the *n*-dimensional niche space are the focus of attention. In temperate USA and Australia bird species diversity is predictable from a foliage height diversity (habitat complexity) index based on three foliage height layers (Recher 1969). This relationship underestimates bird diversity in a high diversity area, the tropical forests of Panama, and over

estimates bird diversity in a low diversity area, the island of Puerto Rico. However, good fits are again obtained if one calculates the habitat complexity index based on four height layers in Panama, and two in Puerto Rico. Compared with the USA and Australia, in Panama birds recognise and partition their habitat niche space using an additional layer, whilst in Puerto Rico they only sub-divide on two layers. If the three regions are ranked from low to high diversity thus, Puerto Rico < Australia = USA < Panama, habitat niche breadth follows the reverse pattern Panama < Australia = USA < Puerto Rico (MacArthur *et al.* 1966). Similarly bird species on Fiji's largest island, Viti Levu, used more apparent habitats per species than birds on New Guinea, a much larger, and more species rich island. Some individual species occurred in both places allowing for direct comparison. The kingfisher *Halycon chloris* can be found on all aquatic habitats in Viti Levu, but on New Guinea, where five other species of the same genus occur in sympatry, *H. chloris* utilises only the mangrove habitat. Likewise the golden whistler *Pachycephala pectoralis* is the only species of its genus living on Viti Levu, but it occupies New Guinea with several other congeners. In New Guinea it only utilises lowland habitat, whilst on Viti Levu it uses all the habitats used by all its congeners on New Guinea. The thrush *Turdus poliocephalus* occurs at all elevations in several habitat types on Viti Levu, but only in forest clearing above 3000m or above the tree line on New Guinea. The white-breasted wood swallow *Artamus leucorhynchus* lives only in dry savannah in New Guinea, but utilises a much broader range of habitats in Viti Levu (Gorman 1975). The same patterns were observed for birds in the West Indies. Where bird diversity was higher, the number of different habitats used by each species was lower (Cox & Ricklefs {1977} and Wunderle {1985} in Rosenzweig {1995}). Gorman (1979) noted a similar effect in the lizard *Anolis sagrei*, with respect to perch-height variability in the West Indies. Similar niche shifts have also been noted in other studies of *Anolis* lizards with respect to perch height (eg Schoener 1975). In allopatry, the smallest and scarcest desert gerbil *Gerbillus henleyi* prefers stabilised sand habitat, but when in sympatry with either of the larger and more abundant species, *G. allenbyi* or *G. pyramidum*, *G. henleyi* switched to using semistabilised dune habitat. Interspecific competition from either of the two conspecifics accounted for 90.3% of the reduction in *G. henleyi* density relative to when it was alone (Abramsky *et al* 2005). A bioenergetics model, incorporating variables such as body size, thermal physiology, prey abundance, etc., successfully predicted elevation related variation in the abundance of *Anolis* lizards in the Lesser Antilles Islands for islands occupied by just a single species, but not for islands occupied by two species. In this latter situation one species was always more abundant at lower altitude than expected and the other species more abundant at higher altitude than anticipated by the model. Species interactions in sympatry modified species responses to elevation gradients (Buckley and Roughgarden 2005).

Optimal Foraging theory suggests that as resource levels increase, organisms become more specialised in their utilisation of the resource; they become more selective (Krebs & Davies 1981; Stephens & Krebs 1986). Increasing resource levels thus encourage a reduction in niche breadth. This allows increased niche packing, more niches of less breadth, enabling more species to coexist along the resource spectrum. As lizard species richness in the deserts of North America, South Africa and Australia increases, the niche-width of individual species decreases and the amount of niche overlap decreases (Pianka 1975). The species richness of several major vertebrate groups, including mammals, birds, reptiles and amphibians, are all positively correlated with measures of potential evapotranspiration, a surrogate for productivity (Wright 1983; Currie 1991). Rodent species diversity in the Great Basin, Sonoran and Mojave deserts, southern USA, is positively related to the minimum amount of rainfall expected in 83% of years. In desert environments, precipitation is strongly linked to seed production (Schaffer & Gadgil 1975), the principal food resource of the rodents. Thus in areas where food resources are more abundant, rodent communities contain a greater number of species (Brown 1975). Similar results were found in the northern Chilean arid region (Meserve & Glanz 1978). Species diversity in harvester ant communities in desert habitats in the south-western USA was also positively correlated to annual precipitation, which was again considered to be a reliable index of local seed productivity.

Resource partitioning was on the basis of seed size and foraging strategy. Resources, in terms of a particular seed size category, too scarce to support a species in low productivity habitats, were able to provide additional niche space in higher productivity habitats. There was some indication that niche width was reduced in higher productivity, higher diversity, more competitive habitats. Variance in body size of the size poly-morphic species, *Veromessor pergandei*, was lower in these habitats (Davidson 1977). These two positive relationships, between mean annual precipitation in south-western North American deserts and the species diversity of seed-eating ants and small rodents, show almost identical slopes (Brown & Davidson 1977). At both global (Reichle 1970) and local (Adams & Woodward 1989) scales, plant species diversity is correlated with primary productivity.

Competition and Niche theory would seem to suggest that increased productivity should always result in an increase in species diversity. But other results have also been forthcoming. Many negative relationships between species richness, or diversity, and productivity have been observed and this has been termed the “paradox of enrichment” (Rosenzweig 1971). The addition of nutrients to aquatic systems results in increased algal productivity (eutrophication). This invariably leads to a reduction in the species diversity of algae and other aquatic organisms (Patrick 1963). The species diversity of zooplankton communities in Danish freshwater lakes is negatively correlated with productivity (Whiteside & Harmsworth 1967). Along natural gradients of soil fertility, plant species diversity increases with increasing soil fertility (Mellinger & McNaughton 1975). However, adding fertilizer to herbaceous plants communities generally results in a reduction in species diversity (Silvertown 1980; Tillman 1982; Aerts & Berendse 1988). Unlike the desert rodent studies undertaken in the southern USA and northern Chile (Brown 1975; Meserve & Glanz 1978), Abramsky & Rosenzweig (1984) noted that above a certain level of productivity in both sandy and rocky habitats in Israel, small mammal diversity declined with further increase in productivity.

There would thus appear to be considerable controversy regarding the nature of the relationship between productivity and species richness and diversity. One hypothesis that reconciles these apparently contradictory studies is that the relationship between productivity and community diversity is actually unimodal, rather than monotonically increasing or decreasing, and that these studies cited above only covered productivity ranges lying on one side or other of the mode. Tilman (1982) developed a mathematical model that predicted such unimodal relationships. In contrast to the desert communities of the southern USA and northern Chile already discussed (Brown 1975; Meserve & Glanz 1978), Owen (1988) showed that in the more mesic habitats of Texas, small rodent diversity declined as an index of productivity increased. Since the productivity levels in the southern USA desert study (Brown 1975) reached a maximum that was approximately equal to the lower end of the productivity range in Owen’s (1988) data set, Rosenzweig (1995) suggested that these data actually revealed the two sides of the same unimodal relationship between rodent community species diversity across the whole USA and productivity. Mammalian carnivores in Texas actually did display a unimodal relationship between diversity and productivity (Owen 1988). Unimodal relationships between species diversity and productivity have been observed in several other studies: for example, Australian tropical mammals (Rosenzweig & Abramsky 1993) and zooplankton in Canadian freshwater lakes (Rosenzweig {1992} after Patalas {1990}). As with many of the studies examining the effect of productivity on species diversity already cited, much of the evidence supporting the unimodal relationship relies on the measurement and use of variables that are surrogates for productivity (eg. the use of precipitation data as an index of desert seed production, Davidson 1977). In tropical mountainsides, productivity declines with increasing elevation due to the corresponding decline in ambient temperature (Lonsdale 1988). Thus the fact that bryophyte (Gradstein & Pocs 1989), fern (Tyron 1989), Arthropod (Janzen *et al.* 1976), bird (Terborgh 1977), and small mammal (Heaney & Rickart 1990) species diversities all peak at mid elevations in tropical mountain habitats has been taken as evidence in support of the unimodal relationship (Rosenzweig 1995). It has been suggested that

the relationship between diversity and productivity is “context-dependent”. Each system has a critical level of nutrient availability, possibly determined by the level of nutrients typically available within the system. Below the critical level, increases in nutrient availability increase diversity, while above the critical level, further nutrient enrichment reduces diversity (Bracken & Nielsen 2004).

Mittelbach *et al* (2001) carried out a meta-analysis of 257 data sets originating from 171 separate studies. A wide range of relationships between diversity and productivity were observed. On balance Mittelbach *et al* (2001) concluded that humped (unimodal) relationships predominated in plant communities at small spatial scales. As spatial scale of the study increased, relations tended to become monotonic positive, before reverting back to unimodal at the largest spatial scales. Mittelbach’s *et al* (2001) analyses and conclusions were criticised by Whittaker & Heegaard (2003) and their criticisms rebutted by Mittelbach *et al* (2003). Steiner & Liebold (2004) suggested that the spatial scale dependency of the shape of the diversity-productivity relationship was because as spatial scale of a study increased, so the measure of diversity moved from local (α) diversity to habitat-related diversity (β). They suggest that β diversity may be positively related to productivity until at the regional scale, diversity once again tends to be unimodally related to productivity.

Several models determining community species diversity based on competition and niche theory have been proposed. The diversity, D , of a community consisting of species utilising a common resources depends on three parameters: R , the amount and distribution of the resource; \bar{U} , the range of the resource exploited by each species; and \bar{O}/H , the average overlap in resource utilisation between species. The relationship takes the form, $D = R / (\bar{U} - \bar{O}/H)$ (MacArthur 1972). A theory of limiting similarity suggests that maximum tolerable overlap in resource utilisation by coexisting species is related to resource predictability in variable habitats, but approaches a constant value as environmental variability, indicated by the variance to mean ratio (σ^2/χ) of resource productivity, tends to unity (May & MacArthur 1972).

There has been considerable debate regarding the importance of competition as a force structuring communities. Schoener (1983) and Connell (1983) both reviewed a large number of published studies, with many studies common to the two reviews, and attempted to determine how frequently species experienced competition in nature. Both authors judged the importance of competition as a community structuring force by this frequency of occurrence measure. Schoener suggested that 77% of the species studied experienced competition, whilst Connell believed that only 55% did so. Ferson *et al.* (1986) maintain that the difference between these two figures implies that Schoener and Connell disagreed about the importance of competition in communities. This seems a bit picky on the part of these latter authors since Schoener and Connell both agree that in over 50% of instances, the species concerned were experiencing inter-specific competition. In any considered judgment, this makes competition an important process. Nevertheless, Ferson *et al.* (1986) analysed the two reviews in great detail. They concluded that there was little difference between Schoener and Connell in the way that they interpreted the data before them. However, Connell was far more restrictive with respect to the literature he reviewed, examining only papers published over an eight-year period in only six journals. Schoener applied no such limitation, casting his net much more widely, examining data published at any time in any journal. Connell also applied selection criteria to determining whether a study was suitable for inclusion that were much stricter than Schoener’s. Thus, Connell excluded experiments that, in his view, did not have adequate controls, and he excluded papers that only reported one species at one time and place. According to Ferson *et al.* (1986), these selection criteria preferentially excluded studies where Schoener may have recognised competition. Furthermore, in comparison with Schoener, Connell had much stricter requirements for the recognition of competition, once again leading Connell to underestimate the importance of competition relative to Schoener. This detailed analysis of the two reviews leads to only one conclusion: competition is an important force in the structuring of

communities. How important perhaps lying somewhere between Connell's (1983) lower estimate of 55% of species examined, and Schoener's (1983) upper limit of 77% of species studied.

However, if competition is not the principal force imposing structure on communities, what other process might operate to dictate the species composition and diversity of biological communities? Hairston (1986) suggests that for salamanders of the genus *Desmognathus* in the southern Appalachian Mountains, which to all intents and purposes appear to be perfect examples of competitive niche partitioned communities, predation is in fact the more important structuring process.

5. PREDATION AND DISTURBANCE (TOP DOWN CONTROL)

Competition and Niche theory concentrates on inter-specific interactions within trophic levels. This is almost always the case, even in situations where the limiting resource may not be food, such as in competition for space, or micro-habitat type. Even under these circumstances, the competing species are generally competing for access to a food resource where their prey requirements overlap considerably. By definition, predator-prey interactions take place between trophic levels, and these can have a major influence on the structure of communities. Predators may restrict prey species populations to such low levels that resources no longer become limiting. Thus for example, in the absence of predators, field vole (*Microtus agrestis*) populations expand until they become food limited. Predation pressure maintains their populations below the carrying capacity (Huitu *et al* 2003). Under such circumstances, competing species may be able to coexist, where in the absence of the predator, one would always out-compete the other (Connell 1971; 1975; Paine 1966). Grazing by rabbits prevented grasses from out-competing and displacing dicotyledonous herbs. Elimination of the rabbits by myxomatosis resulted in a decline in plant species diversity. Grasses invaded, forbes disappeared and woody vegetation started to appear (Thomas 1960). Similarly, exclusion of voles from Californian grasslands revealed that their grazing had imposed a particular distribution of species relative abundance within the plant community (Batzli & Pitelka 1970). Variability in predation pressure can effect the outcome of top-down control, introducing variability in the prey trophic level (Benedetti-Cecchi 2005). Conversely predation pressure can serve to damp down variability in prey trophic levels. Phytoplankton sensitivity to pulses of nutrients is reduced when predation pressure from zooplankton is high (Cottingham *et al* 2004).

Predators can directly influence prey population dynamics, thereby affecting their competitive capacity and altering the outcome of competitive interactions within the prey trophic level. In the presence of their predators, the pumpkinseed sunfish *Lepomis gibbosus*, the snail *Physa acuta* spent less time feeding and more time seeking refuge in sub-optimal habitat. As a result snail growth rates were markedly reduced and populations of species competing with the snail increased (Dill *et al* 2003). A similar situation has been described for young trout. When in the presence of their predators, juvenile trout also tended to use sub-optimal habitats as part of their predator avoidance behaviour and again growth rates were reduced as a consequence (Biro *et al* 2003). Bottlenose dolphin distributions match the distributions of their prey when their predators, tiger sharks, are absent. But when tiger sharks are present, they tend to utilise shallow sea grass habitats, which the dolphins then consequently avoid, even though densities of their prey are highest in this habitat (Heithaus & Dill 2002). Often in such situations, survival rates are ultimately affected (Svanback & Persson 2004).

Tilman (1982) has argued that in a system where competitive exclusion limits species diversity to a one resource one consumer rule, the addition of a predator allows the coexistence of two consumers. The population size of the competitively dominant consumer (the only one in the system utilising the resource prior to the addition of the predator) is kept below its carrying capacity

by the feeding activities of the predator, this frees up some of the resource for utilization by the closest subordinate consumer. Tilman proposes that in a system consisting of J resources, I consumer species and K predators, equilibria will only occur when $I \leq J + K$, and $K \leq I$, ie. the number of consumers will be less than or equal to the sum of the number of resources and the number of predators, the number of predators must be less than or equal to the number of consumers.

The classic key-stone species concept considers critical predator-prey interactions that impose structure on communities. If this interaction is altered in some way, then the resultant changes in the community can be dramatic. The predator thus dictates the structure of the community, and species performing such roles have been termed “key-stone” species. Communities structured in this way can be considered to be top-down controlled. Intertidal rocky-shore habitats appear to provide ideal circumstances where keystone species operate to control the structure of the communities present. Many of the examples of such top down control of community structure have originated from such environments. In a departure from previous form, these marine examples of a community structuring process are discussed here because they have been so pivotal in the development of the theory. The text book example of such a community structuring process is the interaction between the starfish *Pisaster ochraceus* and the mussel *Mytilus californianus*, which appears to play a critical role in the structure of the rocky intertidal communities of western North America. The mussel is the dominant competitor for space on the rocky shore. Predation by the starfish limits the population growth of the mussel, preventing it from reaching its potential carrying capacity. This allows other competitors for the same resource to co-exist with the mussel. When the starfish was removed, population growth of the mussel was no longer checked, and its population expanded to utilise much more of the resource. This resulted in the elimination of some of its competitors and the species richness of the system declined from fifteen species to eight (Paine 1966; 1969; 1974).

Similarly, on a Chilean rocky intertidal shore, removal of the starfish *Heliaster helianthus* from an experimental site resulted in a 90% reduction in the population of these predators in the area. The mussel *Perumytilus purpuratus* made up over 70% of the diet of *H. Helianthus*. The reduction in predation pressure from the starfish resulted in an increase in the amount of space occupied by the mussel, from 59% to 79%. Space occupancy by the other common species, the barnacle *Jehlius cirratus* decreased from around 34% to approximately 15%, presumably through competitive exclusion. Dominance in the experimental area increased considerably. On a nearby control site no such population trends were observed so that one year into the experiment, populations of the barnacle and mussel differed significantly between the experimental and control sites. Four years after starfish removals ceased and the site had been allowed to recover, starfish abundance on the experimental site was almost back up to pre-experimental levels, levels equivalent to those observed on the control site, and the mussel population had once again been reduced to levels similar to those found on the control area. However, the population of *J. cirratus* had continued to decline and significant differences in population size between the experimental and control sites were still apparent. No other species appears to have invaded, or taken over the space previously occupied by the barnacle (Paine *et al.* 1985).

Competitive interaction over space in Sonoran Desert rocky intertidal zones between the barnacle *Chthamalus anisopoma* and an encrusting alga of the genus *Ralfsia* was influenced by grazing pressure on the alga by the limpet *Collisella strongiana*. *C. strongiana* reduced algal abundance, releasing the barnacle from competition so that its population increased. No effect direct effect of the limpet on the barnacle was detected. High abundances of the barnacle affected *Ralfsia* directly, through competitive pre-emption of space, and indirectly by limiting limpet densities. A negative feedback loop was also suggested by the data: removal of the barnacle allowed limpet numbers to increase, this suppressed growth in the algal population, which in turn left space to

encourage an increase in the barnacle population. The state of this three-species interacting system was further influenced by predation pressure on the barnacle from the gastropod *Acanthina angelica* (Dungan 1986).

Keystone species control of community structure is not limited to the just the intertidal zone, examples from sub-tidal marine communities are also common. In the sub-tidal communities of the east coast of Canada, lobster populations have declined markedly due to commercial exploitation. Released from predation pressure, the population of the sea urchin *Strongylocentrotus droebachiensis* in the area increased considerably. Sea urchins are herbivores that can have a large impact on algal abundance and distribution (Kitching & Ebling 1961). As a result of the increase in the sea urchin population off the east coast of Canada, *Laminaria* and *Alaria* seaweeds have been largely eliminated (Mann & Breen 1972). Similar effects have been observed down the western coasts of Alaska, Canada and the northern USA. Once again the kelp algal communities were strongly influenced by whether *Strongylocentrotus* spp. sea urchins were abundant in the area or not. If they were abundant, then kelp densities were low and tended to be dominated by *Agarum* species. If sea urchin populations were small, then kelp densities were considerably higher and the kelp community was dominated by *Laminaria* species. Once again it was the presence or absence of a top predator that determined the size of the sea urchin populations. When the sea otter *Enhydra lutris* was present they kept sea urchin populations under control, but where they were absent, sea urchin populations were much larger (Estes & Palmisano 1974; Estes 1996). In both instances, the abundance of a top predator determined the structure of the community in the lower trophic levels.

African elephants have been cited as terrestrial example of a keystone species. Their feeding activities tend to reduce shrub and small tree cover, allowing grasses to invade. As grass cover increases, so does the fire risk in an area and bush fire encourage the conversion of the woodland habitat to grassland. Grasses alone are insufficient to sustain elephant populations and they are forced to move elsewhere, leaving behind a habitat far more suited to other ungulate species (Laws 1970). Other situations considered to be examples of keystone species control include Michigan streams where the grazing activity of the crayfish *Orconectes propinquus* altered the distribution of the filamentous alga *Cladophora glomerata*. In areas where the crayfish was absent, the autotrophic level was dominated by *C. glomerata* and the abundance of diatoms was very low. Diatom abundance was twenty times higher in areas where *C. glomerata* was virtually excluded by crayfish grazing activities, and two sessile grazing insects *Psychomyia flavida* and *Leucotrichia pictipes* were two to three times more abundant (Creed 1994). In the Baltic Sea, the distribution of razorbills *Alca torda* has changed markedly since the invasion of mink in 1994. Previously widely distributed, razorbills now only breed on the most isolated islands where the numbers of mink predators is lowest. Consequently, contrary to Island Biogeography Theory (see section 7.7) ground-nesting bird abundance and diversity is now highest on the most isolated islands in the Baltic Sea. In experiments involving mink removal the effect of island isolation on breeding bird diversity was lost. Predation by mink determined the structure and composition of the breeding bird community (Nordström & Korpimäki 2004). Predator identity can be important in determining the outcome of top-down control, since selection for different prey species may affect the outcome of competition within the prey resource guild (Chalcraft & Resetarits 2003). Two lakes in Wisconsin, USA, differing in their dominant native planktivorous fish species had very different zooplankton communities. Following invasion and replacement of these dominant planktivores by rainbow smelt *Osmerus mordax* the zooplankton communities of both lakes converged, becoming dominated by cyclopoid copepods. The zooplankton communities in both lakes were structured by the predator forces imposed by dominant planktivorous fish predators present, despite evidence of resource limitation and competitive interactions within the zooplankton (Beisner *et al* 2003).

There are many examples in the literature where top down control effects have been propagated through at least two trophic levels. The presence of predators firstly reduces the abundance of their prey, altering the relative abundance of species one trophic level down. Then secondly, it alters the interaction strength between its prey and its prey's prey, thereby affecting relative abundance of organisms two trophic levels below the original predator. This introduces the concept of trophic cascades. Nutrient mediated increases in periphyton algae on plants was thought to determine whether shallow lakes were dominated by plants or phytoplankton, implying bottom up control of plant community structure in such lakes. However, in 17 plant dominated lakes in Norfolk varying in nutrient concentration, the density of periphyton on plants was related to grazing invertebrate density, which in turn was determined by the biomass of fish present. In these lakes top down control was manifest, fish controlled the densities of grazing invertebrates, which in turn controlled periphyton density, which determined the composition and structure of the plant community (Jones & Sayer 2003). In a similar situation in streams, fish preying on the grazer, baetis, reduce their populations. Consequently grazing pressure on algae decreased, resulting in increased algal growth covering stream bed boulders (McIntosh *et al* 2004). Crayfish *Paraneohaps zealandicus* prey selectively on Tanypodinae, and as a result their prey, *Deleatidium* mayflies, increase in abundance (Usio & Townsend 2004). Such effects need not arise only through direct predation, indirect effects can also cause similar changes through trophic levels. Crabs feeding on snails alter the behaviour of their prey, eliciting more refuge seeking behaviour, suppressing snail feeding rates and causing growth rates to decline. Reduced grazing pressure from snails on barnacles results in an expansion of barnacle populations (Trussel *et al* 2003). The toadfish *Opsanus tau* controls the abundance of mud crabs *Panopaeus herbstii*, which preys on juvenile oysters *Crassostrea virginica*. When toadfish are present in sufficient numbers, predation on juvenile oysters by the crab is reduced and the oysterbeds build up (Grabowski 2004).

The keystone species concept is often linked with populations that exhibit 'boom and bust' patterns of abundance. These patterns have been well illustrated in communities with sea urchin 'keystone species' (Barnes *et al*. 2002). The mechanisms that drive boom/bust population patterns are not always straightforward and may follow a chain of events and the additive effects of a combination of external factors (Barnes *et al* 2002). In such top-down controlled systems, harvesting the top predator can allow its prey populations to boom to their carrying capacity, resulting in a marked decline in prey populations in the next trophic level down. Fishing for lobsters at the Channel Islands National Park, California, reduced lobster abundance. Sea urchin densities subsequently increased to the extent that they over-grazed their algal prey, eventually becoming food limited (Estes & Dugan 1995; Sala *et al* 1998; Tegner & Dayton 2000). At this point urchin populations became more vulnerable to disease and epidemics frequently occurred reducing urchin populations and allowing algal re-growth. However, urchin populations were never reduced by epidemic to the extent to which they had been controlled by predation; therefore disease did not fully replace predators in the trophic cascade (Lafferty 2004).

In the two examples cited above involving the effect of sea urchin herbivory on algal communities, the top-down control operated through at least two trophic levels, suggesting a possible cascade effect. In both examples, sea urchin herbivore populations were either controlled by top predators (lobster or sea otter), or they weren't. In the absence of control, the herbivore population expanded to the point where it became resource limited, as evidenced by the reduction of algal density to very low levels (Estes 1996), or to the point where the habitat was reduced to large areas of bare barren rock (Mann & Breen 1972). At this point, with resource limitation so clearly in evidence, sea urchins so dominated the herbivore trophic level that, presumably, species diversity at this trophic level was low. Conversely, with algal density restrained well below its carrying capacity, there being little likelihood therefore of resources (nutrient, space, light) being limiting, species diversity at the autotroph trophic level should have been relatively high. On the other-hand, in the presence of top down control by otters or lobsters, sea urchin numbers were maintained at low levels and their food

resource, kelp, was abundant and not limiting. Under these circumstances, species diversity at the herbivore trophic level might be expected to be high. Conversely, with little herbivory to check algal growth, *Laminaria* kelps dominated the autotroph trophic level, winning the competition for space and light, and so lowering species diversity at this trophic level. Unfortunately the data are not presented in the cited papers to allow us fully to check this pattern. However, Estes (1996) suggests that the pattern does exist in his observation that when sea urchin populations were controlled by otters, the algal community was dominated by *Laminaria* species, but when sea urchins were abundant, *Agarum* species dominated the autotroph trophic level. The genus *Laminaria* consists of species which are strong competitors, but which are poorly defended (chemically) against herbivory. Thus when top down control from otters is absent, *Agarum* species are able to survive under conditions of heavy herbivory that *Laminaria* species cannot sustain. When top down control is present, and herbivore pressure is reduced, *Laminaria* species out-compete and replace *Agarum* species.

H Hairston *et al.* (1960) noted that the widespread destruction of vegetation was rare, so grazers could not be food limited. Their abundance must therefore be restricted by predation, thereby preventing them from depleting their plant food resources. Under these circumstances the grazers could not be competing. But if the predators were restricting the population growth of grazers, then it follows that the predators must themselves be food limited and therefore competing for the grazer resource. Initially these ideas were developed for terrestrial systems, but the concepts were later adapted to aquatic habitats (Brooks & Dodson 1965; Persson *et al.* 1992). Thus a pattern to food web community structure, resulting from cascading top-down control, begins to emerge. Assume that the highest trophic level is bottom-up controlled with predator populations limited by the supply of prey resources. Thus, this trophic level, controlled by competition, is dominated by the top competitors and so has low species diversity. Populations of species occupying the penultimate trophic level, kept in check by this predation mortality, are prevented from reaching their carrying capacities. Resource supplies to the penultimate trophic level are therefore not limiting, so competitive exclusion is prevented allowing competing species to coexist. Under these circumstances, species diversity in the penultimate trophic level might be expected to be high. Since resource supply to the penultimate trophic level is not limiting, and predator populations at this trophic level are maintained below their carrying capacity, species' populations in the next trophic level, the third one down, are subjected to little or no predation control. These populations can therefore expand to utilise more fully the resources being supplied to them from the fourth trophic level down. Competitive processes should therefore operate in the third trophic level, leading to the exclusion of competitively subordinate species and the dominance of the trophic level by a few prevailing species, resulting in low species diversity. This process then continues down to the basal, autotroph, trophic level. The fact that resources from the fourth to the third trophic levels down are limiting implies strong predation control of populations in the fourth trophic level. Populations of competitively dominant species are prevented from expanding to utilise all the resources available to them, freeing this unused resource for exploitation by other competitively weaker species, so species diversity will be high in this trophic level. Thus cascading top-down control of multi-trophic level communities may result in the alternation between high and low species diversity moving from one trophic level to the next (McQueen *et al.* 1986; 1989; Carpenter *et al.* 1987; Fox 2004).

Models of top-down control suggests that invertebrate and ectotherm predators and herbivores should propagate top-down cascades to a greater degree than endotherms and vertebrates because of their higher metabolic efficiency. Increased herbivore to plant body size ratios strengthened cascade effects, while predator body size had no effect. Increased system productivity magnified cascades. Because herbivore:plant body size ratios and plant production:biomass ratios are higher in aquatic ecosystems than in terrestrial systems, the model

predicts that cascade effects should be stronger in water than on land, a prediction that appears to be born out by published studies (Shurin & Seabloom 2005).

The notion of top down control operating through more than one trophic level has been utilised in the achievement of management objectives for communities and ecosystems. Since the mid-1960s, the shallow freshwater lakes of the Norfolk Broads have become increasingly affected by nutrient pollution. As a result of this eutrophication, the lakes have become dominated by phytoplankton during the summer months. The fish assemblage, once the basis for a renowned recreational fishery, has become characterised by numerous small fish, mainly roach *Rutilus rutilus* and bream *Abramis brama*, and aquatic macrophyte vegetation has mostly disappeared. In the 1980s active management to restore the Broads commenced with the reduction of phosphorus in sewage effluent. However, despite a 90% reduction in phosphorus levels entering Barton Broad, the lake remained dominated by phytoplankton (Phillips 1984). Grazing pressure from large bodied cladoceran zooplankton can significantly reduce Phytoplankton standing crops in the Broads (Phillips & Kerrison 1991), however, these zooplankton populations are in turn significantly limited by predation pressure from fish (Cryer *et al.* 1986; Perrow *et al.* 1994). This indicated the possibility for top-down control manipulation. Small scale experiments revealed that the exclusion of fish allowed populations of large bodied cladocerans to grow and be maintained, and these in turn kept phytoplankton populations at low levels, resulting in clear water within the experimental cages (Phillips & Kerrison 1991). Following these encouraging results a long-term programme of biomanipulation was implemented. Removal of fish to keep their populations down, resulted in maintenance of relatively large populations of large-bodied cladocerans, mainly *Daphnia hyaline*, but also *D. magna*, with the result that phytoplankton biomass was kept at low levels and the water was sufficiently clear for macrophyte vegetation to start to develop. The presence of macrophyte was important because it provided refuges for the larger cladocerans, providing them some natural protection from grazing by small roach and bream (eg. Hall *et al.* 1970), but it also provided cover for pike *Esox lucius* and perch *Perca fluviatilis*, which are both natural predators of roach and bream (Moss *et al.* 1996; Phillips *et al.* 1996).

Increased levels of predation need not always result in increased species diversity in the prey trophic level. Selective predation on only certain species within a trophic level, leaving other species unaffected, can result in the expansion of the populations of these un-grazed species so that they dominate the trophic level. As a consequence, species diversity is reduced (Patrick 1970; 1975). In such circumstances, diversity would be most adversely affected if predators preferentially selected rarer species, or if predatory activity had a relatively greater affect on rare species (Birkeland & Neudecker 1981; Hairgreaves & Lebrasseur 1985; Spiller & Schoener 1998; Williams *et al.* 2003). Examples of such a situation include coral reef fish communities in Australia and the Bahamas (Almany & Webster 2004). Alternatively, the mortality levels inflicted by a non-selective predator on some prey species may be unsustainable, with the result that these prey species are driven to extinction by the activities of the predator. Predation by a generalist predator, the backswimmer *Notonecta hoffmani*, generally reduced the densities of all potential prey, resulting in the extinction of some species, tending to reduce diversity in freshwater communities (Murdoch *et al.* 1984). In 1955 zander *stizostedion lucioperca* were introduced into Lake Egidir in south-western Turkey and quickly established themselves. By the late 1980s, nine of the original native fish species in the lake had been extirpated (Campbell 1992; Adams 1996). Similarly, the Nile Perch *Lates niloticus* was introduced into Lake Victoria in the late 1960s. Prior to this the lake held a very high diversity of different fish species. Nile perch fed mainly on Haplochromines, of which there were some 300 species present in the lake. By the late 1970s, native fish abundance and species diversity had diminished drastically (Achieng 1990). The slopes of species-area relationships for fish communities living in lakes in northern Wisconsin where piscivorous fish were present were less steep than those calculated for lakes where piscivorous fish were absent (Tonn & Magnuson (1982).

The highest levels of species diversity may occur at intermediate levels of predation. Algal diversity in intertidal rock pools was highest when intermediate densities of herbivorous gastropods were present. When no gastropods were present a single species of algae, *Enteromorpha*, dominated the community, excluding other algal species. At the highest densities of gastropods, populations of the edible species were greatly reduced and the community was dominated by a single inedible algal species, *Chondrus* (Lubchenco 1978). The diversity of carrion-breeding diptera communities on non-mammalian carcasses was highest at intermediate levels of feeding disturbance by non-dipteran arthropod scavengers (Kneidel 1984). Freshwater benthic invertebrate communities are more species rich at intermediate levels of predation pressure, although species evenness was highest at relatively high levels of predation. Predators operated by influencing prey density and preventing dominant competitor populations from booming (Thorp & Cothran 1984).

Given the extensive coverage given here to top-down control, one might be forgiven for believing that top-down control dominates the processes imposing structure on biological communities. However, the wealth of studies cited in section 7.3 bear testament to the fact that this is not necessarily so. Furthermore in studies explicitly examining the relative strengths of top-down control versus bottom up limitation, the over-riding importance of bottom up processes have been demonstrated. In a sap-feeding insect herbivore assemblage, all six herbivores increased in density when nitrogen content of *Spartina* was elevated. Only one species, the dominant herbivore, was affected in any way by predation by spiders (Denno *et al* 2003). In arthropod communities associated with a dominant tree species, *Metrosideros polymorpha*, bottom up effects had the greater impact on community structure. Energy input to the community had a more fundamental influence on higher trophic level harvesting dynamics. Top down effects tended to be attenuated through the food web and did not cascade down to basal trophic levels (Gruner 2004). Both songbird (Schmidt & Ostfeld 2003) and desert ant (Sanders & Gordon 2003) community structure varies in response to variability in resources.

Predation is a biological process that contributes to the overall mortality rate experienced by prey species. Non-biological processes that lead to increased mortality rates appear to affect community species diversity and richness in a similar manner. Disturbance can play a critical role in influencing patterns of distribution, abundance and diversity of species (Paine & Levin 1981; Sousa 1984; Pickett & White 1985; Petraitis *et al* 1989; Shea *et al* 2004). Pond permanence for example explains 54% of variance in species diversity (Urban 2004). Disturbance increases mortality rates, but can also release resources that are of benefit to some species (Grime 1973; Connell 1978; Huston 1979; 1994; Connell *et al* 1997). Increasing disturbance can to have an inhibitory effect on species diversity. Increased forest disturbance reduced the species richness of tropical soil nematodes (Bloemers *et al.* 1997), while major flood disturbance on the Glenfinnish River, County Cork, Ireland caused a massive reduction in the overall density of macro-invertebrates in the river, as well as reducing taxonomic richness (Giller *et al.* 1991). As a system is increasingly disturbed, species relative abundance distributions depart from the canonical log-normal distribution. In effect, the process of succession tends to run in reverse, with communities becoming increasingly dominated by a few species able to tolerate the disturbance (May 1986). Examples of this are provided in the Rothamstead grass plots experiments (Tillman 1982), diatom communities in streams subject to organic pollution (Patrick 1973), and pollinator communities on blueberry heaths subjected to pesticides (Kevan *et al.* 1997). The reverse trend has also been demonstrated. On recovery from pollution, cumulative species richness of the fish community in the River Thames increased and the distribution of species relative abundance was increasingly better fitted by the Log-normal distribution (Andrews & Rickard 1980). Disturbance effects can cross ecosystems affecting different communities. Thus terrestrial disturbance that resulted in reduced plant cover and diversity, had similar depressing effects on the communities present in nearby streams (Quist *et al* 2003).

Other studies have suggested that the opposite relationship holds, that disturbance has a stimulatory effect on species diversity. In the arid American southwest the native Sonoran topminnow *Poeciliopsis occidentalis* is generally extirpated when mosquitofish *Gambusia affinis* are introduced into a water system within a period of one to three years. However, the topminnow is better able to withstand the effects of flash flooding and in areas where flooding is frequent, both species coexist over prolonged periods (Meffe 1984). In desert streams, maintenance of high variability in flow regimes is important for maintaining native fish species assemblage structure and composition. If flows reduce, exotics tend to invade with subsequent reductions in species richness (Eby *et al* 2003). In Mediterranean bee communities, as time since the last disturbance (scrub fires) increased, so the population size of the dominant bee species increased. Species dominance increased and diversity declined. The frequency of disturbance was important in maintaining the diversity of the bee community (Potts *et al* 2003). Computer model simulations suggested that species diversity in the deciduous forests of east Tennessee was likely to be highest on the driest and most frequently disturbed areas, and least on the wettest and least disturbed locations (Pastor & Post 1986). Disturbance leading to environmental fluctuation may allow the coexistence of competitors by providing each species with the competitive advantage in alternating time periods. Providing the fluctuations occur sufficiently frequently that neither species is given the advantage for too long, then both species populations may be maintained (Blandine & Gonzalez 2005).

Disturbance leading to variation in resource availability promotes coexistence in the consumer trophic level through a variety of mechanisms, but primarily by providing circumstances that first favour one competitor, then favour a second, and so on. Coexistence is most likely with non-linear consumer responses, when consumers are relatively inefficient and when resource variability occurs with long periods and moderate amplitude (Abrams 2004). Variation in the frequency or the intensity of disturbance can affect community structure in different ways (Bertocci *et al* 2005). Periodic disturbance can dictate the composition and species richness of plant communities. The type, frequency and timing of disturbance can critically influence the outcome through the disruption of particular species. Non-linearities and storage effects were also important (Crawley 2004). Disturbance may not operate to maintain diversity just through limitation of the population growth of dominant competitors, ie within trophic levels. Disturbance can also promote diversity and coexistence across trophic levels by reducing the strength of predator-prey interactions that might drive a prey species into extinction. Mosquitofish (*Gambusia affinis*) typically extirpate Sonoran top-minnows (*Poeciliopsis occidentalis*) via predation within one to three years of introduction. This occurs most rapidly in streams that never flood. Long-term coexistence occurs in localities that flood frequently. Mosquitofish are less well adapted to surviving flood than the top-minnow. Abiotic disturbance promotes coexistence by periodically reducing the population size of the exotic predator before the native prey is eliminated (Meffe 1984).

In some communities, freshwater *Testes* damselfly communities for example, varying abiotic disturbance (pond permanence) and biotic predation regimes (fish predators, dragonfly predators, both predators, no predators) both combine to dictate the structure of the community present (Stoks & McPeck 2003). In the Blue Oak savannas and chaparral communities a complex combination of grazing and disturbance maintains plant community structure. In the savanna habitat, grazing maintains species richness by preventing native plants from dominating the assemblage, so providing opportunities for alien plants to establish themselves. In the chaparral, total plant diversity and alien plant diversity both increase following disturbance from fire. Alien plants colonise the chaparral from the nearby savanna, so grazing pressure on the savanna increases the potential for fire disturbance to increase diversity on chaparral (Keeley *et al* 2003).

As with the paradox of enrichment discussed in the section above, where both positive and negative relationships between productivity and species richness/diversity were resolved by the conclusion that these represented the two different sides of a unimodal relationship, the same

would appear to be the case with respect to disturbance. Diversity is highest at intermediate levels of disturbance – the intermediate disturbance hypothesis (Connell 1978; Grubb 1977; Huston 1979). In a series of algal microcosm experiments, species richness was highest in microcosms disturbed at intermediate frequencies (every 7 days), but the highest evenness and species diversity was observed in microcosms with the lowest frequency of disturbance (every 28 days) (Robinson & Sandgren 1984). In intertidal boulder fields, the frequency and extent to which boulders get rolled around by waves is dependent upon size; smaller boulders get rolled further and more frequently than larger ones. Algal and barnacle species richness on the boulder surface was greatest on boulders of intermediate size (Sousa 1979). Vegetation species richness peaked in areas of intermediate wave exposure along the shore of Lake Axe, Ontario (Keddy 1983). In Finland, the species richness of moth and butterfly communities showed a unimodal relationship with vegetation height. Since vegetation height was linearly related to grazing pressure, this meant that species richness was highest at intermediate levels of disturbance from grazing (Poyry *et al* 2004). Roxburgh *et al* (2004) concluded that promotion of coexistence through disturbance related variation in resources was a complex situation. Diversity was highest at intermediate levels of disturbance, but at least two mechanisms were involved – the storage effect and relative non-linearity. Other studies have suggested that spatial scale may influence the relationship between disturbance and diversity. In tropical forest bird communities, the relationship between diversity and disturbance was positive at large spatial scale and negative at small spatial scale (Hill & Hamer 2004).

6. HUSTON'S (1994) DYNAMIC EQUILIBRIUM MODEL

“The dynamic equilibrium theory applies specifically to the local species diversity among competing organisms, but it influences and is itself influenced by species diversity at the landscape and regional scales.” (Huston 1994)

One of the difficulties in determining the role of competition in governing the present day structure and composition of communities is the fact that competitive exclusion does not occur instantaneously. Often it occurs slowly and the populations of “losing” species decline gradually, possibly over many generations. In essence, even in competitively controlled communities, the species diversity we see today may not be the product of competitive exclusion, because exclusion of the losing species has yet to take place. In other words, the system is not yet at, but is moving (slowly) towards, competitive equilibrium (Huston 1994). A modeling, combined with experiments, approach indicated that the largest of the two competing bruchid beetles species, *Callosobruchus maculatus*, was able to out-compete the smaller, *C. chinensis*, in gaining access to food resources and oviposition sites in single-generation time-scale experiments. However, multi-generation time-scale experiments revealed that the faster development rate of *C. chinensis* gave this species competitive superiority in the longer-term because it was able to oviposit earlier than *C. maculatus* in subsequent generations. Despite this longer-term competitive dominance, at least five generations, and often many more, were required before the competitive exclusion of *C. maculatus* occurred (Bellows & Hassel 1984). Such considerations led to increased interest in the behaviour of mathematical models near their equilibria (local stability). Stability was deemed to mean the continued coexistence of a suite of species. Instability involved the loss of one or more species in the simulated communities. These studies brought to light a totally unexpected result – large, strongly interconnected systems were less stable than smaller, weakly interconnected systems (May 1972; 1973). Food webs in communities where levels of environmental fluctuation are high are characterised by low levels of connectance, compared with the food webs of communities located in more stable environments (Briand 1983).

One explanation for this contradiction to the generally held belief that increasing diversity should impart increased stability, was that the model assumptions of linear responses, randomly assembly of the model food webs, etc, underpinning the equilibrium analysis rarely held true in the natural world. However, an alternative explanation is that species coexisted in highly diverse communities because competitive exclusion was prevented, either by environmental variation (disturbance) or other factors (eg. predation mortality). In other words, coexistence is a non-equilibrium, not an equilibrium phenomenon (Hutchinson 1961). At the scale of the single patch, competitive exclusion can be prevented in three principal ways (Huston 1994): by reducing the populations of the dominant competitors before they achieve competitive exclusion; by slowing the process of competitive exclusion to the point where competitive equilibrium is never reached; or by changing the conditions under which competition occurs to the extent that the competitively dominant species become competitively subordinate before exclusion occurs. Immigration is a regional-scale process, which in effect “props up” the subordinate species, serving to compensate for the negative ratio of mortality over births, thereby preventing or delaying competitive exclusion. Even if competitive exclusion does occur, immigration can cause the subordinate species to become re-established (Huston 1994). The importance of competition as a force imposing structure on natural communities should vary as a function of environmental variability (Wiens 1977; Rottenberry 1978; Rottenberry *et al.* 1979; see above). Competition was an important factor in determining the organisation of waterfowl guilds in the prairie-pothole regions of North America where breeding habitat variability was low, but as environmental variability increased, the importance of competition as a structuring force declined (Nudds 1983).

Competitive exclusion can be prevented by any disturbance that reduces the population of the dominant competitor species before expansion of this species' population can drive subordinate species populations to extinction (i.e. before the dominant competitor has reached the carrying capacity with respect to the environment). Huston (1994) applies the term disturbance only to processes that cause mortality. Mortality reduces the abundance of dominant species, thereby preventing competitive exclusion. Such mortality can be caused by abiotic factors, eg. flood, frost, wave action, winds, drought, fire, etc., and biotic processes, eg. predation, herbivory, disease, parasitism, etc. Disturbance mortality that kills only the dominant competitor is the most effective at promoting high species diversity (Huston 1994). Such mortality can arise through density-dependent and species dependent mechanisms. Generalised predators tend to concentrate on the most abundant prey and switch between prey species as prey populations fluctuate, depending upon which species is the most abundant/profitable (Murdoch & Oaten 1975; Murdoch *et al.* 1975; Pyke *et al.* 1977; Rauscher 1978; Stephens & Krebs 1986;). The net-spinning caddis larvae *Plectrocnemia conspersa* is a generalist predator in freshwater streams. It aggregates in areas where prey capture rates are high, thus tending to concentrate in areas where its prey density is greatest. Thus, as the density of its different prey vary both in time and space, the caddis larvae switches between prey, concentrating on which ever prey species is the most abundant (Hildrew & Townsend 1980; 1982).

Even density independent mortality, by serving to slow the progress towards competitive equilibrium, will tend to enhance species diversity (Huston 1979). Increasing the frequency of mowing slowed down the competitive exclusion of grass species by the most dominant species (Harris & Thomas 1972). Increased grazing pressure from sheep also reduced the rate of competitive exclusion of the competitively inferior grass species (Berendse 1985). However, at the point at which disturbance intensity and/or frequency is too high for the most vulnerable species to cope with (eg. species with slow population growth rates which cannot recover sufficiently in the time between disturbance events, or rare species wiped out by a single intense mortality event), these then go extinct, then disturbance will start to reduce species diversity (Huston 1979).

Relationships between disturbance and diversity appear also to be tempered by variation in productivity. Predators have different effects on the diversity of their prey guild at either high or low basal resource levels (Proulx & Mazumder 1998; Kneitel & Miller 2002). Fire disturbance of chaparral plant communities has less effect on diversity in low productivity serpentine communities, but were longer-lasting, than on the higher productivity sandstone chaparral (Safford & Harrison 2004). Grazing disturbance models predict different relationships between disturbance and diversity depending on whether resource levels are high or low (Cingolani *et al* 2005). The species diversity of Mediterranean bee communities tends to be positively related to resources, but this relationship is influenced by disturbance frequency (Potts *et al* 2003). Along gradients of disturbance and nitrogen level in old-field grasslands, species richness was highest at intermediate disturbance in the absence of nitrogen as species with different life-histories are able to coexist. But at all levels of disturbance, species diversity tended to decline with the addition of nitrogen (Wilson & Tilman 2002). Kneitel & Chase (2004) suggested that the additional consideration of a second factor might shift the relationship between diversity and the other factor either to the left or to the right (eg Worm *et al* 2002), or dampen or increase the magnitude of the relationship (eg Wootton 1998; Wilson & Tilman 2002). They suggested that the effects of one factor on diversity might be greatest when the influence of the other factor is least. At low resource levels, increased predation pressure or disturbance should always reduce diversity.

After exhaustive review of the literature, Huston (1994) proposed that the two unimodal relationships that we have discussed in detail in the preceding sections actually underpin the species diversity of communities (Figure 6.1:A). That both relationships are indeed unimodal is explained on the basis that competition is the major force in structuring communities (eg Schoener 1983; Connell 1983; Ferson *et al* 1986, and see preceding sections). At low levels of productivity, resources would be insufficient to support specialist species and the community is dominated by a small number of generalists. As resources increase, the resource supply becomes sufficient to support specialists, thereby effectively allowing species niche widths to decrease enabling increased niche packing. More species can be supported and diversity increases. As productivity increases further, limitations to population growth are reduced allowing dominant competitors populations to expand so that they utilise an increasingly broad spectrum of the resource, resulting in the elimination of competing species and lowering diversity. At low levels of disturbance, the population growth of dominant competitors is not limited by anything other than resource supply. Populations of dominant competitors therefore expand till they reach their carrying capacity, out-competing and excluding subordinate competitors for the same resource and keeping diversity low. As disturbance increases, population growth of the dominant competitors is checked, leaving resources available for subordinate competitors so that diversity increases. As disturbance increases still further, some species in the assemblage, increasingly unable to sustain the rising levels of mortality, go extinct causing diversity to decline.

Huston (1994) combined these two unimodal relationships to form a three dimensional model, the dynamic equilibrium model (Figure 6.1:B). Essentially this model maintains that community structure is not a stable equilibrium between resource supply and utilisation, rather that the equilibrium between community structure and resources is constantly disturbed by perturbations that vary in their extent and frequency. The outcome of this model is that it predicts different relationships between diversity and productivity, depending on the disturbance regime and different relationships between diversity and disturbance, depending on the productivity regime (Figure 6.1:C). Thus Huston's dynamic equilibrium model provides specific hypotheses regarding the relationship between disturbance and species diversity; it suggests that in areas of low productivity, we should expect to find a negative relationship, but that positive relationships might be anticipated in areas of high productivity. Huston (1994) examined species abundance data originating from a wide range of habitats and environments, varying in disturbance and productivity, to demonstrate the "universal nature" of his dynamic equilibrium model.

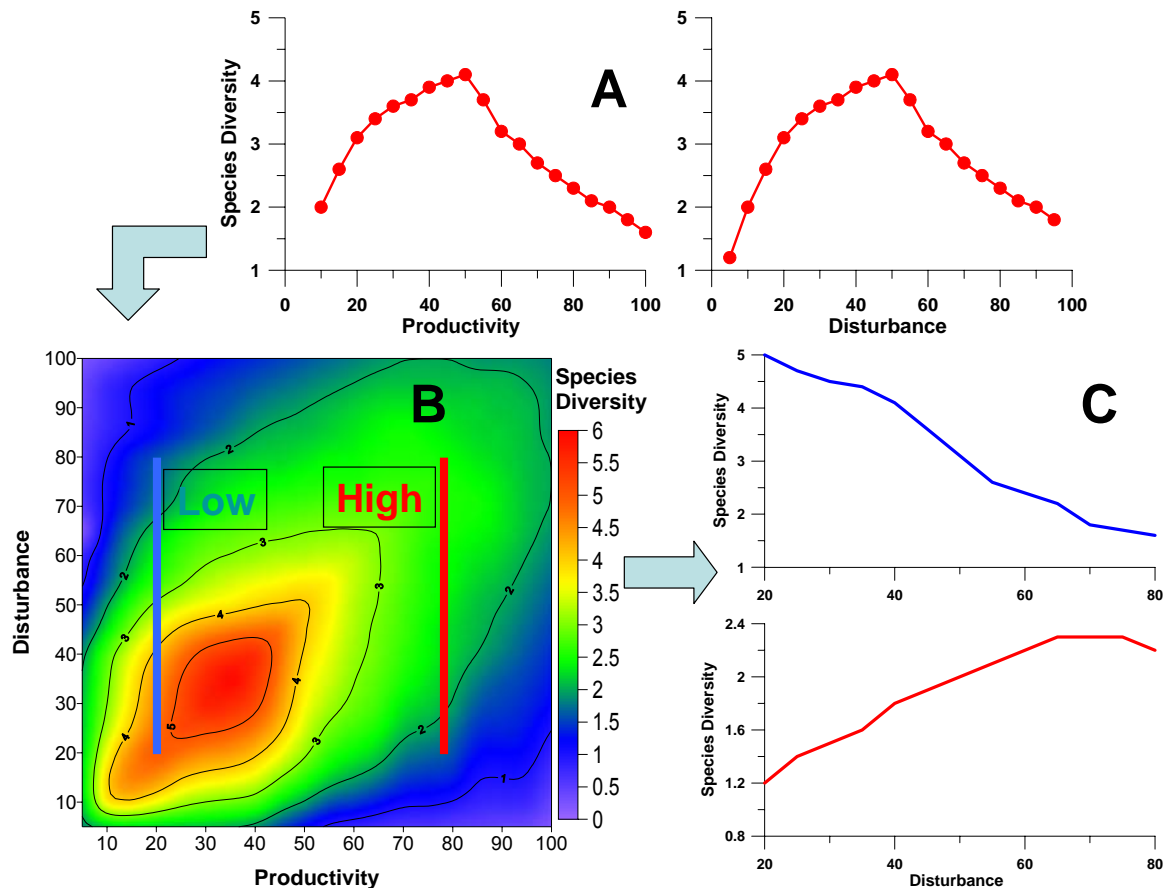


Figure 6.1. Schematic illustrating the evolution of Huston's dynamic equilibrium model and the relationships between species diversity and disturbance predicted by the model at low and high levels of productivity. A: unimodal relationships between species diversity and productivity and between species diversity and disturbance. B: Combination of the two relationships to produce the three dimensional "model" relating species diversity simultaneously to both productivity and disturbance. C: Predicted relationships between diversity and disturbance at the two productivity levels indicated in panel B.

7. SPECIES – AREA RELATIONSHIPS

One of the most obvious patterns in the structure of communities is that of the species-area relationship: the larger the area sampled the greater the number of species that will be included. According to Rosenzweig (1995), this rule was the first diversity pattern to be recognised, sometime between 1835 and 1859, and it has more evidence to support it than any other pattern. Indeed as one increases the area sampled, thereby increasing the number of individuals included in the sample (eg. Williams 1964), theoretical distributions such as the log-normal discussed in section 7.2.2., suggest that the number of species included in the sample is bound to rise. Because the species-area pattern is so pervasive it has a section all of its own, rather than simply treating it as another one of the patterns discussed in section 7.2. The species-area relationship has also implications for other aspects of this review, particularly the application of meta-population dynamics and the role of these in structuring communities on global and local scales. This is a further reason for considering the species-area pattern in its own section.

Species-area curves are traditionally plotted on a log-log plot, with both species and area log-transformed (all bases are equivalent [Rosenzweig 1995]). There has been some debate about the

actual form of the species – area relationship, some authors suggesting that the data, particularly at small spatial scale, better fit a “Gleason” (1922) type exponential model where only area is log-transformed in the linear regression (Whittaker 1972; van der Maarel 1988; Stohlgren *et al.* 1995). However, most studies log-transform, both variables prior to performing the linear regression, resulting in the more usual “Arrhenius” power law function of the form $S=cA^z$, where S is the number of species encountered in the sampled area A , and where c is the constant, and the exponent z the slope, of the log-log linear plot (MacArthur & Wilson 1967; Williamson 1988; Rosenzweig 1995; Tilman & Lehman 1997). Few empirical studies have systematically examined variation in the form of the relationship, across a range of spatial scales with numerous independent samples collected using a consistent survey protocol. However, in a study of plant communities across North and South Carolina and adjacent parts of Georgia and Tennessee in the southeastern USA, “Arrhenius” power function provided a significant better fit to the species richness – area sampled data than the “Gleason” exponential model across all spatial scales (Fridley *et al.* 2005). In non log-transformed plots of the data, the parameter c is not an intercept, but contributes to the slope. In fact c is the slope of S plotted on A^z .

Rosenzweig (1995) argues that there are in fact four species-area patterns, which are in fact scale related. At the smallest scale he suggests that one should consider species-area curves among tiny pieces of single biotas. These are not linear in log-log space, but instead tend to be convex upwards in shape, having a negative second derivative. Next are the species-area curves that are to be found among large pieces of single biotas. Examples of this sort of species-area pattern include the cumulative species-area plots for British plants arising from the addition of contiguous sub-areas to the area sampled, starting with a single county and building up to the whole British Isles (Rosenzweig {1995} from data in Dony {1963}). Similar examples, both in respect of spatial scale and the biota involved, include the cumulative species-area plots for plants in California (data from Johnson *et al.* {1968} in Rosenzweig {1995}) and for plants in France (data from Williams {1964} in Rosenzweig {1995}). Another example of this type of pattern, again involving plants but this time at a much reduced spatial scale, involves the cumulative species-area plots for plants in a Michigan aspen forest arising from the addition of contiguous sub-areas to the area sampled, starting with a single 1m² quadrat and building up to the whole 240m² area of the study area (Gleason {1922} in Rosenzweig {1995}). Other examples, in these cases involving birds, are the cumulative species-area plots for South American neo-tropical birds at different elevations (C. Rahbek’s data in Rosenzweig {1995}), and the cumulative species-area plots for birds using Mediterranean habitats in Chile, California and South Africa (data from Cody {1975} in Rosenzweig {1995}).

The third type of species-area curves are those that occur among islands belonging to a single archipelago. Numerous examples of this type of species relationship are to be found in the literature. These include the species-area relationships described for: plants on islands off the Californian coast (data from Johnson *et al.* {1968} in Rosenzweig {1995}); plants on the Channel Islands (data from Williams {1964} in Rosenzweig {1995}); vascular plants on the Azores (Eriksson *et al.* 1974); ants on Connecticut islands (data from Goldstein {1975} in Rosenzweig {1995}); terrestrial invertebrates living in caves in West Virginia (Culver *et al.* 1973); arthropods living on islands of *Spartina alterniflora* in Oyster Bay, Florida (Rey 1981); molluscs in lakes in New York State (Browne 1981); birds and reptiles in the West Indies (Wright 1981); birds on páramos (sky islands) mountain-tops in the northern Andes (data from Vuilleumier & Simberloff {1980} in Rosenzweig {1995}); birds on the Solomon Islands (Diamond & Mayr 1976); boreal mammals living on montane islands of the Great Basin (Brown 1971).

The fourth type of species-area pattern is the one that is observed for areas that have had separate evolutionary histories. If the cumulative species richness on separate continents is plotted on cumulative area on a log-log plot, a straight line is again obtained. Thus the same relationship

$S=cA^z$ appears to hold, but the exponent, z , is much greater than for the previous two patterns (Rosenzweig 1995). Plots for the number of phytophagous insect species feeding on bracken in different and quite isolated parts of the world related to the area occupied by bracken in each region (Lawton 1984), and plots of the number of phytophagous insect species feeding on cacao in different countries related to the area occupied by cacao in each region (Strong 1974) provide two examples of this type of species-area curve.

Rosenzweig (1995) supports his case for the existence of these four separate species-area patterns on the basis that there is a clear difference between the exponent values z in the relationship $S=cA^z$. Such variation in z value as area sampled increased from local scale to regional scale, and larger, was clearly demonstrated in the nested analysis of plant communities in the southeastern USA (Fridley *et al* 2005). Values for z on a mainland which is successively subdivided, ie pattern 2, species-area curves among large pieces of single biotas, routinely lie between 0.12 and 0.18 whilst those for pattern 3, species-area curves among islands of one archipelago routinely fall between 0.25 and 0.35. Rosenzweig claims that, despite some methodological problems, the data in Begon *et al.* (1990) support his contention that island archipelago z values exceed mainland sub-division z values. Any reduction in mainland area sampled results in a smaller reduction in the number of species encountered, than a similar reduction in island area. Data in the examples listed above support this. In addition, Rosenzweig (1995) plots data from Wilson (1961) for ponerine and cerapachyine ants on the New Guinea mainland and other islands in the archipelago. For subdivisions of the New Guinea mainland the value for z determined was 0.088, whilst for the various islands, $z=0.298$. Species richness on the islands was lower than if they had been similar sized parts of the New Guinea mainland. In pursuing this argument, Rosenzweig (1995) demonstrates that whilst the parameter c is scale dependent, z is not. Thus if comparisons of c are required it is important to ensure that the data are determined using the same unit of area, ie km^2 or m^2 , but not a combination of the two. However, z is independent of the units used to measure the area sampled. He goes on to qualify this argument, pointing out that, islands close to a mainland and only recently isolated from the mainland, have z values only slightly higher than the mainland value (Johnson & Simberloff 1974). The degree of isolation of islands from the mainland can influence z values, though in contradictory ways (Schoener 1976; Lomolino 1984).

It has also been argued that the parameters used to describe the species area relationship hold no theoretical significance, and that the restriction of the z values to a limited range was a statistical artifact (Connor & McCoy 1979; Connor *et al.* 1983). Gilbert (1980) provides several examples where no significant relationship between area and species richness can be detected. The biological significance of species-area relationships has been questioned in other ways also. It has been claimed, for example, that they are simply just sampling artefacts. As we include more area in the sample, we include more individuals and are therefore likely to include more species. This leads to the problem of sample size dependence of many indices of diversity, a problem that needs to be taken into account when interpreting the results of any analysis (see Magurran 1988, Southwood 1978). Rosenzweig (1995) examines whether species-area patterns are simply an artefact of sampling and discounts this possibility – they are real!

Most studies occur within the scale of a province. In other words, they are at island or mainland scales, rather than comparing separate biogeographical provinces. Mainland scale patterns are usually a function of habitat variability. The larger the area, the greater the number of different habitats included within the area. The greater the niche space, the higher the potential species diversity. Rosenzweig (1995) argues that in mainland species-area patterns, habitat heterogeneity explains nearly all the variance. Fox (1983) identified several different types of microhabitat in south-east Australia. As his sample area increased, so did the number of micro-habitats included within it. This accounted for the species-area relationship he observed. In 18 lakes in northern Wisconsin at least one or two different measures of habitat complexity were at least as good a

predictor of fish species diversity as lake area. This observation held true when all 18 lakes were included in the analysis and when the two groups of lakes with quite different fish assemblages and species-area relationships were treated separately (Tonn & Magnuson 1982). In natural reserves in the wheatbelt area of western Australia, habitat variety, as indicated by the different plant associations, was closely correlated with reserve area. The relationships between bird, lizard and small mammal species richness and reserve area could almost entirely be explained by the effect of area on habitat complexity (Kitchener *et al.* 1980a; 1980b 1982). The creation of nature reserves in areas of intensively managed farmland with chronic over-grazing in itself tends to create a mosaic of land-use that enhances regional species diversity (Fabricius *et al* 2003). Similarly, in the Italian Alps land abandonment resulted in grassland meadows reverting back, first to shrub-land and ultimately to forest. As habitat heterogeneity increased, with an associated increase in plant structural heterogeneity, avian diversity increased. The maintenance of some grazed grassland meadow served to increase the land-use mosaic and to further enhance bird diversity by allowing the continued survival of grassland birds (Laiolo *et al* 2004). The species-area relationships describing the species richness of phytophagous insect communities on plants either have a more positive slope (Strong & Levin 1979) or larger constant (Lawton & Schröder 1977) on a log-log plot as one moves from plants with a low structural complexity, eg. herbs and monocotyledons, through to plants with a high architectural complexity, e.g. trees. Even within genera, such as the prickly pear cacti *Opuntia*, the number of phytophagous species associated with a particular species was dependent on its architectural complexity rating (Moran 1980).

In explaining island scale species area patterns one first needs a definition of an “island”. Ultimately, every landmass on the earth is surrounded by water, so at what point does an island become a mainland? “Inaccessibility” provides a possible answer, one that underpins many of the example studies already cited. Inaccessibility, or barriers to movement, characterise biogeographical islands (Vuilleumier 1970; Brown 1971), but how inaccessible does a region have to be – how big the barrier? Rosenzweig (1995) suggests an alternative definition, one based in biology. An island is a “self-contained region whose species originate entirely by immigration from outside the region”. He also points out that the alternative to this defines mainland scale regions. A mainland is a “self-contained region whose species originate entirely by speciation”. Rosenzweig recognises that most real places, large or small, accessible or inaccessible, do not fall into either one of these categories, but instead lie somewhere in between. He points out, however, that these definitions introduce a continuum whose identifying measure is “the proportion of immigrant species”. The latter definition suggests that different mainlands would have no species in common. I would argue that this definition identifies instead “biogeographical provinces”, with “mainlands” falling somewhere within this continuum between “islands” and “provinces”. Reed (1981) noted that, even when the effects of island size and the number of habitats present on each island had been taken into account, the distance between the island and the main land and the number of species in bird communities on British islands were still significantly negatively correlated.

Many studies again indicate the importance of habitat heterogeneity in underpinning the species-area relationships observed on islands (Johnson *et al.* 1968; Johnson & Simberloff 1974; Abbott & Black 1987). For example, the numbers of species of birds on the Åland Archipelago (Haila 1983; Haila *et al.* 1983), snails on Bahamian Islands (Maly & Doolittle 1977), plants on the Galapagos Islands (Hamilton *et al.* 1963), insects and birds on islands in the Southern hemisphere (Abbott 1974), and arthropods on the Seychelle Islands (Muhlenberg *et al.* 1977) all appear to be determined by extent of habitat variability on the islands concerned. The species richness of bird communities on the Californian Islands was more closely predicted by measures of habitat heterogeneity on each island than by island area (Power 1972). Similarly species richness of the bird communities on British islands was best predicted by the number of habitats on each island (Reed 1981). However, even among these examples, instances of apparently empty habitat,

where a species could have been supported, were reported (Maly & Doolittle 1977), suggesting that habitat heterogeneity may not have been the complete answer.

This begs the question - is there any inherent effect of island size, independent of habitat heterogeneity, on species richness? Rosenzweig (1995) argues that as island area decreases, the total number of individuals on the island declines. Thus, the populations of the rarer species get smaller, running an increasingly high risk of extinction. Thus island species-area curves are also influenced by the greater extinction risk on smaller islands. Simberloff (1976a; 1976b) examined this question by artificially altering the size of mangrove islands by removing some of the trees on the islands' peripheries, ensuring that only island size was reduced, not the variety of different habitats on each island. Invertebrate species richness tended to decline on islands that had their area artificially reduced, while on a control island, species richness actually increased slightly. In a second experiment, Schoener & Schoener (1981) created artificial "islands", varying in their area over three orders of magnitude, out of textured Formica panels. All the panels were made of the same material, so had the same habitat heterogeneity. These panels were suspended in Puget Sound, Washington where they were colonised by sessile marine invertebrates including hydroids, polychaetes, bryozoans, sponges, tunicates, arthropods and molluscs. By the end of the experiment, species richness on the suspended Formica panels was closely related to panel area. In looking at the number of species in the bird communities present on British islands, area was found to be the second best predictor, after the number of habitats on each island had been taken into account. On the smallest island, although a particular habitat may be present, in many cases its extent was too small to support a single breeding pair of the bird species that might utilise it (Reed 1981).

8. ISLAND BIOGEOGRAPHY THEORY

The emergence of the discipline of metapopulation biology, and particularly its relevance to the control of community structure has been heavily influenced by island biogeography theory (MacArthur & Wilson 1963; 1967). Island biogeography theory is based upon several simple premises. Smaller islands have species higher extinction rates than larger islands. This assumption is based upon the probability that individual populations are likely to be smaller on smaller islands and that the risk of extinction is higher in smaller populations. Because islands are separated from the mainland by a dispersal barrier, once a species goes extinct, recolonisation by the same species would take longer than would be the case between adjacent similarly sized areas on the mainland. Thus once a species was lost from an island it would take longer for it to return. The greater the dispersal barrier between the island and the mainland, ie the further the distance offshore of the island, the longer the time interval would be between immigration recolonisation events. In summary, species richness on an island decreases with decreasing island size and increasing distance between the island and the mainland. Or to put it in another way - species richness in a region decreases with increasing risk of extinction and decreasing rates of immigration. The number of species on the island is the equilibrium balance between these two rates. Rosenzweig (1995) paraphrases MacArthur & Wilson's (1963; 1967) island biogeography theory along the following lines. Immigration is the appearance on the island of sufficient individuals of species j to propagate a population (a propagule), providing species j is not already present on the island. Assume that each species from a mainland pool of p species sends propagules to the island at a rate i_j and this rate is independent of the species already present on

the island. The total rate of propagule arrival is then $I = \sum_{j=1}^p i_j$. Now separate these arriving propagules into two groups, those consisting of the s species already present on the island and the

p -s species that are not. The propagule arrival rate is now $I = \sum_{j=1}^s i_j + \sum_{j=s+1}^p i_j = \sum_{j=1}^p i_j$. Since all

elements i_j are positive, and assuming that the number of species present on the island is zero or positive, the immigration rate, I_s , is smaller than the rate of propagule arrival,

$I_s = \sum_{j=1}^p I_j \leq \sum_{j=s+1}^p I_j \quad s \geq 0$. The more species already present on the island, the lower the

immigration rate should be. If there are no species present on the island there is nothing to go extinct, thus if $s=0$, then $E=0$. Each species j added to the island community has its own species

extinction rate E_j . Thus the total extinction rate on the island, $E_s = \sum_{j=1}^s E_j$, rises with s . The total

extinction rate therefore rises from zero, while the total immigration rate declines to zero, with increase in the number of species on the island, the two curves must cross at some point between $s=0$ and $s=p$. At this point losses equal additions and we arrive at the equilibrium number of species on the island, \hat{S} . This equilibrium is stable since, if s increases beyond \hat{S} , then I_s decreases and E_s increases, driving s back towards \hat{S} , but if s drops below \hat{S} , then the reverse occurs, I_s increases and E_s decreases, again driving s back towards \hat{S} .

This argument, that the number of species on an island is the equilibrium result of two opposing processes, immigration and extinction, has been developed without the need to implicate any other community structuring processes, such as competition or predation (Rosenzweig 1995). In other words, one should expect to observe communities consisting of relatively constant and predictable numbers of species simply as a result of dispersal and extinction processes, there being no need to explain this consistency on the basis of complex competitive or trophic interactions between the species making up each community. In the next two sections we examine factors that can affect the rates of immigration and emigration, ie competition and predation. Even if the relationships between I_s and E_s with s are modified away from linear functions by such processes, this does not alter the fact that an equilibrium number of species, \hat{S} , will still exist simply as a balance between immigration and extinction (Rosenzweig 1995). Thus we now have two alternative views of the way in which ecological communities might be structured, the *niche-assembly perspective* (Cody 1975; Diamond 1975), which has derived most attention so far in this review, and this new concept, dubbed the *dispersal-assembly perspective* (Hubbell 1997; 2001; Weiher & Keddy 1999). *Niche-assembled* communities are limited-membership assemblages. The composition of the community, the species present in or absent from it, is dictated by inter-specific competition for limited resources. Competitive interactions within a trophic level may be modified by predator-prey interactions between trophic levels. This alters the outcome of competition, and as a consequence, often causes the composition of the community to be revised. *Dispersal-assembled* communities are open, random assemblages of species thrown together by chance and history. Species come and go, their presence or absence determined by random dispersal and extinction events (Hubbell 2001).

8.1. What Affects Extinction Rates?

An underlying tenet of conservation biology is that small populations have a greater risk of going extinct than larger populations, leading to the concept of minimum viable population size (Soule 1980; Shaffer 1981; 1987; Gilpin & Soule 1986). Genetic drift has a far greater impact on smaller populations than larger, and can lead to extinctions in small populations (Lande & Barrowclough 1987). It is generally accepted that rarity is strongly linked to extinction risk (Goodman 1987). Rosenzweig & Clark (1994) demonstrated the importance of larger population size in reducing the risk of extinction in populations of breeding birds on some British Islands. The extinction rate of

four species of orb-web spider on small Bahamian islands was strongly negatively correlated with population size (Schoener & Spiller 1992). Rarer species on the islands frequently went extinct, followed by recolonisation events, whilst common species tended to maintain relatively constant populations (Schoener & Spiller 1987). But even abundant species can go extinct over relatively short times: Rosenzweig (1995) recounts the fate of the passenger pigeon *Ectopistes migratorius* in the USA. In the early 1800s this species numbered up to 5 billion individuals – one of every two birds in the USA would have been a passenger pigeon. In 1914 the last passenger pigeon died and in the space of 100 years, one of the most abundant vertebrates in the USA had disappeared. Habitat fragmentation, reducing the populations present in remaining fragments, can certainly increase extinction risk (Fagan *et al* 2002).

Competitive and predatory interactions can lead to the loss of species as species richness increases. If species richness has no effect on the extinction rate per species, and if this rate is μ , then the total extinction rate in the community is $S\mu$, where S is the number of species in the community. Thus even if species richness has no effect on the probability of any one species going extinct, the overall extinction rate in the community rises as a linear function of species richness. MacArthur & Wilson (1963; 1967) did not accept this linearity. They believed that the function was concave upwards, that on average across the community, the risk of extinction to individual species increased as the number of species in the community rose. With increasing competition for limiting resources, populations of several species would decline, bringing with it the greater risk of extinction. Competitive exclusion would lead to the increased risk of the loss of some species. Forty-nine species of birds have been introduced to Hawaii and neighbouring islands. Physical properties of the phenotype of each species were plotted so that each species occupied a point in n -dimensional space. The shortest line linking all surviving colonists in this space was significantly longer than lines joining the same number of species selected randomly from surviving species and species that had gone extinct. The survivors were more different phenotypically than would be expected from random extinction of the invading birds. These results were interpreted as suggesting that competition had increased the risk of extinction of species which were too similar to others, and were the less good competitors (Moulton & Pimm 1987). Similar results were obtained for birds on the islands of Tahiti and Bermuda (Lockwood *et al.* 1993; Lockwood & Moulton 1994). Following the introduction of rabbits to islands, the addition of competitors (hares) is more effective at eradicating them on smaller islands (Flux 1993).

As species richness in an area increases, the likelihood that more trophic levels will operate within the community increases: some of the incoming species will be predators. Predation can lower prey population sizes and increase the chances of extinctions, this in turn could lead to the loss of the predator. On Bahamian islands occupied by lizards, populations of orb-web spiders were reduced by an order of magnitude, leading to a reduction, by a factor of two, in spider species richness (Toft & Schoener 1983). The populations of lizards were in turn limited, again by about an order of magnitude, by the presence of mongooses on some of the islands, leading to some lizard species extinctions (Case & Bolger 1991). When the spider, *Metapeira datona* was introduced to small islands in the Bahamas, these propagules were much more likely to go extinct on islands where lizard predators were present, than on island not inhabited by islands (Schoener 1986). Following the introduction of rabbits to islands, the addition of predators (cats) or disease (myxoma virus) was more effective at eradicating them on smaller islands (Flux 1993).

8.2. What Affects Immigration Rates?

MacArthur & Wilson (1967) suggested that species varied in their rates of propagule arrival to an island, some species were good dispersers, others not so good. In all likelihood good dispersers would reach an island and establish populations before poor dispersers. Diamond (1974; 1975)

identified bird species that he termed “supertramps”. These were highly efficient dispersers that arrived quickly and at high rates at islands. Other species had much lower immigration rates. As the number of species, s , on the island increased therefore the remaining pool of possible immigrant species on the mainland, $p-s$, would increasingly consist of poorer dispersers. The reduction in I_s caused by the arrival of the first few species would be much greater than the reduction caused later on by the arrival of a similar number of poor dispersers. They considered that total immigration rate to the island would be unlikely to be a linear negative function of s , but would instead be concave downwards, the slope of the curve should decrease as species richness on the island increased.

MacArthur & Wilson (1967) also proposed that less isolated islands would have higher immigration rate curves, and therefore support a higher equilibrium species richness for a given area than more isolated islands; the greater the immigration rate, the higher the species richness. Species-area plots for less isolated islands tend to lie above those of more isolated islands (Williamson 1981). Reed (1987) noted that the degree of isolation explained much of the residual variation in the species-area regressions for birds on Bahamian islands and similar results were obtained for bird communities in the West Indies (Lack 1970). However, ferns (Pteridophytes) do not appear to fit this rule. Species-area curves for ferns on the Azores, isolated islands in the middle of the Atlantic Ocean, were almost identical to those determined for the Channel Islands, close to mainland Europe. Ferns reproduce through the production of very light spores that get carried very great distances on the wind at no cost. They arrive after huge journeys just as capable of propagating than if they had travelled only a short distance (Williamson 1981). Distance *per se* is not the important factor in island biogeography theory, immigration rates are, but for many species distance from the mainland source is an adequate surrogate for immigration rates to an island (Rosenzweig 1995). Wilcox (1978) demonstrated the importance of immigration rates in determining the species-area relationships of different taxon, varying in their dispersal capability, on 19 West Indian islands. Reducing island size had a much greater negative effect on taxa with relatively low dispersal ability, such as reptiles, compared with taxa such as birds and bats with higher dispersal capabilities. Islands separated from the mainland by water characterised by strong currents and unstable ice-bridges in winter held fewer mammals than islands of similar size and distance from the mainland, but which were separated from the mainland by water with little current and stable ice-bridges in winter (Lomolino 1994). The more difficult the passage between the mainland and an island, the lower the immigration rate.

8.3. Species Richness and the Importance of Local Versus Regional Processes

Many studies have highlighted the apparently linear relationship between regional and local species richness (Cornell & Karlson 1999; Findley & Findley 2001), so that in many instances, estimates of the size of the regional species pool have provided the best predictors of local species richness (eg Angermeier & Winston 1998). This has lead some authors to suggest that local communities are simply a sub-sample of the regional species pool, with some form of proportional sampling inferred (Cornell & Lawton 1992). In inference here is that the composition of local communities, far from being stable, assembled, species assemblages, are actually random sub-sets of the overall regional species pool, and that the composition of the local community at any one time is the result of the vagaries of the dispersal process and immigration. There can be little doubt that dispersal is important in maintaining high species diversity (Levine 2003; Cottenie *et al* 2003). For example in grassland communities, the positive relationship between resources and diversity was only apparent when supplies of potential colonists were high (Foster & Dickson 2004). In coastal Ecuador, high species turnover (extinction and recolonisation) in abandoned coffee and forest habitats accounted for their higher species diversity over other land-use habitats (Tylianakis *et al* 2005).

However, many studies examining the relative importance of regional and local processes in dictating local species richness have demonstrated a phenomena termed “saturation” (eg Cornell & Lawton 1992). That is plots of local vs regional species richness deviate away from the linear relationship expected from the arguments presented above, instead displaying an asymptotic curvilinear relationship (Figure 8.3.1). Such relationships suggest that processes, such as competition, operating at the local scale place a limit on local species richness; that local communities become full or saturated, with no further scope to accommodate new potential colonists. The species richness of macro-invertebrates communities in stream head-waters in Finland was strongly related to region species richness. Nevertheless, local factors placed limitations on the subset of the regional species pool present in each stream (Heino *et al* 2003). Similarly, local species richness in butterflyfishes tended to be related to regional species richness, but at local scale communities tended to become saturated and richness reached an asymptote (Findley & Findley 2001). In temporary pools in Galilee in Israel, species richness was primarily determined by regional pool species richness, but local habitat characteristics related to island biogeography theory, pool size and permanence, placed limits on local species richness (Kiflawi *et al* 2003). In interconnected pond systems, high dispersal rates maintained high levels of species richness in the zooplankton communities occupying them, such that richness in each pool tended to be related to the regional species richness. Even so, local processes were strong enough to place limits on local species richness (Cottenie *et al* 2003). In a few studies explicitly examining the relative importance of local and regional processes in governing community structure, local structuring processes have been shown to be so pervasive that dispersal had very little impact on the maintenance of diversity. In plant communities in wetland beaver meadows, for example, local factors such as age of meadow or the drainage regime were the most important determinants of diversity (Wright *et al* 2003)

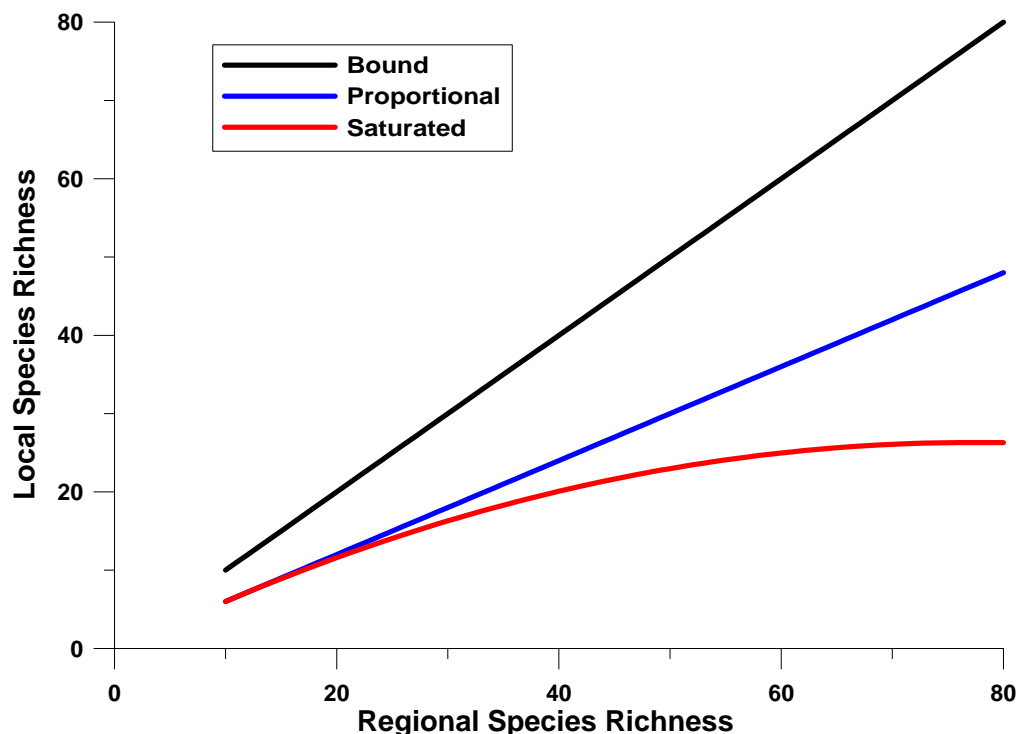


Figure 8.3.1. Relationships between regional and local species richness under situations of proportional sampling of the regional species pool and where local processes lead to saturation in local species richness.

9. METAPOPOPULATION DYNAMICS AND COMMUNITY STRUCTURE

Another explanation for high species diversity in competitively controlled communities, where competition equilibrium is reached and competitive exclusion does occur, relies on the patchiness of the environment. Thus a species might be excluded, and go extinct, on one patch, but continue to survive on another (Tilman 1982). Emigration from this second patch could provide the immigrants required to reinvade and repopulate the first patch at a later point in time. At the larger spatial scale, across all patches in the entire habitat, high species diversity is maintained by the presence of each species on one or more patches, whilst being absent on others, depending on the particular equilibrium point, or state of departure from competitive equilibrium, at each individual patch. Changes in one patch are balanced by opposing changes in others. At larger temporal scales, high species diversity at each patch is maintained by the stochastic interaction of extinction and immigration perturbing local dynamics to and from competitive equilibrium (Levin & Paine 1974; Levin 1976; Paine & Levin 1981; Lehman & Tilman 1997). Computer simulation of tree-fall gap formation and forest succession indicated high levels of variability at extremely local and short-term spatial and temporal scales – i.e. non-equilibrium conditions. At larger temporal and spatial scales, this variability was eliminated by the stochastic asynchrony of gap formation to form an apparently stable equilibrium situation (Smith & Urban 1988).

These sorts of arguments have led to the modern day study of metapopulation dynamics and its role in the structuring of biological communities (Hanski & Gilpin 1997; Hanski 1999; Hubbell 2001). If space is considered as a resource, such that a habitat is divided up into units sufficiently large to contain a single individual of a species, then Levins' (1969) model can be used to determine the level of occupancy of sites (Tilman *et al.* 1997). Levins' (1969) model considers a population whose individuals have a finite probability of dying, m , the mortality rate, and which produce propagules at a rate c , the colonization rate. A propagule entering an empty site occupies it. Occupants of sites are capable of producing propagules. These propagules disperse randomly across all possible sites, but a propagule cannot establish in an already occupied site. Propagules landing on already occupied sites are effectively lost; they die. To keep track of the population dynamics, all that is necessary is to monitor p , the proportion of all possible sites that are occupied. This is given by: $dp/dt = cp(1-p) - mp$, which states that the rate of change in site occupancy depends on the rate of propagule production cp multiplied by the proportion of currently open sites $(1-p)$. Subtracting losses through mortality mp from this gives the net change in the number of sites occupied.

This model has several interesting emergent properties. A species will persist in the habitat provided that $c > m$. Populations will grow in a logistic fashion. When $c > m$ the proportion of occupied sites will approach an equilibrium p_e , when $dp/dt = 0$, where $p_e = 1 - m/c$. This equilibrium is globally stable, p will approach p_e from any starting density, and from any perturbation that reduces p , so long as $p > 0$ (Hastings 1980). Most importantly, since no species is immortal, none are capable of completely filling the habitat at equilibrium. An unavoidable result of living in a spatial habitat therefore is that a proportion of sites will be empty. The proportion of viable sites left unoccupied at equilibrium, s_e , is $s_e = 1 - p_e = m/c$. The fundamental conclusion to be drawn from this implicit consideration of space (implicit because the actual geographic co-ordinates play no part in the logic) is that not even the most dominant of competitors can occupy all of the viable habitat.

Lehman and Tilman (1997) expand Levins' (1969) model to develop an abstract model for interspecific competition. This is given by $dp_i/dt = c_i p_i (1 - \sum_{j=1}^i p_j) - m_i p_i - \sum_{j=1}^{i-1} c_j p_j p_i$. Here p , c and

m have the same meaning as above, but they are now indexed by species rank, where the dominant competitor holds the first rank, 1. Colonisation and mortality are explicit, through c_i and m_i respectively, but the competitive hierarchy is implicit. The hierarchy results because the summations include terms for superior competitors, those of index value lower than i , but exclude terms for inferior competitors (index values higher than i). In a non-spatial model the best competitor wins and only this species occupies the habitat (Tilman 1982), but when space is taken into account (albeit implicitly) using the equation above, any number of species can stably coexist in a homogeneous environment (Tilman 1994). Coexistence occurs even though a superior competitor propagule entering a site immediately displaces a lower ranked species already occupying the site because neither the best competitor, nor any group of competitors, is able to occupy all of the habitat. It does, however, require a trade-off between competitive ability and dispersal ability, with a limit to the similarity of these traits. Some sites will always be empty, and these can provide a “home” for the most sub-ordinate competitor, provided their dispersal ability is sufficient to reach it quickly enough. Poor competitors are displaced by superior competitors, but because of their superior dispersal capability, poor competitors are much more likely to replace a superior competitor in a site, when the superior competitor individual occupying it eventually dies. There will therefore be constant turnover in the occupancy of sites (Lehman & Tilman 1997). Superior competitors will never be able to occupy all the sites, and no individual lives for ever. Sufficiently mobile fugitives will therefore always manage to occupy some of the habitat, albeit transiently (Horn & MacArthur 1972; Armstrong 1976; Crawley 1990). The fundamental trade-off between competing species, the ability to get to a site (good coloniser) against the ability to displace previous occupants and hold on to a site (good competitors), has been explored in several fauna (MacArthur & Wilson 1967; Levin & Paine 1974; Werner & Platt 1976; Platt & Weiss 1977). It can be as simple as the energy allocated to roots, improving nutrient acquisition and local competitive ability, versus the energy allocated to seeds, improving colonisation ability (Tilman 1990).

The existence of spatial structure, acting through individual mortality and colonisation, alters conclusions regarding the outcome of competition. Despite the pre-ordained outcome of competition at the local scale, regional co-existence does occur. Thus, meta-population can maintain species coexistence across a network of patches through a balance between frequent within patch extinctions and recolonisation events (Hanski 1999). However, this requires fairly restrictive conditions on migration. Dispersal rates have to be high enough for recolonisation to balance extinctions, but not so high as to cause local populations to start to fluctuate in synchrony (Earn *et al* 2000). The role of meta-population theory in determining community structure is dependent on patch dynamics. Theory needs to incorporate a patch-dynamics perspective of a landscape in a dynamic mosaic of successional states, taking account of links between colonisation and extinction processes and local succession (Ellner & Fussman 2003),

10. PATTERNS IN THE STRUCTURE OF MARINE COMMUNITIES

In the preceding review of the various processes believed to impart structure to the composition of animal communities, the vast majority of examples in support of particular mechanisms involve terrestrial systems and organisms. Terrestrial and marine ecosystems differ considerably in the way that key functions and process are organised. The processes that control the population dynamics of marine organisms also vary markedly to those operating in terrestrial populations. Table 10.1 presents 44 different characteristics of ecosystem processes and functions, and community and population attributes, in which, generally speaking, clear differences between marine and terrestrial systems can be demonstrated. This table was developed at the MAFCONS Community Theory Workshop convened in Ghent, Belgium, in April 2003. It is meant to be exemplary, and is almost certainly not exhaustive.

Characteristic	Marine	Terrestrial
Primary producers	micro-organisms	higher order plants
Primary producers	do not create habitat	create habitat
Primary production	not limited by water	water limiting
Primary production	dependent on diffusion processes	readily available
Temporal variability in primary production	greater	less
Dimensionality	3D	2D
Biogenic habitat structuring	by higher trophic level	by lower trophic level
Light	remote and directional	all around
Buffereing of environmental variation	greater	less
Adaptability to opposite environment	greater	less
Environment	poorly known	well known
Population Growth	variable stochastic recruitment	Lokta-Voltera per capita growth
Dispersal	wide range	narrow range
Dispersal	non-random direction	random direction
Broadcast spawning	common	rare
Body growth	indeterminate	determinate
Fecundity	indeterminate	determinate
Ontogenetic development	many niches	few niches
Functions	no parallel function	unique functions
Relative importance of homeothermy	low	high
Water conservation (osmosis)	unimportant	important
Canibalism	higher	lower
Omnivory	more	less
Mixotrophy	higher	lower
Pred-prey distributions	loosely coupled	tightly coupled
Number of trophic levels	higher	lower
Food chain length	longer	shorter
Connectance	higher	lower
Herbivores	micro-phages	macro-phages
Grazer foodweb importance	less	more
Detritus foodweb importance	more	less
Ecological efficiency (transfer)	higher	lower
Carbon Cycling	faster	slower
Carbon storage	higher	lower
Top predator diversity	higher	lower
Longest lived organisms	top of foodweb	base of foodweb
Periodic cycles	more	less
Succession	arrival of mobile animal	driven by plants
Succession times	shorter	longer
Phylum level diversity	high	low
Competitive exclusion	rare	common
Species geographical ranges	bigger	smaller
Vulnerability to invasion	more	less
Management impact at regional scale	greater	less

Table 10.1. Differences between marine and terrestrial ecosystems and communities.

Given these differences between marine and terrestrial ecosystems, the question as to whether current community structure theory, developed mainly with regard to terrestrial studies and experiments, holds any pertinence to marine ecosystems and communities is certainly germane. In

the following sections, some of the patterns of community structure described previously, and the processes considered to have given rise to these, are re-examined but now marine cases are considered specifically. Two questions underpin this re-examination: “Are patterns of community structure in marine and terrestrial ecosystems similar?”, and “Are the processes that produce the patterns of community structure observed in marine ecosystems the same as those that operate in terrestrial ecosystems?”

10.1. Community Assembly Rules

Similar evidence for the presence of community assembly rules has been documented for marine communities as has been presented previously in Section 7.2.1. Reef fish communities recovered to approximately the same species composition and richness following total fish removal by the atomic testing programme, provided that the appropriate recruit resource was present. In this study the importance of habitat structure in dictating the type of community present was confirmed. Habitat structure was unaffected by the atomic tests (Planes *et al* 2005).

10.2. Theoretical Species Abundance Distributions

Compared with most terrestrial data sets, data from marine soft sediment habitats have high species richness. Communities tend to include large numbers of rare species. Fitting log-normal distributions to species abundance data suggests that more than one log-normal distribution occurs. Models of species abundance distribution have therefore been developed that comprise of two nested log-normal distributions, one fitted to the more abundant species and the second fitted to species assigned to the rare category (Gray *et al* 2005).

10.3. Marine Latitudinal Gradients

As with many terrestrial studies, negative latitudinal gradients (a decrease in diversity as one moves progressively further north or south from the equator) appear to be common in marine ecosystems (Stevens 1989). Latitudinal gradients have been indicated among plankton communities, such as copepods (Turner 1981). Angel (1997) suggests a decline in diversity with increasing latitude in the North Atlantic for several groups of pelagic organisms, a pattern seen to a depth of at least 2000m. Latitudinal gradients have been noted among several benthic invertebrate groups (Heck 1979), bivalves (Fischer 1960; Stehli *et al.* 1967; Sanders 1968; Roy *et al.* 1994; 2000), predatory gastropods (Taylor & Taylor 1977; Vermeij 1996) epi-zooplankton (Grice & Hart 1962), and reef-building scleractinian corals (Fischer 1960; Stehli & Wells 1971; Veron 1993; 1995). Latitudinal gradients have also been observed in deep-sea regions, including North Atlantic deep-sea macrofauna (Rex *et al.* 1993; 2000; Poore & Wilson 1993) and global deep-sea habitats for foraminifera (Culver & Buzas 2000). Rex *et al* (2005) describe negative latitudinal diversity gradients in coastal molluscan communities both north and south of the equator, but show that the patterns are highly asymmetrical between the hemispheres.

Despite this, the extent to which such clines are a general characteristic of marine communities remains uncertain, particularly in southern hemisphere regions (Clarke 1992; Poore & Wilson 1993; Brey *et al.* 1994 Clarke & Crame 1997). For example, whilst Thorson (1957) reported a negative gradient in hard substrate communities, he observed no such gradient in sedimentary communities. Similarly, within benthic shelf fauna communities, negative gradients have been proposed for gastropods (Valentine 1966; Roy *et al.* 1998) and molluscs (Crame 2000; Roy *et al.* 2000), but other studies have not found gradients (Kendall & Aschan 1993; Boucher & Lamshead 1995). Patterns at regional scales have also been inconsistent. Ellingsen & Gray (2002) found no

latitudinal gradient in the species richness of soft-sediment benthic macrofauna along the Norwegian coastline. Similar conclusions were drawn for North Atlantic shelf bryozoans (Clarke & Lidgard 2000) and for the Atlantic Ocean as a whole (Price *et al.* 1999). Pelagic copepod diversity in North Pacific shelf ecosystems suggests negative gradients, but these tend to be obscured somewhat by regional variation in oceanography (McGowan & Walker 1985; Russell-Hunter 1970). As with their terrestrial counterparts, the exact shape of the relationship between species diversity and increasing latitude in marine systems has also been questioned. Rather than being a simple linear relationship, it has again been suggested that as latitude increases, diversity first increases as you move away from the equator, before declining as one proceeds further towards the pole (Taylor & Taylor 1977; Roy *et al.* 1998). Rather than being linked to changes in sea temperature, this may in fact be more closely linked to changes in seasonality (Taylor & Allinson 1998).

To further confuse the picture, and just as with some terrestrial communities, positive gradients have also been described in some marine assemblages. The diversity of organisms found on coral reefs, for example, is generally lower in the tropics and tends to increase at higher latitudes (Paine 1966; Sanders 1968; Abele 1974). Seabird species diversity, unlike their terrestrial counterparts, is lower in the tropics and increases towards higher latitudes in both hemispheres (Stehli 1968; Scott 1974 in Huston 1994). Deep-sea nematodes may also exhibit a positive gradient (Lambhead *et al.* 2000). Reverse latitude gradients of lower diversity near the tropics, and higher diversity nearer the poles, have been reported on a number of occasions for marine benthic organisms: for example, continental shelf infauna (Thorson 1957; Sanders 1968), invertebrates (Paine 1966), and algae (Gaines & Lubchenco 1982) from rocky intertidal coastlines and deep-sea benthos (Sanders 1968; Stuart & Rex 1989). Soft-sediment macro-benthos species richness was higher at middle latitudes on the Norwegian coast. However, an alternative indicator of species diversity, taxonomic distinctness, which measures the degree of relatedness between organisms occupying a location, did reveal latitudinal gradients, but again the picture was confusing. When all taxa were considered together the relationship with latitude was positive. However, when individual taxon groups were considered, negative relationships were observed for crustaceans and annelids and no relationship was apparent for molluscs (Ellingsen *et al.* 2005).

These studies, when considered together suggest that mismatched data sets, or analytical approaches, can produce conflicting patterns, or perhaps that different faunal groups may exhibit different responses to whatever variable(s) are responsible for these gradients.

Perhaps of greatest relevance to the present discussion is the presence of latitudinal gradients in both North Sea benthos and fish communities. In each case these gradients are the reverse of the more general negative gradient; species diversity, or species richness, of both benthic and demersal fishes communities is higher in the northern North Sea than in the southern North Sea (Heip *et al.* 1992; Daan *et al.* 1990). The strongest inflows of Atlantic waters into the North Sea are provided by The Fair Isle, East Shetland and Norwegian Trench currents, all of which flow into the northern North Sea (Turrell 1992; Turrell *et al.* 1990; Turrell *et al.* 1996). It is conceivable that the reverse latitudinal gradients observed for both fish and benthic assemblages may be maintained by high immigration rates into the north of the region. These inflows are considered to provide the mechanism by which the adult copepod, *Calanus finmarchicus*, invades the North Sea each spring (Backhaus *et al.* 1994), and there is some evidence of fish invasion into the northern North Sea via these currents, for example the bluemouth *Helicolenus dactylopterus* (Heessen *et al.* 1996). In the Mediterranean and Black Seas, decreasing trends in Polychaete species richness have been observed as one moves from west to east across the region. Polychaetes colonised these seas primarily from the Atlantic via the Straits of Gibraltar, and the decline in polychaetes diversity, as one proceeds in an easterly direction, has again been explained by the increase in distance from the source of colonisation (Arvanitidis *et al.* 2002). These authors suggest that Polychaete diversity in the Mediterranean and Black Seas is determined by the balance between colonisation and

extinction, as suggested by the equilibrium model of MacArthur & Wilson (1963; 1967). A similar explanation, based on the equilibrium model, has been presented to explain variation in the species richness of deep water mollusc communities in the Mediterranean Sea. In these communities, species richness is determined by the balance between larval influx into the deep water basins, and mortality rates (Bouchet & Taviani 1992). It is worth noting that harpacticoid data seem to exhibit a reverse trend in that more southern areas of the North Sea appear to be more species rich. It is clear that careful, parallel analyses that consider sampling effort and abundance differences are needed to establish whether these patterns hold up under closer scrutiny.

Multiple explanations have been invoked to explain latitudinal patterns (see previous section above), most developing primarily from the terrestrial ecology literature. Most of these explanations assume that latitude represents a proxy for some other causative variable. It has been suggested that the high primary productivity in high latitude oceans (Steemann-Neilsen 1954; Harvey 1955; Koblenz-Mishke *et al.* 1970; Barnes & Hughes 1988) may explain the reverse latitudinal gradient observed in seabird species diversity (Stehli 1968; Scott 1974 in Huston 1994). Rex *et al.* (2005) point out that water availability, an integral feature of recent developments in the energy/water dynamics diversity theory as it pertains to terrestrial biotas, is presumably irrelevant in the oceans. Here we consider a few of the possible causes of latitudinal gradients and discuss their possible relevance with respect to marine systems generally, and the North Sea specifically.

- Longer time period for speciation without interruption by glaciation. To some extent glaciation must have influenced some environments more than others, and certainly contributed to the reduced species diversity in the Arctic, but this explanation does not help in explaining gradients at more southerly latitudes and is not particularly useful for North Sea. In this instance it is likely that glaciation did play a role in defining modern benthic and demersal fish communities, but the spatial scale of the North Sea and predominant currents suggest that differential recolonisation of different areas of the North Sea is probably not a contributing factor. Specific tests of this hypothesis would involve genetics data that probably don't exist at this time.
- Climate stability (Slobodkin 1969). Climatic stability can influence species diversity in several ways. First, variability in climate might limit rates of speciation, and secondly it might reduce diversity by limiting colonization to only species with a relatively high tolerance to seasonal variation. For the North Sea case, speciation differences are almost certainly not relevant given the temporal and spatial scales, but it is possible that seasonal variability could place limits on species because of physiological tolerance. One approach might be to look at species distributional ranges and known physiological tolerances in order to determine whether there is any spatial difference in terms of environmental niche breadth between northern and southern areas of the North Sea.
- Greater total solar input allows higher total production and more species (Currie 1991). In the oceans, solar input correlates poorly with primary production because of nutrient limitation in most marine systems. In deep ocean molluscan fauna, latitudinal and bathymetric gradients suggest that diversity is a function of the rate of nutrient input from surface production (Rex *et al.* 2005). But the potential relationship between diversity and production is a complex one, in that parabolic relationships have been proposed for a variety of habitats (Rosenzweig & Ambransky 1993). In marine systems, the depth-diversity parabolic relationship (Rex 1983) could be attributed to production differences, as could declines in diversity in eutrophied environments (e.g. Pearson & Rosenberg 1975). If production and diversity represent cause and effect, then the diversity response appears to be group dependent. A very crude negative relationship for shelf gastropods and deep-sea macrofauna is noted in Snelgrove *et al.* (2000) though a more detailed analysis in Watts *et*

al. (1992) suggests no functional relationship. The reverse relationship is reported by Lambshead *et al.* (2000) for deep-sea nematodes. Thus, the framework for prediction in the North Sea is not clear, though there are clear differences in production in the North Sea with greater production in the central and southern regions than in the north (Reid *et al.* 1990; Joint & Pomroy 1993). The relationship with diversity could be tested by comparing alpha diversity in grabs with sedimentary chlorophyll measurements or by contrasting beta diversity at larger scales but by using a similar approach. One final point with respect to production is that there are clear depth differences across the North Sea; Sanders (1969) noted an increase in diversity with depth in shelf environments off the western United States, and the potential contribution of depth could be removed using regression residual analysis techniques to remove depth effects (e.g. Etter & Grassle 1992).

- Area of continents greater at low latitudes (Rosenzweig 1995). For the oceans, the reverse is likely to be true in that continental shelf area is greater at higher latitudes, although for deep-sea habitat it is true that the tropical Pacific and Atlantic are larger in area than the temperate and polar areas and could therefore conceivably provide more habitat variety and higher diversity towards the equator. Total habitat area could contribute to some of the spatial differences in the North Sea, particularly as it relates to habitat heterogeneity (see below). Examination of species-area curves, and specifically their structure in moving across habitats (smooth or stepped) could clarify whether assemblages are patchier in one area compared to another and whether this is consistent with diversity differences.
- Rapoport's rule. Species latitudinal ranges are greater with increased distance from the equator (Stevens 1989). This explanation is based on the idea that at temperate and polar latitudes, organisms are more broadly distributed and therefore exhibit lower beta diversity. Rapoport's rule does not appear to underpin diversity gradients in eastern Pacific mollusc communities (Roy *et al.* 1994). In the North Sea this hypothesis could be tested by determining whether there are more southern species that also occur in the north, compared with the number of northern species that also occur in southern areas. A related question is whether degrees of local endemism are higher in the northern areas.
- Habitat heterogeneity. (MacArthur 1957) simply argues that greater habitat heterogeneity begets more niches, which in turn encourages higher diversity. This idea has been applied to coral reef gastropods (Kohn 1967) and as a key issue in the deep-sea patch mosaic model (Grassle & Sanders 1973). In the North Sea, it is possible the reverse latitudinal gradients in benthic and demersal fish communities might be explained by greater habitat complexity in northern latitudes, perhaps from biogenic contributions. This is certainly a testable hypothesis.
- The latitudinal gradient is a statistical artifact – the mid domain effect (Colwell & Hurtt 1994; Colwell & Lees 2000; Colwell, Rahbek & Gotelli 2004). Fish fauna along the Tropical East Pacific exhibit a strong latitudinal gradient in species richness. The mid-domain effect provided the strongest predictor of the latitudinal gradient (Mora & Robertson 2005). No effect of energy (water temperature) was observed. In the North Sea it should be possible to analyse groundfish survey data to explore the relationships between the numbers of ranges overlapping at various latitudes to determine the extent to which a process, similar to the mid-domain effect, might explain latitudinal gradients in diversity.

Above and beyond these explanations, a complex suite of alternative possibilities, some invoking niche and competition theory, have been proposed. Specifically, niche breadths and interspecific interactions may differ, and that in the tropics, these may be biologically rather than physically accommodated (Sanders 1969). Thus, it is possible that the tropics have more interspecific than

intraspecific interactions, higher niche overlap, greater competition, greater specialization, greater predation control, more parasitic and pathogenic interactions, and more mutualistic interactions. Over the scale of the North Sea it is difficult to envisage that differences in these variables might exist and be sufficient to explain the observed latitudinal gradients. However, the possibility cannot be fully discounted without more careful consideration.

One of the greatest problems in interpreting latitudinal gradients is that the analysis is easily biased by sampling design, particularly failure to correct for differences in sampling effort and the numbers of individuals collected. There are, nonetheless, techniques such as rarefaction and regression residual analyses that could be used to ascertain whether patterns are real or represent sampling artefacts. This approach can help in teasing out effects of individual variables (including fishing disturbance) that confuse interpretation, and are clearly a priority action item for North Sea benthos and demersal fish data.

10.4. Depth Gradients

Depth gradients in community composition provide the marine equivalent of the elevational gradients found in terrestrial ecosystems. The effect of depth on community marine communities has been widely noted (eg Merret & Marshall 1981; Hecker 1990; Gordon & Bergstad 1992; Fujita *et al* 1995; Moranta *et al* 1998; Hoines *et al* 1998; Jones *et al* 2003).

11. THE ROLE OF COMPETITION AND NICHE THEORY IN MARINE COMMUNITY STRUCTURE

11.1. Evidence of Competitive Exclusion

In the intertidal rocky zone, the smaller barnacle, *Chthamalus stellatus*, is excluded by the larger *Balanus* species. Only when *Balanus* barnacles were removed could *Chthamalus* persist (Connell 1961). The two starfish *Pisaster ochraceus* and *Lepasterias hexactis* tend to occur in sympatry. There is considerable overlap in their diet (Menge & Menge 1974) and their standing crops were negatively correlated in the study area, suggesting a competitive interaction between the two species. When all the *P. ochraceus* were removed from one reef and added to a second, the average weight of individual *L. hexactis* increased on the reef from which its competitor was removed and decreased on the reef where it was added (Menge 1972).

11.2. Resource Partitioning – Character Displacement

The shell length-frequency distributions of two marine snails, *Hydrobia ulvae* and *H. ventrosa* are almost identical in allopatry. In sympatry, however, the modal length of *H. ventrosa* is shifted downwards, while the modal length of *H. ulvae* is larger. These differences in shell length have been related to the variation in particle size selection (Fenchel 1975).

11.3. Resource Partitioning – Behavioural Displacement

The portunid swimming crab *Liocarcinus depurator* occurs only in the sublittoral zone. Examination of the free-running locomotor activity rhythms of freshly-captured *L. depurator* in constant conditions in the laboratory revealed a circadian activity pattern with highest activity levels during the night. The morphologically similar *L. holsatus* occurs in both the intertidal zone and the sublittoral zone. *L. holsatus* captured in the intertidal zone, where *L. depurator* were absent,

showed strong circatidal activity rhythms with maximum activity at high tide. However, *L. holsatus* captured in the sublittoral zone, where they coexisted with *L. depurator*, displayed a clear tendency towards circadian activity rhythms with highest activity during day-time hours. Thus where the two crabs occurred together, the activity patterns of *L. holsatus* were altered in such away as to avoid competing for resources at the same time as *L. depurator*. That this altered behaviour pattern was actually induced by the presence of *L. depurator* was strongly indicated by the observation that when exposed to hydrostatic pressure cycles of tidal amplitude and periodicity in the laboratory previously tidally arrhythmic *L. holsatus* developed circatidal activity rhythms. They thus displayed similar behaviour patterns to conspecifics captured from intertidal zone where *L. depurator* were absent (Abelló, Reid & Naylor 1991). Another study has suggested that predation by *L. depurator* in sublittoral habitats had little effect on the abundance of benthic prey (Hall *et al.* 1990). If food resources are not limiting then can competition be responsible for the alteration in the foraging behaviour of *L. holsatus* described above? These studies were, however, carried out in geographically quite separate locations.

Competition was observed to be the main source of density dependent mortality of planktivorous damselfish on the Great Barrier Reef. The consequence of competition was to alter behaviour so as to make the damselfish more vulnerable to predation. Thus, although predation was the proximate agent of mortality, competition was the driver (Hixon & Jones 2005).

11.4. Resource Partitioning – Habitat Displacement

The codel goby *Gobiosoma robustum* and clown goby *Microgobius gulosus* are common, ecologically similar species, found throughout the Gulf of Mexico and southeastern Atlantic Ocean. In Florida Bay, where these species coexist in sympatry, they exhibit habitat partitioning; *G. robustum* is most abundant in seagrass-dominated areas while *M. gulosus* is most abundant in sparsely vegetated habitats. In situations of allopatry in a laboratory aquarium, both species tended to select seagrass habitat, but when both species were placed in the aquarium together, *M. gulosus* showed a much increased tendency to occupy bare sand habitat. When occurring in sympatry, interspecific competition from *G. robustum* appears to directly modify the habitat choice of *M. gulosus*. When a predator, the toadfish *Opsanus beta* was added to the aquarium, both gobies showed an increased preference for bare sand habitat. The outcome of competition for a particular resource can therefore be altered by the presence of predators (Schofield 2003).

11.5. Resource Partitioning and Avoidance of Competitive Exclusion

The diel and habitat-dependent resource utilisation by the four dominant deep-sea fishes of the Great Meteor seamount fish community, *Zenopsis conchifer*, *Macroramphosus* spp., *Antigonia capros* and *Capros aper*, suggested sufficient resource partitioning among species so as to avoid competitive exclusion (Fock *et al.* 2002). Stomach content analyses of the fifteen commonest species of an assemblage of demersal fishes present on a soft-sediment bottom off the west coast of Scotland in the late summer-autumn suggested at least five distinct diet groups (Gibson & Ezzi 1987). Cod *Gadus morhua*, haddock *Melanogrammus aeglefinus*, pollack *Pollachius pollachius* and saithe *Pollachius virens* were abundant predatory fish on herring *Clupea harengus* spawning grounds off southwestern Norway. Generally the diets of these four predators are quite distinct (Daan 1989; Hislop 1997). However, under circumstances where a single prey resource becomes exceptionally abundant, for example herring eggs following herring spawning, and in no way limiting to these predators, all four species switch to this prey, and at these times the diets of these four gadoid predators exhibit considerable overlap (Høines & Bergstad 1999). That food resources for demersal fish may be limiting at other times is strongly implied by the difficulties found in balancing the energy flow pathways through the benthos to demersal fish in foodweb studies of

both the North Sea and Georges Bank in the northwest Atlantic (Steele 1974; Jones 1982; 1984; Greenstreet *et al.* 1997). In all cases estimates of consumption by fish exceeded realistic estimates of the resources available to them, generated by the production of benthic invertebrates.

11.6. Resource Partitioning Along Multiple Resource Spectra

Seven species of shallow-water squirrelfishes made up >99% of the nocturnally active benthic-crustacean feeding fishes at five tropical reef sites at St. Croix in the Virgin Islands. Food was partitioned by taxon between the four predominantly shrimp consuming species and the three species that mainly preyed on crabs. Secondary food resource partitioning was on the basis of prey size, particularly in the principal prey category. In addition, differences in foraging micro-habitat were just as important as foraging differences in separating species (Gladfelter & Johnson 1983).

Barnes (2002) describes refuge-use and dynamic niche overlap in semi-terrestrial subtropical hermit crabs. Three sympatric species coexisted at high abundance along the south-western Madagascar coastline even though they shared similar resource requirements, some of which were restricted. Niche overlap was found to change dynamically over a temporal scale, in response to physical drivers such as tidal phase, shade and refuge potential of site

11.7. Habitat Heterogeneity as an Additional Resource Spectrum

In marine benthic environments, increased heterogeneity in the substrate, in terms of variation in sediment particle size, and/or increased habitat complexity due to the presence of structure forming, or biogenic, organisms such as corals, algae, sponges and bivalves, has been demonstrated to have a positive effect on the species diversity of associated fish (Gladfelter & Gladfelter 1978), macrobenthic fauna (Thrush *et al.* 2001), gastropod communities (Kohn 1967; 1968) and microbe communities (Pringle 1990). Even relatively low-density features creating small-scale structure on the seafloor (e.g. sponges<2; hydroids<1; horse mussels<17 individuals per 0.3m²) have been found to significantly influence macrobenthic diversity on the 100s to 1000s of metres scale (Thrush *et al.* 2001). At a particular level of habitat structure however, diversity was over-estimated by the models used, suggesting a threshold in the relationship between biodiversity and habitat structure. Organisms that inhabit the sediment create much of the structure in soft-sediment habitats (Thrush & Dayton 2002). It has been shown that the removal of both epifaunal and infaunal structure by trawling and dredging creates a more homogenous and less diverse ecosystem (Mayer *et al.*, 1991; Dayton *et al.*, 1995; Jennings & Kaiser, 1998; Thrush *et al.*, 1998).

Highly structured habitats can provide refuges for both predators and prey. Topographic complexity has a significant and positive influence on the growth and survivorship of juvenile life stages of commercially valuable fish species (Thrush & Dayton 2002). On the Australian Northwest shelf, Sainsbury (1988) showed a decrease in the number and variety of epifauna, particularly sponges, collected as bycatch over time. This reduction was directly associated in a concurrent shift in the fishery from high- to low-value species. It was suggested that this could be explained by the positive role that the epifauna played in affecting the survivorship of the commercially valuable species.

11.8. Relationships Between Productivity and Diversity

Productivity in the mid-ocean gyre zones of the world's open oceans is low (Steemann-Nielsen 1954; Harvey 1955). Plankton densities are low, but species diversity is high in these areas. In

contrast, in high productivity areas, such as nutrient upwellings and the shallower coastal zones, the density of organisms is higher, but their species diversity tends to be lower (Russell-Hunter 1970; McGowan & Walker 1985; Springer *et al.* 1989). In marine systems depth is often used as a surrogate for productivity. The greater the depth, the further the seabed is from the photic zone at the surface where primary production takes place. As distance between the surface and the seabed increases, so does the chance that organic material raining down on to the sea floor will be intercepted on route. Thus the amount of material reaching the seabed to fuel benthic communities decreases with depth. At many coral reefs around the world, coral species richness has been found to increase with increasing depth (Loya & Slobodkin 1971), for example at Eilat in the Red Sea (Loya 1972) and Discovery Bay in Jamaica (Huston 1985).

Unimodal relationships between marine species diversity and depth (a surrogate for productivity, productivity decreases with increase in depth) have been demonstrated for several groups of organisms, including Antarctic brachiopods (Foster {1974} in Rosenzweig & Abramsky {1993}), decapods, fishes and echinoderms (Haedrich *et al.* 1980), cumaceans, gastropods, protobranchs and polychaetes (Rex 1981). Species diversity on the coral reefs at the Chagos Atolls in the Indian Ocean initially increased with increasing depth, a result similar to those described above for Eilat and Discovery Bay. However, as transect depth increased, species richness peaked at a depth of around 20m and then started to decline (Sheppard 1980), suggesting a unimodal relationship between diversity and productivity. More recent studies at Discovery Bay, extending the transe to greater depth, have also revealed the negative side of a unimodal relationship between diversity and productivity at this location as well (Liddell *et al.* 1984).

Considering recent advances in deep-sea ecology, it is perhaps over-simplistic to predict a clear relationship between depth and productivity. There is now clear evidence that deep-sea habitats appear to have extraordinary levels of local, and potentially, global diversity (Hessle & Jumars, 1974; Grassle & Maciolek, 1992; Levin *et al.* 2001; Snelgrove & Smith, in press). Glover *et al.* (2002) measured the relationship between productivity and local polychaete species diversity in the central equatorial Pacific abyssal plain. Instead of relying on depth as a proxy for productivity, measures of particulate organic carbon (POC) flux to the seafloor and average annual surface productivity were recorded for each site. It was expected that there would be a strong diversity-productivity relationship across the sites, which varied from the food-poor central Pacific gyre to the relatively productive equatorial zone. In fact only a weak positive relationship was observed between productivity and diversity in the Pacific abyss, not the unimodal, relationship that was anticipated. Extreme oligotrophy does not appear to limit local diversity in the deep-sea, rather diversity may be controlled by a suite of environmental factors (see Levin *et al.* 2001).

11.9. The “Lottery” and “Storage” Models: Recruitment Competition

Findlay & Findlay (1985) studying butterfly fish communities in the Caribbean and south-central Pacific, varying in species richness from 2 to 17 species, could find no evidence of niche-width compression as the number of species in the community increased. Resources did not appear to be limiting. There was no indication that ecologically similar species were replacing one another when the species suites at different locations were compared. Coexistence of similar species at particular location was much more common than expected. They concluded that, although these communities did not appear to be competitively structured, neither were they random assemblages of the species of which they were composed. They suggested that perhaps these communities might be “dispersal assembled”, with vacancies on the reef being occupied by the chance settlement of a larva belonging to a limited guild of species adapted to that particular type of habitat, effectively the lottery model of Sale (1977; 1978).

The lottery model considers a community in which, once individuals are settled, they cannot be displaced by other individuals, regardless of species. When an occupant dies and a site becomes available, it is filled on a random basis (first come, first served) from the pool of available dispersal stages (larvae) (Sale 1977; 1978). Thus the species compete for space through the production of dispersal forms and the probability that an individual of a particular species will occupy a site is equal to that species proportion of the total population of dispersing forms (Chesson & Warner 1981). A competitive “lottery” for vacant space best explained the co-existence of two ecologically equivalent closely related coral dwelling gobies at Lizard Island on the Great Barrier Reef (Munday 2004).

Recruitment fluctuation can promote coexistence in communities of long-lived animals (Chesson & Warner 1981). Strict resource limitation results in one species increasing at the expense of the other so that competitive exclusion is encouraged. However, if environmental fluctuation results in highly variable recruitment rates, then it is possible for the lower density competitor to give rise to occasional large recruitment events, resulting in a sudden increase in population size. For this to result in the coexistence of the two competitors, the adult populations must be highly fecund so that small adult populations are capable of producing very much larger numbers of recruits. The adult population must also decline slowly so that they are able to survive over periods of poor recruitment. Thus, even a remnant adult population can produce a strong recruitment event, giving rise to a cohort of long-lived adults capable of surviving over a number of potential reproductive periods. This model has been called the “storage model” because the gains made by a single good recruitment event are “stored” in the adult population. The storage model requires that competition among adults should not greatly influence adult survival, nor should adult mortality be unduly influenced by environmental variability (Warner & Chesson 1985). This sort of pattern is particularly true of many fish stocks where natural mortality is low. In the North Sea herring enter the fishery at age 3. In 1907 such fish constituted the vast majority of the catch. In 1908, the same cohort, now 4 years old made up the majority of the catch, and this outstanding cohort continued to sustain the greater part of the fishery until 1913 (Hjort 1914). Fish species have indeterminate growth and fecundity is related to body mass. Thus as individuals get older, and therefore larger, their fecundity increases. Thus, even with the demise of some of the adult population in each generation time during periods of low recruitment, the impact of this mortality on total potential population fecundity will be relatively much less, since *per capita* fecundity within the remaining adults in the population will have increased. Communities maintained through a storage model process are particularly threatened by perturbations that principally threaten the older age classes of populations; the components that carry out the bulk of the storage of future population growth potential. In many fish populations as the age structure of the population declines, offspring become less viable. Growth rates of offspring decline and ability to survive starvation reduces. Much of the benefits of the storage model are lost because as the “quality” of offspring falls, their chances of “winning the lottery” are reduced (Berkeley *et al* 2004).

12. THE ROLE OF PREDATION AND DISTURBANCE IN MARINE COMMUNITY STRUCTURE

Many examples of predation or disturbance control of marine communities have already been discussed in the preceding sections of this review where this theme was initially introduced and developed. The fact that so many of the examples of top-down or disturbance control of biological communities have been derived from studies of marine organisms tends to suggest that such control of the structure of marine communities is common, perhaps more common than in terrestrial systems.

12.1. Trophic Cascades

Verity & Smetacek (1996) reviewed several studies of marine planktonic food webs and concluded that there was little evidence of strong or continuous top down control. However, some evidence of trophic cascade effects were apparent, but the importance of these in structuring plankton communities may have varied seasonally and historically. Despite intense predation pressure from herring *Clupea harengus* and mysid shrimps *Myis mixta*, the role of predation in structuring the zooplankton community in the north-western Baltic sea was minimal (Hansson *et al.* 1990).

Without the need for skeletal support, top predators in marine ecosystems can reach much larger body-size compared with top predators in terrestrial system. Such predators can have very high energy demands, particularly if warm-blooded, so that relatively small numbers of predators can exert considerable top-down pressure on prey populations in resource trophic levels. As few as 40 killer whales would be sufficient to explain the declines in Steller sea lions in the Aleutian islands, while a pod of just five killer whales is sufficient to account for the reduction in sea otters (Williams *et al* 2004), with consequent knock on effects on their prey.

12.2. Disturbance Permits Coexistence

Two sympatric predaceous seastars, *Asterias forbesi* and *A. vulgaris* co-occur over a broad geographic range, from central Maine to Cape Hatteras. Both are of similar body size and occupy similar depth ranges, from the low intertidal to at least 50m. Their diets, size of prey, and feeding activity periodicity show considerable overlap. Variations in these characteristics occur from site to site but are generally positively correlated between the two species. Such similarity along resource dimensions is generally taken to indicate that species compete for resources. However, interspecific competition rarely occurred and food resources were not generally limiting. Mortality arising from periodic disease outbreaks and storm disturbance helped to maintain the two seastar populations below their individual carrying capacities. This disturbance mortality allowed the two potential competitors to coexist and the apparently high level of niche overlap between the two species reflected the absence of pressure to subdivide resources (Menge 1979).

12.3. Disturbance May Reduce Diversity

In benthic invertebrate communities, recovery is linked to physical recovery of the seabed sediment following perturbation. Physical recovery (infilling of holes, etc) is faster in sand habitats than in mud, consequently benthic communities in sand recover more quickly than they do in mud habitats (Dernie *et al* 2003). However, recovery of benthic communities can still take a very long time, often much longer than the physical recovery process. Recovery is strongly dependent on the physical environmental conditions; wave disturbance, flow velocities, wetting/drying regimes, etc. Composition of the macrobenthic fauna in adjacent areas is also critical, as a supply of potential colonists (Thrush *et al* 2003). High frequencies of disturbance can therefore be critical for benthic communities, preventing recovery and resulting in altered communities over prolonged periods.

Under normal conditions the two hermit crabs *Pagurus bernhardus* and *P. prideaux* occur sympatrically, despite the fact that their diets show considerable overlap. *P. bernhardus* shows a strong tendency to aggregate in areas disturbed by fishing trawls where they consume animals damaged in the trawl path, whereas *P. prideaux* do not. Morphometric analyses revealed that *P. prideaux* have smaller chelae relative to *P. bernhardus*. *P. prideaux* may avoid dense aggregations of the more aggressive *P. bernhardus*. These behavioural differences, coupled with higher fisheries mortality for *P. prideaux*, may provide a mechanism whereby *P. bernhardus* could out-

compete *P. prideaux* in areas where fishing disturbance is a frequent occurrence (Kaiser *et al.* 1998).

On the basis of Connell's (1978) Intermediate Disturbance Hypothesis, it has been suggested that fishing disturbance can positively affect benthic biodiversity. Thrush & Dayton (2002) dispute this. They argue that, because there has been little demonstration of direct competition for food and space in soft sediments, particularly over broad spatial scales (Olafsson *et al.*, 1994; Wilson, 1991), it is unlikely that diversity will be enhanced through any reduction in resource monopolisation by dominant competitors whose populations become constrained by disturbance. Their argument is based on the premise that such monopolisation never existed in the first place. They consider that the Intermediate Disturbance Hypothesis is unlikely to apply in soft sediment communities.

13. HABITAT COMPLEXITY: POSITIVE INTERACTION AND BIOENGINEERING

Communities are not only shaped by processes repressing species or population densities, such as physical disturbance, predation and competition, but also by positive processes, usually as a result from interaction between species. Positive interaction potentially promotes species diversity, population size and density. Lawton (1994) pointed out that the very existence of some ecosystems depends on particular species. Although positive interaction is widely reported as an important factor determining the structure of communities it receives less attention than other processes such as predation or competition. However, there are some comprehensive descriptions and discussions of the subject. The journal *Ecology* published eight articles on the subject in a special feature in 1997 ('Positive Interactions in Communities', Vol 78, No 7) covering the concept of positive interaction and providing examples from both terrestrial and marine systems. Reise (1985) discussed the hierarchy of ecological processes shaping populations of tidal shores and compared positive interactions, which he called promotion, with repressive processes (Figure 13.1).

Positive interactions are mainly based on some form of bioengineering. One species actively or passively increases the three-dimensional complexity of a habitat, or transforms the physical state of a habitat, thereby creating suitable living conditions for other species, which would not otherwise have been able to occupy the site. The concept of bioengineering was established by Jones *et al.* (1994), although they called it ecosystem engineering. In marine systems few species shape entire ecosystems (e.g. corals), but most affect the habitat on a smaller spatial or temporal scale. Bioengineering could be regarded as a general term, of which ecosystem engineers represent those species with the most severe effects on the community. Most species may not be dependent on a particular bioengineer, but the relationship may develop over (evolutionary) time into an active association in the shape of commensalism or mutualism. The following paragraphs deal with bioengineering and active association, bearing in mind that there is certainly overlap between the categories.

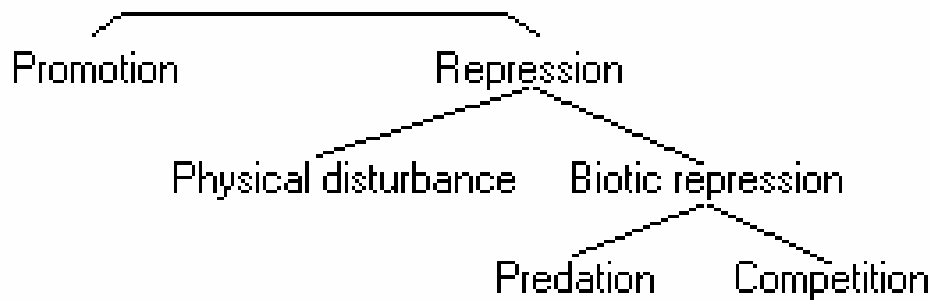


Figure 13.1. Conceptual hierarchy of ecological processes affecting population sizes of tidal flat organisms. Simplified after Reise (1985)

13.1. Bioengineering

The concept of bioengineering was comprehensively reviewed in Bell *et al.* (1991), although the term bioengineering was not used. Jones *et al.* (1994, 1997) and Lawton (1994) first coined the term 'ecosystem engineers' for species affecting the physical state of a habitat. They defined ecosystem engineers as "organisms that directly control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials" (Jones *et al.* 1997). They continue, "Physical ecosystem engineering by organisms is the physical modification, maintenance, or creation of habitats. Thus for example, crayfish *Paraneohrops zealandicus* reduce levels of fine sediment in stream beds, leading to increases in the abundance and diversity of benthic invertebrates (Usio & Townsend 2004). The ecological effects of engineers on other species occur because the physical state changes, which directly or indirectly control resources used by these other species." They suggested that ecosystem engineers have different impacts, depending on population density, spatial distribution patterns, persistence of the population at a site, and the number and types of resources that are directly or indirectly controlled. These factors also demonstrate that the spatial scales engineered can differ considerably, which in turn may affect the size of species interacting with the bioengineer, i.e. large organisms or organisms requiring greater functional space may not benefit from fine-scale engineering. Jones *et al.* (1997) differentiate allogenic engineers, transforming the environment actively (e.g. beaver, earthworm) from autogenic physical engineers, which change the environment merely by providing a physical structure, i.e. their living or dead tissue (forests, coral reefs). For the deep-water coral *Lophelia pertusa* it was shown that most associated individuals were found in dead coral blocks from the inner parts of the bank or colony, but few species were found close to the terminal branches of live coral blocks (Jensen & Frederiksen 1992).

Effects of bioengineers, including ecosystem engineers, do not necessarily have to be positive for other species. Physical state changes may destroy the ecological demands of species, which would have inhabited a site without the bioengineer. For those species the bioengineer has a negative effect. Bioengineers may also be competitors or predators of other species. However, in general it is suggested that the net effects of bioengineering will increase species richness at larger scales, encompassing engineered and non-engineered environments in ecological and evolutionary space and time (Jones *et al.* 1997). Hacker and Gaines (1997) calculated that species diversity in a New England salt marsh community increased by at least 35% as a result of positive interactions.

For a rocky shore community it was calculated that 40-50 % of change in the community could be attributed to indirect interaction (Menge 1995), and that 60% of those interactions were positive effects (Hacker & Gaines 1997).

Generally bioengineers provide an attachment surfaces (Dean 1981; Bartol *et al.* 1999; Callaway 2003), stabilise sediments (Fager 1964; Featherstone & Risk 1977; Eckman 1983; Jones & Jago 1993), ameliorate the sediment by irrigation or fertilization (Reise 1983; Jones & Jago 1993; Ragnarsson & Raffaelli 1999; Lackschwitz & Reise 1998), extend the oxygen supply into deeper layers (Forster & Graf 1995), change hydrodynamic properties (Gallagher *et al.* 1983, Qian *et al.* 1999, Friedrichs *et al.* 2000), increase local productivity (Wright & Jones 2004), or provide refuge from predation (Woodin 1978, Crowder & Cooper 1982, Lubchenco 1983, Pederson & Peterson 2002). Reise (2002) categorised the functional groups of bioengineers in coastal sediments as phototrophically generated mats and vegetation, sliming motile benthos, suspension feeder beds and reefs, dead hard parts of the benthos, burrow builders, infauna reworking and irrigating the sediment and visiting disturbers reworking the sediment. These categories broadly cover the wider marine environment, although phototrophic bioengineers probably play a minor role in sub-littoral areas, while epibenthic sessile animals structuring the habitat immediately above the seafloor play a greater role as bioengineers. Bioengineers do not necessarily shape the habitat for a particular suit of species. Comparisons between banks *Lophelia pertusa* from the Faeroe shelf, Norway and the Bay of Biscay showed very little overlap in the associated species (Jensen & Frederiksen 1992). They concluded that a highly diverse and rich but facultative fauna is associated with the *Lophelia* banks.

13.2. Active Association

Positive, active associations can benefit both partners, called mutualism (+,+), or benefit one partner while the other is unaffected (0,+; commensalism). Begon, Harper & Townsend (1990) devote a whole chapter to mutualism and give many examples of terrestrial as well as marine species. The relationships can be facultative, where partners benefit from the link but are not dependent on each other or they can be obligate for one or both partners. Positive associations are often based on improved access to food and improved shelter or protection from predation for the partners. Commensals, as the name suggests, help themselves to food provided by the partner, without harming the associate apart from reducing its provisions. For example *Pinnotheres* spp. (pea crabs) can be found inside mussels and ascidians, feeding on the mucus bound plankton strand produced by the filter feeders. Although pea crabs appear to be dependent on the host for food, they are not necessarily dependent on one species alone. *Pinnotheres pisum*, for example, can be found in *Mytilus edulis*, *Modiolus modiolus* or *Tapes decussatus*. Several species of hermit crabs provide examples of mutually beneficial associations with sessile species. Colonies of *Epizoanthus papillosus* and the sponge *Suberites pagurorum* can be associated with *Anapagurus laevis*. The hydroid *Hydractinia echinata* colonises the gastropod shell inhabited by *Pagurus bernhardus* and the actinia *Adamsia carciniopados* embraces and overlaps the shell of *Pagurus prideaux*. The sessile associates of the hermit crabs all benefit from having an attachment surface in an environment poor in terms of hard substratum, unhindered access to food and no risk of being smothered. The hermit crabs benefit from extra protection and most importantly from the ability of the associates to extend the housing shell, allowing them to stay longer in one gastropod shell while growing and thereby avoiding the dangerous process of changing house.

In one interesting study, a strongly competitive interaction that would quickly have resulted in the competitive exclusion of one species, was simultaneously ameliorated by a mutualistic interaction. Two competitive damselfishes, the three spot dascyllus (*Dascyllus trimaculatus*) and the orange-fin anemone fish (*Amphiprion chrysopterus*) compete for shelter on the sea anemone (*Heteractis*

magnifica). The anemone fish is the dominant competitor and quickly depresses the density of three spot dascyllus on anemones. This interaction is sufficient that in the absence of other factors, three spot dascyllus would be quickly irradiated from the reef. However, anemone fish stimulate an increase in the size of anemones, with the result that there is sufficient of this resource to maintain three spot dascyllus populations. This indirect mutualism negates much of the impact of the competitive interaction (Holbrook & Schmitt 2004).

The borderline between active association and bioengineering is not always clear-cut. Peterson & Heck (2001) found that mussels (*Modiolus americanus*) present in a seagrass meadow (*Thalassia testudinum*) elevated seagrass production through either increased nutrient resource pool or reduced epiphytic loads on the leaves, while the seagrass increased survivorship. They call the positive interaction 'facultative mutualism', but it could also be argued that both species merely modified the abiotic environment, which happen to facilitate conditions for each other. Hence they could be described as two bioengineers.

13.3. Positive Interaction in Huston's (1994) Dynamic Equilibrium Model

Hacker and Gaines (1997) consider the effect of positive interaction in relation to varying rates of competitive displacement and mortality due to physical disturbance, stress or predation. They place keystone facilitators (equivalent to bioengineers & mutualists) into Huston's dynamic equilibrium model, suggesting that they are most important in situations of high mortality but low rates of competitive displacement (Figure 13.3.1). An example by Bertness & Leonard (1997) supports this concept. They found that in the environmentally stressful upper intertidal rocky shore the limits of dominant sessile species were strongly influenced by positive interaction between species.

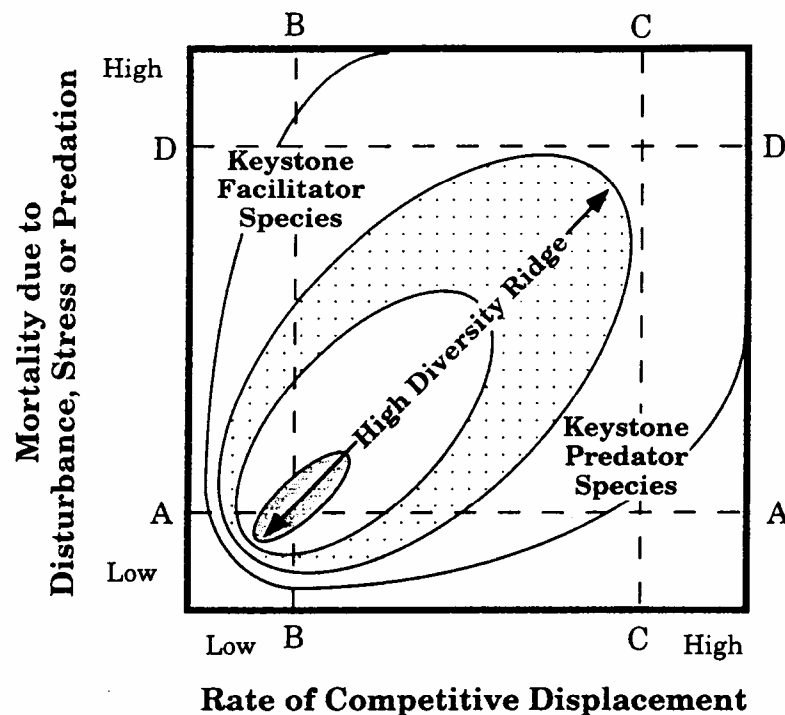


Figure 13.3.1. After Hacker & Gaines (1997). Modified diagram of the 'dynamic equilibrium model' proposed by Huston (1979, 1994), in which it is predicted that keystone predators are most important under high rates of competitive displacement and low rates of physical disturbance and stress. In contrast, keystone facilitator species are most important under low competitive displacement but high disturbance, stress, or predation.

14. BENTHIC INVERTEBRATE COMMUNITY STRUCTURE

14.1. Succession in Benthic Invertebrate Communities

Rhoads & Boyer (1982) describe the relationship between benthic animals and the sediments they inhabit. Early definitions of benthic communities were centred round characterising species and 'steady-state' systems (Peterson 1913; Thorson 1957). A more ecologically realistic concept was proposed by Johnson (1971, 1972), who suggested that a benthic community is a temporal and spatial mosaic, "parts of which are at different levels of succession...in this view the community is a collection of relics of former disasters." This successional perspective has its origin in plant ecology as popularised by Clements (1916). It can also be described to be a mosaic that reflects the disturbance history and organisms' response (Huston 1994). Subsequent experimental and field work by McCall (1977), Myers (1977a,b), Pearson and Rosenberg (1978), Rhoads *et al.* (1977), Wolff *et al.* (1977), Santos & Bloom (1980), and Santos & Simon (1980), helped to define the taxonomic and functional structure of these "temporal mosaics".

14.1.1. Pioneer communities

Rhoads & Boyer (1982) describe the pioneering stages of successional communities. Control of the development of such communities is related directly to intensity and frequency of disturbance (Osman & Whitlatch 1978). There are also quantitative estimates of densities of communities and qualitative descriptions of the characterising communities at particular times in a successional development. This again may help in developing models of productivity. For example, Rhoads & Boyer (1982) quote densities of around $10^5/\text{m}^2$ small, opportunistic, tube-dwelling polychaetes in pioneer communities. They also describe tubicolous amphipods appearing shortly after the polychaete acme. Pioneer communities are limited to the near-surface region of the bottom (<2cm) and they are made up of dense tube aggregations of organisms feeding on surface deposits or in suspension. The surface of the seafloor is covered with faecal pellets.

Most pioneering species are described to feed near the surface of the sediment, or directly from the water column. They are also frequently described as r-selected species (McCall 1977; Rhoads *et al.* 1978). There are however problems with the simplistic r/k strategists role in the successional framework. Vermeij (1978) points out that the full range of possible adaptive strategies are not covered, as there should also be a classification for a 3rd end member called stress-tolerant. These species predominantly inhabit physiologically stressful areas such as the intertidal zone. It's also possible that in frequently trawled areas such tolerant species, rather than just pioneer communities, will dominate communities.

14.1.2. Equilibrium stages

High-order successional stages are unlikely to be found in areas of relatively frequent disturbance. They are only found where major physical disturbances rarely occur. This point does however emphasise the need to consider hydrographic factors in any model considering disturbance. Even in areas of very low trawling effort, for example, you may find communities in pioneer stages due to other forms of physical disturbance such as frequent intense storms (Hall 1994). Brey (1991) does however point out that hydrodynamic disturbance to benthic communities is really only likely to occur in shallow seas.

Rhoads & Boyer (1982) describe late successional stages dominated by infaunal deposit feeders, many of which are represented by “head-down” conveyor belt feeders (*sensu* Rhoads 1974). Some of these species are tubicolous, but many are free-living. Rhoads & Boyer (1982) describe equilibrium assemblages that are associated with a deeply oxygenated sediment surface, where the redox boundary commonly reaches depths of 10cm. Feeding is concentrated along the redox boundary and this zone has also been described to be a region of high micro-organism productivity (Yingst & Rhoads 1980). Pioneering species are often excluded from late successional and equilibrium communities by competitive exclusion mechanisms, such as trophic group amensalism (Rhoads & Young 1970).

Importantly, in some cases it is believed that pioneer and equilibrium species may coexist in the same sediment, namely where physical disturbance is very shallow. This emphasises the importance of knowing how deeply the trawl penetrates and that this may be a factor in allowances related to different types of gear use.

14.2. Soft Sediment Benthic Invertebrate Diversity

About 70% of the earth’s seafloor is composed of marine soft sediments (Wilson 1991; Snelgrove 1999). Although these habitats do not always appear as highly structured as some terrestrial or marine reef habitats, they do support extremely high species diversity (Etter & Grassle 1992; Grassle & Maciolek 1992; Coleman *et al.* 1997; Gray *et al.* 1997; Snelgrove 1999). Marine soft sediments are often considered to be vast homogeneous expanses of mud or sand. However, small biogenic structures are common in such regions and these provide small scale habitat heterogeneity that is very important in maintaining diversity (Hewitt *et al.* 2005). Pen shells (*Attrina rigida*) help to develop rich communities of both sessile and motile benthic invertebrates (Mungia 2004).

Spatial and temporal heterogeneity in community structure of soft-sediment systems are related to the spatial extent and/or frequency of disturbance events; for disturbance to create patchiness it must be small relative to the colonisation potential of the benthic community, but not so small as to enable the adjacent assemblage to quickly infill the disturbed patch (Thrush & Dayton 2002). Turner *et al.* (1993) encapsulate this concept in a simple ratio-based model of the effect of disturbance on landscapes. The ratio of disturbance interval (time between events) to recovery time determines the temporal dimension, while the ratio of the size of the disturbed area, to size of habitat determines the spatial dimension. Significant threats to the integrity and resilience of marine benthic communities will arise when the rate of human-induced change exceeds the rate at which nature can respond (Thrush & Dayton 2002). It is suggested that this scenario is particularly likely to occur where habitat structure and heterogeneity are reduced and where large areas of habitat have been modified.

Colonisation of patches following disturbance is influenced by the “type” of patch involved (Watling & Norse 1998). Type I patches are those surrounded by undisturbed communities and are colonised both from the perimeter and by dispersed propagules. Type II patches are undisturbed patches, surrounded by larger areas of disturbed communities. Type II patches are the source of colonisers, especially over short distances. Recolonisation of patches is likely to be affected by seasonality and by community composition of surrounding patch communities. For example, some components of benthic ecosystems, including amphipods, isopods and other small crustaceans do not have planktonic larvae and thus dispersal by such groups will be slow. Further to this, of those taxa that do have planktonic larvae, production of propagules is often seasonal, certainly in temperate systems, and so disturbed systems may be subject to delay in colonisation dependent on the season

14.3. Trophic Cascades

Selectivity by fish feeding on benthic invertebrates, particularly size-selective predators, can be an important factor in determining benthic community structure (Newman & Waters 1984). In the Gulf of Maine, the removal of top fish predators through intensive fishing has apparently released other predators such as crabs and starfish, thus changing the benthic communities (Whitman & Sebens 1992; Thrush & Dayton 2002). The creation of marine reserves often results in increased densities of fish and invertebrate predators, raising predation pressure on adjacent invertebrate communities, altering the composition and structure of these communities (Langloise *et al* 2005; Guidetti, 2006). Changes in fish biomass in the North Sea, with consequential changes in predation pressure on benthic invertebrate prey, were associated with changes in the overall taxonomic composition of the benthos (Frid *et al.* 1999). In drawing such conclusions, however, one should always bear in mind the inherent difficulties involved in tracking effects through marine food webs. There is therefore a potential risk of attributing actual cause and effect situations to what are in effect only inferred relationships.

14.3.1. Food web theory and marine ecosystems

Several food web metrics can provide insight into the dynamics of biomass partitioning and production in an ecosystem (Link 2002; e.g. May 1973; Pimm 1982; Cohen *et al.* 1990). Link (2002) suggests that species richness S and the number of species interactions or links can be particularly useful, especially as many other metrics can then be derived from them. However, their use must be validated against certain uncertainties. These include the usefulness of reporting topological web statistics or the validity from which the data were derived (e.g. Polis 1991; Hall & Raffaelli 1993; Warren 1994; Winemiller & Polis 1996) and the effects of spatial, temporal and taxonomic resolution on detecting S and linkage L (e.g. Hall & Raffaelli 1991 1993; Martinez 1993; Goldwasser & Roughgarden 1997; Solow & Beet 1998; Martinez *et al.* 1999).

14.3.2. Connectance & species richness

There is contradiction in the hypotheses that describe the relationship between connectivity C and S . Some argue that an increasing S will cause connectivity to hyperbolically decline (Cohen & Newman 1988; Winemiller 1990; Martinez 1992; Hall & Raffaelli 1993; Warren 1994). Link (2002) argues that this is true with changes in the level of taxonomic, spatial or temporal aggregation in a single web or across webs with different numbers of species. An implication from this relationship is that another inference derived from S , L and C is an assessment of system Lyapunov stability (May 1973; Pimm 1982; DeAngelis 1992), where Lyapunov stability relates to local, or neighbourhood, equilibria (e.g. a ball on top of hill; it is not locally stable if perturbed). There is disagreement whether higher C increases, decreases, or has alternating effects on overall stability, regardless of whether we are even solving for or assuming equilibrium conditions (Link 2002).

Much of the work on food webs has been derived from freshwater or terrestrial systems (Link 2002). Link (2002) constructed a food web for the Northeast US shelf ecosystem based primarily upon stomach content evaluation. When examining the number of linkages and number of species across a time series of 2, 3 and 5-year time blocks, he found no change in species number and a 1 to 2% decline in L . A similar exercise for different spatial components of the ecosystem resulted in a similar response, primarily lowering the number of species in any given region by 2 to 5%. Link gives methods for calculating connectivity and stability.

The number of species has tended to increase in recent (post 1990s) food web work on the same systems (Link 2002). This may reflect the higher levels of taxonomic resolution now available for

diet data etc. The allocation of species across trophic levels was similar to most other food webs, with the intermediate species (non-basal & non-top predator (– less than 2 predators)), generally comprising at least 50% of all species. There are still problems however with the poor treatment of lower trophic levels, although Link's web does include 33 invertebrate groups.

The mean number of interactions per species was of a linkage density of 19.3, confirming that these systems are highly connected food webs. Link (2002) suggests that only the studies of Martinez (1991) and Reagan *et al.* (1996) of tropical lakes and tropical rain forest, respectively, exhibit similar magnitudes of linkage density. Link suggests that these high linkage levels (>5) are associated generally with tropical or neotropical ecosystems, and so the North Sea system may show much lower densities of linkage. The US Northeast Shelf ecosystem is a system where biogeographical provinces, ranging from boreal to temperate to sub-tropical, converge to produce high species richness (Sherman *et al.* 1996). Link suggests that the high number of species contribute to the high linkage density observed in the ecosystem. So species are broadening their resource utilisation rather than decreasing niche breadth as competition increases.

There is evidence that generalist, omnivorous predators are also more common than previously thought. Two major points arise from the high connectivity observed for the Link food web; (1) there are a lot of generalists; and (2) there is a high degree of omnivory for these component organisms. Some interesting questions thus arise regarding differences between marine and freshwater/terrestrial systems. Notably, are organisms in marine systems more generalist and omnivorous, especially since systems with more specialists tend to have lower connectance? Or are these observations the result of the high sampling intensity and long duration of this and more recent studies?

14.3.3. The uniqueness of marine food webs & implications for stability

Link's (2002) foodweb is extraordinary considering the relationship normally observed between connectivity and species richness. Most large food webs ($S > 40$) have a connectance of around 10%. Link provides credible reasons why this contentious result is not merely an artefact. He suggests that the openness of marine ecosystems and the orders of magnitude in size across the ontogeny of the organisms involved both contribute to this result. In fact given that the data do not fully cover the entire size range and trophic levels across the life history of the animals, it is feasible that including egg, larval and juvenile interactions would increase the connectivity even more. Link therefore concludes that it is likely that marine ecosystems are inherently very different to terrestrial or freshwater ecosystems for the (cf. Steele 1985).

These findings could have real implications on the value of competitive exclusion in marine systems. Given the high dietary overlap and generalist feeding nature of these organisms, plus the well documented diet switching of the organisms in these systems (Sissenwine *et al.* 1982; Garrison 2000; Garrison & Link 2000; Overholtz *et al.* 2000, Link & Garrison 2002b), it appears that no one organism is highly and directly dependent on, nor highly and directly impacted by, populations of another species. Link is less sure of the implications of this loose connectivity on system stability. For a system as complex as this to persist, overall interaction strengths must be extremely low (McCann *et al.* 1998).

15. 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 (Eccard & Ylönen (2003). 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). For populations with multiple age (size) cohorts interactions between cohorts may be an important source of density dependence. Such interactions may be especially intense because of the differences in body-size that give rise to disparity in competitive ability and potential for trophic interaction. In the planktivorous fairy basslet (*Grama loreto*), juvenile mortality increases as a function of adult density. As density increased, predators tended to aggregate around fairy basslet shoals (Webster 2003). Juveniles tended to feed around the edges of such shoals, where they were more vulnerable to predator attack (Webster 2004). As a consequence of all these possible processes, 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).

Even in terrestrial systems, for example small mammal communities in North America, body size plays a major role in community structure and dynamics (Ernest 2005). Predator size is an

important factor in determining community structure (Cohen 1978; Williams & Martinez 2000). The size of prey that predators of a given body size can take determines food web structure (Warren 1996). Studies of the Ythan Estuary food web model demonstrated that predator-prey size relationships were important in determining the stability of the food web model (Emmerson & Raffaelli 2004). Large predators do not necessarily specialise on large prey, rather their maximum size of prey taken tends to increase so that larger predators take a wider range of prey sizes (Radloff & Du Toit 2004). In fish communities, variation in predator and prey size need not be tightly linked to trophic level, prey of a wide range in size may all be at the same trophic level, resulting in a wide range of different predator body sizes all being located at the same trophic level, one level higher than their prey (Layman *et al* 2005). Because of the importance of body-size as a determinant of community dynamics in marine communities characterised by non-deterministic growth, variation in growth rates can have a major influence on community structuring processes. Both top down and bottom up processes are likely to be affected. Early-hatched fast growing large-mouth bass switch to piscivory as much as a year earlier than their slower growing con-specifics in the same age cohort. After the switch, piscivores grow at twice the rate than non-piscivores (Post 2003). Variable environmental conditions leading to variation in resource levels can actually stimulate faster growth rates in juvenile hybrid striped bass than constant environmental conditions with more constant higher levels of resources (Skalski *et al* 2005).

In addition, models such as the dynamic equilibrium model, and indeed much of the theory relating to the mechanisms believed to structure communities, assume Lotka-Volterra 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 (section 7.10.9). 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; Daly 1972; 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 15.1). In the example illustrated in Figure 15.1, 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. This argument as to how the “storage” model might operate in fish populations assumes that reproductive potential is tightly and linearly linked to individual fecundity, but some caution is needed here. Many fish are broadcast spawners, and as density decreases, fertilisation efficiency may also decline, giving rise to an Allee effect – reproductive capacity might decline more rapidly than density. This could result in the abrupt emergence of severe stock-recruit relationships and negate much of the benefit gained from the “storage” effect.

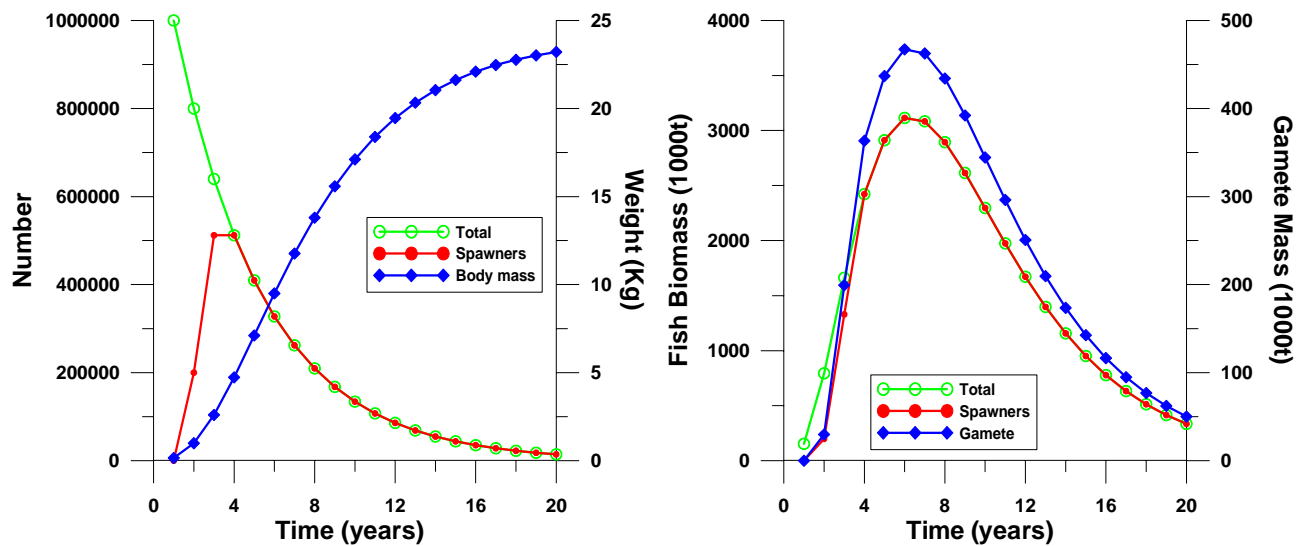


Figure 15.1. Illustration of the “storage” model based on life-history characteristics of a cohort of cod. Growth in length is driven by the von Bertalanffy growth function with $L_{\infty}=123.1$ and $K=0.230$. Conversion to weight assumes values of $c=0.0051$ and $b=3.192$ in the weight at length power 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.

16. AN ALTERNATIVE SIZE-STRUCTURED SPECIES-INTERACTIVE MODEL

Figure 16.1 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 Length_{∞} 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.

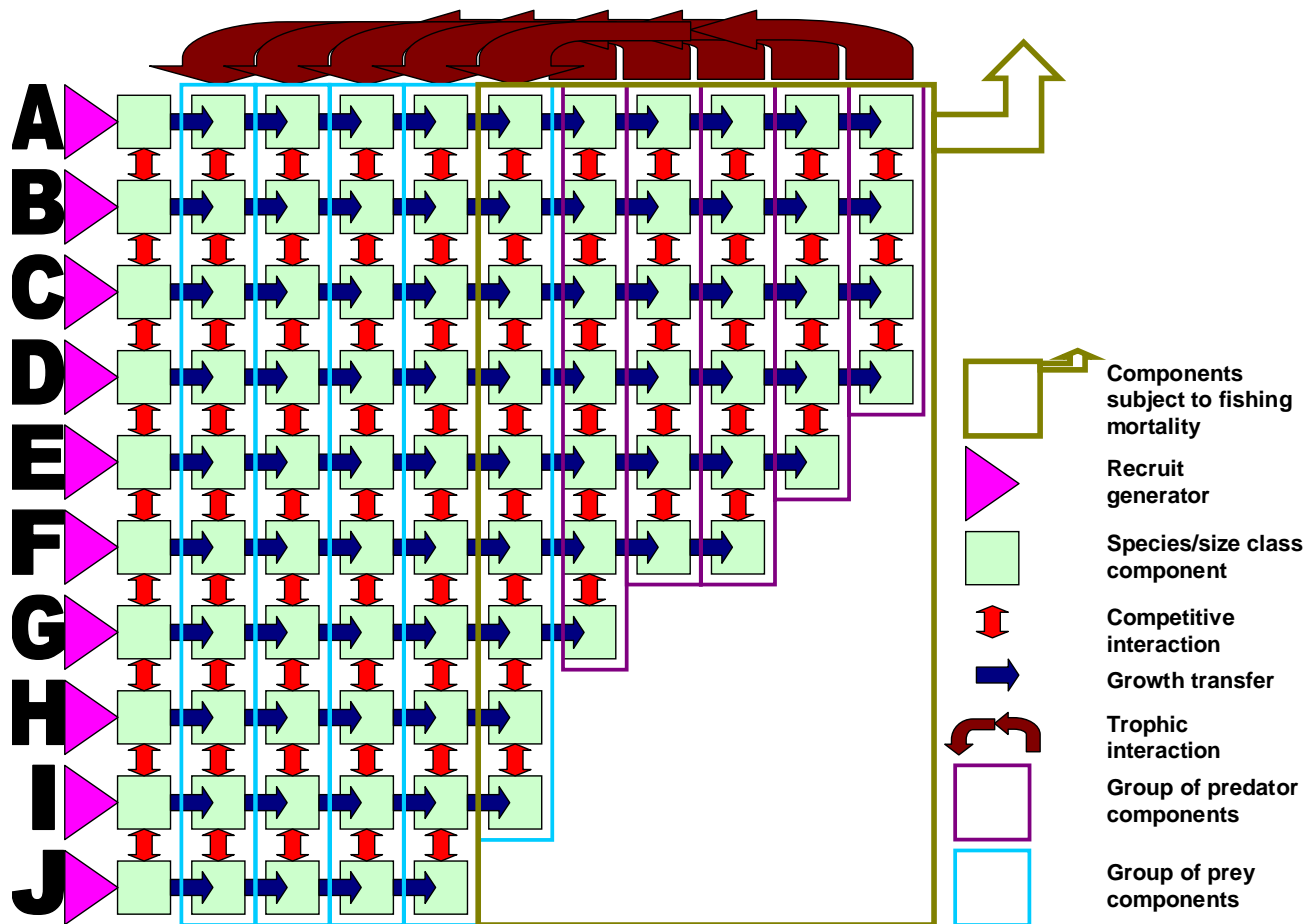


Figure 16.1. Proposed form for a size-structured species-interactive model to simulate the effect of fishing disturbance on the relative abundance of species with differing life-history characteristics.

To model top-down predatory forces, specific predator mass – prey mass ratios would be assumed (e.g. 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 $0.3\% \text{bw} \cdot \text{day}^{-1}$, 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 (Greenstreet & 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.

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