

**Spatial self-organising as an important determinant of
community dynamics in a temperate marine epibenthic
community**

by

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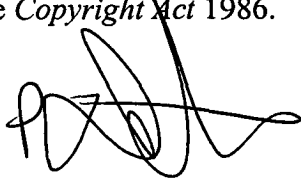
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DECLARATION

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A handwritten signature in black ink, appearing to read 'Piers K. Dunstan', with a stylized, cursive script.

Piers K. Dunstan

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Abstract

Despite widespread acceptance of the spatial structure of ecosystems and the spatial nature of processes acting within them, critical tests of the importance of spatial phenomena to the structure and dynamics of ecosystems have not been forthcoming. In most marine epibenthic communities, the single limiting resource is space. Here I investigate the spatial dynamics of an epibenthic community in a shallow subtidal system in Tasmania and a spatial model of this community to examine how spatial process influences invasion resistance, stability, interactions among species and the growth rates of individuals.

In Chapter 2 I examine the relationship between invasion resistance and species richness in the natural community. The rate of invasion increases with local species richness by two distinct mechanisms. Opportunistic colonisers invade species rich patches at higher rates because speciose patches are dominated by small colonies and mortality rates of small colonies are greater than that of large ones. Thus, mortality provides bare space for opportunists to colonise more frequently in speciose patches. However, some species avoid colonising free space but preferentially associate with established colonies of particular other species. In this case, a given preferred associate is more likely to occur in more species rich patches, and so colonisation rates are greater in more speciose patches.

In Chapter 3 the importance of spatial context on the outcomes of pair-wise species interactions and neighbour-specific growth rates is examined. The outcomes of competitive (overgrowth) interactions among species and neighbour-specific growth rates in experimentally contrived pair-wise interactions are often dissimilar to their counterparts in the non-manipulated natural community. I use a spatial model

and its non-spatial equivalent to demonstrate that these differences in outcomes and growth significantly affect predicted community dynamics.

In Chapter 4 I develop a spatial simulation model parameterised by empirical observations of the recruitment, growth, interaction outcomes and mortality of the natural community. I compare the model dynamics to the dynamics of manipulated and non-manipulated natural communities. The model self-organises to form distinct colonies and adequately captures many features of the short-term dynamics of manipulated communities observed over a 16 month period, although some model behaviours are not reflected in the natural community. When compared to the longer-term dynamics of the non-manipulated communities (*ca.* 12 years), the model accurately predicts the species evenness, diversity, size structure and multivariate variance of these communities. None of these emergent features is evident from equivalent non-spatial (mean field) models.

In Chapter 5 I use the model developed and tested in chapter 3 to examine the relationships between species richness, area, persistence stability of total cover, resilience stability and invasion resistance. Communities occupying small areas are less stable and less resilient than those in larger areas. While richness is positively correlated with persistence stability in small landscapes ($<900 \text{ cm}^2$), in larger landscapes richness is negatively correlated with stability. Moreover, the stability of landscapes is a strong determinant of invasibility. Thus, in landscapes $\geq 900 \text{ cm}^2$ the number of invasions increased with species richness. The underlying mechanisms are emergent in the model and are the same as shown in Chapter 1. None of these features arise in equivalent mean field models.

In conclusion, marine epibenthic communities have strong spatial dynamics and processes. These can be represented accurately by spatial models which self-organise

to form colonies. The dynamics of these models and of the natural communities are contrary to much of established ecological theory. For example, the relationships between richness and persistence stability, and between richness and invasion resistance, depend on patch size, largely because patch size determines the extent of spatial self-organising. For large patches ($\geq 900 \text{ cm}^2$) of a given size, both persistence stability and invasion resistance decrease with species richness. This is an important demonstration that community level properties such as stability and invasion resistance are determined by the properties of the component species and the emergent dynamics of each particular community, and are not an intrinsic function of richness or any other aggregate property.

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Chapter 1: General Introduction

While the importance of spatial context in regulating the dynamics of ecological systems is widely acknowledged, there have been few attempts to determine under what conditions, and exactly how spatial processes act to determine the dynamics of particular systems. Many biotic processes that act to 'organise' a community tend to act over limited distances because individuals are more likely to interact with others in their local neighbourhood than with individuals from afar. Thus, in systems where biotic processes dominate, individuals on a spatial landscape (either actual or virtual) will interact largely with their immediate neighbours. The maximum number of possible interactions for a particular species sets the limit to its neighbourhood size. In this way, the influence on individuals removed from the local neighbourhood will be limited to sequential interactions of multiple neighbours. For a particular species, multiple neighbourhoods are possible, particularly where a species interacts in several different ways. For example, while physical interactions occur over short distances, dispersal and recruitment can extend the influence of an individual over very large distances through the production of new colonies. In the absence of abiotic processes (that can act over larger distances) or long distance biotic processes (e.g. chemical signals) the only structuring forces will occur locally at the scale of the individual.

A neighbourhood view of organisation has its roots in the science of complexity, originated by Alan Turing and John von Neumann. von Neuman described the first self-reproducing automaton (cellular automata) to simulate biological processes. Cellular automata belong to a class of models where individuals are simulated explicitly and the individual components (e.g. individual cells, animals

or zooids) are arranged in a grid on a landscape. Each cell interacts with only its nearest neighbours (its neighbourhood), as defined by the rules for the simulation. An algorithm that accounts for the states of a central cell and its neighbours determines the outcomes of interactions, and algorithms can be developed to approximate neighbourhood biotic processes. The neighbourhood can be structured as either the four adjacent cells to the central cell (von Neumann neighbourhood), eight adjacent cells (Moore neighbourhood) or six adjacent cells arranged in a hexagonal lattice. In most cases, the choice of neighbourhood structure does not influence the qualitative nature of the systems (Durrett and Levin 1994a). The interaction between many individual components at a local scale can generate complex patterns that emerge at a larger scale (Wolfram 1984). As there are no meso-scale rules that define the dynamics of emergent meso-scale structures, the systems are considered to be self-organising. When the tendency for self-organisation is strong, these systems are characterised by strong intra and inter-specific correlations between adjacent cells. Depending on the rules, these models display a wide range of behaviours ranging from static large-scale structures to unpredictable chaotic dynamics. Cellular automata have been used to describe a wide range of biological and physical systems, including grassland communities (Silvertown *et al.* 1992), marine epibenthic communities (Burrows and Hawkins 1998, Karlson and Buss 1984, Karlson and Jackson 1981), chemical reaction-diffusion systems (Madore and Freedman 1983) and generalised Ising models (Domany and Kinzel 1984).

A neighbourhood model of community interactions contrasts with the more common numerical approach in most ecological models (e.g. Haydon 2000, Hughes and Roughgarden 2000, May 1972, 1974, Pimm 1979, Lehman and Tilman 2000). Numerical models have two implicit assumptions. First, in these models the strengths

of interactions are directly proportional to the abundances of each species and consequently species abundances are essentially smeared over the landscape. In this case, the neighbourhood of a species is potentially infinite, there are no spatial refuges, and any two interacting species interact at all times. For this reason these models are referred to as 'mean-field' approximations. Second, individuals do not exist per se and populations can become infinitely small without going extinct. Consequently, species abundances and the carrying capacity of the ecosystem can be scaled to any size and, by definition, the dynamics are independent of scale. While these assumptions may be appropriate for some physical systems (although even here they must break down at some point), they cannot be justified in an ecological context other than as gross generalisations. The most cursory examination of an ecosystem reveals that these assumptions are not often satisfied, individuals are not randomly arranged across a spatial landscape, species abundances cannot be expressed as a fraction of an individual, and scale and patch size invariably influence community dynamics. Mean-field models can only approximate community dynamics if individuals are homogenised across a sufficiently large (in theory, an infinitely large) patch size. In the same way, spatial models can simulate mean-field models if the positions of individuals on a large landscape are randomised between each successive iteration of the model.

Although spatial models may be more relevant than mean-field models to empirical ecologists, they still lack the credibility of empirically tested predictive models (Smith 2000). To date, there have been no empirical tests to validate spatial models and very few validations of mean-field models (i.e. Fussmann *et al.* 2000, Wootton 2001), despite nearly a century of their use in ecology. Ecological models are difficult to test against natural systems due to the long time span of ecological

dynamics and the number of possible variables involved. Consequently, predictions of the models constructed to simulate communities are often beyond the ability of empirical ecologists to test within an appropriate time scale.

If we are to achieve the next step and develop validated models, an appropriate starting point is not to model complex systems with simple models but rather to attempt to model a simple community with the most parsimonious models. A suitable 'model' community would be characterised by simple interactions and demographics, and consequently be modelled with a relatively simple rule structure; in essence a mesocosm in the real world. At least in the first instance we need to include spatial context into our models to validate them. It may then be possible to generalise the validated spatial models into numerical models although this may not be necessary or possible. All we need from the models is the ability to make predictions that can be tested against the dynamics of natural communities. Once the models are validated it will be possible to extrapolate the conditions and test theories in ecology.

A model community

What are the characteristics of an ideal model community? First, it must be possible to generate appropriate models of the communities, therefore the communities must be easy to census. Individuals must be discrete and the outcomes of interactions between them must be obvious. This allows the generation of appropriate algorithms and neighbourhood structures. The processes acting on species (e.g. interspecific interactions, growth, recruitment and mortality) must be measurable to facilitate parameterisation of the algorithms. Second, the communities must be reasonably easy to manipulate so that models can be tested and we have some idea of the starting conditions of the communities.

Colonial sessile marine invertebrate communities meet both of these criteria.

First, the whole colony is visible, making census easy. Interactions for space are clearly visible, and no part of the colony is hidden, making measurement and parameterisation easy. Competition is primarily for space (Barnes and Dick 2000, Buss and Jackson 1979, Jackson and Buss 1975, Lopez Gappa 1989, Nandakumar *et al.* 1993, Rubin 1982, Sebens 1986) and the outcomes of spatial interaction can be measured with sufficient precision to generate algorithms. Although some species may compete for food (Buss 1979, Buss 1990, Okamura 1992) or through chemical interactions (Jackson and Buss 1975), the manifestation of these unseen interactions is expressed in the outcomes of visible interactions in space. It is also possible to design algorithms that simulate both recruitment and mortality in these communities.

Previous studies have found a wide range of possible mortality regimes, either partial (Hughes and Jackson 1980, Jackson 1977, 1979) or total mortality (Hughes 1990) of colonies and it is possible to design rules that simulate either possibility. Recruitment can be simulated simply as a rate per unit area or as more complex fine scale species-specific recruitment events such as induction (Hurlbut 1991, Keough and Downes 1982) or suppression (Grosberg 1981, Osman and Whitlatch 1995).

Second, colonies of sessile invertebrates can be transplanted and arranged into specific patterns (e.g. Stachowicz *et al.* 1999) to allow testing of models. Although survival of each transplanted colony is not assured, sufficient numbers can be manipulated to cover any losses. The initial conditions of natural communities on anthropogenic structures (e.g. jetties) can be assumed to be bare space, and in these cases it is usually possible to estimate the age of the communities.

Implications of self-organisation in a sessile marine invertebrate community

Because spatial models often yield quantitatively different results to mean-field models, it is likely that inclusion of spatial context in models may yield behaviours that differ from those predicted by theory based on non-spatial models. All the models designed to examine relationships between the persistence stability of communities and diversity (or more accurately species richness) have been non-spatial (e.g. Doak *et al.* 1998, Haydon 2000, Hughes and Roughgarden 2000, Lehman and Tilman 2000, May 1972, 1974, Pimm 1979, Tilman 1999) and more recent models, designed to be stable, have found that species richness is positively linked to stability. The results of empirical studies have tended to agree with these models (e.g. Frank and McNaughton 1991, Hector *et al.* 1999, McNaughton 1977, 1985, Tilman 1996, 1999, Tilman and Downing 1994), although there are exceptions (Silvertown *et al.* 1994). However, important objections to the design and analysis of these experiments have been raised (Cottingham *et al.* 2001, Givnish 1994, Huston 1997, Huston *et al.* 2000, Wardle 1998). Similarly, models linking richness and invasion resistance have been non-spatial (e.g. Case 1990, 1991, Law and Morton 1996) and have identified a positive relationship between invasion resistance and richness. While empirical studies show both positive (e.g. McGrady-Steed *et al.* 1997, Stachowicz *et al.* 1999, Symstad 2000, Tilman 1997) and negative (e.g. Robinson *et al.* 1995, Wiser *et al.* 1998) trends between richness and invasion resistance, the consensus view supports a weak positive relationship between the two (Levine and D'Antonio 1999), in keeping with Elton's (1958) initial suggestions. However, many modelling and empirical studies can be criticised as being insensitive to the effects of scale and patch size. Early theoretical studies suggested that patch size influences invasion rate (MacArthur and Wilson 1964, 1967). The few studies of invasion

dynamics that have considered different scales of observation have found both positive and negative relationships depending on the scale of the experiment (Levine 2000, Stohlgren *et al.* 1999).

If communities self-organise then structures emerge at a scale larger than the most basic unit and may not be randomly distributed across the landscape. In the case of cellular models of sessile marine invertebrate communities, the system self-organises to form multicellular colonies, and colonies may also self-organise to form higher order structures at a larger spatial scale (Johnson 1997). Colonies will be evident as positive spatial correlations between adjacent cells of the same species. Meso-scale organised (i.e. non-random) structures comprised of many species will be evident as positive interspecific correlations between adjacent cells. These structures are the result of the synergistic interaction between neighbourhood rules, the network of interactions between species, and the demography of colonies for particular species. If self-organisation is an important determinant of community dynamics in sessile marine invertebrate communities we would expect that both the formation of colonies and non-random associations between colonies would affect the dynamics, stability and invasion resistance of communities.

In this thesis I develop and validate spatial models of a sessile marine invertebrate community and examine the dynamics of the community across a range of possible conditions. The objective is to use a validated a model to study community dynamics over spatial and temporal scales that are not normally accessible to ecologists.

In chapter 2, I explore the relationship between species richness and invasion resistance in the natural community. I show that the mechanisms that generate these patterns are related to the spatial context of the community. In chapter 3, I examine

the effect of spatial context on pair-wise interaction outcomes and neighbour-specific growth rates. I demonstrate that simple and complex spatial contexts yield dissimilar outcomes for given interspecific interactions and that impacts on the dynamics of model communities. In chapter 4, I develop a spatial model to simulate the natural sessile marine invertebrate community and test this model against manipulated and non-manipulated communities. In chapter 5, I use the model developed in chapter 4 to examine the links between persistence stability, resilience stability, invasion resistance and landscape size.

Chapter 2: Invasion rates increase with species richness in a marine epibenthic community by two mechanisms.

ABSTRACT

It is widely held that the likelihood of species invading established assemblages decreases with increasing species richness of the recipient community. We found that invasions of a community of sessile marine invertebrates increase with local species richness by two distinct mechanisms. In the first, opportunistic colonizers with traits of typical invasive species colonize species rich patches at higher rates because speciose patches are dominated by small colonies and mortality rates of small colonies is greater than that of large ones. Thus, mortality provides bare space for opportunists to colonize more frequently in species rich patches. In the second, some species avoid colonizing free space but preferentially associate with established colonies of particular other species, and a given preferred associate is more likely to occur in species rich patches. These patterns are the result of particular properties of individual species and local species dynamics, and show that reduced risk of invasion is not an intrinsic property of species rich communities.

INTRODUCTION

With increasing numbers of invasions of exotic species worldwide and significant concomitant impacts on community structure and dynamics (eg Carlton and Geller 1993, Parker *et al.* 1999, Ricciardi *et al.* 1997), it is important to understand how the properties of communities determine their vulnerability to

invasion. Elton's (Elton 1958) hypothesis that resistance to invasion increases with species richness approaches the axiomatic (Levine and D'Antonio 1999) and is supported by several theoretical and empirical studies. Observation and manipulation of grassland (e.g. Prieur-Richard *et al.* 2000, Symstad 2000, Tilman 1997), marine invertebrate (Stachowicz *et al.* 1999) and mesocosm (McGrady-Steed *et al.* 1997) communities has demonstrated decreased likelihood of invasion with increasing richness. Similarly, non-spatial models also indicate a negative relationship between invasion success and local species richness (Law and Morton 1996, Case 1990, Case 1991), and they have emphasized that invasions may be influenced more by global properties of the recipient community, such as species richness, than the biology of the invading species (Case 1990, Case 1991). In contrast, a small body of experiments with natural assemblages in grassland and riparian communities show that invasibility may increase with local richness (Levine 2000, Planty-Tabacchi 1996, Robinson *et al.* 1996, Stohlgren *et al.* 1999, Wiser *et al.* 1998). Levine and D'Antonio (1999) reviewed the evidence supporting a negative relationship between species richness and invasions and concluded that the hypothesis was weakly supported. Most importantly, they drew attention to the critical lack of studies on the mechanisms that underpin links between richness and the likelihood of invasions. Here we examine invasions of a natural community of sessile marine invertebrates as an analog of invasions by exotic species and identify two distinct mechanisms that act to increase invasibility of the assemblage as local richness increases.

STUDY SITE AND METHODS

We intensively monitored an established sessile marine invertebrate community over 446 days, recording species' interactions, recruitment and mortality on 11 census

dates. Space is the principle limiting resource in the system. We examined how invasibility was influenced by local species richness, availability of free space, associations between recruits and resident colonies, and associations between resident colonies. Our study was conducted in the Maria Island marine reserve (42°34' S, 148°3'E) on the east coast of Tasmania. Darlington jetty extends into the marine reserve and supports a diverse and extensive assemblage of sessile invertebrates. Concrete slabs extend to approximately 3 meters below the low water mark, providing a low-light habitat under the jetty platform that is free of macro algae. Twenty-three fixed quadrats (each 0.1 m²) were established along ca. 30 m of jetty. The quadrats were sampled photographically on 11 occasions at approximately monthly intervals between 19 November 1996 and 6 January 1998 (using 35mm color transparencies). Photographs were digitized and the identity, position, area and interactions with other organisms of each colony recorded. We recorded an interaction whenever the edges of two colonies of different species were in contact.

Only larval recruits were counted as successful invaders. Colonies established outside the fixed quadrats that grew into the quadrat area were not recorded as recruits. Recruits were identified once they reached a size of approximately 15mm².

Since Tasmania has a highly diverse and endemic invertebrate marine fauna (estimated ca.70% endemism), a large number of marine invertebrate species are undescribed. Voucher specimens of the species in this paper have been deposited with the Tasmanian Museum and Art Gallery for sponges from family Halichondriidae species 1 (K1741), family Halichondriidae species 2 (K1742), family Halichondriidae species 3 (K1743), family Leucetiidae sp. (K1745), Cnidarian *Corynactis australis* (K1746), Bryozoans *Celleporaria* sp. (H2543) and *Parasmittina* sp. (H2544) and ascidian *Didemnum* sp. (D2474).

COLONISATION RATES INCREASE WITH LOCAL SPECIES RICHNESS

Data from photographs yielded information on 8,471 colonies from 46 species of sessile colonial invertebrate, but we concentrate our analysis on the 8 most abundant species that account for 72% of the colonies and 75% (on average) of the total area covered by organisms. Sponges comprised the majority of the species present (22 species), while there were 15 species of ascidian, 6 species of bryozoan, and 3 species of cnidarian. Sponges were the dominant space occupiers, covering between 4.8% and 75.5% of available space. On average, *Corynactis australis* accounted 18.6% of the total area covered by organisms, Halichondriidae species 1 14.6%, Halichondriidae species 3 10.3%, Halichondriidae species 2 8.5%, Leucetiidae sp. 7.2%, *Celleporaria* sp. 6.6%, *Didemnum* sp. 5.6%, and *Parasmittina* sp. 3.3%.

The dynamics of space occupancy depends strongly on local species richness. The number of species invading a patch is positively related to local species richness (figure 1a). This is not the result of very localized recruitment from established colonies within each quadrat, since the relationship also holds for colonizing species not represented as established colonies in each quadrat (figure 1b). Similarly, colonization rates of the 8 most abundant species increase with number of species occupying a quadrat, although the relationship is not significant for Halichondriidae species 2 (figure 1). The rate of increase in maximum colonization rates with increasing richness is greatest for the ascidian *Didemnum* sp. and lowest for the anemone *Corynactis australis*.

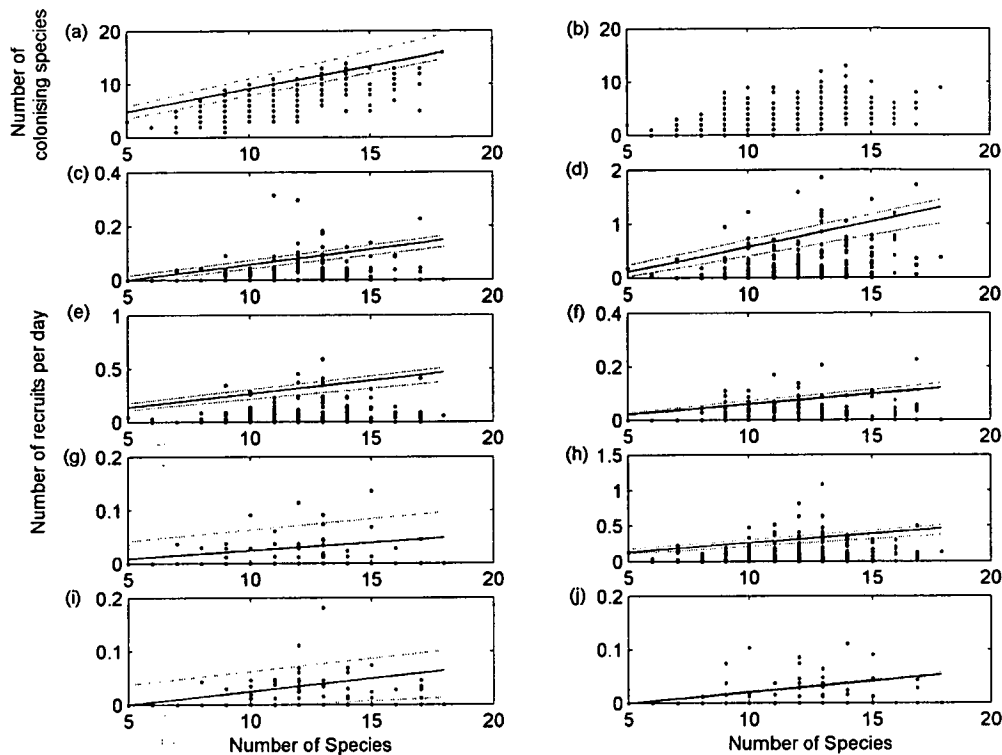


Figure 1. Relationship between species richness and colonization rate in 0.1 m² quadrats. Considering the upper bounds of the relationship, recruitment for all species combined and the 8 most common species separately all show increased rates of colonization with local species richness. Lines represent quantile regressions (32) on the 90th quantile with 70% confidence intervals. Species and relationships are: (a) Number of recruits from all species (slope = 0.85714, $t_{1,196}$, $P = 0.0000$), (b) Number of recruits of species not present in quadrats, (c) *Parasmittina* sp. (slope = 0.01136, $t_{1,196} = 10.06306$, $P = 0.0000$), (d) *Didemnum* sp. (slope = 0.09171, $t_{1,196} = 3.23093$, $P = 0.00145$), (e) *Celleporaria* sp. (slope = 0.02503, $t_{1,196} = 2.08916$, $P = 0.03798$), (f) Leucetiidae sp. (slope = 0.00758, $t_{1,196} = 2.42877$, $P = 0.01605$), (g) Halichondriidae species 2 (slope = 0.00303, $t_{1,196} = 1.04924$, $P = 0.29536$), (h) Halichondriidae species 3 (slope = 0.0252, $t_{1,196} = 2.17601$, $P = 0.03075$), (i) Halichondriidae species 1 (slope = 0.00493, $t_{1,196} = 2.40805$, $P = 0.01696$), (j) *C. australis* (slope = 0.00413, $t_{1,196} = 2.03602$, $P = 0.04309$).

In all cases these relationships are triangular suggesting that richness is limiting but not a direct causal factor. The upper bounds of the relationships were estimated using quantile regressions. Quantile regressions are based on a weighted absolute deviance model and provide a robust estimate of location, are resistant to outliers and provide an efficient estimator when the residuals are not normal (Buchinsky 1998, Scharf 1998). The selection of the quantile for the dependent variable weights the analysis and can be selected to provide upper and lower bounds for a scattered distribution. Here we use the upper 90th quantile since all our data are bounded by zero. This was more conservative than using the 95th or 99th quantile while still providing an accurate estimate of the limits of the distribution. Co-efficients and confidence intervals were estimated using the R package (<http://cran.r-project.org/>).

Importantly, species show both positive and negative associations with free space (figure 2), which reflects two distinct underlying mechanisms that generate the observed positive relationship between colonization rate and local species richness. Six of the 8 most abundant species respond as typical opportunistic invaders, with colonization rate increasing with availability of bare space. The strongest positive response to free space is the colonial ascidian *Didemnum* sp. followed by Halichondriidae species 3, *Celleporaria* sp., *Parasmittina* sp., Leucetiidae sp. and Halichondriidae species 2. In contrast, colonization rates of *C. australis* and Halichondriidae species 1 decrease with increasing availability of free space (figure 2).

A mechanism based on size-dependent mortality

The positive relationship between colonization rate and species richness for species showing opportunistic use of bare space depends on a complex mortality

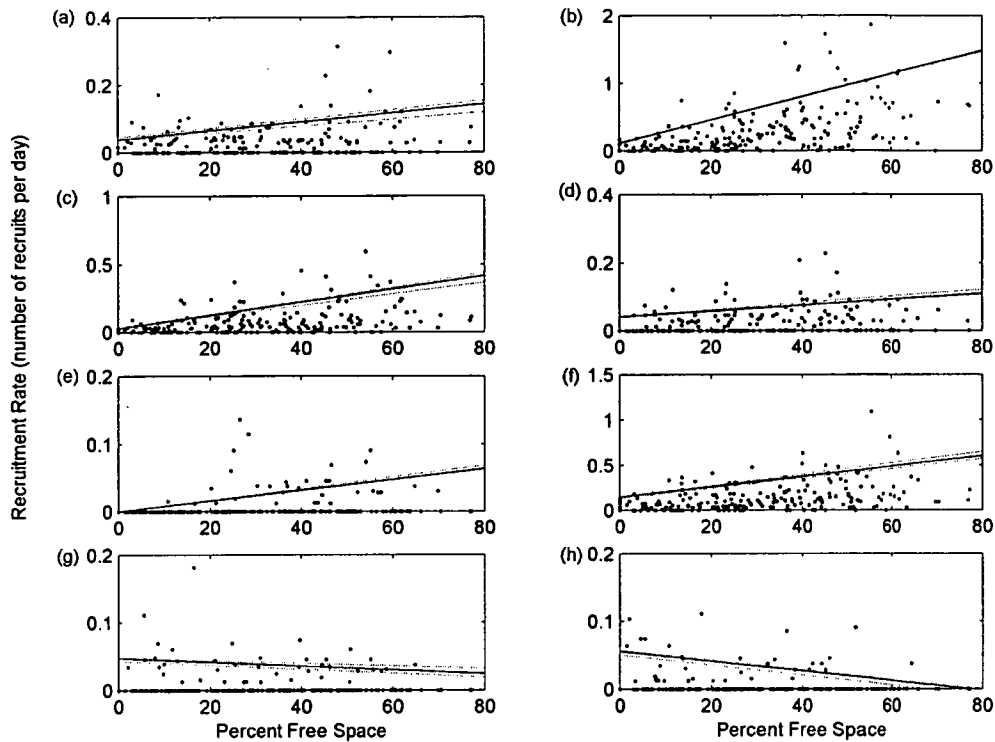


Figure 2. Relationship between the percentage free space in a quadrat and colonisation rate (number of recruits per day) for the 8 most abundant species. Considering the upper bounds of the relationship, 6 species ((a)-(f)) show increased recruitment with increasing availability of bare space, while colonisation rates of the other 2 species ((g)-(h)) declined with increasing bare space. Lines represent quantile regressions on the 90th quantile with 70% confidence intervals. Species and relationships are (a) *Parasmittina* sp. (slope = 0.00132, $t_{1,196} = 1.97714$, $P = 0.04943$), (b) *Didemnum* sp. (slope = 0.01711, $t_{1,196} = 4.80175$, $P = 0.0000$), (c) *Celleporaria* sp. (slope = 0.00483, $t_{1,196} = 4.00377$, $P = 0.00009$), (d) Leucetiidae sp. (slope = 0.00086, $t_{1,196} = 2.08457$, $P = 0.0384$), (e) Halichondriidae species 2 (slope = 0.00079, $t_{1,196} = 3.64397$, $P = 0.00034$), (f) Halichondriidae species 3 (slope = 0.0057, $t_{1,196} = 3.17995$, $P = 0.00171$), (g) Halichondriidae species 1 (slope = -0.00029, $t_{1,196} = -1.88811$, $P = 0.06049$), (h) *C. australis* (slope = -0.00072, $t_{1,196} = -2.28922$, $P = 0.02313$)

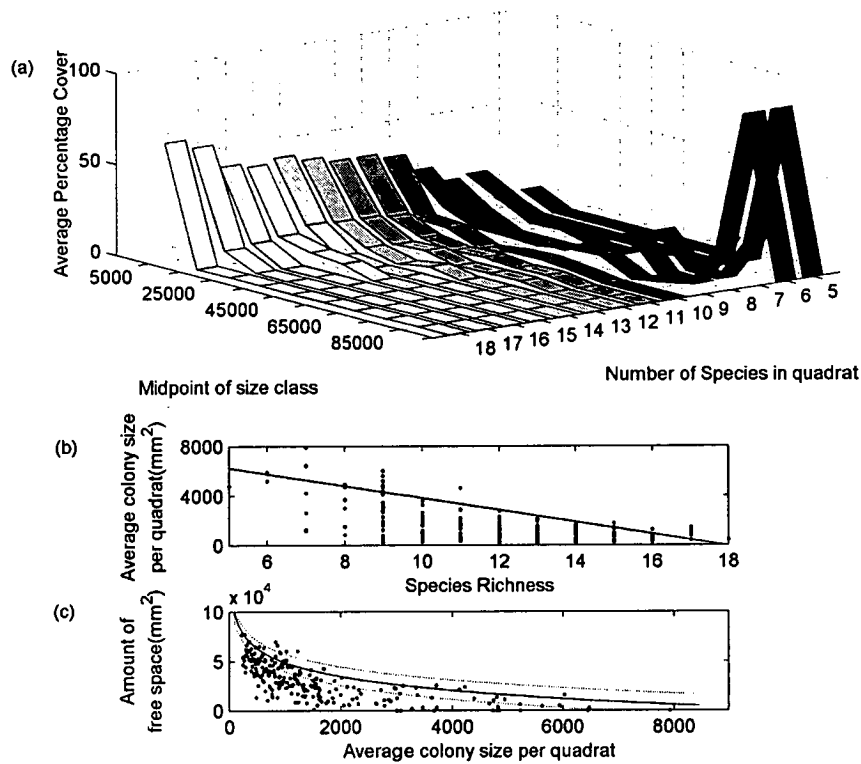


Figure 3. (a) Relationship between species richness per quadrat, size of colonies and average total cover (relative to total quadrat area) of species-size groupings. When local species richness is low, space is dominated by large colonies, while small colonies proliferate when richness is high. (b) Upper bounds of relationship between species richness and average colony size per quadrat using quantile regression, (slope = -485.13, $t_{1,219} = -5.7434$, $P = 0.0000$). (c) Upper bounds of relationship between average colony size and the amount of free space, modeled on the equation $y = \text{slope} \cdot \log(x) + c$ using quantile regressions, (slope = -20,648.08, $t_{1,219} = -12.284$, $P = 0.0000$).

dynamic. For all species there is a clear relationship between local richness, colony size and the amount of cover of colonies of a particular size (figures 3a,b). When richness is low, space is dominated by large colonies (80,000 – 90,000 mm²). As

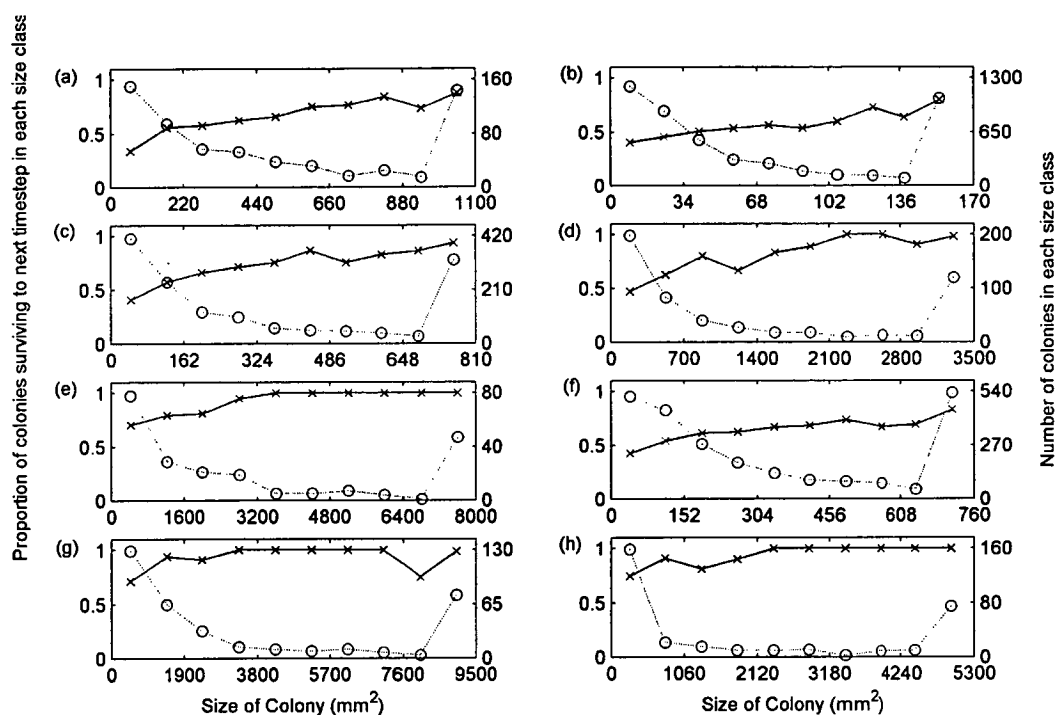


Figure 4. Survivorship increases with colony size for the 8 most common species. 'x' = percentage survivorship of size class, 'o' = number of colonies in size class. (a) *Parasmittina* sp., (b) *Didemnum* sp., (c) *Celleporaria* sp., (d) Leucetiidae sp., (e) Halichondriidae species 2, (f) Halichondriidae species 3, (g) Halichondriidae species 1, (h) *C. australis*.

richness increases colonies become progressively smaller until space is dominated by small colonies between 0 and 10,000 mm². This reflects the usual dilemma of species packing; the more species occurring in a given area, the smaller the size of individuals and/or fewer the number of individuals per species. Importantly, mortality is size-specific, with survivorship increasing with size in all 8 species (figure 4). Thus, because colony size is smaller in more speciose patches, and mortality rates of small colonies are greater than that of larger colonies, free space is made available to opportunistic colonizers more frequently in species rich patches (figures 3a,c). The dynamics of recruitment and mortality generally occur over a shorter time-scale than growth into free space. Thus, it is relatively rare that a colony survives sufficiently

long to grow to a large size. As a consequence, most colonization of new areas is through larval recruitment, rather than growth of existing colonies, contrasting with the predictions of Connell and Keough (1985).

A mechanism based on positive associations between species

Despite that free space is required for a colonization event, colonization rates of *C. australis* and Halichondriidae species 1 decline with increasing availability of free space. This reflects significant positive associations between these species and established colonies. A randomization test was used to test the null hypothesis that the number of interactions between two species was as expected by chance given the particular abundance of colonies observed. The test kept the number of interactions for each species constant while selecting an interacting species at random from the group of species present, preventing a species from interacting with a con-specific. This maintains the observed relationship between the area of a colony (and the size frequency distribution for the species) and the number of interactions with other colonies. The interactions were randomized 50,000 times and the distribution of the number of interactions for each pair of species was compared to the observed pattern of interactions. If the number of initial interactions was below the 2.5 or above the 97.5 percentile of the distribution, the species were considered to be negatively or positively associated respectively. The test was repeated for each census date to avoid the confounding effects of colonies present at multiple dates. A similar test was conducted on recruits of all species to determine whether associations between recruits and adjacent colonies were random. In this test recruits were pooled over all census dates, and recruits that did not interact with any other species were considered to interact with bare space.

The distribution of interactions between recruits and established colonies often departed from the null model of random association in space, and two distinct patterns emerge (Table 1a). *Didemnum* sp. and *Celleporaria* sp. preferentially colonize bare space and avoid locations where immediate interaction with established colonies will occur. Accordingly, the number of interactions between *Didemnum* sp. recruits and established colonies of *Celleporaria* sp., Halichondriidae species 1, Leucetiidae sp., Halichondriidae species 3, and *C. australis* is less than expected by chance, and *Celleporaria* sp. recruited adjacent to Halichondriidae species 2 and Leucetiidae sp. less often than expected. Recruits of all other species are associated with colonies of particular species more often than expected by chance, preferentially colonizing space where the chance of interaction is higher. Recruits of *Parasmittina* sp., *C. australis*, Halichondriidae species 1 and Leucetiidae sp. interact with established colonies of this species complex more frequently than expected. This pattern of positive associations is temporally stable in that long established colonies of this group are positively associated with each other over many census dates (Table 1b). Established colonies of *Didemnum* sp. also display a similar pattern to recruits, avoiding interacting with *Celleporaria* sp. and Halichondriidae species 3. Thus, patterns of association generated by recruitment are not transient and appear consistently in assemblages of established colonies over multiple census dates.

For species that preferentially colonize sites adjacent to established colonies of particular taxa, colonization rates will increase with availability of preferred associates. As the richness of a given patch increases, the likelihood of an established colony of a preferred species occurring in that patch must also increase. By this mechanism, colonization rate tracks local richness. These species do not respond to free space as do the ‘opportunists’, and strong positive associations between recruits

Table 1. Summary of spatial associations among the 8 most common species as calculated from randomisation tests. (↑) indicates that the number of interactions was more than expected by chance (> 97.5% of the distribution according to the null hypothesis), or in referring to free space, that the number of recruits entirely surrounded by free space was greater than expected by chance; (↓) indicates that the number of interactions was less than expected by chance (< 2.5% of the null distribution), or in referring to free space, that the number of recruits entirely surrounded by free space was less than expected by chance. (a) gives results for the distribution of interactions between recruits and resident colonies; (b) gives results for the distribution of interactions between established colonies, where each cell shows the results of 9 census dates with positions 1 to 9 corresponding to 19/10/96, 11/12/96, 15/1/97, 11/2/97, 5/5/97, 3/6/97, 20/8/97, 12/9/97 and 4/11/97.

(a)

		Resident Colonies								
		<i>Didemnum</i> sp.	Halichondriidae species 3	<i>Celleporaria</i> sp.	Halichondriidae species 1	<i>Parasmittina</i> sp.	Leucetiidae sp.	<i>C. australis</i>	Halichondriidae species 2	Free Space
Recruits	Halichondriidae species 2			↑	↑					↓
	<i>C. australis</i>					↑	↑			↓
	Leucetiidae sp.				↑			↑		↓
	<i>Parasmittina</i> sp.		↑		↑		↑	↑		↓
	Halichondriidae species 1	↑		↑		↑	↑	↑		↓
	Halichondriidae species 3		↑			↑			↑	↓
	<i>Celleporaria</i> sp.						↓	↑	↓	↑
	<i>Didemnum</i> sp.		↓	↓	↓		↓	↓		↑

Table 1(b) cont.

	<i>Didemnum</i> sp.	Halichondriidae	<i>Celleporaria</i> sp.	Halichondriidae	<i>Parasmittina</i>	Leucetiidae sp.	<i>C. australis</i>
		species 3		species 1	sp.		
Halichondriidae species 2			↑ ↑ ↑				
<i>C. australis</i>	↑ ↓		↑ ↑ ↑ ↓ ↑ ↓	↑ ↑ ↑ ↑ ↑ ↑	↑ ↑ ↑ ↑ ↑	↑ ↑ ↑	
Leucetiidae sp.		↓ ↓ ↓ ↓		↑ ↑ ↑ ↑	↑ ↑ ↑		
<i>Parasmittina</i> sp.	↑ ↓ ↓		↑ ↓ ↓	↑ ↑ ↑ ↑			
Halichondriidae species 1		↑	↑	↑ ↑			
<i>Celleporaria</i> sp.	↓ ↓ ↓ ↓ ↓						
Halichondriidae species 3	↓ ↓ ↓ ↓	↑					

1	4	7
2	5	8
3	6	9

and established colonies (Table 1a) may yield significant negative associations with free space (figure 2). Where positive associations occur among a particular group of species, this group may form a patch that resists invasion by species outside the group, particularly the opportunistic colonizers, by limiting the availability of free space.

Thus, the 8 common species form a continuum of colonization strategies. At one extreme *Didemnum* sp. and *Celleporaria* sp. are highly opportunistic and invasive. They rapidly colonize free space and recruit most readily to sites where they avoid interaction with other colonies, as is typical of other invasive cosmopolitan

genera (Oren and Benayahu 1998). At the other extreme, colonization rates of *C. australis* and Halichondriidae species 1 are positively associated with the presence of established colonies of particular species and their recruitment is adversely affected by increasing availability of free space. Between these extremes, the remaining species also associate positively with particular other species, enabling significant recruitment when bare space is rare providing that diversity is sufficiently high to ensure the presence of the preferred species. However, this does not preclude them from colonizing free space when it becomes available.

LOCAL PROCESSES AND INVASIBILITY

The relationships we observed between colonization rate (of both species and individuals) and species richness are triangular, suggesting that richness is a limiting factor but not a direct determinant of invasion rate. The two underlying mechanisms depend on local processes and species specific properties (size-specific mortality in one case and positive associations between recruits and established colonies in the other) that determine how space (as the principal limiting resource in the system) is utilized. These two mechanisms are influenced by species diversity in different ways. The dynamics of sessile marine invertebrate (Grosberg 1981, Keough 1984, Keough and Downes 1982, Osman and Whitlatch 1995, Patzkowsky 1988), grassland and other vegetation (Levine 2000, Stoll and Weiner 2000) communities in general are strongly dependent on local processes in that settlement of larvae (marine systems), and recruitment, growth and survivorship are influenced by the identity of neighboring individuals. We might therefore expect that similar relationships between local interactions, invasion and species diversity would hold for these types of communities. However, while our observations of a positive relationship between

invasion rate and local richness are similar to observations for some grassland (Robinson *et al.* 1995, Stohlgren *et al.* 1999, Wiser *et al.* 1998) and riparian (Levine 2000, Planty-Tabacchi *et al.* 1996) assemblages, they are diametrically opposite those reported recently for a different marine epibenthic assemblage (Stachowicz *et al.* 1999), and other grassland (Prieur-Richard *et al.* 2000, Symstad 2000, Tilman 1997) systems. It may be that this dichotomy can be resolved by deeper analysis of the particular local mechanisms, and complexity of the resource spectrum involved.

If the self-organized spatial structure of species and communities (i.e. Johnson 1997, Herben *et al.* 2000, Silvertown *et al.* 1992) are important the properties of experimental systems with contrived spatial arrangements and species complements might not behave globally as do the natural assemblages from which they were derived. For example, it is likely that the act of manipulating our assemblages would disrupt the mechanisms that generate the patterns of invasions, thus generating a different result. In our systems, manipulation of colonies on small tiles (as in Stachowicz *et al.* 1999) would cancel the effect of size-specific mortality, as all colonies would be of similar sizes. As we have shown here, many small colonies have higher rates of turnover than a single large colony of the same area. Thus, we might expect that in manipulated communities a negative rather than positive relationship would exist between richness and invasions. Regardless, it is clear that invasibility of communities is determined largely by species properties and local interactions among species rather than being an inherent function of local species richness.

Chapter 3: Competition coefficients in a marine epibenthic assemblage depend on spatial structure.

(Oikos in press)

ABSTRACT

We investigated the importance of the spatial context of interactions in a multispecies marine epibenthic assemblage with respect to the outcomes of interspecific interactions, neighbour specific growth rates, and the dynamics of spatial and mean-field models of the system. We compared the outcomes of interactions and overgrowth rates of pair-wise combinations of species in spatially simplified contrived interactions with the same combinations in an unmanipulated assemblage. While estimates of neighbour specific growth rates were similar in both sets of interactions, the probability of a species winning a particular interaction was strongly dependent on whether the interaction was contrived or occurred in the unmanipulated assemblage. The dynamics of a spatial model and its mean-field equivalent parameterised from estimates of interaction outcome and neighbour specific growth from contrived interactions were significantly different to the dynamics of models based on estimates of interaction outcome and neighbour specific growth obtained from non-manipulated assemblages. Differences in the dynamics of models based on parameters from unmanipulated and contrived interactions are primarily due to differences in interaction outcomes while fluctuations in growth rates contribute to the variability around these dynamics. Our results suggest that conclusions about interspecific interactions and community dynamics examined in simplified spatial

associations (e.g. in manipulative experiments) will be limited to assemblages with a similarly simplified spatial structure, an unlikely occurrence in nature.

INTRODUCTION

The dynamics of multispecies assemblages depend strongly on the topology of interaction networks and the nature and strength of interactions among each pair of species. It follows that to understand and predict the dynamics of multispecies assemblages, it is necessary to identify processes that influence interaction strengths, and to accurately parameterise interaction outcomes and strengths in attendant models. Interaction coefficients describing interaction effects of pair-wise combinations of species are used widely in theoretical (e.g. Lotka 1925; MacArthur & Levins 1967; May 1973) and empirical (e.g. Neill 1974; Silvertown *et al.* 1992; Vandermeer 1969) ecological models.

Techniques used to estimate competition coefficients vary from simple *in situ* measurements of overgrowth in non-manipulated marine invertebrate (e.g. Buss & Jackson 1979) and grassland (Law *et al.* 1997) communities, to more complex manipulative procedures such as replacement series, and simple and full additive designs, in greenhouses (see Freckleton and Watkinson 2000; Gibson *et al.* 1999). It is not usually apparent whether these different approaches, particularly with respect to the simplified spatial structures usually associated with manipulative procedures, influence estimates of interaction coefficients. However, the possibility that the outcomes of interactions may be altered in artificial conditions is recently acknowledged for plant assemblages (Freckleton and Watkinson 2000; Gibson *et al.* 1999). Greenhouse experiments arrange species in contrived interactions in artificial conditions, introducing the two separate artefacts of contrived interactions (where species are placed in spatially simplified conditions) and the greenhouse environment

(which is usually more benign and less variable than environmental conditions in nature).

Marine epibenthic invertebrate communities are unique in that space is the primary limiting resource and direct observation and measurement of competitive outcomes are possible, unlike the situation for terrestrial plant assemblages where interactions below the surface of the soil are unobservable. Here we quantify the growth and overgrowth dynamics of 5 sessile marine invertebrate species in a non-manipulated assemblage and compare these parameters to those observed in contrived *in situ* interactions at the same site. If the presence of other species modifies the outcome of particular pair-wise interactions as posited by Bilick and Case (1994) and Wootton (1993, 1994) or the artificial nature of manipulations are important in determining the outcomes of interspecific interactions, then we might expect that interaction outcomes of simple contrived pair-wise interactions will be different to those for the same species pairs in non-manipulated natural assemblages where pairs of interacting species occur in a variety of spatial arrangements with other species. We also assess the effect of the observed differences in interaction outcomes on the dynamics of spatially explicit and non-spatial multispecies models. Even if multispecies models are only used heuristically, the dependence of their dynamics and subsequent conclusions on estimates of interaction outcomes is an important issue. We compare the estimates of interaction outcome and neighbour-specific growths both directly (using inferential statistics) and indirectly (by examining their effects in spatial and equivalent mean-field models). We show that the outcomes of interactions of pairs of species depend on the spatial context in which these interactions occur, and that spatial and non-spatial models based on the different estimates predict dissimilar community dynamics.

MATERIALS AND METHODS

Study Site

Our study was conducted in the Maria Island marine reserve (42°34' S, 148°3' E) on the east coast of Tasmania. Darlington Jetty extends into the reserve and supports a diverse assemblage of sessile invertebrates. Concrete slabs extend to approximately 3 metres below the low water mark, providing a low-light habitat under the jetty platform that is free of macro algae. Twenty-three fixed square quadrats (each 0.1 m²) were established along ca. 30 m of jetty. The quadrats were sampled photographically on 11 occasions between 19th November 1996 and 6th January 1998. The mean number of individual colonies per quadrat was 68.7.

Analysis of data from non-manipulated assemblages

Photographs were digitised and the identity, position, area and interactions with other organisms of each colony recorded. We recorded an interaction whenever the edges of two colonies of different species were in contact. Although interactions over longer distances may be facilitated by chemical interactions (Buss 1979, Jackson and Buss 1975) and feeding interference (Buss 1990, Okamura 1992), we had no method of estimating these types of interaction from photographs and so our interpretation is conservative. Each interaction edge was followed through time to determine the direction and distance (calculated as the average of each colony's growth over the length of the edge) of growth between successive census dates. Neighbour-specific growth rates and the proportion of wins to losses for each interacting pair were calculated using two methods: (1) from space-time interactions where each

measurement of growth at each census date was counted as a replicate observation and the colony with the highest overgrowth rate along the interaction edge was counted as 'winning' the interaction, and (2) from unique interactions (true independent replicates), where growth rates were averaged over the entire sequence of observations for each interaction edge and the colony with the highest average growth rate along the edge was given as 'winning' the interaction.

Analysis of data from contrived pair-wise interactions

On the basis of their ease of manipulation and ability to survive when transplanted onto a tile, five species of epibenthic invertebrate were selected for manipulation in contrived interactions, *vis.* two bryozoans (*Celleporaria* sp. and *Parasmittina* sp.) two sponges (Halichondriidae species 2 and Halichondriidae species 4) and one ascidian (*Didemnum* sp.). Voucher specimens of all species have been lodged with the Tasmanian museum and are catalogued as H2543, H2544, K1742, K1744 and D2474 respectively. Halichondriidae species 2 and Halichondriidae species 4 are so named for consistency with the species discussed in chapter 2.

Monospecific cultivations of each species were established beneath Darlington Jetty on shards of terracotta tile (50 * 50 mm²). After 8 months growth to allow transplants to attach firmly and cover tiles, 10 replicate pair-wise interactions of all 10 possible combinations of the 5 species were established. Two tiles, each covered with a different species, were juxtaposed on plastic mats to form a 50 mm interaction edge. Each pair-wise combination was separated by a distance of at least 50 mm. The pair-wise combinations were sampled photographically on four occasions over 6 months from the 20th August 1997 to 12th February 1998, and the result of each unique

interaction (i.e. each independent replicate combination) calculated in the same way as for non-manipulated unique interactions.

Spatial Model

Interactions between the 5 selected species were modelled using a spatial model and its mean-field approximation. The spatial model was implemented as a cellular automata on a toroidal landscape (i.e. with periodic boundary conditions), using a von Neumann neighbourhood, synchronous updating, a landscape size of 100*100 cells and 100% initial random cover. The local rules governing interaction outcomes between adjacent cells are:

1. If a cell is empty, one of the 4 adjacent cells is selected at random and if the selected cell is occupied, it grows into the empty cell with a probability of g_{iFS} , where g_{iFS} is the growth rate of species i over free space. We included these rules for redundancy since cover was never less than 100%, as the model contained no elements for mortality.
2. If a cell is occupied, one of the 4 adjacent cells is selected at random. If the selected cell is occupied by species i , this species overgrows the central cell, j , with a probability of $a_{ij} * g_{ij}$, where a_{ij} is the probability of species i winning an interaction with species j and g_{ij} is the growth rate of species i over species j .

Any cell in the neighbourhood has a probability of $0.25 * a_{ij} * g_{ij}$ of overgrowing the central cell. This scales the probabilities for the presence of multiple cells of the same species in the neighbourhood. Thus 2 neighbours of same species have a probability of overgrowing the central cell of $0.50 * a_{ij} * g_{ij}$, 3 cells $0.75 * a_{ij} * g_{ij}$ and 4 cells $1 * a_{ij} * g_{ij}$. The stochastic elements in the rules allow synchronous updating without artefacts of isotropy.

Models were parameterised using data from either the contrived unique interactions or the non-manipulated unique interactions. Because interaction outcomes are a binomial response, a meaningful variance about each point estimate cannot be estimated. However, variances were calculated for neighbour-specific growth rates, and so parameters for models were determined from a normal distribution described by the observed mean neighbour-specific growth rate ± 1 standard deviation. Model community assemblages were estimated from Monte Carlo simulations of 100 runs of 500 iterations.

To determine the relative importance of interaction outcomes and neighbour-specific growth rates in affecting the dynamics of the models, growth data from both contrived and non-manipulated interactions were combined to determine overall average neighbour specific growth rates. Separate models were parameterised with the overall growth rates and interaction outcomes from each type of interaction. Predicted community assemblages were estimated from Monte Carlo simulations of 100 runs of 500 iterations.

Mean-field model

A non-spatial equivalent of the cellular model can be expressed as a mean-field equation where the probability of interaction is proportional to the abundance of the species. It is equivalent to randomising the landscape of the spatial model between every iteration.

The mean-field equation is:

$$N_{i(t+1)} = N_{i(t)} / K(K - \sum \alpha_{ij} N_j)$$

where $N_{i(t)}$ and $N_{i(t+1)}$ are the abundances of species i at time t and $t+1$ respectively and K is the capacity of the landscape (10,000 in all simulations).

Although the value of K does not affect the dynamic of the system, we use 10,000 to allow direct comparison with the spatial models. The elements of the interaction matrix are comprised of the difference in interaction probability and growth for each species, i.e. $\alpha_{ij} = a_{ij}g_{ij} - a_{ji}g_{ji}$, where a_{ij} is the probability of species i overgrowing species j ($a_{ij} + a_{ji} = 1$) and g_{ij} is the growth rate of species i over species j when i overgrows j . The mean-field model is similar to the generalised Lotka-Volterra competition equation (Mac-Arther and Levins 1967). Assemblages were predicted from Monte Carlo simulations of 100 runs of 500 iterations.

Mean Competition Coefficient

The mean competition coefficient (MCC), modified after Kokkoris *et al.* (1999), was calculated for both matrices of interaction outcome (i.e. contrived and non-manipulated):

$$MCC = \frac{\sum_{i=1}^n \sum_{j=1}^n |a_{ij} - 0.5|}{elements}$$

where n is the number of species and *elements* is the number of elements in the matrix. Calculations for elements in the matrices were only conducted where the number of replicate observations was ≥ 10 for each pair-wise interaction, in keeping with the number of replicate observations of contrived interactions. Unlike the models used by Kokkoris *et al.* (1999), a_{ij} and a_{ji} are linked and must sum to 1. Subtracting 0.5 gives the difference between the point at which each species will overgrow with equal probability, and so provides a measure of the relative strengths of interaction outcomes.

Comparison of models

Assemblage structures predicted by the different models were compared using NPMANOVA (Anderson 2001) with 10,000 randomisations for each test. In a system where the dynamics can be observed completely (i.e. species with abundances of zero are extinct) Euclidean distance is an appropriate measure of multivariate distance. Thus, examination of the principle components of the covariance matrix yields a graphical representation of the multidimensional dispersion of the communities. The simulations of both mean-field and spatial models parameterised using data from non-manipulated or contrived interactions were compared by considering community structure in Euclidean space at 50 and 500 iterations.

RESULTS

Comparison of neighbour-specific growth rates and competitive outcomes among contrived and non-manipulated interactions

All 5 species were characterised by high variance in neighbour-specific growth rates (figure 1). Accordingly, when neighbour specific growth rates from non-manipulated interactions were compared with the equivalent growth rates from the contrived interactions, only 2 out of a possible 13 *t*-tests were significant ($\alpha = 0.05$). However the clear trend for most species was that the growth rates in the contrived interactions were higher.

The matrices of unique interaction outcomes generated from the contrived interactions and non-manipulated interactions (Table 1) were compared using log-linear modelling (Caswell 1989). The *states* of an assemblage are the species that lose an interaction, (i.e. the columns in the interaction matrix) and the *fates* are the species

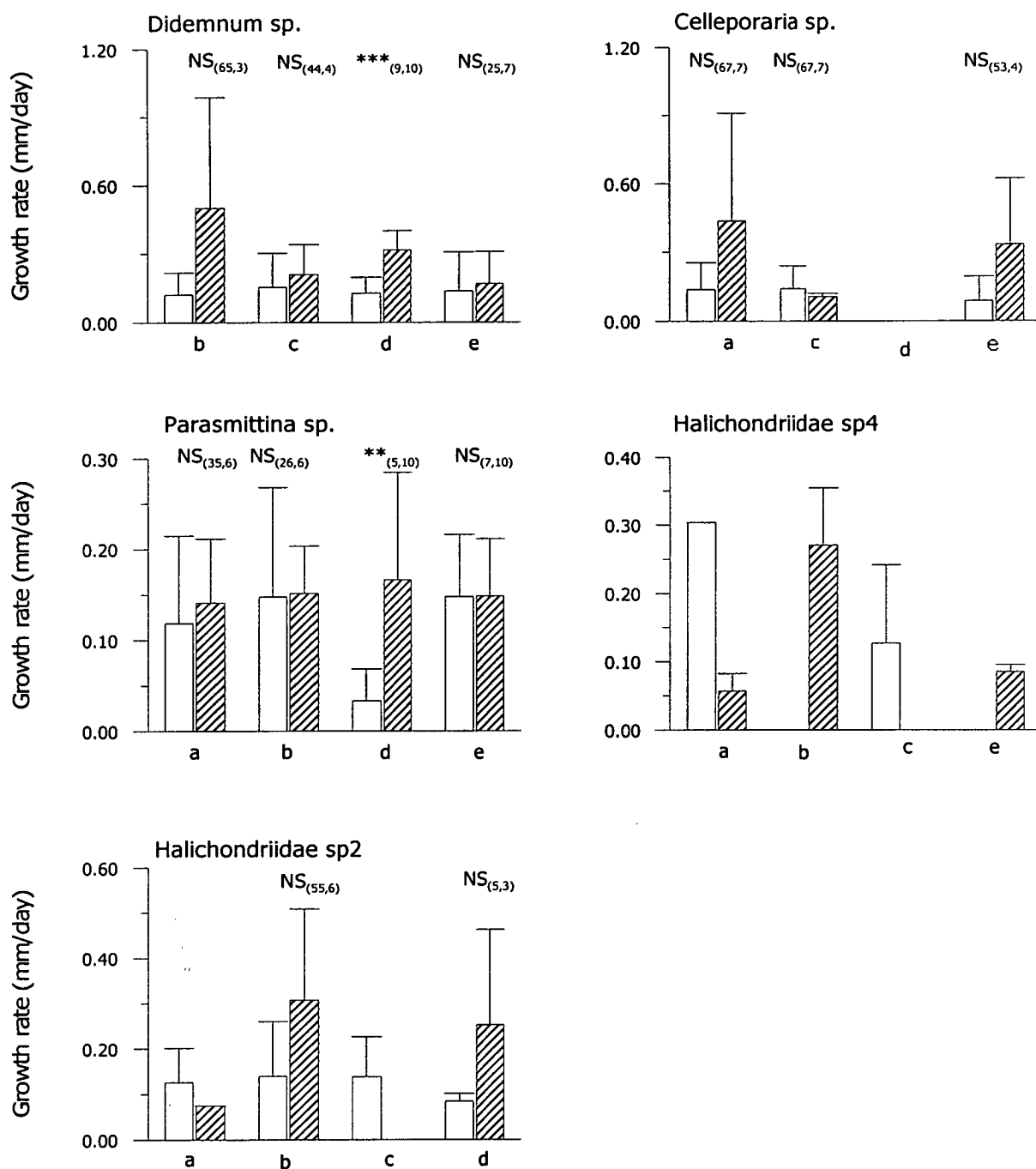


Figure 1. Average neighbour-specific growth rates (mm per day) + 1 standard deviation for each species (data from non-manipulated interactions are open, data from contrived pair-wise interactions are shaded). Where statistical comparisons are possible (i.e. $n > 1$), the significance of t -tests is given as NS = not significant, $P > 0.05$; ** = $0.01 > P > 0.001$; *** = $P < 0.0001$. The number of replicates in each test is given in parenthesis beside the significance value as (number from non-manipulated interactions, number from contrived interactions). (a) *Didemnum sp.*; (b) *Celleporaria sp.*; (c) *Parasmittina sp.*; (d) Halichondriidae species 4; (e) Halichondriidae species 2.

that overgrow existing species. In this way, two or more interaction matrices can be compared and any interaction between *state* or *fate* and *interaction matrix type* indicates that the interaction matrices differ. The interaction between *state*fate*interaction matrix type* was significant ($\chi^2 = 20.4677$, $df = 9$, $P = 0.0152$) indicating that the matrix of interaction outcomes estimated from contrived and non-manipulated assemblages were different.

Table 1. The probability of overgrowth (a_{ij}) for each pair-wise combination of species from contrived and non-manipulated interactions. The numbers of replicate observations for each pair-wise combination are in parenthesis. The significance of comparisons using Likelihood ratio tests (Bonferroni adjusted) between contrived and non-manipulated interactions for each pair-wise combination of species are given as NS, $P > 0.05$; *, $0.05 > P > 0.01$; **, $0.01 > P > 0.001$.

	Losing species (state)				
	<i>Didemnum sp.</i>	<i>Celleporaria sp</i>	<i>Parasmittina sp</i>	Halichondriidae sp4	Halichondriidae sp2
Winning species – contrived interactions (fate)					
<i>Didemnum sp.</i>	0	0.3 (10) NS	0.4 (10) NS	0.83 (12) NS	0.88 (8) NS
<i>Celleporaria sp.</i>	0.7	0	0.4 (10) NS	0 (10)	0.4 (10) NS
<i>Parasmittina sp.</i>	0.6	0.6	0	1 (10) **	1 (10) **
Halichondriidae sp4	0.17	1	0	0	0.4 (10) *
Halichondriidae sp2	0.12	0.6	0	0.6	0
Winning species – non-manipulated interactions (fate)					
<i>Didemnum sp.</i>	0	0.5 (96)	0.54 (61)	0.86 (7)	0.55 (29)
<i>Celleporaria sp.</i>	0.50	0	0.53 (30)	0 (0)	0.44 (50)
<i>Parasmittina sp.</i>	0.46	0.47	0	0.50 (4)	0.40 (10)
Halichondriidae sp4	0.14	0	0.50	0	0 (1)
Halichondriidae sp2	0.45	0.56	0.60	1	0

Comparison of mean competition coefficient among contrived and non-manipulated interactions

The MCC for the matrix of contrived unique interaction outcomes was 0.281, while the MCC for the matrix of identical species but derived from observations of non-manipulated unique interactions was 0.125 (Figure 2a). The mean relative strength of interaction outcomes estimated from contrived pair-wise interactions are stronger than for the same pairs of species in non-manipulated assemblages. Space-time interactions were examined to determine whether the total number of interactions in which a colony was engaged at any one point in time influenced the likelihood of overgrowth. The MCC for colonies interacting with just one other colony (MCC = 0.1648) is only 59% of the MCC obtained from the contrived interactions (MCC = 0.281). The MCC further decreases as the number of interactions increase (Figure 2a). The effect of increasing the number of interactions beyond three could not be examined since there were relatively few appropriate pair-wise combinations that interacted with > 3 colonies and provided ≥ 10 independent replicates.

Examining space-time interaction outcomes for each species shows that *Didemnum sp.* (Figure 2b) and *Celleporaria sp.* (Figure 2c) are equally likely to overgrow or be overgrown by all other species independent of the number of neighbours per colony. In contrast, *Parasmittina sp.* (Figure 2d) and Halichondriidae sp2 (Figure 2e) were more likely to overgrow competitors as the number of interactions increased. The mean response across all species is that interaction outcomes become more even with increasing numbers of neighbours, with a concomitant decrease in the MCC.

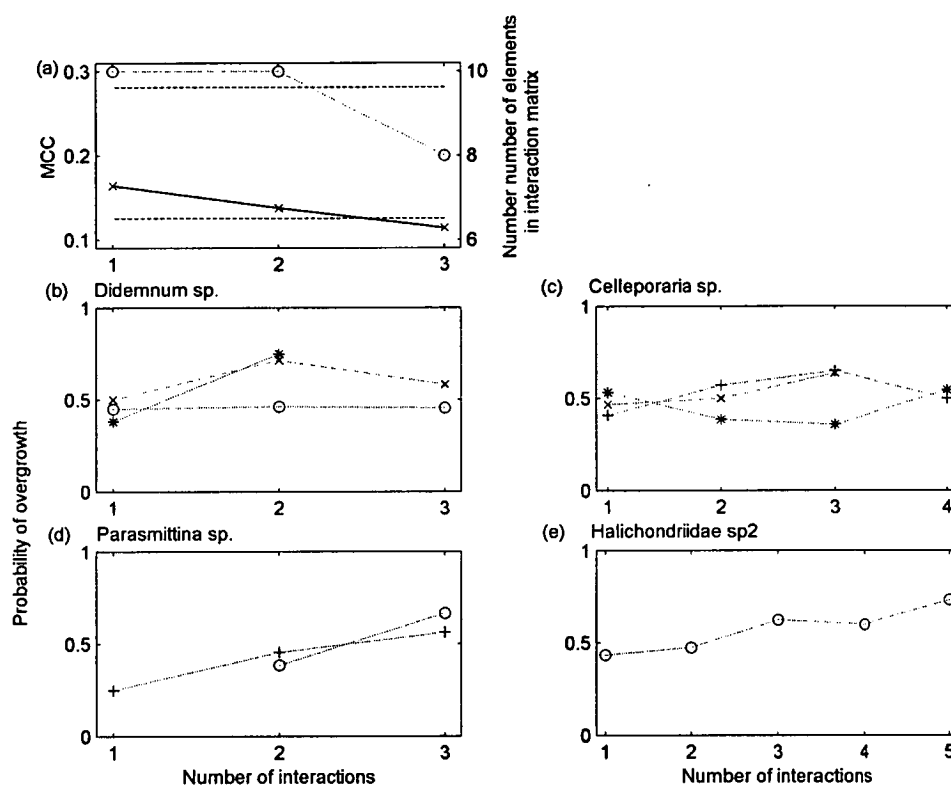


Figure 2. The effect of the total number of interactions per colony of the winning species on the probability of overgrowth in non-manipulated assemblages (number of replicate observations ≥ 10). (a) Effect of the number of interactions per colony of the winning species on mean competition coefficient (MCC). Upper and lower dashed lines represent the MCC of the matrix of contrived unique interactions and the MCC of the matrix of non-manipulated unique interactions respectively; x = MCC determined from space-time interactions where the total number of interactions per colony are limited to 1, 2 or 3; o = the number of elements in the matrix used to calculate the MCC. Other graphs show the probability of overgrowth by (b) *Didemnum sp.*, (c) *Celleporaria sp.*, (d) *Parasmittina sp.* and (e) *Halichondriidae sp2*. with increasing numbers of interactions per colony; for figures b-e '+' represents an interaction with *Didemnum sp.*, 'o' an interaction with *Celleporaria sp.*, 'x' an interaction with *Parasmittina sp.* and '*' an interaction with *Halichondriidae sp2*.

Comparison of model predictions using data from contrived and non-manipulated interactions.

After 50 iterations, community configurations predicted by spatial models based on parameters derived from contrived unique interactions and from non-manipulated unique interactions were significantly different in Euclidean multidimensional space (1-way NPMANOVA, $F_{1,198} = 199.4385$, $P = 0.0$), and the models did not converge after 500 iterations (1-way NPMANOVA, $F_{1,198} = 112.1687$, $P = 0.0$). Principle component analysis similarly revealed separation of predicted assemblages based on the different parameter estimates along the first PC after 50 iterations (Figure 3a) and 500 iterations (Figure 3b). The eigenvectors of the first PC (Table 2) showed that separation of communities after both 50 and 500 iterations was most strongly influenced by the abundance of the bryozoan *Parasmittina sp.*, reflecting that this species is predicted to be significantly more abundant when models are parameterised using estimates from contrived interactions. The PCA shows a triangular distribution in 2 dimensions. Each vertex represent landscapes with only one species present, in this case (Figure 3b) *Parasmittina sp.* on the middle right, *Didemnum sp.* on the upper left and *Celleporaria sp.* on the lower left. The distribution has 2 other vertices in the 3rd and 4th dimensions representing landscapes with only Halichondriidae sp2 and Halichondriidae sp4 respectively. Each vertex is joined to each other vertex by a straight line representing communities where only 2

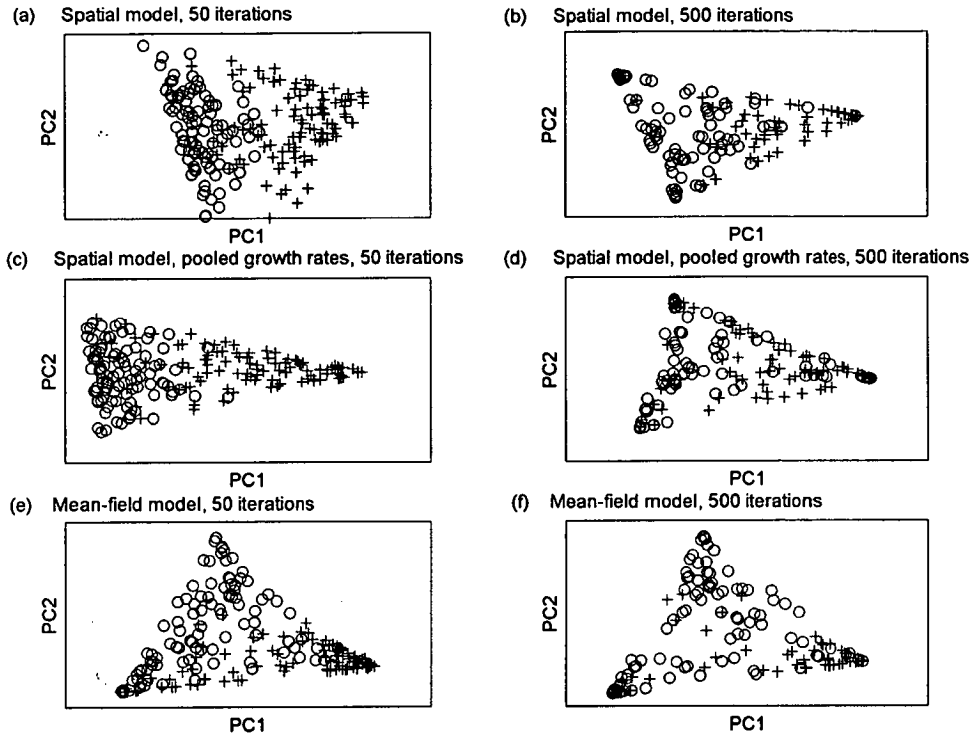


Figure 3. Comparison of predicted dynamics of 5 species system based on principle component analysis of spatial and mean-field models after 50 and 500 iterations. 'o' represent runs of models based on parameters from observations of pair-wise unique interaction outcomes and neighbour-specific growth rates in non-manipulated assemblages; '+' represent runs of models parameterised from observation of pair-wise unique interaction outcomes and growth rates estimated in contrived interactions.

species are present in varying proportions. Spatial models parameterised by pooling growth rates from contrived and non-manipulated interactions, but retaining separate estimates of interaction outcome for contrived and non-manipulated interactions were also significantly different at both 50 and 500 iterations (1-way NPMANOVA, $F_{1,198} = 105.221, P = 0.0001, F_{1,198} = 45.2564, P = 0.0001$, respectively). The PCAs showed identical patterns those derived from spatial models parameterised using

separate interaction outcomes and neighbour-specific growth rates from each interaction type (*cf.* Figures 3a, 3b versus Figure 3c, 3d; Table 2).

Table 2. Eigenvectors of principle components from covariance matrices with the cumulative proportion of variance explained by each vector.

VARIABLE	PC1	PC2	PC3	PC4
50 iterations – spatial model				
<i>Didemnum sp.</i>	-0.5376	0.6352	-0.2585	-0.2017
<i>Celleporaria sp.</i>	0.0015	-0.6209	-0.6199	-0.1736
<i>Parasmittina sp.</i>	0.8108	0.3325	0.0405	-0.1744
Halichondriidae sp4	-0.0484	-0.0314	0.1057	0.8863
Halichondriidae sp2	-0.2263	-0.3153	0.7322	-0.3365
Cumulative proportion	0.7221	0.8974	0.9919	1.000
500 iterations – spatial model				
<i>Didemnum sp.</i>	-0.4981	0.6806	-0.1980	-0.2223
<i>Celleporaria sp.</i>	-0.1809	-0.6534	-0.5439	-0.2109
<i>Parasmittina sp.</i>	0.8368	0.2242	-0.1037	-0.1967
Halichondriidae sp4	-0.0224	-0.0074	-0.0378	0.8933
Halichondriidae sp2	-0.1354	-0.2439	0.8079	-0.2635
Cumulative proportion	0.5609	0.8150	0.9594	1.000
50 iterations spatial model with overall growth rates				
<i>Didemnum sp.</i>	-0.3122	0.7198	-0.3704	-0.2172
<i>Celleporaria sp.</i>	-0.2725	-0.6923	-0.4247	-0.2572
<i>Parasmittina sp.</i>	0.8648	0.0306	0.0032	-0.2263
Halichondriidae sp4	0.0035	-0.0239	-0.0335	0.8935
Halichondriidae sp2	-0.2835	-0.0342	0.8254	-0.1927
Cumulative proportion	0.5467	0.8473	0.9842	1.000
500 iterations spatial model with overall growth rates				
<i>Didemnum sp.</i>	-0.4369	-0.6527	-0.3665	-0.2209
<i>Celleporaria sp.</i>	-0.2467	0.7483	-0.3464	-0.2432
<i>Parasmittina sp.</i>	0.8494	-0.1170	-0.1243	-0.2224
Halichondriidae sp4	0.0019	0.0147	-0.0171	0.8941
Halichondriidae sp2	-0.1639	0.0067	0.8544	-0.2078
Cumulative proportion	0.4868	0.8068	0.9912	1.000

50 iterations mean-field model				
<i>Didemnum sp.</i>	-0.6344	-0.5814	-0.1556	-0.1880
<i>Celleporaria sp.</i>	-0.0260	0.2558	0.8015	-0.3025
<i>Parasmittina sp.</i>	0.7650	-0.3785	-0.1789	-0.1988
Halichondriidae sp4	0.0036	0.0316	0.0766	0.8906
Halichondriidae sp2	-0.1081	0.6725	-0.5436	-0.2012
Cumulative proportion	0.5938	0.8731	0.9919	1.000
500 iterations mean-field model				
<i>Didemnum sp.</i>	-0.6038	-0.6074	-0.1774	-0.1870
<i>Celleporaria sp.</i>	-0.0794	0.2684	0.7948	-0.3000
<i>Parasmittina sp.</i>	0.7863	-0.3522	-0.1304	-0.2018
Halichondriidae sp4	0.0011	0.0325	0.0738	0.8908
Halichondriidae sp2	-0.1041	0.6587	-0.5607	-0.2020
Cumulative proportion	0.5832	0.8492	0.9753	1.000

Mean-field models showed similar patterns. After 50 iterations the predicted assemblages using each estimation were significantly different (1-way NPMANOVA, $F_{1,198} = 51.9874$, $P = 0.0$), and the models did not converge after 500 iterations (1-way NPMANOVA, $F_{1,198} = 43.954$, $P = 0.0$). However, distinct from the pattern for the spatial model, separation of predicted communities based in parameters derived from contrived and non-manipulated systems was on the second PC, not the first (Figure 3e & 3f). The second PC is dominated by the abundance of Halichondriidae sp2. (Table 2), which is represented as a monoculture at the upper vertex. Vertices on the lower left and lower right represent dominance by *Didemnum sp.* and *Parasmittina sp.* respectively.

DISCUSSION

The spatial context of pair-wise interactions, in terms of the total number of colonies interacting with the two of interest, and the species identity of each colony, is

rarely considered in calculating interaction outcomes and neighbour-specific growth rates. Many studies of competitive interactions place species into artificial conditions with a simplified spatial structure (i.e. Freckleton & Watkinson 2000; Gibson *et al.* 1999). Indeed, >60% of all papers published in the journal *Ecology* between 1981 and 1990 examined at most two species (Kareiva 1994). Our results demonstrate consistent differences between matrices describing outcomes of contrived pair-wise interactions in a simplified spatial structure and interactions among the same species in non-manipulated assemblages where spatial structure varies from simple to complex arrangements. In contrast, differences in neighbour-specific growth rates among contrived and non-manipulated systems were slight, and most comparisons between contrived and non-manipulated pair-wise outcomes were insignificant. Differences in interaction outcomes and the network topology, coupled with slight changes in neighbour-specific growth rates, lead to marked differences in the dynamics of model communities.

These results highlight the possibility that models parameterised on the basis of results of simple manipulated interactions may result in predicted dynamics that are not characteristic of natural assemblages.

Effect of number of interactions

Contrived interactions in manipulative experiments are most often limited to pair-wise interactions (i.e. Freckleton & Watkinson 2000; Gibson *et al.* 1999) or to a small number of specified interactions in which the spatial context is highly constrained. This situation is unlikely to arise in a natural (non-manipulated) assemblage, where the number of interactions experienced by a single individual or colony, will be limited only by its size and shape and the size and shape of the

interacting individuals or colonies. At a species level, we observed two different responses to increasing numbers of interactions. The probability of *Didemnum sp.* and *Celleporaria sp.* winning an interaction showed no consistent pattern (figure 2b & 2c) with the total number of interactions. In contrast, the likelihood that a colony of *Parasmittina sp.* and Halichondriidae sp2 (figure 2d & 2e) won an interaction increased as the number of interactions with the colony increased.

As the number of interactions per colony increased from one to three in the non-manipulated assemblage, the absolute probabilities of winning an interaction tended to become more even for all species. Consequently, with increasing interactions per colony, the MCC. Importantly, the MCC from the contrived interactions was almost double that for the identical set of interactions in the non-manipulated assemblage.

If the only difference between contrived and non-manipulated interactions was the total number of interactions affecting each colony, then we would expect that interaction outcomes for colonies in non-manipulated assemblages with only one interaction would be similar to those from contrived interactions. However, outcomes of contrived interactions were notably more one-sided than equivalent interactions in the non-manipulated assemblage, even when there were only a pair of interacting species. Thus, the change in the number of interactions was not the only cause of the difference between contrived and non-manipulated interactions. It is likely that size plays an important role in influencing interaction outcomes. Several studies of non-manipulated marine assemblages have shown that interaction outcomes may be influenced by differences in colony size (e.g. Buss 1980; Harvell & Padilla 1990; Russ 1982; Winston & Jackson 1979; but see also Nandakumar & Tanaka 1997). Similarly, Grace *et al.* (1992) showed that in manipulated experiments with plants,

‘winning’ a pair-wise interaction was biased toward the larger plant. However, in our experiments any effect of differences in colony size should be reduced by limiting species in contrived interactions to an initial size of 2500 mm² and growing colonies on raised shards.

Changes in models with different estimations of interactions

The importance of differences in interaction outcomes and neighbour-specific growth rates are highlighted by comparing the dynamics of models parameterised using estimates from contrived interactions with model dynamics parameterised from estimates of non-manipulated assemblages. The trajectories of the both spatial and mean-field models parameterised with different interaction types diverged rapidly. Differences in interaction outcomes described by the two parameter sets proved critical in producing differences in predicted assemblages, as demonstrated by the dynamics of models parameterised using pooled growth rates (Figures 3c & 3d). Since pooled growth rates were identical in these two sets of simulations, the clear distinction between models based on observations of contrived and non-manipulated interactions can only be due to the differences in the interaction outcomes. The separation of predicted communities based on pooled (Figures 3c, 3d) and separate (Figures 3a, 3b) growth rates is qualitatively identical, and eigenvectors show similar patterns for both analyses (Table 2). We conclude that the clear separation stems largely from differences in interaction outcomes between the contrived and non-manipulated systems, while variability in neighbour-specific growth rates introduces ‘within-group’ variability into the predicted assemblages, which vary between successive runs in Monte Carlo simulations.

Predicted assemblages from models parameterised with estimates from non-manipulated assemblages are more evenly spread in state space, having communities on all 3 possible vertices in 2 dimensions, all 5 possible vertices in 4 dimensions, and show states in which all species are present at varying levels (Figure 3). In contrast, models parameterised with estimates from contrived interactions are more aggregated around 1 or 2 vertices (Figure 3). The relatively weaker interactions in the non-manipulated assemblages (i.e. where the likelihood of winning an interaction is more even among species) contribute less to the dynamics of the system than the variability in growth rates, hence the assemblages are more evenly spread across multidimensional space. Where interaction outcomes are relatively stronger (i.e. one-sided), variability in growth becomes less important and the predicted assemblages are driven, on average, toward a different point in multidimensional space.

Changes in the estimates of competitive coefficients as a result of removing colonies from non-manipulated assemblages (where spatial associations are complex) and placing them in spatially simplified contrived interactions were unpredictable. We have shown that multispecies models developed from observations of contrived interactions are unlikely to represent non-manipulated communities of the same species. Conclusions can only be drawn about the dynamics of a similarly contrived assemblage where individuals have spatially simplified associations. Differences in the development of these assemblages are likely to be further exacerbated if contrived manipulations are undertaken in artificial conditions (e.g. aquaria or greenhouses). This highlights the need for long term (relative to the scale of the interactions involved), spatially resolved quantitative observations of non-manipulated assemblages - a rare commodity in ecology.

Chapter 4: Predicting global dynamics from local interactions: do models marine epibenthic communities reflect reality?

ABSTRACT

Although spatially explicit community models have generated a wide range of complex dynamics and behaviours, the conclusions of many of these models have yet to be tested empirically. Here we develop a spatially explicit model of a marine epibenthic community and test its ability to predict the community dynamics and behaviours of the natural community. We use measurements of species in the natural community to parameterise outcomes of pair-wise interspecific interactions and neighbour-specific growth rates and species-specific recruitment and mortality rates. The model was defined with rules acting at two spatial scales: (1) between individual cells on the spatial landscape that define the nature of interactions, growth and recruitment, and (2) at the scale of whole colonies (blocks of contiguous cells) that define size-specific mortality and limitations to the maximum size of colonies for some species. The model was compared to manipulated communities and to the existing non-manipulated community. We found that the model was a good descriptor of the range of possible communities from which the manipulated and non-manipulated communities were drawn, and of the multivariate variances of natural communities. The size-frequency distributions of individual species and overall pattern of species evenness in the natural community were well predicted as emergent features of the models. Both the models and natural communities show high variability in community structure that arises from the variability of model parameters

for each species. This feature underpins an insensitivity of the dynamics to the initial spatial arrangement and abundances of colonies and the coexistence of many species.

INTRODUCTION

Predicting the dynamics of species through space and time is a major challenge for community ecology and the explicit goal of some ecological models. The development of robust and well validated predictive models would allow examination of community dynamics at spatial and temporal scales beyond the scales easily observed in natural communities and may help to test and subsequently generate ecological theory. Recent studies on marine intertidal communities (Wootton 2001) and mesocosm communities (Fussmann *et al.* 2000) have both demonstrated that is possible to generate broadly predictive numerical non-spatial models. Non-spatial numerical models contain two implicit assumptions, (1) the strengths of species interactions are proportional to their abundances, and consequently the neighbourhood of a species is potentially infinite, and (2) individuals do not exist per se and populations can become infinitely small without going extinct. For many communities, particularly those dominated by sessile species, the assumptions of numerical non-spatial models are not appropriate and introducing spatial context is warranted.

Interactions between neighbours at a local scale can generate population and community dynamics that are both complex and interesting (e.g. Herben *et al.* 2000, Law and Dieckmann 2000, Silvertown *et al.* 1992, Silvertown and Wilson 2000, Tilman 1994). Where individuals interact largely with their neighbours, a weak competitor may find itself isolated from other species that would otherwise out compete it for a specific resource (Tilman 1994, Johnson 1997, Stoll and Weiner

2000). Thus, in a community where interactions are modelled within a local neighbourhood, dynamics are complex and more species may coexist than in numerical models of the same systems (e.g. Johnson 1997). The development of individual based spatial models has flourished in recent decades (Judson 1994). Species in these models interact as individuals, and the frequency of interaction is not determined merely by the abundances of each species. Spatial models have provided insights into many aspects of ecology that were not apparent in nonspatial models. In a homogenous landscape (i.e. where there is only one resource) multiple species may coexist (e.g. Johnson 1997, Molofsky *et al.* 1999, Silvertown *et al.* 1992, Silvertown and Wilson 2000), and where intransitive loops exist in the network structure, the strongest competitor may not always become the dominant species (Johnson 1997). When competition for a single resource is extended to a metapopulation, multiple species may coexist, even when competitive outcomes follow a transitive hierarchy (e.g. Tilman 1994, Goldwasser *et al.* 1994).

Predictive ecological models

Unlike many models developed in the physical sciences, ecologists often have difficulty in demonstrating that the dynamics displayed of their models are similar to the dynamics of the natural systems they are intended to represent. Smith (2000) criticises models in theoretical ecology as being unfalsifiable, and consequently suggests that they fall outside a strict definition of science. Durrett and Levin (1994a) suggest that models should be used in a qualitative rather than in a quantitative way, principally because local interactions are not modelled accurately. If this is true, then interpreting whether even the qualitative dynamics reveal anything about the natural systems is problematic and these models are no longer strictly falsifiable. To develop

a predictive model that can be validated, the algorithms defining species interactions and demography, and the parameters used to determine the outcomes of these interactions and the species demography, should be representative of observations in nature. If either of these requirements is not met, then the dynamics of the models are unlikely to reflect their natural counterparts.

To create a model that in some way represents reality, both of these requirements must be satisfied. Neither is a trivial task. The natural community must be sufficiently well understood to derive appropriate model algorithms and it must also be possible to measure empirically the interactions between species and the demography of particular species. An appropriate model would also predict variance structures, and this too is a challenging task. Most ecological models use point-estimates as parameters despite that in nature most parameters are not invariant and thus should be estimated as a mean (the point estimate) and variance. While stochastic processes can be introduced as an external forcing to add variability to a model (e.g. Ives *et al.* 1999, Goldwasser *et al.* 1994) this approach is unlikely to generate variability seen at both species and ecosystem levels. Here, we include measures of variance in the empirical estimates of several parameters, and seek to validate that appropriate variability in the model is an emergent dynamic of the system.

A 'model' community

Marine epibenthic assemblages are appropriate model communities for which spatial models may be developed and tested. The interactions between species at a local level between colonies, and the dynamics of individual colony recruitment and mortality have been well studied. Space is the limiting resource (Barnes and Dick

2000, Buss and Jackson 1979, Jackson and Buss 1975, Lopez Gappa 1989, Nandakumar *et al.* 1993, Rubin 1982), although competitive outcomes may be influenced by competition for food via feeding currents (Buss 1979, Buss 1990, Okamura 1992). Interactions occur along the entire edge of contact between two colonies and the outcome of the interaction may vary along a single interaction edge (i.e. the winning species may change at different points along the edge of contact). Colony mortality may be either partial (Jackson 1977, 1979, Hughes and Jackson 1980) or total (Hughes 1990) and may be the result of predation (Russ 1980, Jackson and Winston 1982), disturbance (Connell and Keough 1985, Jackson and Winston 1982) or senescence. Recruitment dynamics are complex. Recruitment rates may be either enhanced (Hurlbut 1991, Keough and Downes 1982, chapter 2) or suppressed (Osman and Whitlatch 1995, Grosberg 1981, chapter 2) by adult colonies or particular topographic refuges. Because the entire colony is visible, it is possible to census the entire community photographically.

Here we develop the simplest possible spatial model of a marine epibenthic system, based on the characteristics of individual component species, that captures the basic ecology of the community. This model is superficially similar to those of Karlson and Jackson (1981) and Karlson and Buss (1984) who also simulated local interactions but more simply than the approach we use here. Our model simulates local dynamics on two scales: at the scale of individual cells to simulate growth, recruitment, and interaction processes, and at the scale of individual colonies (contiguous blocks of cells of the same species) to simulate mortality and impose maximum size limitations on colonies of some species. We compare the dynamics of the model with manipulated and non-manipulated communities *in situ* to assess how

well our models based on local interactions predict the global dynamics of the real system.

SAMPLING A MARINE EPIBENTHIC COMMUNITY TO DERIVE PARAMETERS

Our study was conducted in the Maria Island Marine Reserve (42°34' S, 148°3' E) on the east coast of Tasmania, Australia. Darlington Jetty extends into the reserve and supports a diverse assemblage of sessile marine invertebrates. Concrete slabs (5 m high * 1 m wide) extend from 2 m above the high water mark, providing a low-light habitat under the jetty platform free of macro algae. Two steel girders run horizontally along each slab at approximately 0.5 m and 2.5 m below the high water mark, partitioning an area 2 m high * 1 m wide. Within this area 23 square quadrats (each 0.1 m²) were established along ca. 30 m of the jetty, one quadrat per slab, fixed by steel thread holes. The quadrats were sampled photographically on 11 occasions between 19th of November 1996 and 6th January 1998. The photographs were digitised and the identity and size of each colony was recorded. Changes between census dates were examined to determine the number of recruits of each species, rates of whole colony mortality, the outcomes of interactions and neighbour-specific growth rates for each species.

Estimation of interaction outcomes and neighbour-specific growth rates

The photographs yielded data on 8471 colonies from 46 species of sessile marine invertebrate. We selected 14 species that comprised on average 84.3% of the total cover to parameterise multispecies models of manipulated and non-manipulated communities. These species were *Didemnum* sp. (D2474), *Botrylloides leachi*,

Celleporaria sp. (H2543), *Parasmittina* sp. (H2544), *Watersipora subtorquata*, *Phloeodictyidae* sp., *Leucetiidae* sp1 (K1745), sp2, *Halichondriidae* sp1 (K1741), sp2 (K1742), sp3 (K1743), sp4 (1744), *Microcionidae* sp., and *Corynactis australis* (K1746) (codes in parentheses are identification numbers for voucher specimens lodged at the Tasmanian Museum). As all data was collected photographically, we were unable to collect information of the importance of competition for food (Buss 1990, Okamura 1992) or particular chemical interactions (Buss 1979, Jackson and Buss 1975) other than manifested as direct contact interactions. A total of 6832 interactions were recorded and measurements were taken along each 'interaction edge' between two colonies. Each interaction edge was followed over successive census dates. A total of 4646 interaction sequences were recorded and each sequence was considered as one unique replicate interaction for a particular pair-wise combination of species. In this way, changes in outcome between census dates were described in terms of interaction outcomes and average neighbour-specific growth rates. The growth rates of each colony were averaged over the entire sequence of observations for each particular interaction edge and the colony with the highest average growth rate along the edge was counted as 'winning' the interaction. The probability of a species winning an interaction was calculated as the proportion of wins verses losses across all replicates of each pair of species (Table 1). Average neighbour-specific growth rates and standard deviations were calculated from replicate observations of species winning an interaction (Table 2). Growth over free space was calculated in the same way, except that the probability of a species 'winning' an interaction with free space was always one.

Estimation of recruitment and mortality rates

Recruits were recorded by comparing sequential photographs and identifying newly recruited colonies. Rates of recruitment of each species were standardised as the number of recruits per day per mm^2 to adjust for the period between censuses and the size of the quadrat sampled (Table 3).

Mortality was calculated as the probability of complete colony mortality per day. As demonstrated in chapter 2, mortality of sessile marine invertebrate colonies beneath the Maria Island Jetty is size dependent, decreasing with increasing colony (Figure 1). Partial mortality other than overgrowth by other colonies was extremely rare with only a single recorded event. Colonies were divided into 15 size classes and mortality rates calculated as the proportion of colonies in each size class that died, weighted by the number of days between census dates for each colony. In selecting the size classes, two conflicting needs had to be balanced: (1) to maximise the precision of the estimate for each size class by increasing the number of colonies in each size class, and (2) to maximise precision in estimating the relationship between size and mortality by increasing the number of size classes. These needs were best met by using 14 size classes on the first 80% of colonies and 1 final size class for the remaining 20%. This maximised the information on small colonies where mortality was most likely and provided a precise estimate of the mortality of large colonies, which were relatively rare. The overall relationship did not change significantly when greater numbers of size classes were selected, although the variance around these estimates did increase. For 8 of the 14 species (the bryozoans, ascidians and small sponges) this relationship was best described as a linear function (Table 4 and Figure 1). For the remaining 6 species (large sponges or cnidarians) the best fit was obtained

Table 1. The interaction outcomes (a_{ij}) for each pair-wise combination of species used in the models with the number of observations in parentheses. Since Halichondriidae sp4 was only present in the manipulated communities, outcomes are only presented for the species in those models.

	Phloeodictyidae sp.	<i>Didemnum</i> sp.	Halichondriidae sp3	<i>Celleporaria</i> sp.	Halichondriidae sp1	<i>W. subtorquata</i>	Microcionidae sp.	Leucetiidae sp2	<i>Parasmittina</i> sp.	Leucetiidae sp1	<i>C. australis</i>	<i>B. leachi</i>	Halichondriidae sp2	Halichondriidae sp4
Phloeodictyidae sp.	0	0.34 (68)	0.67 (27)	0.52 (21)	0.6 (5)	0 (0)	0.63 (8)	0.4 (15)	0.44 (9)	0.8 (15)	0 (0)	0.2 (5)	0.5 (10)	-
<i>Didemnum</i> sp.	0.66	0	0.64 (181)	0.5 (96)	0.38 (56)	1 (6)	0.57 (53)	0.56 (63)	0.54 (61)	0.71 (95)	0.35 (62)	0.53 (30)	0.55 (29)	0.86 (7)
Halichondriidae sp3	0.33	0.36	0	0.54 (153)	0.42 (59)	0.36 (14)	0.43 (61)	0.34 (77)	0.37 (62)	0.48 (33)	0.51 (93)	0.39 (18)	0.25 (28)	-
<i>Celleporaria</i> sp.	0.48	0.5	0.46	0	0.47 (49)	0.43 (7)	0.4 (35)	0.37 (81)	0.53 (30)	0.56 (30)	0.38 (21)	0.4 (5)	0.44 (50)	0.0 (0)
Halichondriidae sp1	0.4	0.63	0.58	0.53	0	0 (0)	0.73 (11)	0.44 (16)	0.56 (39)	0.74 (47)	0.57 (23)	0.69 (13)	0.43 (7)	0.0 (0)
<i>W. torquata</i>	0	0	0.64	0.57	0	0	0 (4)	0.5 (8)	0.33 (6)	0.4 (5)	0 (1)	0.5 (2)	0.5 (4)	-
Microcionidae sp.	0.38	0.43	0.57	0.6	0.27	1	0	0.27 (15)	0.33 (6)	0.5 (26)	0.5 (34)	0.5 (6)	0.38 (13)	-
Leucetiidae sp2	0.6	0.44	0.66	0.63	0.56	0.5	0.73	0	0.83 (6)	0.72 (32)	0.36 (11)	0.4 (5)	0.54 (13)	-
<i>Parasmittina</i> sp.	0.56	0.46	0.63	0.47	0.44	0.67	0.67	0.17	0	0.71 (38)	0.46 (29)	0.45 (11)	0.4 (10)	0.5 (4)
Leucetiidae sp1	0.2	0.29	0.52	0.44	0.26	0.6	0.5	0.28	0.29	0	0.35 (4)	0.34 (29)	0.38 (8)	-
<i>C. australis</i>	0	0.65	0.49	0.62	0.43	1	0.5	0.64	0.54	0.65	0	0.5 (4)	0.33 (6)	-
<i>B. leachi</i>	0.8	0.47	0.61	0.6	0.31	0.5	0.5	0.6	0.55	0.66	0.5	0	0.67 (3)	-
Halichondriidae sp2	0.5	0.45	0.75	0.56	0.57	0.5	0.62	0.46	0.6	0.63	0.67	0.33	0	1 (1)
Halichondriidae sp4	-	0.14	-	0.0	0.0	-	-	-	0.5	-	-	-	0.0	0

Table 2. The mean neighbour-specific growth rates (g_{ij} ; mm/day) ± 1 standard deviation for each pair-wise combination of species used in the models and the mean growth rates over free space (g_{iFS}) ± 1 standard deviation. Since Halichondriidae sp4 was only present in the manipulated communities, growth rates are only presented for the species in those models.

	Manipulated free space	Free Space	Phloeodictyidae sp.	<i>Didemnum</i> sp.	Halichondriidae sp3	<i>Celleporaria</i> sp.	Halichondriidae sp1	<i>W. subtorquata</i>	Microcionidae sp.	Leucetiidae sp2	<i>Parasmitina</i> sp.	Leucetiidae sp1	<i>C. australis</i>	<i>B. leachi</i>	Halichondriidae sp2	Halichondriidae sp4
Phloeodictyidae sp.	-	0.19 ± 0.14	0	0.13 ± 0.09	0.14 ± 0.14	0.12 ± 0.05	0.11 ± 0.11	0.00 ± 0.00	0.11 ± 0.07	0.24 ± 0.17	0.08 ± 0.03	0.09 ± 0.08	0.00 ± 0.00	0.04 ± 0.00	0.12 ± 0.09	-
<i>Didemnum</i> sp.	0.91 ± 0.28	0.21 ± 0.16	0.14 ± 0.08	0 ± 0.00	0.19 ± 0.15	0.13 ± 0.10	0.13 ± 0.09	0.22 ± 0.12	0.13 ± 0.08	0.17 ± 0.13	0.18 ± 0.16	0.17 ± 0.15	0.12 ± 0.08	0.19 ± 0.13	0.19 ± 0.19	0.12 ± 0.08
Halichondriidae sp3	-	0.22 ± 0.16	0.14 ± 0.08	0.15 ± 0.13	0 ± 0.10	0.14 ± 0.10	0.13 ± 0.09	0.09 ± 0.10	0.15 ± 0.10	0.18 ± 0.15	0.26 ± 0.25	0.12 ± 0.09	0.10 ± 0.08	0.24 ± 0.18	0.24 ± 0.17	-
<i>Celleporaria</i> sp.	0.12 ± 0.04	0.19 ± 0.13	0.13 ± 0.09	0.15 ± 0.12	0.11 ± 0.08	0 ± 0.12	0.13 ± 0.12	0.11 ± 0.05	0.10 ± 0.06	0.11 ± 0.07	0.13 ± 0.09	0.17 ± 0.14	0.10 ± 0.07	0.20 ± 0.02	0.12 ± 0.15	0.0
Halichondriidae sp1	0.06 ± 0.01	0.28 ± 0.17	0.55 ± 0.24	0.16 ± 0.17	0.17 ± 0.18	0.17 ± 0.22	0 ± 0.00	0.00 ± 0.00	0.21 ± 0.27	0.27 ± 0.20	0.12 ± 0.11	0.14 ± 0.13	0.12 ± 0.09	0.18 ± 0.11	0.12 ± 0.02	0.0
<i>W. torquata</i>	-	0.22 ± 0.19	0.00 ± 0.00	0.00 ± 0.00	0.15 ± 0.12	0.24 ± 0.08	0.00 ± 0.00	0 ± 0.00	0.00 ± 0.00	0.16 ± 0.13	0.11 ± 0.07	0.09 ± 0.08	0.00 ± 0.00	0.31 ± 0.00	0.06 ± 0.01	-
Microcionidae sp.	-	0.21 ± 0.16	0.16 ± 0.03	0.16 ± 0.14	0.14 ± 0.12	0.12 ± 0.09	0.07 ± 0.06	0.17 ± 0.12	0 ± 0.05	0.08 ± 0.07	0.13 ± 0.07	0.12 ± 0.06	0.13 ± 0.09	0.16 ± 0.11	0.15 ± 0.09	-
Leucetiidae sp2	-	0.23 ± 0.19	0.11 ± 0.06	0.14 ± 0.10	0.15 ± 0.13	0.15 ± 0.11	0.27 ± 0.20	0.14 ± 0.07	0.10 ± 0.06	0 ± 0.04	0.13 ± 0.09	0.16 ± 0.09	0.18 ± 0.09	0.11 ± 0.01	0.27 ± 0.23	-
<i>Parasmitina</i> sp.	0.26 ± 0.08	0.24 ± 0.17	0.10 ± 0.07	0.14 ± 0.10	0.12 ± 0.08	0.16 ± 0.13	0.12 ± 0.08	0.10 ± 0.03	0.09 ± 0.06	0.28 ± 0.00	0 ± 0.10	0.13 ± 0.11	0.12 ± 0.11	0.11 ± 0.07	0.15 ± 0.05	0.05 ± 0.05
Leucetiidae sp1	-	0.29 ± 0.21	0.08 ± 0.04	0.16 ± 0.22	0.13 ± 0.09	0.13 ± 0.11	0.12 ± 0.12	0.16 ± 0.10	0.12 ± 0.06	0.20 ± 0.14	0.13 ± 0.10	0 ± 0.09	0.12 ± 0.09	0.14 ± 0.12	0.10 ± 0.02	-
<i>C. australis</i>	-	0.32 ± 0.17	0.00 ± 0.00	0.14 ± 0.09	0.15 ± 0.10	0.15 ± 0.10	0.14 ± 0.10	0.28 ± 0.00	0.17 ± 0.18	0.11 ± 0.06	0.14 ± 0.11	0.15 ± 0.11	0 ± 0.02	0.20 ± 0.12	0.39 ± 0.12	-
<i>B. leachi</i>	-	0.33 ± 0.17	0.26 ± 0.15	0.44 ± 0.38	0.18 ± 0.19	0.15 ± 0.02	0.10 ± 0.05	0.17 ± 0.00	0.44 ± 0.19	0.19 ± 0.06	0.17 ± 0.13	0.26 ± 0.24	0.09 ± 0.00	0 ± 0.27	0.30 ± 0.27	-
Halichondriidae sp2	0.18 ± 0.07	0.31 ± 0.21	0.08 ± 0.02	0.14 ± 0.07	0.13 ± 0.07	0.15 ± 0.14	0.12 ± 0.12	0.05 ± 0.04	0.13 ± 0.08	0.17 ± 0.07	0.13 ± 0.07	0.13 ± 0.08	0.08 ± 0.03	0.08 ± 0.00	0 ± 0.00	0.09 ± 0.0
Halichondriidae sp4	0.43 ± 0.16	-	-	0.30 ± 0.0	-	0.0	0.0	-	-	-	0.20 ± 0.12	-	-	-	0.0 ± 0.0	0

Table 3. The mean recruitment rates per day \pm 1 standard deviation of the 14 species modelled.

	Mean Recruitment Rate (Number of recruits/mm ² /day)	Standard Deviation
Phloeodictyidae sp.	2.854 e-7	5.725 e-7
<i>Didemnum</i> sp.	2.928 e-6	3.409 e-6
Halichondriidae sp3	1.371 e-6	1.534 e-6
<i>Celleporaria</i> sp.	6.668 e-7	9.473 e-7
Halichondriidae sp1	8.618 e-8	2.152 e-7
<i>W. torquata</i>	1.325 e-7	4.588 e-7
Microcionidae sp.	5.397 e-7	1.121 e-6
Leucetiidae sp2	5.331 e-7	9.028 e-7
<i>Parasmittina</i> sp.	2.941 e-7	4.682 e-7
Leucetiidae sp1	2.479 e-7	3.793 e-7
<i>C. australis</i>	6.998 e-8	1.904 e-7
<i>Botrylloides leachi</i>	1.237 e-7	3.174 e-7
Halichondriidae sp2	6.778 e-8	1.967 e-7
Halichondriidae sp4	4.192 e-8	1.582 e-7

with a power curve. To prevent the fitted relationships from exceeding the bounds of biologically reasonable values, upper and lower limits were set. As the predicted probability of mortality can be less than 0 in a linear relationship, a lower limit was set as the probability of mortality shown by the largest size class (Table 4). Where no mortality was observed in the largest size class the probability was set to 0.0001, an arbitrarily small number similar to the lowest mortality observed for other species with a linear relationship. For species with a power relationship (where the predicted relationship can exceed 1 for very small colonies), the upper limit was set at the probability of mortality shown by the smallest size class (Table 4).

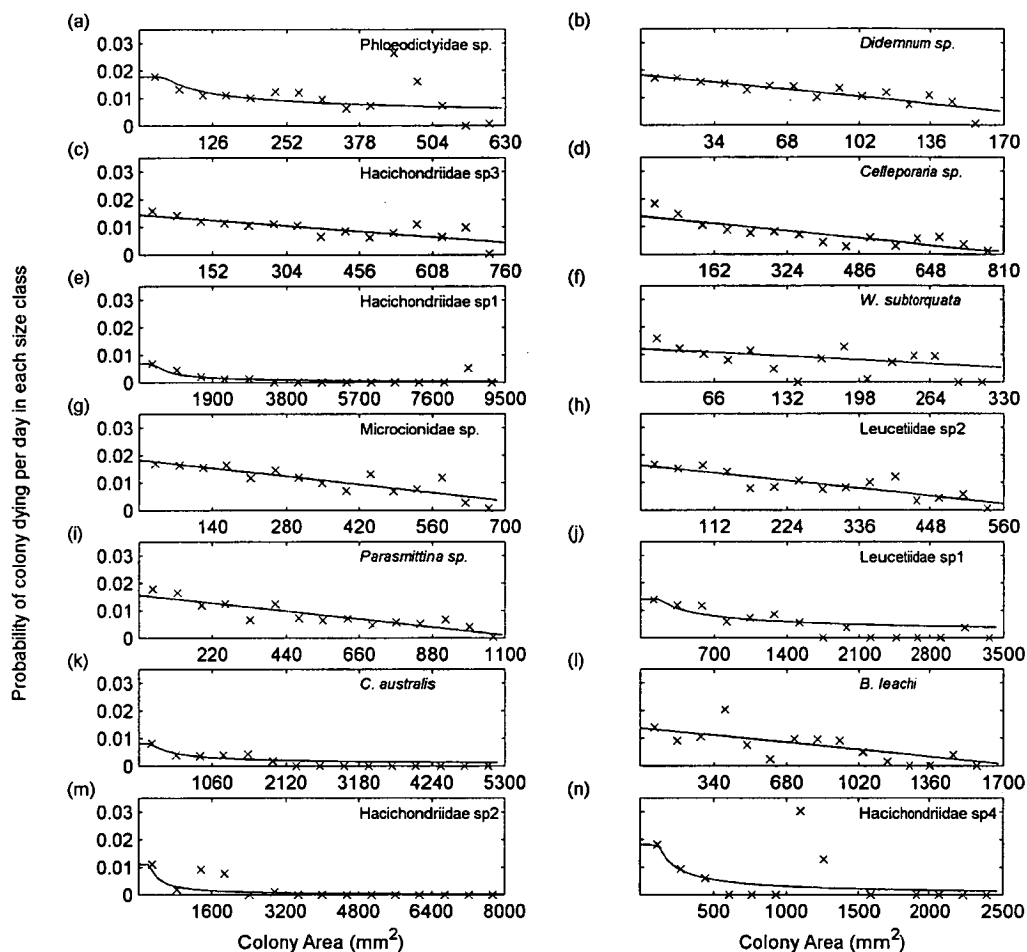


Figure 1. Size specific mortality rates of the 14 species used in this study. The empirical probability of mortality per day of a colony in each size class is represented by 'x', and the fitted relationship is shown as a solid line. The upper limits for power curve relationships are shown (the probability of mortality of the smallest size class), while the lower limits for linear relationships are set by the probabilities of mortality for the largest size classes (fits are given in Table 4).

Table 4. The relationship between mortality rates (per day) and colony size (mm²). Where the relationship is linear, the coefficients refer to $y = mx + c$, and the limit sets the lower limit of mortality. Where the relationship is a power curve, the coefficients refer to $y = c \cdot x^m$, and the limit sets the upper limit to mortality.

	Relationship	C	M	Limit	R ²
Phloeodictyidae sp.	Power curve	-2.58887	-0.38235	0.0179	0.1695
<i>Didemnum</i> sp.	Linear	0.018261	-7.8E-05	0.0005	0.7536
Halichondriidae sp3	Linear	0.014462	-1.3E-05	0.0003	0.6207
<i>Celleporaria</i> sp.	Linear	0.013775	-1.6E-05	0.0012	0.7170
Halichondriidae sp1	Power curve	0.259883	-0.8775	0.0068	0.9221
<i>W. torquata</i>	Linear	0.012157	-2.1E-05	0.0001	0.2105
Microcionidae sp.	Linear	0.018323	-2.1E-05	0.0007	0.74261
Leucetiidae sp2	Linear	0.016295	-2.5E-05	0.0006	0.7329
<i>Parasmittina</i> sp.	Linear	0.015656	-1.3E-05	0.0003	0.7981
Leucetiidae sp1	Power curve	-1.92948	-0.44334	0.0140	0.7812
<i>C. australis</i>	Power curve	-1.86155	-0.56307	0.0082	0.8437
<i>Botrylloides leachi</i>	Linear	0.01372	-7.7E-06	0.0001	0.3854
Halichondriidae sp2	Power curve	0.963215	-1.01051	0.0110	0.8994
Halichondriidae sp4	Power curve	0.006982	-0.83625	0.0180	0.9971

MANIPULATION OF SPECIES INTO ARTIFICIAL COMMUNITIES

Six species were selected (on the basis of ease of manipulation and ability to survive when transplanted) for manipulation into 'artificial' communities, two bryozoans *Celleporaria* sp. and *Parasmittina* sp., an ascidian *Didemnum* sp. and three sponges, Halichondriidae species 1, 2 and 4. Colonies of each species were removed from the concrete wall and transplanted onto terracotta tiles of dimensions 50 * 50 mm and held in place with rubber bands. The colonies were left for 8 months, to allow growth and attachment to the tiles prior to manipulation into artificial

communities on the 13th November 1997. Transplanted colonies were arranged onto roughened PVC boards (500*500 mm) in four spatially distinct patterns (Figure 2), with each pattern replicated 5 times. Tiles were attached to the boards with cable ties threaded through holes in the boards. Two patterns had a random arrangement of the 6 species with either 12% or 24% initial cover (Figure 2). The remaining two patterns contained the 6 species at 12% initial cover, in either a pattern with all species grouped in the centre of the mat or in a pattern where each colony was equidistant to the two adjacent colonies. The mats were weeded each month to remove any species other than the original six. Each mat was sampled photographically three times, on 24th March 1998, 22nd August 1998 and 16th March 1999 (131, 313 and 488 days respectively after the communities were established).

SPATIAL MODEL

Local rules at two scales

The dynamics of the multispecies assemblage were modelled using stochastic cellular automata with a von Neumann neighbourhood, synchronous updating and an open landscape (i.e. absorbing boundaries). Unlike other individual based models, individual colonies in our models are blocks of contiguous cells of the same species. Growth, interaction and recruitment take place at the scale of individual cells (local cell rules), while mortality occurs at the scale of the individual (local individual rules). The local rules of interactions between cells are:

1. If a cell is unoccupied (i.e. in a 'free space' state), one of the four adjacent cells in the neighbourhood is selected at random, and if the selected cell is occupied it grows into the empty cell with a probability g_{iFS} , where g_{iFS} is the growth rate of species i over free space.

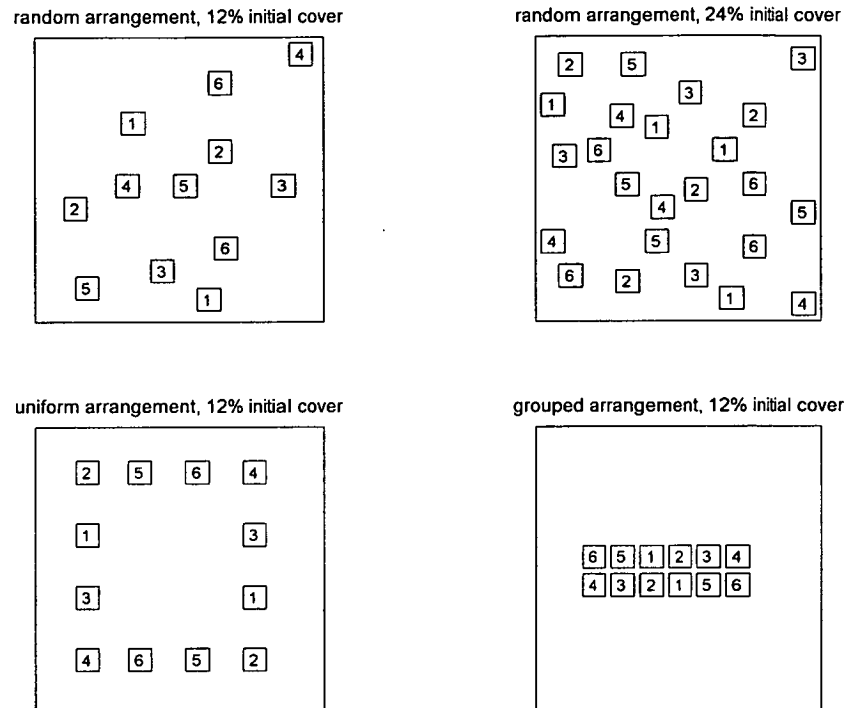


Figure 2. The spatial arrangement of the 6 species in the manipulated communities. Species codes are, 1 = *Didemnum* sp., 2 = *Celleporaria* sp., 3 = *Halichondriidae* sp1, 4 = *Parasmittina* sp., 5 = *Halichondriidae* sp4 and 6 = *Halichondriidae* sp2.

2. If a cell is occupied by species i , one of the four adjacent cells in the neighbourhood is selected at random. If the selected cell is occupied, it grows into the central cell with a probability $a_{ij} * g_{ij}$, where a_{ij} is the probability of species i winning an interaction with species j and g_{ij} is the growth rate of species i over species j .

Any cell in the neighbourhood has a probability of $0.25 * a_{ij} * g_{ij}$ of growing in to the central cell. This scales the probability for the presence of multiple cells of the same species in a neighbourhood. Thus with 2 cells of the same species (i) surrounding a central cell (species j) the probability of i overgrowing j is $0.5 * a_{ij} * g_{ij}$, with 3 cells the probability is $0.75 * a_{ij} * g_{ij}$ and with all neighbours of j being i , i overgrows j with

a probability of $1 * a_{ij} * g_{ij}$. Neighbour-specific growth rates for each simulation were selected from a normal distribution, described by the observed mean neighbour-specific growth rate ± 1 standard deviation (Table 2).

New recruits of each species were introduced onto a single empty cell in the landscape with a probability r_i , the recruitment rate of species i (Table 3).

Mortality was calculated using local individual rules (rather than local cell rules) to simulate size-specific mortality. Despite size-specific mortality being a deviation from strict local rules, the models are individual based in the sense that each block of contiguous cells of the same species can be considered an individual colony. The area of each 'colony' on the landscape was calculated by counting the number of contiguous cells of the same species, and the probability of the whole colony dying was determined from the predicted relationships between colony size and mortality from the empirical data for that species (Table 4). If a random number was less than this probability, the entire colony was removed from the landscape, returning all cells to a state of 'free space'.

Scaling space and time in the model

The model parameters were scaled so that a single cell was equivalent to $10 * 10$ mm (100 mm^2) in the natural system and each iteration of the model was equivalent to 1 day. Neighbour-specific growth rates were scaled to represent the probability of growth over a distance of 10 mm over the period of one day and the probability of a new recruit was scaled as the probability recruitment per 100 mm^2 per day. As a consequence of scaling space, the area of model 'colonies' could be converted from cells to mm^2 and used to calculate the probability of mortality.

Tests to compare models with manipulated and non-manipulated communities

Models were compared with manipulated and non-manipulated real communities using two multivariate statistical approaches. The first tested the null hypothesis that the distance between multivariate centroids describing replicate model and real communities in Euclidean space was less than expected by chance. The second method tested the null hypothesis that the centroid of the modelled assemblage was an equally efficient measure of central tendency of the multivariate replicates of the real observed community as the centroid describing the observed community. This test compares the distances of empirical data points (either from manipulated or non-manipulated real communities) of replicate communities to the centroid of these data points with the distances of the same empirical data points to the centroid predicted by the replicate model assemblages.

To test whether model centroids were closer to the empirically observed centroid than expected by chance, *t*-tests assuming differences in sample sizes and variances were adapted for a multivariate case. The test was conducted as a randomisation procedure on the raw data describing the total cover of each species on each replicate (real or simulated) patch (randomisation *t*-test). The area occupied in model communities was converted from cells to mm² using our knowledge of the scale of each cell to allow comparison with real communities. An initial t_{obs} statistic was calculated using the formula:

$$t_{obs} = \frac{\left(\sum_{i=1}^p (\bar{y}_{i,model} - \bar{y}_{i,emp})^2 \right)^{1/2}}{\left(\frac{s_{model}^2}{n_{model}} + \frac{s_{emp}^2}{n_{emp}} \right)^{1/2}} \quad \text{eq. (1)}$$

$$\text{where } s_{\text{model}}^2 = \frac{\sum_{i=1}^p \sum_{j=1}^n (y_{ij \text{ model}} - \bar{y}_{i \text{ model}})^2}{n_{\text{model}} - 1} \quad \text{eq. (2)}$$

and s_{emp}^2 is calculated in the same way using empirical data (either from manipulated or non-manipulated communities); p is the number of species, n the number of replicates from either models or empirical data points and $y_{ij \text{ model}}$ and $y_{ij \text{ emp}}$ are the i^{th} and j^{th} observation from model and empirical communities respectively. It should be noted that the variance measure s^2 is the trace of the covariance matrix, i.e. the sum of the variances of each component species. The raw data was then allocated randomly across the two groups (i.e. model and empirical communities) retaining the appropriate sample size, and a $t_{\text{randomise}}$ calculated. The randomisation procedure was iterated 20,000 times and the value of t_{obs} compared to the distribution of $t_{\text{randomise}}$ to calculate a significance value. This test does not have associated degrees of freedom, nor does it assume multivariate normality in the data. However, because the number of replicate empirical data points is much less than the number of data points generated from different runs of the model, and each empirical data point exerts a greater influence on the position of its associated centroid than does each replicate data point from the model.

The second method tested the distribution of empirical data points relative to the centroids of both the empirically and model derived data (distance t -test). The distance in Euclidean space between each empirical data point and the empirical centroid was calculated and compared to the distances between same the empirical data points and the centroid of the replicate modelled assemblages using a standard t -test. Unlike a standard t -test on raw data, which is relatively insensitive to the distribution of points around a centroid (the mean), this test is sensitive to both

differences between centroids and the distribution of points around the centroid. The test is balanced with respect to the number of observations.

The two tests quantify different aspects of the relationship between model and empirical communities. The randomisation *t*-test explores the difference between the centroids of the communities and largely ignores the variance around these means. While this may be appropriate in situations where experimenters are interested in only the mean response of a treatment (and partitioning out natural variance) it does not adequately test if one cluster of data points could potentially be a subsample of a 'global' cluster. In this case the 'global' cluster is the data points predicted by the models and the subsample is the natural community. We are trying to predict possible communities with the models and discern if the natural communities belong to that multivariate distribution. Distances are minimised from the subsample cluster to its centroid. If the subsample data points are not tightly clustered around their centroid relative to the cluster of model data points, then distances do not change significantly with a different centroid (i.e. the model centroid) and we can conclude that the subsample could be derived from the 'global' cluster.

DYNAMICS OF MANIPULATED COMMUNITIES WITH DIFFERENT INITIAL CONFIGURATIONS

The structure of each manipulated community based on total cover of component species was compared 131, 313 and 488 days after the communities were established using NPMANOVA (Anderson 2001). Communities were tested at each time to avoid repeated measurements on the same community over multiple times. After 131 days the communities were significantly different ($F_{3,16} = 4.1978$, $P = 0.0058$; Figure 3a). *A posteriori* comparisons showed that communities in the initial

12% cover 'grouped' arrangement were significantly different from communities with an initial 24% cover in a random arrangement ($t = 2.8776$, $P = 0.0176$, unadjusted for multiple comparisons). However, after 313 days the communities were no longer significantly different ($F_{3,16} = 2.1912$, $P = 0.0828$; Figure 3b), and this trend continued to the final census 488 days after initial establishment ($F_{3,16} = 1.0561$, $P = 0.3887$; Figure 3c). At each time all species had high variance, consequently the communities had high multidimensional variance (Figure 4).

MODELLING MANIPULATED COMMUNITIES

The manipulated communities were modelled using the spatial model with a landscape size of 50 * 50 cells, corresponding to a cell size of 10 * 10 mm and a total patch area of 500 * 500 mm. The initial spatial conditions of the models were set to the initial spatial arrangement of each of the manipulated communities and a separate model was run for each of the four spatial configurations. The models were parameterised with the six species used in the manipulated communities, viz. *Celleporaria* sp., *Parasmittina* sp., *Didemnum* sp. and Halichondriidae species 1, 2 and 4 (Table 1, 2, 3, 4). Model communities were simulated as 300 Monte Carlo runs of 488 iterations, each run equivalent to 488 days.

Some species on the roughened PVC mats displayed much higher growth rate into free space than was observed in the quadrats on the jetty wall. Free space on mats was contained no other species, whereas free space on the concrete wall was covered with entoprocts. Species still grew into free space on the walls but the rate

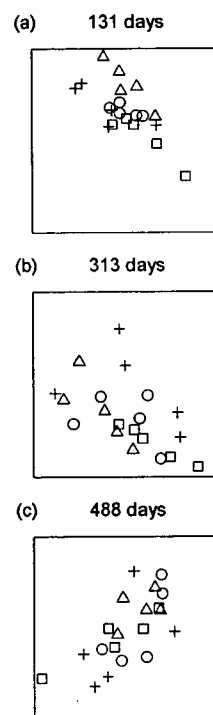


Figure 3. Metric multidimensional scaling of manipulated communities at (a) 131, (b) 313 and (c) 488 days after each community was established. '+' represents communities with an initial configuration of 12% cover, randomly distributed; 'o' represents communities with an initial configuration of 12% cover, uniformly distributed; 'Δ' represents communities with an initial configuration of 12% cover with colonies grouped in the centre; '□' represents communities with an initial configuration of 24% cover, randomly distributed.

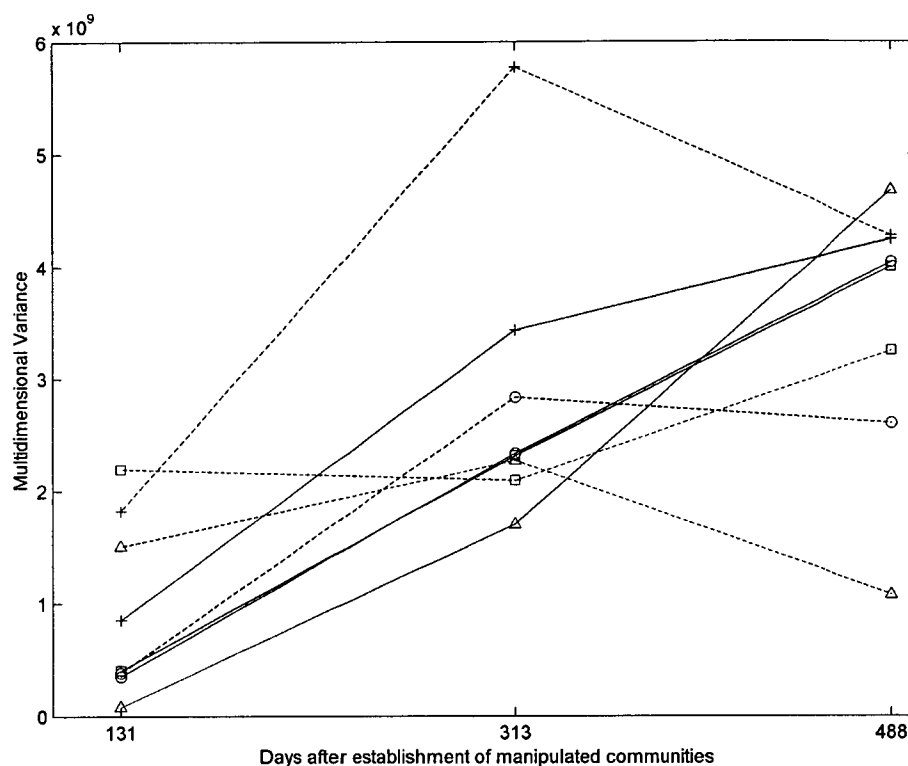


Figure 4. The multidimensional variance (calculated using eq. (2)) of manipulated (dashed lines) and model (solid lines) communities. '+' represents communities with an initial configuration of 12% cover, randomly distributed, 'o' represents communities with an initial configuration of 12% cover, uniformly distributed, 'Δ' represents communities with an initial configuration of 12% cover with colonies grouped in the centre, '□' represents communities with an initial configuration of 24% cover, randomly distributed.

was slowed. Thus, in parameterising these models it was appropriate to use empirical measures of the mean and standard deviation of growth into free space on the PVC mats than the measures of colony growth into free space on the concrete walls.

The cover of each species in model runs sampled at 131, 313 and 488 iterations (equivalent to 131, 313 and 488 days) were compared with the corresponding manipulated communities using both the randomisation multivariate *t*-test and the distance *t*-test. In 75% of tests, significant differences were found between the

centroids of modelled and manipulated communities (Table 5, randomisation *t*-test).

Tests using the distance *t*-test showed similar results, with 66% of tests indicating significant differences between model and manipulated communities (Table 5, distance *t*-test).

Table 5. Results of tests comparing model communities with manipulated communities 131, 313 and 488 days after establishment.

	Randomisation <i>t</i> -test	Distance <i>t</i> -test
Random 12% arrangement		
After 131 days	$t = 2.52, p = 0.059$	$t = 1.89, df = 8, p = 0.096$
After 313 days	$t = 1.99, p = 0.120$	$t = 0.55, df = 8, p = 0.604$
After 488 days	$t = 3.92, p = 0.0333$	$t = 2.498, df = 8, p = 0.037$
Even 12% arrangement		
After 131 days	$t = 8.23, p = 0.000$	$t = 12.665, df = 8, p = 0.000$
After 313 days	$t = 2.433, p = 0.050$	$t = 1.844, df = 8, p = 0.1025$
After 488 days	$t = 4.46, p = 0.005$	$t = 3.215, df = 4.4, p = 0.292$
Grouped 12% arrangement		
After 131 days	$t = 3.41, p = 0.01$	$t = 1.712, df = 8, p = 0.125$
After 313 days	$t = 3.03, p = 0.031$	$t = 3.084, df = 8, p = 0.015$
After 488 days	$t = 7.78, p = 0.0008$	$t = 8.435, df = 8, p = 0.000$
Random 24% arrangement		
After 131 days	$t = 4.84, p = 0.0004$	$t = 3.251, df = 8, p = 0.018$
After 313 days	$t = 3.59, p = 0.008$	$t = 4.173, df = 8, p = 0.0031$
After 488 days	$t = 3.33, p = 0.019$	$t = 3.19, df = 8, p = 0.0128$

It should be noted that the tests were not adjusted for multiple comparisons, which is conservative in evaluating whether the models accurately predicted the dynamics of the real system. While both model and manipulated communities were dominated by *Didemnum sp.* (Figure 5), abundances of *Parasmittina sp.* and Halichondriidae sp4 were considerably higher in the manipulated communities than in their model counterparts. The overall total variance for each community

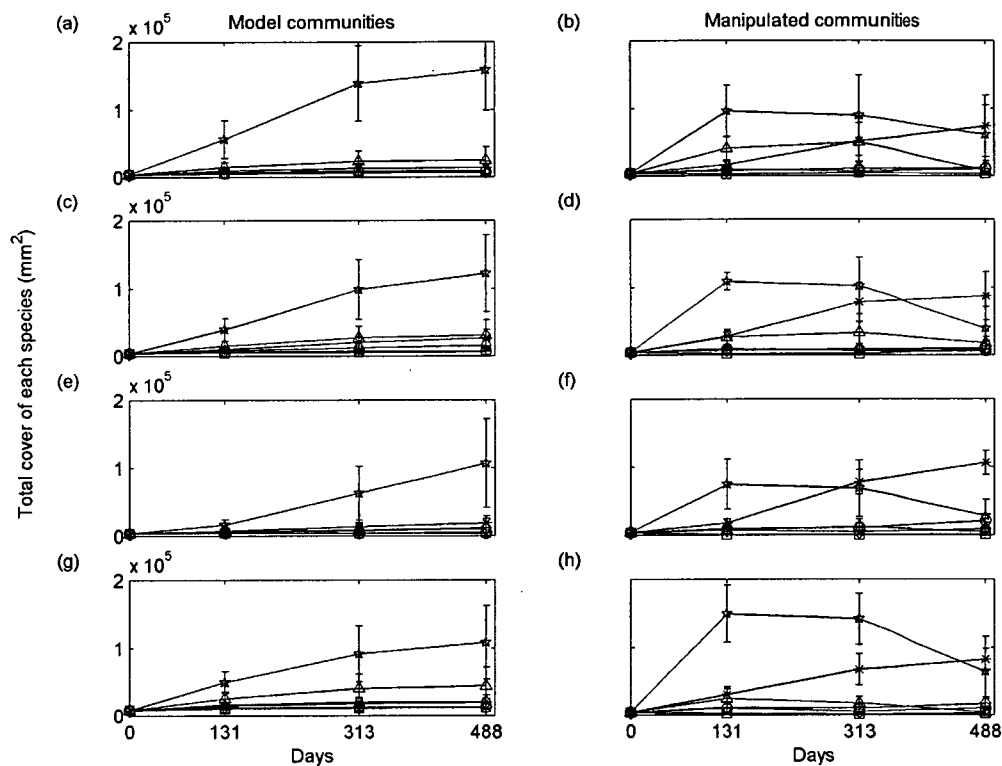


Figure 5. Mean abundances (± 1 standard deviation) of species in manipulated and corresponding model communities sampled 131, 313 and 488 days after establishment. Abundances are shown for model and manipulated communities with initial conditions of 12% randomly arranged (a and b), 12% cover, uniformly arranged (c and d), 12% cover, grouped arrangement (e and f), and 24% cover, randomly arranged (g and h). '☆' represents *Didemnum* sp., ' ' represents *Parasmittina* sp., '△' represents *Halichondriidae* sp4, 'o' represents *Celleporaria* sp., '□' represents *Halichondriidae* sp1 and '◇' represents *Halichondriidae* sp2.

configuration was similar in models and manipulated communities (Figure 4). The variability of manipulated communities was generally higher than model communities after 131 days. Variability in model communities increases (approximately) linearly with time, whereas in most cases variability in the manipulated communities was observed at the 313 day census.

MODELLING NON-MANIPULATED COMMUNITIES

A multispecies model of the 13 most common species on the wall of jetty was used to simulate a quadrat on the jetty wall. These species, *Didemnum* sp., *Botrylloides leachi*, *Celleporaria* sp., *Parasmittina* sp., *Watersipora subtorquata*, *Phloeodictyidae* sp., *Leucetiidae* sp1, sp2, *Halichondriidae* sp1, sp2, sp3, *Microcionidae* sp. and *Corynactis australis* accounted for 84.3% of the total cover and 89.1% of the total colonies. The parameters used for each species are outlined in Tables 1-4. The model was simulated on a 100 * 200 cell landscape and the cell size was scaled to 10 * 10 mm, thus the landscape size was equivalent to the area of concrete between the girders from which the quadrats were sampled. The landscape had open boundaries. Model communities were simulated as 400 Monte Carlo runs, each of 6000 iterations, equivalent to 6000 days (16.4 years) and the cover of each species was sampled every 300 iterations. The landscape was initialised with 0% cover, and recruitment was the only source of new species and colonies. This corresponds with the initial conditions of the jetty when it was constructed in 1985. Within the landscape, an area corresponding to the size a quadrat (32 * 32 cells) was subsampled. The position of each subsample was fixed for the duration of each run.

These subsamples of the model community were compared to the cover observed in the equivalent sized quadrats on the jetty wall. To remove effects of repeated observations of the same quadrats (23 in total), species cover in each sampled quadrat was averaged over the 11 censuses taken between 19th of November 1996 and 6th of January 1998. This yielded 23 replicate empirical observations to compare with the 400 runs of the model community. The species dynamics of the 23

empirical observations was compared with subsamples taken from model communities.

For these runs of the model, the size of a single colony was not limited and several colonies of the same species could coalesce to form a super colony. Thus, colonies could potentially dominate the entire landscape. The size-frequency distribution (expressed as the percentage of total colonies in each size class) for each

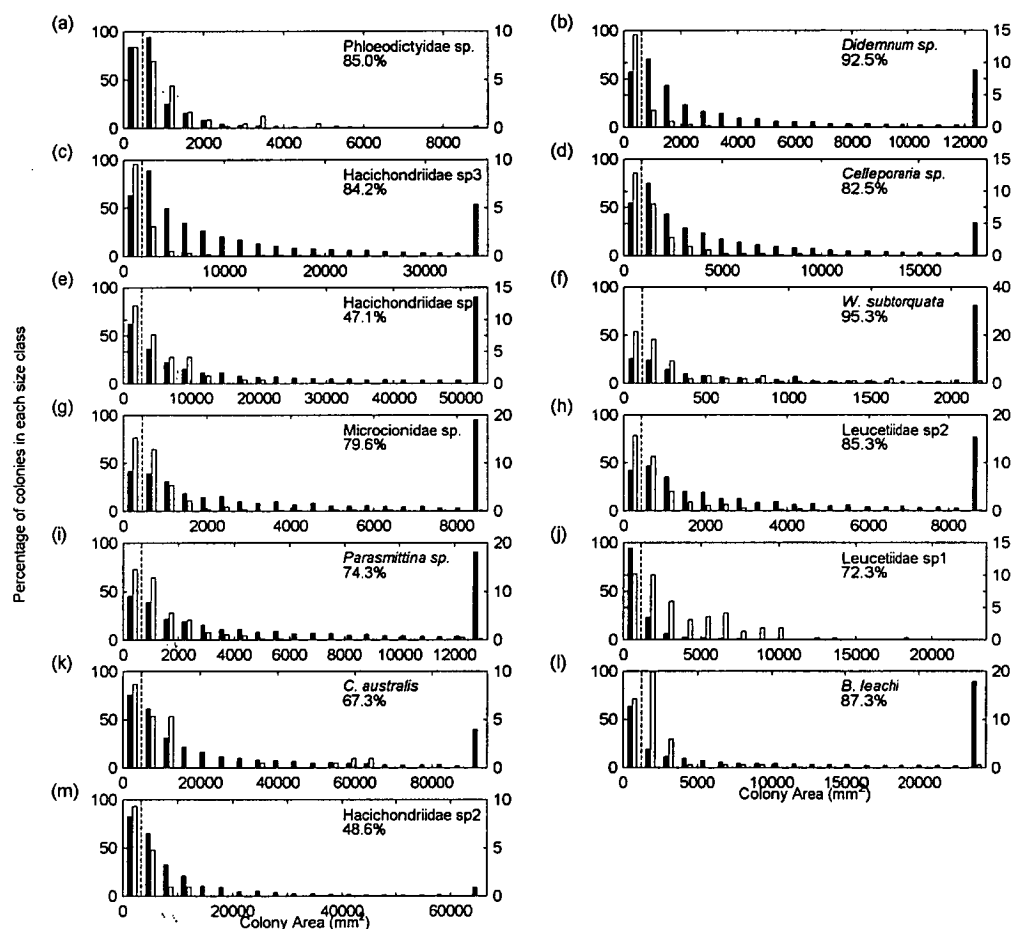


Figure 6. Size frequency distributions of species in model communities (closed bars) and in quadrats on the jetty wall (open bars) expressed as a proportion. Size classes to the left of the dashed vertical line refer to the left-hand axis and size-classes on the right of the dashed line refer to the right-hand axis. The proportion of complete colonies in quadrats on the jetty wall is shown in the upper right corner for each species.

species from the model was compared with the size-frequency distribution of complete colonies within the 23 observed quadrats on the jetty walls (Figure 6). Any colony whose boundaries were completely within a quadrat on the jetty wall, so that area could be accurately measured, was counted as a 'complete' colony. 'Complete' colonies on the jetty wall were divided into 20 size classes, encompassing the entire range of sizes observed. The proportions of colonies in each size class were compared to the equivalent proportions from the models (Figure 6). Colonies from models were sampled from the entire landscape. While the size-frequency distributions are similar over much of the size range, it is clear that many species have proportionally many more of the largest colony size in model communities than exist in natural communities on the jetty wall. Note that the percentage of complete colonies was high in quadrats on the jetty wall, indicating the 0.1 m² quadrat was sufficiently large to capture a representative picture of the size frequency distribution.

Limiting the maximum size of colonies

For species where the percentage of complete colonies in quadrats on the jetty wall was >70% but the percentage of the largest size class of colonies in the models was disproportionately greater than that observed on the jetty wall, the maximum size of a colony in the models was limited to the maximum size of complete colonies observed in the quadrats on the jetty wall (Table 6). While a single colony (a block of contiguous cells) could not grow beyond this limit, smaller colonies could grow and fuse to form larger colonies. These new colonies formed by fusion were then unable to grow any larger unless another smaller colony grew and fused with the larger one.

Table 6. The limits to the sizes of colonies for each species.

Species	Size Limit
Phloeodictyidae sp.	No limit
<i>Didemnum</i> sp.	11512
Halichondriidae sp3	36282
<i>Celleporaria</i> sp.	10365
Halichondriidae sp1	No limit
<i>W. torquata</i>	2216
Microcionidae sp.	8730
Leucetiidae sp2.	8922
<i>Parasmittina</i> sp.	13193
Leucetiidae sp1	No limit
<i>C. australis</i>	No limit
<i>Botrylloides leachi</i>	24477
Halichondriidae sp2	No limit

The multivariate variance of empirical quadrats was compared to the variance of equivalent sized subsamples of model communities (Figure 7). The variance ratio of empirical to model variance did not differ significantly from unity after 2400 iterations ($F_{22,399} = 1.3091$, $p = 0.1597$), equivalent to 6.6 years. The variance of the models was greater than the observed variance after 3000 iterations and continued to increase steadily. Models with additional parameters defining size limits had significantly different centroids at 2400 iterations ($t = 3.735$, $P = 0.000$; randomisation t -test) to the empirically observed quadrats. However, the distances from replicate empirical quadrats to the centroids of empirical quadrats and of the models subsamples were not significantly different ($t_{44} = 1.804$, $P = 0.0781$; distance t -test).

Metric multidimensional scaling diagrams at 300, 2400, 3900 and 6000 iterations (Figure 8a-8d) show the changes in community structure over time. After 3900 iterations, the approximate age of the jetty when photographs began (10.7

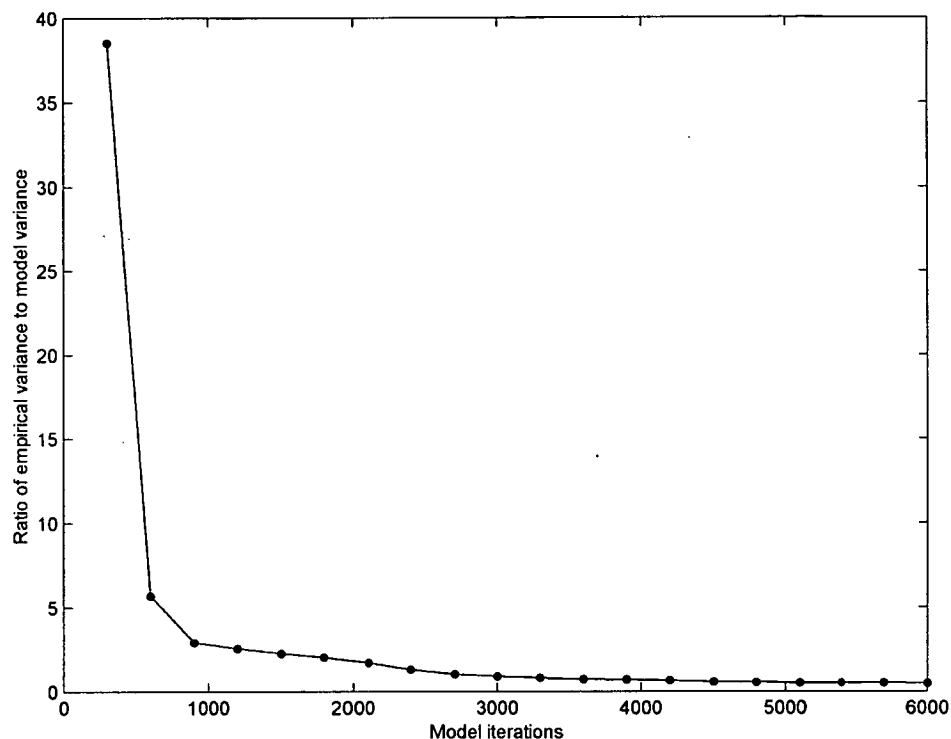


Figure 7. The change in the ratio of multidimensional variance of non-manipulated quadrats on the jetty wall and model subsamples, calculated using eq. (2).

years), model and empirical distributions overlap ($t_{44} = 1.8521$, $P = 0.1356$; distance t -test; Figure 8c) although the centroid are still significantly different ($t = 3.198$, $P = 0.000$; randomisation t -test). Empirical observations lie largely within the distribution of points from replicate runs of the model community. The distance t -test indicates that after 2400 iterations natural communities are effectively a subset of the possible communities predicted by the models. The three quadrats slightly outside the distribution of model community structures are all characterised by high covers of *C. australis*. After 6000 iterations (16.4 years), the community configuration of quadrats in MDS space lies within the distribution of the model space.

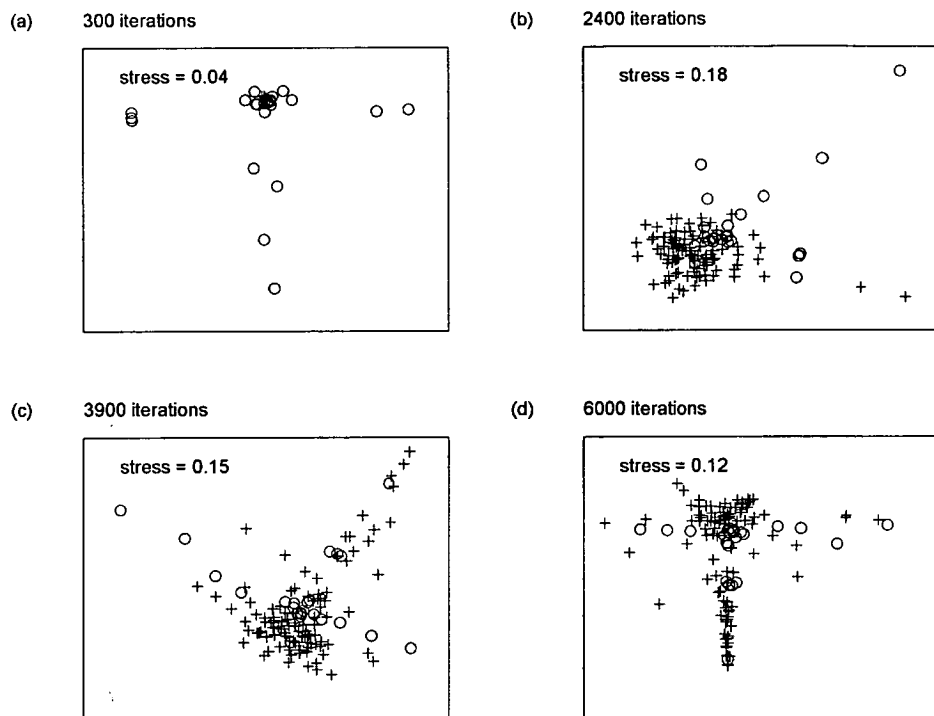


Figure 8. Metric multidimensional scaling of community structure in the 23 quadrats on the jetty wall (o) and in equivalent sized subsamples from replicate runs of the model community (+) at 300, 2400, 3900 and 6000 iterations.

Didemnum sp. rapidly acquires space in the model community and continues to hold that space over time (Figure 9a). This is due to its relatively high recruitment rate. *B. leachi* and Halichondriidae sp3 also acquire space rapidly. In contrast, Halichondriidae sp1 and *C. australis* are slow to occupy a significant amount of space but their cover gradually increases through time. A notable characteristic of these two species is that as their average cover increases, so does the variance in their cover (Figure 9b). When these species are present, they are likely to eventually completely dominate space. The cover of Halichondriidae sp1 and *C. australis* in quadrats on the jetty wall showed similar patterns, with colonies dominating space in some quadrats or small or absent in others (Figure 9a).

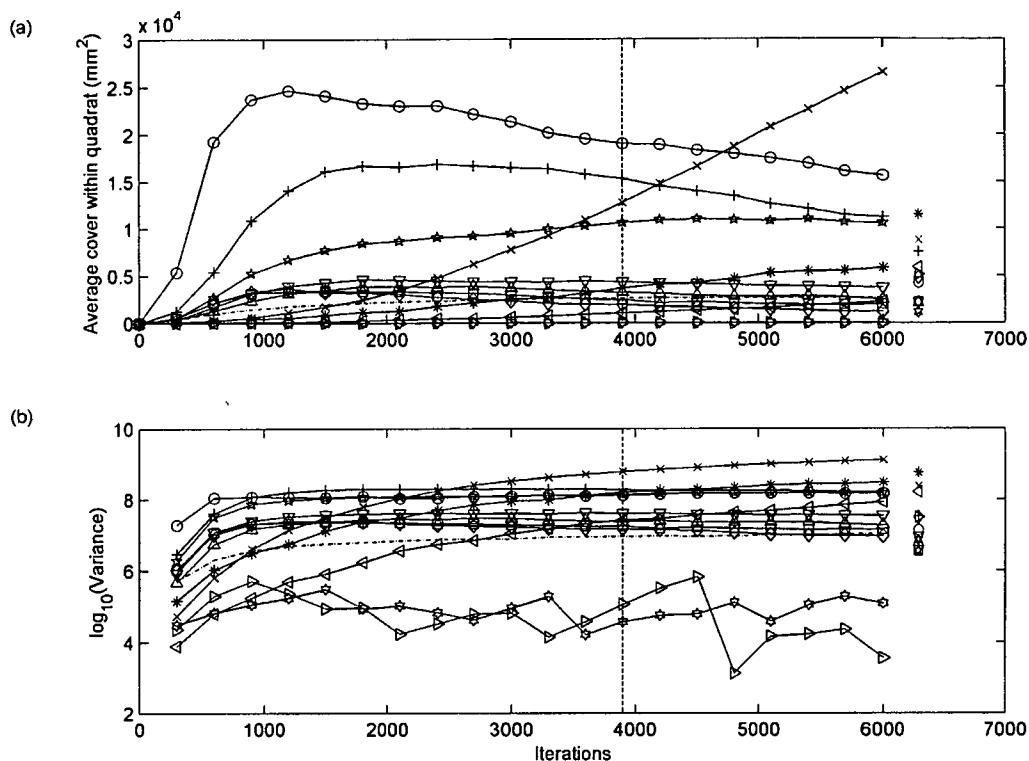


Figure 9. The average cover (a) and variances (b) of species in subsamples of model landscapes and from quadrats on the jetty wall (shown on the far right). 'o' represents *Didemnum* sp., '+' represents *Halichondriidae* sp3, '☆' represents *Botrylloides leachi*, 'x' represents *Halichondriidae* sp1, '*' represents *Corynactis austalis*, '◇' represents *Celleporaria* sp., '▽' represents *Parasmittina* sp., '•' represents *Watersipora subtorquata*, '☆' represents *Phloeodictyidae* sp., '▷' represents *Leucetiidae* sp1, '◁' represents *Halichondriidae* sp2, '□' represents *Microcionidae* sp. and '△' represents *Leucetiidae* sp2.

The distribution of the Shannon diversity of subsamples from the model communities was similar to that of the empirical quadrats on the jetty wall (Figure 10). However, quadrats on the jetty wall had a spike in diversity above 2.7, possibly due to the consistently higher numbers of species in the jetty wall (Figure 10). Despite the jetty wall having higher species numbers, the evenness of species in quadrats and in models was very similar.

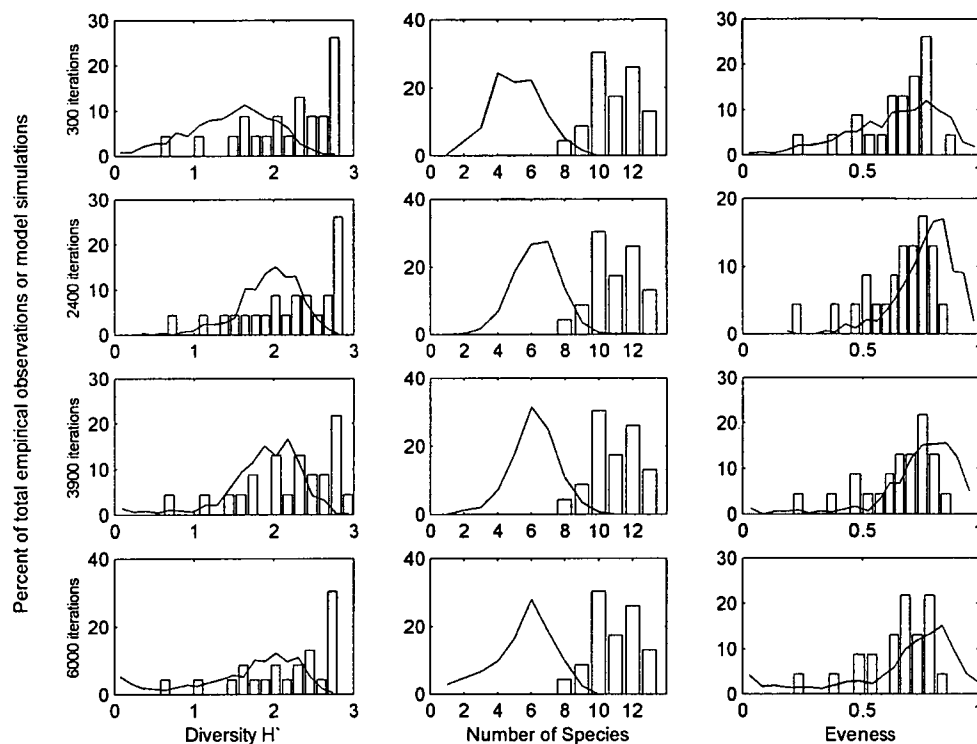


Figure 10. The distribution of Shannon-Wiener diversity, species number and evenness of replicate quadrats on the jetty wall (represented by open bars) and of equivalent sized subsamples from replicate runs of the model community (solid line) at 300, 2400, 3900 and 6000 iterations.

DISCUSSION

Spatially explicit models are no longer novel in ecology and have shown that local interactions at the scale of individual 'cells', can generate a wide range of non-trivial global behaviours (e.g Durrett and Levin 2000, Johnson 1997, Kendall and Fox 1998, Savill and Hogeweg 1999). Despite their wide application, critical tests of the dynamics of these models in the form of comparisons of the dynamics of the models with that of the natural systems they are intended to represent have not been forthcoming. Difficulties in sampling a community sufficiently intensely to generate appropriate parameters has meant that examples of these sorts of models are rare.

This study required measurements of ca. 15,000 colonies and 20,000 pair-wise interactions in total. Even with this level of census, estimates of some parameters may have low precision and in some cases are unobtainable (e.g. no interactions were recorded between *Halichondriidae* sp1 and *Watersipora subtorquata*).

Predicting the dynamics of manipulated communities

The dynamics of the model systems presented here well reflected many features of the natural marine epibenthic community they represented. However, like the flickering shadows cast on the walls of Plato's cave, the models sometime present a distorted picture. The models were relatively poor predictors the mean dynamics of the manipulated communities but they were notably better in predicting the range of possible manipulated communities. The dominant species in all simulations and in the manipulated communities was *Didemnum* sp. (Figure 4), but the dynamics of *Parasmittina* sp. and *Halichondriidae* sp4 tended to differed between manipulated and model communities. Despite this, in 25-33% of comparisons there were no statistical differences between models and reality, and when tests are adjusted for multiple comparisons (Bonferroni or Dunn-Sidak) then models and manipulated communities are rarely significantly different.

Differences between the dynamics of the manipulated communities and the dynamics of model communities may be due to either inaccurate/unobtainable parameters or differences in the dynamics of communities on PVC mats and on concrete walls. Inaccuracies in parameter estimates many arise due to the short time span of sampling and that we were unable to estimates the effects of seasonality on growth, recruitment and mortality. Differences may also arise from the differences in the nature of 'free space'. On the walls of the jetty, 'free space' is not truly free of

macro invertebrates (i.e. vacant) but rather a conglomerate of dead organisms and entoprocts. This conglomerate was not present in the free space of the manipulated communities, with the result that growth rates over free space on PVC mats are much higher than growth over 'free space' on the concrete walls. It is also possible that transplanting the colonies into artificial communities may alter the interaction outcomes, and particularly neighbour-specific growth rates of species (chapter 3).

Predicting the dynamics of non-manipulated communities

The 13 species model of the non-manipulated jetty wall community preformed better in predicting the dynamics of the natural community. However, several species tended to dominate the model communities (notably *Didemnum* sp., Halichondriidae sp1 and sp3; Figure 9). Colony sizes of most species in models were usually larger on average than those we observed in nature. Larger colony sizes imply that fewer species can be packed into the same area and consequently the species density in models was less than that observed in quadrats on the jetty wall (Figure 11). Whether the self-organised colony size is smaller in a community with a larger species pool or that a trade-off exists between colony size and another parameter (e.g. reproduction/recruitment and colony size; see Tilman 1994) cannot be determined. It is also possible that the growth of large colonies in the natural community is in some way constrained by increasing numbers of interactions. Increasing numbers of interactions tended to change the likelihood of a species winning a single interaction (chapter 3) which could effect the global community dynamics as species density increases. Alternatively, differences that do arise between the natural community and the models are possibly the result of biological processes that are not represented in the models (i.e competition through feeding and long-range chemicals or changes in

growth rates with colony size). Regardless of detailed differences between models and reality, the models well reflected the broad dynamics of the natural community, particularly patterns of species evenness and variability in community structure. Importantly, the structures of natural communities are within the cluster of possible community configurations predicted by the models after approximately 6.6 years. These dynamics are emergent behaviours of the models, and demonstrate that it is possible to generate global scale dynamics from the interactions between individual colonies.

Variability in community structure

The communities generated from models constructed with the present rules reveal several non-trivial characteristics of spatially extended ecosystems. First, variability is an intrinsic component of ecological systems. Natural systems have stochastic elements to their signals of recruitment, growth and mortality. Thus, in addition to a mean trajectory, a representative model of an ecosystem would desirably estimate the variability about that mean. These models would describe possible community configurations that do not necessarily exist in the natural systems at any point in time. In the case of our models, variability arises through the stochastic elements of parameter values and local rules. Levels of variability commensurate with the natural system can be generated without the need to add random variables as external forcings to describe environmental noise or disturbance (e.g. see Ives *et al.* 1999). Models that describe only the mean behaviours of systems are unlikely to represent the complete range of possibilities, especially as the number of species and parameters increases.

That we did not need to include a component of large-scale disturbance is unsurprising given the sheltered nature of the community we observed. This demonstrates that the high variability observed in natural communities is not necessarily dependent on external forcing by large-scale environmental stochasticity, and that many species can coexist on a single resource dimension (i.e. space in the models) without obvious disturbance to generate spatial heterogeneity. In natural communities with high variance in community structure similar to this marine epibenthic community, it is unlikely that the mean state actually contains much information about the complete range of community processes. For example, small-scale stochastic variability in recruitment may result in two significantly different communities (using tests based on means) developing despite having the same source larval pool. Coupled with the variability in growth rates, interaction outcomes and mortality rates, the variance in systems and not the centroid, is more likely to represent community processes.

As a consequence of high variability in community configurations, community trajectories are relatively insensitive to the initial starting arrangement of colonies. Replicate manipulated communities starting with the same species complement and spatial arrangement of colonies and the models of these manipulated communities both demonstrate a wide range of possible states through time (Figures 4 & 5). The final state of these communities was insensitive to the initial state. Thus, after 488 days of development, the magnitude of differences among communities with different starting conditions were no larger (and often smaller) than differences among replicates with identical starting configurations. This was true for both manipulated and models of manipulated communities. Any effect that initial conditions may have is obscured by the variability in processes acting on these communities. In contrast,

sensitivity to initial conditions, either in the spatial arrangement of individuals or the abundances of species, is axiomatic for many other spatial and non-spatial multispecies models (e.g. Saravia *et al.* 2000, Silvertown *et al.* 1992). Again, parameters in these models are point estimates and ignore any variability in community processes. From any particular starting configuration, variability drives communities toward multiple states that may have little in common in terms of their mean abundances. These results emphasise the need to closely examine variances in natural communities and that mechanisms that are important in models may not necessarily be important in natural systems.

Coexistence of multiple species on a single resource

High variability in observed growth rates, mortality and recruitment rates contribute to the high variability we observed in this system. Goldwasser *et al.* (1994) found that, in model communities high variability within and between sub-communities in a metacommunity contributed to the retention of species that would otherwise go extinct. In addition to variability and spatial structure, weak interactions may act to stabilise communities and to promote coexistence (Benedetti-Cecchi 2000, Berlow 1999, Kokkoris *et al.* 1999, McCann 1998). The interaction outcomes we observed here were highly intransitive and no one species had an advantage over all others. These interactions could be characterised as ‘weak’ since there are no consistent winners in any pair-wise interaction, and growth rates are slow relative to the stochastic influences of mortality and recruitment. Most new recruits are rapidly eliminated (Figure 6) and only a very small number grow to a sufficient size to escape high levels of mortality. Relatively slow growth rates and high levels of mortality mean that this community does not form self-organised multispecies

structures similar to those seen in other models (e.g. Johnson 1997). Interactions are still important, but only to the extent that a weak competitor can be swiftly overgrown and have a low likelihood of outlasting a competitor with which it comes into contact. Communities with weak interactions may be more stable simply because there is more time for mortality and disturbance to disrupt an interaction than if interactions were ended swiftly. If growth was faster relative to mortality rates, colonies would be larger, less likely to die, interact more often and the community may evolve interspecific self-organised structures. Thus, a continuum of possibilities exists depending on the relative speeds of grow, recruitment and mortality.

Despite the weakness and symmetry of interactions, large clonal organisms (i.e. sponges and cnidarians) still become the dominant species. Butler and Connolly (1999) found that after 13.5 years a sessile marine invertebrate community in South Australia had not reached a 'climax' community and large clonal organisms were dominating space. Our results show similar patterns and suggest that a sessile invertebrate community may have no 'climax' structure, but rather continue to change and diversify (i.e. increase variance). This suggests that the communities we have modelled have a fuzzy attractor than exists over a large area of multidimensional space. The attractor is not defined by specific species but rather the range of possible relationships that can exist between species properties. Thus, the variable growth rates, mortality rates and recruitment rates, coupled with weak interactions between species on a spatial landscape contributed to the community variability, and subsequently to the coexistence of all 13 species.

A testable model?

The model presented here shows that it is possible to construct a multispecies ecological model that displays the same broad dynamics as natural communities. A key point is that the dynamics are emergent from the local rules and their parameters and are not 'hard wired' by fitting large numbers of parameters. The complex dynamics seen in marine epibenthic communities can be generated from the interactions between individual colonies, without the need for global rules or ecological processes. The model captures the important processes and dynamics of these communities and importantly, reflects the variability inherent in these systems. That the model behaviour well approximates that of the natural communities lends power to conclusions drawn from the model and affords some confidence in extrapolations to situations beyond those seen in the natural community.

Chapter 5: Linking richness, stability and invasion resistance with area in model marine communities.

ABSTRACT

Notably absent in the debate on nature of the relationship between species richness and stability (persistence and resilience) and species richness and invasion resistance has been the influence of patch size on these relationships. Species-area relationships are among the oldest and most accepted ecological relationships studied and regulate species richness within a patch of a given size. Here we use an empirically validated spatial model of a marine epibenthic community to link the effects of patch size to the stability, invasion resistance and richness of communities. The relationship between community stability (persistence and resilience) and species richness is determined by the size of the model landscape. In small landscapes persistence stability increases with species richness. However, beyond a critical landscape size stability decreases with increasing richness. Invasion resistance is strongly correlated with the community persistence stability. Hence, the relationship between species richness and invasion resistance is also determined by the size of the model landscape. These patterns are generated by the interaction between species recruitment, species mortality and interactions between species. Our results suggest that a continuum of possible relationships can exist between species richness, stability, invasion resistance and area and that these relationships are emergent behaviours generated by the properties of species within communities.

INTRODUCTION

In the search for general theories in community ecology, linking species richness with community persistence stability would be a major achievement, although despite intense study, a resolution to this debate remains elusive (Cottingham *et al.* 2001, Johnson *et al.* 1996). The dominant hypothesis, initiated largely by Elton (1958) and MacArthur (1955), proposes that increasing species richness increases the temporal stability of an aggregate community property (e.g. biomass, total productivity, nutrient cycling). A positive link between stability and species richness is an appealing explanation of the high diversity seen in natural communities. This hypothesis has received considerable support in empirical studies on grassland communities (Frank and McNaughton 1991, Hector *et al.* 1999, MacNaughton 1977, 1985, Tilman 1996, 1999, Tilman and Downing 1994) and microcosm communities (McGrady-Steed *et al.* 1997, Naeem *et al.* 1994, Naeem and Li 1997). However, many of these studies have been criticised on the basis of experimental design (Cottingham *et al.* 2001, Givnish 1994, Huston 1997, Huston *et al.* 2000, Wardle 1998) and other work has found a negative or insignificant relationship between richness and stability (Rodriguez and Hawkins 2000, Silvertown *et al.* 1994). Despite this, the general consensus has been that the empirical evidence supports the hypothesis (Cottingham *et al.* 2001).

The apparent discrepancy between empirical results and theoretical models has been a source of disquiet. Early theoretical models generally show that stability should decrease as complexity (i.e. connectance or species richness) increases (e.g. May 1972, 1974, Pimm 1979). These models were generally randomly constructed communities so that biologically unrealistic interaction networks could readily arise, and they were modelled using either differential or difference equations. However,

recent work has shown that highly connected systems can be stable providing that the communities are not connected at random (Haydon 2000). Hughes and Roughgarden (2000) examined the dynamics of selected stable communities perturbed away from equilibrium and found that more diverse communities were most resilient to change. This suggests that existing stable communities are not an assemblage of random species, rather a subset of all possible communities. Increasing richness may stabilise aggregate community properties by dampening the fluctuations of a single species (Doak *et al.* 1998). When the cover of a particular species decreases as more species are packed in to the same area the relative effect of fluctuations on total cover will correspondingly decline. Incorporating the work of Doak *et al.* (1998) and Tilman (1999), Lehman and Tilman (2000) attempted to provide some closure on the debate, suggesting that both sides were correct “but one addressed population stability and the other addressed community stability” (Lehman and Tilman 2000).

Elton (1958) proposed a second important hypothesis, namely that increasing richness resulted in increasing invasion resistance of the recipient community. Modelling has supported this hypothesis (e.g. Case 1990, 1991, Law and Morton 1996) but empirical evidence has been more ambiguous. Some studies have found that resistance increases with richness (e.g. Tilman 1997, Symstad 2000, Stachowicz *et al.* 1999, McGrady-Steed *et al.* 1997), other studies have found the reverse situation (e.g. Robinson *et al.* 1995, Wiser *et al.* 1998), while some work suggests that both patterns arise but at different scales (Levine 2000, Stohlgren *et al.* 1999).

Overall, studies of how invasibility and stability vary with richness are problematic for reasons of generality, the modelling approach and scale. Firstly, empirical results on stability are almost exclusively from grassland or contrived communities, limiting the generality of the empirical results (Contingham *et al.* 2001).

Grassland communities also dominate debate about invasibility (Levine and D'Antonio 1999). With few other community types considered, it is difficult to evaluate the generality of the patterns.

Secondly, the models used to describe relationships between richness and stability are, without exception, non-spatial numerical models. Numerical models are attractive because the stability of a system is readily determined and they are analytically tractable. However, these models assume that the strengths of species interactions are directly proportional to their abundances, and if the carrying capacity of each species is identical then 'individuals' are completely mixed within an infinite landscape. Consequently, the interaction neighbourhood of an 'individual' is potentially infinite. While they are useful for describing some physical systems, numerical models fail to capture the full complexity of ecological processes, including local interactions, the effect of spatial scale on ecosystem process and spatial correlations between and within species. In contrast, individual based spatial models allow interactions between individuals on a landscape to occur at a local scale (e.g. Judson 1994, Herben *et al.* 2000, Silvertown *et al.* 1992, Silvertown and Wilson 2000). The emergence of spatial aggregations within species and spatial separations between species allows individuals to escape from superior competitors through spatial refuges (Stoll and Weiner 2000, Tilman 1994). Spatial models display non-trivial behaviours that lead to qualitatively and quantitatively different results to non-spatial models (Durrett and Levin 1994a, 1994b, Molofsky *et al.* 1999, Johnson 1997).

Thirdly, the effects of scale on the invasibility/species richness and stability/species richness relationships have not been explicitly tested either empirically or theoretically. Elton (1958) observed that communities inhabiting smaller islands were less stable and therefore more likely to be invaded, a claim

further reinforced by MacArthur and Wilson (1963, 1967). Since then theories of species-area relationships and diversity-stability relationships have diverged although Wardle *et al.* (1997) provides some evidence to suggest that aggregate ecosystem properties may be influenced by island size. Interestingly, numerical models of diversity stability relationships can be scaled to any size providing that space to live is a parameter in the models. These models suggest that the diversity-stability relationship would hold irrespective of the patch size.

To provide a counterpoint to empirical and modelling studies and to explicitly examine questions of scale, we examined the dynamics of a spatial model of a marine epibenthic community. We have previously reported that the dynamics of the model reflect the dynamics of a natural marine epibenthic community predicting the relative abundances, size structures of species, diversity and species evenness (chapter 4). Here, we examine the relationships between persistence stability, resilience stability, invasion resistance and species richness within the context of changing patch size.

THE MODEL

Sessile marine invertebrate communities were simulated using a probabilistic cellular automata with a von Neumann interaction neighbourhood, synchronous updating and an open landscape (i.e. absorbing boundaries). The model is described in detail in chapter 4. We compared the dynamics of the models to manipulated and unmanipulated sessile marine invertebrate communities and found that the models provided a good approximation of the development and dynamics of these communities. The model is parameterised from species in a marine epibenthic community from Tasmania. The model has a rule structure that operates at two scales: (1) growth and competition between species at the scale of cells on the

landscape, and (2) mortality and size limitation at the scale of individual colonies (blocks of contiguous cells of the same species). The local rules of interactions between cells are:

1. If a cell is unoccupied (i.e. in a 'free space' state), one of the four adjacent cells in the von Neumann neighbourhood is selected at random, and if the selected cell is occupied it grows into the empty cell with a probability g_{iFS} , where g_{iFS} is the growth rate of species i over free space.
2. If a cell is occupied by species i , one of the four adjacent cells in the neighbourhood is selected at random. If the selected cell is occupied, it grows into the central cell with a probability $a_{ij} * g_{ij}$, where a_{ij} is the probability of species i winning an interaction with species j and g_{ij} is the neighbour-specific growth rate of species i over species j .

We modelled the community of 13 species, *Didemnum* sp., *Botrylloides leachi*, *Celleporaria* sp., *Parasmittina* sp., *Watersipora subtorquata*, Phloeodictyidae sp., Leucetiidae sp1 sp2, Halichondriidae sp1, sp2, sp3, Microcionidae sp., and *Corynactis australis* that exists beneath Darlington Jetty, Maria Island, Tasmania, as in chapter 4. Probabilities of interaction outcomes (a_{ij}) and neighbour-specific growth rates (g_{ij}) were determined empirically from observations of growth and overgrowth of 8,471 colonies in 0.1m² quadrats over a period of 446 days. Recruitment and colony mortality were also calculated using these empirical observations. Both the mean and the variance in recruitment and growth rates were calculated using observations of different colonies over time. Interaction outcomes and colony mortality were probabilistic events. New recruits of each species were introduced onto a single empty cell in the landscape with a probability r_i , the recruitment rate of species i .

Colony mortality in the natural community was strongly dependent on colony size (chapter 2). We calculated the probabilities of colonies of particular sizes dying from observations of the natural community and applied these probabilities to 'colonies' in the model. The area of each 'colony' on the landscape was determined as the number of contiguous cells of the same species. The probability of the whole colony dying was calculated using the estimated relationships (either linear or power curve) between colony size and probability of mortality.

After comparing the size-frequency distributions of models and natural communities it was apparent that for some species, the maximum sizes of colonies in models was considerably larger than colonies found in the natural community. The maximum size of colonies for these species (8 out of 13 species) was limited to the maximum size of naturally observed complete colonies. In this way we limited the growth of certain species to an absolute maximum size. Models with this additional parameter set provided significantly better descriptions of the natural communities than models without it.

The complete parameter set used here is detailed in chapter 4. In all simulations we have scaled the size of each cell to 100 mm^2 and iterations represent daily timesteps. We select neighbour-specific growth and recruitment rates for each simulation randomly from normal distributions described by their observed means and standard deviations in the natural systems. Landscapes were initialised as empty space and individual colonies were allowed to recruit and grow as would be expected in a natural community.

LINKING AREA, RICHNESS, STABILITY AND INVASIBILITY

To determine whether the models displayed richness/area relationships we simulated communities on square landscapes of a range of sizes. Landscape areas (ℓ^2) simulated were square grids ranging from 25 - 62500 cells. We simulated 100 communities for each landscape size. Communities were simulated for 4000 iterations but all analyses were based on the last 1000 iterations (i.e. at the stage of community development most representative of our natural system (chapter 4).

Species area relationships

To determine if our model predicts similar species-area relationships and relationships between species invasion and extinction to those hypothesised by MacArthur and Wilson (1964,1967) we examined the richness-area relationship over the range of landscape sizes simulated (figure 1). The number of species on a landscape was limited only by the capacity of that landscape to support the species present. In all cases up to 13 species could potentially coexist. We fitted both a power curve (the usual description of a species area relationship) and an extreme value function (EVF, Williams 1995) to the relationship. The EVF provides the best fit, as the predicted maximum number of species is limited to the total species pool (in this case 13 species). While the EVF and the power curve both provide a good fit when $\ell^2 < 40000$ cells, the power curve predicts an unrealistic number of species in larger landscapes (figure 1). However, the variance about the means for each landscape size is high (e.g the minimum number of species on landscapes where $\ell^2 = 62500$ is less than the maximum number in landscapes where $\ell^2 = 400$). The full complement of

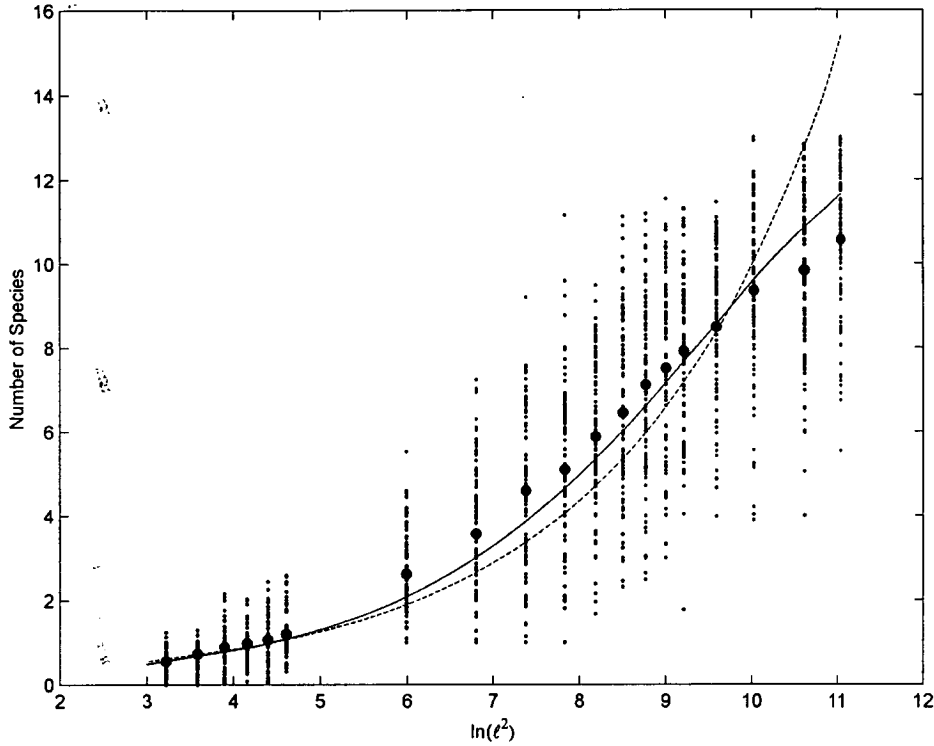


Figure 1. The relationship between species richness and landscape area (ℓ^2). Each data point represents mean richness between 3000 and 4000 iterations. Large circles are the means of 100 simulations. A power curve (dashed line, richness = $0.1585 * (\ell^2)^{0.4142}$, $R^2 = 0.7847$) and an extreme value function (solid line, richness = $13 * (1 - \exp(-\exp(0.506688 * \log_e(\ell^2) - 4.782)))$, $R^2 = 0.8146$) are fitted to the data.

13 species was never represented on a single landscape until landscape size equalled 22500 cells, (equivalent to 2.25 m²).

MacArthur and Wilson(1964,1967) suggested that species area relationships are an emergent property of a dynamics equilibrium between the immigration of new species into and extinction of existing species within a patch. We examined the relative likelihood of extinction compared to immigration events for each landscape (figure 2). We calculated the likelihood of immigration as the number of times species richness increased as a proportion of the total number of times that species

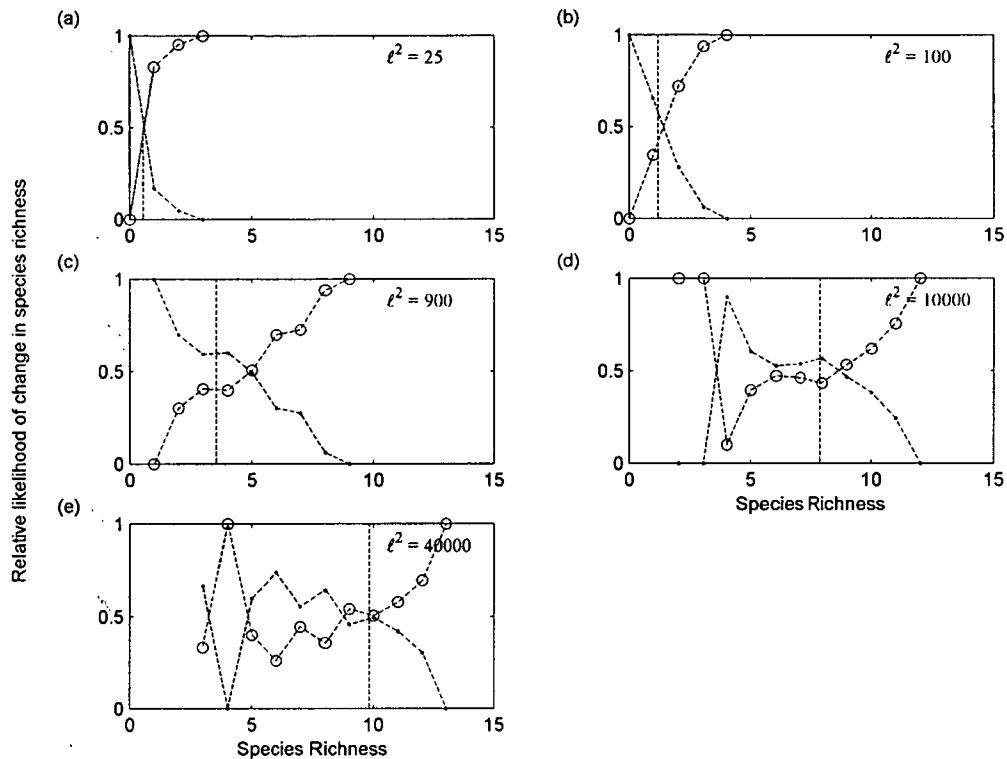


Figure 2. The relative likelihood of extinction ('o') and immigration ('.') of species on landscapes of size ℓ^2 . Vertical dashed lines represent the mean number of species for each landscape size.

richness changed in any direction (i.e. number of increases in richness + number of decreases in richness). The likelihood of extinction was calculated as $1 -$ the likelihood of immigration. In extremely small landscapes ($\ell^2 = 25$) an increase in richness is highly unlikely irrespective of the number of species. However, on larger landscapes, communities with fewer species than the mean number of species for that landscape size are more likely to gain new species than lose them. Conversely, when richness increased beyond the mean for that landscape size, species extinction was more likely. The mean number of species for each landscape size is a rough indicator

of the equilibrium point where the relative likelihood of species invasion balances the relative likelihood of species loss.

Persistence stability depending on patch size

The persistence stability of total cover in each community, and cover of each species within the community, on each landscape size was estimated between 3000 and 4000 iterations. To estimate population persistence stability we calculated an index of stability, the coefficient of variation:

$$S_i = \frac{\sqrt{\text{Var}(x_i)}}{\overline{x_i}}$$

over the time interval of 1000 iterations, where x_i is the time series of species i .

Because the variability of total cover (community persistence stability) in a community depends on the covariances between species in addition to the variances in species cover over time, we estimated community stability as

$$S_T = \frac{\sqrt{\sum_{i=1}^N \text{Var}(x_i) + 2 \sum_{i=1}^N \sum_{j=1}^{i-1} \text{Cov}(x_i, x_j)}}{\sum_{i=1}^N \overline{x_i}}$$

over the same time interval for a community with N total species. Small values of S_T and S_i represent stable communities (i.e. less variable) while large values indicate relatively unstable communities. While standardising by the mean removes the influence of landscape size on this measure, it means that the measure is insensitive to large increases in stability as the variance measure (the numerator) tends toward zero. Unlike a system with a stable global equilibrium, our systems are dynamic with constant small perturbations (i.e mortality and recruitment) and consequently, are always variable through time.

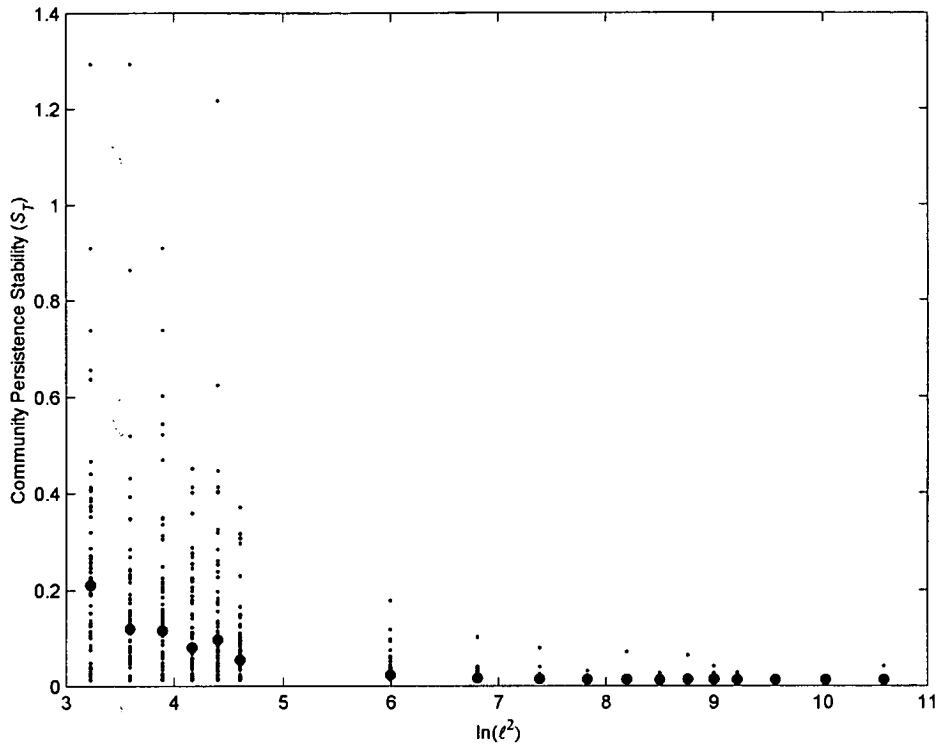


Figure 3. The relationship between community persistence stability (S_T) and landscape size. The mean value of S_T for each landscape size is represented by the large circle and each separate simulation by small circles.

We found that both the mean and range of values for S_T decrease as landscape size becomes larger, showing that larger landscapes are more stable (figure 3). The range of values of S_T also decreased with landscape size. However, when landscapes of different sizes are examined separately we find two distinct relationships. For small landscapes ($\ell^2 < 900$), S_T decreased as a function of richness (figure 4a & 4b). In landscapes of this size, space is strongly limiting, so that no colony is able to grow large enough to escape mortality (mortality is size-specific) and all colonies are of a similar size. Hence, the more species present, the less likely a single mortality event will dramatically effect the overall cover so that total cover is more stable at higher

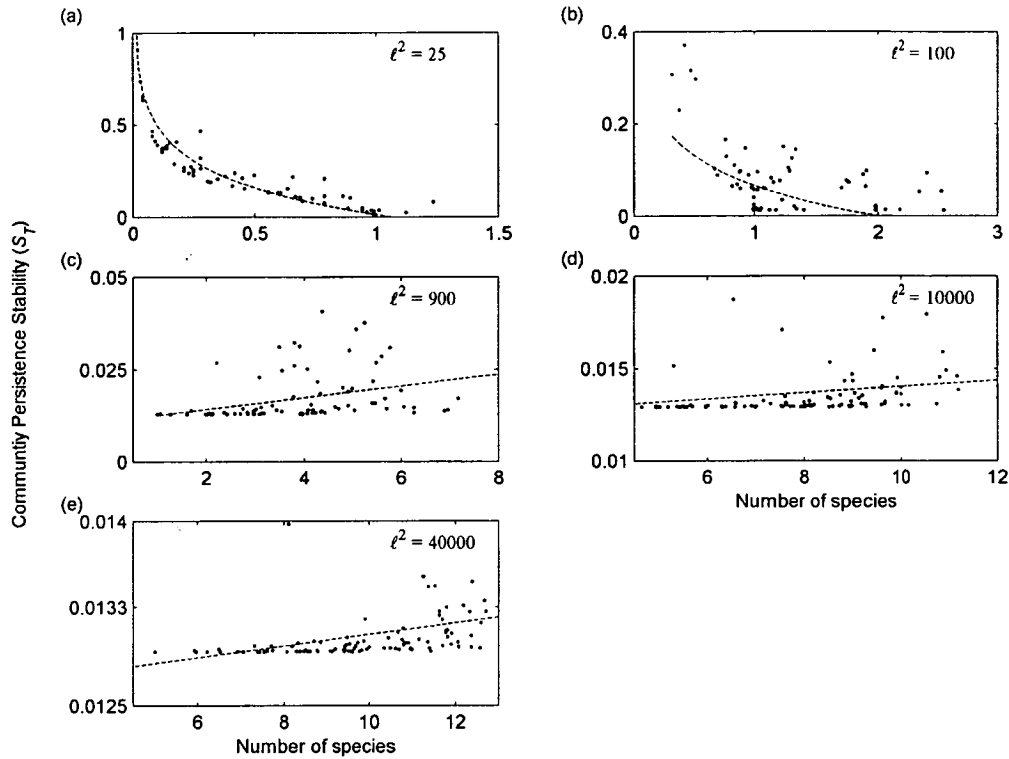


Figure 4. The relationship between average species richness and community persistence stability (S_T) for five selected landscape sizes. The correlations between richness and S_T are given in Table 1; (a) for $\ell^2 = 25$, $S_T = -0.208984 \cdot \log(\text{richness}) + 0.012780$; (b) for $\ell^2 = 100$ $S_T = -0.093634 \cdot \log(\text{richness}) + 0.064849$; (c) $\ell^2 = 900$, $S_T = 0.001595 \cdot \text{richness} + 0.010994$; (d) $\ell^2 = 10000$, $S_T = 0.000202 \cdot \text{richness} + 0.011942$; (e) $\ell^2 = 40000$, $S_T = 0.000047 \cdot \text{richness} + 0.012607$.

richness. S_T is stabilised at higher species numbers because the mortality of a single species has proportionally less effect on total cover than at lower richness when colonies occupy more space. Thus, in small landscapes, communities are stabilised through species averaging (Doak *et al.* 1998). Individual species populations are more stable as richness increases (Table 1) increasing richness also increases the likelihood that single species will be present

Table 1. Pearson correlation coefficients over the range of ℓ^2 simulated for S_T and S_i (for most abundant species in the models) correlated with average species richness.

ℓ^2	S_T	$S_{\text{Halichondriidae sp3}}$	$S_{\text{Didemnum sp.}}$	$S_{\text{Halichondriidae sp1}}$	$S_{\text{C. australis}}$
25	0.80842 P = 0.0001 N =93	-0.70561 P = 0.0001 N =45	-0.50833 P = 0.0112 N =24	-1 P = 0.0001 N =7	-0.68263 P = 0.3174 N =4
100	-0.32644 P = 0.0009 N =100	-0.18021 P = 0.1509 N =65	-0.16789 P = 0.3426 N =34	-0.40147 P = 0.0712 N =21	0.01067 P = 0.9932 N =3
900	0.38196 P = 0.0001 N =99	-0.38675 P = 0.0007 N =74	-0.2004 P = 0.1123 N =64	0.43953 P = 0.0002 N =67	0.13019 P = 0.6438 N =15
10000	0.33113 P = 0.0008 N =99	-0.49554 P = 0.0001 N =98	-0.28791 P = 0.0051 N =93	0.46005 P = 0.0001 N =95	0.1217 P = 0.3761 N =55
40000	0.28254 P = 0.0046 N =99	-0.55451 P = 0.0001 N =98	-0.45676 P = 0.0001 N =94	0.36283 P = 0.0002 N =98	-0.22518 P = 0.0309 N =92

In contrast, for landscapes of $\ell^2 \geq 900$, individual colonies are released from the constraints of total area, and the relationship between richness and stability reverses. In landscapes of these sizes, S_T increases as a linear function of richness (figure 4c – 4e). In large areas species can attain a wide range of sizes, and in species where growth is unlimited, some species can attain very large sizes (relative to the landscape size). Because mortality is size specific, larger colonies are less likely to die. Consequently, landscapes where colonies attain large sizes (specifically, colonies of *Halichondriidae* sp1, sp2 and *Corynactis australis*) are very stable (i.e. low S_T values) when compared to landscapes where large colonies are absent or present only

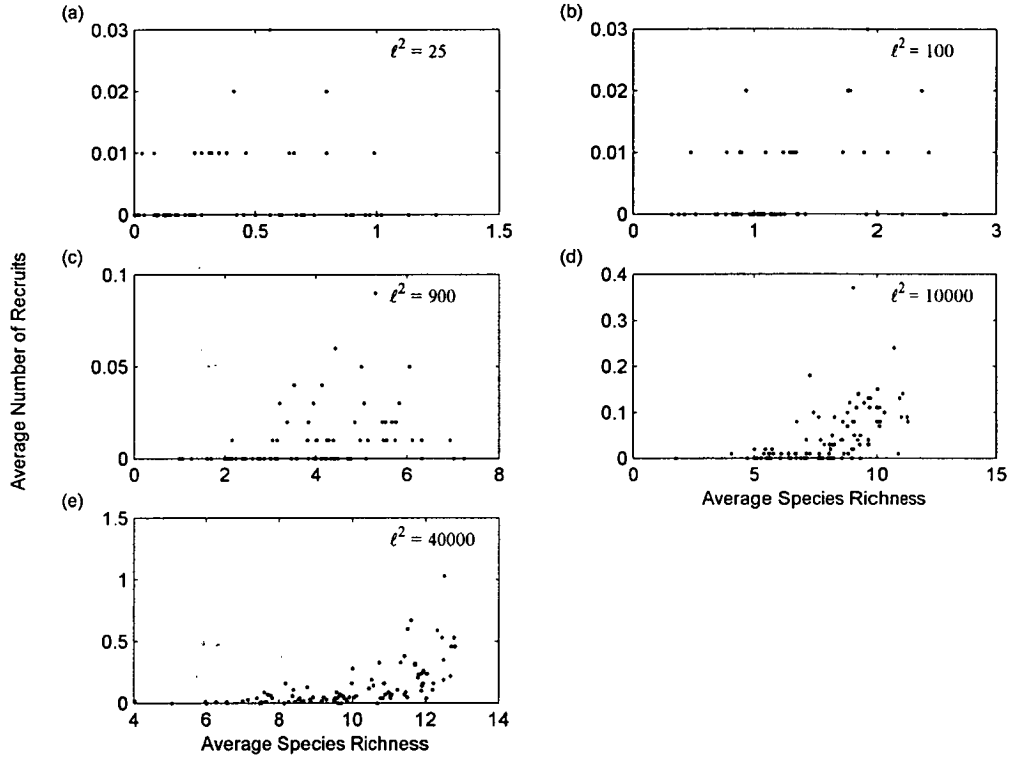


Figure 5. The relationship between species richness and average recruitment per day from 3000 to 4000 iterations. Relationships are estimated using the Pearson correlation coefficient; (a) $\ell^2 = 25$, $r = -0.0589$, $P = 0.5599$, $N = 100$; (b) $\ell^2 = 100$, $r = 0.29742$, $P = 0.0027$, $N = 100$; (c) $\ell^2 = 900$, $r = 0.40961$, $P = 0.0001$, $N = 100$; (d) $\ell^2 = 10000$, $r = 0.5613$, $P = 0.0001$, $N = 100$; (e) $\ell^2 = 40000$, $r = 0.6037$, $P = 0.0001$, $N = 100$;

as small colonies. Large colonies of *Halichondriidae* sp1 in particular dominate space and maintain species richness at low levels. However, when these species are absent or occur as small colonies the populations of most other species are more stable, thus S_i for other species that do not produce large colonies is positively correlated with species richness. Individual species are always less stable than the community from which they were drawn (i.e. $S_i > S_T$), irrespective of the species richness. Thus, while S_i was negatively correlated with richness (i.e. population stability increases with

richness) for most species over all ranges of ℓ^2 , species forming large colonies such as *Halichondriidae* sp1 are most stable when richness is low when $\ell^2 \geq 900$.

The relationship between species richness invasibility, persistence stability and landscape size

We used recruitment into the community as an analogue of invasions into patches. In all landscapes of $\ell^2 \geq 900$ cells, average recruitment rates are positively correlated with richness (figure 5, figure 6 ‘.’). This is identical to the pattern found in the natural community on which the model is based (chapter 2), but contrasts with the patterns found in some grasslands (e.g. Tilman 1997). However, in smaller landscapes of $\ell^2 < 900$ cells correlations were weak and did not show any consistent pattern with richness (figure 5, figure 6 ‘.’). Because recruitment in our models and in the natural community is a function of available free space, it follows that as cover increases average recruitment decreases across all landscape sizes considered (figure 6, ‘o’). Similarly, since S_T is a function of variance in total cover over time (i.e. the amount of free space over time), it follows that that the average cover in a landscape was strongly correlated with the measure of stability, S_T (figure 6, ‘x’). As S_T incorporates both the mean and variance in total cover, it provides a better estimate of free space over time than simply the mean cover. Thus, over the entire range of landscape sizes (with the exception of $\ell^2 = 25$) average recruitment was strongly correlated with the persistence stability (S_T) of the community (figure 6 ‘*’). In this way, species poor communities are relatively more resistant to invasion by new recruits compared with species rich communities because stability decreases with increasing richness.

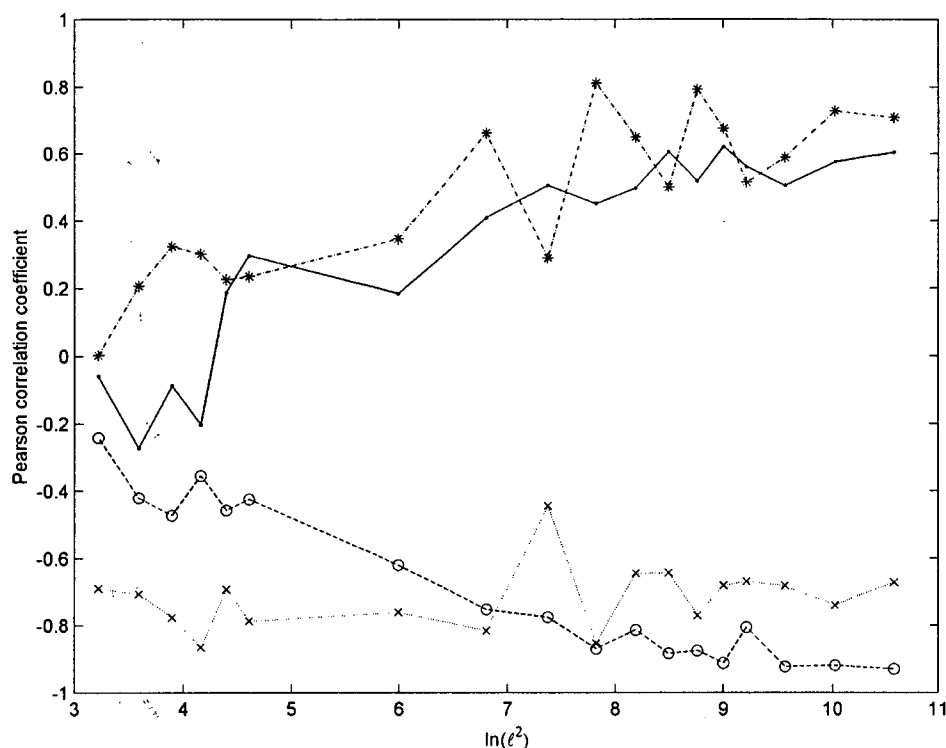


Figure 6. Dependence of correlations (Pearson correlation coefficients) between species number and average recruitment (.), average recruitment and average cover (o), average cover and stability, $S_T(x)$, and average recruitment and stability, $S_T(*)$ on landscape size.

Over the range of landscape sizes simulated, recruitment per unit area (in this case 1 cell) is a function of the landscape size (figure 7). Larger landscapes receive on average proportionally fewer recruits than smaller landscapes. Again, recruitment is a function of the stability of the landscapes. Larger landscapes, being more stable (figure 3), have a lower proportion of free space for recruitment and consequently have a lower recruitment rate per unit. This implies that the invasibility of a group of small landscapes is considerably higher than the invasibility of a single large landscape of the same total area. The variance in recruitment density to small landscapes was also much greater due to the smaller landscape sizes (i.e. less total area for recruitment compared to larger landscapes) and the stochastic nature of

recruitment to these landscapes. Thus, a negative link exists between stability and invasibility but not necessarily between species richness and invasibility.

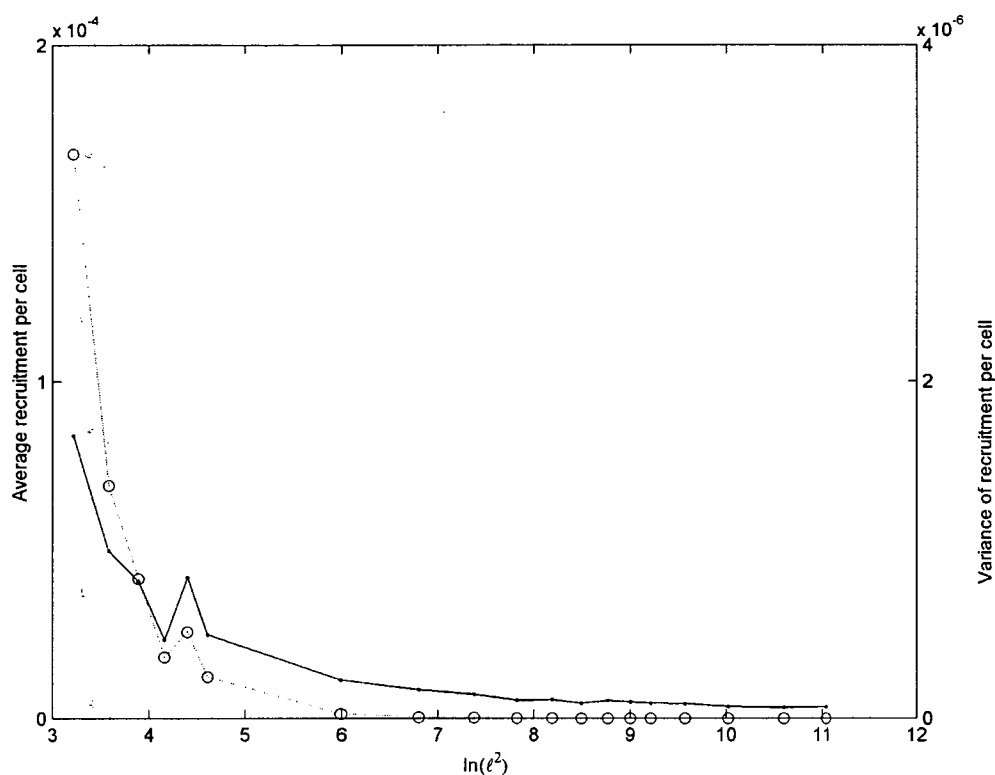


Figure 7. The relationship between recruitment per unit area and landscape size (ℓ^2); average recruitment per unit area (.) on the left axis and variance in recruitment per unit area 'o' (right axis).

The relationship between species richness and resilience stability

The resilience of communities to change was examined by simulating a disturbance in which the most common species were removed after 3000 iterations. Species richness at the time of removal (including the species removed) and time taken for community cover to return to the level prior to removal, was measured. The dissimilarity between the community prior to the disturbance event and the

community at the point where total cover equalled or exceeded the cover prior to removal was calculated using the Bray-Curtis measure (Bray and Curtis 1957).

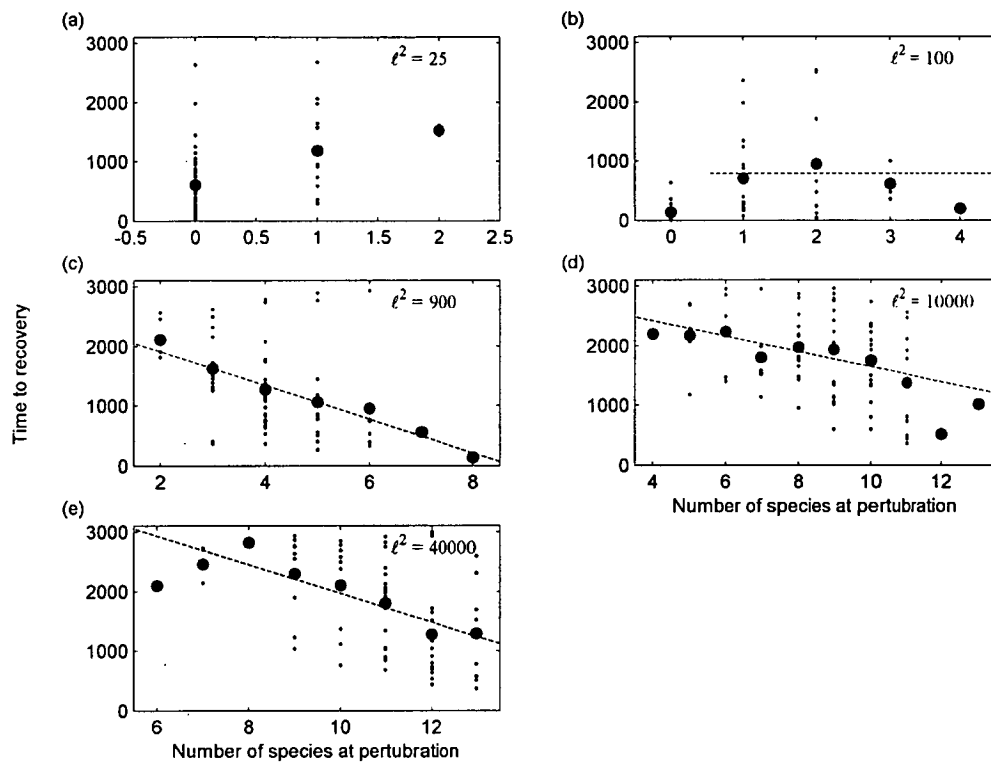


Figure 8. Time to recovery of cover after removing the dominate species at 3000 iterations. Five landscapes, with the appropriate lines of best fit, are shown; (a) for $\ell^2 = 25$, Return time = $527 * \text{species richness} + 619$; (b) for $\ell^2 = 100$, Return time = $200 * \text{species richness} + 364$; (c) for $\ell^2 = 900$, Return time = $-284 * \text{species richness} + 2486$; (d) for $\ell^2 = 10000$, Return time = $-128 * \text{species richness} + 2936$; (e) for $\ell^2 = 40000$, Return time = $-242 * \text{species richness} + 4382$.

For small landscapes ($\ell^2 < 900$) there is no consistent relationship between species richness and the time taken for the total cover to recover (figure 8a & 8b). These communities are unstable and stochastic effects of recruitment and mortality tend to dominate the dynamics (figure 3). However, in larger landscapes recovery time is negatively correlated with species richness at the time of perturbation (figure

8c-8e, Table 2). The slopes of lines of best fit between richness and recovery time are not significantly different for landscapes between 900 and 40000 cells (Table 2). The intercept of each regression line is the recovery time of a landscape where species richness equalled zero, the starting conditions of the model. The intercepts for all landscapes where $\ell^2 \geq 900$ are not significantly different (Table 2). Thus, in large landscapes ($\ell^2 \geq 900$ cells) species rich communities have faster recovery times than species poor communities. This is because species poor communities were generally dominated by large colonies and the removal of large colonies (i.e. the most abundant species) results in a large decrease in total cover. In contrast, the removal of the most abundant species in species rich communities results in only a small decline in total cover since more species are packed into the same area. Thus, while species poor communities have higher persistence stability than more species rich communities because mortality of large colonies is relatively rare, the resilience stability of species poor communities is lower than in more speciose communities.

Table 2. Analysis of Covariance of the relationship between initial species richness and the time taken to recover from a perturbation event for $\ell^2 \geq 900$.

Source	df	SS	F-value	Pr > F
Initial Richness	1	583385.96	123.21	0.0001
ℓ^2	10	60972.37	1.29	0.2329
ℓ^2 * Initial Richness	10	57160.16	1.21	0.2823
Error	797	3773705.42		

We used the Bray-Curtis measure of dissimilarity to assess the similarity of communities before perturbation and after recovery. Both the mean and range of dissimilarity decreased as landscape size increased (figure 9). While small landscapes may contain no species in common with the original community after total cover has recovered, larger landscapes invariably contained at least some species in common with the community prior to perturbation.

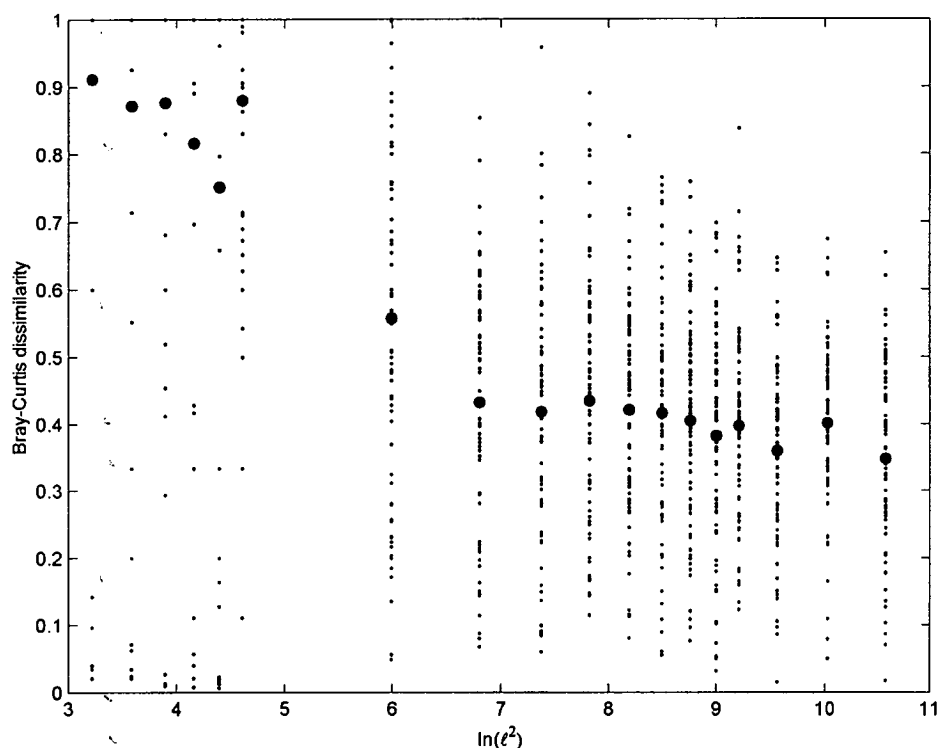


Figure 9. The mean Bray-Curtis dissimilarity (large circles) and the distance for each simulation (small circles), between the community prior to perturbation and the community at the point when total cover equalled or exceeded the cover at the point of perturbation.

DISCUSSION

The importance of spatial context

Our results provide a counterpoint to the relationship between stability and diversity reported for terrestrial plant communities (e.g. Frank and McNaughton 1991,

Hector *et al.* 1999, MacNaughton 1977, 1985, Tilman 1996, 1999, Tilman and Downing 1994). The patterns of stability and diversity in our community are the result of specific mechanisms involving the size structure of populations and the interactions between these populations. These mechanisms do not operate in any other model that we are aware of, but may arise commonly in other natural communities. Individual colonies (i.e. aggregations of contiguous cells of the same species) are an emergent property of the models as cells self-organise on a spatial landscape. When colonies are formed, the likelihood that adjacent cells contain the same species is greater than the likelihood that adjacent cells contain different species. This condition could never be achieved in the models of Lehman and Tilman (2000) where intra-specific competition is always set to be greater than inter-specific competition as an artifice to ensure stability. Our models also differ from other theoretical studies of diversity and stability (i.e. King and Pimm 1993, May 1972, 1973, Lehman and Tilman 2000), in that the likelihood of interactions between species are not proportional to species abundances. Non-spatial models can not estimate the spatial effects of aggregations of 'individuals', or in our case the dynamics of whole colonies. Lotka-Volterra equations can be considered as mean-field approximations of our models on infinite landscapes where individual cells can potentially interact with all other cells. The differences between our models and others arise as a consequence of the spatial nature of our models.

The demonstrated importance of spatial context in models of the marine epibenthic community we studied does not infer that spatial context is likely to be equally relevant in all systems. The correspondence between the stability/diversity relationship of models and natural grassland and mesocosm communities suggests

that these communities are effectively well mixed where individuals are all of similar size and mortality is independent of the size of individuals or aggregations.

Species richness, persistence stability and invasibility

We found that the persistence stability of a community was an important determinant of its invasibility. More stable communities are more resistant to invasion than unstable communities. Since stability is higher in species poor communities, these communities are more resistant to invasion than species rich communities. This is because species poor communities are dominated by large colonies that are less likely to die and create free space than are smaller colonies. The relationship between species richness and invasion resistance has been examined in many other studies (i.e. Case 1990, 1991, Levine 2000, Stachowicz et al. 1999, Tilman 1997), although the mechanisms that generate these patterns have not been studied and may vary from system to system (Levine and D'Antonio 1999). We have showed previously that the natural community on which the model is based demonstrates an identical relationship between richness and invasibility for similar reasons (chapter 2). The results of our model, and parallel observations in the natural community are contrary to most existing theory which suggests that invasibility should decrease with richness (e.g. McGrady-Steed *et al.* 1997, Tilman 1997, Stachowicz et al. 1999), although there are notable exceptions (see below).

It is likely that a continuum of relationships exists between diversity, stability and invasion resistance, depending on the emergence of larger scale aggregated structures (i.e. colonies or aggregations of individuals) within the system and the properties of these structures. When little or no spatial structure exists within the community (i.e. well mixed) the models of Lehman and Tilman (2000) suggest that

increasing richness stabilises communities. However, as larger scale structures emerge (i.e. the dynamics have a higher spatial component) and if larger structures have enhanced survivability, the relationship will reverse and increasing richness will destabilise the community. It is possible that the effects of spatial structuring are important in other communities. Communities that are manipulated in experiments often have their spatial structure disrupted so that the types of mechanisms we have identified here are prevented from operating. For example, the randomly arranged colonies used in experiments by Stachowicz *et al.* (1999) were no larger than 2 cm by 2 cm, homogenising the sizes of colonies and breaking any spatial structure. Thus, it follows that many manipulated communities show a positive relationship between richness stability and invasion resistance (e.g. Levine 2000, Symstad 2000). Huston (1997) noted that by manipulating species diversity in grasslands, species poor communities were less likely to contain species resistant to drought, thereby reducing their stability. This contrasts with studies of invasions in non-manipulated natural communities where spatial structure remains intact, in which invasions increase with richness (i.e. Levine 2000, Robinson *et al.* 1995, Wiser *et al.* 1998) as we observed in our models and non-manipulated community.

Species richness and resilience stability

While persistence stability is negatively correlated with richness in landscapes of $\ell^2 \geq 900$ cells, resilience stability is positively correlated with richness (figure 8c-8e). More interestingly, this relationship is constant over all landscapes of $\ell^2 \geq 900$ cells. Because most colonies on a landscape do not have unlimited growth, cover will only increase with new recruits, and rates of recruitment will be proportional to area (ℓ^2). Species poor communities are more strongly affected where the size of the

disturbance is greatest, particularly if the species removed is the largest and most stable species in the system. In this situation, communities may have to recover from a state close to the initial starting conditions of zero total cover. In species rich communities, in which only a single species is affected by disturbance, the total cover is buffered by the presence of other species that are unaffected (Doak *et al.* 1998). These systems are characterised by smaller colonies, as more species are packed into the same area. Thus, more speciose systems minimise both the size of the disturbance and consequently, the return time of the community.

The importance of patch size

Many of the system properties observed here change when the landscape size is less than 900 cells. This is a dynamic specific to this model with these parameters. Small landscapes do not allow species to grow sufficiently large to escape high rates of colony mortality irrespective of their species. The critical patch size at which the patterns seen here emerge depend explicitly on the interaction between the mortality regime for the species present in the community and the size of the patch. With different relationships between colony size and mortality it is conceivable that both the ‘critical’ patch size and the relationship between persistence stability/invasion resistance and species richness could change.

The size of the landscape had a profound effect upon the persistence stability, resilience stability and invasion resistance of a community. While temporally stable communities are possible on small landscapes, the mean and variance in S_T (i.e. more unstable) was higher than in larger landscapes (figure 3). Consequently, on average there is proportionally more space available on smaller landscapes than on larger landscapes, facilitating an increase in the numbers of recruits per unit area.

Importantly, there is a rapid switch between unstable highly invulnerable communities on small landscapes and stable invasion resistant communities on large landscapes with only a small increase in landscape size. The emergence of similar behaviours in other systems could have important ramifications for conservation strategies, particularly in the design of reserves.

Species-area and species invasion/extinction relationships are emergent behaviours of the 'metacommunity' of all landscapes for a particular landscape size. Thus, for any community there are multiple scales of emergent dynamics and the emergent behaviours are determined by the balance between recruitment, mortality and interactions. This corresponds with the views of MacArthur and Wilson (1963, 1967) who suggested that smaller islands would have higher extinction rates than their larger counterparts and Elton (1958) who also suggested that smaller islands were less stable and more prone to invasion.

Although smaller islands are less stable than large islands, within small islands increasing species richness increases the stability. If this pattern also arises in other communities, it could explain why the relationship between richness, stability and invasion resistance has been inconsistent among several empirical studies. If other communities also demonstrate a critical landscape size below which there is a positive relationship for richness and above which the relationship is negative, then the scale of experimental manipulations would determine the result. For example, both Levine (2000) and Stohlgren *et al.* (1999) found that in small areas richness was positively correlated with invasion resistance, while in large areas invasion resistance was negatively correlated with richness, as suggested by the results of our models. Coupled with the effects of disrupting spatial structure through manipulations, this

offers a very good explanation of the range of relationships between richness and stability/invasions observed in natural communities.

Thus, relationships between richness, stability (both persistence and resilience) and invasion resistance depend explicitly on the scale of observation. We suggest that the patterns observed in empirical studies (and to some extent in models) and our models are not contradictory but that each represents one facet of a complex relationship. In the absence of external disturbance, the results for any study at a particular scale will be influenced by the degree of mixing within the community, the emergence of large scale structures (i.e colonies), and the properties of these aggregate species structures. The dynamics we have observed here suggest the existence of a much larger continuum of possible relationships between richness, stability (both persistence and resilience), invasion resistance, species invasion/extinction and area than have been explored previously.

Chapter 6: Conclusions

The emergence of spatial-organisation in a sessile marine invertebrate community

This work suggests that spatial self-organising is an important force structuring the dynamics of these marine epibenthic communities. In models of sessile marine invertebrate communities self-organisation leads to the development of colonies and consequently the dynamics are different to those of mean-field models. Self-organisation into colonies in models confers advantages to larger colonies that smaller units do not have. The development of colonies in models is analogous to the growth of sponges, bryozoans, ascidians and cnidarians in natural communities. If a colony encounters a superior competitor it is able to grow in other directions, prolonging the survival of the colony as an entity, despite losses through competition at one section of their perimeter. Increasing colony size also offers refuges from mortality. This mechanism, apparent from observations of the existing natural community, was an emergent behaviour in the models. The development of large colonies maximises both the persistence stability and invasion resistance of a community. This is a novel result with wide ramifications. Where this occurs it is likely that the dynamics observed would be similar to those seen in this study.

In the natural community we studied, certain species are positively associated with other species (chapter 2). These positive associations may be the result of non-random recruitment and ostensibly not due to self-organisation of colonies over time. Unlike in natural systems, the models show no consistent inter-species self-organisation over time. Strong inter-species correlations can arise in spatial models systems where the network structures are in the relatively rare configurations (i.e.

Gurney *et al.* 1998, Johnson 1997) with relatively little stochastic input from mortality and recruitment. It may be that the networks that develop strong inter-species correlations are as rare in nature as are globally stable mean-field models (i.e. May 1974). Because growth rates of colonies over free space and their neighbours were slow relative to the rates of recruitment and mortality, patterns that may arise over long time scales (c.a. years) as consequences of network structures are likely to be disturbed by the effects of recruitment and mortality that occur over much shorter time scales (c.a. days). However, increasing growth rates would at some point balance and then exceed the stochastic input of recruitment and mortality. At that point it could be expected that interactions between colonies would structure the communities. Non-random associations between colonies of different species could then develop as a consequence of growth and interaction rather than recruitment and mortality. Both possibilities (i.e. none/weak and strong inter-species organisation) represent extremes of a continuum described by the relative importance of short-term stochastic versus long-term structuring processes.

The influence of spatial structure on community dynamics

The model developed here and the experiments to used validate this model reveal several unique behaviours not previously reported. First, the global dynamics in terms of relative abundances of species is relatively insensitive to the initial spatial arrangement of the colonies. The variable nature of growth rates, mortality and recruitment means that communities can explore a wide range of possible structures from the same staring configuration. It suggests that it is not sufficient to look at the mean behaviour of the system using the mean parameters, but necessary to also consider the variability around means. This feature is conspicuously absent from

most other ecological models. Our models generated all the variability seen in the global dynamics of the natural community simply from the measured variability in the parameters. The natural variability in the global dynamics is an emergent property of the variability of processes acting within the community, without the input of any external disturbance or other forcing. In this context, it is interesting to note that by using ANOVA and similar univariate and multivariate models, which dominate the analysis of ecological experiments, experimenters are focusing on means and not variances. While in many cases filtering out environmental noise and focusing on the means is appropriate, in some cases the community variances will contain more useful information on the processes acting within the community than the means.

Differences in means may be due to stochastic events or chaotic dynamics and may not reflect differences in ecological processes. To determine whether the processes acting within a community are similar irrespective of stochastic events it is necessary to compare variances.

The second behaviour is that the total amount of space available (i.e the patch size) determines the relationships between species richness, stability (both persistence and resilience) and consequently invasion resistance. The implication is that for the same species complement, a wide range of relationships between these community descriptors can exist, depending on the size of the landscape. The nature of these relationships are driven by the spatial structure of colonies and the properties of these larger aggregated structures. Across a range of landscape sizes, stability and consequently invasion resistance is influenced by the ability of species to form large colonies which have relatively reduced mortalities. For landscapes of the same size, the stability of the community as a whole is a function of the stability of each species, their respective size distributions and the covariances between species. In the

smallest landscapes all species are vulnerable to mortality because available space limits the maximum size that colonies can attain. However, as landscapes size increases individual colonies are able to grow larger with a commensurate reduction in the mortality rate. The exact relationship will be determined by the size mortality distributions for each species. Beyond a critical landscape size, very large colonies are more stable than equivalent cover of many small colonies for the time period examined.

There is no doubt that spatial structuring into colonies is a major determinant of the community dynamics in this marine epibenthic community. However, self-organisation plays a lesser role, except if colonies are considered as self-organising entities. To a large extent, other stochastic processes acting within the community obscures any organisation. It is possible that spatial structure is important in other communities (e.g. grassland communities) in their undisturbed states. Species in communities with these emergent properties will display certain characteristics (i.e. differences in mortality with size) and this could be easily investigated. The results found in this thesis raise two important questions (1) how do the processes outlined previously effect metacommunity dynamics and (2) how do these processes effect scaling on a single large landscape.

Metacommunities and scaling

First, do the dynamics of each separate community change when linked together as a metacommunity comprised of many varying landscapes? The communities modelled here are in essence a metacommunity with open global recruitment defined by a probability distribution. The next step is to link recruitment to abundances within a landscape. When considered as a metacommunity, each physically separate

community will represent a point in a continuum of possibilities. Within a single community large colonies inevitably die through stochastic events. At this point the total cover will drop and the community will take a considerable period of time to recover, as shown by the resilience stability (chapter 5). Is a single community with a cycle of large colonies that dominate space over long periods of time more stable than one with a constant but rapidly changing cover of small colonies and does this answer change if time scale of observation changes? This would require an examination of dynamics over much longer time periods, perhaps in the order of decades. A community with a cycle of large colonies would also have cycles of increased invasibility over time. On the scale of the metacommunity what proportion of communities have large colonies compared to those with only small colonies at one point in time and does this proportion change with time?

In answering these questions, it is difficult to untangle issues of time from issues of space. The measures of stability I have used here contain an implicit assumption about the appropriate time scale used to measure persistence stability. A time scale that at one spatial scale may capture the important community dynamics may miss dynamics that occur at larger spatial scales. What this does highlight is that measures of stability and invasion resistance can be influenced by the period of observation, the scale of observation and the overarching metapopulation dynamics.

Second, while I have examined the relationship between richness, stability and invasibility in islands/patches, I have not explored the relationship between these measures on a single landscape at different scales of observation. The question of stability on a single landscape across a range of observational scales can be approached from two directions. One approach, similar to that used in chapter 5, is to generate a coefficient of variance or similar statistic, and observe changes in the

statistic with the scale of observation (e.g. DeRoos *et al.* 1991). Alternatively, the characteristic length scale of the community could be estimate (e.g. Durrett and Levin 2000, Keeling *et al.* 1997, Pascual and Levin 1999, Rand and Wilson 1995). This is an approach derived from statistical physics that is a measure of the ordering of a system over multiple scales. Both methods are statistically similar (they both used measures of spatial residuals). Again, the determination of these statistics is dependent on the time scale of observation. It would be difficult to answer questions of metacommunities with first determining how spatial and temporal scaling effect dynamics on a single landscape. If scaling affects community dynamics in any way, and it does for patches of varying size (chapter 5), it follows that the range of patch sizes in a metacommunity will influence the overall dynamics. I suspect that not only will communities have a characteristic length scale (irrespective of the measure) but also a characteristic time scale and these measures reflect important community and metacommunity processes.

Conclusions

The dynamics of these sessile marine invertebrate communities are strongly dependent on the spatial structure of the community and that spatial structure is emergent in models, depending on the properties of species. The spatial nature of colonies of particular species influences the overall community stability and invasion resistance and interacts in non-intuitive ways with the total amount of space. It should be expected that different communities, with different species complements would behave globally in different ways. The exact dynamics will be determined by the species present and will not be a function of any particular aggregate property. However, this does not imply that generalisations are not possible across communities

and ecosystems. Because the processes acting here are so simple to is easy to see how they might act in other ecosystems. The generalisations possible will reflect the complexity of the systems described. Ecosystems are much more complex than the simple models and hypothesised relationships that have been used to now, and it is necessary to develop more sophisticated syntheses of how species properties generate the emergent community dynamics. It is not simply enough to say that species richness influences stability, without also qualifying how area changes that relationship. Ecological theory need to take the next step and embrace the complexity of ecosystems and generate new hypotheses.

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