UNIVERSITY OF SOUTHAMPTON

INFLUENCE OF RECRUITMENT ON POPULATION PERSISTENCE IN OPEN AND CLOSED SYSTEMS

Adam Kent

Thesis submitted for the degree of Doctor of Philosophy

School of Biological Sciences

October 2000

UNIVERSITY OF SOUTHAMPTON
ABSTRACT
FACULTY OF SCIENCE
SCHOOL OF BIOLOGICAL SCIENCES
Doctor of Philosophy

INFLUENCE OF RECRUITMENT ON POPULATION PERSISTENCE IN OPEN AND CLOSED SYSTEMS

by Adam Kent

This thesis examines the influence of recruitment on the persistence of populations in open and closed systems. Three systems were modelled, addressing questions concerning the influences on consumer dynamics of prey recruitment, consumer behaviour, and prey behaviour. Theoretical concepts were developed with mathematical models, and tested on observations from field experiments and empirical data collected from the literature. The following focal questions were addressed:

1. How do consumer populations respond to migration of their limiting prey into or out of the system? A Lotka-Volterra type model revealed that even a small prey outflux had catastrophic consequence for predator persistence. In contrast, the predator population was stabilised by subsidising it with prey influx. These outcomes for prey subsidy were compared to those for prey enrichment, which is known to destabilise populations (Rosenzweig's 'paradox of enrichment'). This research has implications for conservation and pest management. An influx to conserve a threatened population or an outflux to eliminate a pest population may have more effect when applied to the limiting resource than to the focal species itself.

2. How do populations of colonists respond to conspecifics in an open system? Recruitment of barnacles to rocky shores was monitored in experimental tests of alternative models for recruitment dynamics. Two species were analysed: *Semibalanus balanoides* and *Chthamalus montagui*. The position and number of barnacle settlers was found to depend directly on the presence of conspecifics and the availability of free-space. The reproductive success of some sessile barnacle species, including *S. balanoides*, depends on individuals lying within a penis length of conspecifics. Other sessile species, including *C. montagui*, are able to self-fertilise and their spatial positioning therefore has less effect on total reproductive success (though they may still prefer to cross-fertilise). A simulation model was used to determine the relative effect of penis length and territorial repulsion on spatial patterns in both species. Random settlement within a penis length of conspecifics successfully mirrored observed settlement patterns. This mutual attraction of conspecifics was found to generate exponential growth of recruits in some populations from an arithmetic influx of settlers, and consequently gave population dynamics with properties similar to those found in closed systems. Analytic models were developed to distinguish density-dependent (arithmetic) growth from density-independent (exponential) growth. The model for exponential growth revealed a maximum value of free space above which a barnacle population could not be supported. This was identified as an extinction threshold and could be interpreted as the density of barnacles at which all individuals are greater than a penis length apart.

3. How do prey respond to dietary switching by their predators? A two-prey model was applied to tundra microtine populations (the 'predators') eating vegetation (the 'prey') with wound-induced toxic defences to predation. Parameter values were gathered from the literature, and model outputs were tested against five empirically derived criteria that characterise population cycles in this group. For plants without chemical defences the model met only four of these criteria. Supplementing the model with a parameter to describe periodic toxin production resulted in the model output meeting all five criteria. The delayed onset of toxin production was shown to be crucial if all criteria were to be matched.

“Nature has no stake in being understood by ecologists”

Hairston (1994)

CONTENTS

Title: INFLUENCE OF RECRUITMENT ON POPULATION PERSISTENCE IN OPEN AND CLOSED SYSTEMS

ACKNOWLEDGEMENTS

I would like to thank the University of Southampton's High Performance Computing Centre and the School of Biological Sciences for funding the Studentship under which this research was carried out. My supervisor Dr Patrick Doncaster who has been instrumental in the production of this thesis, and has given me so much time and help over the past three years. Professors Tim Sluckin and Steve Hawkins have also made time in their busy schedules to help me follow certain lines of enquiry.

Collaborations with the members of the BED rocky shore group have been both informative and enjoyable. In particular I would like to thank Malcolm Roberts for his assistance in counting all of those barnacles, even if it did mean having to spend long summer days on the beaches around the Isle of Wight. A big thanks must also go to Kieran Hyder for all the words of wisdom and help he has given me since day one, cheers mate!

My three years in Southampton would not have been the same without all my new friends. Thanks to Adam H., Adam J., Adam M., Cam, Carol, James, Natalie, Mark, Matt H., and Stevey B. Thanks must also go to everyone from the old skool who have kept me in touch with the real world, thanks to Ben, Bridie, Chris, Dave, Emma & Phil, Hel & Sal, Scott and Wendy G., with an especially big thanks to Morg, Olly and my brother Matthew.

I would finally like to profusely thank and applaud Wendy and my Mum, Anne, and my Dad, Mike. All three have put up with my (sometime excessive) moaning and groaning but have always offered words of encouragement, enthusiasm and rationale. They always seem to be there at the right time physically, mentally and financially! However, I would like to take this opportunity to assure them all that one day I will get a job!

1 GENERAL INTRODUCTION

As the world's remaining natural habitats divide and fragment in the face of human exploitation, it becomes increasingly important to understand the ecological and evolutionary dynamics of local populations in order to effectively manage and preserve them. In this thesis, both analytical and experimental approaches have been used to investigate the dynamics of populations subject to regulation and recruitment in open and closed systems. As a result of this research we have been able to draw inferences about the consequences of different recruitment dynamics on population persistence.

Current theoretical population research is very much bimodal, with models describing systems that are either closed (e.g. Levins, 1969; Burkey, 1989; May, 1991; Hanski, 1991, Harrison, 1991) or open (e.g. Roughgarden & Iwasa, 1986; Gotelli, 1991; Hanski, 1994a). The defining characteristic of a closed system is that recruitment entirely depends on the local birth rate; in an open system, in contrast, recruitment depends on colonisation from external sources and is independent of local births. These two extremes are artificial in the sense that natural systems are never entirely open or closed. Both extremities have categorically different outcomes to population persistence. Research enabling a better understanding of the interface between the two is needed if ecological models are to be effectively implemented in species conservation or eradication programmes. In this thesis I aim to answer such questions. The findings are therefore intended to be of general interest to both pure and applied ecologists.

In this introductory chapter I review the role and use of population models in studying open and closed systems. First I examine the function of modelling in ecological research. I next present some classical population models, which form the basis of the research presented in this thesis. I also outline what predictions these models give with regard to population persistence. Finally, I discuss the merits and requirements of an inter-disciplinary approach combining both empirical and modelling techniques. In conclusion I outline specific objectives for each data chapter. The principal function of this chapter is to introduce the reader to the key processes that drive population dynamics, which inform the conceptual models of these dynamics.

1.1 MATHEMATICAL MODELS: THEIR ROLE IN ECOLOGICAL RESEARCH

One way in which we can make predictions concerning the natural world is through modelling. Mathematical models can give an insight into how population numbers fluctuate in space and time and they play a vital role in current ecological research (see Nisbet & Gurney, 1982; Murray, 1993; Renshaw, 1995; Hilborn & Mangel, 1997). Models provide standards of 'ideal' behaviour against which real ecological situations can be compared. Their aim is to capture the essence of a problem and allow the user to explore different solutions and processes under consideration (Begon *et al.*, 1990; Grimm, 1999). A model is therefore usually considered to be the formal statement of a hypothesis (Lomnicki, 1987).

The incorporation of mathematics into ecology has generally contributed directly to our theoretical knowledge of ecological systems (Caswell, 1988). However, considerable scepticism still prevails amongst some researchers as to the role of modelling in ecology (May, 1999). Stenseth *et al.* (1977) state that the general objectives of mathematical models in ecology are to organise ideas and data, expose implicit assumptions, polarise thinking, pose pertinent questions, explain earlier observations, predict the outcome of further experiments, pinpoint ambiguities, and establish where further studies are needed. Models can also generate hypothesis relatively cheaply, when compared to the time and money required testing such hypothesis using equivalent field or laboratory experiments.

Biological models should never be constructed without a good understanding of the biological relationships and biological meanings to which they are applied (Wissel, 1992). Equally, models should not be made so complicated by the inclusion of so many parameter values that they make it impossible to answer basic biological questions (Uchmanski, 1999). Typically, these models are of little use in enabling us to understand natural processes (Stenseth, 1993). As the numbers of parameters in a model increases the model gains in precession but loses generality. The mathematical analyses must be sufficiently transparent to enable useful biological conclusions to be drawn from them (Renshaw, 1995). Models in ecology should be both realistic, and precise (Holling, 1965; Levins, 1969).

The construction of ecological models is a complex process, which depends on the questions that the model aims to address (Hilborn & Mangel, 1997). Modellers rarely build a model completely from scratch, they generally borrow many, if not most, designs and ideas from other models (Grimm, 1999). Models are constructed so as to improve our understanding of a theoretical problem, just as experiments are conducted to improve our understanding of an empirical problem (Caswell, 1988). However, neither the model nor the experimental system need duplicate every detail of the real world (Caswell, 1988). When constructing a model it is important to not only clarify the aims of the model but also the extent to which individuals are to be represented (McGlade, 1999).

Most simple population models assume that all individuals within a system are homogenous, evenly mixed in space and that they interact equally (McGlade, 1999). These systems are typically represented by either difference (eqn 1.1), or differential equations (eqn 1.2).

$$\text{difference equation :} \quad N_{t+1} = f(N_t) \tag{1.1}$$

$$\text{differential equation:} \quad \frac{dN}{dt} = f(N) \tag{1.2}$$

Both eqns 1.1 and 1.2 describe how N changes over time according to some function f. Whether to use difference or differential equations depends upon the organism, the life history, the life strategy and the habitat to be modelled. Difference equations relate to population at time $t + 1$, in terms of the population N_t at time t (Murray, 1993). Difference equations are typically used for models that have discrete occurrences such as population changes over set time intervals; consequently they are applied to systems with distinct generations.

Differential equations apply where generations overlap completely so that birth and death processes are continuous. The net rate of population increase is represented by

$\frac{dN}{dt}$. The increase in size of the population is the sum of the contributions of the various individuals within it (Begon *et al.*, 1990). Differential equations are therefore associated with continuous models. Differential equations can posses a rich spectrum of dynamical behaviour (May, 1976). The use of differential equations has remained an invaluable tool in the elaboration of population modelling, and this approach permeates much of current ecological thinking (Arditi & Ginzburg, 1989). As the change in size of the populations modelled in this thesis are assumed to be continuous and not discrete I have used differential rather than difference equations. In Chapter 4 I analyse the growth of barnacle populations which do have discrete generations. However, it remains appropriate to use differential equations to model the increase in size of one generation.

1.2 PREDATOR-PREY MODELS

One of the major problems faced by ecologists is to understand the role of prey in the regulation of their predator populations (Hastings, 1990; Berryman, 1992). Predator-prey models allow the stability of a two-species system to be calculated at a local level. In both Chapters 2 and 5 we model local populations using predator-prey models and in Chapters 3 and 4 we compare empirical results to predator-prey models. Although there is much variation in current predator-prey models (e.g. see Murray, 1993; Renshaw, 1995) they are all based on the framework identified in classical population models; population size depends on the balance of inputs to outputs. However, the exact form of the model depends upon whether the inputs are generated within the system or come from outside it.

1.2.1 Closed system models

A closed community is defined as an autonomous unit. Its population size depends on the balance of births and deaths within the population itself. Only birth-death processes regulate populations within closed systems and there is no immigration or emigration. If an extinction event occurs it happens once and for all; populations cannot be re-seeded from external sources. Models for population growth in a closed environment are based on two fundamental premises: that populations have the potential to increase exponentially through self-replication of the component individuals and that there is density-dependent feedback that progressively reduces the actual rate of increase.

1.2.1.1 The Lotka-Volterra model

The simplest and one of the earliest closed system models is the Lotka-Volterra model of predator-prey interactions. Volterra (1926), an Italian mathematician by training, first proposed a simple model for the predation of one species by another to explain the oscillatory levels of certain fish catches in the Adriatic. Lotka (1932), an American physical chemist by training, also proposed a similar model independently of Volterra to explain prey-dependent population regulation. The Lotka-Volterra equations adopt the chemical principles of mass action. In other words, they assume that the response of the population is proportional to the product of their biomass densities (Berryman, 1992).

The Lotka-Volterra density-independent model assumes initially that in the absence of consumers the prey population increases exponentially, and can be expressed by:

$$\frac{dS}{dt} = r \cdot S \tag{1.3}$$

where r is the net reproductive rate per capita and S is the number of prey in the population. If prey are removed from the population by predators, and prey removal occurs at a rate that depends on the frequency of the predator-prey encounters, then the encounters will increase as the numbers of predators increase and as the number of prey increase. The exact number of prey encountered by each predator will ultimately depend on the search and attack efficiencies of the predator for each prey, which can be represented by a parameter constant c. The consumption rate of the predator population will therefore be $c \cdot S \cdot N$, where N is equal to the number of predators. This is known as the predator functional response to prey. The overall equation for prey rate of change is then the sum of these two components:

$$\frac{dS}{dt} = r \cdot S - c \cdot S \cdot N. \qquad (1.4)$$

The Lotka-Volterra equations assume that if the predator population is unable to capture prey the numbers within the population will decline exponentially; thus the equation for predator mortality is given by:

$$\frac{dN}{dt} = -d \cdot N \qquad (1.5)$$

with, *d*, being equal to the natural mortality rate of the predator population. The death of predators is counteracted by the births of new predators. The rate of births is assumed to depend upon only two factors:

1. The rate at which prey are consumed: $c \cdot S \cdot N$.
2. The predator's efficiency at turning the consumed prey into new predator biomass (generally through births), given by a conversion constant, *b*.

Predator birth rate is added into eqn 1.5 to give the Lotka-Volterra predator rate equation:

$$\frac{dN}{dt} = b \cdot c \cdot S \cdot N - d \cdot N. \qquad (1.6)$$

The dynamic properties of the coupled rate equations (eqn 1.4 and 1.6), which constitute the Lotka-Volterra model, can be investigated by finding their zero isoclines (see Figure 1.1). The prey zero isocline is the line of points at which a prey population maintains itself at a constant equilibrium, neither increasing, nor decreasing in numbers for a given number of predators. This is given by setting eqn 1.4 to $\frac{dS}{dt} = 0$. The predator zero isocline is the line of points at which a predator population maintains equilibrium for a given number of prey. This is given by setting eqn 1.6 to $\frac{dN}{dt} = 0$. The single point of equilibrium for both prey and predators is then given at the intersection of the two isoclines.

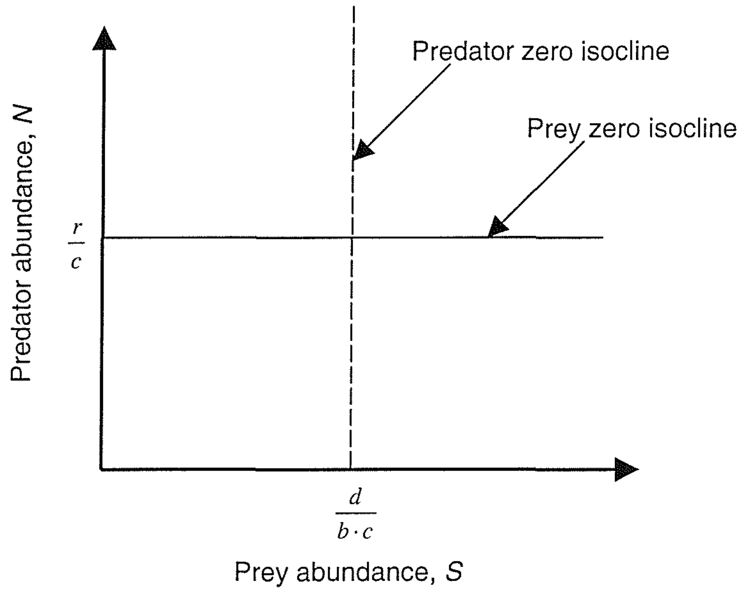


Figure 1.1. A graphical representation of zero isoclines, for the classical Lotka-Volterra model (eqns 1.4 and 1.6). A zero isocline is the line of points at which a population maintains equilibrium. The predator zero isocline is represented by a broken line and the prey zero isocline a solid line.

The system described by the rate eqns 1.4 and 1.6 can at any time be expressed by the values of S and N. Which direction the system will move at a chosen point can be determined by combining predator and prey density vectors. If we plot enough points and join them up to form trajectories, we can see in which direction the system moves from a stationary point at $t = 0$. Figure 1.2 displays the system dynamics of the Lotka-Volterra equations; this type of diagram is referred to as phase plane diagram.

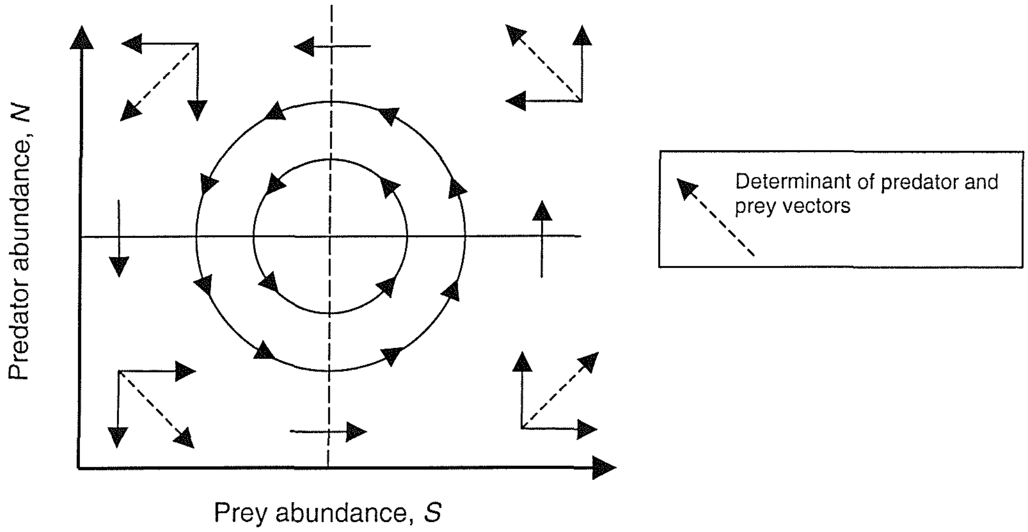


Figure 1.2. Combined Lotka-Volterra predator-prey vectors for eqns 1.4 and 1.6. The determinant of the vectors gives the direction of movement for both populations. The population moves with time from low predator-low prey, to low predator-high prey, to high predator-high prey, to high predator-low prey (see Figure 1.1 for a description of isoclines).

The dynamics shown by Figure 1.2 indicate that the coupled populations undergo perpetual oscillations around the equilibrium point. The size and amplitude of the closed orbits are determined by the initial conditions (Bulmer, 1994). The mechanism for the cycles are as follows: high prey densities tend to result in high predator densities, which in turn tend to depress prey density which result in lower predator densities and so forth (May, 1981). This carries on until another factor influences the values, after which the oscillations follow new cycles indefinitely, until they too are affected by other conditions. Uniform cyclic oscillations are never seen, as chaotic environmental factors continually shift the cycles into new orbits. The population cycles described by the Lotka-Volterra equations are known as neutral stable limit cycles as once perturbed the cycles never return to their original position.

The Lotka-Volterra equations are often not satisfactory when making comparisons to reality. There are two main problems with the model (Brown & Rothery, 1993; Bulmer, 1994).

1. There is no self-limitation of prey populations in the absence of predators.

2. The rate at which prey is eaten is directly proportional to the product of the densities of the predators and the prey; i.e. the model assumes no density-dependence in the consumption of prey by predators.

1.2.1.2 Lotka-Volterra with density-dependence and self-limitation

It has been realised since the early work of Verhulst (1888), and Pearl & Reed (1920), that many biological populations exhibit negative feedback mechanisms that restrict their growth. This negative feedback process within the population has been termed 'density-dependence' and is an important factor when considering population models.

Relatively realistic models can be obtained by modifying the predator free growth term within the prey Lotka-Volterra equation, to include density-dependence. In the original Lotka-Volterra equations the prey population grows indefinitely to infinity in the absence of predators. This limits its use as even without the threat of predation other factors such as food, space, and disease are going to limit prey population size. Malthus (1798) was the first to recognise that animal populations have the capacity to increase geometrically, whereas their food supplies increase arithmetically, and consequently animal population growth is liable to be limited by resources. To correct the assumption of unlimited growth a logistic self-limitation term is often added to the prey equation. The limiting term is known as the carrying capacity, K. The carrying capacity is the maximum number of individuals a specific environment can sustain. The inclusion of carrying capacity in the original Lotka-Volterra prey rate equation (eqn 1.4) gives:

$$\frac{dS}{dt} = r \cdot S \cdot \left(1 - \frac{S}{K}\right) - c \cdot S \cdot N \tag{1.7}$$

This modification produces a prey zero isocline with a negative slope rather than a horizontal one (see Figure 1.3), i.e. prey reach a maximum K in the absence of predation; few prey are sustained when the predator is close to its own carrying capacity. The predator population can then exploit nearly all of the prey population leaving few prey uneaten as standing crop. The negatively sloping isocline confers stability. The intersection is now a stable focus.

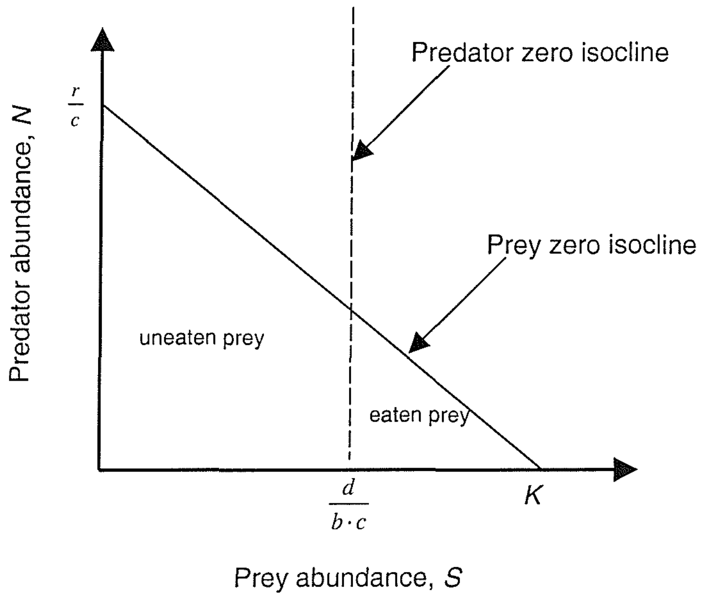


Figure 1.3 The introduction of density-dependence into the prey rate equation results in a sloped prey isocline rather than a horizontal isocline as shown in Figure 1.1. The point at which the prey isocline intercepts the prey axis is known as the carrying capacity, and represents the maximum density of prey that can be sustained by the environment.

The Lotka-Volterra model assumes that the number of encounters between a predator, and its prey increases linearly with prey density. Realistically, there must be an upper limit to the predation rate (Brown & Rothery, 1993). Predators may also require a constant handling time for each prey regardless of prey density.

Although the length of time spent by a predator searching for each prey item is a function of prey density the amount of handling time per prey can be expected to remain constant. The functional response describes the predator search rate and prey density relationship. Holling (1959) was the first to formally present theoretical and experimental evidence supporting the idea that consumption rate may depend on prey-dependent search time and constant handling time. The detailed response by a single predator to increases in prey density was classified into three types by Holling (1959) (see Figure 1.4). A type I functional response shows a linear increase in predation rate, until a plateau is reached. A type II functional response follows a rectangular hyperbola with a decelerating increase in consumption rate. A type III functional response follows a sigmoidal curve, with an initially accelerating increase in consumption rate, then decelerating.

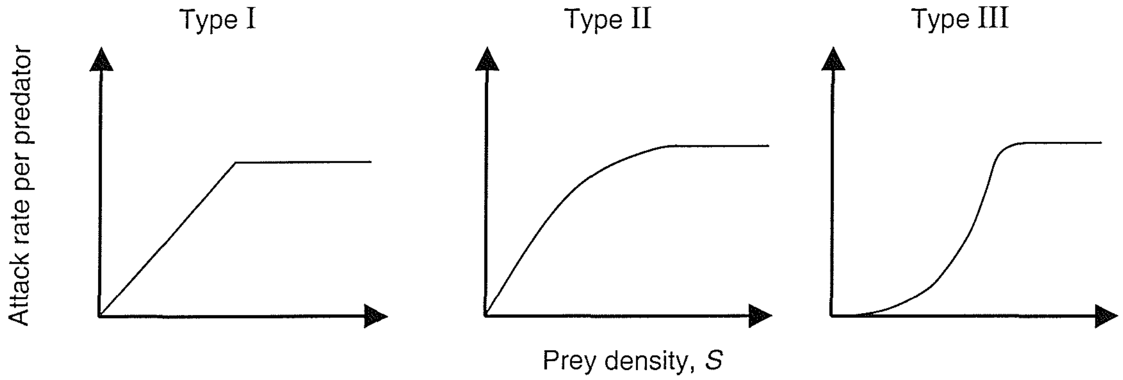


Figure 1.4 The three types of relationships between prey density and the attack rate of a predator i.e. the functional response as originally described by Holling (1959). Type I shows a constant increase, type II follows a decelerating increase and type III a accelerating increase.

At high prey densities a type III functional response is similar to a type II response, both exhibit inverse density-dependence. A type III functional response can occur when an increase in prey from low densities leads to an increase in the predator's searching efficiency or a decrease in prey handling time (Begon *et al.*, 1990). The type of response exhibited typically depends on the organism and the system being studied, though a type I response is considered to be rare in natural systems (Putman & Wratten, 1984).

Where the functional response describes predator behaviour, the numerical response describes the relationship between prey density and the number of predators recruited to the system as a function of the proportion of prey consumed. As the density of prey increases the proportion of prey consumed by the predator population decreases. However, as prey density increases predators generally become more abundant due to increased reproduction rates. The functional and numerical responses are therefore directly linked as shown in Figure 1.5.

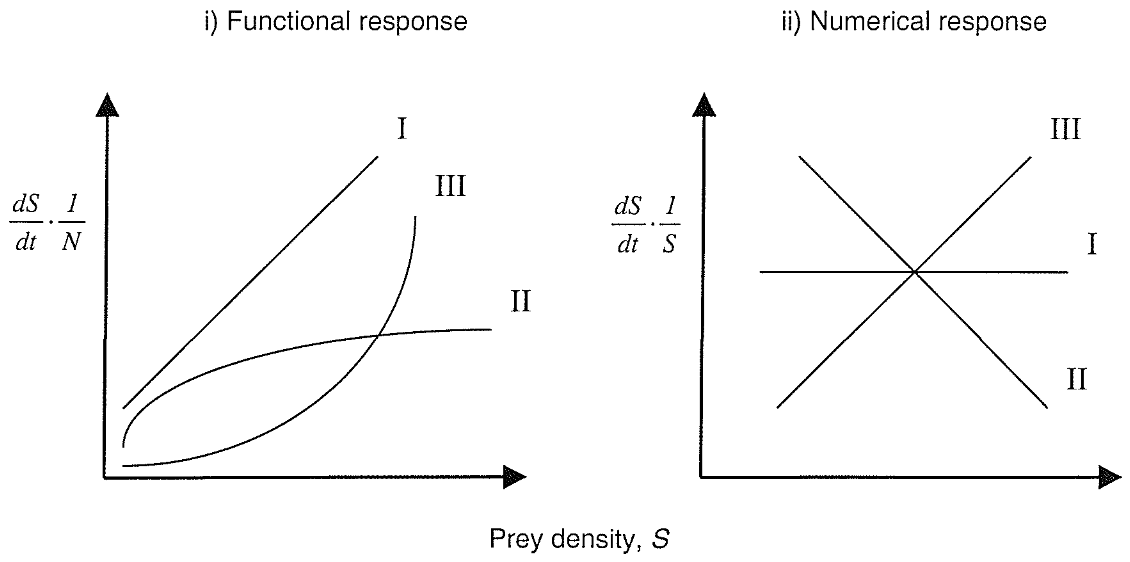


Figure 1.5 The relationship between the i) functional response which describes the association between prey density and predator attack rates and the ii) numerical response which describes the association between prey density and the number of predators.

The zero isocline given by the Lotka-Volterra predator rate equation (eqn 1.6) is vertical (see Figure 1.1). A vertical isocline can successfully represent predators that do not interfere with conspecific survival directly. Interference is the decline in resource use resulting from the behaviour of other conspecifics, though this does not include depletion, in which the resource is removed (Sutherland, 1996). Predators that do not display interference never battle over the same individual prey item, engage in cannibalism, or exhibit territorial defence (Rosenzweig, 1971). Under this regime predators can be regulated by the over exploitation of prey. The absence of mutual interference results in a density-independent numerical response of predators to prey, which gives the vertical predator isoclines (e.g. Rosenzweig, 1971; Gilpin, 1972; Tanner, 1975, see also Chapter 2).

Mutual interference between predators and other abiotic factors can increase self-regulatory mechanisms in the predator population. Hassell & May (1974) have shown that both predator aggregation and interference increase stability. The appetite of an individual predator has also been shown to be an influencing factor in the amount of prey required, this has been termed the 'developmental response' (Murdoch, 1971). If prey individuals are all of a similar calorific content, then appetite defines the maximum number of prey which can be eaten in a given time. This sets an upper limit to which a predator can deplete the prey population (Crawley, 1975), and consequently alters the predator isocline from a vertical line to a hyperbola indicating density-dependent consumption (see Figure 1.6). The precise form of the function which relates appetite to body weight will vary between species (Kendeigh, 1970).

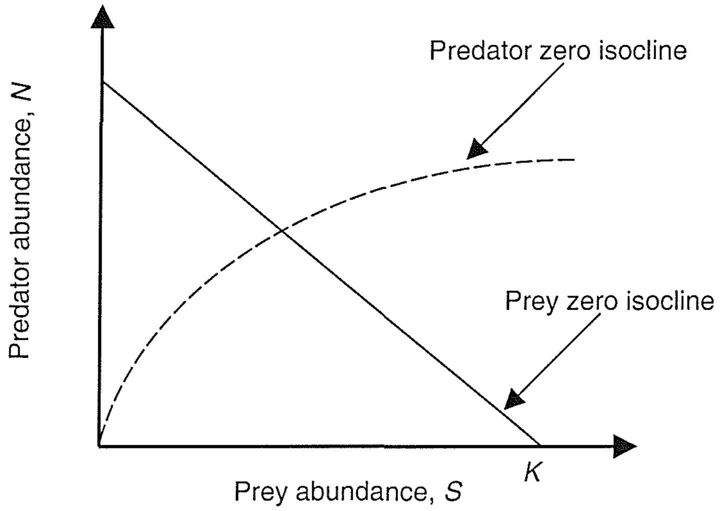


Figure 1.6 The introduction of density-dependence in the form of mutual interference to the predator rate equation and the resulting effect on the predator zero isocline (broken line) which now takes the appearance of a hyperbola curve rather than a vertical line.

Density-dependence may not operate to regulate populations at all times. There are times of increase and times when density-independent factors cause a decrease without compensating effects from the density-dependent factors (Nicholson, 1958). Density-dependence is necessary for a population to have an abundance in a range definable by the properties of the system of which it is a part of (Chesson, 1998). Stable dynamics are not the only equilibrium condition displayed by density-dependent equations, as they can also lead to stable limit cycles and even to irregular and apparently chaotic population fluctuations (Hassell *et al.*, 1976). Stable limit cycles are characterised by well-defined cyclic changes in population numbers over time (May, 1973). Stable limit cycles can be distinguished from neutral cycles (as given by the original Lotka-Volterra model) as they have self correcting mechanisms that enable the populations to return to the original trajectory once a perturbation has occurred. The stability of the cycles relies upon density-dependence either in predation or the resource. Many predator equations which include a density-dependence function exist in the literature and display a full range of predator-prey dynamics, (e.g. see Nicholson, 1935; Maynard-Smith & Slatkin, 1973: Bellows, 1981: May *et al.,* 1981; Royama, 1981; Crone, 1997). However, density-dependence can act indirectly through a resource (competition) or predator (density-dependent predation or 'apparent competition'), and therefore may operate with a time lag (Chesson, 1996).

For a predator-prey interaction to persist, the parameters of the appropriate population model should be such that the model implies either a locally stable equilibrium or a limit cycle. Beddington *et al.* (1976) have shown that this is a necessary but not a sufficient condition for persistence. Sufficiency may only be guaranteed only when the component population densities occur and stay within some well defined region around the equilibrium or cycle. Throughout this thesis we comment upon the persistence of populations we have modelled and studied, and therefore in the next section I highlight some of the theoretical background behind extinction theory which is applicable to predator-prey interactions in closed systems.

1.2.1.3 Extinction thresholds and theory of deterministic extinction

The stability of ecological systems and the persistence of species within them are fundamental concerns in ecology (Myerscough *et al*., 1996), though extinction, or the absence of persistence is a phenomenon that is notoriously difficult to document convincingly (Walde, 1994). In general, predators and competitors tend to have a negative effect on population density thereby increasing extinction probability (Bengtsson, 1989).

In a closed system only birth and death processes regulate the number of inhabitants. If the net population growth rate is negative and remains negative then eventually the population will go extinct. As the system is closed from immigration the population remains extinct indefinitely. The actual time to extinction depends on the difference between birth and death rates at different densities. It will be greatly variable from species to species (Burkey, 1999). Equilibrium in the system is achieved when the density of prey is reduced to that level at which a predator gives rise to a single progeny before dying (Nee, 1994). If the prey density drops below this equilibrium value and the predator is unable to produce one progeny then within time the population will reach extinction. On a global scale (which itself can be considered a closed system) all populations will decrease to zero in the far future. Populations are doomed to extinction in accordance with the paleontological argument that all species are destined to eventual extinction (Alvarez, 1998). The planet is not devoid of life, however, because species give rise to new species before going extinct. The dynamics of births and deaths thus applies equally to species or to populations.

Conservationists are interested in minimum viable populations (MVP) (Shaffer, 1981) which are able to persist over a given period of time with a certain probability. MVP are linked to the amount of suitable habitat or resource available to sustain such populations. The amount of habitat that can just sustain a single population has been termed by Lande (1987) as the extinction threshold. By using a predator-prey system Nee (1994) has shown that the deterministic extinction threshold of a predator is equal to the uneaten fraction of the prey population. Therefore, a population well buffered against extinction is one that maintains the equilibrium density of limiting prey well below what it would be in the absence of predation i.e. it has a small uneaten fraction (Doncaster *et al.*, 1996). Such predictions assume density-independent predator dynamics (i.e. a vertical predator isocline in Figure 1.3), and no stochasticity (see next section).

The verbal description of an extinction threshold given above can be represented by the set of zero-isoclines shown in Figure 1.7. The equilibrium predator population is given by N^*. If the carrying capacity of the environment is reduced from K_1 to K_T the prey isocline moves so it intersects the S axis at K_T. As the parameter K does not effect the predator isocline, it remains stationary. The reduction of the carrying to K_T results in the predator equilibrium density dropping from N^* to 0. This K_T is the deterministic extinction threshold. The concepts and the application of extinction thresholds are discussed further in both Chapters 3 and 4.

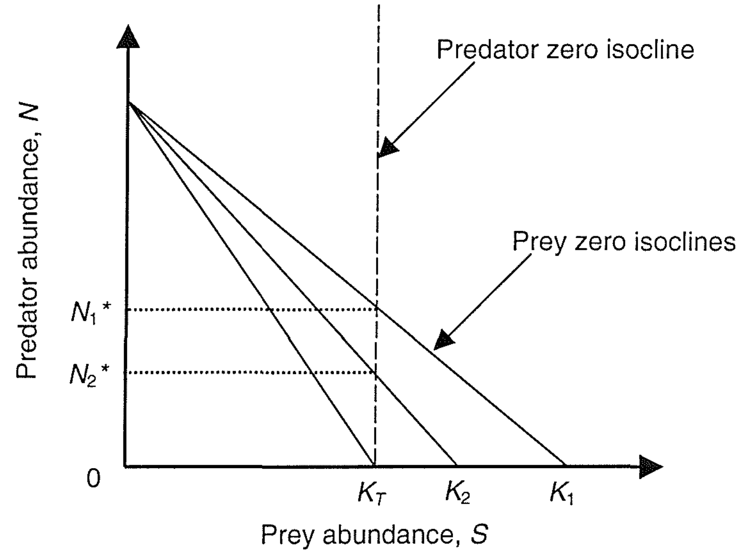


Figure 1.7 The effect of altering the prey carrying capacity on the persistence of the predator population using a deterministic approach. At K_1 the equilibrium population of predators is given by N_1*. A reduction in the carrying capacity of the environment to K_2 reduces the equilibrium predator population to N_2*; further reduction to K_T reduces it to zero. At this point the carrying capacity has dropped too far to sustain a predator population. This point is known as the extinction threshold (Lande, 1987).

The existence of extinction thresholds highlights the danger of habitat fragmentation. If habitats are made smaller by the introduction of non-traversable barriers such as roads or fences, then the carrying capacity of the environment is immediately depleted, affecting first the prey then the predator populations. Although the time to extinction depends on species, the effect of fragmentation may be relatively invariable across species (Burkey, 1999). Throughout the world, populations of endangered species are increasingly restricted to relatively small fragments of formerly extensive habitat (Groombridge, 1992). In many practical applications actual persistence times can be estimated by multiple realisations of modelling techniques (Middleton & Nisbet, 1997).

In Figure 1.7 the reduction of the carrying capacity increases the likelihood of extinction as the equilibrium population of predators is also reduced. Rosenzweig's (1971) extension of this model looks at it in the opposite direction. His 'paradox of enrichment' model predicts that enriching the system (by increasing the carrying capacity) will cause an increase in the equilibrium density of predators but not prey. This leads to instability, which increases the probability of extinction. Rosenzweig (1971) explains this behaviour by showing that if the predator is quite proficient at reproducing in the presence of a few of its prey then the predator will be far from extinction threshold but predator-prey dynamics will be unstable. If on the other hand the victims are relatively proficient at escape or their exploiters have a relatively poor reproductive efficiency or digestive efficiency then the predator will be closer to deterministic extinction, but the system will stable.

In Chapter 2 we compare the effect of enhancing a populations limiting resource through increasing the carrying capacity of the resource stock (Rosenzweig's model), to subsidising the resource through prey subsidy (our prey flux model). We find that these models give contrasting results.

1.2.1.4 Stochasticity

It was MacArthur & Wilson (1967), who first introduced stochasticity into a population model. They studied the probability that the colonisation of an introduced species fails due to the randomness of individual survival and reproduction. Stochasticity will not only affect the model organism it is applied to but also individuals and populations in trophic levels above the organism it is intended to act upon.

Stochastic processes can be sub-divided into two distinct areas, demographic stochasticity and environmental stochasticity.

Demographic Stochasticity: refers to chance variation between individuals in the same environment (Brown, 1993). Fluctuations arise because a population contains a discrete number of members, with population changes being caused by a succession of individually unpredictable births and deaths. Demographic stochasticity results from irregularities on an individual basis, and is only important in small populations (e.g. Lande, 1988; Wissel & Zaschke, 1994).

Environmental Stochasticity: refers to temporal environmental variation (external randomness) acting on a population (Stephan & Wissel, 1999). Environmental stochasticity includes abiotic factors (e.g. the weather) and the biotic impact of other populations (e.g. predators, competition, resources) (Simberloff, 1988).

While tools for the mathematical analysis of demographic stochasticity are well developed, a single consistent measure for the strength of demographic stochasticity has not been available. Such a measure is required for proceeding from examples and case studies to generalisations (Kokko & Ebenhard, 1996). The decision whether to use a stochastic model or a deterministic model is controlled by the magnitude of demographic stochasticity (Nisbet & Gurney, 1982). In practice, the environment does fluctuate and this superimposes an additional risk of extinction on that arising from demographic accidents alone (Pimm, *et al.*, 1988).

Environmental stochasticity leads to population fluctuations distinct from demographic stochasticity (Brown, 1993). Theoretical models of extinction predict that population persistence is more sensitive to environmental variation than demographic stochasticity (Leigh, 1981; Goodman 1996). Levins (1969) has shown that the general effect of environmental stochasticity is to lower the population density below what it would be in a deterministic environment. The primary cause of this is that fluctuations occur around the deterministic mean, but happen at much faster time-scales than those that regulate the mean. The fluctuations reducing the population are more destructive than the upward fluctuations. The severity of environmental stochasticity has considerable significance in population and conservation biology (Hanski, 1992).

Stochasticity can be modelled in a variety of ways depending how the environment and the population are predicted to fluctuate. The stochastic element may feature in the frequency term, or the sequence may perform a random walk in which its value at time *t*, is closely related to its immediate past history (Renshaw, 1995). The effect on the time to extinction in a deterministic model and one that incorporates stochasticity can be shown graphically (see Figure 1.8). In general, stochastic models will predict an extinction event before a similar deterministic model.

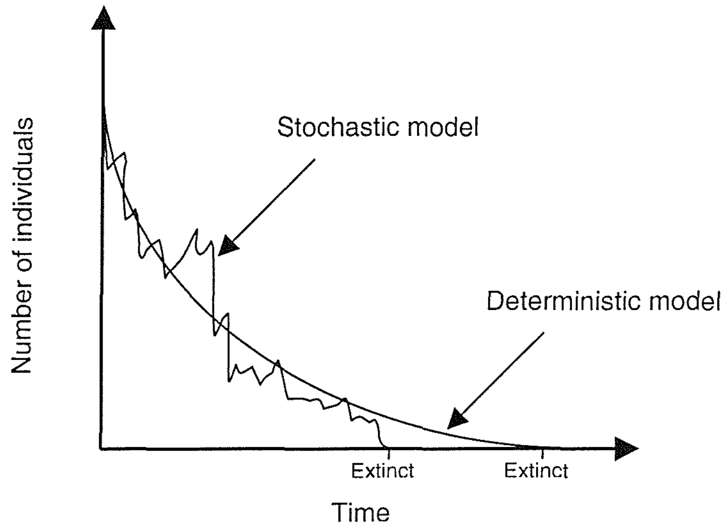


Figure 1.8 The effect of stochasticity on a population. Both the deterministic and the stochastic versions follow the same trend, with the number of individuals decreasing with time. The stochastic model, however, predicts extinction before the deterministic model.

The assumption that an environment is deterministic can only be made if stochasticity is so small it can be ignored. In general if a deterministic model shows a stable equilibrium, then the corresponding stochastic model would predict long term survival, whereas if the deterministic model shows no equilibrium then the stochastic model would predict a high probability of extinction (Maynard-Smith, 1974). Populations with a low intrinsic rate of increase run a higher risk of becoming extinct, as they will consequently recover slowly from a reduction in numbers caused by either demographic or environmental stochasticity.

Environmental stochasticity determines the way the carrying capacity influences the lifetime of a population (Stephan & Wissel, 1999). An increase in the carrying capacity leads to an enormous increase in population lifetime if environmental noise is weak (Goodman, 1996; Lande, 1993). An increase in the carrying capacity has a limited effect if environmental stochasticity is strong, though this is not always the case (Stephan & Wissel, 1999).

Although the advantages of stochastic over deterministic models have been highlighted it is generally considered that both deterministic and stochastic models have important roles to play in the understanding of biological systems (Renshaw, 1995). Stochastic models must be built on deterministic models (Maynard-Smith, 1974), so an understanding and appreciation of the deterministic foundation must occur before fundamental models can be expanded. The models presented in this thesis are of the deterministic kind. I again justify this use of deterministic models in Chapter 6.

1.2.2 Open system models

An open system consists of a mosaic of patches within which interactions proceed. Migration can occur between patches, though the focus of open system models is on the dynamics within a patch. Extinction within a patch of an open system need not be final; the patch can become re-colonised by migrants from occupied patches. Models of open systems consist of a large number of similar components, each of which interacts with some of its neighbours, allowing for both immigration and emigration. In open systems migration between patches may lead to astronomically long delays before equilibrium conditions are met (Begon *et al.*, 1990).

1.2.2.1 Leslie's model

An alternative formulation of the Lotka-Volterra equations was proposed by Leslie (1948), after working extensively on age-structured population models. Leslie's equation for the rate of prey increase is identical to the Lotka-Volterra equation (eqn 1.7). The predator equation is similar to the Lotka-Volterra predator equation, but is modified to include a logistic predator self-limitation term. The constant carrying capacity is replaced by the biomass density of resources in lower trophic levels. The predator consumption rate in Leslie's equation no longer depends on the density of prey (as it does in the Lotka-Volterra model, eqn 1.6) but on the ratio of predators to prey, so that:

$$\frac{dN}{dt} = c \cdot N \cdot (1 - \sigma \cdot \frac{N}{S}) \qquad (1.8)$$

where σ, is the density of prey required to maintain a single predator and to replace itself once before it dies. In effect σ describes the marginal subsistence demand for prey

(Berryman, 1992). The variable $1 / \sigma$ therefore describes the marginal reproductive value of the resource, and N / σ the carrying capacity of predators when provided with a constant supply of prey (Berryman, 1992). The effect is to give a predator isocline with a positive gradient (see Figure 1.9) unlike the isocline described by the Lotka-Volterra model shown in Figure 1.3 which is vertical.

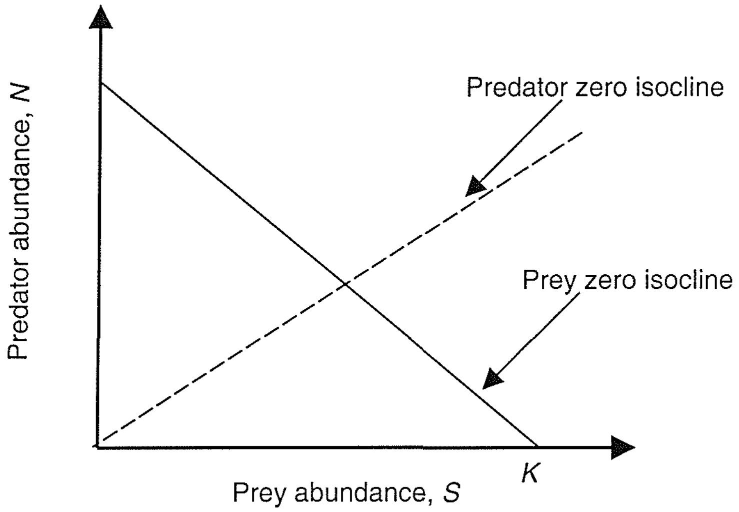


Figure 1.9 The effect on the predator isocline of introducing logistic predator limitation and a prey consumption rate dependent upon the ratio of predators to prey rather than the density of prey. The predator isocline now has a positive gradient rather than being vertical.

The Lotka-Volterra formulation is preferred if rates of change are instantaneous. In Leslie's model there is no relationship between the rate at which a predator eats, and the rate at which it reproduces (Maynard-Smith, 1974). The model does not conform to the law of conservation i.e. the function describing consumption rate does not describe recruitment rate. This would be necessary if the model was designed to model populations in a closed system. In closed systems consumption rate is directly related to birth rates. However, in open systems there is not a direct conversion as the birth or recruitment rate is independent of the local population density (Roughgarden & Iwasa, 1986; Bence & Nisbet, 1989).

1.2.2.2 Ratio-dependent models

Classical density-dependent models (such as the modified Lotka-Volterra model) follow the laws of mass action. The numerical response of the predator population depends solely upon the numbers of prey; the predator and prey rate equations are explicitly coupled. Ratio-dependent models assume that the trophic function of predators depends on the predator-prey ratio, and not on prey abundance alone. Recently there has been an increasing interest in the role that ratio-dependent models play in ecological research (e.g. Arditi & Ginzburg, 1989; Arditi & Saiah, 1992; Akçakaya *et al.*, 1995; Lundberg & Fryxell, 1995) However, ratio-dependent models have no simple mathematical coupling of predators to prey comparable to the law of mass action.

It is assumed in density-dependent models that the number of prey consumed per predator in a unit of time remains unchanged even if the predator population is increased. On a daily time scale the individual feeding rate can probably be modelled as the result of random encounters between predators and prey hunting independently from one another (Arditi & Ginzburg, 1989). If we consider longer time scales, then consumption rate should take into account predator density, as there will be less food available for each individual as predator numbers increase (Arditi & Ginzburg, 1989). Yearly consumption rate should therefore be a function of the prey numbers per population of predators. Typically the greater the number of predators the faster the prey density is reduced.

Ratio-dependent models produce predator isoclines with a positive slope as seen in Figure 1.9. A sloping predator isocline results in greater stabilising mechanisms, and prevents the problems associated with the 'paradox of enrichment' (Luck, 1990; Hanski, 1991). Ratio-dependent predation predicts continuous and correlated increases at all trophic levels in hypothetical food chains as primary productivity increases. (Arditi & Ginzburg, 1989; Berryman, 1992; Ginzburg & Akçakaya, 1992).

The inclusion of a type II functional response (as described by Figure 1.4) in the prey rate equation results in a zero isocline whose shape is described by a parabolic curve. The isocline diagram displayed in Figure 1.10 is characteristic of ratio-dependent predator-prey equations (e.g. see Tanner, 1975; Arditi & Ginzburg, 1989; Lunberg & Fryxell, 1995; Renshaw, 1995).

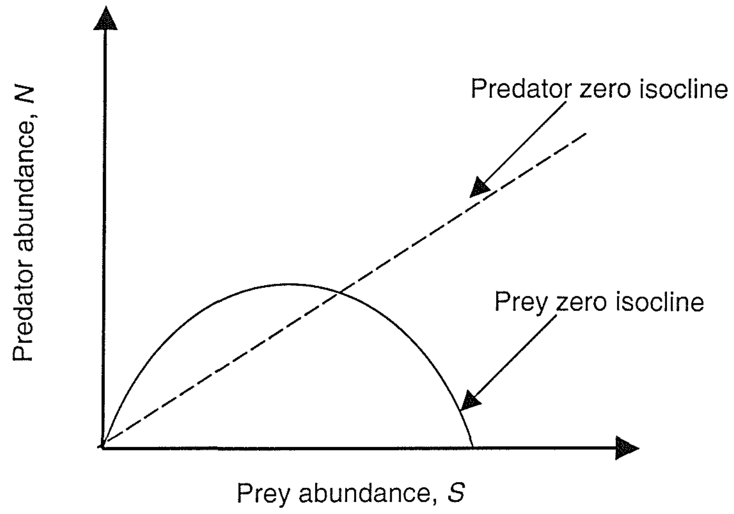


Figure 1.10 The effect of a type II functional response and ratio-dependent predation on the isocline diagram. The predator isocline has a positive slant and the prey isocline is humped.

Ratio-dependent and density-dependent models of trophic interactions make very different predictions concerning the steady states of ecosystems. Arditi & Saiah (1992), suggest that the applicability of ratio-dependent or density-dependent models depends on the degree of heterogeneity of predators spatially. Density-dependent models are appropriate in homogenous situations while ratio-dependent models are more appropriate in heterogeneous situations. Ginzburg & Akçakaya (1992) have concluded from their work on nutrient input and the biomass of phytoplankton, zooplankton and fish across lakes, that ratio-dependent models best explain the occurrences in this relatively open system. This work has been confirmed by McCauley *et al.* (1993) who have shown that relationships between tropic levels in a lake ecosystem are compatible with ratio-dependent models.

The use and consequently the biological reality of ratio-dependent models over prey-dependent models is not held by all (see Gleeson, 1994: Sarnelle, 1994: Abrams, 1994). Ruxton & Gurney (1992) have commented upon results and have suggested that in some cases ratio-dependent models do not distinguish ratio-dependence from other equally plausible forms of density-dependence. Ratio-dependent models make specific assumptions that prevent them from serving as a foundation for general consumer resource theories. The four main criticisms opposing ratio-dependence are given by Akçakaya *et al.* (1995) as:

1. The empirical evidence is insufficient and, or biased.
2. Ratio-dependent models exhibit pathological behaviour at low values of N.
3. Ratio-dependence lacks a logistical or mechanistic base.
4. More general models incorporate both prey and ratio-dependence and there is no need for either of the two simplifications

Strictly limiting functional responses to either prey-dependent or ratio-dependence may not be necessary. A mutual interference parameter, m, can be incorporated into the predator rate equation (eqn 1.6) to allow the two opposing types of dependence to play a role in determining population dynamics, as shown in eqn 1.9.

$$\frac{dN}{dt} = b \cdot c \cdot S \cdot N^{1-m} - d \cdot N \qquad (1.9)$$

If $m = 0$, then predator recruitment per capita is governed by prey density. This is the classical mass action model. If $m = 1$, however, then predator recruitment per capita is ratio dependent. For values of $0 < m < 1$, different degrees of density and ratio-dependence influence the populations depending on the value of m. Hassell & Varley (1969) were the first to combine the two types of dependence in one model. Since its introduction the continuum approach has been used by others (e.g. Arditi & Akçakaya, 1992; McCarthy *et al.*, 1995; Stow *et al.*, 1995; Doncaster, 1999). Although an intermediate model can be constructed, experimental evidence indicates that intermediate situations do not occur frequently in natural populations (Arditi & Saih, 1992), though some plankton populations exhibit density and ratio-dependent characteristics (e.g. see Stow *et al*, 1995).

Predator-prey population models are used in Chapters 3 and 4 to describe certain characteristics of organisms living in the marine environment, which is regarded as an open system (Roughgarden *et al.*, 1985). We use the isocline diagram produced by Leslie's model (an open system model) and the isocline diagram produced by the Lotka-Volterra model with density-dependence (a closed system model) to analyse and compare the growth and persistence of barnacle populations. Intertidal barnacles are used as a model organism to study open systems in two of the experimental chapters presented in this thesis (Chapters 3 and 4). Consequently, some of the general aspects of barnacle settlement and recruitment biology applicable to both chapters are briefly detailed below.

1.2.2.3 Barnacles as model organisms to study open system processes

Larval settlement of sessile marine invertebrates has been widely studied because of the importance the process has on the future growth, survival, and reproductive success of the adults (Hills & Thomason, 1996). Barnacles are dominant intertidal organisms of temperate rocky shores. Although adult barnacles are sessile, the larval phase is planktonic, and individuals can be passively transported kilometres by oceanic processes before settlement (Scheltema, 1986; Farrell *et al.*, 1991; Bertness *et al.*, 1996). As a result the local recruitment rate does not depend on the local birth rate. Intertidal barnacles are therefore considered an exemplary model organism to study recruitment processes in open systems (Wethey, 1984; Gaines & Roughgarden, 1985; Roughgarden *et al.*, 1985; Hyder, 1999).

At large spatial scales, oceanographic features that dictate the transport of barnacle larvae onto a shore are important determinants of potential settlement numbers (Roughgarden *et al.*, 1987; Farrell *et al.*, 1991; Gaines & Bertness, 1992). The concentration of cyprids in the water column is directly related to settlement density (Gaines *et al.*, 1985), though the larval supply to a particular shore can be influenced by the wind (Hawkins & Hartnoll, 1982), tidal range (Shanks, 1986) and wave exposure (Bertness *et al.*, 1992).

Once the barnacle nauplius larva has undergone six planktonic nauplius stages it finally moults into a cyprid larva. The cyprid is the non-feeding specialist settlement stage (Rainbow, 1984). The cyprids develop a negative phototrophic response causing them to avoid light in search of a suitable substratum to settle upon. The settlement of barnacle larvae is generally not random (Knight-Jones & Stevenson, 1950). Three factors determine the distribution of larvae following dispersal, (Gaines, & Bertness, 1993):

1. The density and distribution of reproductive adults.
2. The timing and magnitude of reproductive output.
3. The probability distribution of juvenile transport distances.

Once on a substratum the cyprids undergo an initial phase of broad exploration before undertaking a phase of close exploration (Rainbow, 1984). Towards the end of this exploratory phase the cyprid only searches a small area, moving scarcely more than its own length (Knight-Jones & Crisp, 1953). Factors influencing the settlement of barnacle larvae at small spatial scales have been studied extensively (Caffey, 1982; Minchinton & Scheibling, 1993a and references therein).

Cyprids have a number of cues that they rely upon when searching for favourable settlement sites. These include topography (Crisp & Barnes, 1954; Hills & Thomason, 1996; Wethey 1984b), texture and composition of the substratum (Crisp & Barnes, 1954; Anderson & Underwood, 1994), light (Barnes *et al.*, 1951), the presence of microbial films (Le Thournex & Bourget, 1988; Thompson *et al.,* 1998), macro algae (Hawkins, 1983), and predators (Johnson & Strathmann, 1989) along with the availability of conspecifics (Knight-Jones, 1953; Crisp & Meadows, 1962; Larman & Gabbot, 1975).

Two of the main cues that govern whether the larvae settle on a substratum are the availability of free-space (Crisp, 1961; Minchinton & Scheibling, 1993a; Bertness, *et al.,* 1992) and the proximity to conspecifics (Yule & Walker, 1985; Bertness, *et al.,* 1992; Shkedy & Roughgarden, 1997). Wethey (1984b) concludes that cyprids are attracted more strongly to each other than they are to external stimuli. Barnacles select to settle near conspecifics to enable internal fertilisation, via a penis of limited length (Wu, 1981). Cross-fertilisation must occur in many barnacle species in order for successful reproduction to take place (Barnes & Crisp, 1956). Recognition of conspecifics has been attributed to the identification of adult cuticular proteins especially arthropodin (Knight-Jones, 1953; Crisp & Meadows, 1963; Larman & Gabbott, 1975; Yule & Crisp, 1983). However, chemical cues have been shown to be short lived (Wethey, 1984b).

The specificity of these chemical cues varies between species. Raimondi, (1988) has shown that *Chthamalus anisopoma* cyprids are attracted to chemicals produced by organisms other than barnacles, such as the predator *Acanthina angelica,* which shares the same habitat. Crisp (1990), however, has shown *Balanus amphitrite* larvae to preferentially settle on substratum with conspecifics chemical cues rather than on substratum with chemical cues from other barnacle species. Though, *Elminius modestus* larvae do not discriminate between conspecifics and other adult barnacle species (Hui & Moyse, 1982).

If *S. balanoides* cyprid larvae move over approximately 3 cm and do not find conspecifics they will move on (Hills & Thomason, 1996). *S. balanoides* cyprids can delay settlement for up to 3 - 4 weeks (Lucas *et al.*, 1979). As barnacle larvae do not actively feed during this exploratory period they must rely upon finite stored energy reserves.

The distribution and abundance of barnacle populations will also be influenced by post-settlement processes (e.g. see Connell, 1961; Wethey, 1984a; Connell, 1985; Gosselin & Qian, 1996; Menge, 2000). The possible influence biotic and abiotic post-settlement processes have on our experimental populations will be raised in the specific chapters.

In Chapter 3 we evaluate the strength of conspecific attraction in two barnacle species, in Chapter 4 we calculate the rate of adult barnacle population growth. In nature animals struggle with different trade-offs in the attempt to transfer their genes to future generations (Norrdahl & Korpimäki, 1998). For adult barnacles to transfer their genes to the next generation the motile larvae must settle a penis length from a conspecifics. We find that this mutual attraction between conspecifics alters the growth of the population to a form that is not typically observed in open systems. This has interesting consequences with regard population persistence. A lexicon of terms used in both barnacle chapters can be found in Appendix 3.1.

1.2.3 The Allee effect

Allee (1931) observed that many animal and plant species suffer a reduction in their per capita rate of growth at low population densities. Allee proposed that intraspecific co-operation may result in inverse density-dependence where numbers within a population are low (Begon *et al.*, 1990; Courchamp *et al.*, 1999). The most common use of the Allee effect is to describe the increased difficulty associated with finding potential mates at low population densities (Asmussen, 1979; Gerritsen, 1980; Courchamp *et al.*, 1999). This concept is now widely termed the Allee effect, though it is sometimes referred to as critical depensation in the harvesting literature (e.g. see Myers *et al.*, 1995; Alvarez, 1998). The implications of the Allee effect are important in most areas of ecology (Stephens & Sutherland, 1999).

Our prey flux model in Chapter 2 includes an Allee effect. We show that an Allee effect of even a modest intensity can ultimately result in the extinction of both predator and prey populations. Although we do not directly encompass an Allee effect into the chapters detailing barnacle and vole populations we do comment on its possible effect and consequences to population persistence in Chapter 6.

A shortage of interactions among conspecifics at low densities can result in a reduction of population growth for a number of reasons, though only mechanisms that affect a measurable component of individuals fitness should be included in the definition of Allee effects (Stephens & Sutherland, 1999). Mechanisms for Allee effects at low population densities, other than mate location, include reduced anti-predator defence (Lewis & Kareiva, 1993), less efficient feeding at low densities (Way & Banks, 1967), reduced effectiveness of vigilance and anti-predator defences (Kenward, 1978); social hierarchy disruption and reduced social co-operation (Courchamp *et al.*, 1999).

An Allee effect can ultimately result in a population growth rate that is smaller than the rate of population mortality. In these circumstances extinction is inevitable (Wells *et al.*, 1998). A critical density can therefore exist below which the population is likely to go extinct if subject to Allee effects (Courchamp *et al.*, 1999). Even with recruitment Allee effects may prevent populations from increasing above the extinction thresholds if the number of colonists arriving at a patch is limited (Amarasekare, 1998a). An understanding and inclusion of the Allee effect in both ecological theory and ecological models is therefore important to conservation biology and wildlife management (Lamont *et al.*, 1993; Lande *et al.*, 1994).

The Allee effect has been implemented in theoretical models of local populations (Asmussen, 1979; Lande, 1987; McCarthy, 1997; Alvarez, 1998; Wang *et al.*, 1999), metapopulations (Hanski, 1991; Gyllenberg *et al.*, 1996; Amarasekare, 1998a; Gyllenberg *et al.*, 1999) and invading populations (Lewis & Kareiva, 1993). There is also growing empirical evidence to support the theoretical findings in a variety of organisms e.g. fig trees (*Ficus* sp.) (Courchamp *et al.*, 1999); proteaceae plants (*Banksia goodii*) (Lamont *et al.*, 1993); social spiders (*Anelosimus eximius*) (Aviles & Tufino, 1998); Glanville fritillary butterfly (*Melitaea cinxia*) (Kuussaari *et al.*, 1998); mole rats (*Cryptomys damarensis*) (Jarvis *et al.*, 1998); and African wild dogs (*Lycaon pictus*) (Courchamp *et al.*, 1999).

The Allee effect is more rarely detected in vertebrates, partly due to the evolution of effective mate location traits (Gyllenberg & Hemminki, 1999). The Allee effect is however, a major driving force behind animal sociality, with the degree of sociality dependent upon the severity of the Allee effect (Stephens & Sutherland, 1999). Consequently, a positive correlation can be identified between mate location efficiency and population density (Wells *et al.*, 1998), with density enhancement promoting mating in some species (Wells *et al.*, 1990). However, when mate location traits remain efficient even at low population densities endangered species may not display Allee effects (Wells *et al.*, 1998).

1.3 METAPOPULATION MODELS

The metapopulation concept has a pedigree dating back to the early part of the twentieth century but, until recently this area of research played only a minor and episodic role in the intellectual advance of population biology (Hanski & Gilpin, 1997). The term 'metapopulation' was first introduced in the work of Levins (1969, 1970). Levins coined the term metapopulation for an assemblage of unstable local populations connected by migration. Today the term is employed to mean a 'population of linked populations each prone to occasional extinction followed by recolonisation' (Hanski & Gilpin, 1997; Hanski, 1998; Hanski, 1999). Fundamental similarities can be made between local and metapopulation theory. The colonisation and extinction in metapopulations can be likened to births and deaths of individuals in a local population (Doncaster, 2000).

1.3.1 Closed system models

The closed metapopulation model assumes a number of populations with no mainland from which migrants can originate. All migration in a closed system occurs between the individual island populations; any recolonisation of unoccupied patches is due to immigration of individuals by other island inhabitants.

In Chapters 3 and 4 we investigate the settlement of barnacle species onto substratum. We liken the colonisation of available free-space by barnacles to Levins' closed system metapopulation model and comment on the consequences to persistence at both the local and regional levels.

1.3.1.1 The Levins model

The original metapopulation concept as propounded by Levins (1969) assumed that space is discrete and that it is possible to distinguish between habitat patches that are suitable for inhabitancy. In his model Levins distinguished between the dynamics of a single population and the dynamics of a set of local populations. Levins considered the metapopulation as a population of local populations inhabiting an infinitely large patch network. Levins' model has been found to provide a good approximation of networks with 100 patches or more (Hanski, 1999); stochasticity is therefore considered unimportant at this scale (Hastings & Harrison, 1994).

Levins' model has two underlying assumptions:

1. Patches are scored as being either occupied or not; the actual size of the local population is ignored.
2. All extant populations are assumed to have a constant risk of extinction.

With these assumptions a basic model can be constructed which is similar to the Lotka-Volterra type predator rate equation in a local population (see eqn 1.6):

$$\frac{dN}{dt} = c \cdot N \cdot (K - N) - d \cdot N \qquad (1.10)$$

where N is the number of currently occupied patches, c is the colonisation rate of each habitable patch per occupied patch and d is the extinction rate parameter. Given that $K - N$ is the number of habitable patches, eqn 1.10 has the same structure as the Lotka-Volterra prey equation (eqn. 1.6), with the limiting resource being habitat patches rather than prey. The colonisation rate is therefore density-dependent, and the number of colonised patches cannot exceed K. The model gives an instantaneous rate of change in the fraction of occupied patches (Hanski *et al.*, 1996).

Levins' model predicts that the fraction of occupied habitat at equilibrium will increase with decreasing value of the ratio d / c, and the metapopulation will persist as long as $d / c < K$ (Hanski & Gilpin, 1997). This set of equations provide a simple model for metapopulation dynamics, analogous to the logistic Lotka-Volterra model, as a paradigm of local population growth (Hanski, 1996). As in the logistic Lotka-Volterra predator-prey model, the Levins model has negative density-dependence in the per capita growth rate. Metapopulations may, however, take enormous time spans to eventually reach an equilibrium point after a major perturbation (Hanski & Gilpin, 1997).

The Levins model is best applied to the following situations (Hanski & Gilpin, 1997; Hanski, 1999):

1. Habitat patches have equal areas and isolation.
2. Local populations in the metapopulation have entirely independent dynamics.

3. Exchange rate of individuals among local populations is so low that migration has no real effect on local dynamics.
4. The rate of colonisation is assumed to be proportional to the fraction of currently occupied patches.

Diagrams similar to those used to describe local population dynamics (e.g. see Figure 1.10) can also be used to represent metapopulation models, enhancing comparisons between population dynamics at the metapopulation and local levels as shown in Figure 1.11. The analogy between the logistic predator-prey model and Levins metapopulation model provides a simple way to explore effects of metapopulation dynamics (Amarasekare, 1998b).

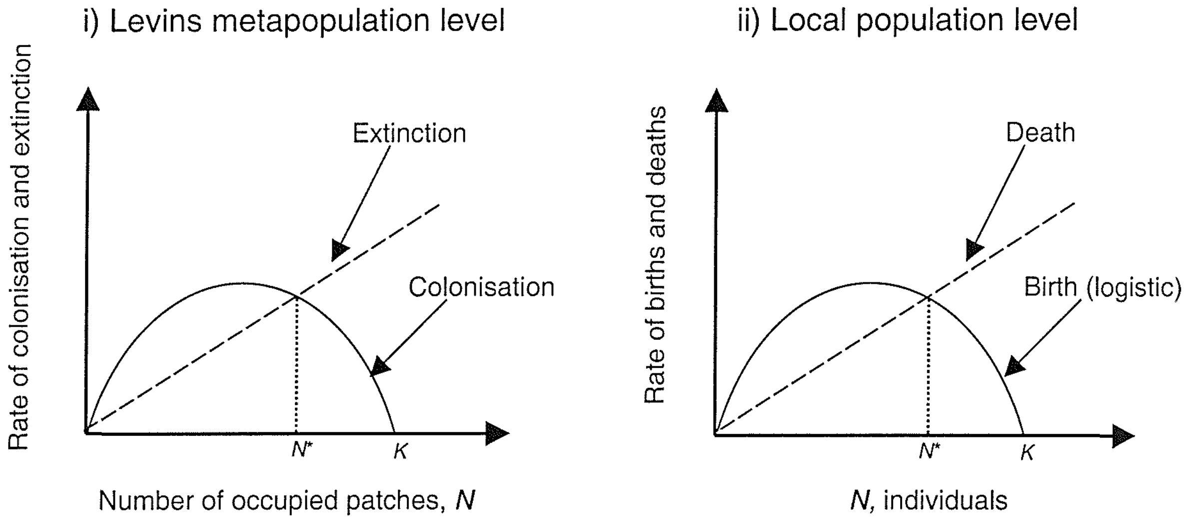


Figure 1.11 A diagrammatic representation of i) the Levins closed metapopulation model and ii) a local closed population model prone to extinction. The same behaviour is represented by both models with N^* equal to the equilibrium population of colonists/individuals and K the carrying capacity.

The Levins diagram for a metapopulation (Figure 1.11(i)) can be extended further to give valuable insights into the population equilibrium position under different colonisation and extinction rates. Figure 1.12 shows the effect of extinction and colonisation on the equilibrium number of occupied patches, N_x. An increase in the extinction rate from E_1 to E_2 results in a marginal drop in the equilibrium number of occupied habitats. However, the same rate of change of extinction at the apex of the colonisation parabola E_3 to E_4 results in a significant decrease in the equilibrium position. If extinction exceeds colonisation as in E_5 then none of the patches are inhabited and the population goes extinct.

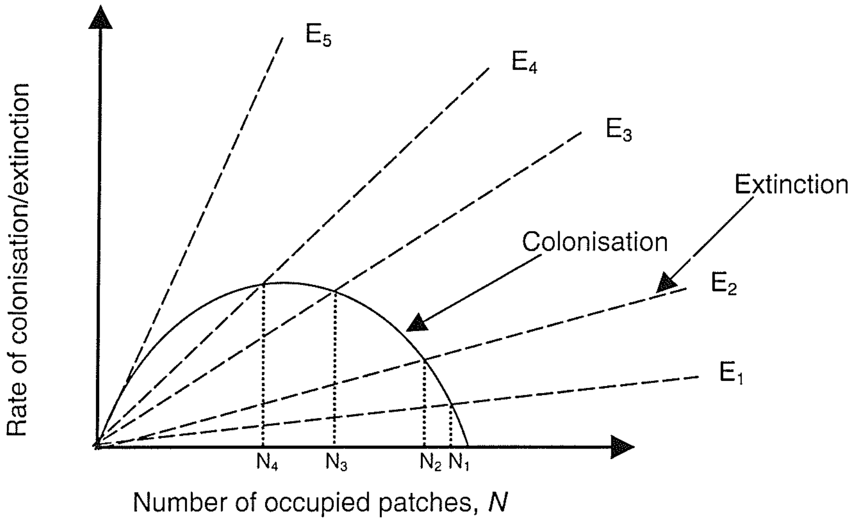


Figure 1.12 The effect extinction and colonisation rates have on the overall equilibrium density of occupied patches *N*. As extinction is increased linearly the equilibrium number of occupied patches decreases at a rate greater than a linear e.g. compare the equilibrium number of occupied patches when the extinction rate is equal to of E_1 and E_2 to those when E_3 and E_4. When extinction exceeds colonisation the population goes extinct, as seen at E_5 (adapted from Levins, 1969).

An important conclusion that can be made from the Levins model is that a species may become extinct in the presence of suitable habitat if the rate of local extinction exceeds the rate of colonisation (Hanski, 1991). The species may reach the extinction threshold (when $K = d / c$) and go below it but, there will be a time delay between this and the consequent extinction of the species. At low habitat occupancy Allee effects can lead to increased metapopulation extinction thresholds (Amarasekare, 1998a). The risk of extinction can be alleviated if immigrants can settle on occupied patches as well as unoccupied patches. This is known as the rescue effect and is discussed in more detail in Section 1.3.3.

In the Levins metapopulation model the spatial arrangement of patches is ignored. The kind and degree of connectedness between patches or populations is however, a critical feature in models of spatially structured populations (Harrison, 1991). Nevertheless, even if migration is distance-dependent the Levins model is still a good approximation for a metapopulation at a stochastic steady state (Nisbet & Gurney, 1982). Consequently, the Levins model is still used as a conceptual basis for much metapopulation research (e.g. Schoener, 1991; Verboom *et al.,* 1991; Gotelli & Kelley, 1993; Hasting & Harrison, 1994; Ives & Settle, 1997), though more complex models have been constructed and investigated (see Hanski & Gilpin, 1997; Hanski, 1999).

1.3.2 Open system models

An open metapopulation is one in which there are a series of habitat patches or 'islands' which are colonised by a single species, from a 'mainland' source habitat. Boorman & Levitt (1973) first suggested the mainland-island structure of an open metapopulation. The mainland can always supply immigrants, as extinction here is negligible (Hanski, 1999). This is the main fundamental difference between a closed metapopulation and one that is open. A closed system relies on colonisation from within (a form of self-replication), whereas open systems rely on an external supply. Open metapopulation theory shows that for a single species the probability with which the species occurs in a patch increases with increasing patch area. Open metapopulations are therefore a single species equivalent of MacArthur & Wilson's (1967) island biogeography theory (see Figure 1.13) which is one of the few valid generalisations in ecology (Hanski, 1994b).

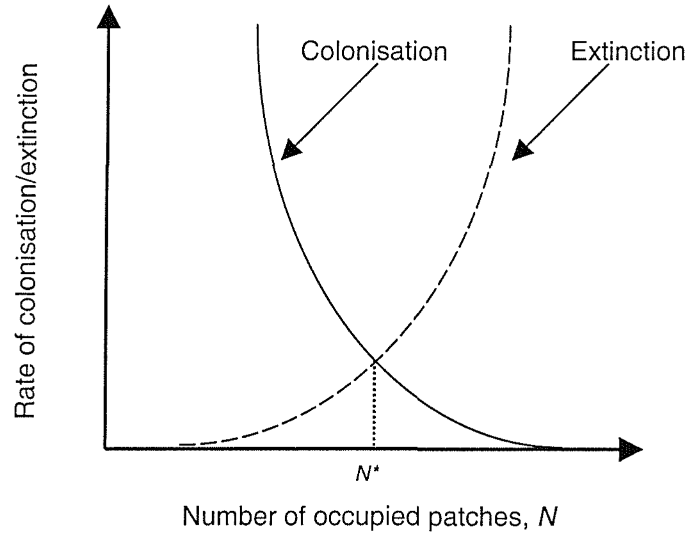


Figure 1.13 The relationship between colonisation and extinction rate in an open metapopulation. The relationship is identical to MacArthur & Wilson's island biogeography theory except they describe the number of occupied niches rather than number of occupied patches. Local extinction affects the distribution of local populations but not regional persistence.

Local extinctions may be frequent but on a larger global scale these may be trivial (Harrison, 1991). High variance in patch or population size means that most local extinctions will probably be unimportant, as they will tend to strike the smallest of the patches and populations, with little influence on the metapopulation (Harrison, 1991).

The extinction-resistant mainland can always provide a source for colonists after a local extinction event, though this may not be immediate.

To date there has been much research conducted into open metapopulations (e.g. see Hanski, 1982; Hanski 1994; Pagel & Payne 1996; Hanski & Gilpin, 1997). As I do not directly include open metapopulation models in this thesis (they are shown here only as a comparison to closed metapopulation models), I will not expand further on their detailed structure. A review of current open-metapopulation theory can be found in the definitive metapopulation textbooks by Hanski & Gilpin (1997) and Hanski (1999).

1.3.3 The rescue effect

The size of a population increases with an increasing migration rate; this in turn reduces the risk of extinction. Brown & Kodric-Brown (1977) were the first to introduce this concept, though it was originally applied to island-biogeography theory with a mainland supply of potential colonisers. Today this concept is widely referred to as a 'rescue effect' and is primarily used and developed in a metapopulation context (e.g. see Gotelli, 1991; Hanski, 1994; Hollyoak & Lawler, 1996; Hanski, 1999; Etienne & Heesterbeek, 2000), though the term rescue effect can be interpreted differently amongst authors (Hanski, 1999). Hanski & Gyllenberg (1993) use the term rescue effect to include a decreasing extinction rate with increasing immigration rate and increasing immigration rate with an increase in the fraction of occupied patches.

A rescue effect can occur where there is no mainland source population. The more patches occupied within a closed system metapopulation, the greater the rate of immigration between patches i.e. the more patches occupied the stronger the rescue effect. A patch is more likely to be occupied the closer it is to another occupied patch (Brown & Kodric-Brown, 1977). Consequently, the size of the rescue effect may depend on the size and the proximity of the source populations and may vary in accordance to dispersal rates (Holyoak & Ray, 1999).

Our prey flux model in Chapter 2 models the influx of a prey species into a predator-prey system. We therefore make comparisons between the rescue effect, which models an influx of colonisers in a metapopulation network and our prey influx, which is modelled at a local population level. We investigate the consequences this has to predator and prey population stability.

The key to metapopulation persistence is the amount of dispersal, just as the key to local population persistence is the rate of births. Low dispersal rates will not balance extinction, while very high dispersal may result in synchronised extinction (Hollyoak & Lawler, 1996). Dispersal balances extinction against colonisation whereas a rescue effect prevents or reduces extinction events. However, as the rescue effect increases, the risk of extinction decreases to a point at which asynchrony breaks down because patches are colonised at similar times and dispersal equalises density across patches (Hollyoak & Lawler, 1996).

If individuals are immigrating into a patch then they must be emigrating from another population within the metapopulation network. However, migration typically occurs from the largest patches, which have the greatest density of individuals. Emigration from the source patch only slightly increases the risk of extinction here, but can prevent extinction in small patches (Hanski, 1999). By augmenting population densities that are low the rescue effects can therefore dampen down the size of population fluctuations (Hollyoak & Lawler, 1996).

The rescue effect primarily influences population persistence in small patches. Levins type models cannot include rescue effects as they assume no immigration and habitat patches within these models are assumed to be of equal size with equal isolation. Hanski (1982) has formulated a metapopulation model that includes rescue effect. However, Levins rule remains valid for metapopulations with low turnover rates of habitat destruction and fragmentation, because the rescue effect has little importance (Hanski *et al.*, 1996).

1.4 AMALGAMATING MODELLING AND EMPIRICIAL APPROACHES

Scientists may want to test certain models so that they can be verified or validated. Validation does not denote the establishment of truth; rather it denotes the establishment of legitimacy typically given in terms of arguments and methods (Oreskes *et al.*, 1994). Testing models is a difficult process, as it requires an independently collected data set from specific locations (Hilborn & Mangel, 1997). Appropriate scales of time and space must be specified for the observations of the responses of the populations, before meaningful judgements concerning stability or persistence can be made (Connell & Sousa, 1983). In field populations natural perturbations are often so frequent that there may be insufficient time for populations to reach stability (Connell & Sousa, 1983). Moreover, some types of dynamical behaviour predicted by theoretical models rarely occur in real populations (Hassell *et al.*, 1976).

In science it is common for natural laws to be discovered from empirical evidence well before theoretical structures are developed to rationalise the law (Bradshaw, 1983). Nevertheless processes must be understood in theory in order to make correct predictions for empirical testing (Sinclair & Pech, 1996). Although an understanding of models is a necessary condition for a full understanding of population behaviour in the field, it is not a sufficient condition for such an understanding (Crawley, 1983). Even if the results from a model are consistent with present and past observational data there is no guarantee that the model will perform at an equal level when used to predict the future (Oreskes *et al.*, 1994).

Empirical data may not always succeed in refuting or validating models completely. There has been much recent interest in providing empirical evidence to support the roles of density or ratio-dependence in regulating populations (e.g. see Hassel, 1975; Possingham *et al.*, 1994; Doncaster & Gustafsson, 1999 for density dependent evidence, and see Akçakaya, 1992; Ginzburg & Akçakaya, 1992; Akçakaya *et al.*, 1995 for ratio-dependent evidence). Even with empirical evidence one model cannot be generally accepted at the cost of the other as different models apply to different situations. Some of the difficulties in determining the role of predators in the regulation of natural populations may be because mathematical models do not mirror all population fluctuations (Dempster, 1983; Hassell, 1985; Hassell, 1987). However, it must be remembered that there is no single best all-purpose model of any system (Levins, 1969).

A major aim of theoretical ecology and especially population modelling is to provide a framework of the rationally conceivable within which empirical observations can be encompassed (Stenseth, 1977). Models can therefore be used check consistency and can be used to generate testable predictions from field generated hypothesis (Lomnicki, 1988; Hansson, 1988). The interpretation of empirical results can be used to refine the model or hypothesis as well as supporting or undermining the theory (Caswell, 1988). Empirically derived data can also improve model assumptions, and can generate specific values for model parameters (Hilborn & Mangel, 1997).

The role of the theoretical ecologist is thus to help bridge the gap between observation (either real or virtual), mathematical description and the analytical foundations of ecology by providing models and methods for practitioners to use (McGlade, 1999). However, there currently exists a division between empirical and theoretically minded ecologists (Lomnicki, 1988), even though the comparison of empirical with mathematical solutions is a critical step in theory development (Oreskes *et al.*, 1994). More could be accomplished if theoreticians and empiricists worked together to increase communication between the two approaches (Hall, 1988; Caswell, 1988). Doak & Mills (1994) suggest that the first step should be for theoreticians to clearly state how data can be productively, and cheaply, collected to assess their models, whereas empiricist should try to collect data that will be useful in parameterising models or distinguishing between alternative models. I support this idea in my thesis and where applicable I suggest experimental designs to test theoretical concepts in my thesis.

1.5 SPECIFIC OBJECTIVES

The overall aim of the thesis is to explore ways in which recruitment dynamics influence the persistence of populations. Since the techniques and study organisms differ between chapters, each one has a discrete set of objectives.

In Chapter 2 I compare and contrast the effects of prey subsidy to the well known effects of stock enrichment. The prey flux model is designed to allow both prey influx and prey outflux. I investigate the effect of both influx and outflux on the stability of a predator-prey system and comment on the effect each has on population persistence.

In Chapter 3 I examine the spatial distribution of two sessile barnacle species *Semibalanus balanoides* and *Chthamalus montagui.* The position between individual settlers and conspecifics at three distinct stages in a barnacle's life cycle is assessed. The two primary factors influencing spatial patterns are considered to be territorial repulsion and penis length. Penis length is important, as adult barnacles are sessile but internal cross-fertilisation must occur if they are to successfully reproduce. These assumptions are applied to a settlement simulation model, which determines the relative effects of spatial constraints during settlement. Conclusions from empirical work are then applied to theoretical open and closed population models.

In Chapter 4 I investigate population growth rates of newly settling barnacle cohorts. To achieve this I experimentally cleared patches of rock to leave bare substratum. At the centre of these patches I left a remnant group of adult conspecifics. Again two species are assessed, *Semibalanus balanoides* and *Chthamalus montagui.* Both settlement and immature adult numbers are analysed in comparison to the numbers of remnant adults. The rates of population growth are compared to a geometric-arithmetic growth continuum. This allows the equilibrium properties to be assessed and compared to open and closed population models.

In Chapter 5 I use a quantitative model to analyse the dynamics of microtine populations that feed on two plant species; a preferred prey type and a less-preferred prey type. By using an existing one-predator two-prey optimal foraging model along with actual parameter values, generated from the literature, I investigate the cyclic dynamics of microtine populations. I go on to develop an extension to the model that includes periodic toxin production by the less-preferred prey type. By comparing simulated data to empirical data I was able to evaluate the accuracy of my models.

In Chapter 6 the results of the previous chapters are summarised and general concepts raised throughout the thesis are discussed. I highlight the limitations associated with each of the specific chapters and suggest possible directions for future work that would extend the conclusions drawn from the current studies.

2 CONSEQUENCE OF PREY FLUX FOR LOCAL STABILITY OF PREDATOR-PREY SYSTEMS

2.1 ABSTRACT

The size of a population can be augmented by enriching the carrying capacity of its limiting resource, or by subsidising the renewal of the resource. Rosenzweig's well known 'paradox of enrichment' models the first case, in which enrichment can force predators and prey into destabilising limit cycles. In this chapter the second case is modelled, of subsidy through prey influx. This type of 'rescue' effect stabilises the system. In contrast to Rosenzweig's outcome, the system is destabilised by impoverishment of the environment under prey outflux. An outflux may be virtual rather than actual, if it expresses an 'Allee' effect of reduced prey recruitment at low density due to the difficulty of finding mates. Limit cycles are not sustained by prey outflux; instead both populations collapse to zero over a large region of the predator-prey phase plane. The presence of a predator is found to exaggerate the impact of rescue and Allee effects. The obvious implications for conservation and pest management are that a rescuing subsidy to conserve an endangered population, or a cull to eliminate a pest, may have more effect if they are applied to the limiting resource rather than to the resource consumer of focal interest itself.

2.2 INTRODUCTION

All models for the coupled dynamics of consumer populations and limiting resources differ qualitatively according to their base-line assumptions about density-dependence in rates of birth and death of consumers and resources. For example, the persistence and stability of predator populations and their prey depend on whether and how the consumption rate per predator changes with prey density and with predator density. The predator functional responses of Holling (1959) describe the range of influences of prey density on consumption, while interference coefficients such as those of Hassell & Varley (1969) or Beddington (1975) describe the range of influences of predator density.

These models all have increasing stability with strength of density-dependence. Many real systems, however, show inverse density-dependence in the predator functional response. The models then predict destabilisation if the predator population is augmented by increasing the carrying capacity of its limiting resource, a phenomenon known as the 'paradox of enrichment' (Rosenzweig, 1971). Less attention has been given to the effects of density-dependence in the renewal rate of prey (see for example McCarthy, 1997). Density-dependence here has a stabilising effect also, and most standard predator-prey models invoke a logistic growth of prey in order to avoid predicting a continuous cycling of predators and prey (Berryman, 1992), which was a feature of the original Lotka-Volterra models of geometric prey growth (Lotka, 1925; Volterra, 1926). Logistic growth may be a reasonable model of intraspecific competition among prey if they have an upper limit on their abundance in the absence of predation (a carrying capacity). Prey renewal may depend on other factors besides competition, however. For example, prey renewal is enhanced by immigration and slowed by emigration.

The aim of this chapter was to analyse the dynamics and stability of a predator-prey system under an influx and conversely an outflux of prey. A prey influx can be considered as modelling a rescue effect on the population of a species, which happens to be a prey to some predator. The rescue effect is well known to stabilise metapopulation dynamics (e.g. Brown & Kodric-Brown, 1977; Hanski, 1999), so prey influx should and does stabilise the population of prey, and consequently also the predator population. The reverse effect of a prey outflux, however, gives rise to novel outcomes for the predator-prey system, not analogous to those of metapopulation dynamics.

Prey outflux can be considered as a reverse rescue effect, or an Allee effect (Allee, 1931), which destabilises the dynamics of our prey species. Any mechanism that can lead to a positive relationship between a component of individual fitness and either the number or density of conspecifics can be termed a mechanism of the Allee effect (Stephens & Sutherland, 1999). The importance of this dynamic process in ecology has been under-appreciated (Courchamp *et al.*, 1999). In the absence of a predator, however, an Allee effect does not predict deterministic extinction except under extreme circumstances. The presence of a predator is found to exacerbate the dynamics, so even a small effect leads to the catastrophic collapse of both prey and predators.

These outcomes have lead to two sets of contrasting predictions for the stability of consumer populations as a result of changing the quality of their limiting resource. Whereas stock enrichment destabilises in the Rosenzweig model, resource subsidy stabilises in our model. Equally for the reverse case, whereas stock impoverishment stabilises in the Rosenzweig model, resource outflow destabilises in our model. Since prey flux may be an extrinsic effect, not necessarily defined by the life-history characteristics of prey or predators, we have explored the consequences of manipulating its magnitude in both positive and negative directions.

In developing our new model for prey flux we initially identified the features of Rosenzweig's paradox of enrichment that we wished to retain. These were the 'humped' isocline of equilibrium prey density for a given predator density (Rosenzweig, 1969), and prey-dependent growth of the predator population. Although others have analysed prey-dependent models with humped prey isoclines (e.g. Arditi & Ginzburg, 1989; Lunberg & Fryxell, 1995), our model is novel in allowing the prey isocline to lie either side of the origin set by an equilibrium of zero predators and prey, depending on a parameter that describes the direction and magnitude of prey flux into or out of the system. We tested the hypothesis that changing the sign of this parameter makes a qualitative difference to system stability.

2.3 PREDATOR-PREY SYSTEMS WITH STOCK ENRICHMENT

Rosenzweig (1971) studied six related deterministic models of predator-prey interaction. In all of these, predators were assumed to find prey in proportion to their abundance, and to require a non-negligible and constant time to process each prey before seeking the next one. This 'handling' time is the defining feature of Holling's (1959) Type II functional response. It gives a numerical response of prey to predation that is inverse density-dependent, and is expressed by a humped shape to the isocline of equilibrium prey for a given predator abundance. Rosenzweig's models additionally assumed that the predator population had a growth in abundance per capita that depended on prey but not predator numbers, so that predators did not interfere with each other directly. This density-independent numerical response of predators is expressed by a vertical predator isocline. The analysis of enrichment was carried out using graphical predation theory, and numerical integration (Gilpin, 1972).

Rosenzweig identified stable equilibria of predator and prey populations for any systems in which the predator isocline intersects the prey isocline on the right-hand side of the apex of its hump. For any such system, enriching the carrying capacity of prey could shift the apex to the right of the predator isocline, as shown in Figure 2.1. The system then becomes unstable and limit cycles are produced. As the resource is enriched yet further, both populations will cycle with increasing amplitude. Eventually with increased enrichment the oscillations may be so great that one of the populations will die out due to demographic stochasticity (Yodzis & Innes, 1992). The 'paradox' of enrichment embodies the fact that enriching the environment leads not to population enhancement, but to cycles of 'boom and bust' with extinction a likely consequence. Since its introduction in 1971 this idea has subsequently been further developed by many authors, among others May (1972), Gilpin (1972), Riebesell (1974), Armstrong (1979), Yodzis & Innes (1992), Scheffer & De Boer (1995), Abrams & Walters (1996), Nisbet *et al.* (1998) and Huxel (1999).

One of Rosenzweig's major goals was to warn ecosystem managers to be careful. Their attempts to increase population productivity by enriching limiting resources in natural systems might have exactly opposite results to their intentions. However, there have been relatively few empirical tests of the predicted destabilising effect of enrichment on predator-prey systems (McCauley & Murdoch, 1990; Yodzis & Innes, 1992; Abrams & Walters,1996). Luckinbill (1974) and Veilleux (1979) used a *Didinium-Paramecium* system to show experimentally that as the predator isocline is moved from right to left the system goes from being stable to unstable in the form of limit cycles (as in Figure 2.1). Hessen & Nilssen (1986) have shown that additions of nutrients to enclosures containing lake water led to large increases in phytoplankton concentrations that were followed by population crashes. The effects of nutrient enrichment on stability are not as well documented for terrestrial systems as they are for aquatic systems. DeAngelis *et al.* (1989) suggest that this is probably due to the longer time scales necessary for studies in terrestrial systems. However, Schwinning & Parson (1996) have found that the paradox of enrichment applies to a legume-grass community.

Others have not found evidence supporting the paradox of enrichment, though empirical studies of all types of food web stability are subject to more ambiguities of interpretation than are theoretical studies (DeAngelis *et al.*, 1989). McAllister *et al.* (1972) found that by adding fertiliser to an oligotrophic lake there was no resultant change in stability. McCauley & Murdoch (1987, 1990) conclude that coupled oscillations of *Daphnia* and algae are common, though destabilisation with increasing nutrient levels does not occur in the field or experimental systems. The enrichment of sunlight can cause trees to produce more carbon-based defences and become less edible to some herbivores (Rousi *et al.*, 1993). Empirical work designed to test the paradox of enrichment can fail due to insufficient resource enhancement (Yodzis & Innes, 1992). Population destabilisation exhibited by enrichment can depend on several factors including metabolic type, the ecological limitation of ingestion, relative body size and the form of functional response (Yodzis & Innes, 1992). Further reasons for the discrepancies between the theory and experimental evidence have been adduced by Leibold (1989), Arditi & Ginzburg (1989), Kretschmar *et al.* (1993), and Abrams & Walters (1996). The empirical validity of Rosenzweig's hypothesis thus remains open. The experimental systems have not always mirrored Rosenzweig's theoretical models explicitly. Alternatively, where theoretical and empirical work have been akin, enrichment has not been forced to a sufficiently far enough extreme to cause system instability.

In the theoretical work presented subsequently in this chapter the objective was to model system enrichment caused by prey influx rather than increased prey carrying capacity. This system seems closely analogous to the Rosenzweig models. Nevertheless we did not find a paradox of enrichment. Indeed we found destabilisation occurring when the prey environment was impoverished. The difficulties in matching empirical and theoretical results may, we suggest, be due to subtle modelling problems. At least in the case when enrichment is only apparent and actually due to immigration, the paradox of enrichment should not occur.

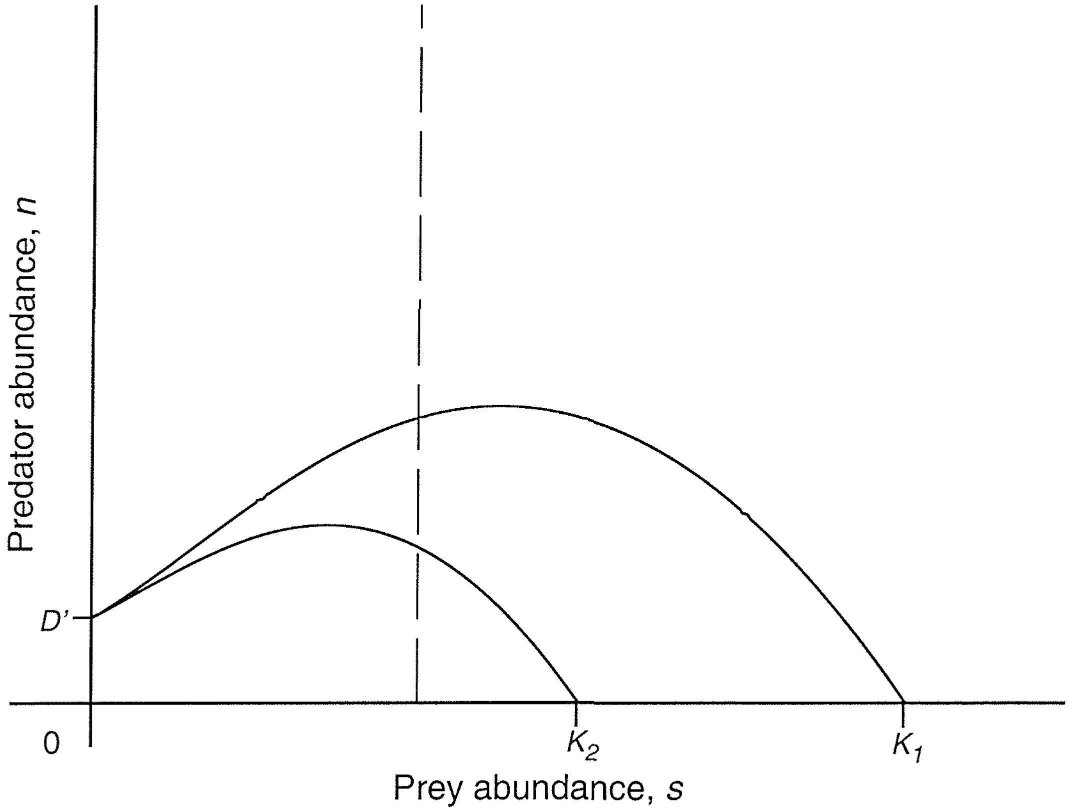


Figure 2.1 Phase plane depicting Rosenzweig's (1971) paradox of enrichment. The constant D' describes the ratio of the predator's search to handling time for prey (Appendix 2.1), and K describes the carrying capacity of prey stock. The continuous lines show the isocline of prey abundance for a given size of predator population. The broken line shows the isocline of predator abundance for a given size of prey population. The system equilibrium is at the intersection of the predator and prey isoclines. Enriching the carrying capacity from K_1 to K_2 increases n but also results in a change in the relative positions of prey and predator isoclines. At K_1 the apex of the prey isocline lies to the left of the predator isocline and the dynamics are stable. At a new K_2 following enrichment, the apex lies to the right of the predator isocline, and the dynamics are unstable.

2.4 PREDATOR-PREY SYSTEM WITH PREY SUBSIDY

2.4.1 Prey flux model

Our model assumes logistic growth of prey to carrying capacity in the absence of predation, and a consumption rate per capita by predators that depends on prey abundance according to the classical disc equation of Holling (1959). Predators are assumed to reproduce in direct proportion to their consumption of prey. This biologically realistic framework is described by coupled prey and predator rate equations:

$$\dot{s} = (D + s)\cdot(1 - s) - \frac{s \cdot n}{D'+s} \tag{2.1}$$

$$\dot{n} = \frac{v \cdot n}{D'+s}\cdot(s - \sigma) \tag{2.2}$$

The variables s and n are non-dimensionalised prey and predator abundances (detailed in Appendix 2.1). The parameter D represents the amount of prey flux into or out of a prey population of given carrying capacity, with positive values for influx and negative for outflux. Parameter D' represents the ratio of intrinsic search to handling time of each prey by each predator, and it takes some positive value greater than zero. The intake rate per predator, $s\,/\,(D'+s)$, describes the predator's functional response to prey (Type II of Holling, 1959). The constant v is a conversion ratio of consumed prey into new predator biomass. The constant σ sets the threshold prey density below which predator density declines, since $\frac{dn}{dt} < 0$ if $s < \sigma$. In this sense it describes the predator's relative marginal subsistence demand for prey.

Together D and D' control the strength of inverse density-dependence in prey dynamics, which is weakened by large positive values of these parameters. Whereas the prey isocline of Rosenzweig's models is humped, as shown in Figure 2.1, the prey isocline given by eqn 2.1 rises sharply as it approaches the n-axis if D is positive (prey influx), as shown in Figure 2.2. In effect, the stabilising influence of prey influx represented by positive D is enhanced by the weakened inverse density-dependence in consumption given by positive D'. The prey isocline makes no such rise under prey outflux, however, regardless of the value of D'. The prey isocline only crosses the n-axis in the region of positive n if $D = 0$ (when it crosses at $n = D'$ and the phase plane is identical to Figure 2.1), or in the limiting case of $D' = 0$ which represents a negligible search time with respect to handling time (when it crosses at $n = D$).

With prey dynamics of this type, the same humped prey isocline as in Rosenzweig's models is retained over most of the region of positive n, s. Our model differs from these and all other predator-prey models with humped isoclines, however, in allowing the prey isocline to lie either side of the origin, as shown in Figure 2.2 (cf. Tanner, 1975; Arditi & Ginzburg, 1989; Lunberg & Fryxell, 1995). Changing the sign of D moves the isocline across the origin. As D is interpreted ecologically as describing prey flux into (positive D) or out of (negative D) the system, the model is called the prey flux model and abbreviate it to PF. Note, however, that PF is kept relatively simple. In particular, it is not a diffusion model, nor does it include resource patches with different carrying capacities.

In PF the rate of prey outflux is constant, and independent of prey density. Consequently, as s tends towards zero the outflux of prey can exceed the density of the stationary prey population, if D is negative. However, before this can occur the prey population will have already gone extinct, once the density of stationary prey is equal to that of the outflux, so that $s - D = 0$. The prey population remains extinct, with further outflux intuitively impossible.

As with the predators in the Rosenzweig (1971) model, the predators in PF exhibit no mutual interference (eqn 2.2). This means the predators never battle over the same individual prey, or engage in cannibalism or territorial defence. The macroscopic consequence of the lack of mutual interference is that the predator isocline in PF is strictly vertical (Figure 2.1 and Figure 2.2).

2.5 EQUILIBRIUM SOLUTIONS

The equilibrium solutions of eqns 2.1 and 2.2 are given by setting $\dot{s}$ and $\dot{n}$ to zero:

$$n = (D + s) \cdot (1 - s) \cdot \frac{(D' + s)}{s} \qquad (2.3)$$

$$s = \sigma \qquad (2.4a)$$

or,

$$n = 0 \qquad (2.4b)$$

Equation 2.3 describes the two prey isoclines in Figure 2.2, and eqn. 2.4a describes the predator isocline (dashed line). Equation 2.3 and eqn 2.4a are referred to as solution I and eqn 2.4b as solution II. Solution I gives the model a non-trivial equilibrium. The vertical predator isocline in Figure 2.2 means that σ is the equilibrium prey density for all equilibrium predator densities. If prey influx is reduced, for example, so that the value of D decreases, the effect is entirely compensated by a reduction in predator density, and there is no change in prey density. The constant σ is a measure of the efficiency of the predators at catching prey. Thus a value of σ close to unity indicates an equilibrium population that makes little impact on the carrying capacity of prey.

Solution II corresponds to equilibrium solutions in which there is no predator population and therefore either $n = 0$ and $s = 1$ (solution IIi), or $n = 0$, $s = -D$ (solution IIii), where solution IIii only applies for negative D. Solution IIi corresponds to the prey reaching its carrying capacity in the absence of predators. This solution is only stable for $\sigma > 1$, i.e. if the threshold prey density for predator population stability is greater than the prey carrying capacity. The threshold $\sigma = 1$ therefore represents an extinction threshold for predators: the minimum carrying capacity of prey that will support any predators (Lande, 1987; Nee, 1994). Solution IIii is never stable and will be discussed in the next section.

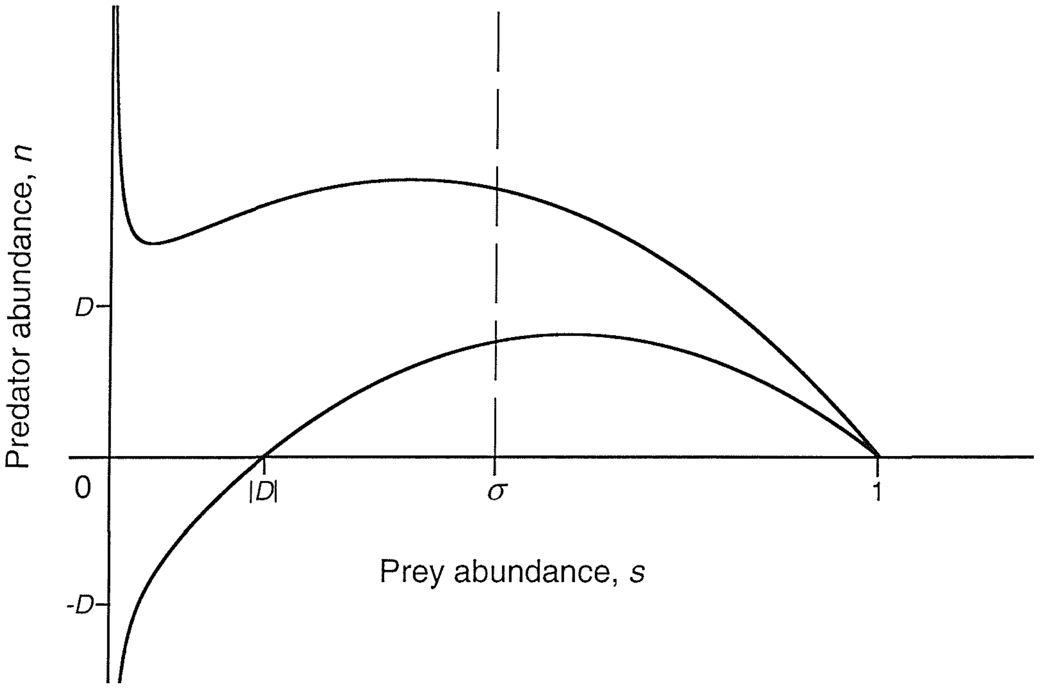


Figure 2.2 Phase plane for the prey flux model under prey influx (upper line, $D = +0.2$) and prey outflux (lower line, $D = -0.2$). Continuous lines show prey isoclines given by eqn. 2.3. The broken line shows the predator isocline given by eqn. 2.4a. At the given value of $\sigma = 0.5$ and with $D' = 0.01$, the dynamics are inherently unstable for prey outflux, since the prey isocline for negative D has an apex lying to the right of the predator isocline

2.6 QUANTITATIVE ANALYSIS

The stability of the steady state solutions introduced in the previous section are examined first. Initially, the ecologically uninteresting case of solution II was analysed. A relatively straightforward analysis showed that if $\sigma > 1$, then IIi is stable. Solution IIi is only stable if the fraction of unused prey population is insufficient to maintain the predator population, or equivalently the predators are below their extinction limit. If this is not the case, this solution is a saddle point pushing the predator population higher, but stabilising the prey population. If D is positive, Solution IIii does not apply. If D is negative, IIii, which exists in addition to IIi, there is a saddle point for small negative values of D.

Next the more interesting case of solution I was analysed. It is a well-established feature of all such models, including Rosenzweig's paradox of enrichment, that an increase in stabilising mechanisms occurs with a larger marginal subsistence demand (σ) for a given strength of inverse density-dependence (D in our model or D' in others: May, 1973; Tanner, 1975). Likewise, stability is enhanced by weaker inverse density dependence (i.e. larger D or D') for a given marginal subsistence demand.

For prey influx given by a positive value of D, the steady state of the predators and prey is stable if the predator isocline in Figure 2.2 intersects the prey isocline on the right-hand side of its apex, as is also seen in Rosenzweig's (1971) model. If the predator isocline intersects the prey isocline on the left-hand side of the apex, as it does for lower values of σ or D, then the steady states are unstable, resulting in limit cycles. Stability is reinstated under prey influx, however, if the predator isocline lies very close to the n-axis.

In Figure 2.3a a metadiagram is presented showing the regions over which eight different kinds of behaviour occur in the full (D, σ) plane for the PF model. Figure 2.3b shows that these same regions apply equally to large as to small values of D'. Appendix 2.2 contains the calculations that were used to produce Figure 2.3. Figure 2.4 and Figure 2.5 illustrates the eight different categories of behaviour in phase planes. Along with the analytical examination, extensive investigations using simulation techniques were also used to confirm the validity of the purely theoretical analysis. Simulations were carried out using MATLAB *simulink* (see Appendix 2.3 for the completed *simulink* model). The distinct regions and behaviours identified are:

1. Region **A**, in which $\sigma > 1$. The prey population is insufficient to maintain a predator population, whatever the value of D. These steady states are nodes with pure relaxation toward equilibrium. In region **A1** (prey influx) the prey equilibrium at $s = 1$ is unique. In region **A2** (prey outflux), there is bistability, and the other stable equilibrium (with extinct prey and consequently no predators), occurs at the origin (Figure 2.5 trajectory (ii)).

2. Region **B**, for lower σ. Here an equilibrium steady state with non-zero predator and prey populations exists in the form of a stable node. Thus relaxation to equilibrium occurs without any population cycling. In region **B1** this equilibrium is unique, whereas in region **B2**, it coexists with system collapse if initial predator populations are large in comparison to prey populations (Figure 2.5, trajectory (ii)).

3. Region **C** with further reduced σ. The stable node is transformed into a stable focus. A non-trivial steady state solution still exists, but the relaxation toward equilibrium involves a (steadily decreasing) degree of predator-prey cycling. Once again, region **C** is divided into region **C1**, with prey influx, in which the equilibrium point is unique, and region **C2**, with prey outflux, in which there is also a null stationary point and a threshold below which both populations collapse (Figure 2.5, trajectory (ii)).

4. Region **D** with still lower σ, and $D > 0$. The steady state of coexisting predator and prey populations becomes unstable. The predator-prey system cycles outward from the steady state and reaches a limit cycle. In Figure 2.6, we show also the time dependence of the population in this limit cycle. This region **D** ceases to exist if $D' \geq 1$.

5. Region **E** (also with low σ, but $D < 0$). The predator-prey system also cycles

outward from the steady state, but now tends towards the zero-population attractor.

6. For $D < -1$ the only stationary state is the trivial empty environment, and the basins of attraction for the non-trivial populations described in **A2**, **B2** and **C2** shrink to zero.

7. For $D > 1$ the prey isocline no longer has a maximum and the limit cycles disappear.

Under the prey outflux regime, the negative value of D always yields an empty environment solution. There is also a coexisting predator-prey solution in restricted regimes (**B2**, **C2** in Figure 2.3) and a coexisting prey-only solution in region A2. Population collapse always occurs with low σ, because prey populations kept at low density by predation decline to zero when the inverse density dependence of consumption combines with that of outflux.

Even when coexistence of predators and prey is a solution under prey outflux, it has rather a restricted basin of attraction. In particular predator populations well above those at the predator-prey equilibrium point (see Figure 2.5, trajectory (ii)) again drive the prey and thus the predator populations to extinction.

In general, predators that achieve a stable point under prey influx will not persist under conditions of prey outflux, unless the outflux is small in relation to the predator's marginal subsistence demand for prey. In other words, only predators that make little impact on prey carrying capacity can persist under conditions of high prey outflux.

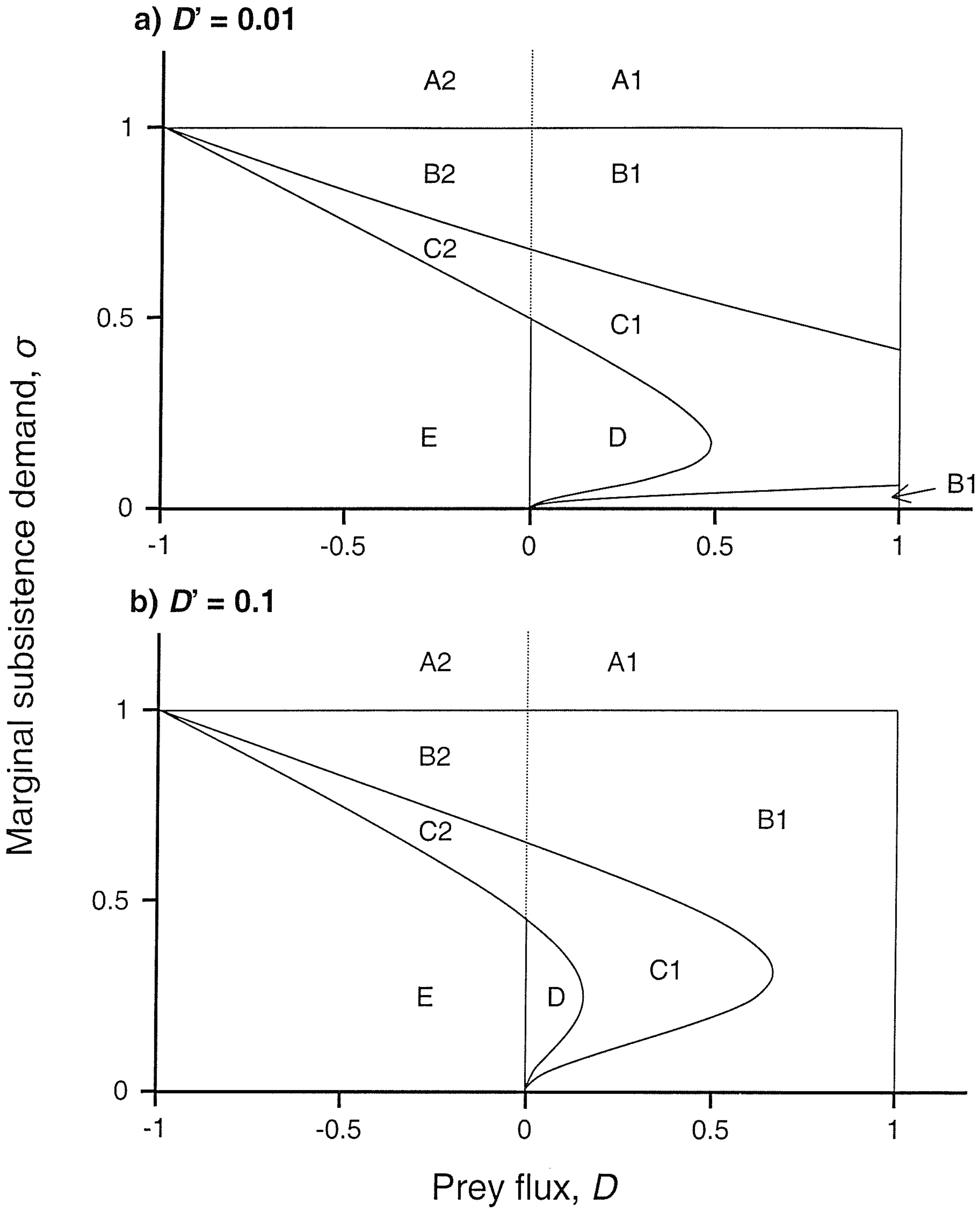


Figure 2.3 Stability regions of σ against D, for the prey flux model at two values of D' (with $\nu = 0.1$). (a) Small ratio of search to handling time ($D' = 0.01$); (b) larger ratio of search to handling time ($D' = 0.1$). Equations for the boundary lines are given in Appendix 2.2. The stability conditions exhibited in each sector are **A1** = prey population insufficient to maintain a predator population; **A2** = bistability: either prey population is insufficient to maintain a predator population or prey population collapses to the origin followed by the predator population; **B1**= a steady state of predators and prey in the form of a stable node; **B2** = a stable node coexists with system collapse for large initial populations; **C1** = a stable focus exists in which relaxation toward equilibrium involves a degree of predator-prey cycling; **C2** = a stable focus coexists with system collapse for large initial populations; **D** = the predator-prey system cycles outward from the steady state and ultimately reaches a limit cycle; **E** = predator-prey system cycles outward from the steady state, but tends towards the origin and extinction.

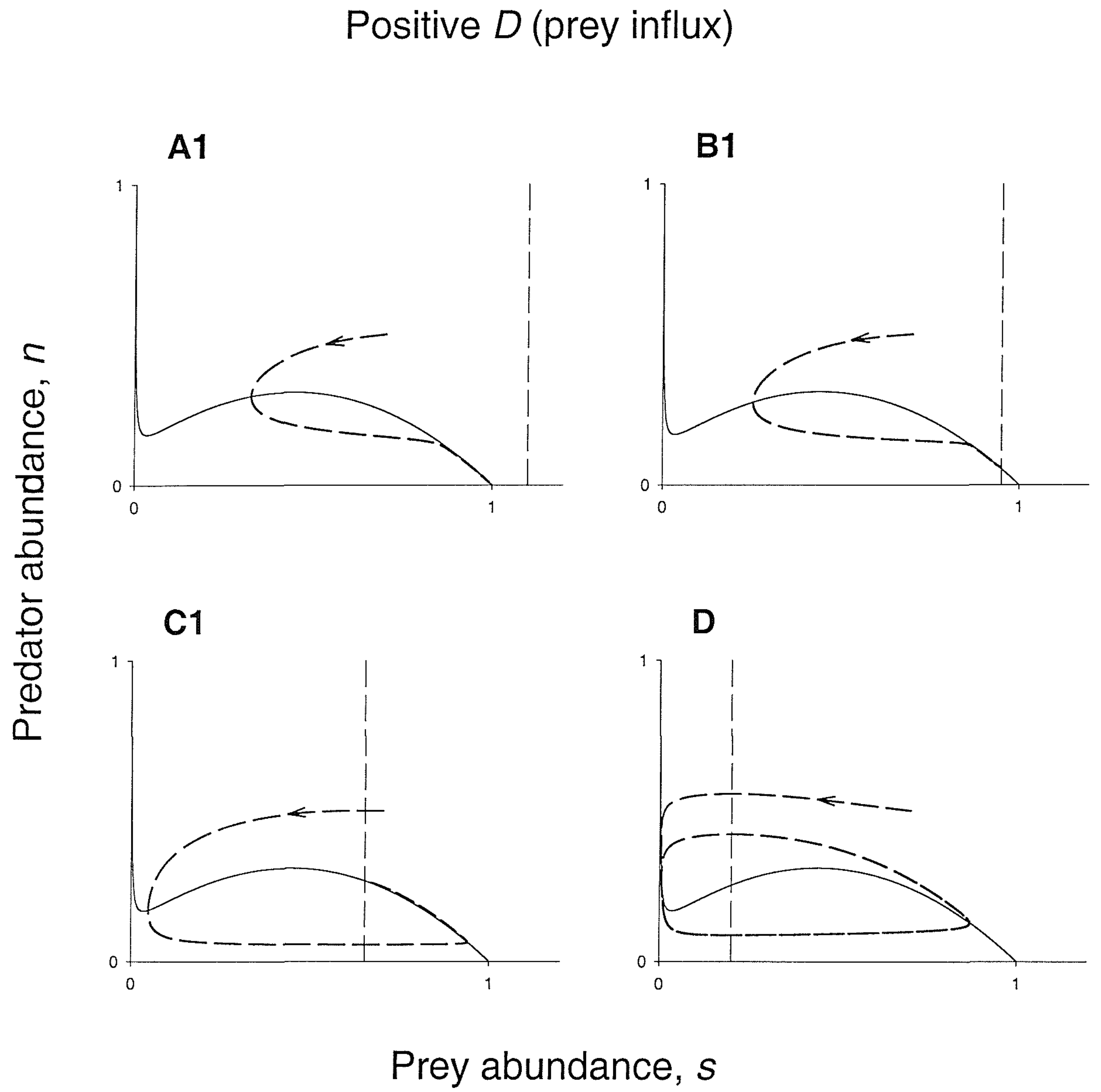


Figure 2.4 Phase planes illustrating dynamic behaviour in the four prey influx regions of the meta-diagram shown in Figure 2.3a. The solid lines show the prey isocline of eqn 2.3 and the thin broken lines shows the predator isocline of eqn 2.4a. Parameter values are: $D = +0.1$, $D' = 0.01$ $v = 0.1$, and $\sigma = 1.1$ (for **A1**), 0.95 (for **B1**), 0.65 (for **C1**) and 0.2 (for **D**). The predator-prey trajectory is shown by a thick dotted line. Population values at $t = 0$ are $s = 0.7$, $n = 0.5$.

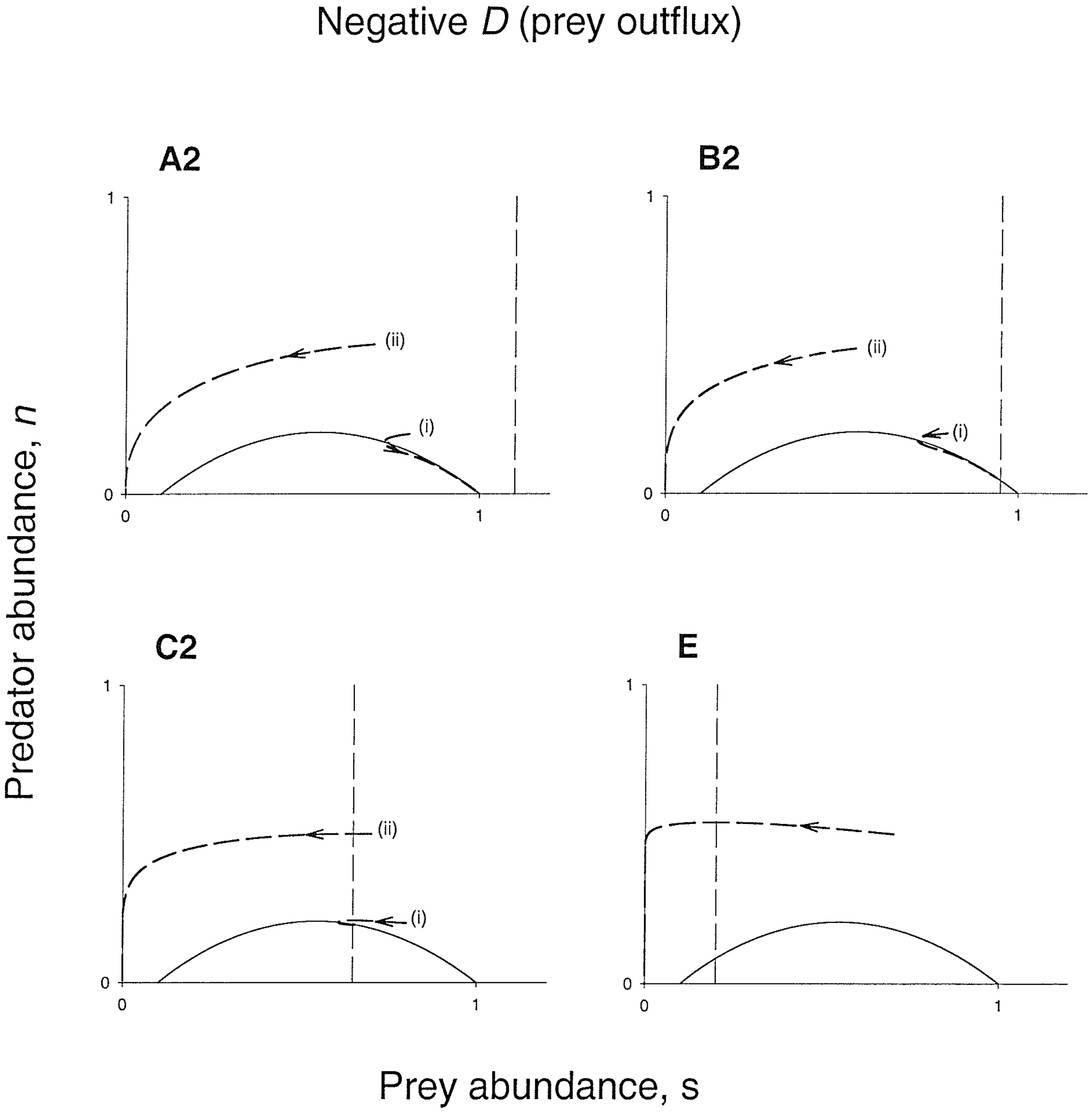


Figure 2.5 Phase planes illustrating dynamic behaviour in four prey outflux regions of the meta-diagram shown in Figure 2.3a. The solid lines show the prey isocline of eqn 2.3 and the thin broken lines shows the predator isocline of eqn 2.4a. Parameter values are: $D = -0.1$, $D' = 0.01$, $v = 0.1$, and $\sigma = 1.1$ (for **A2**), 0.95 (for **B2**), 0.65 (for **C2**) and 0.2 (for **E**). The predator-prey trajectory is shown by a thick dotted line. Two kinds of stability co-exist; which trajectory the predator-prey populations follow depends upon the initial population density. At $t = 0$ (i) s = 0.8, n = 0.2 and (ii) s = 0.7, n = 0.5..

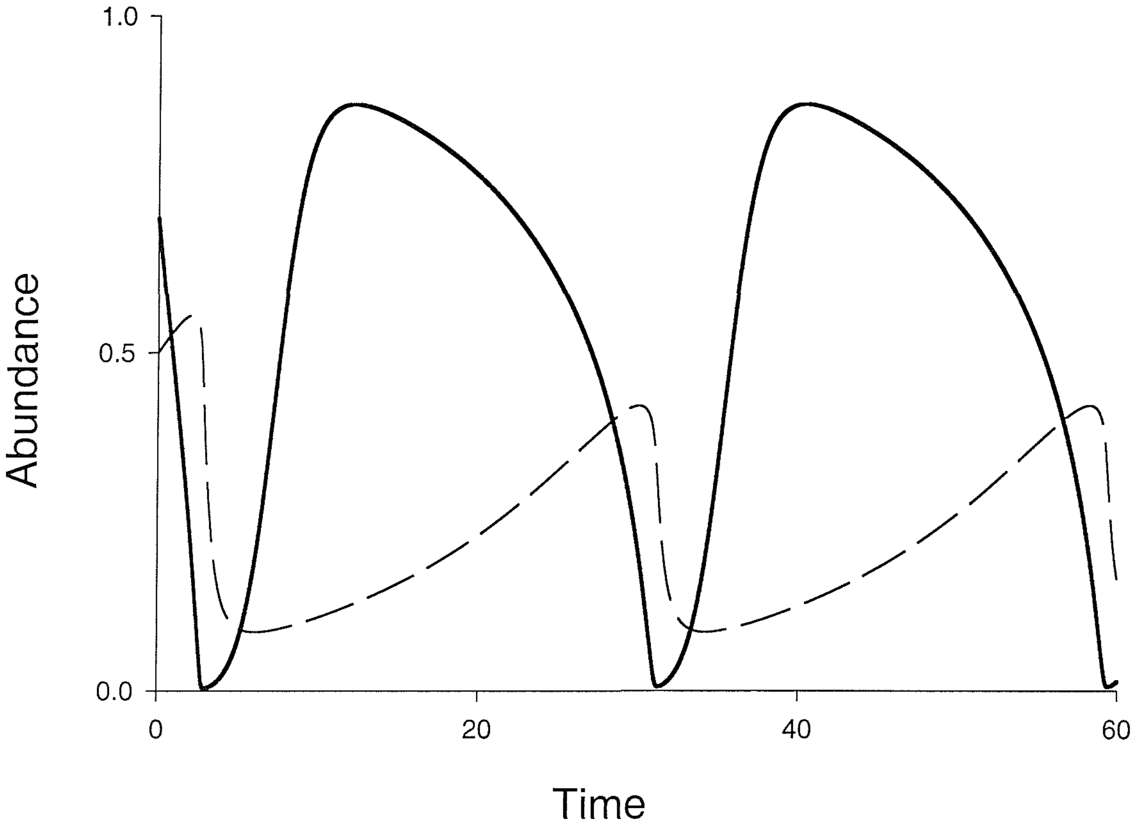


Figure 2.6 Predator and prey periodic behaviour for scenario **D** in Figure 2.4, with time and abundance in non-dimensionalised units ($D = +0.1$, $D' = 0.01$, $v = 0.1$, ,$\sigma = 0.2$). Lines show time dependence for the prey population (solid) and the predator (broken) populations.

2.7 DISCUSSION

In this chapter we have introduced a model to describe predator-prey dynamics incorporating both a prey influx into the system (modelled by positive D in PF) and a prey outflux (modelled by negative D in PF). In contrast to Rosenzweig's paradox of enrichment model we find that an increase in prey subsidy stabilises both predator and prey populations whereas even a modest outflux can result in the extinction of both the prey then the predator population.

Whilst the functional response of predators to their limiting prey is an intrinsic feature of predator behaviour, resource flux is likely to be influenced by extrinsic features which can vary spatially and temporally. For example, Walde (1994) has tested the effects of prey influx for the phytoseiid mite *Typhlodromus pyri* on apple trees. Population densities of *T. pyri* were higher and persistence was greater where immigration rates were higher for its prey, the phytophagous mite *Panonychus ulmi*. In the absence of immigration, *T. pyri* could drive *P. ulmi* to local extinction, although occasional re-colonisation from outside the system prevented extinction at a larger scale. The PF model is consistent with this rescue effect of prey immigration.

Although we have interpreted negative D to represent an Allee effect, an increase in actual outflux (or emigration) at decreasing population densities has been recorded in many territorial mammal species (Wolff, 1997; Diffendorfer, 1998) these include *Peromyscus* sp., (Wolff 1992) and *Microtus* spp., (Jannett, 1978; McShea & Madison, 1984; Lambin, 1994). At high population densities competing conspecifics can impede emigration, and can therefore decrease the per capita rate of outflux, whereas this pressure is alleviated at lower densities. High emigration rates at low population densities can also be a mechanism for individuals to avoid the consequences associated with reproductive suppression, and inbreeding (Wolff, 1997). The outflux may be virtual rather than actual, if negative D expresses a reduced recruitment rate of prey at low density (Alvarez, 1998; Amarasekare, 1998a; Amarasekare, 1998b; Wang, *et al.*, 1999). Outflux then represents not a departure of prey, but rather an outflux of recruitment opportunities known as an Allee effect on prey (Allee, 1931). This effect posits a threshold below which there is negative population recruitment, attributable to a scarcity of mating opportunities as density approaches zero. Populations may also exhibit Allee effects for a wide variety of reasons not directly connected with mating success. These include: reduced-anti-predator defence (Lewis and Kareiva, 1993), less efficient feeding at low densities (Way and Banks, 1967), and reduced effectiveness of vigilance and anti-predator defences (Kenward, 1978).

Whether a declining prey density causes an increase in the per capita emigration rate of prey (actual outflux), or a decrease in their per capita birth rate (Allee effect), the process is one of negative feedback. This is referred to as 'critical depensation' in the literature on resource harvesting, and Alvarez (1998) has demonstrated that its influence on the optimal harvesting strategy is to lower the threshold for depleting a population. Whilst that economic prediction required Itô stochastic calculus, our ecological predictions from simple differential calculus yield a unified result for prey dynamics on a continuum between positive and negative (inverse) density-dependence.

What practical conclusions can we draw for species management from our work? In his 1971 paper Rosenzweig wrote that man must be very careful in attempting to enrich an ecosystem in order to increase its food yield: 'enriching an ecosystem's energy or nutrient flow ... may end in catastrophe'. We emphasise that Rosenzweig's models demonstrate how a catastrophe is provoked by enriching the stock of nutrients, and not its flow per se. Enriching the flow both increases consumer density and stabilises the system, and so does not give rise to a paradox. In contrast, a halted inflow or an outflow of renewing resource can provoke unrecoverable extinction by reducing densities and destabilising the system. This may provide a partial explanation for the ambiguous results from empirical work designed to validate the paradox of enrichment. A stock enrichment involving also resource subsidy can yield counterbalancing effects on stability.

The impact of rescue and Allee effects on population dynamics has been shown to be exaggerated by the presence of a predator. This has obvious implications for conservation and pest management. If a population is to be conserved then instead of restoring habitat to improve consumer recruitment, which can give Rosenzweig's paradox, it may be better to restore habitat to improve prey recruitment. Under PF this approach can lead to system stability and population growth. If a population is to be eradicated then instead of culling the pest consumers themselves (which may then recover) it may be better to cull their resource. Under PF this approach can lead to system instability and a population crash. In summary, populations may be managed more effectively if efforts are directed at the limiting resource rather then the resource consumer of focal interest itself. Given the potential implications of our study in particular with respect to species management of small open communities, there is a continuing need for empirical work to test our conclusions

3 SPATIAL PATTERNS IN A SESSILE MARINE INVERTEBRATE: CONSEQUENCES TO LOCAL PERSISTENCE

Declaration: this work has been done in collaboration with Mr Malcolm Roberts (assistance in data collection), Dr. Patrick Doncaster (assistance with design) and Prof. Steve Hawkins (biological expertise). I have led the design, fieldwork, analysis and interpretation stages.

3.1 ABSTRACT

The reproductive success of some species of sessile inter-tidal barnacles depends on the motile larvae settling within a penis length of a conspecific. One consequence of this is that individuals are spatially constrained if they are to successfully reproduce. Spatial patterns of settlement were measured for two sessile barnacle species *Semibalanus balanoides* and *Chthamalus montagui* in order to estimate the effect of limited penis length on recruitment. *C. montagui* can self-fertilise, whereas *S. balanoides* cannot. Six locations were chosen along the south coast of England with varying levels of recruitment. Experimental replicates were prepared at the start of the settlement season by removing existing adult barnacles to expose patches of bare rock. Treatments were left at the centre of cleared patches comprising small groups of adult conspecifics (1 - 32 individuals). At the end of the settlement season the position of settlers was analysed in relation to these remnant adult conspecifics, to cohort members, and to other cyprids/spat. *C. montagui* were found to settle randomly with respect to adults but were aggregated with respect to other cohort members. *S. balanoides* populations were aggregated in all comparisons. A good approximation to observed settlement patterns was obtained by a model simulating settlement in a restricted random distribution constrained only by a maximum and a minimum inter-individual distance. The parameter values defining these constraints had biological relevance, being equivalent in magnitude to barnacle penis length and territorial repulsion respectively. However, territorial responses were shown to be less influential in dictating the observed settlement patterns as penis length. The strong clumping behaviour exhibited by the recruiting barnacles contributes to a geometric growth of population size. We discuss the consequences to population persistence of this type of growth pattern.

3.2 INTRODUCTION

The spatial patterns of individuals have long been a major concern to ecologists (Clarke & Evans, 1954; Blacksmith, 1958; Pielou, 1960, 1962; Lloyd, 1967), since they are influenced by both biotic and abiotic factors and play an important role in determining the intensity and outcomes of intraspecific interactions (Wethey, 1984a). Typically the spatial pattern of individuals will lie somewhere on a spectrum from random to regular to clumped (Clark & Evans, 1954). Regular spacing in a population is a good indicator of mutual repulsion and therefore reflects some form of territoriality or other manifestation of mutual intraspecific competition. An aggregated pattern in contrast indicates attraction; either to each other or to patchily distributed resources. A random pattern indicates that the distribution of each individual is independent of others. It can also occur when attraction and repulsion both act upon a population, effectively cancelling each other out. All interpretations of spatial pattern must address the scale at which the observations are made, since a distribution may be regular or clumped depending on the resolution with which it is resolved.

Motile organisms can readily influence their own spatial position either by avoiding conspecifics (e.g. to seek food) or by actively locating them (e.g. to seek mates). In contrast, spatial arrangements in sessile organisms are persistent by definition; consequently they have a great impact on the organism's fitness (Satchell & Farrell, 1993). However, field data addressing this subject are scant (Davis & Campbell, 1996).

In populations of barnacles, competitive repulsion is delicately balanced by mutual attraction (Knight-Jones & Stevenson, 1950; Knight-Jones, 1953; Crisp, 1961). Barnacles are hermaphrodite as adults and entirely sessile in habit. Reproductive success in species that cannot self-fertilise (e.g. *Semibalanus balanoides*) therefore depends on individuals settling within a penis length of conspecifics. This requirement must be met if cross fertilisation, and thus reproductive success, is to occur. The actual length of a barnacle's penis depends on the species (see Klepal *et al.*, 1972; Klepal, 1987; Barnes, 1992). The length of a *S. balanoides* penis can be being anything up to 25 mm (Barnes & Crisp, 1956) and so too can the penis of *Chthamalus montagui* (F. Pannacciulli pers comm).

Attraction, however, is balanced by territorial behaviour (Crisp, 1961). The location at which an adult barnacle can be found depends on the site selection made during the cyprid settling stage of their life cycle. It is only this planktonic stage that is actively mobile and thus the ultimate reproductive success of the individual is dictated at an early age. However, a limited degree of mobility (up to 24 mm) is possible by adult individuals when subjected to lateral pressure (Crisp, 1960).

In this chapter we aimed to test the hypotheses that variation in spatial patterns, exhibited by a newly settling barnacle cohort, would be affected by both mutual attraction to adult conspecifics and other cohort members, and also by intraspecific territorial repulsion. We examine the spatial distribution of individual barnacles in relation to conspecifics and apply conclusions from the empirical work to theoretical population models. Barnacles respond to many features of their local environment, and they rely on numerous settlement cues before metamorphosis and permanent attachment. In the next section we outline some of the processes that influence the development of the spatial pattern in barnacle populations.

3.2.1 Spatial arrangement in local barnacle populations

In many barnacle species the spatial arrangement of individuals has an important influence on their survival. Interactions between sessile species are balanced between positive and negative interaction components that depend on the context and the local physical and biotic conditions (Bertness *et al.*, 1998). There appear to be several opposing factors that interact in the development of barnacle spatial patterns. Local population density may influence the success of individual barnacles via several biotic and abiotic processes.

Small-scale patterns of flow dynamics can alter patterns of colonisation (e.g. Crisp, 1955; Butman *et al*, 1988). Settled cyprids may disrupt water flow in their vicinity, and the velocity gradient associated with the presence of a settled cyprid may too attract new arrivals (Crisp, 1955). Chemical cues may then be used to avoid conspecific adults, but the chemical cues that enhance settlement are likely to be short-lived in the intertidal zone (Wethey, 1984b).

Satchell & Farrell, (1993) conducted spatial arrangement experiments on four inter-tidal barnacle species *Balanus amphritie, B. glandula, Chthamalus dalli*, and *Pollicipes polymerus*, they found that only *P. polymerus* showed clumping behaviour and suggested reasons for not seeing aggregation:

1. The cyprids studied did not detect the presence of conspecifics; natural selection behaviour may result in the cost being to high to search for a better location.
2. There may be a weak relationship between later adult abundance and settler abundance.
3. Initial settlement densities may not have been high enough to result in strong intraspecific competition for space.

Wethey (1984b) found significantly non-random nearest neighbour distances among newly settling *S. balanoides* cyprids, between newly settling cyprids and previously settled but unmetamorphosed cyprids and between newly settling cyprids and newly metamorphosed individuals on Massachusetts shores. He also showed that cyprids settle in aggregations with respect to other individuals settling on the same tide, and show an even stronger aggregation response to previously settled cyprids. However, although adult conspecifics were removed the bases of the detached adults were not, also the direct relationship between settlers and adult conspecifics was not explored.

The requirement to settle close enough to allow cross fertilisation to take place is, however, balanced against territoriality in some species (Crisp, 1961). The tendency for barnacles to aggregate may decrease at high densities (Satchell & Farrell, 1993), this may be as a result of an increase in intraspecific competition for space and the resources made available by that space (Wu, 1980; Moyse & Hui, 1981), increased rates of predation (Fairweather, 1988) and parasitism (Blower & Roughgarden, 1989). A territorial response may also prevent individuals from being crushed or overgrown by conspecifics or other species (Connell, 1959). Crisp (1961) has shown that with *S. balanoides* the territorial separation is typically in the region of 1.55 - 1.9 mm depending on the density of conspecifics and the actual length of the cyprid. Barnett &

Crisp (1979) have shown that when nearest neighbour distances are less than 2 mm it is more profitable for *S. balanoides* larvae to swim off. The territorial mechanism exhibited by barnacle cyprids indicates some degree of intraspecific competition. Indeed, Crisp (1964) has shown that settlement greater than 4 spat per cm^2 is wasteful. It results in no additional barnacle biomass per unit area, as individuals are forced to reduce their size inversely to the population density. However, Wethey (1984b) concludes that evidence for territorial behaviour during settlement is minimal, but gregarious territorial settlement can lead to the formation of clear patches over time.

Bertness *et al.* (1998) have shown in laboratory experiments that crowding can actually benefit individuals by resulting in a higher feeding efficiency, as individuals are elevated above the surface and are exposed to higher fluid velocities and particle fluxes than individuals between hummocks. Barnacle crowding can also increase survivorship by buffering individuals from thermal stress (Bertness, 1989), increasing reproductive output (Wethey, 1984a), and decreasing skeletal support costs (Wu, 1980). Aggregations of conspecific adults can also reduce the mortality of settlers by providing a refuge from predators and grazers (Miller & Carefoot, 1989). Barnacles living at low population densities may be more susceptible to mortality caused by battering with wave-tossed debris (Shanks & Wright, 1986). Density-dependent intraspecific crowding is, however, responsible for most *S. balanoides* deaths at low and intermediate tidal heights independent of other biotic and physical pressures (Bertness, 1989). At very high settlement densities *S. balanoides* individuals within hummocks become elongated, fragile and have minimal contact with the substrate they are attached to when compared to isolated individuals (Barnes & Powell, 1950). This consequently reduces individual survival rates. If density–dependent intra-specific competition and facilitation influences barnacle populations, then populations that routinely experience different levels of recruitment could exhibit markedly different within-population patterns of distribution (Bertness, 1989).

A difference in the spatial arrangements of organisms may give an insight into the growth of the population as a whole. If the organism under study displays clumping behaviour, due to the need to carry out a fundamental biological process, then this may influence the way in which the number of individuals in the population increases. The greater the number of conspecifics present within a penis length of an individual the greater the number of offspring that individual can potentially sire, increasing the individuals reproductive fitness. Therefore, individual cyprids should select areas of substratum whereby conspecific numbers are maximised, when free-space is not a limiting factor. We would inevitably expect to find some degree of aggregation in the local population, with the degree of aggregation increasing as the numbers of conspecifics increased. Conversely we would expect the presence of single isolated barnacles to be a rare. Barnacle populations will increase geometrically if individual conspecific all have the same degree of attraction to settling cyprids.

Because local recruitment is supplied from outside, barnacle populations are usually regarded as having no extinction threshold. That is to say, there is no minimum population size below which local persistence cannot be sustained (Nee, 1994). However, the mutual attraction between individuals can produce a geometric (exponential) pattern of population growth, despite an arithmetic influx, which does give the population an extinction threshold at the density at which penises can just reach between individuals. More generally the effect of mutual attraction between individuals is to give the open system some of the population characteristics normally associated with closed systems. This subject will be returned to in the next chapter.

To assess the role that conspecifics play in determining the spatial arrangement of settling barnacles, and consequently the growth rate of the local population, we manipulated adult barnacle populations at various locations. We removed all barnacles from a suitable substratum apart from a remnant central adult group. Patches were then photographed using a digital camera and exact positions of each barnacle mapped out in relation to the remnant central adult group and other cohort conspecifics.

The specific objectives of this chapter were to quantify the degree of aggregation between barnacle settlers and conspecifics from three distinct age classes: adults, yearly cohort members and cyprids at locations with varying recruitment rates. By experimental manipulation we could determine whether the number of barnacle settlers increased in proportion to the number of adult conspecifics. The empirical data also allowed us determine whether there was any movement of adult barnacles or individual barnacle isolation. By simulating a restricted random settlement of barnacles we were able to assess the relative influences of conspecific attraction and territorial repulsion on the observed spatial patterns. By characterising barnacle aggregation behaviour, the rates of population growth could be deduced and applied to classical models.

3.3 METHODS

3.3.1 Study organism and locations

Two species were used to study spatial patterns in barnacles, *Semibalanus balanoides* (L.) and *Chthamalus montagui* Southward, (for a description of *S. balanoides* see Chapter 4). *C. montagui* is a common intertidal sessile marine invertebrate of the class Cirripedia. *C. montagui* is a broad conical barnacle with a kite shaped aperture, which distinguishes it from *C. stellatus* (Southward, 1976). The distribution of *Chthamalus* sp. is regulated by sea temperature. They are typically found on the coasts of Ireland, and Wales and the south west of England (Rainbow, 1984), both species are absent east of the Isle of Wight (Crisp *et al.*, 1981). *C. montagui* can be found on the upper reaches of moderately exposed shores (Hayward *et al*, 1996). *C. montagui* typically breeds in July and August with the settlement of cyprids taking place in the autumn, typically beginning in September (Bassindale, 1964), but this varies with latitude (Burrows *et al.*, 1992; O'Riordan *et al.*, 1995). *C. montagui* is a simultaneous hermaphrodite which cross-fertilises, but with the ability to self-fertilise in isolation (Barnes & Crisp, 1956; Barnes & Barnes, 1958).

The locations used to study barnacle spatial patterns were chosen to reflect the presence of the barnacle species and their level of recruitment based on background density (see Chapter 4, settlement plate results, for confirmation that background density did reflect recruitment rate).

S. balanoides was studied at Cowes, Isle of Wight (1°17'47"W.,50°45'41"N.), in 1998 and at four locations around the Isle of Wight: Cowes, Totland (1°33'36"W., 50°40'45"N.), Ventnor (1°12'25"W., 50°35'49"N.), and Seaview (1°06'49"W., 50°43'02"N), in 1999. *C. montagui* was studied at Portland Bill, Dorset (2°26'35"W.,50°28'42"N.) and Sidmouth, Devon (3°14'13"W., 50° 40'56"N.) in 1998.

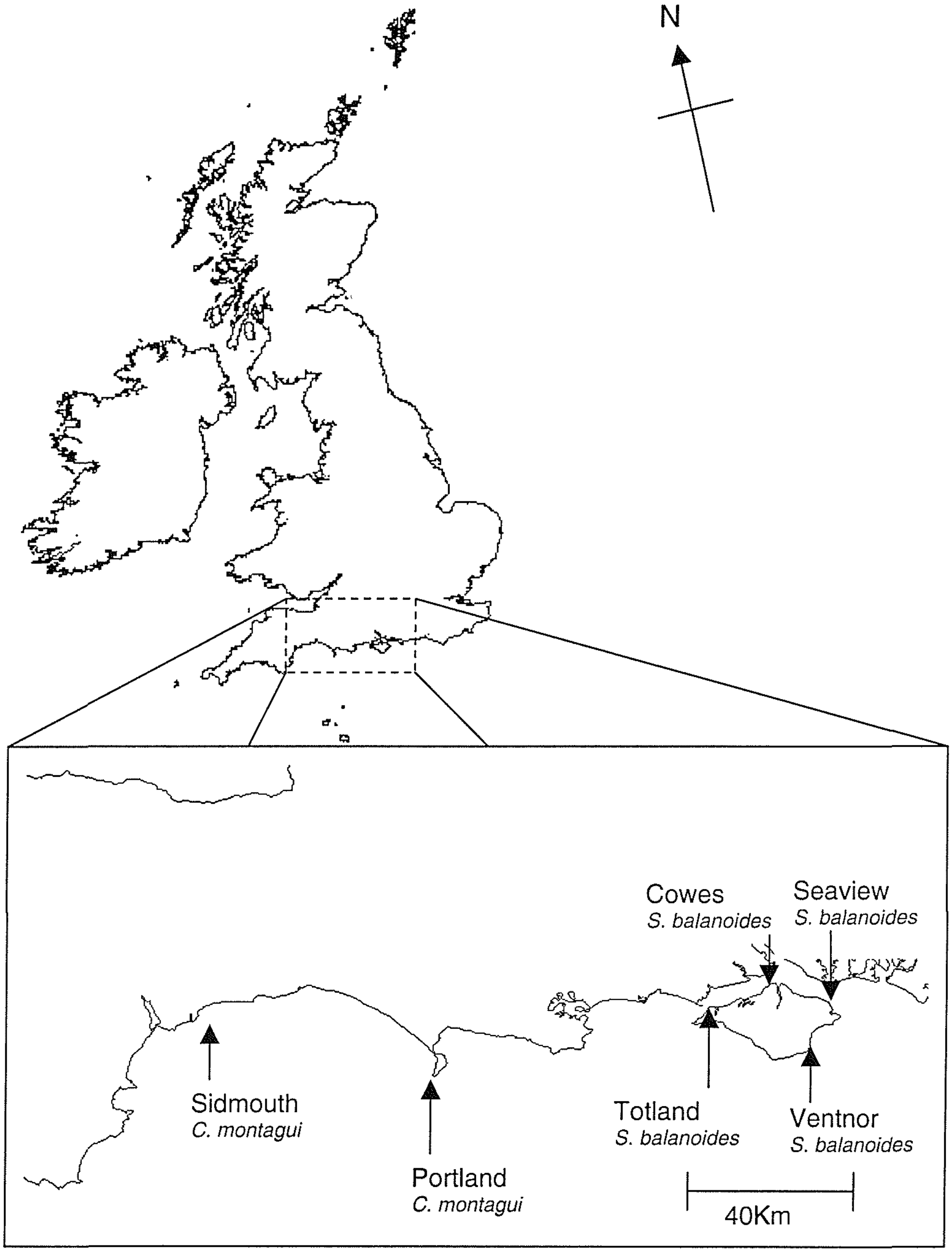


Figure 3.1 The boxed area in the top map shows the study locations with respect to the rest of the United Kingdom. The insert shows the spatial relationship between the locations along the south coast. The location used in 1998 for *S. balanoides* comparisons was Cowes, and for *C. montagui* comparisons Sidmouth and Portland. Locations used in 1999 for *S. balanoides* comparisons were the four locations around the Isle of Wight: Cowes, Totland, Ventnor and Seaview.

Sidmouth is on the coast of Lyme Bay between Lyme Regis and Tor Bay. The rock type is largely Permian and Triassic red breccias and sandstones (Barne *et al.*, 1996). Along the shore however, there are numerous man-made rock out-crops constructed of rock-berm. The Isle of Portland is linked to mainland England via Chesil Beach with the 'island' protruding into the English Channel. Portland is also bordered by Lyme Bay as well as Weymouth Bay and as a consequence strong tidal streams can be found around this peninsula.

Cowes is positioned on the northern tip of the Isle of Wight on the edge of the Solent. Cowes is built on a gravel capped hill and slopes into Bembridge marls descending to Bembridge limestone on the shore (Bird, 1997). Along the shore at Cowes there are also various stretches of flint gravel. The shore at Cowes is bordered by a 3-metre high sea wall. Totland is on the far north west tip of the Isle of Wight at the most westerly part of the Solent. The upper shore at Totland is covered with stretches of flint gravel. Mid and lower shores are comprised of tertiary sands. Along the shore there are numerous man-made rock revetment breakwaters as well as timber groynes. The shore at Totland is bordered by a 2-metre sea wall. Ventnor is on the south-south east coast of the Isle of Wight. The cliffs at Ventnor are comprised of gault clay, upper greensand and chalk. The shore is a mixture of shingle and limestone boulders. Seaview lies on the north east coast of the Isle of Wight and the easterly most extremity of the Solent. The upper to mid-shore is comprised of shingle and limestone boulders. Whereas the lower shore is mainly sand and clay. The shore at Seaview is bordered by a 3 to 6 metre sea wall.

Locations around the Isle of Wight were selected according to the level of *S. balanoides* recruitment. Both Cowes and Seaview were deemed high-recruitment locations, whereas Totland and Ventnor were deemed low-recruitment locations. Recruitment has been found to vary between all locations. Sidmouth is the most westerly location in the study and has higher barnacle recruitment than both Portland and the Isle of Wight (Herbert, in prep).

3.3.2 Experimental design

The study was conducted from April until November 1998 on *S. balanoides* at Cowes, and from September 1998 until February 1999 on *C. montagui* at Sidmouth and Portland. The 1999 study on *S. balanoides* on the Isle of Wight was carried out from April to August.

We designed data collection in order to compare between *S. balanoides* at different locations in a single year (1999 IoW results), *C. montagui* at different locations in a single year (1998 Portland and Sidmouth results), interspecies comparisons in a single year (1998 Cowes and 1998 Portland/Sidmouth results), and between year comparisons for a single species at a single location (1998 Cowes and 1999 Cowes results).

In order to measure settlement rates and spatial patterns of a new cohort at a designated location, we removed adult populations to expose 'virgin' bare rock. Adult barnacles were removed using a paint scraper and a wire brush, ensuring that all physical barnacle structures were removed. The use of a paint scraper to remove adult barnacles is well documented (e.g. Wethey, 1983, 1984a; Minchinton & Scheibling, 1991; Minchinton & Scheibling, 1993a; Thompson *et al.*, 1998). At the centre of each cleared patch a small group of adult barnacles was left in place. The number of 'remnant' adults left at the centre of the patch represented the treatment. Care was taken to prevent any injury or damage to the remnant central adults, and where possible remnant adults were left as a circular group. Treatment patches at locations were prepared at least three weeks before the onset of the new cohort to allow them to reacclimatize. Patches were marked with screws fitted into plastic wall plugs placed in drill holes, to enable relocation. These treatments allowed us to assess the influence of adult conspecifics on the orientation and spatial pattern of a settling barnacle cohort. We hypothesised that the greater the number of remnant adults left the greater the number of settlers that would be subsequently attracted to the immediate area around the central patch.

For each settlement season the experimental design altered slightly as a result of improvements made after each settlement season. Much of the experimental methods, however, remained constant throughout. Experiments were all conducted around the

MW mark to enable the study of new juvenile populations at all low tides, and to ensure all treatments were immersed for approximately the same length of time. Recruitment can increase by up to four times from mid shore to lower shore (Minchinton & Scheibling, 1993a). In our research all of the treatments in each study were placed at approximately the same tidal height to prevent such factors becoming confounded within the results. Where possible vertical rock faces were chosen, if these were not vertical then faces that were close to vertical were used. All treatment patches were prepared on rock surfaces facing seaward. Care was taken in selecting patches with the same relative topography.

It was assumed that the availability of new recruits was constant within a localised area, resulting in all treatments within a shore having the same access to a local recruitment cohort.

3.3.2.1 S. balanoides 1998

Initially before manipulation suitable substrata with both high (> 80 barnacles / 25 cm^2) and low (< 15 barnacles / 25 cm^2) densities of adult *S. balanoides* were selected at Cowes. Suitable patches for manipulation were then selected within shores with different designated recruitment levels at the location. All treatment patches were selected to have a similar initial covering of barnacles. Each patch was randomly assigned a treatment from the choice of 0, 1, 2, 4, 8, 16, and 32 adult barnacles. All adult barnacles were cleared from a square area of at least 10 × 10 cm around the central patch of adults. This set of treatments was replicated three times at each of the recruitment levels (see Figure 3.2 for experimental design).

3.3.2.2 C. montagui 1998

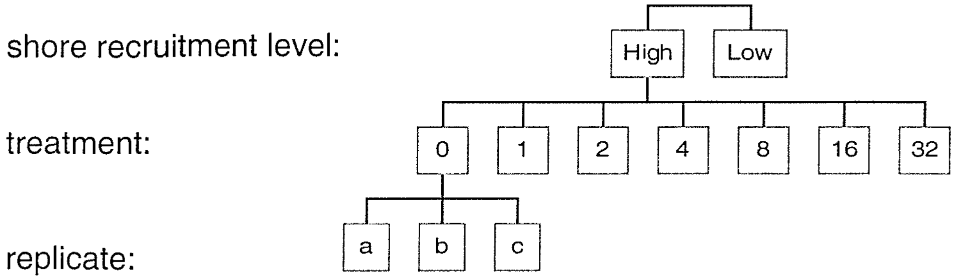
Suitable substrata with both high (> 40 barnacles / 25 cm^2) and low (< 10 barnacles / 25 cm^2) densities of adult *C. montagui* were selected at Portland. The overall background densities at Sidmouth were much higher than those at Portland therefore this was reflected in the division between the high and low-recruitment shores. At Sidmouth the high-recruitment shore had greater than 120 barnacles / 25 cm^2 whereas the low-recruitment shore had < 20 barnacles / 25 cm^2. The categories high-recruitment and low-recruitment were determined by taking population counts at different areas at each of the locations.

At each of the *C. montagui* locations treatment patches were selected for either 0, 8, 16, or 32 adult barnacles. A circular area of 30 cm diameter was cleared of all adult barnacles with the treatment adults at the centre. Each of the treatments was repeated three times. This was then repeated once more within the same recruitment shore to give two areas each with sets of three replicated treatments. This 'nested' design was then replicated at the opposing recruitment shore at the location. All treatment patches were at least 50 cm apart (see Figure 3.2 for experimental design).

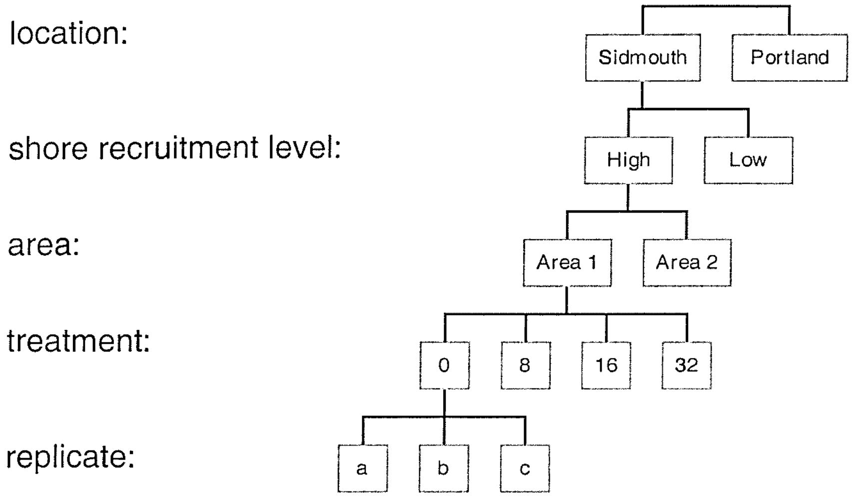
3.3.2.3 S. balanoides IoW 1999

Two high-recruitment and two low-recruitment locations were selected around the Isle of Wight in order to assess any differences in observed barnacle spatial patterns between locations with different barnacle recruitment levels. Locations were chosen after making counts and observations at 20 possible study locations. At each selected location treatment patches were selected at random for preparation with either 0, 2, 4, 8, 16 or 32 adult barnacles. A circular area of 30 cm diameter was cleared of all adult barnacles, except for the treatment adults left at the centre. Each of the treatments was then repeated three times (see Figure 3.2 for experimental design). At Seaview, Totland, and Ventnor treatment patches were all prepared on suitably large boulders and rocks at approximately the same tidal height. At Cowes all treatment patches were prepared on a vertical sea wall at exactly the same tidal height.

i) *S. balanoides* 1998 at Cowes (Isle of Wight)



ii) *C. montagui* 1998 at Sidmouth and Portland



iii) *S. balanoides* 1999 on the Isle of Wight

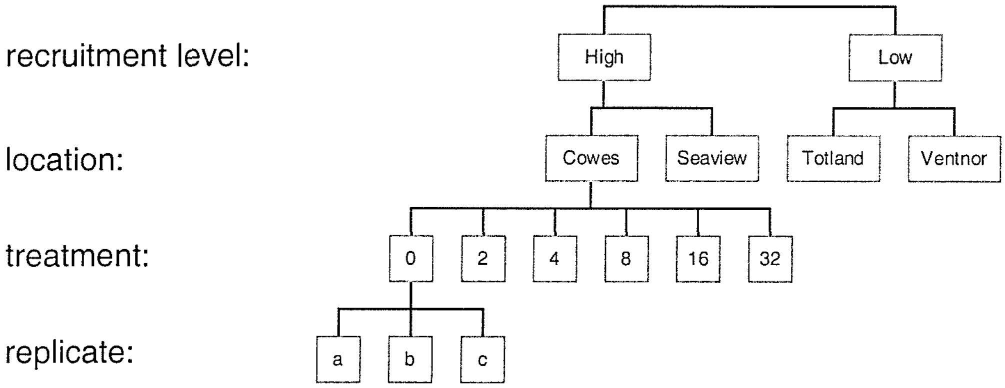


Figure 3.2 The experimental design for i) *S. balanoides* 1998 (note no replication of recruitment level, shores, or location), ii) *C. montagui* 1998 and iii) *S. balanoides* 1999. For each design only one branch of the experimental tree is shown. All other branches are identical to the one shown.

As well as preparing treatment patches settlement plates were also deployed at each of the four locations around the Isle of Wight in 1999. These were designed to allow recruitment comparisons to be made between locations, as well as allowing recruitment to be compared to the background population density.

The settlement plates were adapted from terracotta kitchen tiles. Typically materials such as perspex (Shkedy *et al.*, 1995), plexiglass (Raimondi, 1990), and slate (Barnett, & Crisp, 1979) have been used in the construction of settlement plates. However, preliminary observations, before the 1999 settlement season, suggested that barnacles would readily settle upon terracotta. The tiles used measured 7 cm × 7 cm and were glazed on the front but not on the back. The back of the tiles were used to measure settlement as they were marked with a raised 14 × 14 square lattice design. Each of the squares being 4 mm × 4 mm with a 1 mm trough between each of them. A hole was drilled through the centre of each of the tiles and four titles were screwed onto suitable surfaces at each of the locations. Each time the locations were visited all tiles were removed and replaced by new ones. The removed tiles were returned to the laboratory where numbers of settlers and individual photographs were recorded.

At all the locations the barnacle species under observation were the most dominant barnacle species present. At Cowes there was a very low background density of *Elminus sp.* (< 2 per 100 cm^2). At Portland there was a very low density of *S. balanoides,* (< 5 per 100 cm^2). Although both *S. balanoides* and *C. montagui* occur together at Sidmouth their respective settlement seasons are temporally separate. Settlement counts therefore only include the barnacle species under observation.

The only other animals visibly present at locations at any abundance were limpets. At Portland and Sidmouth there was a low to medium density of both *Patella vulgata* and *Patella depressa* (approx. 5 - 20 per 1 m^2). At Cowes there was a medium density of *Patella vulgata* (approx. 20 - 30 per 1 m^2), and at Totland, Ventnor and Seaview there was a low density of *Patella vulgata* (approx. < 5 per 1 m^2). Limpet populations can influence barnacle populations by knocking cyprids off the substratum during grazing activities (see Hawkins, 1983; Miller & Carefoot, 1989). Due to the detrimental effect limpets can have on newly settled barnacle populations all limpet species from a 1m^2

area were originally removed from around the treatment patches. Other predatory molluscs were not observed at Sidmouth, Portland, or Cowes. A small number of dogwhelks (*Nucella* sp.) were observed at Totland, Ventnor and Seaview. This species is rare at Totland and Seaview, whereas at Ventnor it is frequent (Bray & Herbert, 1998). However, numbers at Ventnor have since declined (AK pers. obs.). Although visible predators were minimal the presence of predators active during barnacle submersion could not be assessed, these may include fish and crab species (Connell, 1961; Milton, 1983; Burrows *et al.*, 1999a).

3.3.3 Sampling and distance calculations

During the 1998 *S. balanoides* and *C. montagui* settlement seasons observations were made in the field weekly for approximately the first two months of settlement then fortnightly thereafter. In 1999 observations were made twice a week for the first month of settlement, then weekly until no further settlement was observed at any of the locations. For both the 1998 *C. montagui* and the 1999 *S. balanoides* studies digital photographs were taken of each treatment when the locations were visited. However, there were a number of occasions in which treatments were not photographed due to time constraints. Photographs were only taken during the 1998 *S. balanoides* study at the end of the settlement season.

All photographs were taken using a Ricoh RDC-4300 digital camera and were downloaded onto a computer on return from the field using DU-4 (Camera Tool) software. The photographs taken encompassed the whole treatment patch, and a 300 mm ruler to enable scaled analysis. The photographs used for the analysis of spatial patterns are those taken on the sampling date in which barnacle numbers were found to be no longer variable. In studies of settlement behaviour it is possible that unobserved post-settlement mortality influences spatial patterns. To reduce problems of this sort both living and dead barnacles were used in the analysis (Satchell & Farrell, 1993).

Once the treatment photographs had been loaded onto a computer, an image analysis program called 'Barnacle Location' was written in Visual Basic to allow the study of spatial locations. The Barnacle Location programme displayed the treatment picture on the computer monitor. The computer mouse was then used to mark the central barnacle patch and each new individual settler, along with known distances on the scale. These marked points on the picture were then stored as Cartesian co-ordinates (the units used here being the number of photograph pixels in the x and y direction). From this information a Microsoft Excel macro was written to convert pixels into millimetres, and to calculate the distance from the newly settled barnacles to the centre patch using Pythagoras' theorem. To calculate the distance from an individual to its nearest neighbour, a macro facility was written in Microsoft Excel. This macro calculated the distance between a barnacle and all other marked barnacles, using Pythagoras' theorem, and stored the distance to the closet barnacle. This process was repeated for all barnacles to give a nearest neighbour value for each individual.

3.3.4 Analysis

3.3.4.1 Analysis of densities in concentric annuli

3.3.4.1.1 General linear models

To determine the force of attraction created by the adult conspecifics left at the centre of each treatment, the density of individuals was calculated in annuli radiating from the centre of the patch outwards. If the adults acted as a strong attractant then the density of settlers would be expected to be inversely related to the distance from the centre i.e. greater settler densities nearer the remnant patch. Once the density of settlers was calculated in each concentric ring, it was then possible to compare these results to a random settlement model, and to a general settlement model with variable attractiveness of the remnant adults, as described below.

Using the Barnacle Location programme and a Microsoft Excel macro distances were measured from each individual barnacle to the centre of the cleared patch which was also the centre of the remnant group. The number of individuals could then be record in radiating circular quadrates whose diameter increased by increments of 15 mm, giving a total of 7 counts for the 1998 *S. balanoides* treatments and 10 counts for each of the *C. montagui* 1998 and 1999 *S. balanoides* treatments. However, the first annulus contained the adult treatment individuals, and for some of the larger treatment numbers so did the second annulus. As the number of adults varied (and therefore so did the net free-space available for settlement) settlement in the inner (and occasionally the second) annulus had to be standardised against net free-space to enable consistent comparisons to be made. The area of the central adult treatments was calculated using the computer package Scion Image (1998 Scion Corporation). The number of settlers into the inner most annulus was then adjusted according. This standardisation allowed the amount of free-space in each inner most annulus to be constant regardless of treatment. As the central adults did not extend into other annuli settlement numbers into the rest of the treatment patch were not altered, consequently this adjustment did not alter the numbers of settlers significantly.

A General Linear Model was used to test for differences between the number of settlers in the 15 - 30 mm annulus between treatment levels, the recruitment level, and the location. As discussed already the penis lengths of the two barnacle species used in this study can be up to 25 mm. If individuals settled 25 mm away from the centre of the remnant adult group then they would be counted in the 15 - 30 mm annulus. Numbers of settlers were converted into densities to give a continuous variable and all data were checked for homogeneity of variances with a Bartlett's test in Minitab. A 2-way ANOVA was adequate for analysing the *S. balanoides* 1998 results as there were only 2 factors 'recruitment' and 'treatment'. The linear model used for *S. balanoides* 1999 was:

$$density = recruitment + location'(\,recruitment\,) + trt + recruitment \times trt + location'(\,recruitment\,) \times trt$$

where *recruitment* is the recruitment level of barnacles (high or low), *trt* is the number of adults left at the centre of the cleared patches, *location* is the location of the field site along the south coast. 'Recruitment' and 'trt' were both treated as fixed effects in the analysis, whereas 'location' was treated as a random factor. An expansion of this model was required for the *C. montagui* data due to the extra factor 'area' included in the experimental design.

$$density = location + recruitment + area'(recruitment) + trt + location \times recruitment + location \times area'(recruitment) + location \times trt + recruitment \times trt + area'(recruitment) \times trt$$

where *background, trt* and *location* are as before, *area* refers to the areas within the different recruitment levels where the experiments were carried out e.g. Area 1 or Area 2 (see Figure 3.2). All factors were treated as being fixed except 'area' which was treated as a random factor.

The relationship between the number of adults within a treatment and the number of settlers in the 15 - 30 mm annulus within a single location was analysed further using Spearman rank correlation coefficient.

3.3.4.1.2 Preferential settlement model

Not only can density comparisons be made between treatments, but also between alternative theoretical settlement patterns such as random settlement and central preference settlement. These comparisons were used to help determine the extent of clumping.

To calculate the barnacle densities obtained from a random settlement we had to find the relationship between the diameter of the quadrat, the total number of settlers and the density of barnacles per concentric ring. The expected patterns under random settlement were calculated by using a set of derived equations, outlined and explained below.

The number of barnacles, N_r, in a given annulus of outer radius r is given by:

$$N_r = D_r - D_{r-w} \tag{3. 1}$$

where D_r is the number in a disc of radius r and w is the width of the annulus. For a uniform density across all annuli, the numbers in any given disc will be a constant proportion of the area of the disc:

$$D_r = constant \times \pi r^2 \quad \text{or} \quad D_r = c \cdot r^2 \tag{3. 2}$$

where c is a constant. If the densities are higher in discs of smaller radius, then the power function in eqn 3.2 will take values < 2. The equation can therefore be generalised to:

$$D_r = c \cdot r^f \tag{3. 3}$$

where for example $f = 1$ gives D_r increasing linearly with density, and therefore N_r is constant for all r (yielding higher densities in discs with smaller r). Putting eqn 3.3 into eqn 3.1 gives the formula:

$$N_r = c \cdot r^f - c \cdot (r - w)^f \tag{3. 4}$$

where $c = T / r^f$, where T = total number of observed barnacles settling in the treatment patch of radius r. This added dimension to the model therefore allowed us to compare the empirical data to a random settlement, and to settlement for various degrees of attraction ($f < 2$) and repulsion ($f > 2$) by the central adult group.

A 2-way ANOVA was also used to compare the expected results generated from the random settlement model ($f = 2$) to the experimental results in the 15 - 30 mm annulus at each individual location used in 1999. All data were checked for homogeneity of variances with a Bartlett's test in Minitab.

3.3.4.2 Identification of general spatial patterns between cohort members

Not only are settling barnacle attracted by adult conspecifics, but they can also be attracted by members of the same cohort (Wethey, 1984b). As the photographs used for analysis were taken at the end of the settlement season, they will have included individuals that had settled at the beginning of the season and others that had of settled at the end. The individuals that settled towards the beginning of the season could be anything up to 4 months old at the end of the settlement season, and therefore may act as attractants to individuals settling late in the season. There is also evidence that a cyprid coming into contact with another cyprid can cue it to settle (Satchell & Farrell, 1993). To determine the effect of intra-cohort attractiveness we tested for spatial patterns in the treatment patches at all the locations. We were also able to analyse spatial patterns of individuals that were all at the cyprid/spat stage by looking at positions of individuals on the settlement plates deployed during the 1999 *S. balanoides* season at the locations around the Isle of Wight.

There are two separate approaches to measure the departure of a population from a random distribution. The first is a random technique, though this is not a truly random method (Pielou, 1969). In this method a point is selected at random then concentric rings of a known dimension are searched around the individual until its nearest neighbour is found, and the distance recorded. The other method takes each individual in turn and measures the distance to its nearest neighbour. Clark & Evans (1954) were the first to suggest such a plotless method for analysing pattern. In their method distances are measured for all individuals in the study patch, and thus there are no problems with random sampling (Krebs, 1989). It also allows for direct comparisons to be made between populations (Clark & Evans, 1954). The Clark & Evans method is consequently the technique we have employed to assess spatial patterns in the two species of barnacle.

3.3.4.2.1 The Clark and Evans Nearest Neighbour analysis

Once the nearest neighbour distance has been calculated for each individual barnacle, the mean distance to the nearest neighbour needs to be calculated:

$$\bar{r}_{obs} = \frac{(\Sigma r_i)}{n} \qquad (3.5)$$

where r_i, is the measured distance to the nearest neighbour for a single individual i, and n is the number of individuals in the treatment. The expected distance to the nearest neighbour (if the population was distributed randomly) can be shown to have a value equal to:

$$\bar{r}_{\exp} = \frac{1}{2\sqrt{\rho}} \qquad (3.\ 6)$$

where ρ, is the density of the organism in the treatment patch (see Clark & Evans, 1954, Appendix 1 for a full explanation on how this formula is derived from a Poisson distribution). The deviation of the observed value from that of the expected random value is given in the form of a ratio which is the index of aggregation, R:

$$R = \frac{\bar{r}_{obs}}{\bar{r}_{\exp}} \qquad (3.\ 7)$$

An index of aggregation $R = 1$ signifies that the spatial pattern is random. A clumped distribution is indicated by values of $R < 1$. A uniform pattern is given by $R > 1$. If maximum spacing exists, individuals will be distributed in an even hexagon pattern, with every individual equidistant from six other individuals (Clark & Evans, 1954). In such a spatial distribution the mean distance to the nearest neighbour will be maximised, when this is the case $R = 2.1491$, therefore R is limited to a range between 0 and 2.1491.

The significance of deviations from $R = 1$ depends on the number of individuals and their density, which can be used to calculate the standard error, S_r, of r_{exp}:

$$S_r = \frac{0.26136}{\sqrt{n \cdot \rho}} \qquad (3.\ 8)$$

The standard normal deviate is then given by:

$$z = \frac{\bar{r}_{obs} - \bar{r}_{exp}}{S_r} \tag{3. 9}$$

The standard normal deviate is a measure of the number of standard deviations the expected value lies away from the observed on a normal distribution around the parametric mean of zero difference. Consequently, if $z > 1.96$ then the probability is <0.05, in which case the observed index of aggregation reflects a real difference from randomness.

The Clark & Evans test in its original form is unbiased only when a boundary strip is included in the study (Ripley, 1985; Krebs, 1989). A boundary strip is a buffer zone around the study patch. If individuals in the buffer zone are the nearest neighbours to the individuals in the study patch then these results are used. If the Clark & Evans test is used without a boundary strip then organisms around the edge of the study patch will tend to have larger nearest neighbour distances compared to those closer to the middle. Sinclair (1985) has shown that this bias is in the favour of regular patterns. If no boundary strip is used then the Donnelly (1978) modification of the Clark & Evans test should be implemented. As we wanted to utilise the whole of the cleared treatment patches, we did not allow for a boundary strip, and results were therefore adjusted using the Donnelly modification.

The Donnelly modification of the Clark & Evans test calculates a corrected nearest neighbour distance, $\bar{r}_{cor}$:

$$\bar{r}_{cor} = \bar{r}_{exp} + (0.051 + \frac{0.041}{\sqrt{n}}) \cdot (L \cdot N) \tag{3. 10}$$

where L is the total edge length of the study patch. The standard error is then given by:

$$S_r = \frac{\sqrt{0.07 \cdot A + 0.037 \cdot L\sqrt{A/n}}}{n} \tag{3.11}$$

where A is the area of the study patch. This standard error value is then used in the Clark & Evans standard normal deviate equation (3.9) to give a z-value, which is analysed in the same way. Donnelly's correction should also be employed when individual density is defined in terms of the sample patch (Davis & Campbell, 1996).

Further analysis of nearest neighbour R-values was performed using an ANOVA after a Bartlett's test was used to determine that variances were homogeneous. The ANOVA was carried out to determine the effect treatment and background density had on the R-values obtained from the Clark & Evans test with the Donnelly's correction. The models used to perform the ANOVAs were the same as those described in Section 3.3.4.1.

3.3.5 Barnacle movement

Crisp (1960) found that certain barnacle species have limited mobility when subject to lateral pressure. He showed that *S. balanoides* individuals could move up to 24 mm in the six months following attachment. If the barnacles in this study moved then this may alter the spatial patterns of the observed populations. As individuals grow Crisp (1960) showed that movement is possible on the edges of barnacle clumps. If all individuals on the edge of barnacle clump move then eventually the spatial arrangement will shift from a clumped to a uniform distribution.

To assess barnacle movement treatment patch photos taken during the beginning of the settlement season were analysed and compared to those taken towards the end of the study. The same individuals were identified and numbered in both the early and late photographs. At least 50 individuals were marked in each set of photos. Five recognisable reference points were also marked in both photos (see Appendix 3.2). Using the 'Barnacle Location' program the position of the centre of each barnacles was calculated in each photo along with the reference points. The position of the barnacle was compared to the reference points to see if there was any temporal movement. This procedure was carried out for 8 treatment patches.

3.3.6 Simulating a barnacle invading front

The requirement for barnacles to settle near conspecifics in order to reproduce is balanced against some degree of intraspecific territoriality. A simulation model was developed that combined both of these biological influences, in order to determine their effects on the spatial patterns exhibited by the barnacles in our study. The simulation was only compared to the empirical data obtained from the settlement seasons on *C. montagui* and *S. balanoides* in 1999, as the shape and area of the cleared patches were constant in both studies.

The model was developed using a Microsoft Excel macro, which simulated random barnacles settling into a patch of the same size as actual patches. Whether settlement took place depended upon certain settlement rules as outlined in Figure 3.3. The simulation model required four inputs: the total number of settlers, the number of adults, the maximum inter-individual distance (relating to penis length), and the minimum inter-individual distance (relating to territorial distance). If a barnacle landed within the maximum distance from a conspecific but further than the minimum distance then it would settle, if not settlement was abandoned. Using the total actual number of settlers for each replicate we were able to simulate settlement into each of the treatments. Simulated barnacle numbers in the inner most annulus were adjusted to allow for variations in available free-space between treatments using the same method implemented with the empirical data. Individual barnacles settled one at a time; as a result a degree of temporal analysis was introduced into the model.

Once the model had been developed simulations were run and parameter values tested using maximum likelihood techniques. Maximum likelihood estimates parameter values that maximise the likelihood of a sample, or equally minimise the negative log-likelihood function. Using maximum likelihood techniques it is possible to find parameter values of a given model that provide the best fit to the observed data (Pascual & Kareiva, 1996; Hilborn & Mangel, 1997). The parameter values for which the likelihood is the highest are the maximum likelihood estimates or MLE (Edwards, 1972).

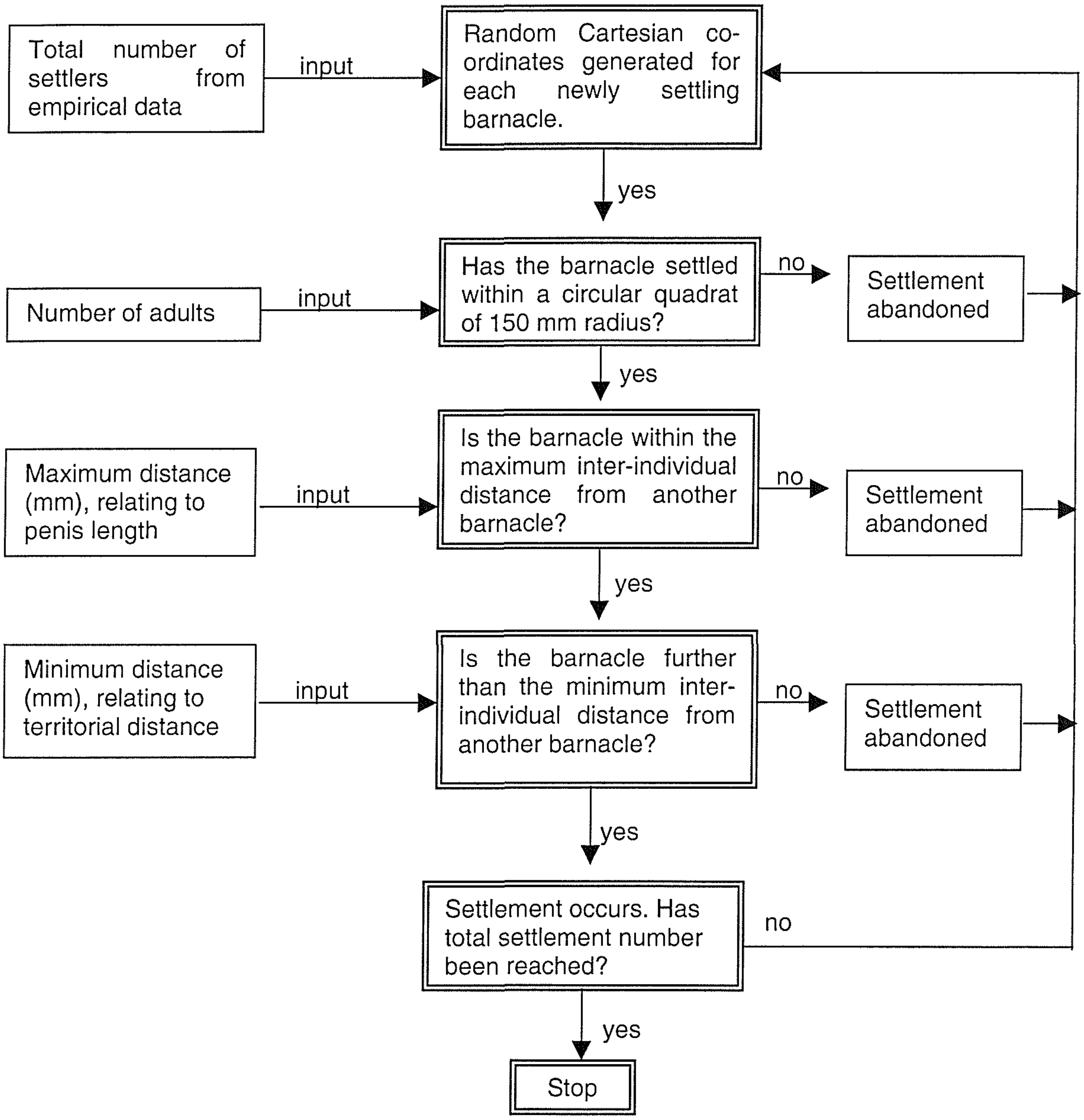


Figure 3.3 The rubric utilised in the barnacle simulation model. Input values include total number of settling barnacles, the treatment number, maximum inter-individual distance (penis length) and minimum inter-individuals distance (territorial distance).

A binomial maximum likelihood estimation was used to obtain minimum (accurate to 0.1 mm) and maximum (accurate to 1.0 mm) inter-individual parameter estimates that gave the best fit between our experimental data and the simulated data.

The technique applied was adapted from the binomial Ln-likelihood function used by Doncaster & Gustafsson (1999). Doncaster & Gustafsson (1999) utilised the technique to compare unoccupied and occupied nest boxes to a resource exploitation model. Similarly we have used the model to compare the actual experimentally derived occupied treatment patch area to the occupied area generated by the settlement simulation model.

To calculate the total area occupied by settling barnacles the average area of a barnacle in each of the photos had to be calculated. The amount of unoccupied area was calculated in each of the treatment patches and in each of the 10 concentric annuli. The mean occupied/unoccupied area for the 3 same treatments at the same location were then compared to the model. The Ln likelihood was calculated by summing terms from the binomial distribution:

$$\text{Ln - likelihood} = \sum_{i=1}^{10} \ln\left[\left(\frac{K_i}{K_i - N_i^*}\right) \cdot {p_i}^{K_i - N_i^*} \cdot (1 - p_i)^{N_i^*}\right] \tag{3.12}$$

where p_i is the simulation estimate of the unoccupied proportion of each of the annuli. The amount of occupied space from the actual results is given by N_i. The total amount of available space is equal to K_i, of which K_i-N_i is unoccupied.

The full simulation model with both parameters, the maximum distance from a conspecific and minimum distance to a conspecific, were then tested against nested models with fewer parameters. That is, sets of simulation data were produced for models using only the maximum parameter and others were simulated using neither parameter, which therefore simulated unrestricted random settlement. These three types of model were set up as competing models (*max* and *min* against *max only* against *random*).

A likelihood ratio test can be used to compare nested models with unequal numbers of parameters (see Hilborn & Mangel, 1997 for a full description of this test). The likelihood ratio test produces chi-squared values, which are equal to twice the difference in the Ln-likelihoods between the two models under comparison. The degrees of freedom are equal to the difference between the models in the number of parameters. A significant *p* value indicates that results obtained from the model with the greater number of parameters fit the empirical data more closely.

Since the treatment patches comprised of cleared areas within natural barnacle populations the area immediately outside the patches often contained adult conspecifics. By referring to the digital photos, we were able to ascertain the number of peripheral adult barnacles in the 150 - 165 mm annulus around the treatment patch. The simulation model was then adapted so that the actual number of adults observed in the 150 - 165 mm annulus could also be simulated to occur outside the treatment patches. Settlers in the simulation model reacted to these peripheral adults in the same way as they did to the remnant central adults and other cohort members. Simulations were run as before and the resulting settlement patterns with peripheral adults analysed and compared to the original model, and the actual observed data.

3.4 RESULTS

3.4.1 Densities of settlers around the remnant adult group

There was considerable variation in settlement numbers of *Semibalanus balanoides* and *Chthamalus montagui* at all shores in all settlement seasons. A consistent general pattern of settlement was apparent, however, in annuli radiating from the centre of the treatment patch. Barnacle numbers tended to increase with the radius of the annulus, reflecting the increasing area of each annulus further from the centre (Figure 3.4 to Figure 3.7, graphs are presented in order of settlement season to allow local comparisons to be made; this trend is also shown in Figure 3.12 to Figure 3.19). The outer-most annuli were characteristically under-populated, as detailed below.

3.4.1.1 S. balanoides 1998

The settlement pattern for the high-density *S. balanoides* in 1998 took a humped form with the apex of the hump towards the outer edge of the patch as shown in Figure 3.4. Comparison of the observed settlement and the random model (eqn 3.4, $f = 2$) showed that a treatment of central adults resulted in an increase in the number of settlers in the first two annuli (0 - 15 and 15 - 30 mm) when compared to expected random settlement. The preferential central settlement model fitted the empirical data more closely than the random settlement model for treatments with central adults. The 95% confidence intervals for the replicates encompassed the preferential central settlement model for 35 of the 49 annuli (i.e. 7 annuli in each of the 7 treatments) compared to 23 for the random settlement model.

Results from the low-recruitment shore were not so well defined (Figure 3.5). A humped pattern was only visible in treatments with 4+ adults. Neither the random nor the preferential settlement model fitted the 0, 1 or 2 adult treatments convincingly.

The number of settlers in the 15 - 30 mm annulus was found to vary significantly with treatment, but also with recruitment level and with the interaction between treatment and recruitment level, as shown in Table 3.1. Treatments with larger remnant groups had higher settlement as did shores with higher recruitment levels, but the positive effect of treatment size was most pronounced at the high-recruitment shore.

Source of Variation	**df**	**MS**	***F***	***p***
Recruitment	1	0.001390	92.63	**<0.0001**
Trt	6	0.000055	3.69	**<0.01**
Recruitment × trt	6	0.000054	3.55	**<0.01**
Error	28	0.000015		

Table 3.1 ANOVA for the density of *Semibalanus balanoides* settlers in the second innermost (15 - 30 mm) annulus in 1998. 'Recruitment' (recruitment level high or low), and 'Treatment' (number of remnant adult barnacles) were treated as fixed factors.

3.4.1.2 *C. montagui 1998*

The majority of *C. montagui* graphs took a humped form with the apex of the hump towards the outer edge of the patch. Figure 3.6 shows the typical 0 adult treatments which reflect the typical pattern (also shown for other treatments in Figure 3.12 to Figure 3.15). In some cases the apex was so far towards the outside of the treatment patch that the graph almost appeared linear (e.g. Sidmouth Area 1 with 8 adults; Portland Area 2 with 32 adults), indicating random settlement. Due to the large 95% confidence intervals, the random settlement and the preferential settlement models could not be confidently distinguished visually for many of the treatments.

The density of settlers into the 15 - 30 mm annulus varied between the two locations (Table 3.2), with generally a greater density at Sidmouth (significant location effect). Settlement densities were not consistent for all areas within a location, the areas with high-recruitment levels having greater settlement than those with low-recruitment particularly at Sidmouth (significant interaction of area' (recruitment) with location). No other factors or interactions contributed significantly to explaining variation in settlement numbers. The absence of a treatment effect indicated that the number of adult *C. montagui* at the centre of the cleared treatment patches did not alter the density of settlers into the 15 - 30 mm annulus.

Source of Variation	**Df**	**MS**	***F***	***p***
Location	1,2	0.16418	30.84	**<0.05**
Recruitment	1,2	0.05715	2.40	0.26 *(ns)*
Area'(recruitment)	2,2	0.02380	4.84	0.20 *(ns)*
Trt	3,6	0.00301	3.11	0.11 *(ns)*
Location × recruitment	1,2	0.01423	2.67	0.24 *(ns)*
Area'(recruitment) × location	2,73	0.00532	3.90	**<0.05**
Location × trt	3,73	0.00096	0.70	0.55 *(ns)*
Recruitment × trt	3,73	0.00162	1.68	0.27 *(ns)*
Area'(recruitment) × trt	6,73	0.00097	0.71	0.65 *(ns)*
Error	73	0.00136		

Table 3.2 GLM ANOVA for the density of *Chthamalus montagui* settlers in the second inner most (15 - 30 mm) annulus in 1998. 'Location' (Portland or Sidmouth) 'Recruitment' (recruitment level, high or low), 'Treatment' (number of adult barnacles) were treated as fixed factors, *ns* = not significant.

3.4.1.3 S. balanoides 1999

The settlement pattern in concentric annuli was similar for three of the locations (Cowes, Seaview and Totland) used in the 1999 analysis. Figure 3.7 shows 0 adult treatments, which reflect the typical pattern (also shown for other treatments in Figure 3.16 to Figure 3.19). Ventnor, however, showed large variations in data with the linear random settlement model fitting the observed data more closely than the preferential central settlement model.

The settlement pattern at the three similar locations (Cowes, Seaview and Totland) showed that settlement in the 0 adult treatment was best represented by the random settlement model. Random settlement was the best fitting model for the inner most annulus (0 - 15 mm) in all patches, except for the 16 adult treatment at Totland. This pattern was not however, reflected in the next radiating annulus (15 - 30 mm).

The number of barnacles settling in the 15 - 30 mm annulus at the four locations was analysed against recruitment level, location and treatment using a 3 factor ANOVA (Table 3.3), to give a similar comparison to the analysis carried out in the other studies. There were no significant differences ($p > 0.05$) in the density of settlers in the 15 - 30 mm annulus at high- or low-recruitment levels (although this was tested with only 2 error d.f.), or at different locations. Treatments with more adults attracted more settlers at Cowes, Totland and Seaview (the treatment by location'(recruitment) interaction was significant at the $p < 0.001$ level).

Source of Variation	**Df**	**MS**	***F***	***p***
Recruitment	1,2	0.001153	16.83	0.06 *(ns)*
Trt	5,10	0.000426	2.25	0.13 *(ns)*
Location'(recruitment)	2,10	0.000069	0.36	0.71 *(ns)*
Recruitment × trt	5,10	0.000075	0.39	0.84 *(ns)*
Trt × location'(recruitment)	10,48	0.000019	4.2	**<0.0001**
Error	48	0.000005		

Table 3.3 GLM ANOVA for the density of 1999 *Semibalanus balanoides* settlers in the second most inner annulus 15 - 30 mm in 1999. 'Treatment' (number of adult barnacles), 'Recruitment' (recruitment level, high or low), were treated as fixed factors, *ns* = not significant.

ANOVAs were carried out to compare actual densities in the 15 - 30 mm annulus (observed from the experimental data) to those generated by the random settlement model at the separate locations. It was decided to analyse each of the locations separately as graphical comparisons suggested a deviation from random in all locations except Ventnor. Indeed, the 15 - 30 mm annulus do contain more settlers than expected from the random settlement model at all locations except Ventnor (Table 3.4). However, treatment was found only to have a significant effect on the density of settlers into the 15 - 30 mm annulus at Totland and Seaview ($p < 0.0001$).

Settlement numbers in the next annulus (30 - 45 mm) were more comparable to the random settlement model in 14 of the 16 treatments. Treatment patches also showed settlement numbers in general that were greater than the background population observed in the 150 - 165 mm annulus (see Appendix 3.3).

	Cowes (high-recruitment)				**Seaview (high-recruitment)**			
Source of variation	**df**	**MS**	***F***	***P***	**df**	**MS**	***F***	***p***
Type	1	0.00131	4.39	**<0.05**	1	0.00727	10.02	**<0.001**
Trt	5	0.00064	2.13	0.1 *(ns)*	5	0.01395	19.24	**<0.0001**
Type × trt	5	0.00020	0.67	0.65 *(ns)*	5	0.00117	1.64	0.19 *(ns)*
Error	24	0.00030			24	0.00073		

	Totland (low-recruitment)				**Ventnor (low-recruitment)**			
Source of variation	**df**	**MS**	***F***	***P***	**df**	**MS**	***F***	***p***
Type	1	0.00865	20.56	**<0.0001**	1	0.00084	1.44	0.24 (*ns*)
Trt	5	0.00381	9.06	**<0.0001**	5	0.00099	1.69	0.18 (*ns*)
Type × trt	5	0.00041	0.98	0.45 (*ns*)	5	0.00013	0.23	0.95 (*ns*)
Error	24	0.00042			24	0.00058		

Table 3.4 Two-way ANOVAs comparing observed (experimental) and expected (random settlement) densities of *Semibalanus balanoides* settlers in the second most inner annulus 15 - 30 mm at each location used during 1999. 'Type' (observed or expected), and 'Trt' (number of adult barnacles) were treated as fixed factors. Densities are square root transformed, *ns* = not significant.

3.4.1.4 Overall comparison between recruitment level, treatment and the number of settlers in the 15 - 30 mm annulus

The relationship between recruitment level, treatment and the number of settlers in the 15 - 30 mm annulus was explored using a Spearman rank coefficient (Figure 3.8). The locations displayed in Figure 3.8 are ranked from left to right according to the overall settlement density in the 32 adult treatment patch. This allowed us to assess the treatment effect in relation to the density of settlers.

Figure 3.8 shows the range of total settlement in the 15 -30 mm annulus was greater for *C. montagui* than for *S. balanoides*. For both species, however, as the total settlement number decreased (from left to right) so too did the number of settlers found in the 15 -

30 mm annulus. This was reflected by a steep to shallow progression in regression slopes from high to low settlement densities for both species.

At all locations except Sidmouth high 2 there was a positive regression of settlement with number of remnant adults. The negative regression slope at Sidmouth high 2 was not significantly different from zero.

Although positive regressions between treatment and settlement numbers were identified for both species at all other locations the significance of the regressions and the relationship with the overall settlement density seemed to vary between species. For *S. balanoides* a significant regression was only identified at the highest of settlement densities, Seaview, and at one of the low-recruitment locations, Totland. Settlement was ranked according to the overall density of settlers in the thirty-two adult treatments. However, the 15 - 30 mm annulus in the sixteen adult treatments had more settlers than the 15 - 30 mm annulus in the thirty-two adult treatments in 9 of the 14 individual cases. If settlement were to be assessed in relation to the number of settlers in the 15 - 30 mm annulus occurring in the sixteen adult treatment Totland would be ranked second behind Seaview. Using this ranking method, the two highest settlement locations would exhibit significant positive regressions between treatment and settlement numbers in the 15 -30 mm annulus. Similarly, a significant treatment effect was also identified only at Seaview and Totland (Table 3.4).

The significance in regressions between the number of settlers in the 15 -30 mm annulus and the treatment effect over differing settlement densities was reversed for *C. montagui* when compared to the *S. balanoides* results. Again at only two of locations were the regressions identified as being significant. However, both of these areas (Portland High 2 and Portland Low 2) were identified as having the least overall *C. montagui* settlement.

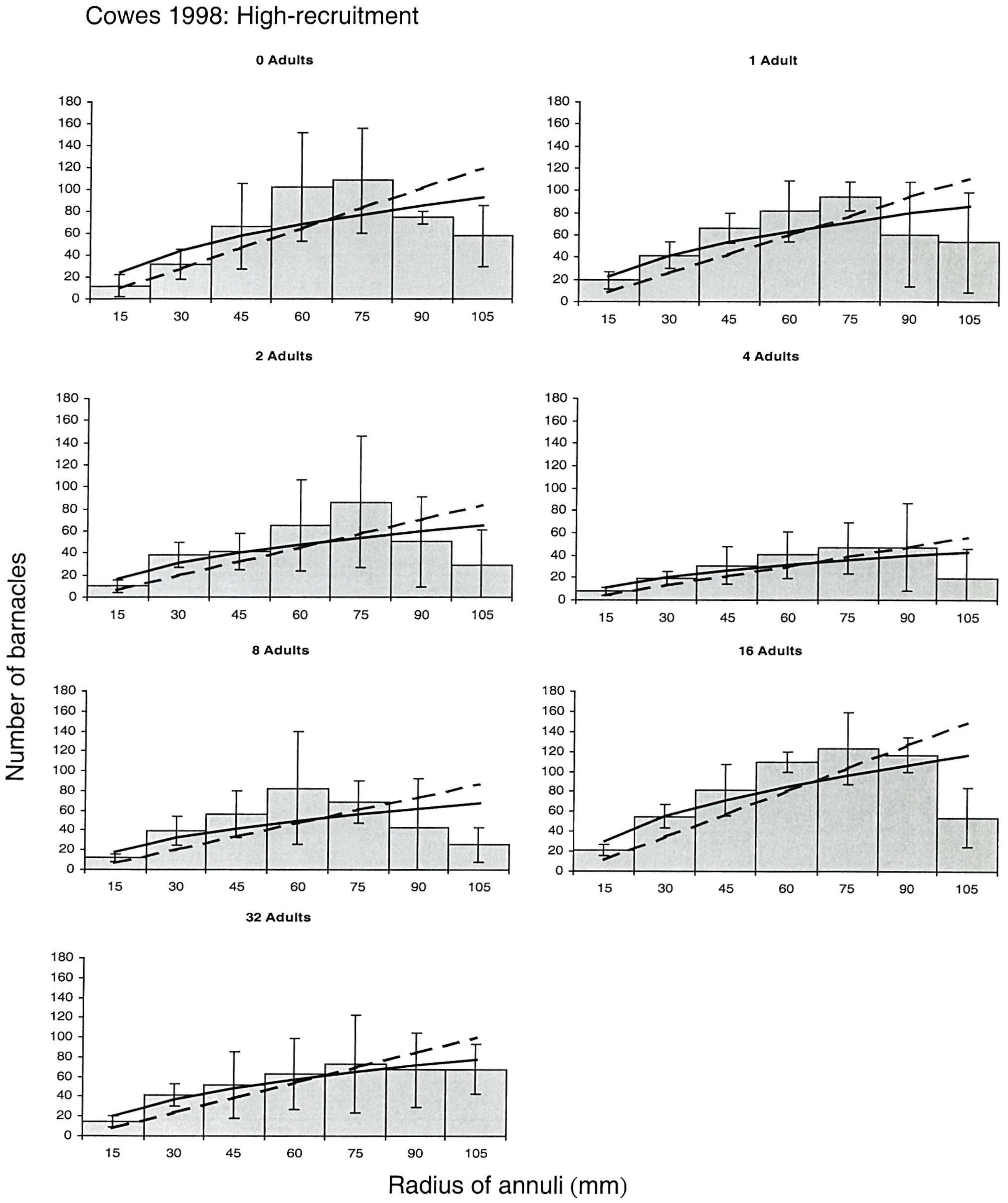


Figure 3.4. *S. balanoides* 1998 Cowes high-recruitment. The observed number of barnacles in annuli of increasing radius, compared to an expected uniform random settlement given by $f = 2$ in eqn 3.4 (dashed line), and an expected settlement for a density of individuals that increases towards the centre of the patch, given by $f = 1.5$, (continuous line). Error bars shown represent 95% confidence intervals from 3 replicates.

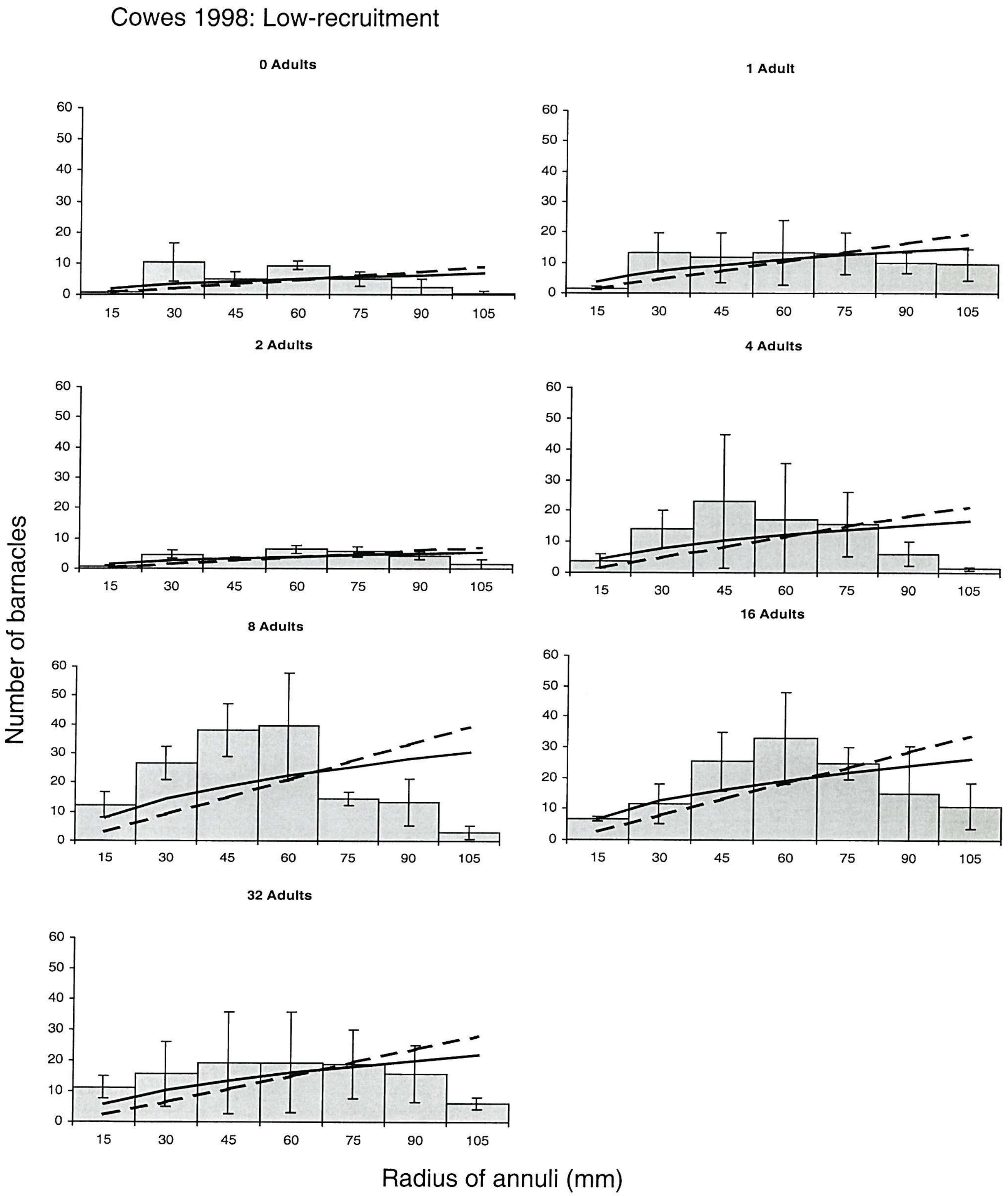


Figure 3.5. *S. balanoides* 1998 Cowes low-recruitment (see Figure 3.4 legend for meaning of terms)

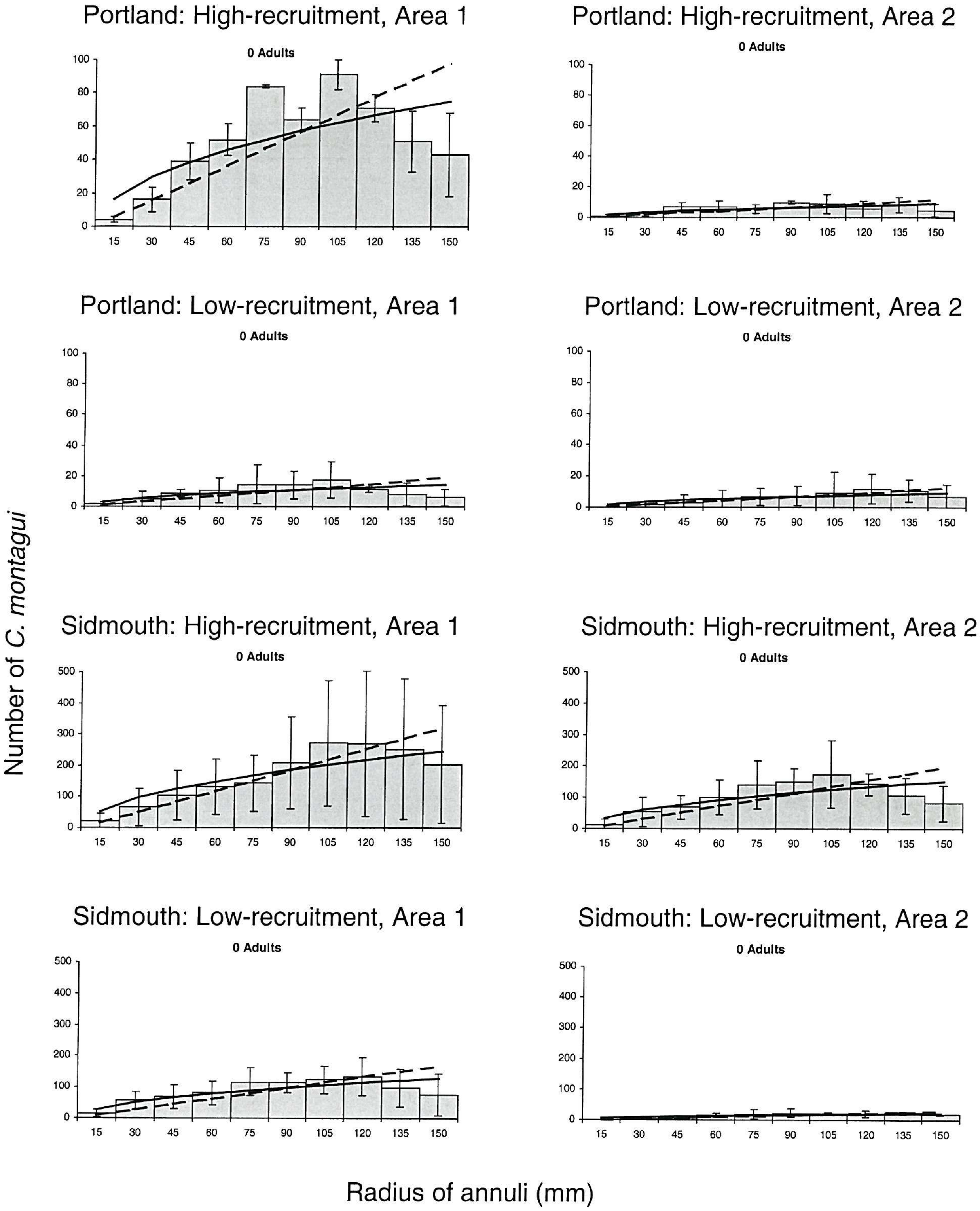


Figure 3.6 *C. montagui* 1998 0 adult treatment patches at Portland and Sidmouth (see Figure 3.4 legend for meaning of terms).

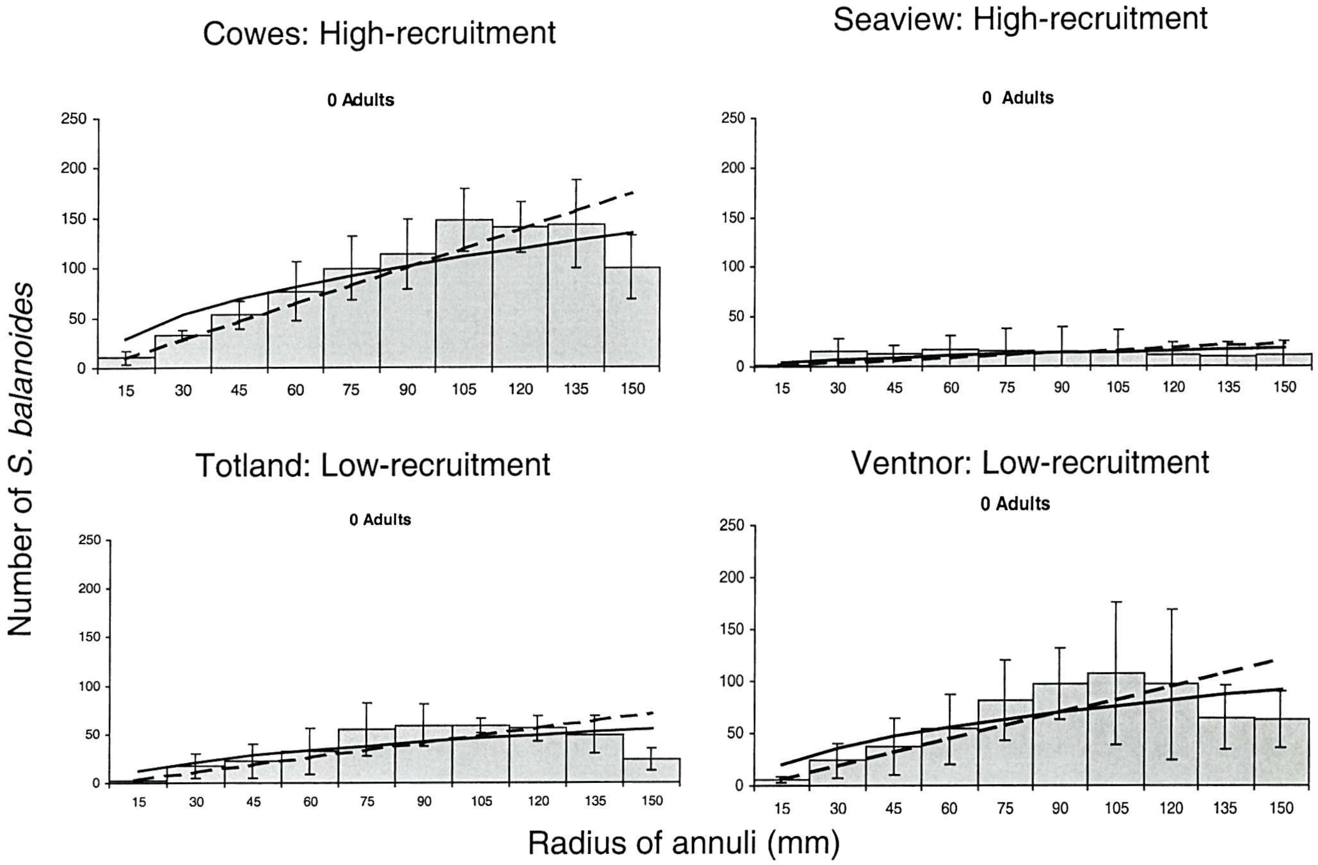


Figure 3.7 *S. balanoides* 1999, 0 adult treatment patches at the four locations around the Isle of Wight (see Figure 3.4 legend for meaning of terms).

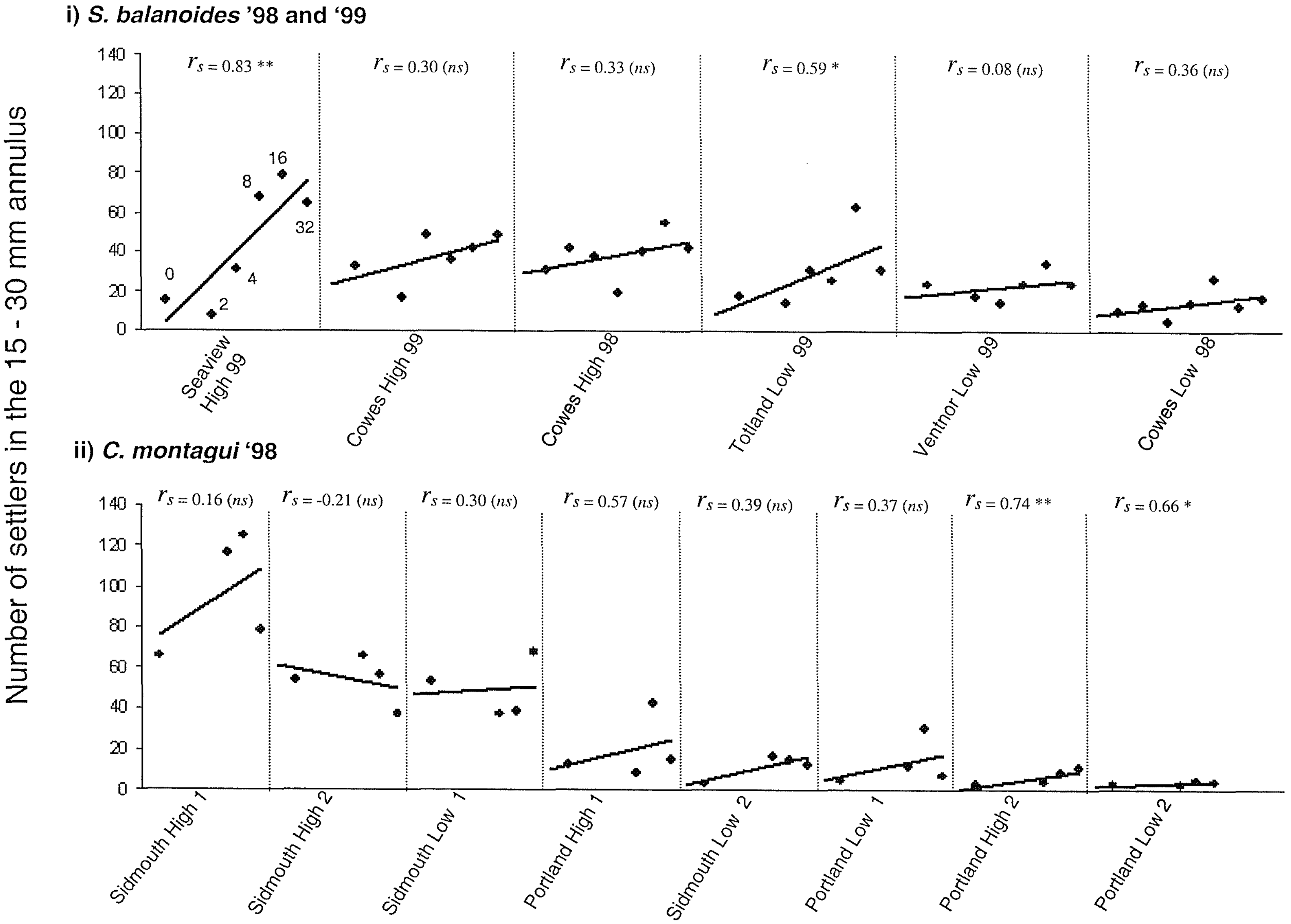


Figure 3.8 The mean final number of i) *Semibalanus balanoides* and ii) *Chthamalus montagui* settlers in each 15 - 30 mm annuli in each treatment at each location taken from 3 replicates. Locations are displayed from highest settlement on the left to lowest on the right (where settlement is indexed by the density of barnacles in the thirty-two adult treatments as described in Chapter 4). Within locations, treatments are displayed in increasing order from left to right as shown in i) Seaview (0, 2, 4, 8, 16, 32 for *S. balanoides*, with an additional 1 adult treatment in 1998, and 0, 8, 16, 32 for *C. montagui*). The Spearman rank correlation coefficients are shown for each of the plots, using the data from all 3 replicates, * = $p < 0.05$, ** $p < 0.01$, (*ns*) = not significant.

3.4.2 Nearest neighbour analysis

Using the adjusted Clarke & Evans test barnacle spatial patterns were shown to vary markedly both within locations and between locations as shown in Figure 3.9. Using the total density of settlers in the thirty-two adult treatment as an index of settlement there appeared to be no direct relationship between settlement density and the degree of aggregation for either *S. balanoides* or *C. montagui*. Consequently, each study is examined separately allowing local comparisons to be made.

In 1998 settling *S. balanoides* at Cowes displayed a mixture of uniform ($R > 1$), random ($R = 1$) and clumped ($R < 1$) spatial patterns according to treatment and recruitment level (Figure 3.9). However, a significantly uniform spatial pattern was only recorded at the high-recruitment shore in the two treatments with the most adult barnacles (16 and 32 adults) along with the totally cleared treatment patch (0 adults). None of the remaining spatial patterns differed from random at the high-recruitment shore. Uniform distribution was not observed at the low-recruitment shore with 4 of the 7 treatments displaying random settlement, and the other 3 treatments having aggregated settlement. Analysis of variance revealed that recruitment did influence spatial pattern, but the spatial pattern due to the treatment effect was not dependent on recruitment levels (Table 3.5).

C. montagui displayed strong aggregated settlement in all treatments at all densities at both Portland and Sidmouth. Analysis of variance revealed no significant differences between the R-values at each location, recruitment level, area or between treatments (Table 3.6).

Results from the *S. balanoides* 1999 study showed once more strong evidence for aggregation. Clumping was observed in 23 of the 24 treatment interactions with only 1 of the 24 showing random settlement. The only location where random settlement was observed was at Cowes (high-recruitment) in the 16 adult treatment. R-values appeared to be smaller (and therefore barnacles were more clumped) at the low-recruitment locations (Totland and Ventnor) than at the high-recruitment locations (Cowes and

Seaview) in 1999. An analysis of variance revealed a significant difference in the *R*-values between locations, with Cowes having the highest and Totland the lowest, but not between recruitment levels (Table 3.7). The effect of the treatment was consistent between locations with the same recruitment levels (i.e. Cowes and Seaview, Totland and Ventnor) but not between locations with different recruitment levels.

Source of Variation	**Df**	**MS**	*F*	*p*
Recruitment	1	0.2003	5.93	**<0.05**
Trt	6	0.0192	0.57	0.75 *(ns)*
Trt × recruitment	6	0.0260	0.77	0.60 *(ns)*
Error	28	0.0337		

Table 3.5 Analysis of variance for factors influencing spatial patterns (*R*-value) in *Semibalanus balanoides* during 1998. 'Recruitment' (recruitment level high or low), and 'Trt' (number of adults left at the centre of the treatment patch) were treated as fixed factors, *ns* = not significant.

Source of Variation	**Df**	**MS**	*F*	*p*
Location	1,2	0.4366	3.49	0.20 *(ns)*
Density	1,2	1.0596	0.96	0.43 *(ns)*
Area'(recruitment)	2,2	0.1102	2.27	0.27 *(ns)*
Trt	3,6	0.0044	0.21	0.89 *(ns)*
Location × recruitment	1,2	0.0440	1.14	0.40 *(ns)*
Area'(recruitment) × location	2,73	0.0412	3.09	0.06 *(ns)*
Location × trt	3,73	0.0049	0.37	0.78 *(ns)*
Recruitment × trt	3,73	0.0133	1.00	0.45 *(ns)*
Area'(recruitment) × trt	6,73	0.0207	1.55	0.17 *(ns)*
Error	73	0.0134		

Table 3.6 Analysis of variance for factors influencing spatial patterns (*R*-value) in *Chthamalus montagui* in 1998. 'Location' (Portland or Sidmouth), 'Recruitment' (Recruitment level high or low), and 'Trt' (number of adults left at the centre of the treatment patch) were treated as fixed factors. 'Area' (High 1/2 Low 1/2) was treated as a random factor, *ns* = not significant.

Source of Variation	**Df**	**MS**	*F*	*p*
Recruitment	1,2	0.2960	1.75	0.32
Location'(recruitment)	2,10	0.1688	5.42	**<0.05**
Trt	5,10	0.0154	0.49	0.77 *(ns)*
Trt × recruitment	5,10	0.0287	0.92	0.51 *(ns)*
Trt × location'(recruitment)	10,48	0.0311	2.55	**<0.05**
Error	48	0.0122		

Table 3.7 Analysis of variance for factors influencing spatial patterns (*R*-value) in *Semibalanus balanoides* during 1999. 'Recruitment' (recruitment level, high or low), and 'Trt' (number of adults left at the centre of the treatment patch) were treated as fixed factors. 'Location' (field site around the Isle of Wight) was treated as a random factor, *ns* = not significant.

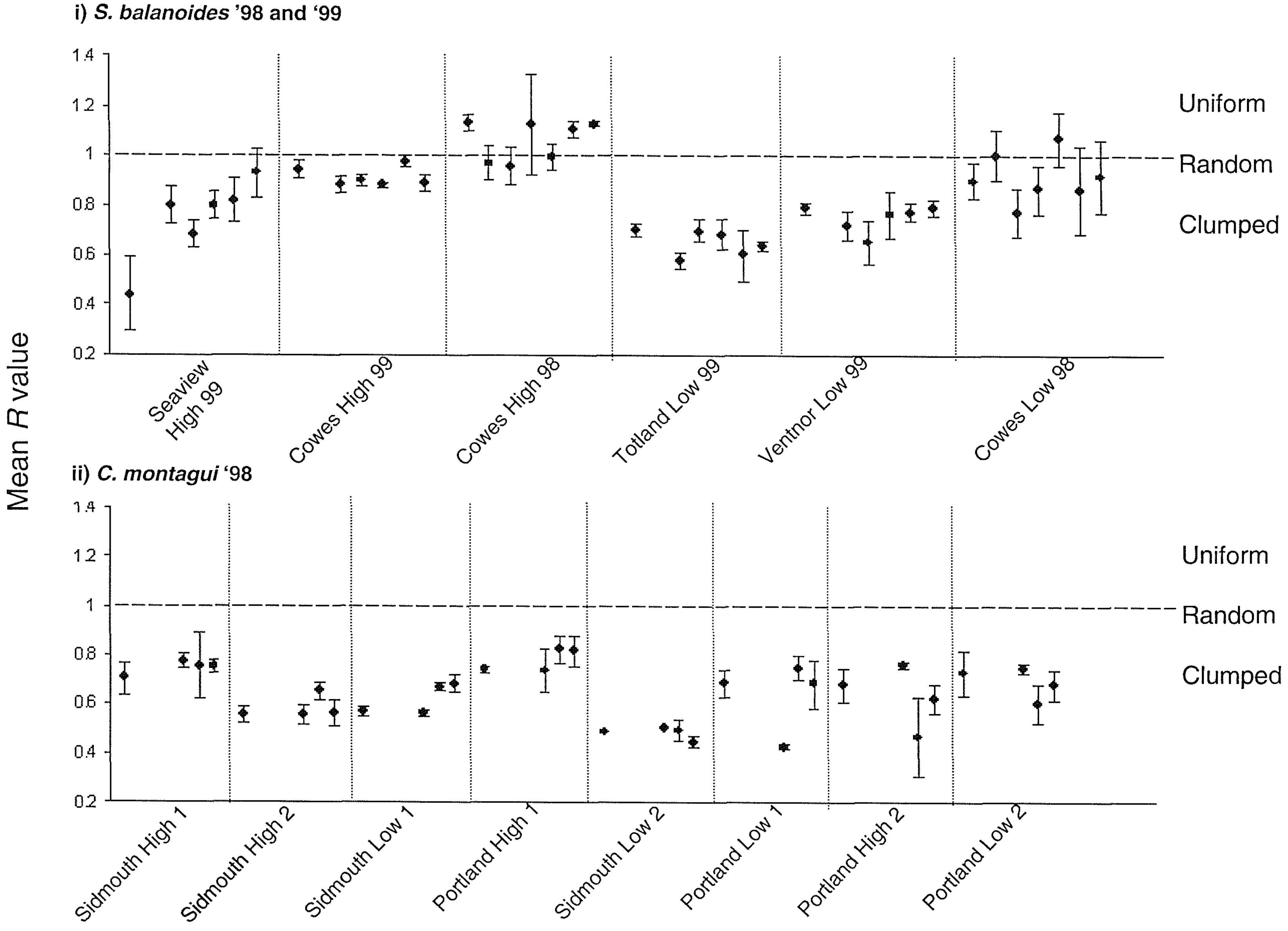


Figure 3.9 Spatial patterns exhibited by i) *S. balanoides* and ii) *C. montagui* displayed as the mean taken from 3 replicates. Locations are displayed from from highest settlement on the left to lowest on the right (where settlement is indexed by the density of barnacles in the thirty-two adult treatments as described in Chapter 4). Within locations, treatments are displayed in increasing order from left to right (0, 2, 4, 8, 16, 32 for *S. balanoides* with an additional 1 adult treatment in 1998, and 0, 8, 16, 32 for *C. montagui*). *R*-values are derived from a Clarke & Evans nearest neighbour test adjusted for no buffer zone. $R > 1$ indicates a uniform distribution, $R = 1$ and random distribution and $R < 1$ a clumped distribution. The resulting *R*-value was then tested for a significant deviation away from a random spatial pattern (see text). Error bars shown = S.E. from the 3 replicates.

Spatial patterns were analysed with the *S. balanoides* cyprid and spat populations that recruited onto settlement plates deployed around the Isle of Wight during 1999, using the same method that was utilised to analyse the treatment patches. The majority of settlement onto the plates occurred at the two high-recruitment locations Seaview (87% of total plate settlement) and Cowes (11%). Settlement onto the plates at the two low-recruitment locations was minimal with Totland accounting for 1.7% and Ventnor 0.3% of the total settlement onto plates during the 1999 settlement season. (see Chapter 4 for a detailed account of the results obtained from the settlement plates).

S. balanoides that settled onto the settlement plates displayed an apparently clumped spatial distribution with a mean $R < 1$ at all analysed locations (Figure 3.10). Results obtained from Ventnor are not displayed due to insufficient settler numbers. In contrast to the results obtained from the treatment patches it was settlement onto the plates at Cowes that showed the greatest deviation from a random spatial pattern towards clumping. There was no obvious relationship between location settlement density and the spatial pattern on settlement plates.

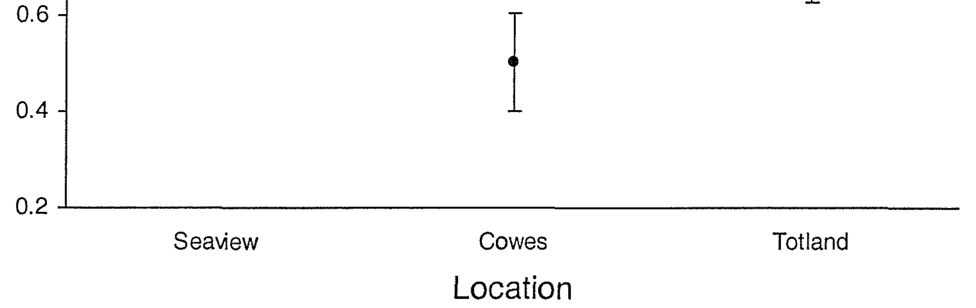


Figure 3.10 Spatial patterns exhibited by *S. balanoides* during 1999 on settlement plates at three of the four locations (see Figure 3.9 legend for meaning of terms).

3.4.3 Variations in barnacle-to-barnacle distances

Using the data extracted from the nearest neighbour analysis we were able to calculate the percentage of individuals in the total population at each location that were a certain distance from a conspecific (Table 3.8).

For all *S. balanoides* locations in both 1998 and 1999 at least 90% of all barnacle-to-barnacle distances were < 10 mm, with very few individuals occurring more than 25 mm from a conspecific. The general pattern of results obtained from the *C. montagui* study differed between the two locations. Barnacle-to-barnacle distances appeared to be much smaller at Sidmouth, than at Portland. The maximum distance found between barnacles at Sidmouth was 25 mm, whereas at Portland some individuals were found to be at least 35 mm away from a conspecific.

	Barnacle-to-barnacle distance							
	0-5mm	5-10mm	10-15mm	15-20mm	20-25mm	25-30mm	30-35mm	35mm+
Cowes High 1998 -*S.b.*	81.4	16.9	1.4	0.2	0.1	0.0	0.0	0.0
Cowes Low 1998 -*S.b.*	65.8	24.2	6.4	2.0	0.8	0.3	0.4	0.1
Portland High1 -*C.m.*	69.8	24.3	4.5	1.0	0.4	0.1	0.1	0.0
Portland High2 -*C.m.*	42.4	33.1	10.7	6.5	3.2	1.5	1.0	1.6
Portland Low1 -*C.m.*	49.2	31.1	12.2	3.8	2.4	0.6	0.3	0.5
Portland Low2 -*C.m.*	42.3	32.6	11.4	5.2	3.7	1.3	1.4	2.1
Sidmouth High1 -*C.m.*	97.4	2.5	0.1	0.0	0.0	0.0	0.0	0.0
Sidmouth High2 -*C.m.*	92.8	6.3	0.7	0.1	0.1	0.0	0.0	0.0
Sidmouth Low1 -*C.m.*	88.7	9.7	1.2	0.3	0.1	0.0	0.0	0.0
Sidmouth Low2 -*C.m.*	78.7	15.3	4.3	1.0	0.6	0.1	0.0	0.0
Cowes 1999 -*S.b.*	80.5	18.9	0.6	0.0	0.0	0.0	0.0	0.0
Seaview -*S.b.*	75.9	20.6	2.5	0.7	0.1	0.1	0.0	0.0
Totland -*S.b.*	79.8	17.0	2.5	0.5	0.1	0.1	0.0	0.0
Ventnor -*S.b.*	87.0	11.7	0.9	0.2	0.1	0.1	0.0	0.0

Table 3.8 The barnacle-to-barnacle distances expressed as a percentage of the total number of settlers at each location. *S.b* = *Semibalanus balanoides*, *C.m.* = *Chthamalus montagui*. The increment for conspecific distance is 5 mm. Treatment effect has been ignored and all results are pooled.

3.4.4 Barnacle movement

Using photographs of the treatment patches taken at the beginning (27th May 1999) and the end (2nd August 1999) of the 1999 *S. balanoides* study it could be ascertained whether any settlers had moved between photographs. Analysis of the results indicated slight movement exhibited by some individuals over a period of 10 weeks. However, any movement observed was in the order of 1 - 3 mm and may be an artefact of the technique employed. The two sets of photographs were not always taken in exactly the same position; a slight offset could have accounted for the apparent movement. Because the co-ordinates for a barnacle were taken as its centre, if the centre moved due to the barnacle tilting this would suggest actual movement by the entire barnacle. We conclude that we have no evidence of movement by adult barnacles in our study.

3.4.5 Simulating barnacle settlement

For each treatment maximum likelihood estimates (MLE) were obtained for the two model parameter values: maximum inter-individual distance (relating to reproductive separation constrained by penis length) and minimum inter-individual distance (relating to territorial separation). The maximum and minimum distances obtained by MLE are displayed in Figure 3.11 for both species; locations are displayed in order of settlement density. The line linking the maximum and minimum distances represents all points between the two extremities, which a simulated barnacle would have been able to settle without rejecting the patch. Also displayed in Figure 3.11 are the MLE Ln-likelihood values. These give an indication of how well the simulated data fits the observed data; the closer to zero the better the fit.

In general the maximum inter-individual distance for *C. montagui* increased as settlement density decreased between locations, though there was no such trend for minimum distance (Figure 3.11). Although there appeared to be a similar relationship between maximum inter-individual distance and settlement density at the various *S. balanoides* locations the relationship was not as pronounced as it was for *C. montagui.*

There was no identified relationship between treatment number and maximum or minimum inter-individual distance for either species within a location or area.

Minimum distances estimated by the MLE analysis ranged from 1.5 to 3.1 mm for *C. montagui* with 20 out of the 24 minimum distances occurring within a 5 mm range (1.8 - 2.2 mm). Analysis of the *S. balanoides* experiments showed that the minimum value ranged from 0.5 to 1.8 mm with 15 out of the 20 minimum distances occurring within a 3mm range (1.5 - 1.8 mm).

The maximum distances obtained from the MLE analysis for both barnacle species were more variable than the minimum distance. They ranged between 12 and 80 mm for *C. montagui*, and between 17 and 60 mm for *S. balanoides*. However, in 10 out of the 24 cases the maximum distance could be found between 15 and 25 mm for *C. montagui*, and in 13 out of 20 cases the maximum distance could be found between 15 and 25 mm for the *S. balanoides* experiments.

The parameter values estimated by maximum likelihood were then used to generate data sets of simulated settlement with which to compare to the observed data. The graphical comparisons are shown according to settlement season to allow local comparisons to be made (Figure 3.12 to Figure 3.15 for *C. montagui* 1998 and Figure 3.16 to Figure 3.19 for *S. balanoides* 1999).

Graphical comparisons between the actual experimental data and the simulated data gave a visual indication of how well the model was able to reproduce observed settlement patterns from random settlement constrained only by maximum and minimum conspecific separation. Overall the comparison was a favourable one, with the generated data fitting the observed data well. However, one area in which the simulated data failed to mirror the observed data convincingly was the last recorded annulus (135-150 mm). The observed data showed that typically the number of barnacles dropped considerably in the last annulus. Although the simulation technique was not capable of reproducing some of the more pronounced declines in the 135 - 150 mm annulus (e.g. Figure 3.12 (i) 16 adults), it did model the more moderate ones (e.g. Figure 3.14 (ii) 8 adults).

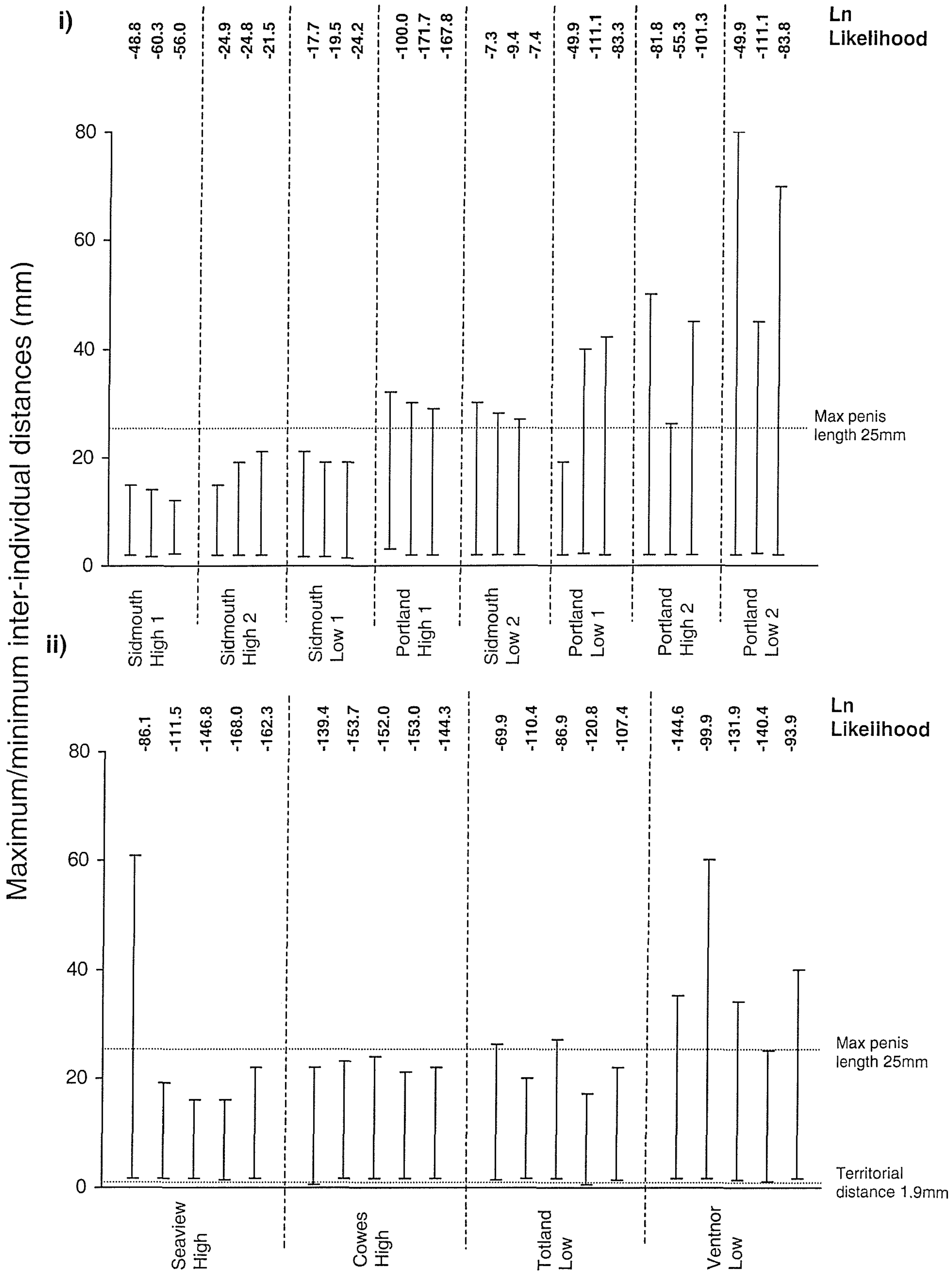
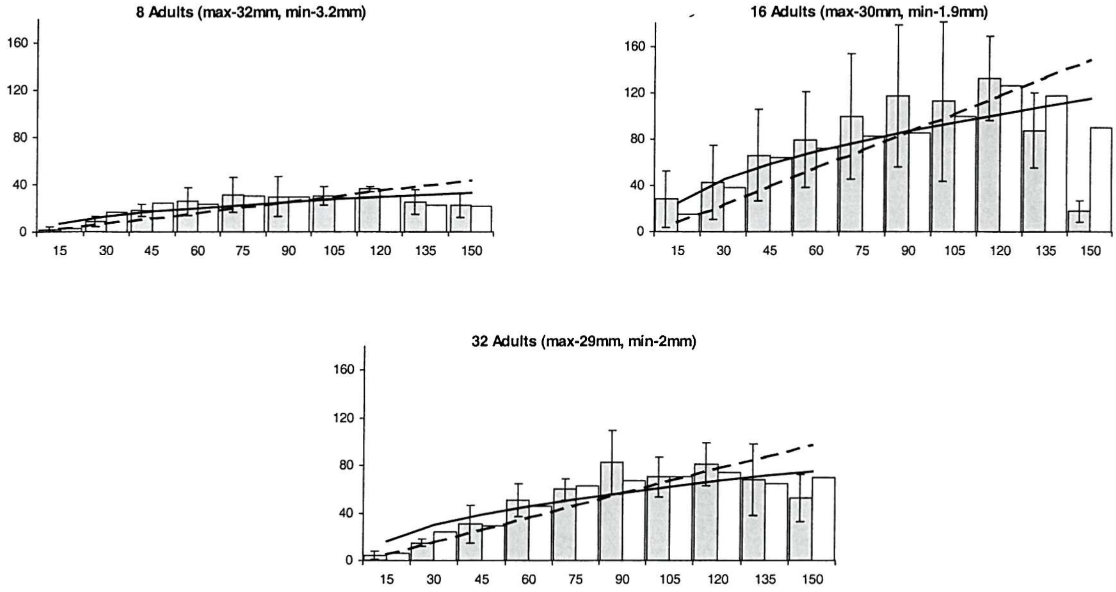


Figure 3.11 MLE of minimum to maximum inter-individual distance for i) *C. montagui* 1998 and ii) *S. balanoides* 1999 simulation models. Locations are displayed from highest settlement on the left to lowest on the right (where settlement is indexed by the density of barnacles in the 32 adult treatment as described in Chapter 4). Within locations, treatments are displayed in increasing order from left to right (8, 16, 32 for *C. montagui* and 2, 4, 8, 16, 32 for *S. balanoides*). The Ln likelihood values given indicate how well the simulated data fitted the observed data. Also displayed is the maximum penis length for both species and the territorial distance for *S. balanoides* as given in the literature (see Section 3.1).

i) Portland: High-recruitment, Area 1



ii) Portland: High-recruitment, Area 2

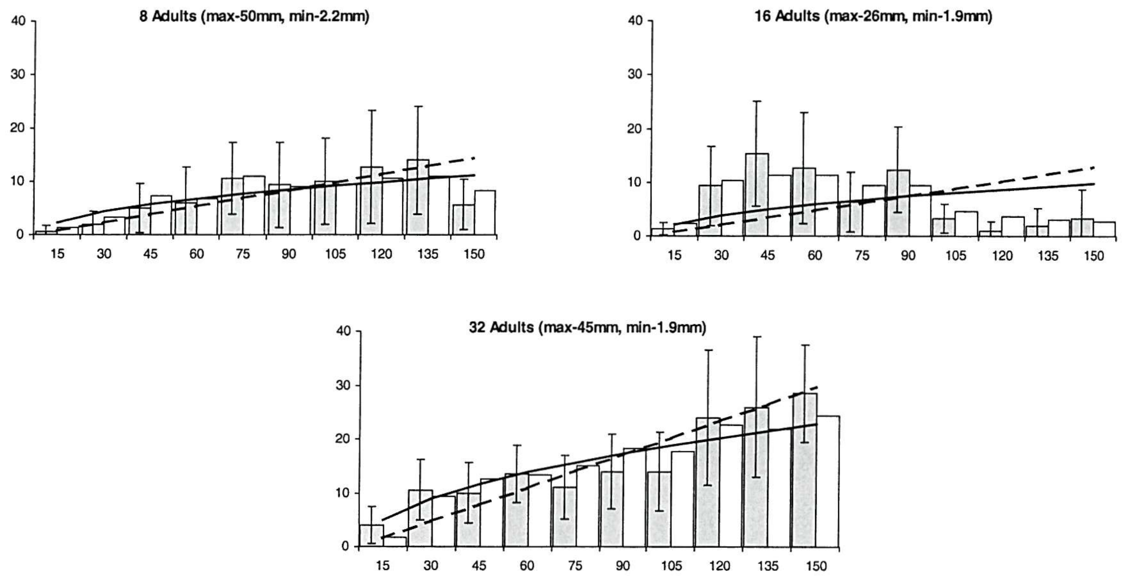
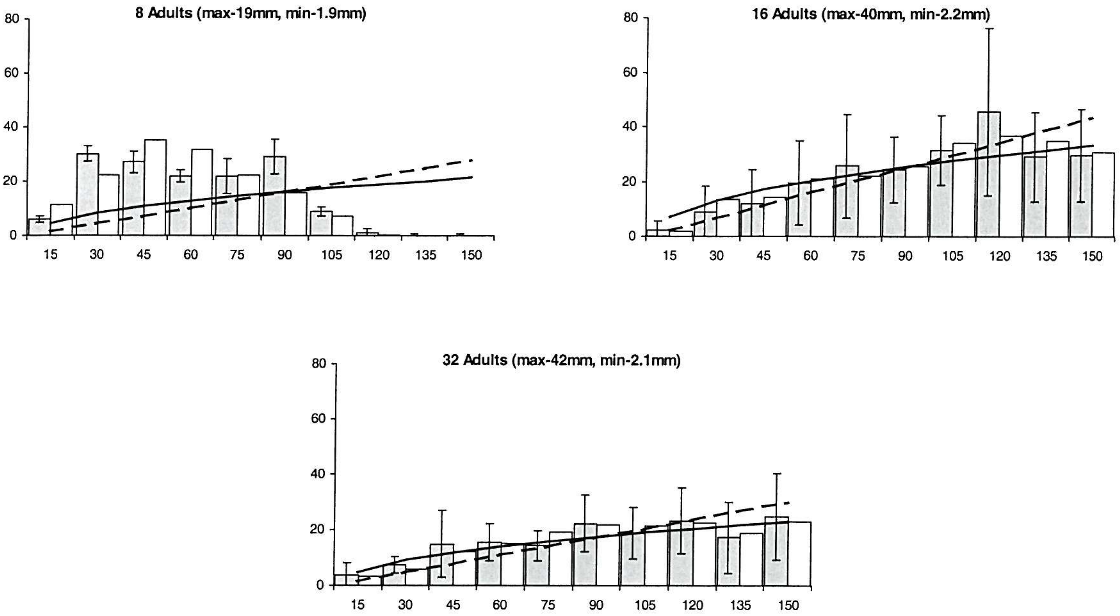
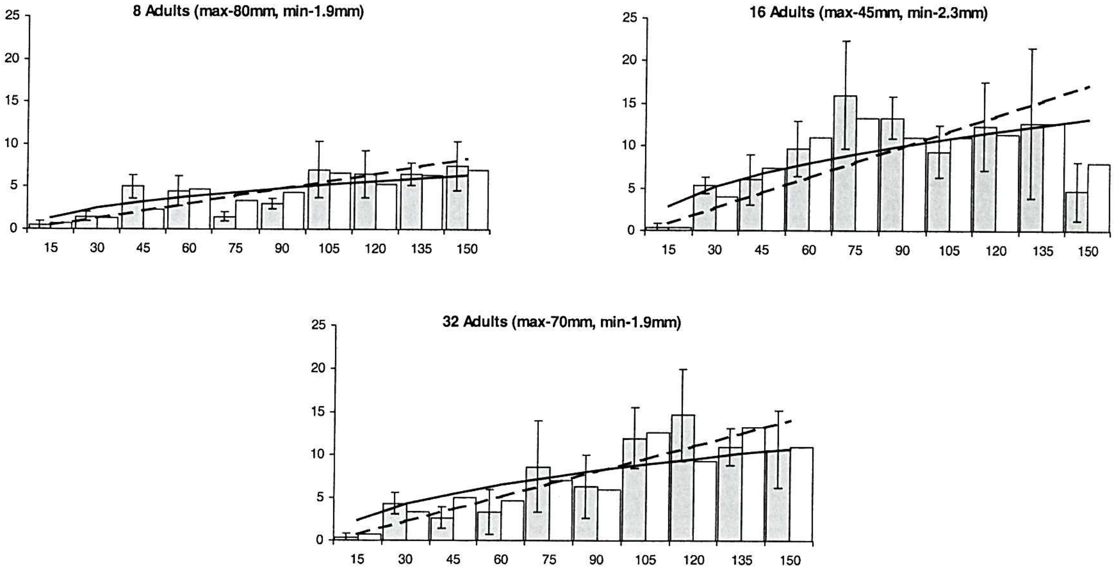


Figure 3.12 Graphical comparisons between empirical settlement data (grey bars), and data produced from the barnacle simulation model (white bars) for *C. montagui* 1998, Portland high-recruitment i) Area 1, ii) Area 2. Parameters are generated using maximum likelihood calculations and are shown for each individual graph. Observed results are also compared to an expected uniform random settlement given by $f = 2$ in eqn 3.4 (dashed line), and an expected settlement for a model where the density of individuals increases towards the centre of the patch, given by $f = 1.5$, (continuous line). Error bars = 95% confidence intervals for 3 replicates. Note that the scale given to the *y*-axis differs between i) and ii); this allows a detailed comparison to be made between treatments within each of the areas.

i) Portland: Low-recruitment, Area 1



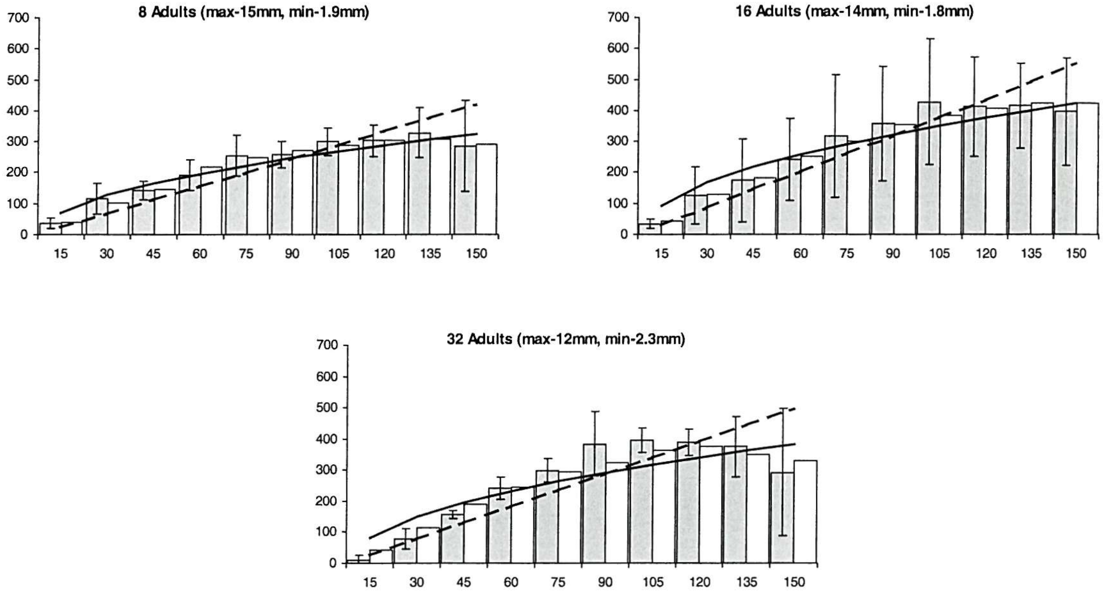
ii) Portland: Low-recruitment, Area 2



Radius of annuli (mm)

Figure 3.13 *C. montagui* 1998, Portland low-recruitment i) Area 1 ii) Area 2. (see Figure 3.13 legend for meaning of terms).

i) Sidmouth: High-recruitment, Area 1



ii) Sidmouth: High-recruitment, Area 2

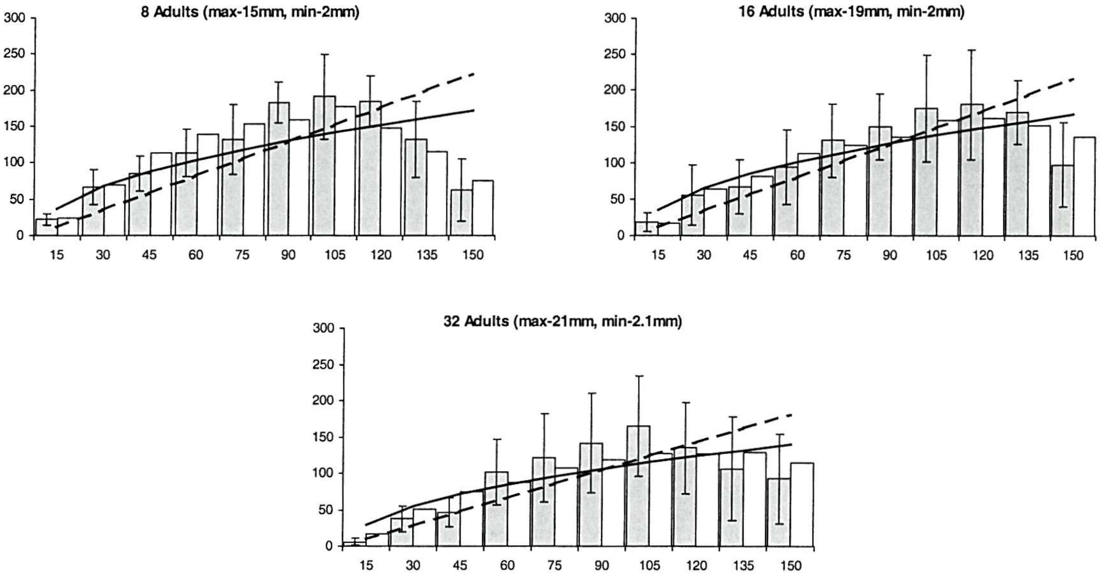
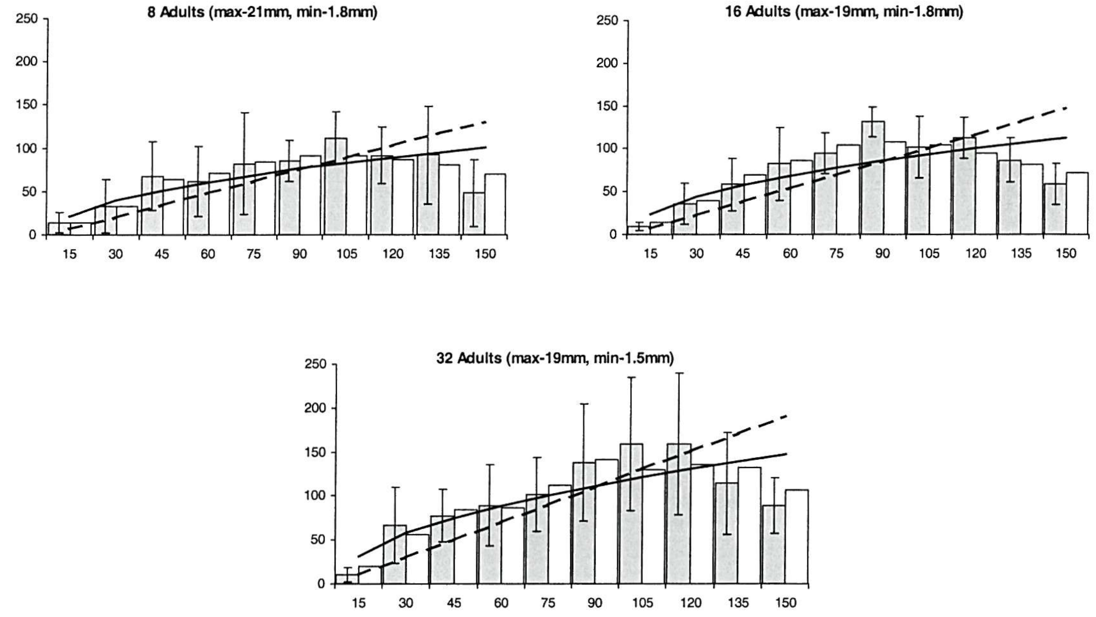


Figure 3.14 *C. montagui* 1998, Sidmouth high-recruitment i) Area 1 ii) Area 2. (see Figure 3.13 legend for meaning of terms).

i) Sidmouth: Low-recruitment, Area 1



ii) Sidmouth: Low-recruitment, Area 2

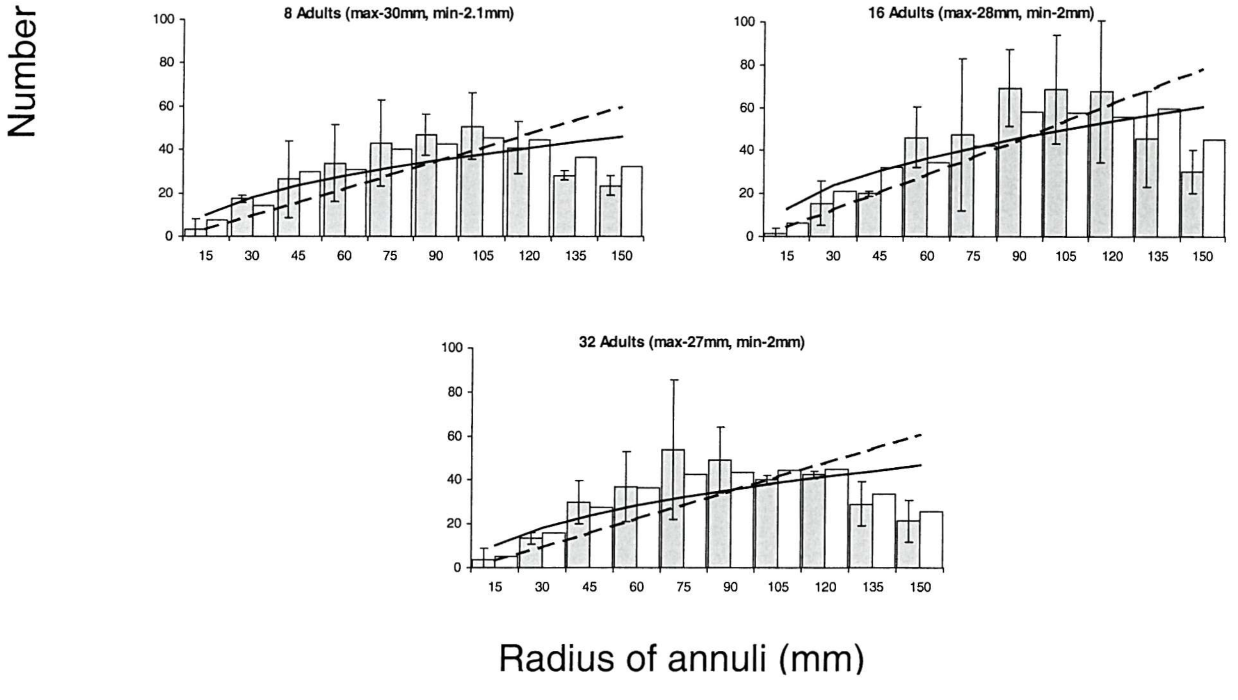


Figure 3.15 *C. montagui* 1998, Sidmouth low-recruitment i) Area 1 ii) Area 2. (see Figure 3.13 legend for meaning of terms).

Cowes: High-recruitment

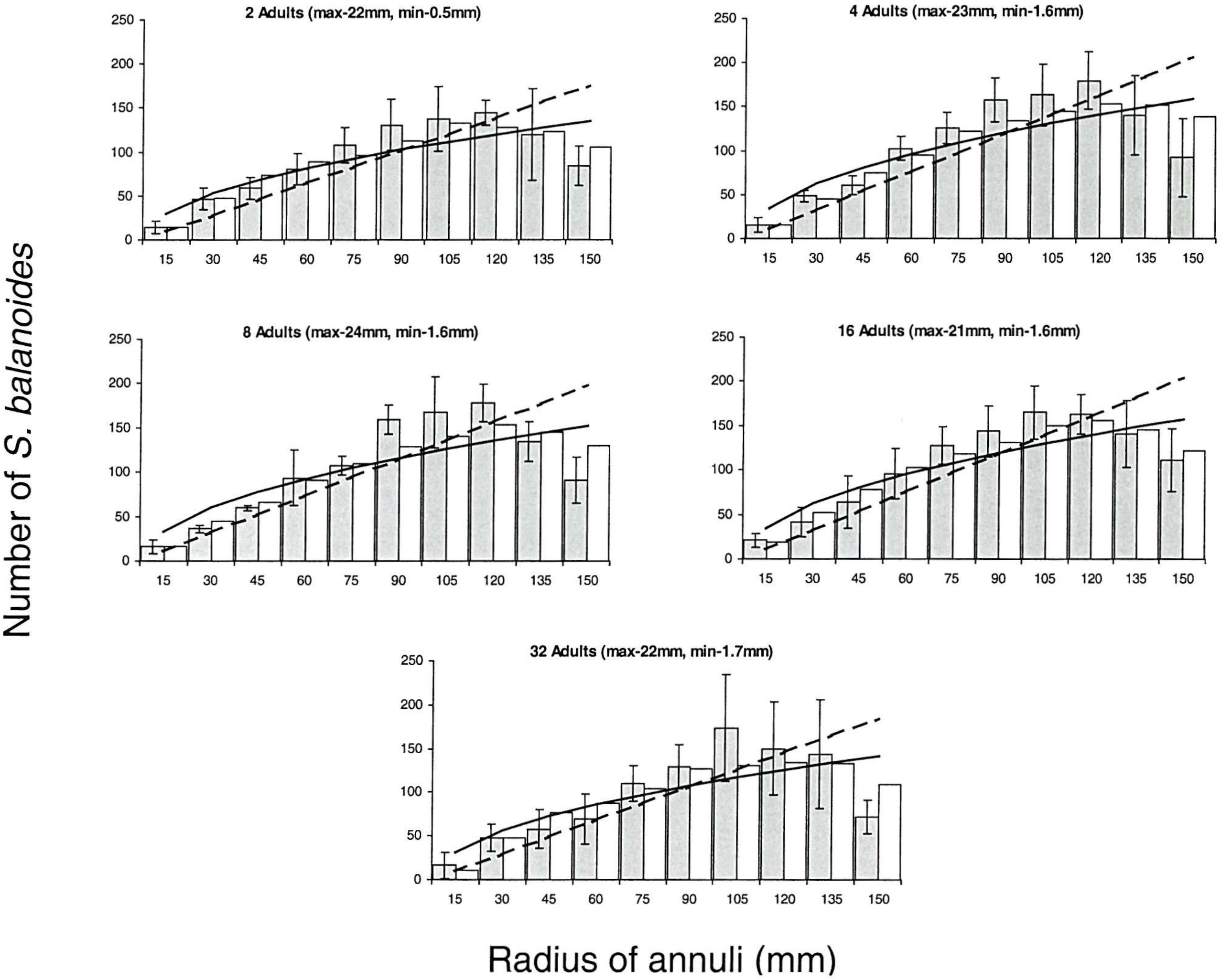


Figure 3.16 *S. balanoides* 1999, Cowes high-recruitment (see Figure 3.13 legend for meaning of terms).

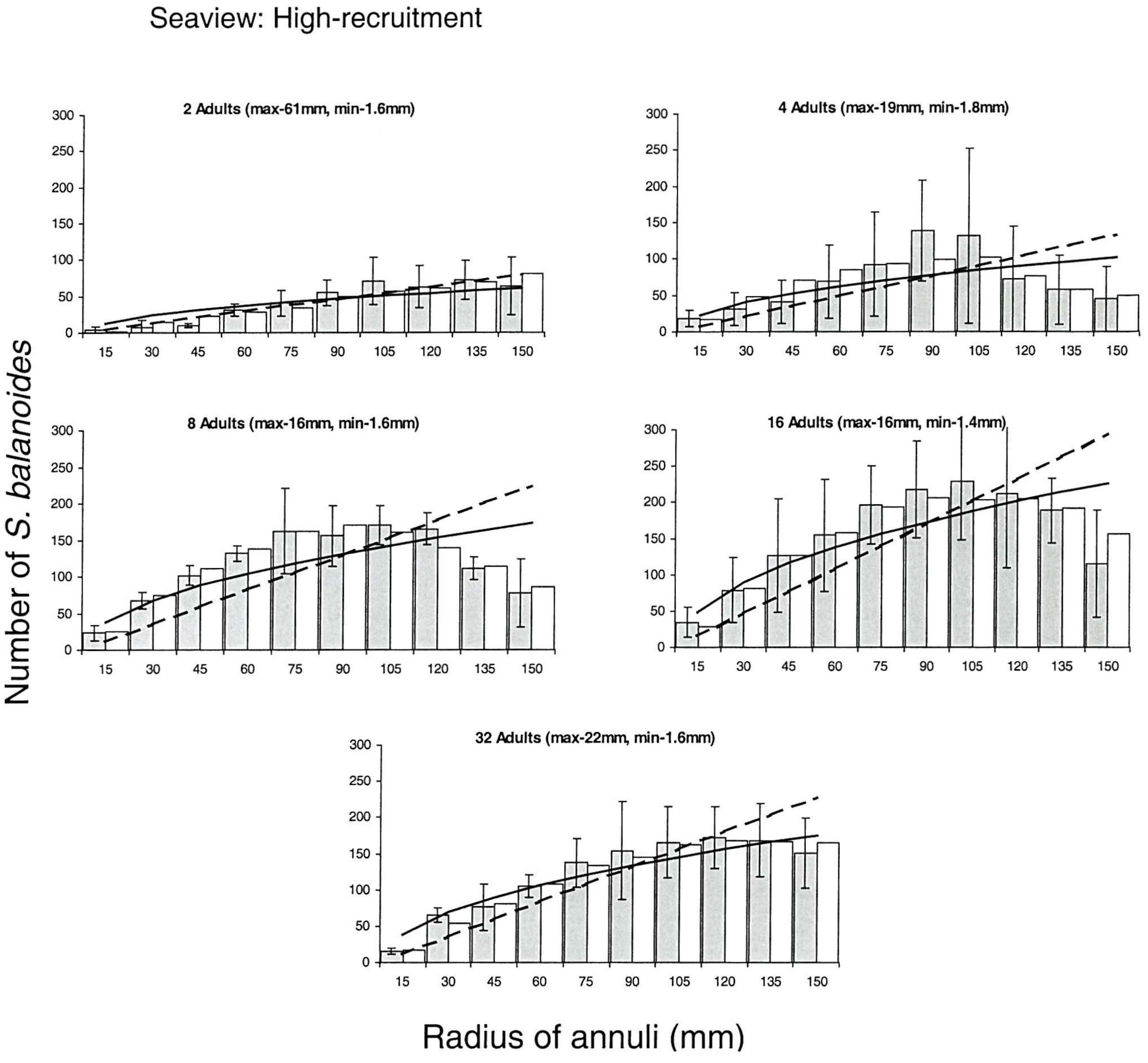


Figure 3.17 *S. balanoides* 1999, Seaview high-recruitment (see Figure 3.13 legend for meaning of terms).

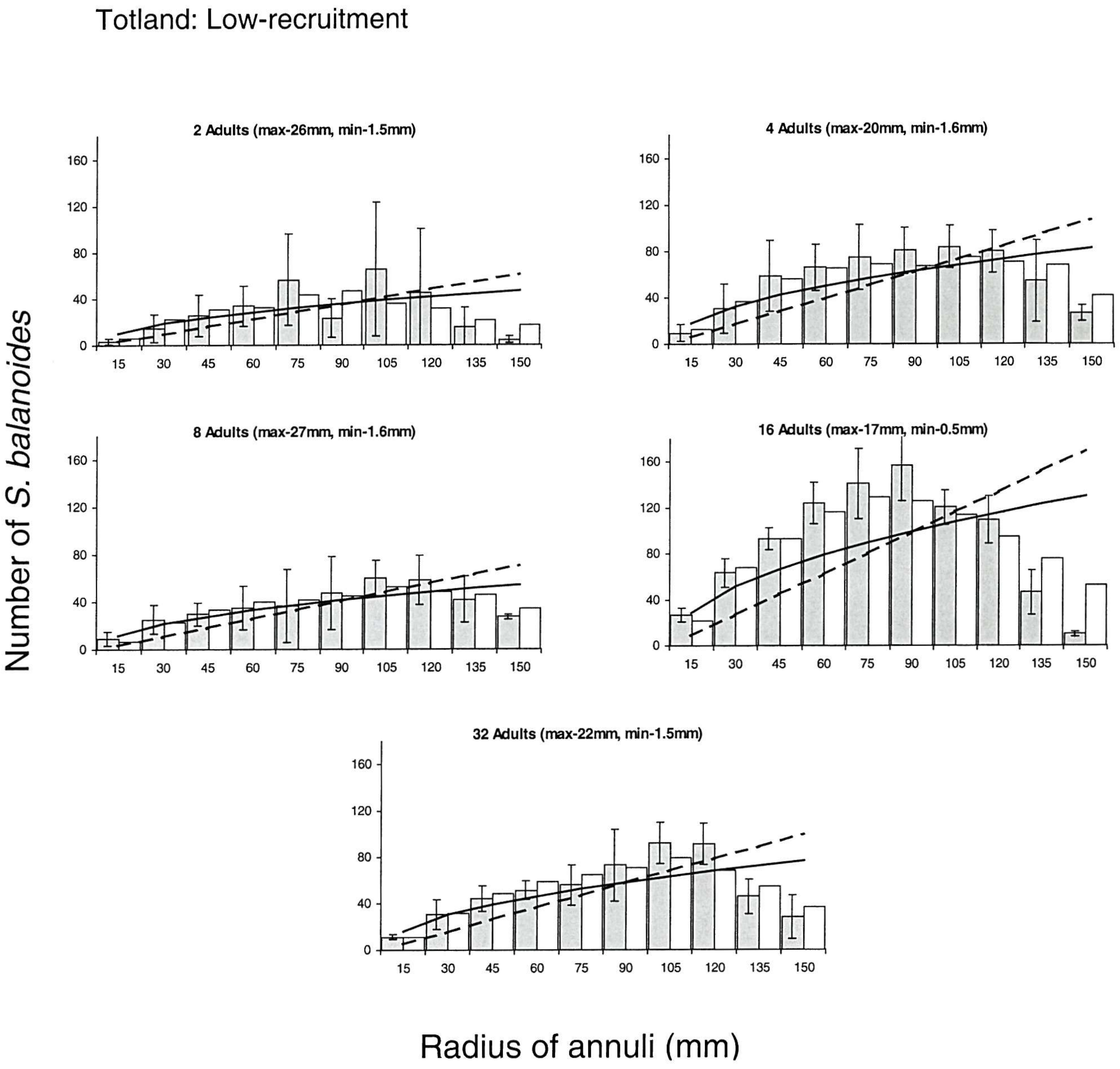


Figure 3.18 *S. balanoides* 1999, Totland low-recruitment (see Figure 3.13 legend for meaning of terms).

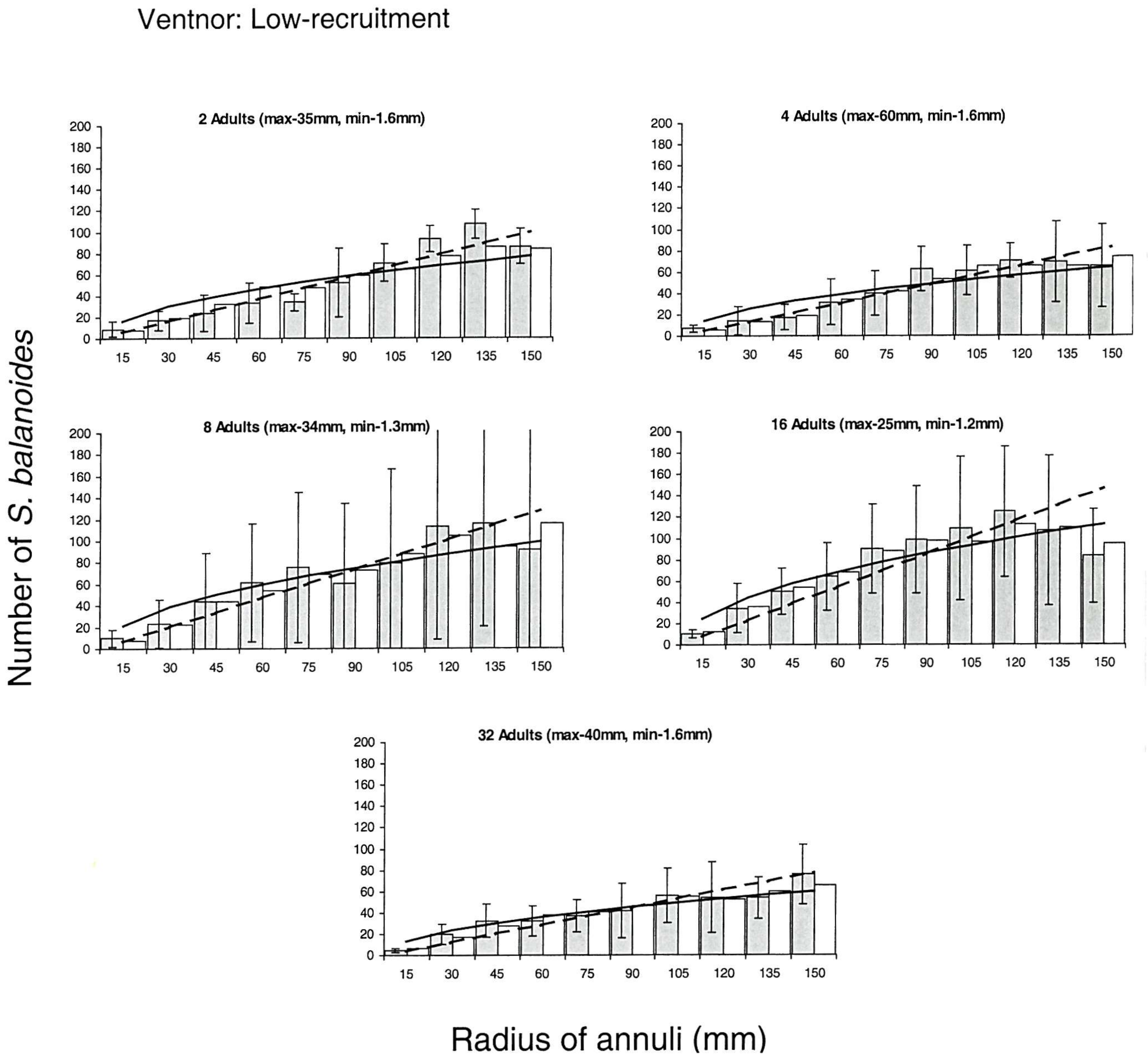


Figure 3.19 *S. balanoides* 1999, Ventnor low-recruitment (see Figure 3.13 legend for meaning of terms).

The full model, with inputs of both minimum and maximum inter-individuals distances was compared to nested competing models with fewer than two parameters using the likelihood ratio test.

For only 3 of the 24 *C. montagui* comparisons the full model with both parameters fitted the observed data significantly more closely than the model with no minimum distance (Table 3.9). For the majority of cases, neither the original two-parameter model (min and max) nor the nested one-parameter model (max only) represented the observed settlement patterns any more convincingly than the fully random zero-parameter model. The two parameter model only simulated 4 of the 24 cases more accurately than the random model, whereas the one-parameter (max only) was only more accurate in 3 of the 24 cases.

The two-parameter model (min and max) gave a better fit to the *S. balanoides* data than the one parameter (max only) model in only 2 of the 20 cases. However, in the majority of cases both the two (min and max) and the one-parameter (max only) versions of the model fitted the data significantly more closely than the fully random zero-parameter model. However, the one-parameter model (max only) was a better fit than the fully random zero-parameter model more often than the two-parameter model (min and max).

It was once more apparent that the recruitment of *S. balanoides* was different at Ventnor when compared to the three other 1999 locations (Cowes, Seaview and Totland), with the one and two parameter models only fitting the 16 and 32 treatment results more closely than the zero-parameter random model. At the other three locations there was a significant difference between the zero-parameter random settlement model and the two and one parameter models in all cases where central adults were present, except for one treatment at Totland (8 adults). Apart from the 0 adult treatments there was no evidence for any direct relationship between treatment number and the significance of the model.

		***C. montagui* model comparisons**		
		max+min versus max only	max+min versus random	max only versus random
		2 v's 1 parameter	2 v's 0 parameter	1 v's 0 parameter
Shore	Trt	1 d.f	2 d.f.	1 d.f.
Portland High 1	8	*ns*	*ns*	**
	16	*	**	*ns*
	32	*	*	*ns*
Portland High 2	8	*ns*	*ns*	*ns*
	16	*ns*	***	***
	32	*ns*	*ns*	*ns*
Portland Low 1	8	*ns*	***	***
	16	*ns*	*ns*	*ns*
	32	*ns*	*ns*	*ns*
Portland Low 2	8	*	*ns*	*ns*
	16	*ns*	*ns*	*ns*
	32	*ns*	*ns*	*ns*
Sidmouth High 1	8	*ns*	*ns*	*ns*
	16	*ns*	*ns*	*ns*
	32	*ns*	*ns*	*ns*
Sidmouth High 2	8	*ns*	*ns*	*ns*
	16	*ns*	*ns*	*ns*
	32	*ns*	*ns*	*ns*
Sidmouth Low 1	8	*ns*	*ns*	*ns*
	16	*ns*	*ns*	*ns*
	32	*ns*	*ns*	*ns*
Sidmouth Low 2	8	*ns*	*ns*	*ns*
	16	*ns*	*ns*	*ns*
	32	*ns*	*ns*	*ns*

Table 3.9 *C. montagui* 1998 likelihood ratio test results for nested simulation models. 'Trt' represents the number of barnacle left at the centre of each patch. Chi-square values and corresponding p values were calculated, with the resulting significance displayed, *ns* = not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

		S. balanoides **model comparisons**		
		max+min versus max only	max+min versus random	max only versus random
		2 v's 1parameter	2 v's 0 parameter	1 v's 0 parameter
Location	Trt	1 d.f	2 d.f.	1 d.f.
Cowes High-recruitment	2	*ns*	*ns*	*
	4	*ns*	*	**
	8	*ns*	*	*
	16	*ns*	*	*
	32	*ns*	*	*
Seaview High-recruitment	2	*ns*	*ns*	*ns*
	4	*ns*	**	**
	8	*	***	***
	16	*	***	***
	32	*ns*	*	*
Totland Low-recruitment	2	*ns*	*	**
	4	*ns*	***	***
	8	*ns*	*ns*	*
	16	*ns*	***	***
	32	*ns*	**	**
Ventnor Low-recruitment	2	*ns*	*ns*	*ns*
	4	*ns*	*ns*	*ns*
	8	*ns*	*ns*	*ns*
	16	*ns*	*	*
	32	*ns*	**	***

Table 3.10 *S. balanoides* 1999 likelihood ratio test results for nested simulation models. 'Trt' represents the number of barnacle left at the centre of each patch. Chi-square values and corresponding *p* values were calculated, with the resulting significance displayed, *ns* = not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

The number of adults in the 150 - 165 mm peripheral annulus varied within and between locations during the 1999 *S. balanoides* study (see Appendix 3.3). Using the same MLE technique as before and the adapted two-parameter random settlement model (to account for adult barnacles present in the 150 - 165 mm annulus as detailed in Section 3.3.6) the maximum and minimum inter-individual distances were recorded along with the Ln-likelihood function for the mean treatment values. Results were obtained for two locations Cowes (high-recruitment) and Totland (low-recruitment) (Table 3.11). The parameter values estimated by maximum likelihood were then used to generate data sets of simulated settlement with which to compare to the observed data and the original model (Figure 3.20 and Figure 3.21).

Adult barnacles in the 150 - 165 mm annulus increased the values of both the minimum and maximum distances when compared to the original model without peripheral adults. The maximum distance increased most at Totland with all maximum distances being 30 mm or more. Some variation in the maximum distance increase can be attributed to differences in the numbers of adults in the 150 - 165 mm annulus. The value of Ln likelihood gave an indication of how well the model fitted the observed data. The original model fitted the experimental data more closely than the model with peripheral adults. The parameter values generated from the MLE analysis using the peripheral adult model produced graphs that were comparable to random settlement given by eqn 3.4 when $f = 2$. If the maximum distances were reduced then the corresponding graphical output appeared bimodal: the majority of individuals settled towards the centre and the edge of the treatment patch with very few in-between.

	Trt (no adults)	No. of adults in 150-165mm annulus	Min distance (mm)	Max distance (mm)	Ln Likelihood
Cowes High-recruitment	2	67	1.9	26	-142.561
	4	101	2.1	29	-157.024
	8	53	2.0	32	-154.4341
	16	96	2.0	25	-156.298
	32	40	2.2	26	-147.658
Totland Low-recruitment	2	60	2.0	40	-74.179
	4	64	2.2	30	-117.010
	8	67	1.8	34	-89.855
	16	50	2.0	35	-144.374
	32	31	1.9	60	-112.3614

Table 3.11Maximum likelihood estimated of parameters minimum distance (relating to territorial behaviour) and maximum distance (relating to penis length) for the *S. balanoides* 1999 barnacle simulation model with adults in the 150 - 165 mm annulus.

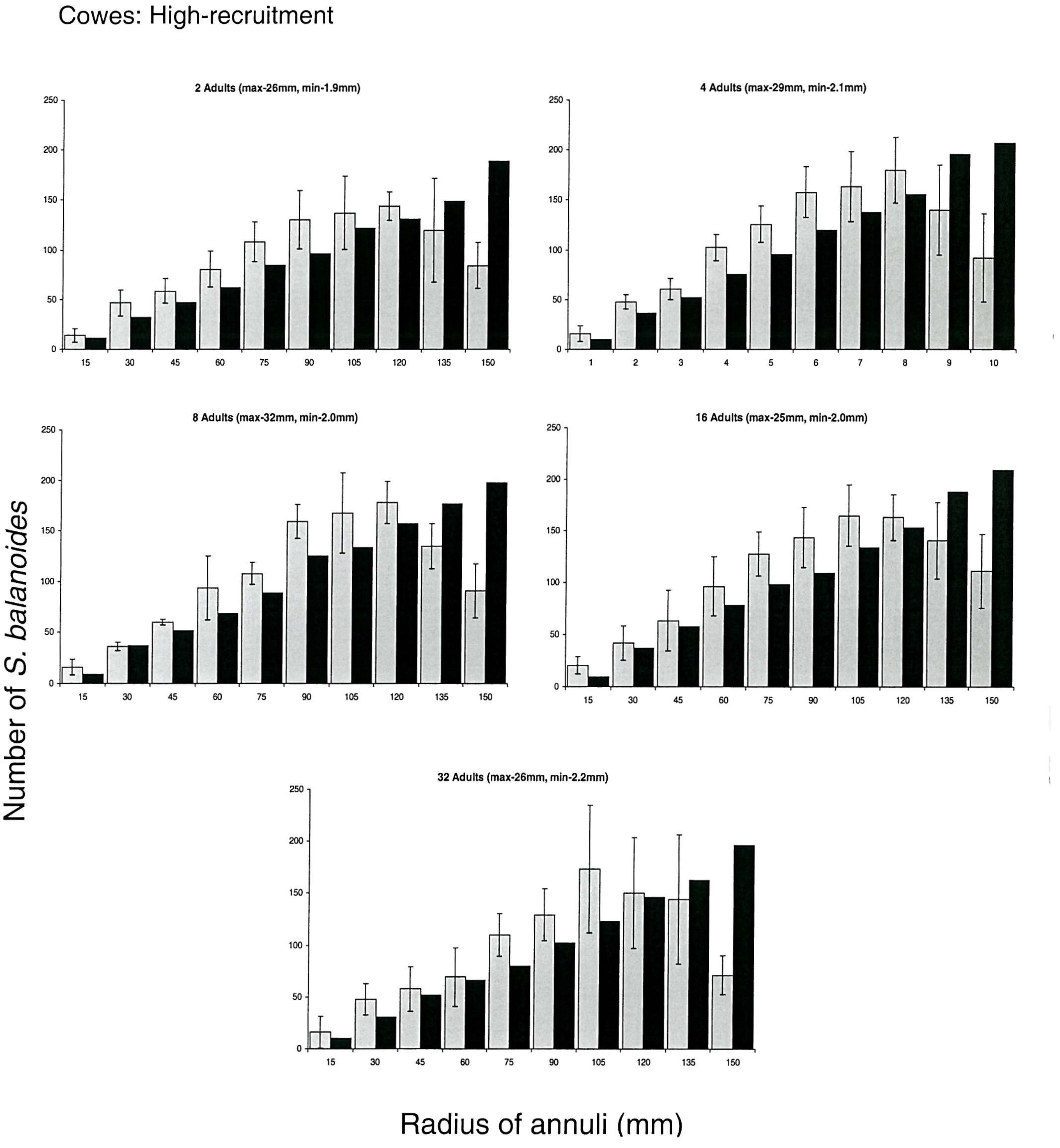


Figure 3.20 Graphical comparisons between empirical settlement data (grey bars), and data produced from the barnacle simulation model with peripheral adults in the 150 - 165 mm annulus (black bars) for *S. balanoides* 1999, Cowes high-recruitment. Parameters are generated using maximum likelihood calculations and are shown for each individual graph. Error bars = 95% confidence intervals for 3 replicates.

Totland: Low-recruitment

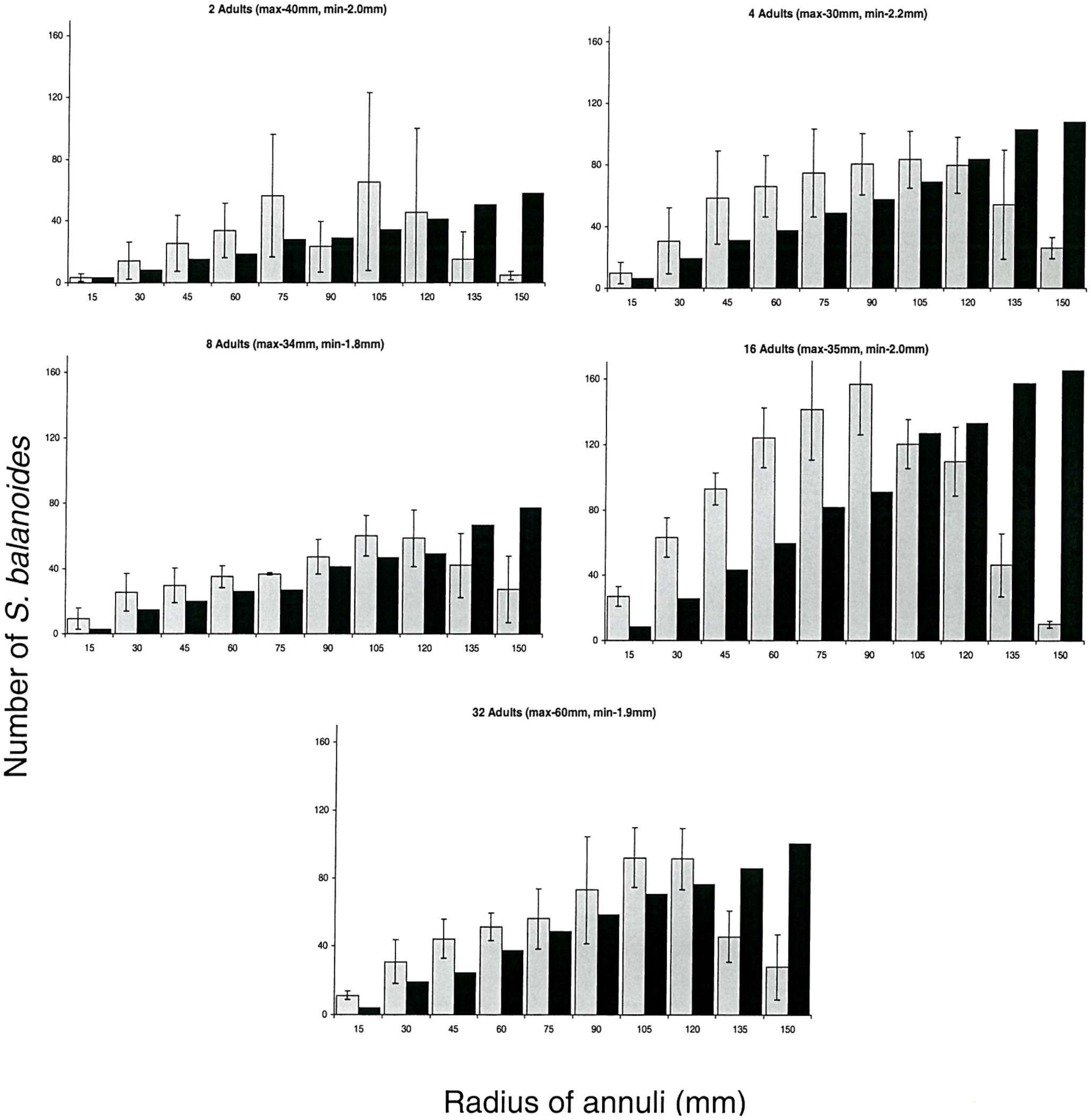


Figure 3.21 *S. balanoides* 1999, Totland low-recruitment (see Figure 3.20 legend for meaning of terms).

3.5 DISCUSSION

The aim of this chapter was to seek evidence for aggregation between newly settled barnacles and conspecifics at three distinct stages of development 1) 1+ year old adults, 2) cohort members from the same settlement season and 3) cyprid/spat (only with *S. balanoides*). We then went on to develop a barnacle settlement simulation model whereby simulated barnacles settled into a virtual treatment patch only if their initial position obeyed certain spatial constraints with respect to conspecifics. Settlement patterns of *S. balanoides*, which cannot self-fertilise, were compared to those of *C. montagui*, which can.

3.5.1 Settler-adult attraction

Graphical plots of *S. balanoides* and *C. montagui* individuals occurring in radiating annuli suggest that the attraction of adult conspecifics differs between different barnacle species at different settlement densities. Wethey (1984b) has also noted that spatial patterns exhibited by barnacles are not always consistent between species. Settlement per unit area of free space in *Chthamalus* is inhibited long before free space is limiting, though this is not the case in *S. balanoides* (Raimondi, 1990).

C. montagui settlement into the treatment patches was not only variable between treatments but also within treatments. Apart from the penultimate and the final annulus, settlement into all annuli was consistent with what would have been expected from the same number of recruits settling randomly. Consequently, the random model (eqn 3.4 with $f = 2$) fitted the data more closely than the central clumping model ($f = 1.5$). Due to the analysis being carried out on photographs from the end of the settlement season we cannot be sure if this was the situation throughout the settlement season. Individuals settling later in the settlement season are more randomly orientated than those that have settled earlier (Barnes *et al.*, 1952). The numbers of barnacle settlers at Sidmouth was considerably greater than the number of settlers at the other locations. The observed random settlement may be the result of a reduction in the number of settlement cues exhibited by individual cyprids when the supply of larvae is great (Gaines &

Roughgarden, 1985). However, we were able to show that the density of settlers into the 15 - 30 mm annulus significantly differed between our two locations, with relatively more individuals settling into the 15 - 30 mm annulus at Portland than at Sidmouth. However, Raimondi (1988) has found that significantly more *Chthamalus* recruited to clear areas on stones with barnacles than to similar areas on stones without barnacles. Settlement into the 15 - 30 mm annulus was dependent both the density of settlers and the number of adults left in the remnant group as summarised in Figure 3.8. However, the only significant relationship between settlement in the 15 - 30 mm annulus and the treatment effect was at the two locations with the lowest overall ranked settlement densities. At the lowest of settlement densities the only certain way to guarantee being a penis length from a conspecific is to settle next to the remnant adult group, whereas at higher densities the settlement of other cohort members can also elevate isolation.

Treatments at Portland would have been subjected to more wave action than those at Sidmouth due to Portland's prominent coastal location. Barnacle crowding can increase survivorship by buffering individuals from waves and the debris within them (Murdock & Currey, 1978). This may explain why at Portland we observed settlement at the edge of the treatment patch, i.e. individuals are settling next to the background adult population not so much for reproductive advantages but for protection and shelter.

In the 1998 *S. balanoides* study as the number of remnant adults increased so too did the number of barnacles found in the first two annuli when compared to either random settlement or the 0 adult treatment at the high-recruitment shore. The preferential settlement model ($f = 1.5$) fitted the actual data more accurately than the random settlement model ($f = 2$) for treatments with central adults. At the low-recruitment shore to obtain similar results the treatment patch needed to contain 4+ adults. Settlement differences between the recruitment densities were highlighted by a strongly significant recruitment level effect when comparing barnacle densities in the 15 - 30 mm annulus.

The results from the 1999 *S. balanoides* study indicated a similar general pattern at all locations except Ventnor. Ventnor is positioned on the south coast of the Isle of Wight and is subject to most of the prevailing winds. Barnacle settlement can be influenced greatly by large waves (Raimondi, 1990). The remaining locations were all positioned on more sheltered northerly facing coasts. Settlement into the 15 - 30 mm annulus was greater than could be expected from random settlement. The number of settlers in the 15 - 30 mm annulus was significantly effected by treatment at Seaview (high-recruitment) and Totland (low-recruitment) though not at Cowes (high-recruitment) or Ventnor (low-recruitment) shown in both Table 3.4 and Figure 3.8. Consequently, we did not observe a recruitment level effect (Table 3.3). The large variation in results at Ventnor might explain why the treatment effect was not consistent between locations.

Although a better fit was observed for the model with $f = 1.5$ (central settlement) than $f = 2$ (random settlement), the model constantly over-estimated numbers in outer annuli. This was because settlers were also attracted to other settlers, causing a recruitment wave out from the centre, which was more satisfactorily modelled by the simulation model (see below).

Adult barnacle counts taken from the 150 - 165 mm annulus (which were not cleared at the beginning of the study) gave us some idea of the background populations surrounding the treatment patches. The numbers of adults in this annulus was lower than the number of individuals found in many of the annuli within the treatment patches. If we assume that the background population is at an equilibrium level then temporal mortality of settlers must explain any differences. Hughes & Griffiths (1988) have found that individual growth within cohorts is accompanied by density-dependence disappearance. So we would expect the number of individuals present within the treatment patch to decline over time.

3.5.2 Settler-cohort member attraction

Although the analysis of concentric annuli suggests that settling *C. montagui* cyprids do not settle preferentially towards adults, apart from at very low settlement densities, there was a strong indication of clumping between individuals of the same cohort. All *R*-values for all treatments at all shores at both locations were significantly less than 1 indicating clumping behaviour. The ANOVA gave no evidence for any area, recruitment or location effect on the *R*-values obtained. This suggests that settling *C. montagui* cyprids may seek individuals of the same cohort more actively than those of previous cohorts. The need to settle next to conspecifics may be driven by abiotic factors other than the need to cross-fertilise. The observed cohort clumping may be the result of cyprids actively seeking areas of the surface preferential for survival such as crevices (Wethey, 1984b), damp areas with reduced desiccation (Hoffman, 1989) or microbial films (Thompson *et al.,* 1999). With *S. balanoides,* if adjacent individuals are of dissimilar age then the older ones tend to grow around the younger. When barnacles are very different in size the older individuals may even grow over the younger barnacles and smother them (Stubbings, 1975). If this behaviour is also true for *C. montagui* then it could explain the clumping patterns observed, with newly settled individuals competing more advantageously with cohort members than with older larger conspecifics. Alternatively, cohort aggregation could be seen if reproduction between individuals from the same settlement season was more successful than reproduction with older conspecifics. Although *C. montagui* individuals can self fertilise if necessary (due to isolation), self-fertilised eggs are often less viable when compared to eggs fertilised via non-self (Barnes & Crisp, 1956).

Roughgarden *et al.* (1985) modelled an open system and concluded that shores with high settlement had few gaps of free space within barnacle populations leading to a uniform spatial pattern. We did not find evidence supporting this at the scale of our analysis. At Sidmouth settlement was high relative to the other locations but barnacles were found to be aggregated. This is consistent with work carried out on *Chthamalus anisopoma* by Raimondi (1990). The model devised by Roughgarden *et al.* (1985) assumes settlement is proportional to available free space, but this may not always be the situation in all species (Raimondi, 1990).

Analyses carried out on the *S. balanoides* data showed inconsistencies between years. In 1998 settlement experiments were only carried out at one of the locations used in the 1999 study, Cowes. However, at Cowes high and low-recruitment shores were used during 1998. At the high-recruitment shore barnacle settlers were found to be either arranged uniformly or randomly, whereas, barnacle settlers at the low-recruitment shore were either aggregated or random. The 1999 *S. balanoides* data collected from four locations revealed aggregation at all locations in all treatment, except for one; a random spatial pattern was evident in one of the treatments at Cowes. If barnacles are clumped then at a local scale individuals can be considered as being crowded; the presence of crowding in our *S. balanoides* populations is consistent with other similar studies (e.g. Wethey, 1984b).

The treatment patches differed structurally between years in two respects. In 1998 the cleared patches were 10 × 10 cm squares whereas the patches cleared in 1999 were circular and larger with a diameter of 30 cm. The shape of cleared patches can affect the distribution of barnacle recruits (Raimondi, 1990). Uniform distribution was only observed in 1998 when the cleared patches were significantly smaller than those used in 1999. If settlement numbers in 1998 had been large and available free space low then the small cleared patches would have been at a premium to settlers. The spatial pattern exhibited early on in the settlement season may not have been uniform. However, due to the constant influx and the lack of free space, settling cyprids may have produced a uniform spatial pattern as a result of the territorial response displayed at the time of attachment (Crisp, 1961). There may, however, be a critical density at which individuals start to compete and display territorial behaviour (Satchell & Farrell, 1993). The critical density has been shown to be related to the survival rate and maximal basal diameter of the barnacles (Roughgarden *et al.*, 1985). The tendency to aggregate may also decrease at high densities in some species (Satchell & Farrell, 1993; Hills & Thomason, 1996). A uniform pattern may also have resulted from individuals being forced to move as a result of lateral pressure (Crisp, 1960). We could find no clear evidence for barnacle movement, however.

The treatment patches in 1999 were larger, and therefore barnacle densities may have been lower than Roughgarden *et al.*'s (1985) critical density threshold. Consequently, cyprids would need to seek conspecifics to be sure of being a penis length from an individual and therefore guaranteeing reproductive success in later life. This behaviour would result in aggregation. This can explain why we see aggregation at all locations in 1999. Hills & Thomason (1996) have also observed aggregation and random *S. balanoides* spatial patterns in the Clyde estuary. Differences between the degree of aggregation at each location could be the result of indifferent recruitment levels. The failure to observe aggregated patterns at the 1998 Cowes low-recruitment shore may be caused by cyprids having difficulties locating conspecifics (Satchell & Farrell, 1993) due to the very low numbers of settlers.

3.5.3 Settler-cyprid/spat attraction

Spatial patterns exhibited by *S. balanoides* cyprids were clumped with respect to other cyprids and newly metamorphosed spat. We can be sure that this relationship is primarily due to conspecific attraction, as the majority of other factors were kept constant by using identical settlement plates. Free-space was not limited on settlement plates, as numbers of settlers were never sufficiently high enough to occupy all the potential settlement area. Predation by fish and crabs may, however, influence the spatial patterns observed, but at no time were limpets seen on the plates. This result is consistent with Wethey, (1984b) who showed that cyprids settle in aggregations with respect to other individuals settling on the same tide. Therefore, once cyprids become established they influence individuals from the same cohort and subsequent cohorts. If the presence of conspecifics is such an important factor during settlement how do the first individuals settle onto virgin surfaces if there are no conspecifics present? Hills & Thomason (1996) suggest that there may be a small number of distinct founder cyprids within each population that settle on unoccupied surfaces.

3.5.4 Quantifying separation and attraction

C. montagui individuals are able to self-fertilise whereas *S. balanoides* are not (Barnes & Crisp, 1956). As a consequence we expected barnacle-to-barnacle distances to be more variable for *C. montagui* than for *S. balanoides* individuals. *S. balanoides* individuals were all found within 25 mm of other conspecifics, whereas some *C. montagui* individuals were more than 35 mm away from conspecifics. The penis length in *S. balanoides* can be anything up to 25 mm in length (Barnes & Barnes, 1956); consequently all individuals in our study would potentially have been capable of cross-fertilisation. *C. montagui* penis can also be up to 25 mm in length (F. Pannacciulli, pers comm), therefore some of the individuals would have to undergo self-fertilisation in order to reproduce. However, conspecific-conspecific distances for both species were all collected from photographs taken at the end of the settlement season. Initially some of the individuals settling early on in the settlement season may not have been a penis length from a conspecific. Only as a consequence of further settlement did they appear within a penis length of conspecifics. Likewise, individuals that appeared isolated in our photographs may only be isolated until future settlement in subsequent years, as *S. balanoides* can live for up to six years (Moore, 1934).

Using our barnacle settlement simulation model and MLE techniques we were able to calculate the optimum maximum inter-individual distance (purportedly regulated by penis length) and the minimum distance (purportedly regulated by territorial separation) that would enable us to model the experimental populations most effectively. In the model individual barnacles settled one at a time, as a result we are introducing a degree of temporal settlement into the results that was not present in the analytical model of eqn 3.4.

Just under half of the maximum distances extrapolated from the MLE results in the *C. montagui* study were between 15 and 25 mm, and in the *S. balanoides* study 65% of the maximum distances were between 15 and 25 mm as shown in Figure 3.11. These maximum distances are comparable to the length of a barnacle penis (see Barnes & Barnes, 1956). Therefore, using a simple simulation model along with observed settlement patterns we have been able to extract a fundamental measurement that is consistent with biological fact. In the majority of the *S. balanoides* results the one-parameter model (maximum only) was shown to be as good a fitting model, if not better, than the two-parameter model (maximum and minimum). This highlights the relationship between the settlement patterns observed in the field and the success with which these can be replicated simply using random settlement and a single constraint of inter-individual distance less than a penis length. Maximum distance was, however, inversely proportional to settlement density especially for *C. montagui*. This may be the result of a decreasing availability of free-space as settlement numbers increase, thus forcing individuals closer to conspecifics.

Territorial separation in *S. balanoides* populations is a function of cyprid length, and is inversely related to background barnacle density (Crisp, 1961). Crisp (1961) found territorial separation in *S. balanoides* to be between 1.55 and 1.9 mm. Our model output is consistent with this range in 75% of cases. *S. balanoides* cyprids are typically about 0.9 mm in length (Crisp, 1961), whereas *C. montagui* cyprids are approximately half the size (0.46 mm Burrows *et al.*, 1999; 0.45 mm O'Riordan *et al.*, 1999; under 0.53mm Power *et al.*, 1999). Consequently, if territorial separation in *C. montagui* is a function of cyprid length as it is in *S. balanoides* then we would expect the territorial distance exhibited by *C. montagui* to be smaller than that exhibited by *S. balanoides* (approximately 0.95 mm). The results from the simulation model, however, suggested that the territorial distance is greater in *C. montagui* than in the *S. balanoides* populations, though this did depend on the overall settlement density.

Interestingly, analysis of nested models with reduced numbers of parameters showed that the maximum and minimum parameter model was no more successful at modelling *C. montagui* settlement than a random settlement model in the majority of cases. If we assume that maximum distance is equivalent to penis length and minimum distance is equivalent to territorial distance then our results suggest that attraction is the greatest influence on spatial patterns when compared to repulsion. The simulation model with parameters produced from the MLE analysis did give, in general, a good representation of what was observed experimentally. It could be developed further, however, to allow for the decrease in density towards the edge of the treatment patch by introducing a probability index into the simulation in place of threshold distances

Adult conspecifics were present around the perimeter of the treatment patches. By adapting the barnacle settlement model to include these adults we were able to ascertain their effect on the overall position of settlers within each of the patches at two of the *S. balanoides* locations used in 1999. The presence of these peripheral adults caused simulated individuals to settle initially towards both the central remnant adults and the edge of the treatment patch. Consequently, the best fitting simulations were achieved when maximum distances were larger than those obtained in the original model. The large maximum distance allowed individuals to settle in the middle annuli. Ultimately the settlement patterns produced were comparable to random settlement and therefore this simulation fitted the observed data less closely than the original model without peripheral adults. This result suggests that settlers find the central groups more attractive than the adults outside the treatment patch. The central conspecifics represent a localised high-density of adults, in a cleared area otherwise void of conspecifics, whereas adults outside the patch may be sparse and infrequent. Settlers are therefore in contact with more adults when they settle close to the centre and thereby maximise their chances of reproductive success by settling close to the central groups where barnacle numbers are relatively high at a local scale. Alternatively these results may be caused by grazing limpets (Hawkins, 1983). Although initially limpets were removed from the around the treatment patches, individuals did encroach the cleared areas towards the end of the settlement season. These limpets may have knocked off barnacle settlers and caused an apparent settlement void towards the edge of the treatment patches.

3.5.5 Conclusions

In summary, analysis of spatial patterns in two barnacle species has shown strong evidence for gregarious settlement in at least one of the settler-adult, settler-cohort member, settler-spat/cyprid interactions tested for. One of the main factors controlling aggregation in *S. balanoides* is the need to carry out cross-fertilisation, via a penis of limited length. Wethey (1984a) has likened the reproductive success of *S. balanoides* as a function of conspecific density to an Allee effect (Allee, 1931). At low densities the fecundity of individuals is low due to a reduction in mating opportunities. As density increases so too does the availability of potential mates. As shown in Chapter 2 the Allee effect can result in population collapse if consumer density is well above the consumer-resource equilibrium point. *C. montagui* individuals have the potential to self-fertilise though it would seem that individuals preferentially seek out comparably aged conspecifics. The advantages of cross-fertilisation over self-fertilisation have been reported by others (Barnes & Crisp, 1956).

Although we have attributed much of the aggregation to reproductive success, other advantages for crowding have been documented (see Wu, 1980; Bertness, 1989; Bertness, *et al.*, 1998). However, as an organism's ultimate fitness is determined by its ability to reproduce, other factors can only amplify gregarious settlement.

The mutual attraction exhibited by both barnacle species has fundamental consequences with regard to population increase. In an open system the rate of population increase depends on the rate of influx, with a constant influx giving an arithmetic increase (as described by Hanski, 1994). The barnacles observed in this study occur in an open (marine) system but they increase in numbers geometrically as we will explicitly show in the next chapter. The reason why we see geometric growth is due to the spatial restraint governing reproductive success. To reproduce an individual has to be a penis length from a conspecific. It is the ability of an individual cyprid to locate conspecifics that insures that it can successfully reproduce. The number of conspecifics it can settle near, and consequently reproduce with, will therefore govern a barnacle's evolutionary fitness. These conspecific location and identification traits will then be selected for in subsequent generations. If we assume that a barnacle has double the reproductive success if it settles next to two conspecifics rather than one then a population of such barnacles will increase geometrically. We have shown that the two barnacle species studied in this chapter do show aggregated attraction.

Geometric population growth is typically observed in closed systems where local recruitment is determined by local self-replication. If local recruitment is itself dependent on the availability of limiting resources of food or shelter, then such populations will posses an extinction threshold. The extinction threshold is the minimum density of a renewing resource that will just support a population of the resource user. Extinction thresholds are a characteristic feature of closed systems, but they exist by future of geometric growth. They are not usually associated with open systems, where persistence or extinction are functions of the influx or lack of influx of recruits. With the open system of *S. balanoides*, however, the mutual attraction of new recruits causes geometric growth, which gives the system an extinction threshold. In effect, if suitable habitat for settlement is so sparse that cyprids must settle more than a penis length from each other, the population will be unsustainable. This theme will be taken up in the next chapter and in Chapter 6.

Gregarious settlement, where the presence of conspecific individuals promotes the settlement of newly arriving larvae is widespread in marine benthic invertebrates, occurring in at least 35 invertebrate species (Burke, 1986). If the degree of attraction is as strong in these species as it is in the barnacle species in this study we can expect these populations to increase geometrically, and therefore to have a pronounced extinction threshold. This has not been considered in the literature up to now. Understanding the causes of population growth enables predictions to be made with respect to the future structure of a population. This may be crucial in not only understanding the evolutionary and ecological population dynamics of the species but also in future management schemes whereby the population under question is required to be eradicated, sustained or encouraged.

4 POPULATION SETTLEMENT AND RECRUITMENT RATES IN AN OPEN SYSTEM

Declaration: this work has been done in collaboration with Mr Malcolm Roberts (assistance in data collection), Dr Patrick Doncaster (assistance with design) and Prof Steve Hawkins (biological expertise). I have led the design, fieldwork, analysis and interpretation stages.

4.1 ABSTRACT

Recruitment rates were measured for two species of sessile barnacles settling onto bare rock in the proximity of small groups of adult conspecifics of varying size. Of the two species studied, *Chthamalus montagui* can self-fertilise whereas *Semibalanus balanoides* cannot. The number of barnacle settlers was shown to depend on both the presence of adult conspecifics and the availability of free-space. Free-space was shown to be a limiting factor only at the highest settlement densities for *S. balanoides*. The numbers of settlers was directly related to the size of the adult group for all *S. balanoides* populations and for some *C. montagui* populations. For both species, treatment patches with no adult conspecifics consistently attracted the fewest number of settlers. Settlement plates were deployed at each of the locations used in 1999. These were adapted from terracotta titles and gave an independent assessment of recruitment. Analysis of recruitment to settlement plates, which were replaced on each visit to a location, suggested that the background population density of adults was a good indication of recruitment supply. Settlement to these plates also suggested the occurrence of settlement pulses throughout the settlement season, although these data did not always match the settlement data extracted from the treatment patches. Rates of recruitment into the adult class were examined graphically, to reveal both arithmetic and geometric growth patterns in both species. The rate of geometric growth was quantified. A compressed exponential growth rate best described the growth of certain *S. balanoides* populations at Cowes. Barnacle population growth rates were likened to those typically exhibited by populations in closed systems. Using this comparison a novel model was detailed to represent the population dynamics of a sessile marine invertebrate in an open system.

4.2 INTRODUCTION

On the spatial scale of many ecological studies, populations are often effectively open; i.e. recruitment is from a pool that is decoupled from the local population (Roughgarden *et al.*, 1985; Bence & Nisbet, 1989). Consequently, the local birth rate has little or no direct role in governing the local population size; the recruitment of individuals from elsewhere provides a new population cohort. A constant influx of new recruits inhibits any temporal extinction. Even if a patch does become extinct it will not remain extinct indefinitely; the population can be re-seeded by recruitment from outside the system.

Closed systems can be considered as autonomous units. If an extinction occurs it is irreversible (May & Oster, 1976; Caswell, 1978; Begon *et al.*, 1990). In closed systems population growth depends only upon the rate at which the individuals within the population can give rise to new offspring (e.g. Volterra, 1926; Lotka, 1932). If, however, the death rate is greater than the birth (recruitment) rate then over time the population will go extinct. Once extinction of the population occurs it will remain so, as the system cannot depend upon immigration to re-seed it.

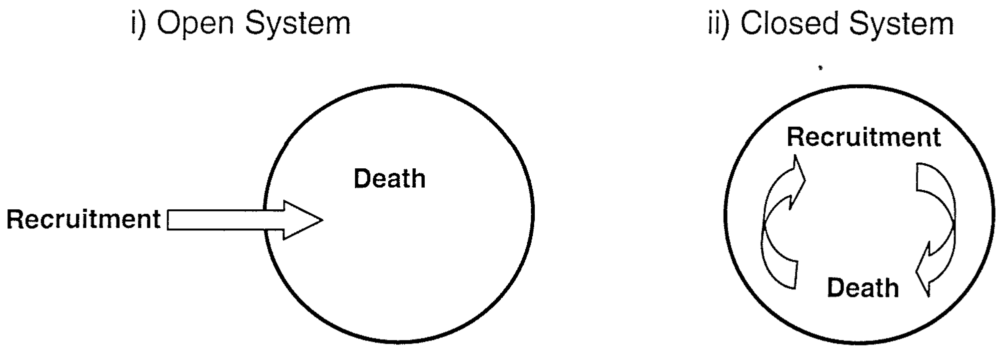


Figure 4.1 The difference between populations in the two types of system. i) In an open system recruitment is via an influx of new arrivals from outside the local system. ii) In a closed system all recruitment is bounded by the system and consequently it is only the birth and death processes within the system that govern the population equilibrium.

The population dynamics of the two systems have different characteristics, making it possible to tell them apart on the basis of empirical data. In an open system, the supply of recruits is independent of the number of residents, which leads to an arithmetic increase in population size if there is a constant supply of recruits. In a closed system the recruitment rate is likely to be proportional to the number of breeding residents, which leads to geometric increase in population size if there is a constant birth rate per capita. Each system has different consequences with respect to persistence of populations within them as shown in Figure 4.2. Under geometric growth (closed system) the minimum resource requirements for a population is found to equal the unused fraction of the limiting resource at equilibrium, this is known as the extinction threshold (Anderson & May, 1991; Lawton, 1994; Doncaster *et al.*, 1996). Under arithmetic growth (open system) there is no extinction threshold as such.

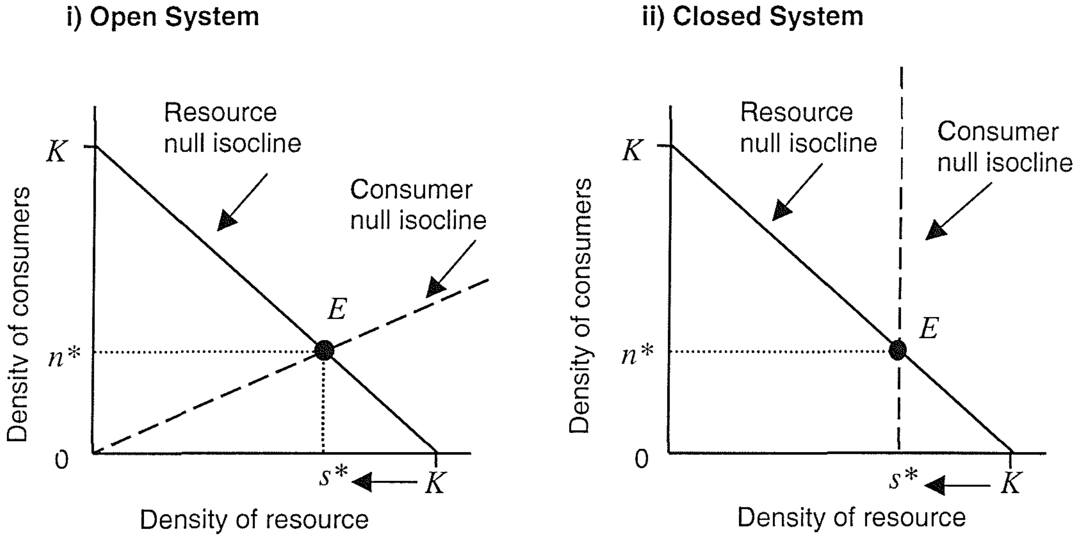


Figure 4.2 The difference between open and closed populations displayed as Lotka-Volterra (1926), type phase plane models. The population equilibrium point E (s^*, n^*) i) With arithmetic growth a reduction in K (the carrying capacity of available space) ultimately leads to a reduction in s^* and n^* but neither reaches zero until $K = 0$. ii) With geometric growth, as K tends towards s^*, then n^* tends to zero and thus to extinction. In the closed system the extinction threshold is at $K = s^*$.

The phase-plane diagrams in Figure 4.2 show the theoretical consequences for equilibrium population persistence in the two models. In a closed system resource density (s^*) is determined only by the ratio of consumer death to birth-rates, and is independent of the resource carrying capacity (K). As the carrying capacity of the environment decreases then resource density remains unchanged but consumer density (n^*) approaches zero. Once $K = s^*$ then $n^* = 0$, which is the point referred to as the extinction threshold (Lande, 1987). If we consider an open system, a reduction in the carrying capacity (K) results in a reduction in both resource and consumer densities. No matter how much the carrying capacity is reduced both s^* and $n^* > 0$, i.e. theoretically there is no extinction threshold. Consumer persistence in the open system is related not only to resource depletion as it is in the closed system but also to a recruitment supply from outside.

The marine environment has long been regarded as an open system (Roughgarden *et al.*, 1985); the water medium can facilitate transport between locations and populations with little energetic cost, unlike terrestrial systems. Much work has been done studying and modelling the recruitment dynamics of organisms found in marine systems (for empirical studies of fish see Doherty, 1982; of coral reefs see Hughes, 1984, of barnacles see Hawkins & Hartnoll, 1982; Gaines *et al*, 1985, Gaines & Roughgarden, 1985; Kendall *et al.*, 1985; Raimondi, 1990; Minchinton & Scheibling, 1991; Bertness *et al.*, 1992, of general open marine systems see Bence & Nisbet, 1989, Caley, *et al*, 1996, and for theoretical studies of barnacles see Roughgarden *et al.*, 1984; Iwasa & Roughgarden, 1986; Roughgarden & Iwasa, 1986; Johnson, 2000). Many of these studies have focused on recruitment dynamics of barnacles, because the mechanisms governing the distribution and abundance of populations of barnacles have still to be unanimously agreed upon.

The recruitment of barnacles is via a free-swimming pelagic larval stage whereas reproducing adults are sessile. The reproductive output of local adults can have little or no direct influence on local recruitment (Gaines, & Bertness, 1993). Cross-fertilisation must occur in many barnacle species in order for successful reproduction to take place (Barnes & Crisp, 1956). Consequently, the mobile larvae must select a suitable settlement site sufficiently close to conspecifics to allow for future reproduction. The limitation of suitable settlement sites and forced conspecific attraction may alter barnacle population growth to forms not typically displayed by populations in open systems.

In this chapter we aimed to measure growth rates of adult barnacle populations. Despite the barnacle system being inherently open, we expect to find evidence of geometric, as opposed to arithmetic growth. By putting the growth pattern into the context of a geometric-arithmetic continuum, we were able to evaluate its equilibrium properties in relation to the extinction behaviour normally associated only with closed systems. The reasons for expecting geometric rather than arithmetic growth stem from spatial reproductive constraints (as seen and described in Chapter 3). In essence the numerical outcome of each resident barnacle attracting one or more recruits is the same as each resident barnacle producing one or more recruits; in both cases the rate of population growth increases in direct proportion to population size. In barnacle species that do not depend on obligate cross-fertilisation we would not necessarily expect to find geometric growth as reproduction is not spatially constrained. The study was conducted on two barnacle species *Semibalanus balanoides* and *Chthamalus montagui*; the former requires cross-fertilisation whereas the latter does not (Barnes & Crisp, 1956). We also aimed to test the effect of recruitment levels on the rate of population increase.

Before a barnacle attaches itself to a surface it preferentially selects a suitable site, if the surface is not suitable the individual will discard the area and search for another. The selection of a settlement site is determined by certain settlement cues as given in Chapter 1. One of the primary settlement cues is the availability of conspecifics to guarantee reproductive success in later life. The following section details the consequence this spatial restraint has on population growth.

4.2.1 Barnacle reproduction and local population growth

The requirement for the cyprid larvae to settle next to other conspecifics stems from the need to reproduce. Many barnacles are hermaphrodite (Barnes & Crisp, 1956). The fertilisation of mature eggs is carried out via internal fertilisation from neighbouring sexually mature adults. However, some species such as *C. montagui* can also undergo self-fertilisation (Barnes & Crisp, 1956). During cross-fertilisation sperm is transferred from one individual into the body cavity of a close neighbour. The ability of an individual to cross-fertilise is primarily dependent on penis length, and the distance from the individual to conspecifics. The length of a barnacle's penis varies between species and individuals (see Barnes, 1992), typically in *S. balanoides* they have been found to extend to up to 25 mm (Barnes & Barnes, 1956) and to 25 mm in *C. montagui* (F. Pannacciulli pers comm). This spatial constraint on reproductive success is likely to affect population dynamics at low equilibrium densities.

In an area with a high-density of adult conspecifics new recruits are not spatially constrained by the availability of nearest neighbours (Figure 4.3i). No matter where a cyprid settles the chances of a conspecific being a penis length away are high. This population will increase arithmetically if there is a constant supply of recruits. Where the density of adult conspecifics is low, recruits will be spatially constrained with regards settlement sites. If successful cross-fertilisation is to take place cyprids must settle within a penis length of a conspecific.

In the low-density scenario presented in Figure 4.3ii cyprids must settle around the central adult population. If recruits are attracted to adults equally then two adults will have double the attractiveness of a single adult and therefore recruit twice the number of cyprids. Four adults will consequently attract double the number of cyprids compared to two adults and four times more than a single adult etc. In this scenario the population will increase geometrically in numbers, albeit within the confines of the resource carrying capacity.

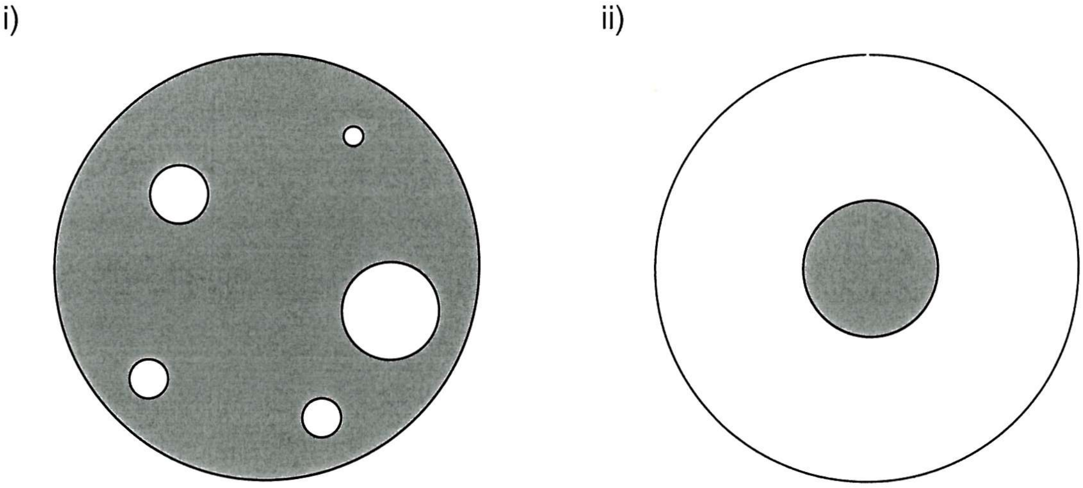


Figure 4.3 Two barnacle populations, the barnacles (consumers) are represented by the shaded area, and the suitable substrate (the resource) is left unshaded. i) High adult density: the new recruits are attracted to the relatively small area of free-space. ii) Low adult density: new recruits to the patch are attracted to the central conspecifics, thus enabling future cross fertilisation to take place.

To test the effects of adult conspecifics on the growth of a new cohort population all barnacles from a suitable substratum were removed apart from a remnant central adult group. The numbers of individuals settling onto the cleared patch were then counted at regular intervals during the settlement season. As well as total counts, cohort counts were also made. Settlement plates were deployed to give an indication of recruitment supply at locations used during the 1999 study.

The specific objective of this chapter was to characterise population growth patterns at high and low-recruitment locations for two barnacle species: *C. montagui* which can self-fertilise and *S. balanoides* which cannot. By clearing patches of rock to leave remnant adult groups of varying size the relative effects of conspecifics and available free-space could be determined. An independent assay of recruitment strength was estimated by deploying settlement plates. These were adapted from terracotta titles and allowed an independent assessment of settlement onto a uniform substrate to be analysed. The rate of population growth under each regime and treatment could then be compared to arithmetic and geometric increase and comparisons to classical open and closed models made. This chapter complements the previous chapter on settlement patterns, and uses data from the same experimental treatments.

4.3 METHODS

4.3.1 Study organism and locations

Two barnacle species were used to study population growth: *Semibalanus balanoides* (L.) and *Chthamalus montagui* Southward (for a description of *C. montagui* see Chapter 3).

S. balanoides is common to abundant around the mid-tidal level on moderately sheltered shores (Connell, 1961; Stubbings, 1975), or alternatively higher up on more exposed coasts (Hayward *et al.*, 1996). *S. balanoides* can be found in large numbers in Western Europe including Arctic Norway, Iceland and on the North Atlantic coast, it is the most widespread British intertidal barnacle (Rainbow, 1984). Gregarious settlement of cyprids has been noted in *S. balanoides* (Knight-Jones & Stevenson, 1950; Barnett & Crisp, 1979; Wethey, 1984b). Cross fertilisation is obligatory and copulation occurs during November and early December (Rainbow, 1984) individuals produce one clutch of eggs per annum (Moore 1935; Barnes & Barnes 1968). These hatched nauplius larvae are generally released in March (Crisp, 1959) with typically 400-8000 larvae released by each individual (Barnes & Barnes, 1968). Planktonic nauplii develop through 6 instars into non-feeding cyprid larvae. These cyprid larvae drift and swim in the plankton for two to three weeks before they actively seek out a suitable substratum to settle upon (Lucas *et al.,* 1979). In the United Kingdom the process of settlement takes place between March and July depending on seasonal fluctuations (Crisp, 1962; Hawkins & Hartnoll, 1982; Kendall *et al.*, 1982). *S. balanoides* individuals can settle and accumulate on numerous types of substratum and are consequently regarded as being of considerable economic importance as a constituent of marine fouling communities (Stubbings, 1975).

The locations of the field sites used in this study depended on the presence of the barnacle species and the level of recruitment based on background density (see settlement plate results, Section 4.4.1, for confirmation that background density did reflect recruitment level). In 1998 the locations chosen were Sidmouth, East Devon (3°14'13"W., 50° 40'56"N.) and Cowes, Isle of Wight (1°17'47"W., 50°45'41"N.) for *S. balanoides* and Portland Bill, Dorset (2°26'35"W., 50°28'42"N.) along with Sidmouth, Devon for *C. montagui*. In 1999 only *S. balanoides* settlement was observed. The locations used in 1999 were all positioned around the Isle of Wight, these were Cowes, Totland (1°33'36"W., 50°40'45"N.), Ventnor (1°12'25"W., 50°35'49"N.), and Seaview (1°06'49"W., 50°43'02"N). Recruitment levels have been found to vary between locations, Sidmouth has significantly higher recruitment levels than both Portland and the Isle of Wight (Herbert, in prep.).

At all of the respective locations the barnacle species under observation was the most abundant barnacle species present. For descriptions of each study location and details of other species found at each location refer back to Chapter 3.

Although Sidmouth was used to monitor both *S. balanoides* and *C. montagui* settlement during 1998 their respective settlement seasons are temporally separate (Rainbow, 1984). The position of the populations on the shore also differs between species, *S. balanoides* are typically found lower on the shore than *Chthamalus* species (Crisp, *et. al.*, 1981). Settlement counts therefore only include the barnacle species under observation. However, care was taken to select remnant adult populations that were solely comprised of the barnacle species being studied.

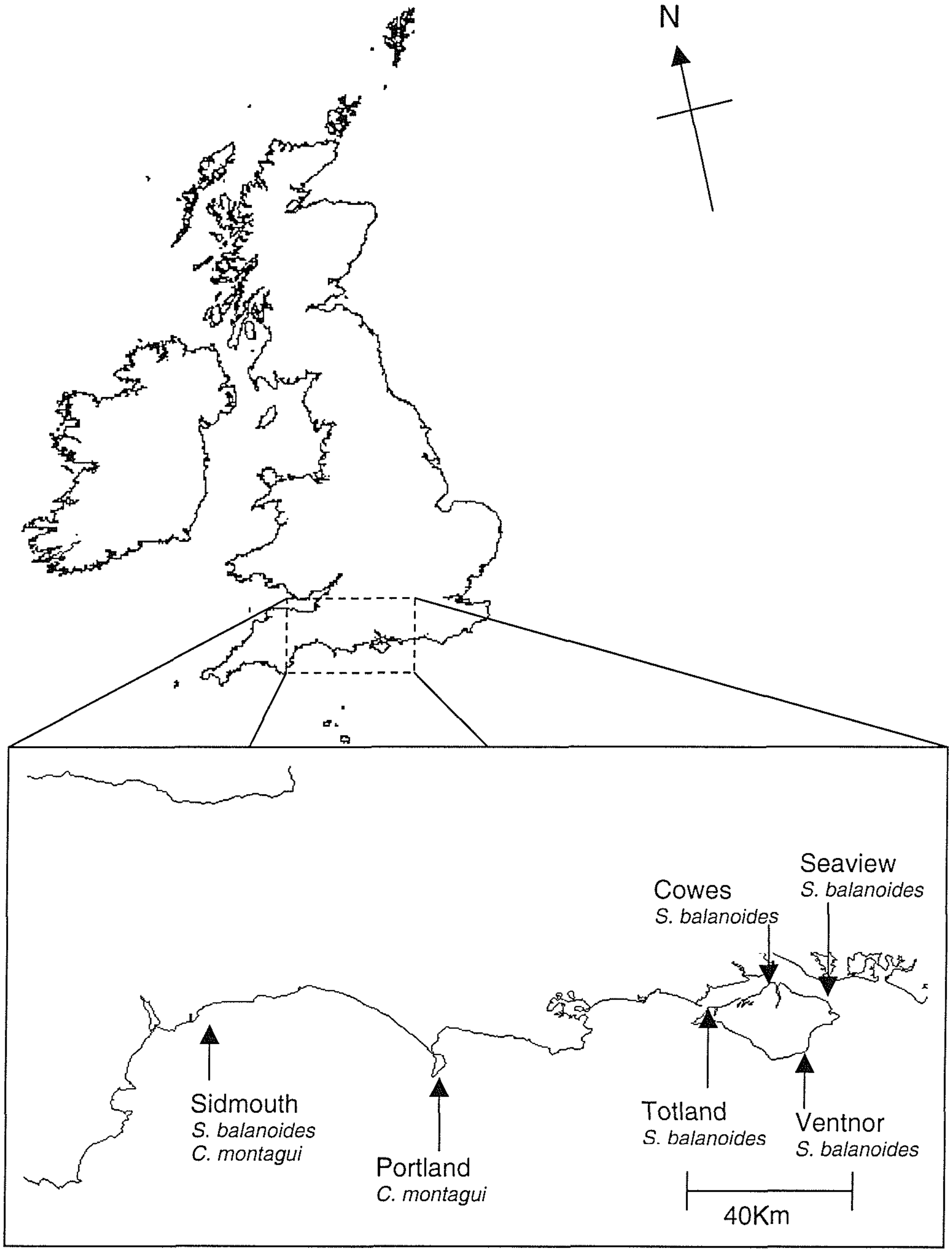


Figure 4.4 The boxed area in the top map shows the location of the study areas with respect to the rest of the United Kingdom. The insert shows the spatial relationship between the locations along the south coast. Locations used in 1998 for *S. balanoides* comparisons were Sidmouth and Cowes, and for *C. montagui* comparisons Sidmouth and Portland. Locations used in 1999 for *S. balanoides* comparisons were the four locations around the Isle of Wight, Cowes, Totland, Ventnor and Seaview.

4.3.2 Experimental design

The study was conducted from April until August 1998 on *S. balanoides* at Sidmouth and from April until November 1998 at Cowes. *C. montagui* counts were made from September 1998 through to February 1999 at Sidmouth and Portland. The 1999 study on *S. balanoides* on the Isle of Wight was carried out from April through to August.

For a description of the general design and experimental methods employed at each of the locations see Chapter 3.

4.3.2.1 S. balanoides 1998

Suitable substratum with both high (> 80 barnacles / 25 cm^2) and low (< 10 barnacles / 25 cm^2) densities of adult *S. balanoides* were selected at Cowes. Since the overall background densities at Sidmouth were much higher than those at Cowes, the division between the high and low-recruitment shores reflected this. At Sidmouth the high-recruitment shore had more than 120 barnacles / 25 cm^2 whereas the low-recruitment shore had < 20 barnacles / 25 cm^2. Suitable patches for manipulation were then selected within the designated recruitment shores at each of the locations. All treatment patches used within a shore were selected to have a similar initial covering of barnacles. Each patch was randomly assigned a treatment from the choice of 0, 1, 2, 4, 8, 16, and 32 adult barnacles. All adult barnacles were cleared from a square area of at least 10 × 10 cm around the remnant adults. This set of treatments was repeated twice more to give three replicates at each recruitment level at each location (see Figure 4.5 for a diagram of the experimental design).

4.3.2.2 C. montagui 1998

The experimental design is detailed in Chapter 3, Figure 3.2. The design differs from that used for the 1998 *S. balanoides* study in that the cleared area was circular with a diameter of 30 cm. Replicates were prepared in two areas within a designated recruitment density shore, though treatments were limited to only 0, 8, 16 and 32 adults.

4.3.2.3 *S. balanoides* IoW 1999

The experimental design is detailed in Chapter 3, Figure 3.2. The design differs from that used for the 1998 *S. balanoides* study in that the cleared area was circular with a diameter of 30 cm. Treatments with 0, 2, 4, 8, 16 and 32 adults were prepared at two low-recruitment and two high-recruitment locations around the Isle of Wight.

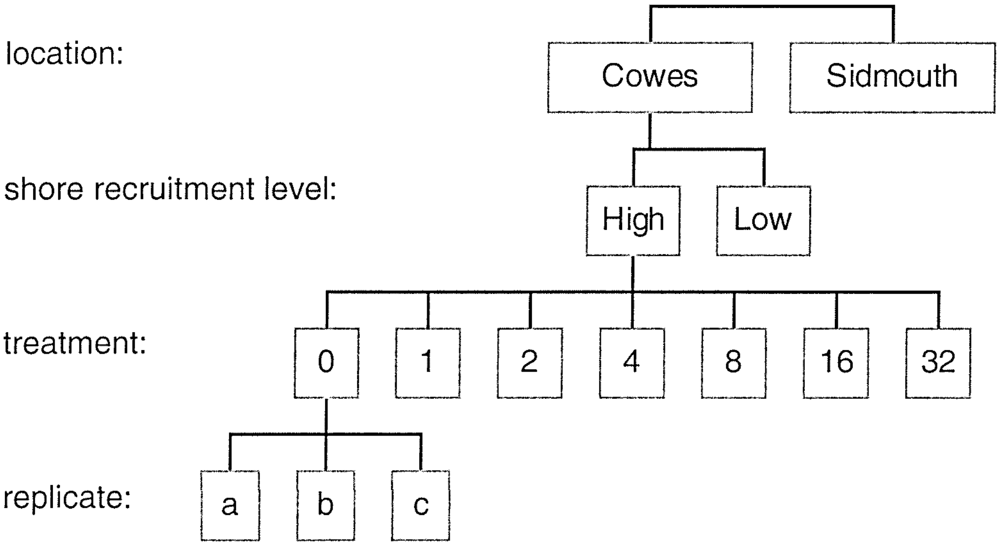


Figure 4.5 The experimental design used in the *S. balanoides* 1998 study (see Chapter 3 for the experimental design used in the other studies). Only one branch of the experimental tree is shown. All other branches are identical to the one shown.

4.3.2.4 *Settlement plates*

As well as preparing treatment patches settlement plates were deployed at each of the four locations used in the 1999 study (as described in Chapter 3). Settlement plates were used to independently assess the relationship between location and recruitment levels. As the plates used were the same at all four locations relative settlement could be compared and ranked.

4.3.3 Sampling

At this point it is important to make clear the distinction between settlement and recruitment. Settlement is used to describe those barnacles which have attached to a surface after habitat selection, whereas, recruitment has been defined as those individuals that have survived settlement and have become part of the adult population (Connell, 1985; Caffey, 1995). However, recruitment has been shown to reflect settlement (Holm, 1990) in barnacles. Consequently, in this study we refer to the number of individuals landing on a treatment patch as settlers, though we use recruitment to describe the supply of individuals.

Numbers of settlers on settlement plates were recorded during the *S. balanoides* 1999 study. Plates were removed from the locations during each visit and returned to the laboratory in sealed containers. Once removed new sterilised plates were immediately deployed in their place. On return from the location the numbers of individuals were counted on each plate. A 5× magnification hand lens was utilised to make identifications. The settlement plates provided an independent assay of recruitment strength with which settlement onto treatment patches could be compared.

During the 1998 *S. balanoides* and *C. montagui* settlement seasons observations were made in the field weekly for the first two months of settlement after which they were reduced to fortnightly. In 1999 observations were made twice a week for the first month of settlement, then weekly until no further settlement was observed at any of the locations. Minchinton & Scheibling (1993b) have documented the effect of sampling frequency and have highlighted the need to sample all treatments within a study with equal frequency.

On each visit to the locations the total number of settlers into each treatment patch was recorded. Because the position of individuals in each quadrat were not recorded these counts represented cumulative settlement. The quadrat sizes used to assess population growth were not consistent between settlement seasons. In 1998 nested square quadrats 5 × 5 cm and 10 × 10 cm were used to count *S. balanoides* settlement. For both the 1998 *C. montagui* and the 1999 *S. balanoides* studies nested circular quadrats were used to ascertain population numbers. The diameters of the concentric quadrats were 5, 10, 15, 20 and 30 cm for *C. montagui* and 5, 10, and 20 cm for *S. balanoides*. Circular quadrats were marked with indelible ink onto acetate sheets. These proved to be a versatile sampling tool, being both waterproof and flexible. However, all settlement results presented in this chapter were ascertained using the largest of the quadrat areas (the others were used for analysis in Chapter 3).

Sampling was only ever carried out at a maximum frequency of twice a week; consequently settlement counts were not absolute. Between sampling, individuals may have died and consequently fallen or been removed from the treatment areas. Even daily sampling is too infrequent for an accurate estimation of settlement (Minchinton & Scheibling, 1993b) as larvae settle on each tide. However, attached larvae and newly metamorphosed *S. balanoides* often remain in place for up to several days after they have died (see Connell, 1985). As the frequency of counts was comparable between locations within a settlement season, the relative settlement numbers could still be compared.

The number of settlers onto the prepared treatment patches was standardised. This was carried out so that the total free-space available to settlers was consistent between treatments i.e. the 32 adult treatments would have taken up a larger proportion of the total space when compared to the 2 adult treatments. The amount of space occupied by the central adult treatments was calculated using an image analysis software package Scion Image (1998 Scion Corporation) and photographs of the treatment patches utilised in Chapter 3. The total count of settlers could then be adjusted accordingly, so that the number of settlers could be attributed to the presence of adults and not to variations in available free-space between treatment patches at the start of the settlement season.

4.3.4 Statistical analysis

A nested General Linear Model (GLM) in Minitab was used to test for differences between the number of settlers to each treatment patch, the number of adults in each treatment, the recruitment level, the location and where applicable the area. Numbers of settlers were converted into densities to give continuous variables and all data were checked for homogeneity of variances with a Bartlett's test. Due to differences in experimental designs the GLM models used differ between the three studies.

For both the *S. balanoides* studies (1998 and 1999) there were three factors in the experimental design. The model used was identical to the *S. balanoides* 1999 GLM model described in Chapter 3, Section 3.3.4.

The model used to analyse *C. montagui* settlement numbers was identical to the *C. montagui* GLM model described in Chapter 3, Section 3.3.4.

Regressions were sought between the final mean density of settlers in each patch at each location and the size of the remnant adult group. A Spearman rank test was used to determine if regressions between treatment and settlement density were significant.

4.3.5 Adult population

Not only were the numbers of new recruits recorded but also the number of individuals that had reached the 0+ adult stage of development. The '0' refers to the 0-1 year old adult age group, and 0+ adults can be distinguished from juvenile barnacles by the clear formation of the six shell plates and a change in shell colour. They are visually almost identical to 1+ year old adults though do not reproduce until the following breeding season (Rainbow, 1984). Therefore, the growth rate of the adult population could be analysed along with the settlement numbers.

A qualitative analysis on the cumulative number of 0+ adults identified arithmetic increase over time at several shores, as might be expected for an open system. These shores fitted a linear model of increase over time and abundance's of adults were not analysed further. However, at some shores adult populations appeared to increase geometrically. Since geometric increase is predicted from mutual attraction between individuals (as described in Chapter 3) we analysed these dynamics further. The geometric model is given by:

$$N_t = N_0 \cdot e^{r \cdot t} \quad \text{or} \quad ln(N_t) = ln(N_0) + r \cdot t \tag{4. 1}$$

Where N_t is the number of adults present in the population at time t, r is the gradient of increasing $ln(N)$ with t and therefore also the per capita rate of increase. For the treatment patches we set $ln(N_0) = 0$ and we define t, as the number of days since the first settlers arrived, where day 0 was the last sampling date at which no adults were observed in any of the treatments.

A variation on this model was used to test for population growth that was either less than exponential and therefore tending towards linearity, or greater than exponential ('compressed' exponential). The modified formula for exponential growth used was:

$$N_t = N_0 \cdot e^{(r \cdot t^b)} \tag{4. 2}$$

where b is a power function. When $b = 1$ population growth is exponential (i.e. geometric). If $b > 1$ then the observed population growth is greater than exponential (i.e. approaching compressed exponential), and if $b < 1$ population growth is less than exponential (i.e. approaching arithmetic).

Using the *solver* function in Microsoft Excel (which uses Generalized Reduced Gradient (GRG2) nonlinear optimization code) we were able to use the compressed exponential growth model (eqn 4.2), to calculate which values of r and b best represented the observed population growth data for adults. The resulting b value then allowed us to place population growth on a continuum between geometric and arithmetic.

To test for significant deviations of b from unity in the samples, an adjusted 2-way t-test was used to identify a difference between the two samples as outlined by Sokal & Rohlf (1994). The adjustment of the standard t-test allows one of the data sets to have a single value, (in this case the single value was $b = 1$), consequently this single observation does not contribute to the degrees of freedom or to the estimate of the within group variance (Sokal & Rohlf, 1994). This single value was tested against the mean value of *b* calculated from each replicate. The modified t-test formula used was:

$$t_s = \frac{Y_1 - Y_2}{\sigma_2 \sqrt{\frac{n_2 + 1}{n_2}}} \tag{4.3}$$

where Y_1 is the single value ($b = 1$), Y_2 is the mean value of *b* from the 3 experimental replicates, σ_2 is the standard deviation of *b* from the 3 replicates, and n_2 is the sample size ($n_2 = 3$). The number of degrees of freedom are given by $n_2 - 1$.

4.4 RESULTS

4.4.1 Independent assessment of recruitment using settlement plates

Whilst making the choice of locations to use in the 1999 *Semibalanus balanoides* study barnacle counts were made at approximately 20 areas of coastline around the Isle of Wight. The four locations chosen where selected on the basis of the background densities of *S. balanoides* populations, with two high-density locations (Cowes and Seaview), and two low-density locations (Totland and Ventnor). By deploying settlement plates at these locations we were able to assess whether there was any relationship between the observed background barnacle population density and recruitment levels.

In total over 660 *S. balanoides* individuals were observed on the settlement plates, 98% of which were onto plates at the high-density locations (see Figure 4.6i). Plates at Seaview attracted the most settlers and accounted for over 87% of all settlement onto plates, with settlement at Cowes contributing towards 11% of the total settlement. Settlement onto the plates at the low-recruitment locations was minimal. Only 1.8% of total plate settlement was observed at Totland. At Ventnor we only counted 2 individuals on settlement plates during the whole of the settlement season, consequently the results from Ventnor are not displayed in Figure 4.6.

The rate of settlement onto plates was not constant over time as shown in Figure 4.6ii. There were 3 settlement pulses onto the plates at the high-density locations; this was most clearly seen at Seaview. An early pulse occurred at the beginning of the settlement season. The largest of the pulses occurred mid-May during the middle of the settlement season (over 70% of all settlement onto the plates occurred during May). A final pulse towards the end of the settlement season was also evident. Settlement pulses at the low-recruitment locations were not as obvious as they were at the high-recruitment locations due to the low settlement numbers. However, there was some evidence to suggest the presence of a settlement pulse during the middle of the settlement season, which coincided with the large pulse at the high-density locations.

Settlement onto the plates was minimal between the first and second settlement pulse; however, there was considerable settlement into the treatment patches throughout the first 60 days (see below). Although there is a difference between settlement onto the plates and the treatment patches, the plates can still be used to compare relative settlement between locations.

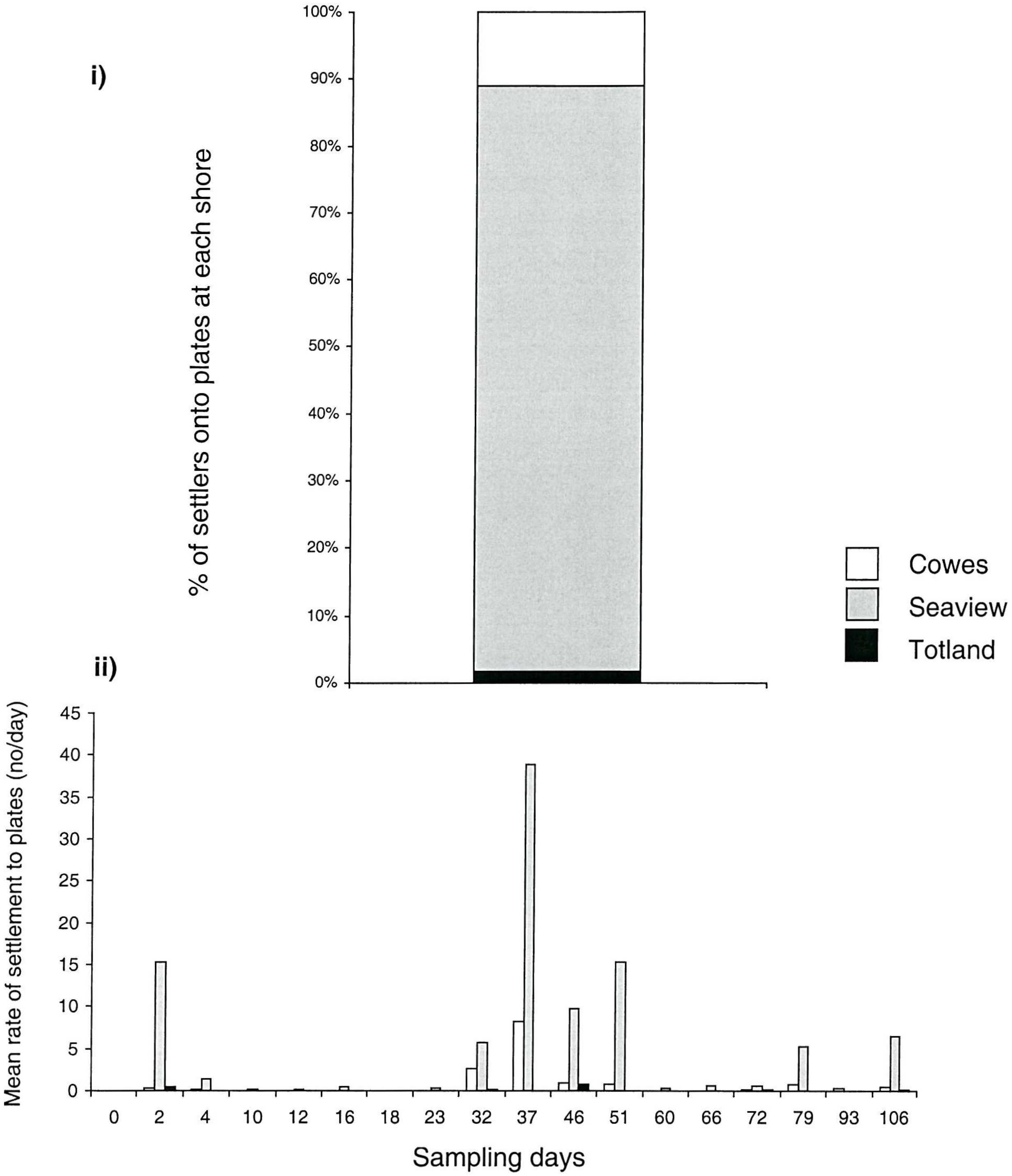


Figure 4.6 A comparison between the number of *S. balanoides* on settlement plates during the 1999 study. i) a comparison of settler numbers at each location expressed as the total number of settlers to all locations. ii) the mean settlement rate to either 3 or 4 settlement plates observed between sampling date after no settlement was observed (day 0). Ventnor is not shown, as settlement at this location was minimal.

4.4.2 Total settlement on treatment patches

Barnacle settlement varied markedly, not only between species but also between locations and in certain cases between recruitment densities. Mean total numbers of barnacle settlers in each treatment from the beginning to the end of the settlement season are presented in Figure 4.7 to Figure 4.11 in chronological order for both species at all locations to allow local treatments to be compared.

4.4.2.1 S. balanoides 1998

At Sidmouth the majority of settlement had occurred by day 50 towards the end of May, as shown in Figure 4.7. After day 50 there was some fluctuation in settlement numbers until day 80. At Sidmouth a marked difference was observed in settlement between shores and also between the treatments. Where recruitment was low most settlement occurred onto those patches with the greatest numbers of adult individuals left at the centre. The least number of settlers were found where there were no central adults. The other treatments fitted between these two with the number of settlers increasing in proportion to the size of the remnant adult group. Where recruitment and background density were high an inverse trend was observed. The treatment patches with the greatest number of remnant adults attracted the fewest number of new settlers, whereas the patches with the least number of adults attracted the most, though this relationship was not entirely proportional.

Sidmouth had higher total settlement than Cowes. Maximum settlement numbers at Sidmouth reached approximately 800 individuals, whereas a maximum of only 170 individuals was observed at Cowes. The first settlement at Cowes was not observed until 10 days after settlement had begun at Sidmouth in late March.

At Cowes 1998 low-recruitment the majority of settlement had occurred by day 50, in early June, whereas where recruitment was high there was still settlement up to day 80, early July (see Figure 4.8). This may explain why there was more overall barnacle settlement into the high-recruitment treatment patches than the treatments subjected to low-recruitment, (maximum high-recruitment = 170, maximum low-recruitment = 80).

At day 50 both the high and low-recruitment treatments had approximately the same number of settlers.

Both the high and low-recruitment shores at Cowes showed a weak general trend with respect to treatment and the amount of settlement. The more adult conspecifics left at the centre the greater the number of settlers found at the end of the study as shown in Figure 4.8. This was not the case at Sidmouth, consequently settlement numbers depended on the interaction of treatment by location'(recruitment): $F_{12,56} = 6.73$, $p < 0.001$.

The relationship between treatment and the number of settlers was not as strong at Cowes as it was at Sidmouth. The association did not hold when comparing exact treatments, i.e. we did not necessarily find that a patch with 2 barnacles at the centre had more settlers than a patch with 1 barnacle at the centre, but a patch with 32 adults at the centre always had more settlers when compared to a patch with 1 adult at the centre. We were surprised to find that the 8 adult treatment had the least number of settlers where recruitment was high, but the most where recruitment was low. Settlement onto the high-recruitment treatment patches appeared at times to fluctuate between visits to the location, suggesting the possibility of recruitment pulses.

4.4.2.2 *C. montagui* 1998

Numbers of *C. montagui* settlers onto treatment patches at Portland increased steadily throughout the first 50 days of recruitment. At Portland most settlement was observed onto the high-recruitment area 1, as shown in Figure 4.9. At Portland the majority of settlement had occurred by day 50, in late September, after which there was some degree of mortality, most noticeably at the high-recruitment area 1. The greatest numbers of settlers were to be found in the 16 and 32 adult treatments though the least number of settlers were not always found in the 0 adult treatment. Consequently, the ANOVA analysis showed that there were no differences between treatments and settlement (location effect $F_{1,2} = 8.87$, $p > 0.05$). However, the treatment effect did influence the number of settlers differently at each of the areas (interaction of area'(recruitment) with treatment effect $F_{6,73} = 9.54$, $p < 0.001$).

Maximum settlement numbers at Sidmouth occurred onto the high-recruitment area 1 as shown in Figure 4.10. Again the majority of settlement had occurred by day 50. The 0 adult treatment had the least number of settlers at 3 of the 4 areas at Sidmouth. The difference in settlement numbers between the high-recruitment area 2 and the low-recruitment areas 1 and 2 was minimal.

4.4.2.3 *S. balanoides* 1999

In the 1999 *S. balanoides* study the low-recruitment locations had fewer settlers onto the treatments patches than the high-recruitment locations (recruitment effect $F_{1,2} = 438.9$, $p < 0.01$). The first settlers were observed on the 13th of April at all four locations, with the majority of settlement having taken place by day 60. The numbers of settlers onto the 0 adult treatments were consistently the lowest, whereas the 16 and 32 treatments always had the highest, as shown in Figure 4.11. The effect of the remnant adults was found to be significant and did not vary between locations or recruitment levels (treatment effect $F_{5,10} = 7.05$, $p < 0.01$). The distinction between the treatments and the number of settlers was most noticeable at Seaview with a clear divide between the 0, 2 and 4 treatments and the 8, 16 and 32 treatments. Although the greatest number of settlers was found in the 8, 16 and 32 treatments at Seaview the 0, 2 and 4 treatments had settlement numbers comparable to the same treatments at the two low-recruitment locations. However, settlement numbers onto the 0, 2 and 4 treatments at Cowes were similar to the numbers obtained from the 16 and 32 treatments at the low-recruitment locations. The rate of settlement was not consistent between visits with rapid increases and decreases in settlement numbers occurring between visits, this was especially noticeable at the high-recruitment locations (e.g. day 60 at Seaview and Cowes).

4.4.2.4 Overall comparison between recruitment level, treatment and settlement density

Settlement density, assessed by indexing shores according the final density of settlers in the 32 adult treatment, or the 0 adult treatment for Sidmouth high-recruitment 1998 (see below), had a marked influence on the magnitude of the treatment effect as shown in

Figure 4.12. The treatment effect was very strong where settlement was high and decreased at lower settlement densities especially at *S. balanoides* locations (from left to right in Figure 4.12). At the highest *S. balanoides* settlement location, which was identified as being Sidmouth high-recruitment in 1998, a negative regression was identified between the density of settlers and the number of adults. This regression was significant at the $p < 0.01$ level. All other regressions at all locations and areas were shown to be positive for both *S. balanoides* and *C. montagui*. Where recruitment was deemed high Figure 4.12 shows there was a significant regression between settlement density and treatment for *S. balanoides* at all but one of the locations (Cowes, 1998). At the low-recruitment locations there was a significant regression between settlement density and treatment at Sidmouth, Totland and Cowes 1998 whereas at Ventnor there was not. Again the settlement results from Ventnor differ from the other three locations used in the 1999 *S. balanoides* study (see also Chapter 3). Results from the *C. montagui* study showed that in general regressions between treatments and the density of settlers was not significant, except at the highest settlement location Sidmouth High 1 and also at Portland Low 1. At both of these locations the regression was significant at the $p < 0.01$ level.

Using Figure 4.12 the relative density of settlers and the identification of high and low-recruitment locations can be compared. For *S. balanoides* the highest settlers densities occurred at the locations deemed high-recruitment. Even though Sidmouth low had the second highest density of *S. balanoides* settlers Sidmouth as a location was deemed a high-recruitment location compared to Cowes 98 (see also Herbert, in prep). The shore used to study low-recruitment at Sidmouth was low relative to other shores at this location. The ranked settlement order of 1999 *S. balanoides* locations in Figure 4.12 was consistent with the ranked order extracted from the settlement plates (Figure 4.6).

The relationship between the recruitment level and the density of settlers is not as well defined at the *C. montagui* locations. In general there was more settlement at Sidmouth than at Portland at all shores except one (Sidmouth Low 2). However, it must be remembered that in Figure 4.12 settlement was indexed by the density of settlers in the thirty-two adult treatments, which did not always contain the maximum density of settlers within a location (i.e. settlement density was greatest in the sixteen adult treatment at Totland low 99 and Portland low 1).

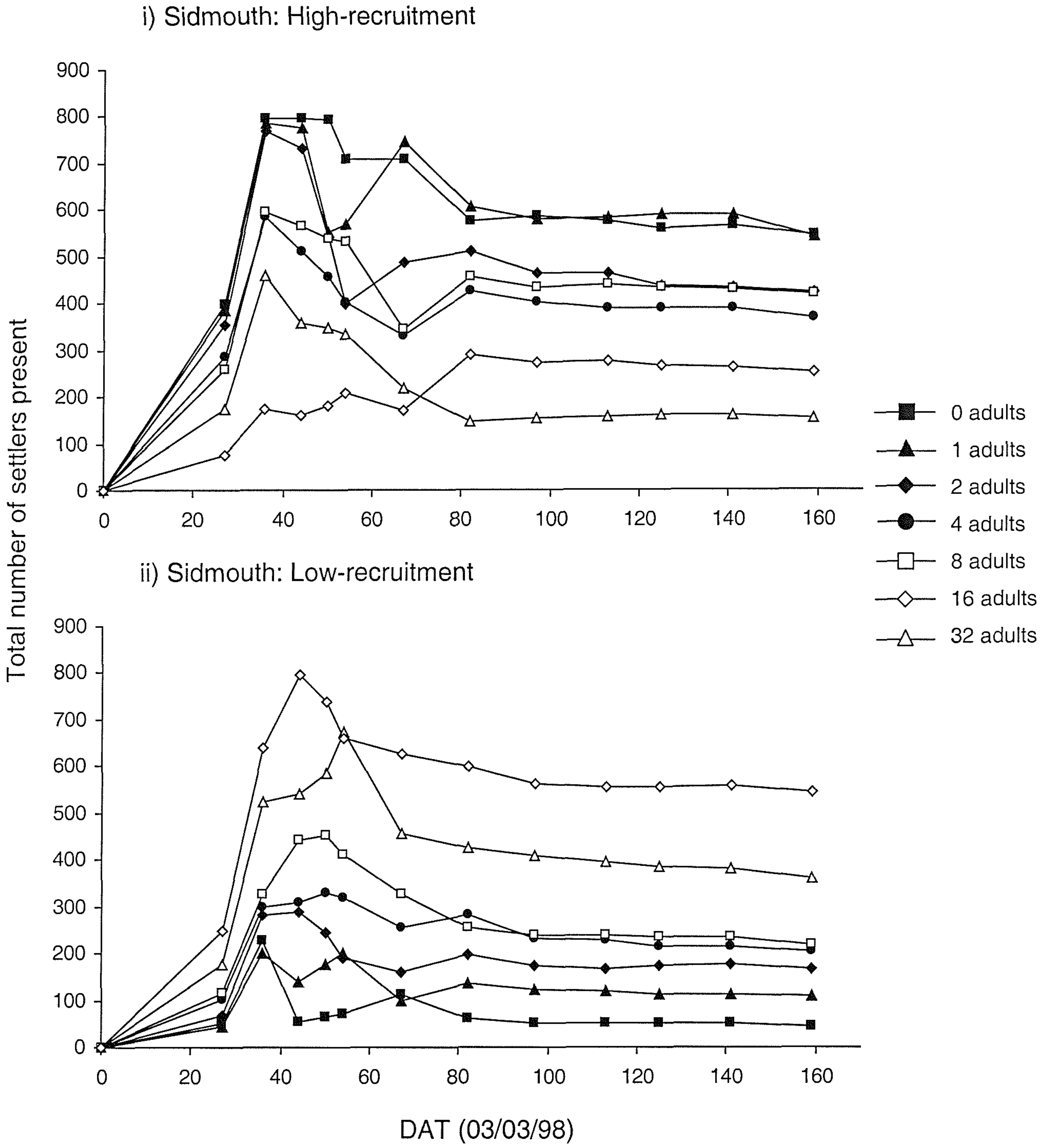


Figure 4.7 Settlement of *Semibalanus balanoides* at shown as the mean of three square patches 10 x 10 cm^2 over time at Sidmouth i) high-recruitment shore, ii) low-recruitment shore. DAT refers to the number of days after the treatment patches were initially prepared (given in parenthesis). The y-axis represents the number of recorded individuals seen at each sampling date. The figure caption identifies the treatment (the number of conspecifics left at the centre of each patch).

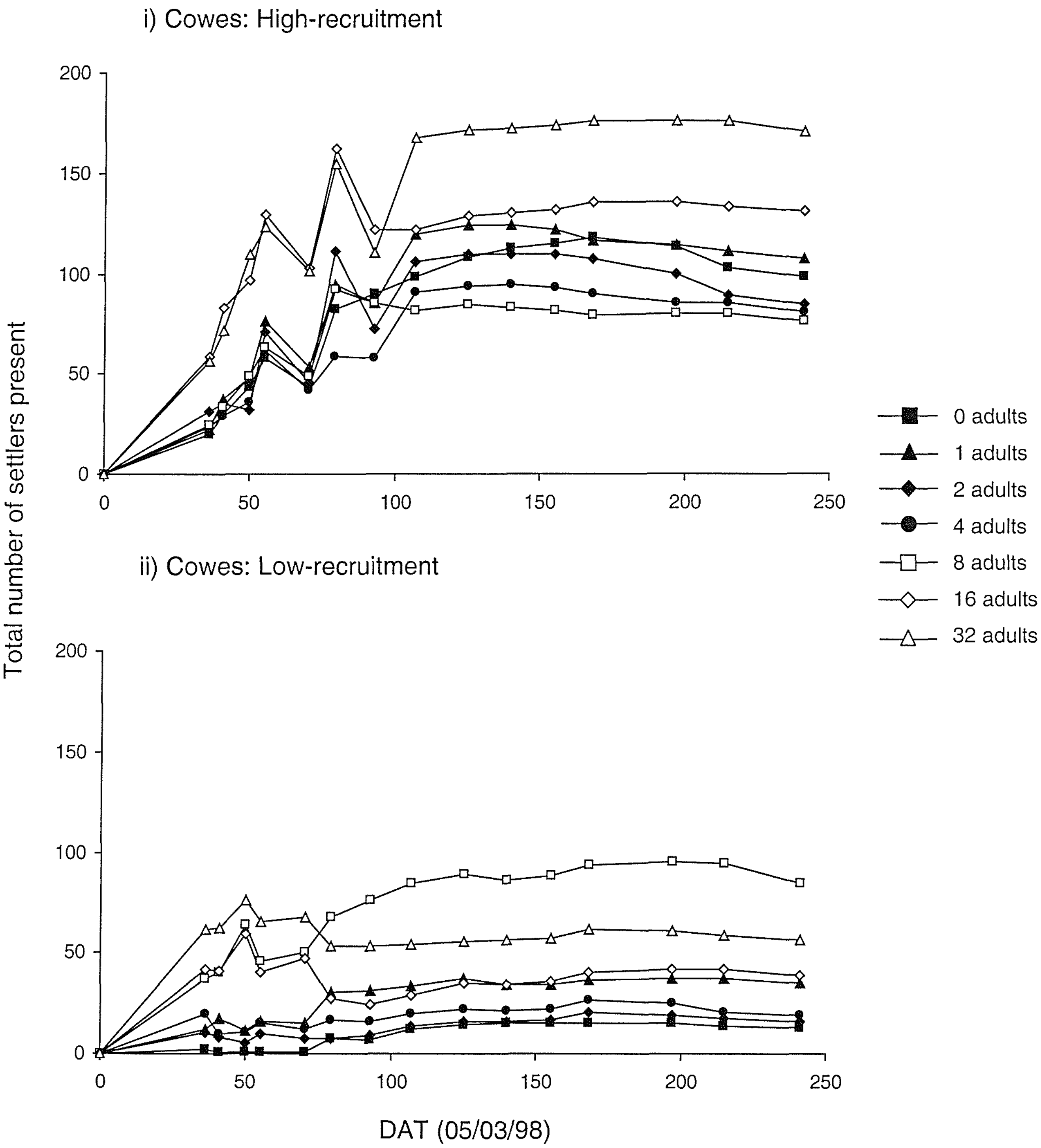


Figure 4.8 *Semibalanus balanoides* settlement shown as the mean of three square 10 × 10 cm^2 treatment patches over time at Cowes i) high-recruitment. ii) low-recruitment (see Figure 4.7 for meaning of terms).

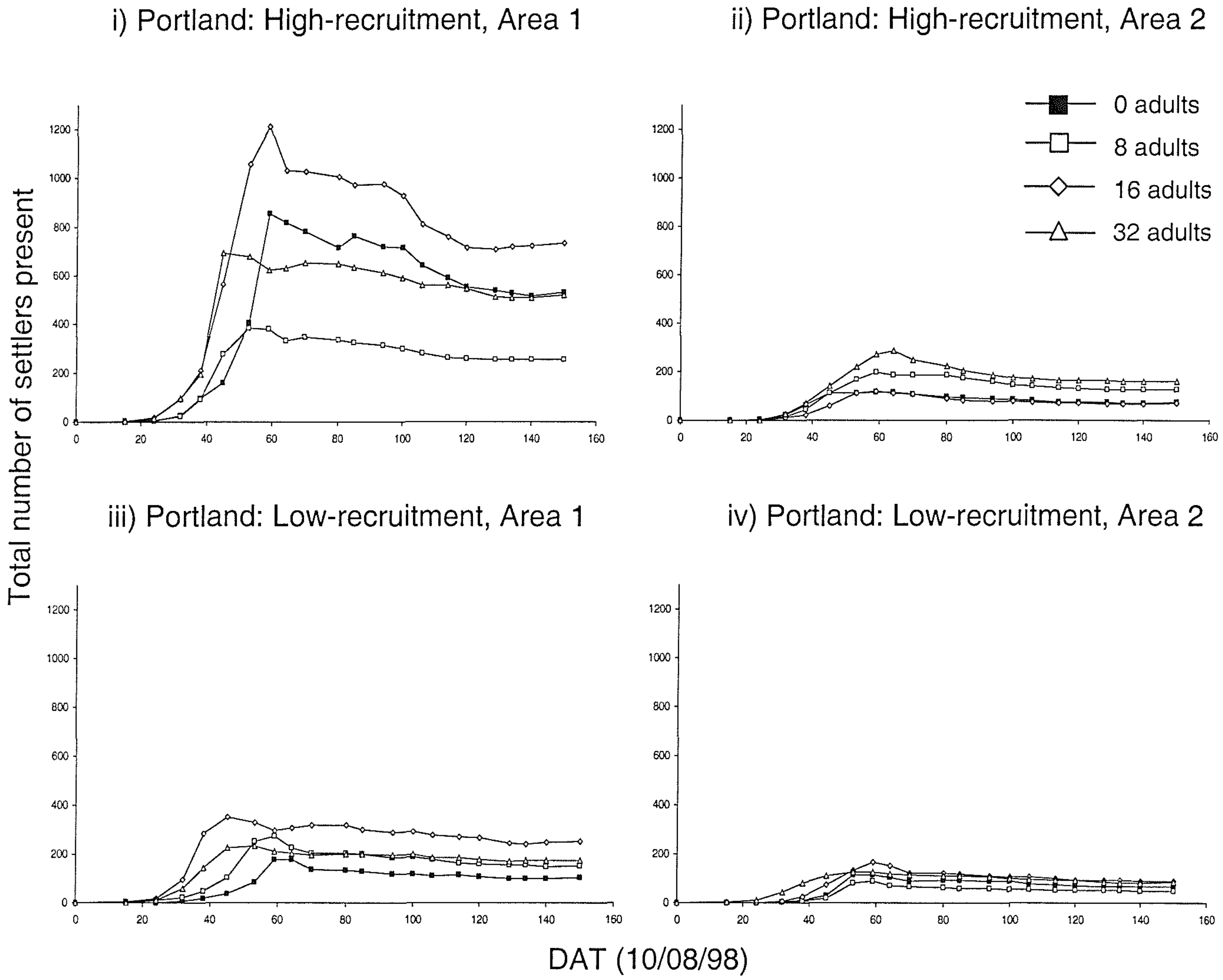


Figure 4.9 *Chthamalus montagui* settlement shown as the mean of three 30 cm diameter treatment patches over time at Portland i) high-recruitment area 1. ii) high-recruitment area 2 iii) low-recruitment 1 iv) low-recruitment area 2. (see Figure 4.7 for meaning of terms).

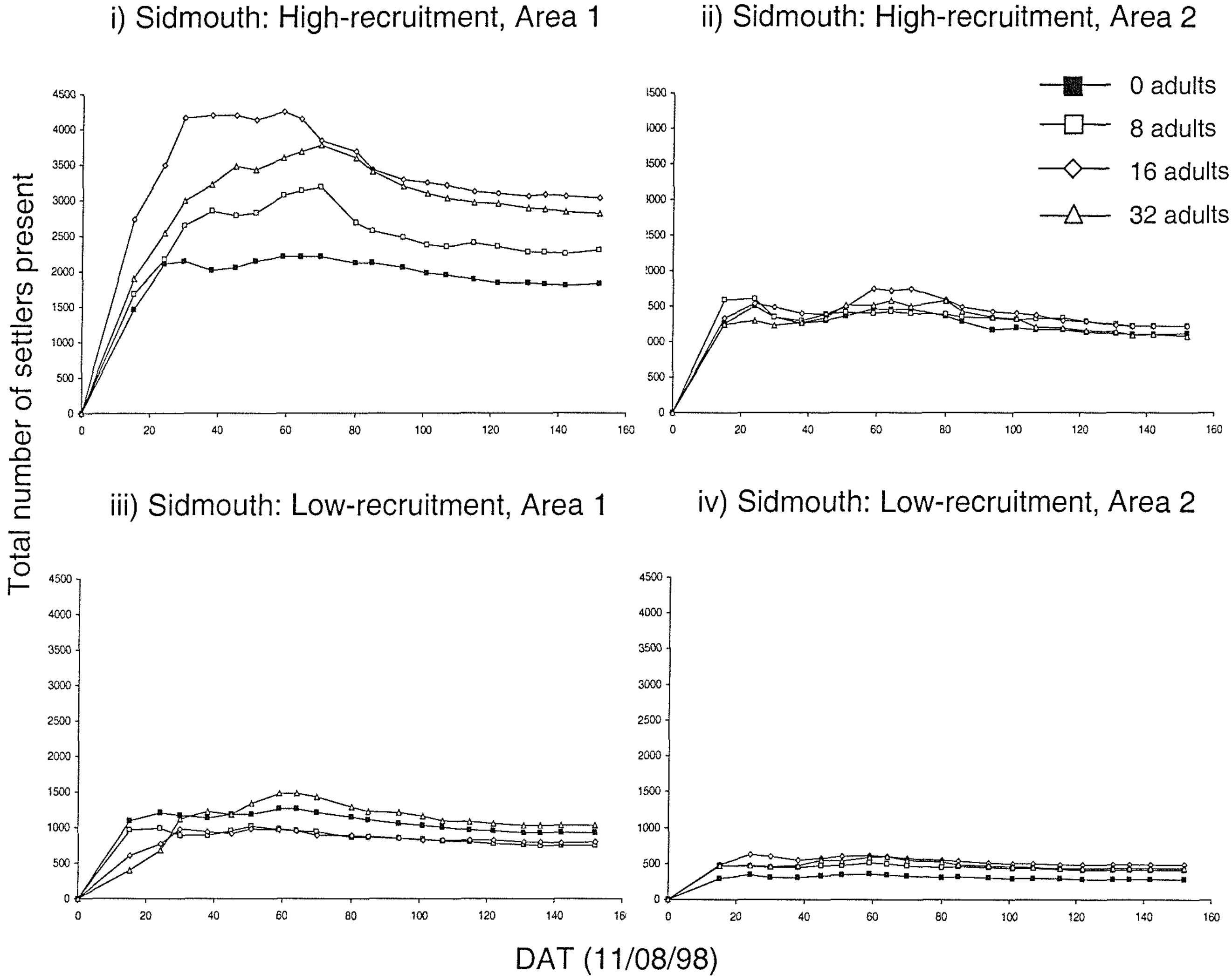


Figure 4.10 A comparison of *Chthamalus montagui* settlement shown as the mean of three 30 cm diameter treatment patches over time at Sidmouth i) high-recruitment-area 1. ii) high-recruitment area 2 iii) low-recruitment area 1 iv) low-recruitment area 2. (see Figure 4.7 for meaning of terms).

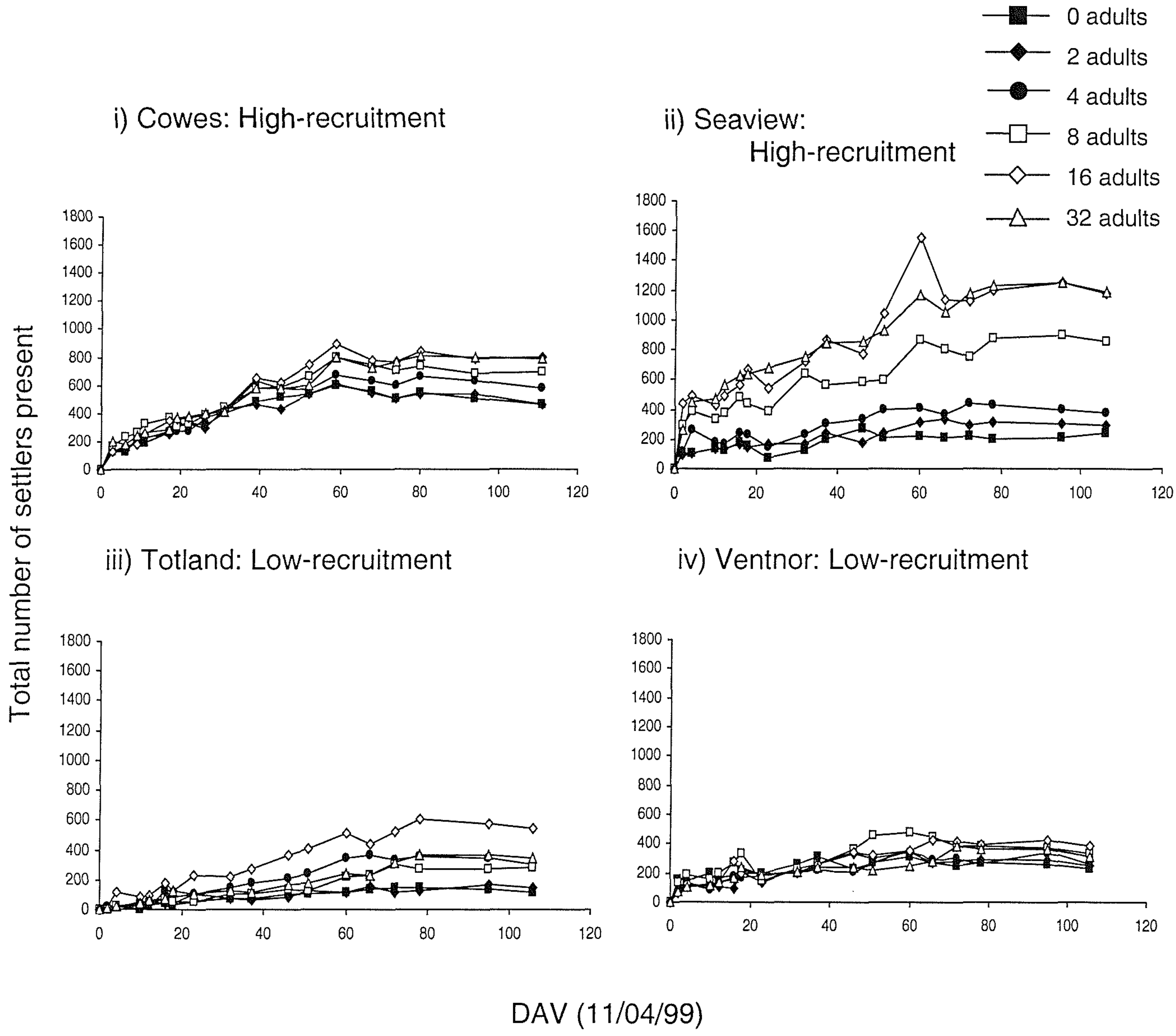
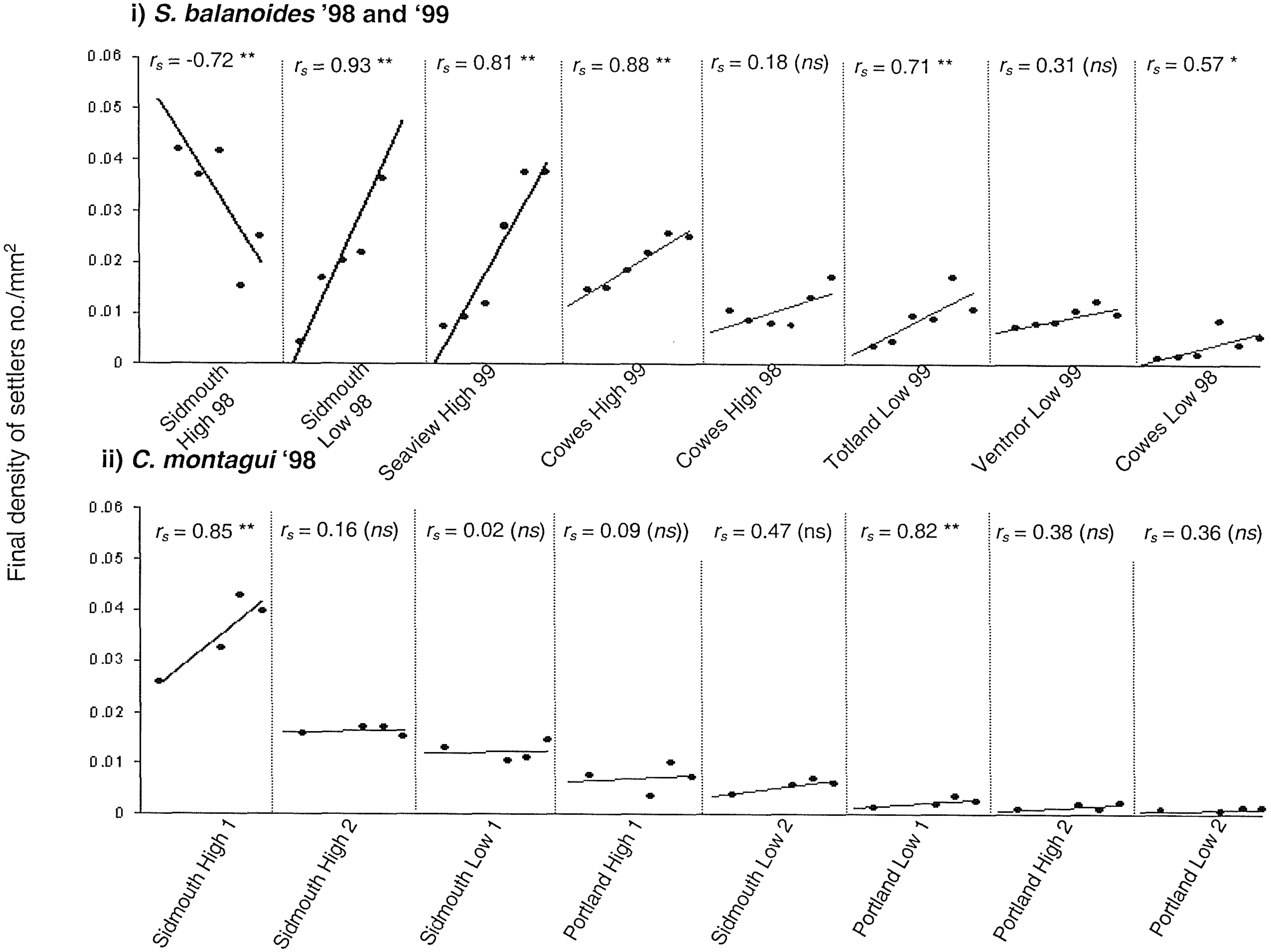


Figure 4.11 A comparison of *Semibalanus balanoides* settlement shown as the mean of three 20 cm diameter treatment patches over time around the Isle of Wight i) Cowes (high-recruitment) ii) Seaview (high-recruitment) iii) Totland (low-recruitment) iv) Ventnor (low-recruitment) . DAV refers to the number of days after the shores were visited relative to the last sampling date before the first settlement was observed (see Figure 4.7 for meaning of terms).



i) *S. balanoides* '98 and '99

ii) *C. montagui* '98

Figure 4.12 The mean final density of i) *Semibalanus balanoides* and ii) *Chthamalus montagui* in each treatment patch at each location taken from 3 replicates. Locations are displayed from highest settlement on the left to lowest on the right (where settlement is indexed by the density of barnacles in the thirty-two adult treatment). Within locations, treatments are displayed in increasing order from left to right (0, 2, 4, 8, 16, 32 for *S. balanoides* and 0, 8, 16, 32 for *C. montagui*. The Spearman rank correlation coefficients are shown for each of the plots, using the data from all 3 replicates, * = $p < 0.05$, ** $p < 0.01$, (*ns*) = not significant.

4.4.3 Between year comparison of *S. balanoides* settlement at Cowes

S. balanoides settlement data were collected at Cowes in both 1998 and 1999 from the same part of the shore. This enabled a general comparison to be made between the treatment effect over two settlement seasons at the same location. However, the experimental design was not consistent between years. To allow the comparison to be made the number of individuals in a 10 cm diameter quadrat was analysed, and the one adult treatment that was used in the 1998 study but not in the 1999 study omitted. A two-way ANOVA was then run with year and treatment as factors (Table 4.1).

Settlement at Cowes was not consistent between years; the number of settlers onto the treatment patches was greater in 1998 than in 1999. The number of settlers differed significantly among treatment types with more settlement present on treatments with the most remnant adults. Although overall settlement numbers differed between years the treatment effect did not alter between years (non-significant interaction).

Source of Variation	**Df**	**MS**	***F***	***p***
Trt	5	0.00094	3.10	**<0.05**
Year	1	0.01449	47.75	**<0.001**
Trt × Year	5	0.00060	1.96	0.12 (*ns*)
Error	24	0.00030		

Table 4.1 ANOVA comparison of the square root transformed density of 1998 and 1999 *Semibalanus balanoides* settlers in each of the treatments taken from counts on the last sampling dates. 'Trt' (number of remnant barnacles) and 'Year' (either 1998 or 1999) were treated as fixed factors, *ns* = not significant. Tests were only carried out after variances were shown to be homogeneous.

4.4.4 Adult population growth

It has been shown earlier in this chapter that initial barnacle settlement is relatively fast. Consequently, it is hard to make any predictions about the rate of population increase. The growth of the adult population was found to be slower (Figure 4.13 to Figure 4.17

displayed in order of settlement season to allow local comparisons to be made). Unsurprisingly the populations with the largest numbers of settlers also had the largest numbers of adults, whereas the populations with the smallest number of settlers had the smallest adult populations.

As also observed in the initial settlement counts there was a strong relationship between the number of remnant barnacles left at the centre of the treatment patches and the number of adults. Again for *S. balanoides* at Sidmouth high-recruitment the greatest number of adults observed were in the treatment patches with the least number of central remnants, the least adults were observed where the treatment numbers were maximised. For the other 1998 *S. balanoides* studies and the 1999 *S. balanoides* studies the number of adults was almost directly proportional to the number of remnants. Again this relationship was not as pronounced in the *C. montagui* 1998 study.

The length of time between first settlement and the first 0+ adult observed varied between locations and species. The average length of time between settlement and the first *S. balanoides* adult in 1998 was 45 days, with individuals at Sidmouth taking on average longer to make the morphological transition. However, treatment patches were only sampled on average once every 14 days, consequently the first adults may have been present any time after 31 days post-settlement. On average it took 28 days post-settlement before the first *C. montagui* adults were observed. With a sampling frequency of 7 days the first adults may have been present after 21 days. Result from the *S. balanoides* studies during 1999 showed that the first settlers took longer to turn into 0+ adults at Cowes than they did at the other 3 locations. On average the first adult was observed 21 days post-settlement during 1999, which was less than half the time it took *S. balanoides* to make the transformation in 1998. It must be noted however, that sampling frequency during the 1999 study was more regular with only a 3-day interval between treatment observations during the initial stages of settlement.

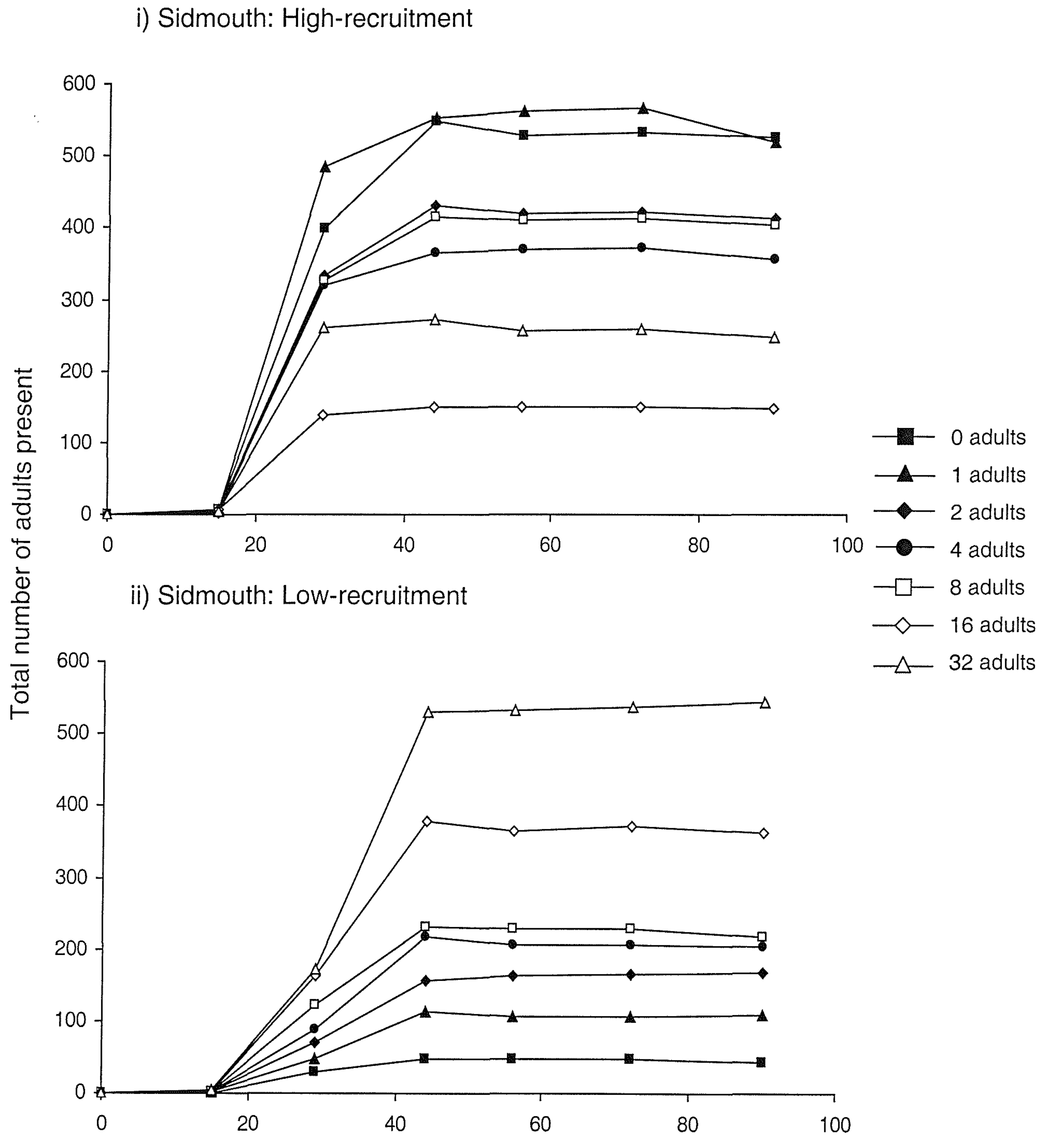


Figure 4.13 Number of *Semibalanus balanoides* adults shown as the mean of three 10 × 10 cm^2 treatment patches over time at Sidmouth i) high-recruitment ii) low-recruitment. Time is relative to the last sampling date before the first adults were observed The figure caption represents the treatment (the number of conspecifics left at the centre of each patch).

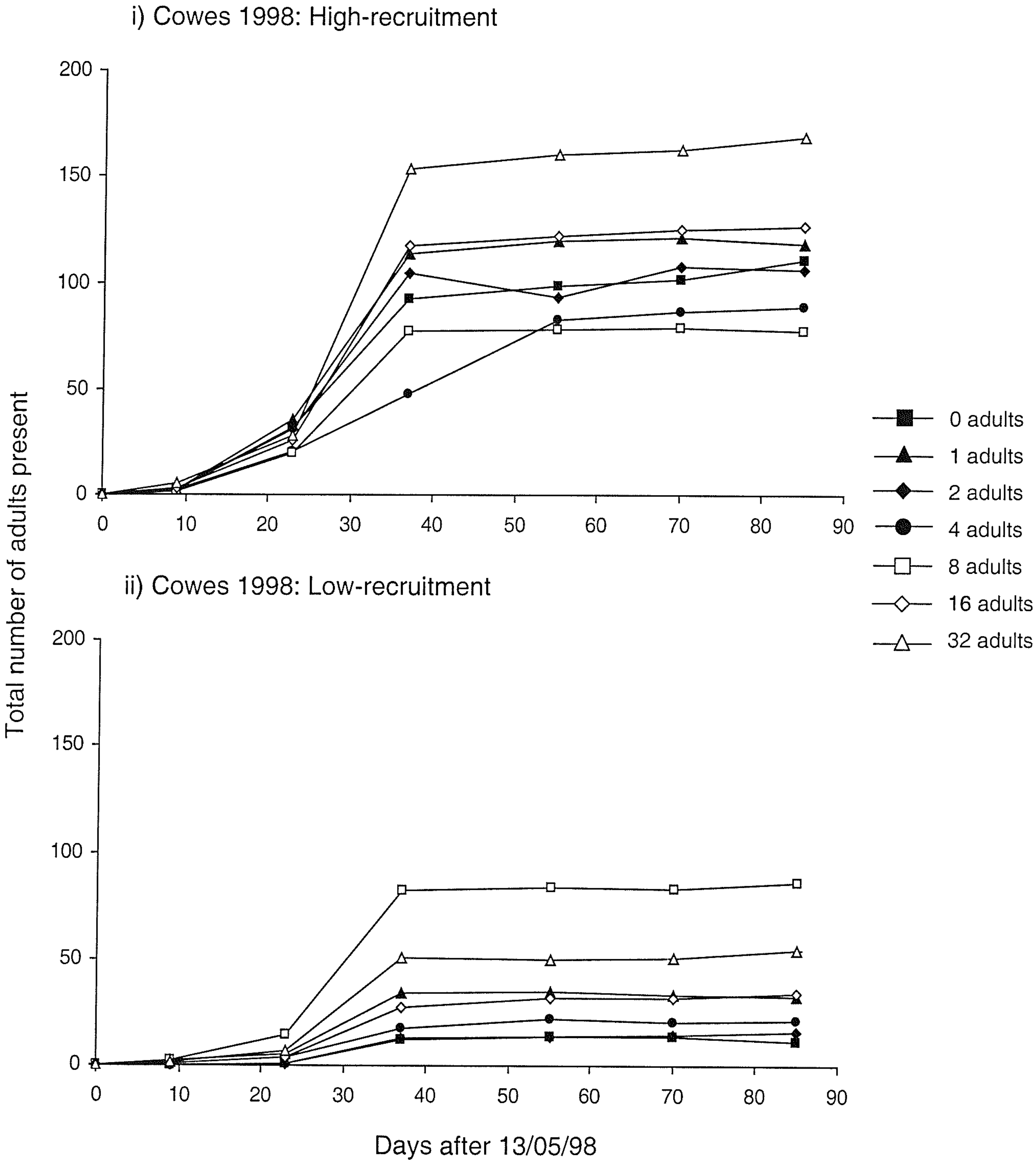


Figure 4.14 Number of *Semibalanus balanoides* adults shown as the mean of three 10 × 10 cm^2 treatment patches over time at Cowes, 1998 i) high-recruitment ii) low-recruitment (see Figure 4.13 for meaning of terms)

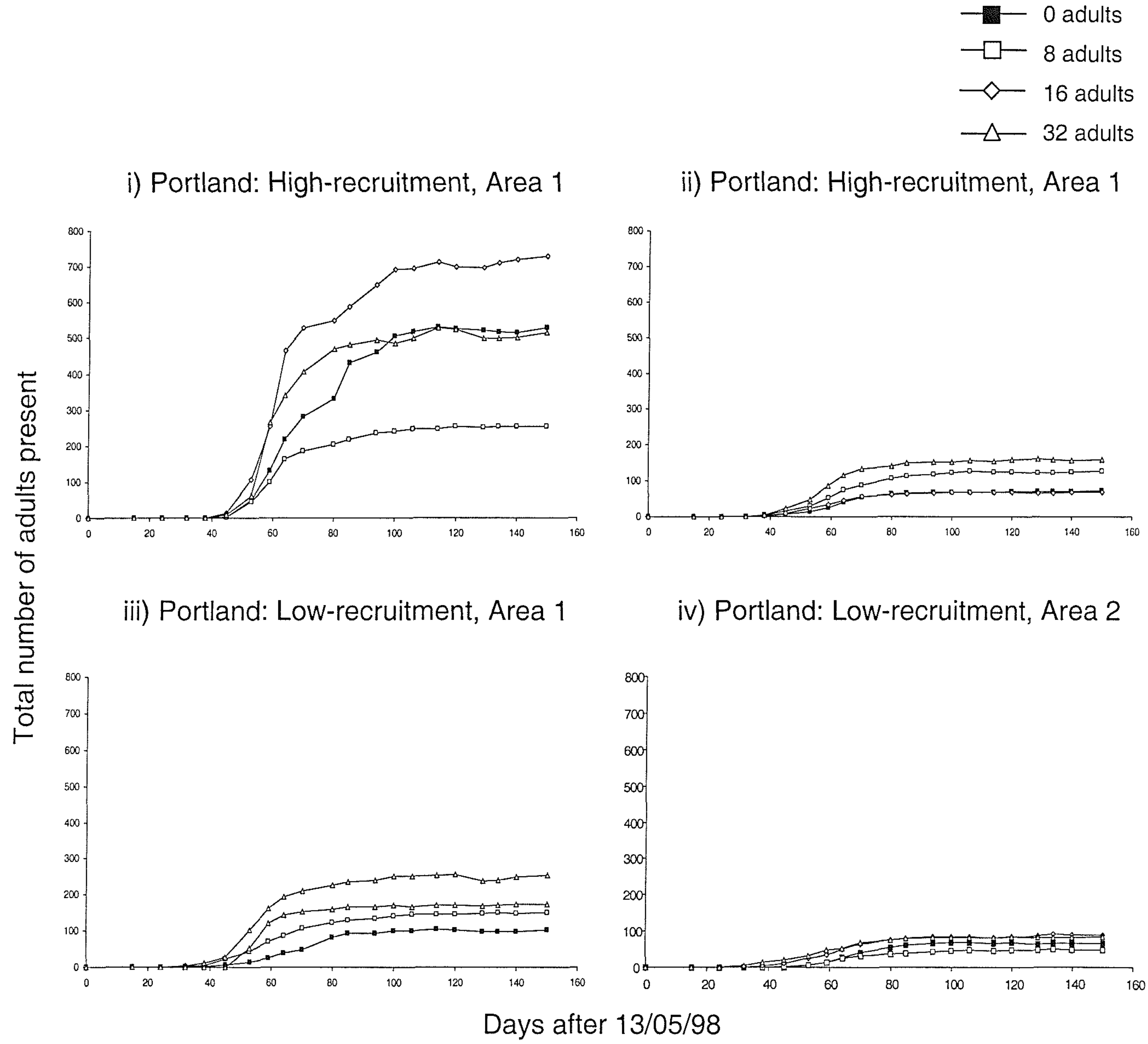


Figure 4.15 Number of *Chthamalus montagui* adults shown as the mean of three 30 cm diameter treatment patches over time at Portland i) high-recruitment area 1 ii) high-recruitment area 2 iii) low-recruitment area 1 iv) low-recruitment area 2. (see Figure 4.13 for meaning of terms).

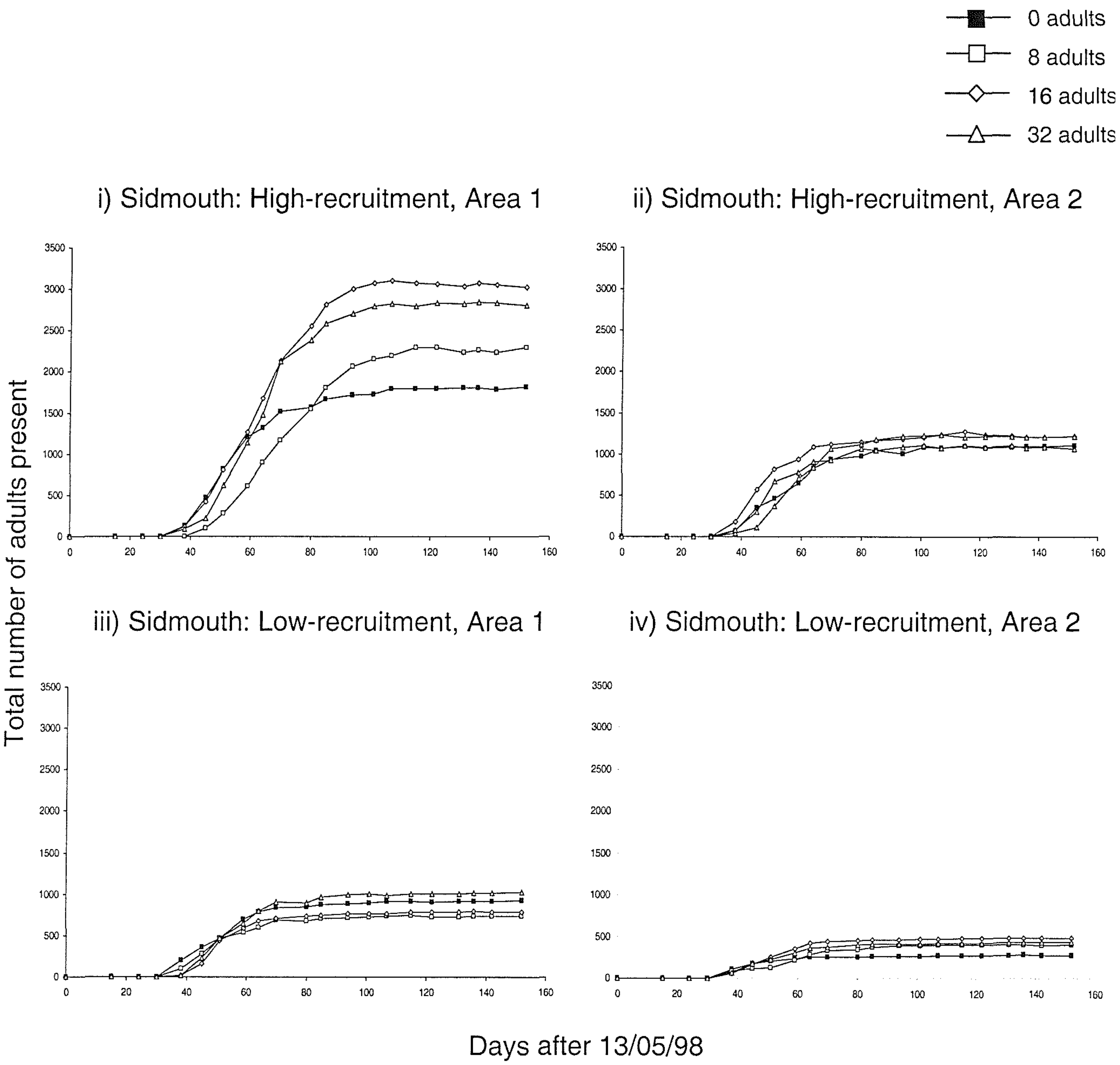


Figure 4.16 Number of *Chthamalus montagui* adults shown as the mean of three 30 cm diameter treatment patches over time at Sidmouth i) high-recruitment area 1 ii) high-recruitment area 2 iii) low-recruitment area 1 iv) low-recruitment area 2 (see Figure 4.13 for meaning of terms).

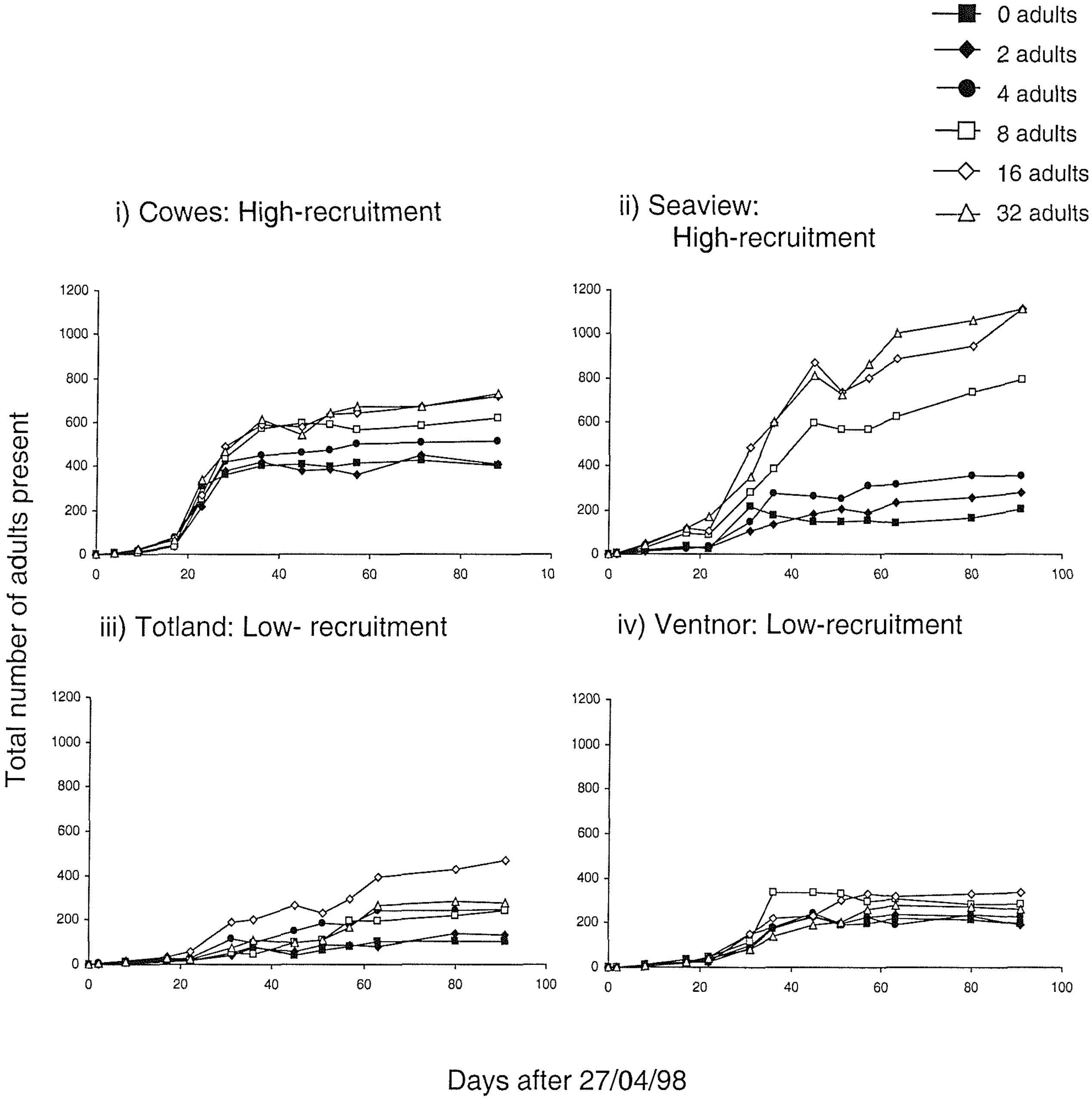


Figure 4.17 Number of *Semibalanus balanoides* adults shown as the mean of three 20 cm diameter treatment patches over time at locations around the Isle of Wight i) Cowes (high-recruitment) ii) Seaview (high-recruitment) iii) Totland (low-recruitment) iv) Ventnor (low-recruitment) (see Figure 4.13 for meaning of terms).

4.4.5 The rate of adult population increase

The graphs of adult population growth enabled us to compare the rate of population increase to two alternative growth models: geometric and arithmetic growth. It appeared that many of the adult populations were increasing linearly e.g. Sidmouth 1998 (Figure 4.13 and Figure 4.16), Totland and Seaview 1999 (Figure 4.17).

A form of geometric increase is logistic growth. The characteristic of logistic population growth is early acceleration in incremental increase with time followed by later deceleration towards zero growth at carrying capacity. Logistic growth equates with a linear decrease in per capita recruitment. Logistic growth appeared to best explain the adult populations increase at some of the locations e.g. Cowes high-recruitment 1998 (Figure 4.14), Portland high-recruitment area 1 (Figure 4.15), and Cowes 1999 (Figure 4.17). The logarithmic numbers of adults in the populations for each of these studies were plotted against time (see Figure 4.18 to Figure 4.20 displayed in order of settlement season). The graphs also included a line of best fit, which was forced to go through the origin as at time 0 there were no adult barnacles present.

There was evidence for geometric adult population growth at Cowes high-recruitment 1998, Portland high-recruitment area 1 and Cowes 1999 except in the 4 and 16 remnant adult treatments. At Portland high-recruitment area 1 adult population growth in treatments with 16 and 32 adults appeared to fit the geometric growth line more closely than the 0 and 8 adult treatments. The variances in the data at Portland, in general, were greater than the variances at Cowes.

A similar graphical analysis was carried out on the number of adults at Cowes 1998 low-recruitment, as shown in Figure 4.21. Although a logarithmic transformation was performed on the data a geometric curve could still be seen in the resulting plots. This suggested that the populations were growing at compressed exponential rates.

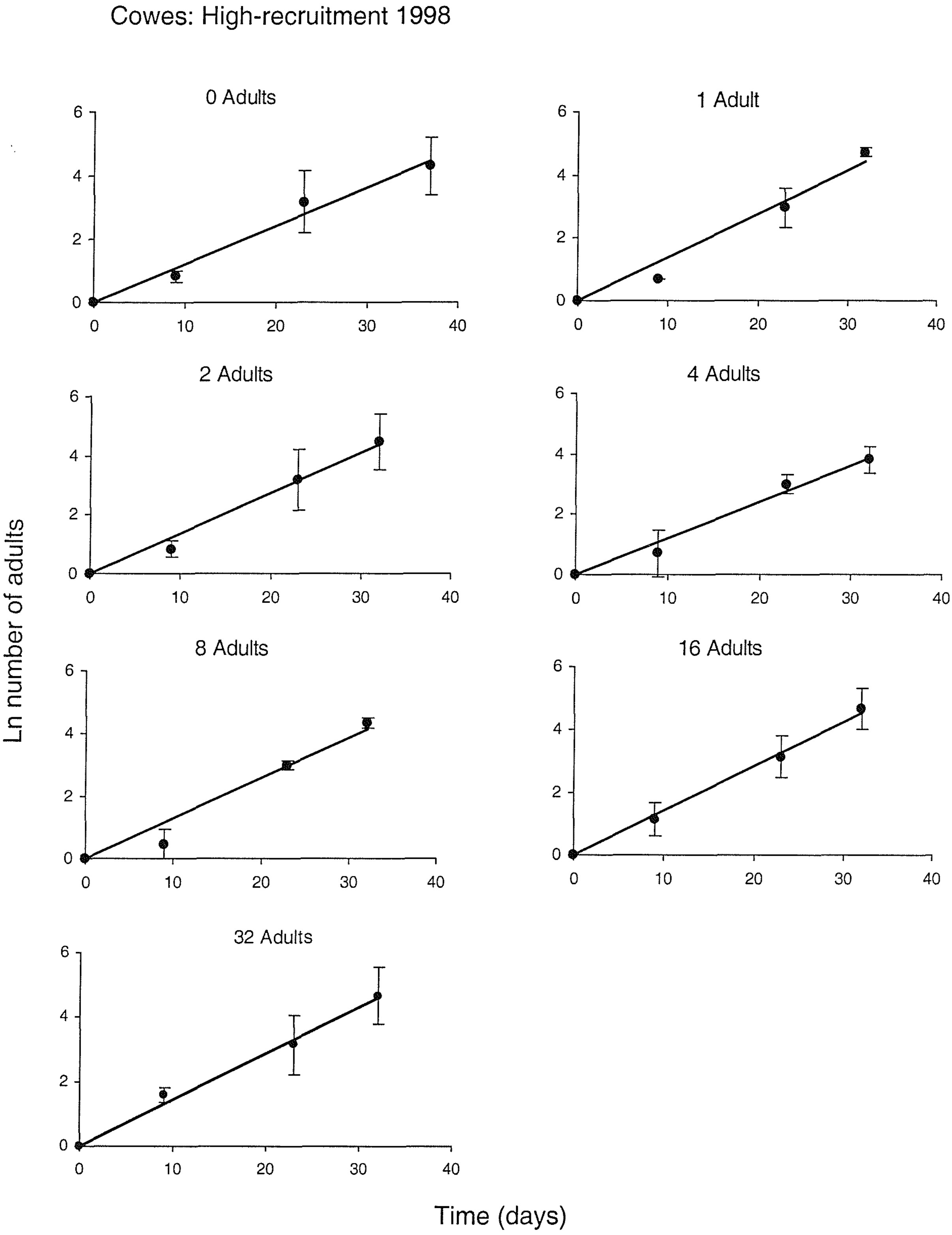


Figure 4.18 Adult population growth at Cowes high-recruitment 1998. The mean Ln number of adult *Semibalanus balanoides* from three 10 x 10 cm^2 quadrat treatment replicates plotted against time, measured in days after 13/05/98, (the last date at which the locations were identified as having no adult barnacles present). Error bars represent the 95% confidence intervals obtained from the three replicates.

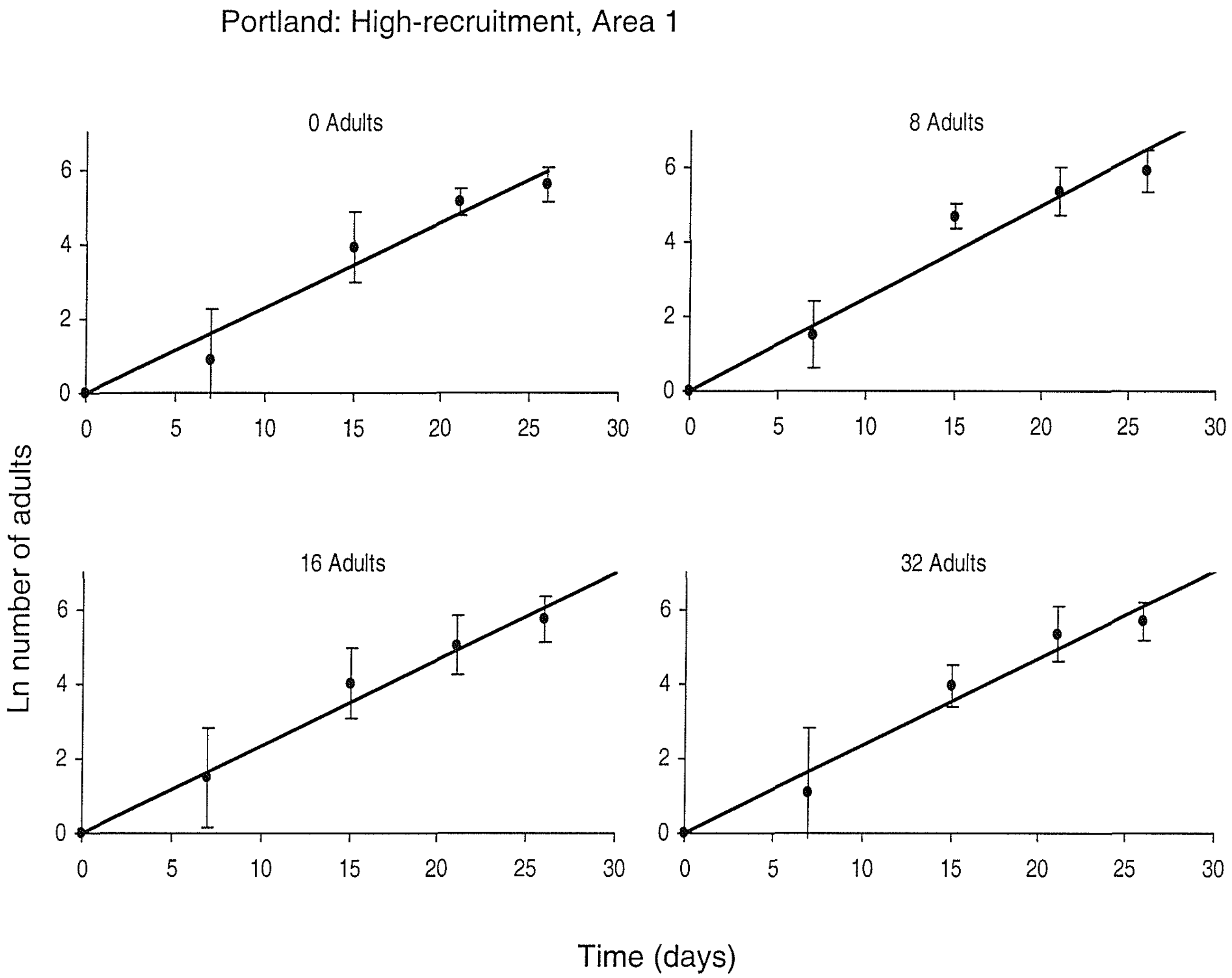


Figure 4.19 Adult population growth at Portland high-recruitment area 1, 1998. The mean Ln number of adult *Chthamalus montagui* from three 30 cm diameter quadrat treatment replicates plotted against time, measured in days after 17/10/98, (the last date at which the locations were identified as having no adult barnacles present). Error bars represent the 95% confidence intervals obtained from the three replicates

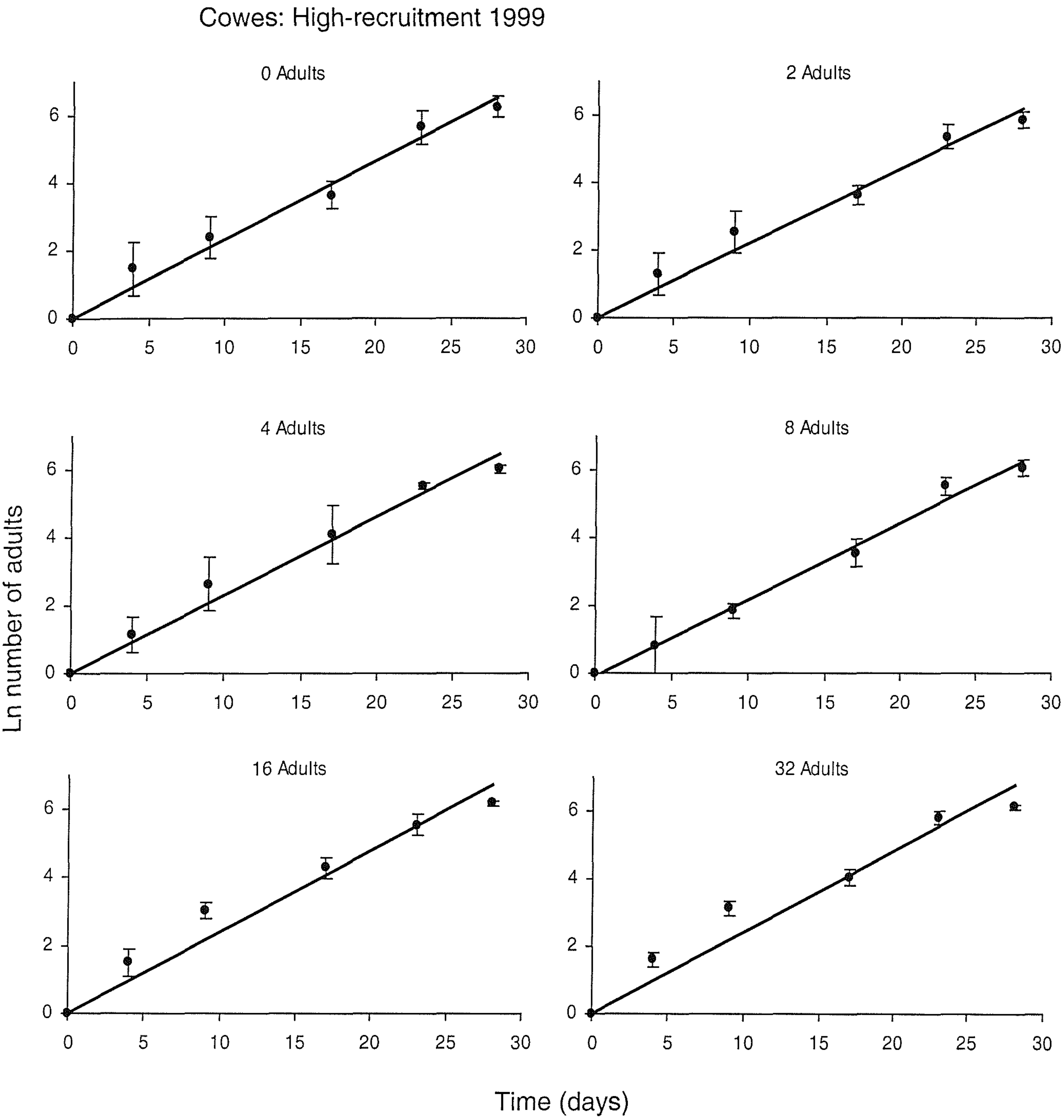


Figure 4.20 Adult population growth at Cowes 1999. The mean Ln number of adult *Semibalanus balanoides* from three 20 cm diameter quadrat treatment replicates plotted against time, measured in days after 03/05/98, (the last date at which the locations were identified as having no adult barnacles present). Error bars represent the 95% confidence intervals obtained from the three replicates.

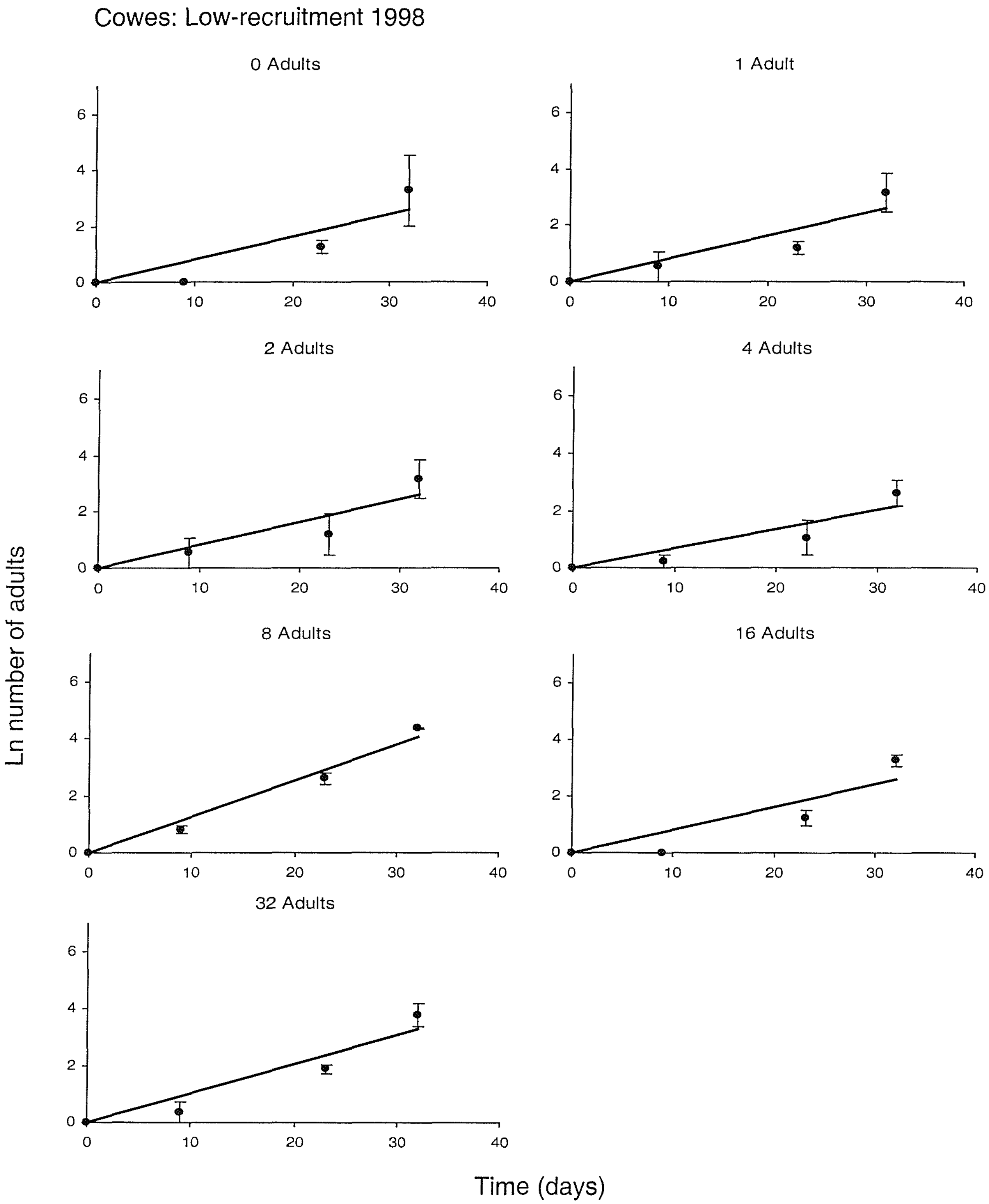


Figure 4.21 Adult population growth at Cowes low-recruitment 1998. The mean Ln number of adult *Semibalanus balanoides* from three 10×10 cm^2 quadrat treatment replicates plotted against time, measured in days after 03/05/98, (the last date at which the locations were identified as having no adult barnacles present). Error bars represent the 95% confidence intervals obtained from the three replicates. Note how the points suggest a geometric growth curve even though they have been transformed.

The adult recruitment data from each treatment were analysed against the compressed exponential growth model using the Microsoft Excel *solver* function as detailed in the Methods section. A two-way adjusted t-test allowed for one observation (i.e. $b = 1$) to be compared to the mean b observation obtained from the samples. The rates of adult population increases displayed in Figure 4.18 to Figure 4.21 were tested against geometric growth. In the majority of treatments the value for b was not significantly different from 1 as shown in Table 4.2, thus indicating geometric growth.

At the high-recruitment locations the general tendency was for less than geometric growth (i.e. approaching arithmetic). The analysis showed that adult population growth was less than exponential in two of the 32 adult treatments both at the same locations (Cowes high-recruitment 1998 and Cowes high-recruitment 1999) with a mean b value significantly less than 1. All treatments at Cowes low-recruitment 1998 had mean b values > 1 and 5 of the 7 had $b > 2$ (Table 4.2, (iv)). Due to the small sample sizes and the large standard deviations, however, only two treatments were found to have b values significantly greater than 1: the 4 and the 16 adult treatments.

The sum of the squares in Table 4.2 gave an indication to how well the compressed exponential model fitted the observed data. The smaller the value the better the fit the model was to the observed data. The sum of the squares was consistently smaller for the *S. balanoides* data than it was for the *C. montagui* data.

By using the cumulative number of settlers onto settlement plates we were able to obtain an indication of whether the recruitment supply was occurring geometrically. This was assessed in the same way as the adult population growth. Settlement onto the plates at Cowes was approaching arithmetic, with a value of $b = 0.78$, although the value was not significantly less than 1 (Table 4.3). Settlement onto the plates at Seaview was closer to arithmetic with $b = 0.67$ and significantly less than 1. For both Cowes and Seaview the value given by the sum of the squares was relatively large. This indicated that the expanded exponential model was not a good model for representing cumulative settlement onto the plates.

		Treatment	Mean b value	σ	Sums of the squares	p
Study locations and year	i) Cowes high 1998 *S. balanoides*	0	1.208	0.157	0.165	*ns*
		1	1.522	0.274	0.122	*ns*
		2	1.259	0.188	0.093	*ns*
		4	1.161	0.309	0.373	*ns*
		8	1.450	0.213	0.191	*ns*
		16	1.131	0.145	0.175	*ns*
		32	0.897	0.005	0.153	**
	ii) Portland high 1 1998 *C. montagui*	0	1.079	0.424	1.582	*ns*
		8	0.814	0.264	2.000	*ns*
		16	0.967	0.461	0.588	*ns*
		32	1.028	0.453	1.622	*ns*
	iii) Cowes high 1999 *S. balanoides*	0	0.871	0.215	0.473	*ns*
		2	0.815	0.196	0.371	*ns*
		4	0.821	0.198	0.298	*ns*
		8	1.056	0.201	0.450	*ns*
		16	0.694	0.083	0.123	*ns*
		32	0.677	0.017	0.423	**
	iv) Cowes low 1998 *S. balanoides*	0	1.335	1.361	0.309	*ns*
		1	2.185	1.226	0.264	*ns*
		2	2.199	1.238	0.260	*ns*
		4	2.750	0.125	0.437	**
		8	1.450	0.312	0.038	*ns*
		16	2.703	0.231	0.069	*
		32	2.257	0.712	0.278	*ns*

Table 4.2. The mean value of b for which the exponential compressed model best fitted the observed data for each treatment shown in Figure 4.18 to Figure 4.21 along with the standard deviation of the sample, σ. The Sum of the Squares gives an indication of how well the model fitted the data. The corresponding p value was calculated using the adjusted two-way t-test and allowed the sample data to be tested against exponential growth ($b = 1$), where *ns* = not significant, * $p < 0.05$, ** $p < 0.01$.

	Mean b value	σ	Sums of the squares	p
Cowes	0.778	0.095	2.218	*ns*
Seaview	0.674	0.065	4.020	*

Table 4.3. The mean value of b for cumulative number of settlers on settlement plates at both high recruitment locations in 1999, (see Table 4.2 for meaning of terms).

4.5 DISCUSSION

In this study *Semibalanus balanoides* and *Chthamalus montagui* settlement rates were measured at six locations with varying recruitment levels, two along the south coast of mainland England and four around the Isle of Wight. These two barnacle species differ in their ability to self-fertilise. *C. montagui* can self-fertilise, whereas *S. balanoides* individuals cannot. The aim of this chapter was to seek the influence of adult barnacles on rates of settlement and growth of a new barnacle cohort.

4.5.1 Recruitment level and supply

Comparisons between the numbers of individual settlers on the settlement plates and the background density of the barnacle populations at the locations confirmed our expectation that population density is a good indication of recruitment. This was also partly confirmed by ranking locations in order of mean settlement density in the thirty-two adult treatments (Figure 4.12).

The settlement plates deployed at the two high-recruitment locations showed settlement occurring in three distinct pulses. This is consistent with Minchinton & Scheibling (1991) who found 2-3 peaks of *S. balanoides* cyprids during the main barnacle settlement period in Nova Scotia, Canada with peaks accounting for 63% of the total cyprids collected. Kendall *et al.* (1982) observed two large *S. balanoides* settlement pulses onto areas of Yorkshire coastline in England whereas Hawkins & Hartnoll (1982) observed three large pulses in settlement on to the shore at Port St. Mary, Isle of Man during 1978. Caffey (1985) has also identified one to three peak periods of settlement for *Tesseropora rosea*. It may also support the idea that locations around the Isle of Wight are subjected to recruitment pulses first from the west then the east (Crisp, 1962). The largest of these pulses occurred during mid-May and was visible at both high-density locations and Totland, a low-density location. These three locations are positioned on the north coastline of the Isle of Wight, whereas Ventnor is on the south. Consequently, any west-to-east followed by east-to-west cyprid movement in the Solent will not have effected Ventnor. Kendall *et al.* (1982) found that peak settlement density occurred 25 days after the start of settlement whereas the results from our settlement plates suggest that it occurred at around 35 days after settlement in our study. Therefore, direct comparisons between settlement patterns exhibited by the plates and the treatment patches are difficult to make, though the plates can still be used to rank recruitment levels between locations.

Although settlement onto the plates occurred readily where recruitment was high, the number of settlers on plates at the low-recruitment locations were less than we expected. The reasons for this are unclear. The material used in the construction of the plates was not a deterrent as settlement onto the plates did occur at the high-recruitment locations. Settlement onto plates at the high-recruitment locations and the relative absence at the low-recruitment locations may be the result of available free-space. If free-space were limiting where recruitment levels were high then a settlement plate would have offered a prime location for barnacle settlement. Individuals arriving at heavily settled locations must search elsewhere to overcome intraspecific territoriality (Crisp, 1961), though this threshold may vary from year-to-year (Kendal *et al.*, 1985).

Cyprids have a finite level of stored energy (Lucas *et al.,* 1979; Miron *et al.,* 1999) which is enough to disperse and explore prospective settlement sites for up to 3-4 weeks in *S. balanoides* (Lucas *et al.,* 1979). Towards the end of this limited time cyprids may become less discriminating when searching for a suitable settlement site (Crisp, 1974; Doyle, 1975; Rittschof *et al.*, 1984). Some of the individuals observed on the settlement plates at the high-recruitment locations may have been approaching the end of their energy reserves; consequently their settlement criteria may have been minimal. This idea is supported by the work carried out by Connell (1961) who found that once preferable sites were occupied by *S. balanoides* the less-preferred sites would then be settled upon. This may also explain why we did not observe much settlement onto plates at the beginning of the settlement season.

4.5.2 General settlement comparisons

The pattern of larval settlement of *S. balanoides* around Britain is known to differ greatly and regularly between geographic areas (Hawkins & Hartnoll, 1982; Kendall *et* *al.*, 1985). During the 1998 *S. balanoides* study settlement occurred first at Sidmouth at the end of March, the first signs of settlement at Cowes were observed 10 days later. However, the settlement season lasted longer at Cowes than Sidmouth. *S. balanoides* larvae are typically released first in the west, then in the east (Crisp, 1962) in the English Channel. Sidmouth was the most westerly location in the study and consequently settlement was found to occur here first. Cowes is centrally positioned on the south coast, and it receives recruitment not only from the west but possibly from the east too. This may explain why at Cowes there appeared to be two distinct settlement peaks during 1998.

The onset of *C. montagui* settlement was observed on the same date in August 1998 at both Portland and Sidmouth. The start of settlement at the four study locations used in the 1999 *S. balanoides* study was also observed on the same date. The spatial distance between these comparative locations was smaller than the distance between Cowes and Sidmouth; therefore the synchronised settlement was not thought to be unusual. Comparisons between the onset of settlement at Cowes 1998 and Cowes 1999 showed that initial settlement occurred 5 days later in 1999. Hawkins & Hartnoll (1982) have shown there to be considerable differences between the onset of settlement in consecutive years at a single shore on the Isle of Man, with the timing of larval release being influenced by water temperature and food availability (Salman, 1982).

The number of barnacles settling onto treatments in general decreased from west to east. Sidmouth had the highest densities of both *S. balanoides* and *C. montagui* settlers with the Isle of Wight and Portland having the least for each respective species. This result is consistent with Herbert (in prep.) who showed that the highest densities of both species are found in the west. Gaines & Bertness (1993) have also found regional variation in the colonisation of intertidal sites by *S. balanoides.* By analysing recruits in New England they discovered that numbers differed by more than two orders of magnitude between locations.

At Cowes the number of *S. balanoides* settlers was not consistent between years. The difference may be attributed to variations in pre- and post-settlement processes. Pre-settlement processes such as wind direction (Hawkins & Hartnoll, 1982), and desiccation (Foster, 1971) have been shown to influence recruitment numbers. Post-settlement processes that can influence barnacle recruitment numbers include the passive removal by limpets (Hawkins, 1983; Miller & Carefoot, 1989) and direct predation (Connell, 1961; Burrows *et al.*, 1999a). Minchinton & Scheibling (1991) found that *S. balanoides* density did not differ significantly between years in high and mid intertidal zones but did in low intertidal zones. Hawkins & Hartnoll (1982) found that the density of settlement varied annually on the Isle of Man. Caffey (1985) observed between year variation in the barnacle *T. rosea* settlement by up to 127-fold in New South Wales.

4.5.3 The effect of treatment on population growth

In general recruitment varies strongly between years and locations and independently of population density (Smith & Peacock, 1990). Bence & Nisbet (1989) have shown through theoretical models that in open systems the settlement rate into a local population will generally not increase in proportion to increases in local population density, even when recruits are attracted to adults. We did observe evidence for a relationship between settlement numbers and the size of the remnant adult group at many of the locations used, as summarised in Figure 4.12, though the strength of this relationship was shown to be proportional to settlement density. However, in the models used by Bence & Nisbet (1989) the availability of free-space was a limiting factor. Free-space was shown to be a limiting factor at only one of the locations in our study (Sidmouth high-recruitment 1998) identified by a negative regression of settlement density to the size of the remnant adult group (Figure 4.12). Others have reported greater densities of settling *S. balanoides* cyprids onto cleared areas rather than uncleared quadrats (e.g. Miron *et al.*, 1999). Minchinton (1995) also found that the settlement of the barnacle *Tesseropora rosea* was consistently greater where conspecifics had been removed.

At Sidmouth low-recruitment, the number of recruits was proportional to the number of adults left in the remnant central group, this reversal of pattern between low and high-recruitment was surprisingly well marked (as shown in both Figure 4.7 and Figure 4.12). The number of settling *S. balanoides* individuals at Cowes 1998 was also generally proportional to the number of adult conspecifics left at the centre of each treatment patch, regardless of recruitment level. Regressions between treatments and the corresponding final settlement density were shown to be significant at all *S. balanoides* 1998 locations except at the Cowes high-recruitment shore. Chabot & Bourget (1988) have also shown that settlement of *S. balanoides* increases with increasing adult cover, though only up to a threshold value of approximately 25% cover.

Cyprid larvae of *S. balanoides* show both gregarious behaviour, facilitating successful reproduction, and territorial spacing behaviour, facilitating successful growth by avoiding competition (Crisp, 1961; and also see Chapter 3). The density of *S. balanoides* is directly related to the amount of free-space in mid- and low-intertidal zones (Minchinton & Scheibling, 1993a). The availability of free-space and the number of conspecifics are directly linked. At both recruitment levels at Cowes and at the low-recruitment shore at Sidmouth, the availability of conspecifics appeared to be the primary settlement cue for cyprids, whereas at the high-recruitment shore at Sidmouth it was the availability of free-space. If the settlement cues used by barnacle cyprids switched between conspecific availability and available free-space, then this would result in settlement patterns similar to those observed in our study.

Cyprids arriving at Sidmouth high-recruitment are likely to be inundated with chemical cues in the water column around the areas of conspecifics due to the sheer density of the background population (Crisp & Meadows, 1962). Under these conditions cyprids may seek out available space, since the density of conspecifics is so large the chances of being a penis length from a conspecific is high, regardless of attachment site. Pineda (1994) hypothesised that the decreased availability of free-space could result in the intensification of settlement in other areas of the habitat where there was available space. This may also help to explain why there were more settlers in the treatment patches with no remnant adults; here the availability of free-space was maximised, in an otherwise dense mat of conspecifics. If settlers are more attracted to conspecifics within their own cohort than those from previous generations then this may also heighten the observed patterns (see Chapter 3). When the density of conspecifics is low and the availability of free-space high, as found at the other three locations, the cyprids actively seek out conspecifics and settle close enough to guarantee successful reproduction (as also observed by other authors e.g. Knight-Jones, 1953; Bayliss, 1993).

Raimondi (1988) found that significantly more *Chthamalus* recruited to areas on stones with barnacles than to similar areas on stones without barnacles. Although in our study the relationship between the number of remnant adults and the number of settlers was not as strong for *C. montagui* as it was for the 1998 *S. balanoides* study there was evidence to suggest that *C. montagui* cyprids were actively seeking out adult conspecifics. Even though the maximum density of barnacle settlers at Sidmouth was similar for *S. balanoides* and *C. montagui* we did not see the inverse relationship between treatment number and the number of settlers in the *C. montagui* study as we did in the similar *S. balanoides* study at the high-recruitment shore. Although the density of settlers was similar the size of the cleared areas were not, and the size and shape of cleared areas are known to affect barnacle settlement (Raimondi, 1990).

At both the *C. montagui* locations the greatest number of settlers was always found on the treatment patches with either 16 or 32 remnant adults though the 0 adult treatment did not always have the least number of settlers. Although *C. montagui* individuals can self-fertilise, self-fertilised eggs are often less viable when compared to eggs fertilised via non-self (Barnes & Crisp, 1956) therefore *C. montagui* cyprids may still actively seek conspecifics. However, there was no evidence to suggest a significant regression between treatment and settlement numbers at all but two of the *C. montagui* shores (Sidmouth High 1, Portland Low 1). The lack of a relationship between the number of remnant adults and the number of settlers suggests that either *C. montagui* cyprids do not always select to settle where adult numbers are maximised or that, *C. montagui* cyprids are unable to recognise variations in the local density of adult conspecifics.

At all locations used in the 1999 *S. balanoides* study generally the more remnant adults left at the centre of the treatment patch the greater the settlement. The treatment effect was shown to be constant across all locations. However, at only three of the four locations (Cowes, Seaview and Totland) was there a significant regression between treatment and final settlement numbers, again the results from Ventnor differ from the other locations used in 1999. Settlement was, however, consistently lowest at all four locations where all adult conspecifics had been removed (0 adult treatment). Minchinton & Scheibling (1993a) have also shown barnacle settlement to be lowest in areas where the total population was removed. Although settlement did vary between years at Cowes the treatment effect did not. This result suggests that the degree of conspecific attraction is constant over a range of settlement densities at this location.

We assumed recruitment to be locally consistent within a shore at a location. Gaines *et al.* (1985), identified differences (up to two orders of magnitude) in settlement rates between patches only a few tens of metres apart. However, they attributed the differences in settlement to the fact that although the same numbers of cyprids were reaching the patches their propensity or ability to settle may have varied. This may explain why *C. montagui* settlement counts differed markedly between the two high-recruitment shores at both Portland and Sidmouth.

Although sampling was only conducted at most twice a week Hills & Thomason (1996) have observed little post settlement mortality of *S. balanoides*, and consequently considered it relatively rare and of little significance to the overall settlement density. Mortality of settlers was evident early on in some of our treatments, and could be identified by fluctuations in cumulative settlement numbers. The greatest fluctuations occurred primarily in the *S. balanoides* study at Sidmouth, though fluctuations were clearly noticeable in some treatments at some of the other high-recruitment locations (e.g. Cowes 1998). As mortality was consistently observed where settlement numbers were highest it is possible that much of the early post-settlement mortality could be contributed to density-dependent factors. Regardless of treatment and settlement density, mortality was relatively consistent within a location once settlers had become firmly established, indicating density-independent mortality.

The extent and onset of density-dependent mortality in *S. balanoides* is unclear from the literature. Connell (1985), concluded that density-dependent mortality only occurs in *S. balanoides* when the population density exceeds approximately 25 individuals / cm^2 whereas Minchinton & Scheibling, (1991) found it to occur in densities as low as 1.3 individuals / cm^2, though no density-dependent mortality was evident in day old recruits (Gosselin & Qian, 1996). The maximum density of settlers observed in our study was approximately 7 - 12 *S. balanoides* individuals / cm^2 at Sidmouth during 1998, suggesting that density-dependent mortality may have taken place in our study if Minchinton & Scheibling (1991) are correct.

Bertness (1989) observed density-dependent mortality at low and intermediate tidal heights, whereas negative density-dependence may be present on the extreme low shore at low population densities (Connell, 1985). Wethey (1984a) however, concluded that in *S. balanoides* populations, crowding is associated with increased survival. Though we have attributed much of the mortality to the effects of crowding some may result from predation. Ideal free theory (see Fretwell & Lucas, 1970; Sutherland, 1996) would predict a higher mortality in the treatments with the greatest density of settlers, if barnacle predators first select patches containing high barnacle densities, as observed by Burrows *et al.* (1999a). We observed no direct evidence for predation when visiting the locations at low tide, though predation is most likely to occur once barnacles are submersed (e.g. see Connell, 1961; Milton, 1983; Burrows *et al.,* 1999a).

Menge (2000) analysed the relationship between recruitment, post-recruitment processes and adult densities. He concluded that for *Chthamalus*, recruitment generally had a stronger impact on adult density than did post-recruitment processes, though for *Balanus* it was post-recruitment factors that had the stronger impact. We too generally observed more mortality in the *Semibalanus* study than in the *Chthamalus* study.

4.5.4 Rate of adult population growth

Both arithmetic and geometric growth was seen in the adult barnacle populations. Logistic growth was initially visually identified. Further graphical analysis of log-transformed abundances supported conclusions made from initial observations. However, at certain locations adult population growth was clearly identified as increasing arithmetically. Discrepancies between locations with respect to the rate of adult population growth may be the result of settlement mortality. Arithmetic growth may be seen where juvenile mortality is highest. The greatest fluctuations in settlement numbers were observed in *S. balanoides* populations at Sidmouth during 1998, the growth of the populations at this location was later shown to be arithmetic.

Geometric growth was identified at each study made at Cowes. Settler mortality is least likely to occur where areas are most shaded and wave protected (Shkedy *et al.*, 1995). The treatment areas used at Cowes were on a sea wall along a sheltered headland.

Having the treatments on a north easterly seawall offered protection from direct sunshine for the majority of the day. The only point in the day when the treatments would have been in direct sunshine would be early morning, when sunlight and temperatures are in general at low levels. Oceanographic features that affect larval recruitment also influence the feeding and growth of benthic filter feeders (Sanford *et al.*, 1994). Cowes is positioned on a 'maritime cross-roads', since not only is it on the edge of the Solent but also at the mouth of a river (the Medina) and opposite the mouth of another (Southampton Waters). This may inevitably mean that there is an abundance of barnacle food around the coastline at Cowes, resulting in low starvation mortality and rapid growth. Surprisingly, the only treatments that did not exhibit geometric growth were the 32-adult treatments, in both the Cowes 1998 high-recruitment shore and the 1999 study, though this may be the result of predation as discussed already.

Hawkins & Hartnoll (1982) have found that the pattern of cumulative metamorphosed juvenile numbers was irregular at high densities due to mortality. Wave exposure has striking effects on the growth of *S. balanoides* (Bertness *et al.*, 1991), and may explain why we did not see geometric adult population growth at the more exposed locations of Ventnor and Sidmouth.

Apart from the 0 and 8 adult treatments, all the other treatments at the Cowes 1998 low-recruitment had values of $b > 2$ indicating compressed exponential growth. Statistical analysis showed that adult growth rate at Cowes low-recruitment was significantly greater than geometric in two of the treatments. Although, these results were ascertained using population counts made from only four temporally separated observations, each was replicated 3 times. Geometric growth in *C. montagui* populations was shown to be evident at Portland in one of the high-recruitment areas. Though the compressed exponential growth model did not fit the *C. montagui* data as closely as it did the *S. balanoides* data. Geometric population growth can be expected in 0 adult treatments, as the establishment of a single cyprid can influence individuals from the same cohort and consequently subsequent cohorts (Wethey, 1984a and evidence from Chapter 3).

The geometric growth consistently identified at Cowes could have reflected a geometric increase in cyprids, since the cumulative settlement of individuals to the settlement plates deployed at this location yielded a value of b not significantly different from unity. Since the value of b was low, however, at $b = 0.78$ the non-significance may be attributed to the small sample. The settlement plates at Seaview did show an arithmetic influx of cyprids, though adult population growth at Seaview was also identified as being arithmetic. Although we compared the growth of the adult population on the treatment patches to the number of settlers on plates, Minchinton & Scheibling (1991) have shown that adult density is directly related to recruit density. However, Connell (1985) has shown that when *S. balanoides* recruitment is sparse it is highly correlated with the abundance of adults but when recruitment is dense it bears no relationship. Therefore direct comparisons between the number of settlers on settlement plates and the rate of growth of the adult population on the treatment patches should be made with caution.

4.5.5 Conclusions

In summary the analysis of settlement numbers of two barnacle species at various locations has shown that there is evidence for preferential settlement by both species where adult conspecific numbers are highest. However, this relationship appears to be delicately balanced against the availability of free-space in *S. balanoides*. Although *C. montagui* individuals are capable of self-fertilisation, the data suggest active identification and orientation towards adult conspecifics by cyprids (this was also shown in Chapter 3). This is supported by the fact that self-fertilised eggs are often less viable when compared to eggs fertilised via non-self (Barnes & Crisp, 1956). Settlement was shown to be temporally variable with distinct pulses throughout the settlement season, though there were discrepancies between settlement plate and treatment patch data.

The growth of the adult populations at some locations suggested an arithmetic population increase, however, this was not the case at others. Graphical and statistical analysis showed that at some locations the adult populations were increasing geometrically, population growth at one location even suggested compressed exponential growth. There are two alternative hypotheses that would both ultimately lead to geometric population growth i) a geometric supply of larvae, and ii) the attraction of cyprids to adult conspecifics.

There was evidence from settlement plate data to suggest that settlement was geometric at one of the locations. However, the insignificant deviation from geometric growth was possibly the result of a large standard deviation and a small sample size; also the exponential model used to test for geometric growth was poorly fitting at this location. In general recruitment tended to be very variable whereas the growth of the adult populations tended to be not so variable. Some factor was therefore reducing variability and tightening up the settlement relationship. We hypotheses that it was the attraction of settling cyprids to conspecifics that was largely responsible. This conclusion is supported by the results obtained in Chapter 3; there we were able to show preferential settlement towards conspecifics by the analysis of spatial patterns.

The aim of this chapter was to assess the population growth of two sessile species, which have a reproductive success that is more or less dependent on being a penis length from a conspecific. We have shown that barnacle larvae are attracted to adult conspecifics when free-space is not a limiting factor and that population growth is geometric at certain locations, rather than arithmetic. We have attributed much of the observed geometric population growth to the recognition of adults by settling cyprids. However, in Chapter 3 we have shown that this recognition behaviour extends not only to adults but also to other conspecifics within the same cohort and even other cyprids. As the selective pressures to settle a penis length from an individual are high, the conspecific location and recognition traits would consequently be strongly selected for in subsequent generations.

Two alternative theoretical models were depicted in Figure 4.2 both showing the relationship between available resource and consumers, in 'typical' open and closed populations. We have shown in this chapter and in Chapter 3 evidence to suggest that at certain locations barnacle populations' increase geometrically. Geometric growth is typically an attribute of populations occurring in closed system, however. Populations occurring in closed systems posses extinction thresholds. Theoretically populations in open systems do not possess extinction thresholds due to an external recruitment supply (Pagel & Payne, 1996). It should be noted however, that model populations in open systems can go extinct if the equilibrium abundance of the consumer is less than a single individual (e.g. Doncaster, 2000).

Barnacles occur in an open system (Roughgarden *et al.*, 1985) though some aspects of their population dynamics have been shown to be typical of closed dynamics. At high resource densities the recruitment dynamics mimic a closed system with density-independent recruitment. When the density of the resource declines (due to a reduction in free-space) recruitment is density-dependent as is seen in a 'typical' open population with constant recruitment influx. These concepts are modelled in Figure 4.22, and can be compared to Figure 4.2 (i) and (ii). The dynamics are compatible with ideal free models of mutually interfering consumers (e.g. Sutherland, 1996). In this case the effect of mutual attraction between barnacles at high resource density mirrors the effect of reduced interference in an ideal free model. The consumer isocline in Figure 4.22 is equivalent to $m \approx 0.1$ in eqn 1.9, which itself is a type of ideal free model (as described again in the General Discussion). Doncaster & Gustafsson (1999) and Doncaster (2000) have also shown a similar behaviour to exist at the population level.

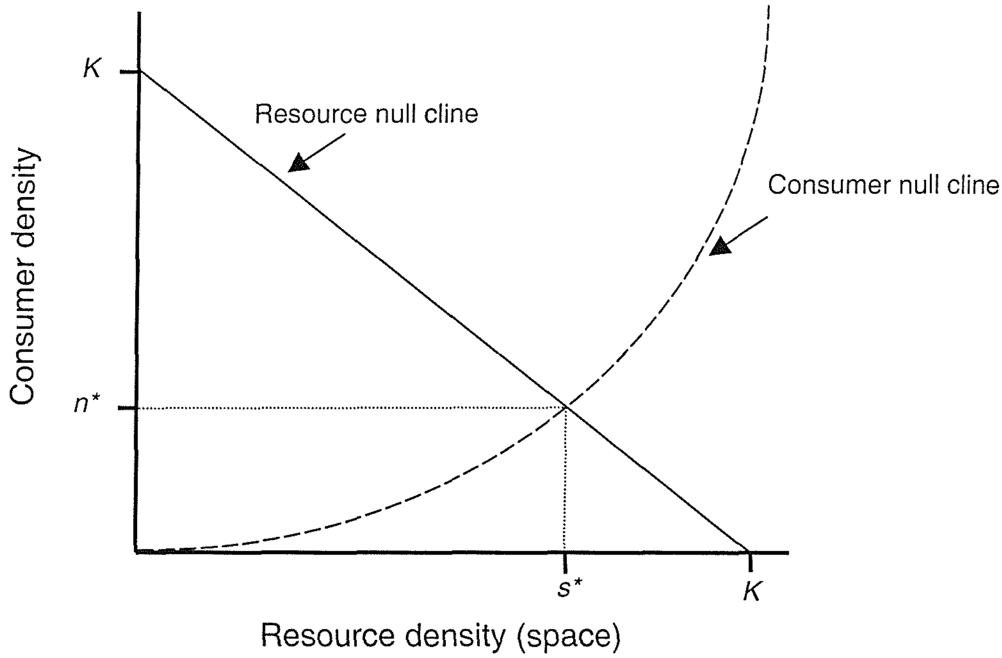


Figure 4.22 A novel conceptual model to illustrate barnacle population dynamics. The model is the result of a combination of both open and closed population models. At high resource densities the population follows closed system dynamics whereas at low densities it follows open system dynamics; consequently no theoretical extinction threshold exists. The population equilibrium point is at *n**, *s**.

Gregarious settlement, where the presence of conspecific individuals promotes the settlement of newly arriving larvae is widespread in marine benthic invertebrates, occurring in at least 35 invertebrate species (Burke, 1986). If conspecific attraction is as strong in these species as it is in the barnacle species observed in this study then we can expect these populations to increase geometrically also, and therefore to have a pronounced extinction threshold. This has not been considered in the literature up to now. As concluded in Chapter 3, understanding the causes of population growth enables predictions to be made with respect to the future structure of a population. This may be crucial in not only understanding the evolutionary and ecological population dynamics of the species but also in future management schemes whereby the population under question is required to be eradicated, sustained or encouraged.

5 ONE PREDATOR TWO PREY: THE CONSEQUENCES TO MICROTINE PERSISTENCE OF LETHAL TOXIN PRODUCTION BY ALTERNATIVE FOOD PLANTS

5.1 ABSTRACT

What drives microtine rodent cycles remains one of the most taxing questions in population ecology, with no single explanation generally accepted in the literature. Jensen & Doncaster (1999) recently detailed a verbal hypothesis to describe a driving mechanism that accounts for many otherwise unexplained features of rodent cycles. They proposed that cycles could be explained by periodic lethal toxin production (PLTP) by a non-preferred plant type. Unlike any other single hypothesis, the PLTP hypothesis is supported by an abundance of experimental and observational data. Possible toxic plant suspects were suggested. Here we model the PLTP hypothesis using a quantitative optimal foraging one-predator two-prey model, as originally derived by Křivan (1996). Rate constants corresponding to each of the model parameters were sought from the extensive microtine rodent literature. Model outputs were tested against five empirically derived criteria: frequency of cycles, maximum and minimum density, maximum to minimum ratio of densities and the occurrence of a catastrophic population collapse. The original model was successful in depicting four out of five criteria, even without inclusion of direct toxin production. With the inclusion of a toxic pulse, and therefore a switch to high microtine mortality, all five criteria were met in toxic prey model outputs. Variations on the original model, whereby the non-preferred plant type was always toxic, or the non-preferred plant type was as nutritionally attractive as the preferred plant type, gave results that matched only a limited number of criteria. The standard Holling-Tanner model was also less successful than the toxic prey model at meeting the criteria. We discuss the implications of periodic toxin production as the driving force behind microtine cycles and consider conclusions derived from the toxic prey model as methods for controlling or conserving microtine species.

5.2 INTRODUCTION

How the size of a population is determined is one of the most fundamental questions in ecology (Dobson, 1995), with the factors regulating population density being the basis for much ecological research (Hairston, 1994). Population cycles present an interesting case of regulation (Krebs *et al.*, 1973). Many small mammal populations have cyclical dynamics recognisably distinct from random fluctuations. The regulatory mechanisms, however, have not been explained by a universally accepted single hypothesis.

In many high altitudes and latitudes of the Northern Hemisphere, though not the Southern Hemisphere, populations of small microtine rodents, particularly voles (*Microtus* spp., and *Clethrionomys* spp.) and lemmings (*Lemmus* spp. and *Myopus* spp.) show population cycling, with a typical periodicity between 2 and 5 years (Myllymäki, 1977a; Remmert, 1980; Begon *et al.*, 1990). This cyclic behaviour was first described in detail by Elton (1924), though outbreaks of small rodents were recorded as far back as the Old Testament, and in Aristotle's writings of 350 BC (Krebs *et al.*, 1973).

All populations have temporally fluctuating densities. In most cases these fluctuations can be attributed to seasonal responses and climatic changes (Jensen & Ball, 1970; Hairston, 1994), though the weather is too irregular to exercise complete control over microtine cycles (Hairston, 1994). While population cycles are never perfectly regular, they are significantly more so than other fluctuations (Keith, 1983). Moran (1952) suggested a statistical procedure to distinguish cycles from random fluctuations. He showed that where a population is cyclic there is a high correlation between population density and the cycle period, whereas with a fluctuating population there is no such correlation. Microtine populations show remarkably regular oscillations, with cycle frequencies longer than a year and much longer than a generation (Hairston, 1994). Many microtine populations usually decline in the summer, autumn and winter following a population peak, with the lowest densities reached by the second summer (Brunnel *et al.*, 1975). Not only are the declines recurrent but they are also characterised by changes in the distribution of microtine body weights and survival rates (Chitty, 1967). It is the regularity of the oscillations that distinguishes cyclic microtine population from those that seasonally fluctuate.

Since microtine populations do persist in time despite undergoing dramatic changes in density, they can be thought of as having equilibrium dynamics described by stable limit cycles. Stable limit cycles are used to describe well-defined cyclic changes in population numbers over time (May, 1973). Populations oscillate in size but there is a self-correcting mechanism that enables the population to return to the original position once a perturbation has occurred (Hairston, 1994). The stability of the cycles relies upon density-dependence either in predation or in the resource. As the prey population increases the predator population will follow. As a result the predator population will become so numerous that it will decimate the prey population, which will cause the predators to starve. Eventually the prey population will recover and the series of events will be repeated. Therefore, the closer to the environmental carrying capacity the population is, the more highly density-dependent are changes in predators and the resource (Crawley, 1983). Microtine rodents have been hypothesised to take the role of the predator by some researchers (e.g. Laine & Henttonen 1983) and the prey by others (e.g. Hanski *et al.*, 1991). Regardless of whether microtine rodents are considered as the predator of plants or the prey to mustelids the dynamics will be cyclic under certain parameter conditions. Turchin *et al.* (2000) have recently hypothesised that lemming and vole cycles are driven by different trophic interactions. By analysing empirical data they conclude that lemmings cycles are driven by the interaction between lemmings and their ‘prey’ species (plants and mosses) whereas voles cycles are driven by the interaction between voles and their predators (mustelids). Although cycling is easily reproduced, simple deterministic models have been unable to successfully model all aspects of empirically derived microtine dynamics. The catastrophic crash and subsequent low phase have presented particular problems (see Section 5.2.1).

Jensen & Doncaster (1999) have recently put forward a novel hypothesis to explain the cyclic behaviour of microtine populations in arctic and alpine tundra regions. They hypothesised that a precipitous decline in microtines can be produced by periodic lethal toxin production by a non-preferred plant species (henceforth referred to as the PLTP hypothesis). The PLTP hypothesis is novel because previous attempts to link toxins with cycles have focused on preferred foods only. In their paper they cite a range of experimental and observational data that indirectly support the PLTP hypothesis. Jensen & Doncaster also claim that the PLTP hypothesis offers explanations for a number of features common to many microtine cycles, which are not explained by any other single theory (see Jensen & Doncaster, 1999 for examples). They go on to suggest that the PLTP hypothesis may be applicable to other polyphagous cyclic vertebrate grazers living in tundra areas that feed on a periodically toxic plant species.

The hypothesis as proposed by Jensen & Doncaster (1999) was a verbal model. The objective of this chapter is to test the PLTP hypothesis with a quantitative model. We use an existing optimal foraging model, and actual predator-prey parameter values obtained from the literature, to examine the effect of a toxic non-preferred plant species on a model microtine population. The qualitative model allows us to analyse the influence of a non-preferred prey type on microtine density and the effect of toxin production on the dynamics of the plant and its target. By comparing simulated data to empirical data we are able to evaluate the accuracy of our model and consequently to discriminate important from unimportant variables.

The evidence for cycling in microtine populations is unequivocal and well documented, and is supplemented by an extensive literature hypothesising the possible mechanisms behind the cycles. In the next section I briefly summarise some of the current proposed hypothesis before describing the detailed mechanisms involved in the PLTP chain of events.

5.2.1 Microtine dynamics

Although much is known about the biology and ecology of both voles and lemmings (e.g. Stenseth & Ims, 1993) the reasons why these populations cycle is one of the long-standing, unsolved problems of population ecology. None of the many hypothesised series of events proposed to explain the causes of microtine cycles have gained general acceptance.

Population cycles follow a repeating four-step pattern of increase - peak - catastrophic decline - low phase (Krebs *et al.,* 1973). For microtine rodents, the period of this cycle is typically anything between 2 and 5 years (Krebs *et al.,* 1973; Akçakaya, 1992; Laine & Henttonen, 1983; Myrberget, 1986; Turchin, 1993), with the period between cycles decreasing at the most northerly latitudes (Hanski *et al.*, 1991; Mackin-Rogalska & Nabago, 1990). Populations in southern Scandinavia have been found to be stable with only seasonal fluctuations (Myrberget, 1973; Hansson & Henttonen, 1985; Hanski *et al.,* 1991). Cycles are not synchronous over large regions nor are population numbers alike in successive cycles or over wide distances (Irving, 1972).

There are four alternative mechanisms currently considered as the driving force behind microtine cycles, two of which rely on intrinsic factors while the other two are based on extrinsic factors. Each is briefly detailed below.

5.2.1.1 Social organisation and dispersal

It is generally accepted that spacing behaviour or social spacing mechanisms result in dispersal, consequently limiting population density (Gliwicz, 1988). Chitty (1960) first proposed a hypothesis to explain microtine cycles based on spacing and dispersal behaviour. He hypothesised that populations were polymorphic with respect to spacing and aggressiveness. At high densities those individuals that can survive crowding and/or are aggressive will be selected for. Since these individuals have a low fecundity, the population declines over time. At low densities, the alternative genotype with a high fecundity is selected for and the population increases. This is a difficult hypothesis to test empirically as changes in aggressive behaviour of small mammals cannot be easily measured in field conditions (Krebs, 1970).

The social fence hypothesis was first put forward by Hestbeck (1982), who went on to model it (Hestbeck, 1988). According to the social fence hypothesis population regulation can result from either spacing behaviour or resource exhaustion (Hestbeck, 1988). If dispersal is prevented by either a physical or social barrier at high densities (e.g. an opposing competing population) limiting resources become depleted and eventually exhausted. The consequence of this is that populations cycle.

Stenseth (1988a) and Stenseth *et al.* (1988) do not agree with Hestbeck. They modelled microtine populations and assumed that all females were territorial. Once a threshold density of females was reached, immature females were forced to leave in search of new habitats causing the crash. Myllymäki (1977b) has shown, however, that it is the mature female and young males that typically disperse in *Microtus agrestis* populations. Watson (1943) witnessed no large-scale emigration of lemmings at peak numbers.

5.2.1.2 Maternal effects

The 'maternal effect' is based on female experiences and the effect they have on the survival and reproduction of her offspring in subsequent generations (Berryman, 1995). Those changes in individual quality in turn affect population growth, preventing population explosions and thus generate cycling (Inchausti & Ginzburg, 1998).

It has been shown by Rodd & Boonstra (1988) that if the density of adult *M. pennsylvanicus* is reduced then juvenile survival rate and individual reproductive rates increase. By manipulating experimental populations they concluded that adult females are responsible for more of the suppression of reproduction than are adult males. Gustafsson *et al,* (1983) found that the rate of maturation was density-dependent, and higher in cyclic populations than in stable populations of bank voles (*Clethrionomys glareolus).* However, the nutritional quality of food intake can also play a major role in reproduction and survival (Batzli, 1986; Koskela *et al.*, 1998).

Whether juveniles are inhibited directly or indirectly by adult conspecifics or whether the young animals delay their own reproduction depends on the species and the location (see Rodd & Boonstra, 1988). An endocrine feedback mechanism has been as suggested as a possible source of this mechanism, with the hormonal responses being triggered by aggressive behaviour (Christian & Davis, 1964). Much work on the effect of density-dependence has been carried out on laboratory populations; effects have only typically been shown where densities have been greater than those found in the field (Hairston, 1994). Stenseth & Antonsen (1988) have developed a maternal effect model and have successfully modelled cycling populations under certain conditions. However, not all parameter values were derived from empirical data.

5.2.1.3 Predation

In recent years there has been much support for the hypothesis that predators are the primary factor driving cyclic microtine populations (e.g. Korpimäki, 1986; Henttonen *et al.*, 1987; Hanski *et al.*, 1991; Akçakaya, 1992; Hanski *et al.*, 1993; Heikkila *et al.*, 1994; Hanski & Korpimäki, 1995; Klemola, 1997). Under this hypothesis, as the microtine population increases so too does the predator population. Eventually the predators become so numerous that they exhaust the microtine population, which ultimately results in the collapse of the predator population due to starvation. The microtine population eventually recovers and the process is repeated. Cycling depends on a faster numerical response by the microtine than by the predator. This presents a problem, as even the presence of mustelids without predation per se is sufficient to slow down the reproductive output of some microtine rodents (Korpimäki *et al.*, 1994; Klemola *et al.*, 1997).

Numerous predator species have been put forward as the primary predatory threat to microtines. These include owls (Lundberg, 1979), mustelids (Hansson & Henttonen, 1985; Henttonen, 1987; Hanski *et al.*, 1991; Hanski *et al.*, 1993), foxes (Angerbjörn *et al.*, 1999), buzzards, domestic cats, and polecats (Erlinge, 1987); (see Hanski *et al.*, 1991 for an extensive predator list).

The non-cyclic seasonal pattern exhibited by southern populations has been attributed to intense predation throughout the year (Hansson, 1971; Erlinge, 1987). At high latitudes predator numbers are typically lower. The result is a reduction in predation, which consequently gives rise to predator-prey cycles (Hanski *et al.*, 1991).

In a series of papers written by Hanski and co-authors (Hanski *et al.*, 1991; Hanski *et al.*, 1993; Hanski & Korpimäki, 1995; Hanski & Henttonen, 1996) a predator-prey model has been put forward to explain cycling microtine populations. The microtine model used was based on a model devised by May (1973), which itself is a variation on the Holling-Tanner model (as shown in Appendix 2.1). Where possible parameter values were ascertained from experimental data, otherwise ranges of suitable values were tested. Many of the parameter combinations resulted in either chaotic or stable microtine populations, though a select few did result in population cycles that were comparable to empirical results. However, the model results did not mirror all empirical observations. There was no extended low phase after a population peak (see Laine & Henttonen, 1983); also population numbers only reached approximately 100 ind·ha^{-1} whereas densities in the field have been known to exceed 300 ind·ha^{-1} for voles (Myllamäki, 1977a) and 500 ind·ha^{-1} for lemmings (Pitelka, 1973).

Predation alone may not be sufficient to account for summer declines following population peaks (Begon *et. al.*, 1990). Predator numbers track the microtine cycles, and do account for many deaths; however, many individuals killed by predators may be doomed anyway (Begon *et. al.*, 1990). Some researchers suggest that predators act as a limiting, but not regulatory, factor in microtine populations (e.g. Jedrzejewski & Jedrzejewski, 1996). Others conclude that resource depletion initiates the decline in microtine rodents, though predation is essential in sustaining it in some instances (Oksanen & Oksanen, 1981). Predator removal experiments have resulted in an increase in prey densities in some studies (e.g. Sih *et al.*, 1985), although in others predator removal had no detectable effect on vole numbers (Marcström *et al.*, 1988).

5.2.1.4 Nutrition and food

The concept that populations are ultimately limited by the amount of food available was initially recognised by Malthus (1798). He noted that populations grow exponentially whereas their resources are renewed arithmetically, some of the population increase is therefore doomed to starve. The interaction between microtine and their food plants has been put forward as a potential driving force behind fluctuating cycles by many authors (e.g. Jensen & Ball, 1970; Tast & Kalela, 1971; Hansson, 1979; Batzli, 1983; Laine & Henttonen 1983; Moen, 1990; Jedrzejewski & Jedrzejewski, 1996). Herbivores of relatively unproductive ecosystems tend to be resource-limited and exert strong grazing pressure upon the vegetation (Oksanen *et al.*, 1981). Both the quality and the quantity of food items have the potential for influencing microtine cycles.

If it is assumed that the quantity of food is the deciding factor, then the population dynamics can be described by a cyclic predator-prey interaction as detailed above.

However, it is the microtine that is now the predator and the vegetation the prey. Unregulated rodent populations will overexploit their food resources (Hansson, 1988). Laine & Henttonen (1988) have found a correlation between the cycling of botanical variables and microtine density in northern Fennoscandia. In peak years there is heavy grazing by microtine. This may influence the production of seeds and flowers in consequent years (Andersson & Jonasson, 1986), where microtine densities have been found to be low (Järvinen, 1987). Vole density and the effect of grazing impact increases continuously from the southernmost to the northernmost localities (Hansson, 1988). However, supplying additional food does not prevent the drop in microtine numbers after a population peak (Chitty & Philips, 1966). Andersson & Jonasson (1986) and Henttonen, *et al.* (1987) also concluded that a food shortage was not responsible for the decline phase in cycling populations.

The quality of vegetation could drive microtine cycles if there was an inverse relationship between grazing and nutrients or alternatively a direct relationship between grazing and the production of secondary toxic compounds (e.g. Freeland, 1974). Nutrient levels have been found to vary significantly over time in potential microtine food plants, with relative synchronisation between species (Andersson & Jonasson, 1986). Stenseth *et al.* (1977) have found that the quality of the food eaten by the field vole *Microtus agrestis* may be reduced as a result of grazing.

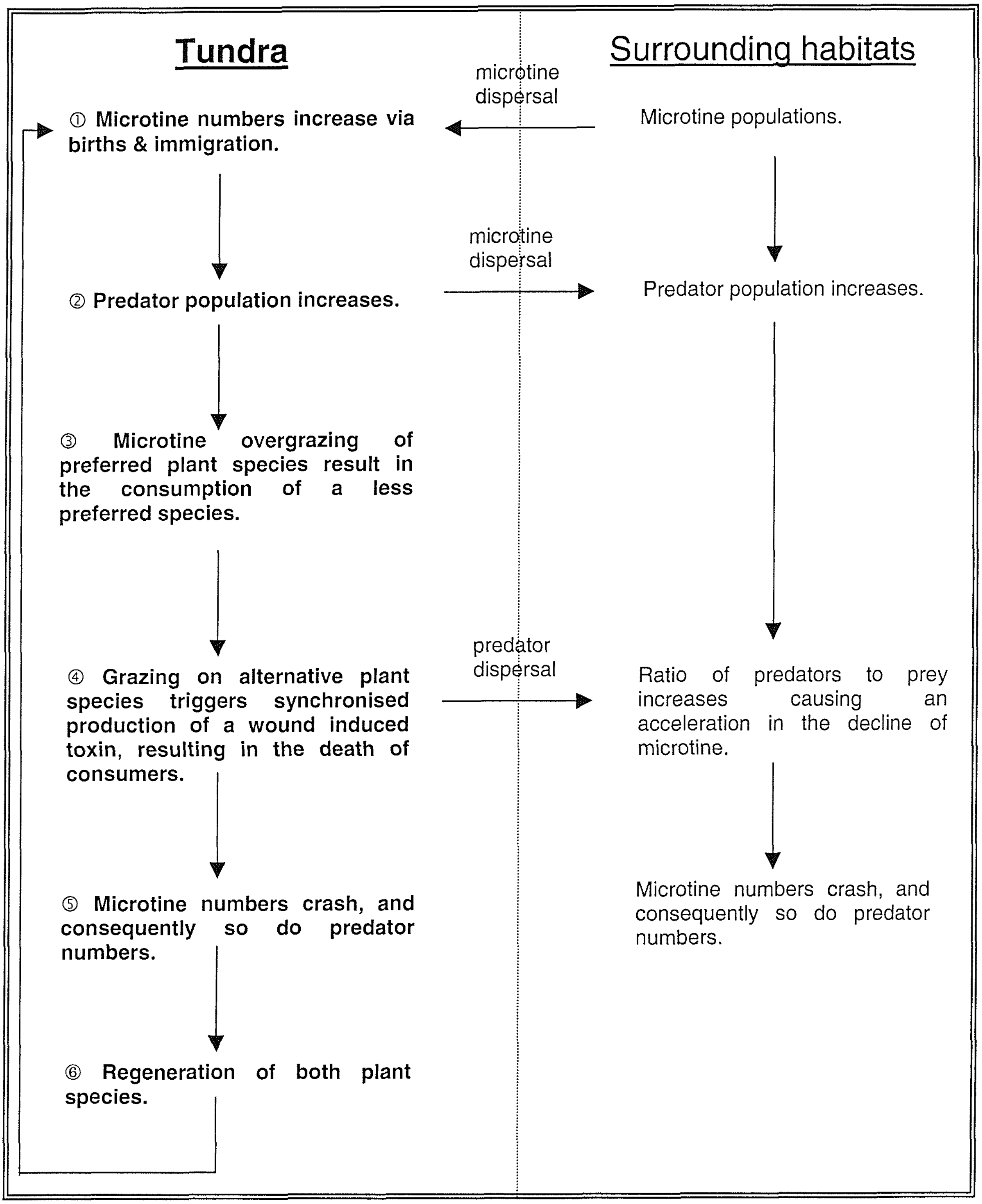
The quality of bilberry sp. leaves has been found to change during microtine cycles with the greatest phenolic content present in the increase to the decline phase of microtine cycles (Oksanen & Oksanen, 1981), though Oksanen *et al.* (1987) have attributed this change to variations in the weather. Conversely other plant compounds have been found to stimulate reproduction in some microtine species (Sanders *et al.*, 1981; Berger *et al.*, 1981), while still other compounds have been found to act as reproductive inhibitors (Berger *et al.*, 1977).

Most researchers have dismissed food toxicity as an explanation for microtine cycles (e.g. Batzli & Pitelka, 1975). The general reason for this dismissal is that if a food source is toxic then either microtine rodents should evolve new preferences for non-toxic food, or they should evolve resistance to the toxin. Since such resistance can develop within only a few generations (Greaves, 1986).

5.2.2 The PLTP hypothesis

A summary of the PLTP hypothesis is presented below and is also shown as a flow chart in Figure 5.1. A geometrically increasing population of a microtine species depletes a preferred food source to levels that can no longer sustain the population. As a result a previously non-preferred food plant is included in the diet. This non-preferred food plant is normally excluded from the microtine diet due to plant chemicals they contain. When over grazed, this plant produces wound induced toxins that are capable of interfering with the grazers' nutrient uptake, suppress breeding and ultimately cause the death of the animals (e.g. Tahvanainen *et al.*, 1991). This results in a population crash, followed by a long phase of low microtine density. A reduction in grazing pressure allows for the regeneration of vegetation (including both the preferred and non-preferred species). The small numbers of microtines that have survived the population crash now increase geometrically in numbers. This population increase is added to by immigration from surrounding areas (to see the overall effects on microtine populations in areas surrounding tundra regions see Figure 5.1).

Freeland, (1974) originally hypothesised that microtines cycles may be driven by a switch between a preferred palatable species and a toxic non-preferred species. Laine & Henttonen (1983) have also reported the switch between qualitative food types at high microtine densities. However, in Freeland's model the switch was to a plant that was constantly accumulating toxins, and not wound induced production as is suggested in the PLTP hypothesis. A direct switch to a food type continually high in toxins should result in the evolution of resistance within a few microtine generations. Batzli & Pitelka (1975) could find no supporting evidence for Freeland's theory. Though Batzli (1983) suggested that in general microtine density levels are set by nutrient availability, whereas oscillations are more likely to be related to interactions between herbivores and inducible secondary plant compounds. According to the PLTP hypothesis, the microtine are unable to evolve resistance because the switch to a non-preferred food type only occurs when the favourable food type has been severally depleted by over grazing. Once the switch to a non-preferred food type has occurred then toxins are only produced when the plant is wounded. This reduces the selection pressure on microtine rodents to evolve resistance. Selection is further reduced by post-crash influx of rodents from surrounding areas not affected by toxin production.



① Microtine numbers increase via births & immigration.

② Predator population increases.

③ Microtine overgrazing of preferred plant species result in the consumption of a less preferred species.

④ Grazing on alternative plant species triggers synchronised production of a wound induced toxin, resulting in the death of consumers.

⑤ Microtine numbers crash, and consequently so do predator numbers.

⑥ Regeneration of both plant species.

Microtine populations.

Predator population increases.

Ratio of predators to prey increases causing an acceleration in the decline of microtine.

Microtine numbers crash, and consequently so do predator numbers.

Figure 5.1 The sequence of events described by the PLTP hypothesis, which cause microtine numbers to oscillate periodically. PLTP acts in tundra but has effects extending into surrounding habitats.

5.3 KŘIVAN MODEL FOR PLTP

Food choice was one of the first aspects of foraging biology studied by ecologists (e.g. Tinbergen, 1961). The switch between the preferred food plant and the non-preferred toxic food plant in the PLTP model was represented by optimal foraging and predator-prey dynamics (for a review on optimal foraging theory see Stephens & Krebs, 1986). Optimal foraging theory predicts that the more profitable prey type is always included in the predator diet whereas the less profitable prey is only included in the diet if the density of the more profitable prey falls below a critical threshold (Křivan & Sikder, 1999). Empirical data have shown that microtine rodents do select forage in relation to a plant's nutritional quality (Batzli, 1983) and they do at times include plant species that are known to produce toxins (see Jensen & Doncaster, 1999).

If a predator follows an optimal diet choice, the strategy of a predator when encountering a prey item depends on the density of the more profitable prey type, which is always chosen when encountered. Křivan (1996) and later Křivan & Sikder (1999), have introduced a simple deterministic model in which the predator follows an optimal diet choice. It is essentially a Lotka-Volterra model expanded to include one-predator species with a Holling Type II functional response to two-prey species. It is therefore similar to an extension of the Holling-Tanner model (as described in Appendix 2.1) with an additional prey type. One structural difference is that the Křivan model has a predator birth rate directly proportional to consumption rate whereas in the Holling-Tanner model consumption rate influences death rate rather than birth rate.

Křivan's model is applied to the PLTP hypothesis, with the microtine rodent as the predator, the more profitable prey type representing the preferred food, and the other representing the non-preferred and potentially toxic food. The Křivan model does not include a specific term to model the toxic pulse. However, we will show that the original model does give a reasonable representation of reality without a direct toxicity effect. The model is then improved by adding a switch in predator mortality rates at a threshold density of non-preferred prey. This represents the toxic pulse as detailed in the PLTP hypothesis.

The Křivan (1996) and Křivan & Sikder (1999) optimal foraging model is summarised below and relevant aspects of its behaviour detailed. The model has three state variables, with dynamics described by continuous rate equations:

$$\frac{ds_1}{dt} = r_1 \cdot s_1 \left(1 - \frac{s_1}{K_1}\right) - \frac{u_1 \cdot q_1 \cdot s_1 \cdot n}{1 + u_1 \cdot h_1 \cdot q_1 \cdot s_1 + u_2 \cdot h_2 \cdot q_2 \cdot s_2} \tag{5.1}$$

$$\frac{ds_2}{\mathrm{dt}} = r_2 \cdot s_2 \left(1 - \frac{s_2}{K_2}\right) - \frac{u_2 \cdot q_2 \cdot s_2 \cdot n}{1 + u_1 \cdot h_1 \cdot q_1 \cdot s_1 + u_2 \cdot h_2 \cdot q_2 \cdot s_2} \tag{5.2}$$

$$\frac{dn}{dt} = \frac{u_1 \cdot e_1 \cdot q_1 \cdot s_1 \cdot n + u_2 \cdot e_2 \cdot q_2 \cdot s_2 \cdot n}{1 + u_1 \cdot h_1 \cdot q_1 \cdot s_1 + u_2 \cdot h_2 \cdot q_2 \cdot s_2} - d \cdot n \tag{5.3}$$

Preferred prey density is described by the state variable s_1, the non-preferred prey density by s_2, and predator density by n. The constant q_i is the search rate of a predator for the ith prey type, e_i is the expected net energy gained by each predator from each unit of the ith prey type (i.e. a conversion ratio of prey into new predator biomass), and h_i is the expected handling time spent with the ith prey type. K_i is the carrying capacity of the environment for the ith prey type, and r_i the intrinsic rate of renewal of the ith prey type.

Each rate equation has a positive component representing birth and a negative component representing death. Essentially the model describes logistic renewal of s_i, towards the carrying capacity K_i, and inverse density-dependent consumption of prey as a function of prey abundance and handling time. Consumed prey then contribute to the production of new predators, which is offset by density-independent mortality of predators. The first prey equation reduces to a Holling-Tanner model of prey dynamics detailed in Appendix 2.1 (eqn 2.3), upon the removal of the second prey from the system. Equally, the second prey equation (5.2) reduces to eqn A2.3 upon removal of the first prey from the system.

The binary variable u_i denote the likelihood that a predator will attack the prey type i. If the predator has optimal prey choice then it will always attack the preferred prey species whenever it is encountered, therefore $u_1 = 1$. Whether the predator attacks the non-preferred prey is dependent on the density of the preferred prey. The non-preferred prey species is attacked ($u_2 = 1$) when the preferred prey species drops below a critical threshold. The critical threshold is a function of the more profitable prey type and is given by Krivan & Sikder (1999) as:

$$s_1^* = \frac{e_2}{q_1 \cdot (e_1 \cdot h_2 - e_2 \cdot h_1)} \tag{5.4}$$

If the preferred prey species is above the critical threshold then the predator will ignore any of the non-preferred prey, therefore $u_2 = 0$.

Under each regime the behaviours of the initial differential equations (eqn 5.1 to 5.3) are altered as the value of u_2 steps between 0 and 1. When $u_2 = 1$ both prey species are included in the predator's diet and the populations are modelled by the complete equations. If the preferred prey species is abundant, and therefore $u_2 = 0$, the predator rate of intake and birth only depend on the renewal rates of preferred prey (eqn 5.1 & 5.3). The dynamics of the non-preferred prey (eqn 5.2) are then independent of the other two populations. This scenario is equivalent to the Holling-Tanner model (described in Appendix 2.1).

The model presented is not intended as a precise representation of microtine population dynamics but rather a tool for studying the dynamical interactions between microtine populations and two prey species with different nutritional values. The model assumes that parameter constants represent population averages with no age structure.

The Křivan optimal foraging model was built in MATLAB *Simulink.* This computer software package allowed us to model the differential equations and also the 'on/off' step function of u_i (see Appendix 5.1 for the complete *Simulink* model). The built model was shown to correspond with output graphs also included in Křivan's work. Simulations were run for at least 200 years. The last simulated 50 years were used to calculate the frequency of cycling populations.

Although Křivan (1996) and Křivan & Sikder (1999) gave a verbal description of each of the parameters used in the original model the corresponding parameter units were not given. To enable us to attach real values to each model parameter required identifying the parameter units. Individual units of measurement were checked by balancing all units across whole equations. The parameter units used are detailed in Table 5.1:

Parameter	**Description**	**Unit**
s_i	Prey density (biomass per ha)	$kg \cdot ha^{-1}$
K_i	Carrying capacity (biomass per ha)	$kg \cdot ha^{-1}$
r_i	Increase in biomass of prey per kg of existing prey per year	$kg \cdot kg^{-1} \cdot yr^{-1}$
n	Predator density (biomass per ha)	$kg \cdot ha^{-1}$
q_i	Area covered per kg of prey per year by each kg of predators	$ha \cdot kg^{-2} \cdot yr^{-1}$
h_i	Time spent by predators consuming not searching for prey	yr
e_i	Net energy gain, conversion factor for predators	$kg \cdot yr \cdot kg^{-1} \cdot yr^{-1}$
d	Decrease in biomass of predators per kg of existing predators per year	$kg \cdot kg^{-1} \cdot yr^{-1}$

Table 5.1 Parameters used in the Křivan optimal foraging model and their corresponding units. Some of these units have terms that cancel each other. They are given in this format to show the underlying structure.

5.3.1 Methods for estimating parameter values

Researchers currently disagree on whether the same mechanisms drive population cycles of both voles and lemmings, with many hypotheses solely concerning one group or the other (e.g. Stenseth *et al.,* 1977; Myllymäki, 1977a; Rodd & Boonstra, 1988; Turchin *et al.*, 2000; Turchin & Batzli, 2000). We have estimated the values of the model parameters from experimental and survey data gathered from the extensive literature. The microtine parameter values discussed below are primarily data obtained from vole studies. A complete list of all parameter values plus other significant values extracted from the literature can be found in Appendix 5.2.

1. **Prey carrying capacity, K_i.** There are two types of prey, the preferred type (with a carrying capacity of K_1) and the non-preferred type (with a carrying capacity of K_2). Each type of prey was assumed to be a single species or species group. A vegetative genus that is preferentially selected by some microtine rodents for consumption is *Salix* (Oksanen & Oksanen, 1981; Batzli & Pitelka, 1983; Rodgers & Lewis, 1985, Moen, 1990). Most calculations of *Salix* sp. carrying capacities come from above ground estimates. As most cyclical microtine species do not primarily consume below ground vegetative components (Batzli & Pitelka, 1971; Lindroth & Batzli, 1984) it was satisfactory to use above ground estimates. In arctic plant communities it is difficult to obtain accurate estimates of above-ground weight components due to variability in vegetation ground cover (Bliss & Kerik, 1973). Above ground biomass estimates vary between 9 kg·ha^{-1} for *S. reticulata,* green parts only (though this can rise to as much as 230 kg·ha^{-1} in southern alpine meadows, Chepurko, 1971) to 1404 kg·ha^{-1} for *S. lanata.* Kjelvik (1973) recorded 150000 *Salix* shoots·ha^{-1} with a single *Salix* shoot weighing 1.28g (Lundberg, 1988) the total carrying capacity of *Salix* shoots is therefore 192 kg·ha^{-1} though there is no discrimination between *Salix* species. We assumed $K_1 = 100\ \text{kg·ha}^{-1}$ as microtine cycles are only predicted in the PLTP hypothesis to initially occur in arctic and alpine tundra regions which have generally infertile soils (Sonesson & Callaghan, 1991).

   Jensen & Doncaster (1999) listed non-preferred food plants with the potential to show toxin production. Their primary suspects were *Empetrum nigrum nigrum, E. n. hermaphroditum* and *Vaccinium uliginosum.* Again the biomass estimates for these species vary. Flower-Ellis (1973) and Kallio (1975) both recorded a typical standing crop of *V. ulginosum* to be 130 kg·ha^{-1}. Estimates of *E. n. hermaphroditum* above ground biomass vary between 129 kg·ha^{-1} (Chepurko, 1971) to 710 kg·ha^{-1} in southern Sweden (Kallio, 1975). As the standing biomass of the toxic prey species appeared comparable to the preferred prey we assumed a similar carrying capacity for both K_2 and K_1 therefore $K_2 = 100\ \text{kg·ha}^{-1}$.

2. **Prey intrinsic rate of increase, r_i.** Exact values for this parameter were difficult to estimate due to the range of factors that can typically influence vegetative growth i.e. light intensity, growing season, crowding, predation, disease, availability of water, soil conditions etc. Consequently, plant growth rates are vary variable (e.g. Wielgolaski, 1972; Bliss, 1975). Growth estimates given in the literature are typically per hectare, so conversions into kg·kg^{-1}·yr^{-1} were dependent upon the carrying capacity values. The intrinsic rate of increase for *Salix* species can range from 0.33 kg·kg^{-1}·yr^{-1} in *S. glauca* (Kallio, 1975) to 6.6 kg·kg^{-1}·yr^{-1} in *S. Lapponum* (Kjelvik, 1973). The rate of increase of the non-preferred species is 0.5 kg·kg^{-1}·yr^{-1} for *V. ulginosum* and 0.8 kg·kg^{-1}·yr^{-1} for *E. n. hermaphroditum* at a single location (Kallio, 1975), though for a similar species with compensatory growth *(V. myrtillus)* the intrinsic rate of increase has been recorded at 5 kg·kg^{-1}·yr^{-1} (Rosswall & Neal, 1975). We explored the dynamics of the model for a range of values. However, to simplify the model we fixed $r_1 = r_2$.

3. **Predator search efficiency, q_i.** No direct data were available for the search rates of voles, though there is known to be considerable variability in vole mobility (Norrdahl & Korpimäki, 1998). The only relevant information we were able to find related to yearly home range. The yearly home range of microtine rodents vary between species e.g. *Microtus agrestis* 0.01 to 0.1 ha, *Cletrionomys rufocanus* 0.03 to 0.1 ha, *C. glareolus* 0.05 to 0.73 ha, *C. rutilus* 0.1 to 2 ha (Macdonald & Barrett, 1993). Lundberg (1988) has recorded that a single *C. glareolus* eats approximately 6 kg of prey per year. If we assume that the average home range to be 0.2 ha then each vole searches 0.2 / 6 ha per kg of food per year. The average weight of a vole is 0.04 kg (see below) yielding 25 voles to the kg, so 1 kg of voles searches 0.2 × 25 / 6 ha·kg^{-1}·yr^{-1}, giving $q_i = 0.8$. We explored the dynamics of the model for a range of values between $q_i = 0.6\text{-}1.0$ ha·kg^{-1}·yr^{-1} due to the variability in home range size. As the preferred prey type is equally abundant as the toxic non-preferred prey type we assumed $q_1 = q_2$.

4. **Predator handling time, h_i.** Handling time includes the time it takes a predator to catch and kill a prey item and the time it takes it to eat the prey item (Krebs, 1994). In other words it covers the fixed interval that is not taken up by searching, so that

the total time interval between eating one unit of prey and the next is $h + 1 / (q \cdot s)$ (see Appendix 2.1). As the predator is a herbivore there is no specific catching or killing time; handling time is primarily the time it takes to eat a prey item. The cropping/chewing rate of *M. pennsylvanicus* is 21.17 $\text{min} \cdot \text{g}^{-1}$ dry weight (or equivalent to eating 1 kg in 0.04 yr) for a monocotyledon species, and 10.97 $\text{min} \cdot \text{g}^{-1}$ dw (or equivalent to eating 1 kg in 0.02 yr) for a dicotyledon species (Belovsky, 1986). Since our prey species are dicotyledons we used the dicotyledon estimate. As we had no reason to suspect otherwise we assumed that handling time is constant for both the preferred and the non-preferred toxic species, so $h_1 = h_2$. Since the Belovsky (1986) estimate is given for dry weight and not wet weight, we estimated h_i to be 0.016 yr for each unit (kg) of food.

5. **Net energy gain from prey, e_i.** A general estimate of the parameter e_1 was obtained by estimating the number of offspring a kilogram of adults are capable of producing that in turn successfully give rise to a new generation.

The weight of voles varies between locations and species (*M. agrestis*: 17-74g in Sweden, (Hannson, 1992), 14-50 g (Macdonald & Barrett, 1993): *C. glareolus* : 12-40 g in Sweeden (Hannson, 1992), 14-40 g (Macdonald & Barrett, 1993), average of 40 g (Gross *et al.*, 1993); *C. rutilus*: 15-40 g (Macdonald & Barrett, 1993); *M. oeconomus*: 25-62 g (Macdonald & Barrett, 1993); *C. rufocanus* 11-30 g (Oksanen & Oksanen, 1981), 15-50 g (Macdonald & Barrett, 1993)). We assumed the average weight of an adult vole to be 0.04 kg; consequently 1 kg of adult voles constitutes 25 individuals. The sex ratio in all *Microtus* species has been observed to be 1:1 (Myllymäki, 1977a). The maximum life-span for *M. agrestis* is 2 years but on average most live for approximately 7 months with females taking approximately 1 month to reach sexual maturity (Macdonald & Barrett, 1993). Therefore a single kg of adult voles consists of 12.5 females, 10.7 of which are reproducing at any one time.

On average *M. agrestis* females give birth to between 4 and 6 individuals per litter, and have between 2 and 7 litters a year (Macdonald & Barrett, 1993). This is consistent with Myllymäki (1977a) who recorded between 21 and 34 offspring a year. Rosswall & Heal (1975) estimated the number of offspring to be lower, at 10 per year. *C. glareolus* females have 4 to 5 litters per year with the average size of a litter being 4 individuals (Macdonald & Barrett, 1993). We assumed that a female would produce on average 20 individuals a year. The total number of individuals born into the next generation from the initial single kg of adults would therefore be 214 individuals per year or 8.56 kg. Of this 8.56 kg we then calculated how many would survive long enough to contribute to the next generation.

M. agrestis males reach reproductive maturity after 40 days, whereas females are reproductively mature after 30 days and have a gestation period of approximately 20 days (Macdonald & Barrett, 1993). Females therefore, make an active contribution to the next generation after 50 days. Using *M. agrestis* life tables compiled by Myllymäki (1977a) the percentage of new-born males alive after 40 days is between 0.9% and 6.4% whereas there are between 2% and 29.5% of new-born females alive after 50 days. These values were calculated by assuming linear mortality between days 30 and 60, and actual mortality data supports this assumption (Myllymäki 1977a). With a 1:1 sex ratio, the initial 1 kg of adults produces between 0.12 kg and 1.56 kg of offspring that survive sufficiently long to contribute to the next generation. We explored a range of values for e_1 of between 0.12 and 1.5 $\text{kg}\cdot\text{yr}\cdot\text{kg}^{-1}\cdot\text{yr}^{-1}$.

The reduced palatability of the non-preferred prey species was expressed in the parameter e_2. As feeding and digestibility is limited for microtines eating the non-preferred plant species (Jensen & Doncaster, 1999) individuals consuming the non-preferred will on average contribute only marginally to future generations. Consequently, the value of e_2 was set close to zero.

6. **Predator mortality rate, *d*.** As discussed earlier the average life span of *Microtus* spp. is approximately 7 months (0.58 yr). This yielded an estimate of $d = 1 / 0.58 = 1.7\ \text{yr}^{-1}$.

Although we estimated many of the parameters to a single value we also explored the consequence to population stability when each of these parameters was increased or decreased. The results of these manipulations will be described in Section 5.3.3.1.

5.3.2 Method of choosing criteria for accepting cyclic behaviour

In order to judge how closely the model predictions fitted empirical microtine population data we compared model output values to five criteria known to characterise microtine cycles: cycle period, peak population density, trough population density, density ratio and the occurrence of a population collapse. Model fit was determined to be good if values for most or all of the criteria lay within observed limits. We now describe what these limits are, based on information generated from the literature.

5.3.2.1 Period of cycles

As discussed already the period of microtine cycles varies between species and location. Many authors have reported observed cycling with peak populations occurring between 2 and 5 years apart (as displayed in Table 5.2).

Period of cycles	Comments (species/location)	Reference
4 years	*Lemmus lemmus*, Alaska	Brunnel *et al.*, 1975
3 to 4 years	*M. agrestis*, C. Scandinavia	Myllymäki, 1977a
5 years	All microtine	Laine & Henttonen, 1983
4 years	Pallasjarvi, Fennoscandian	Henttonen *et al*, 1987
2 to 5 years	Voles	Hanski *et al.*, 1991
3 to 4 years	*C. glareolus*	Marcstrom *et al.*, 1990
3 to 5 years	*M. agrestis*	Macdonald & Barrett, 1993
2 to 4 years	*Lemmus lemmus*	Macdonald & Barrett, 1993
3 to 4 years	Voles	Andersson & Jonasson, 1996

Table 5.2 Average length of time between cycling microtine population peaks.

However, others have reported cycle lengths to be between 2 and 10 years (see Mackin-Rogalska & Nabaglo, 1990). The longest microtine census data comes from Kilpisjärvi biological station, NW Finnish Lapland where annual density estimates have been available since 1946 (Laine & Henttonen, 1983; Hanski & Henttonen, 1996). Microtine rodent population peaks occur at this location on average once every 5 years (Laine & Henttonen, 1983). For our criteria simulated microtine populations had to cycle with a periodicity of between 2 and 5 years.

5.3.2.2 Maximum and minimum population density

The predicted maximum and minimum population densities were compared to empirical results. Again these density values vary between species, location and author (see Table 5.3).

Max (ind·ha^{-1})	Min (ind·ha^{-1})	Comments	Author
300			Chitty, 1971
100	25	*M. agrestis*, S. Scandinavia	Hanssonn, 1974
300		*M. agrestis*, N. Scandinavia	Stenseth *et al.*, 1977
320	0	*M. agrestis*, Ingels	Myllymäki, 1977a
248	8	*M. agrestis*, Ahtaila	Myllymäki, 1977a
332	0	*M. agrestis*, C. Finland	Myllymäki, 1977a
80	10	*C. glareolus*	MacDonald & Barrett, 1993
475		*C. glareolus*, Skomer Island	MacDonald & Barrett, 1993
137	0	Pallasjärvi, Finland	Hanski & Korpimäki, 1995
104	0	Alajoki, Finland	Hanski & Korpimäki, 1995
100	0		Nordahl & Korpimäki, 1998

Table 5.3 Maximum and minimum population densities of cycling microtine populations.

For our criteria values we used a maximum density limit of 100 - 350 ind·ha^{-1} and a minimum density limit of between 0 - 25 ind·ha^{-1}.

5.3.2.3 Maximum to minimum density ratio

There is considerable variation in the ratio of maximum to minimum population density observed during cycles of not only different species but also the same species in different areas (Akçakaya, 1992). Hanski *et al.* (1991) and Hanski & Korpimäki (1995) have used the ratio of maximum to minimum population density as a measure of how well a microtine population model fits empirical data. Where the minimum density is equal to zero Hanski & Korpimäki (1995) replaced it with the next smallest density. Some maximum to minimum density ratios extracted from the literature are presented in Table 5.4.

Max:Min ratio	Comments	Author
10-20	*M. agrestis*, S. Scandinavia	see Stenseth *et al.*, 1977
20-30	*M. agrestis*, C. Scandinavia	see Stenseth *et al.*, 1977
4-70		Hairston, 1994
137	Pallasjärvi, Finland	Hanski & Korpimäki, 1995
104	Alajoki, Finland	Hanski & Korpimäki, 1995
127	Kilpisjärvi, Finland	Hanski & Korpimäki, 1995

Table 5.4 Maximum to minimum ratios for cycling microtine population densities.

Hanski *et al.* (1991) display an extensive maximum to minimum density ratio list in the appendix of their paper. The ratios reported vary between 2 and 168 for different vole species. We assumed a maximum to minimum ratio limit of 100 which is consistent with Korpimäki *et al.* (1994). As a lower limit we set the maximum to minimum ratio criteria to 10.

5.3.2.4 Population collapse

A characteristic of both empirical time series data (e.g. see Laine & Henttonen, 1983; Hanski *et al.*, 1993; Hanski & Henttonen, 1996; Turchin *et al.*, 2000) and the microtine population dynamics described in the PLTP hypothesis (Jensen & Doncaster, 1999) is the rapid collapse of the microtine numbers once at peak densities. In the PLTP hypothesis the catastrophic collapse is a result of toxin production by the non-preferred plant type. The fifth model criteria was therefore related to population collapse. To match the criteria the rate of population decrease during the crash had to be greater than the rate of increase during the recovery phase.

5.3.3 Results of running the Křivan model

The dynamics predicted by the model with the parameter estimates described in Section 5.3.1 ranged from stability to periodic cycling. In a few instances the behaviour was best described as irregular. From the simulations using various combinations of the parameter values, cycling populations were identified as having between 3 and 13 years between population peak densities. Maximum population densities ranged between 783 ind·ha^{-1} and 53 ind·ha^{-1} whereas minimum population densities ranged between 0 and 55 ind·ha^{-1}. A sample of the analysis on all parameter values can be found in Appendix 5.3

Preliminary investigations on parameter values that were not fixed (i.e. r_i and e_1) gave an early indication of approximately what values of r_i and e_1 to use in the more detailed analysis. On this basis the range of r_i fully investigated was between 1.5 and 2 kg·kg^{-1}·yr^{-1} and the range of e_1 investigated was between 0.3 and 0.4 kg·yr·kg^{-1}·yr^{-1}. A summary of the results using these values can be found in Table 5.5 with an example density time plot displayed in Figure 5.2.

5.3.3.1 The effect of individual parameter values on simulated microtine population dynamics

An increase in the intrinsic rate of prey renewal (r_i) results in an increase in the frequency of microtine cycling, although the increase also causes an increase in microtine maximum density and a decrease in microtine minimum density. Consequently, where r_i was sufficiently large only two out of five criteria were met (period of cycles and minimum density). An increase in the microtine search rate (q_i) resulted in a decrease in the frequency of microtine cycling. Again the increase also caused an increase in microtine maximum density and a decrease in microtine minimum density. An increase in the value of q_i was sufficient alone to reduce the number of criteria met by the model from four to one. The final parameter explored extensively in Table 5.5 was the net energy gained from the preferred prey species (e_1). Although the value of e_1 was only explored over a relatively small range it did effect the resulting dynamics. An increase in e_1 brought about an increase in microtine maximum density and a decrease in microtine minimum density. However, it did not alter the periodicity of the cycling populations.

Although variations in the net energy gained from the preferred prey type (e_1) did not alter the periodicity of the cycling populations, variations in the net energy gained from the non-preferred prey type (e_2) did. A reduction in the net energy gained from the non-preferred prey type resulted in an increase in the number of microtine cycles. If e_2 was reduced from 0.04 to 0.02 then the period of microtine cycles decreased from 5 years to 4 years, though the maximum and minimum criteria were no longer met. However, if the search rate (q_i) was also reduced sufficiently ($q_i = 0.6$) then the resulting equilibrium dynamic was stable. In this situation eating any of the non-preferred prey does not advantage the foraging predators. As the search rate and the energy to be gained from eating the non-preferred prey type are low the predator optimises foraging by searching for the preferred prey type only, even at low prey densities. The critical threshold value is high and therefore the predator does not switch between prey species, consequently the non-preferred prey type does not influence the predator dynamics.

The average life span of a microtine rodent was assumed to be 7 months. Investigations into altering the average life span (d) have shown that if d is reduced then there is an increase in cycling periodicity. However, when d was reduced for certain parameter combinations population oscillations appeared irregular. When the average life span was set at 1 year ($d = 1$) all simulations resulted in population cycles with a periodicity of more than 6 years.

An increase in handling time (h_i) and carrying capacity (K_i) also effected the cyclic dynamics of the simulated microtine populations by increasing the length of time between population peaks. However, increasing K_i increased the maximum density and decreased the minimum density whereas increasing h_i decreased the maximum density and increased the minimum density. If handling time (h_i) was reduced to $h_i = 0.1$ then cycling populations were observed that still met four of the five criteria. If handling time was increased to $h_i > 0.2$, however, then the criteria were no longer met.

Inputs			Outputs						
r_i kg·kg·yr^{-1}	q_i ha·yr^{-1}	e_1 kg·kg^{-1}	Threshold Kg·ha^{-1}	Max No.·ha^{-1}	Min no.·ha^{-1}	Ratio max:min	peaks Period (yr)	No. criteria met	Comments
1.5	0.6	0.32	14.9	158.9	21.0	7.6	5.0	****	√ though no population collapse
1.5	0.6	0.36	13.0	160.1	20.6	7.8	5.0	***	√ though no population collapse
1.5	0.6	0.40	11.6	163.8	19.4	8.4	5.0	****	√ though no population collapse
1.5	0.8	0.32	11.2	198.8	4.2	46.9	5.0	***	√ though no population collapse
1.5	0.8	0.36	9.8	214.8	3.0	70.5	5.0	****	√ though no population collapse
1.5	0.8	0.40	8.7	197.0	4.3	46.0	5.0	****	√ though no population collapse
1.5	1.0	0.32	8.9	344.8	0.0	344.8	10.0	**	Ratio too big, not enough cycles
1.5	1.0	0.36	7.8	369.3	0.0	369.3	10.0	*	Ratio too big not enough cycles
1.5	1.0	0.40	6.9	409.8	0.0	409.8	10.0	*	Ratio too big, not enough cycles
1.7	0.6	0.32	14.9	172.4	25.6	6.7	5.0	*	√ though no population collapse
1.7	0.6	0.36	13.0	177.5	24.0	7.2	5.0	****	√ though no population collapse
1.7	0.6	0.40	11.6	175.8	24.5	7.4	5.0	****	√ though no population collapse
1.7	0.8	0.32	11.2	203.1	6.5	31.5	5.0	****	√ though no population collapse
1.7	0.8	0.36	9.8	209.6	5.8	36.2	5.0	****	√ though no population collapse
1.7	0.8	0.40	8.7	215.4	5.6	38.2	5.0	****	√ though no population collapse
1.7	1.0	0.32	8.9	302.5	0.3	302.5	7.1	**	Ratio too big, not enough cycles
1.7	1.0	0.36	7.8	317.9	0.2	317.9	7.1	**	Ratio too big, not enough cycles
1.7	1.0	0.40	6.9	320.7	0.2	320.7	7.1	**	Ratio too big, not enough cycles
2	0.6	0.32	14.9	195.5	31.8	6.1	4.5	***	Min value big
2	0.6	0.36	13.0	196.7	31.4	6.3	4.5	***	Min value big
2	0.6	0.40	11.5	202.4	29.6	6.8	4.5	***	Min value big
2	0.8	0.32	11.2	221.2	9.3	23.7	5.0	****	√ though no population collapse
2	0.8	0.36	9.8	236.9	7.7	30.8	5.0	****	√ though no population collapse
2	0.8	0.40	8.7	245.9	6.8	35.9	5.0	****	√ though no population collapse
2	1.0	0.32	8.9	365.6	0.3	365.6	7.1	*	Max & Ratio too big, not enough cycles
2	1.0	0.36	7.8	400.2	0.2	400.2	7.1	*	Max & Ratio too big, not enough cycles
2	1.0	0.40	6.9	438.8	0.1	438.8	7.1	*	Max & Ratio too big, not enough cycles

Table 5.5 Summary of the dynamical behaviour of the model (eqn 5.1 to 5.3). All populations exhibited periodic cycling. A description of the parameters is given in the text. Fixed parameter values used for these numerical simulations were $K_i = 100$, $h_i = 0.016$, $e_2 = 0.04$, $d = 1.7$. 'Threshold' gives the critical threshold for preferred prey density below which the predator starts eating the non-preferred prey, 'Max' and 'Min' give the maximum and minimum densities of cycling microtine respectively. 'Ratio' is maximum density to minimum density ratio, where $min < 1$, a value of $min = 1$ was used to calculate the ratio. 'Peaks' gives the number of years between maximum densities. The 'number of criteria met' is a measure of how well the model predictions fitted empirical data as detailed in the text (**** = four out of five criteria met). The parameters shown in the highlighted row were used to produce density time plots shown in Figure 5.2.

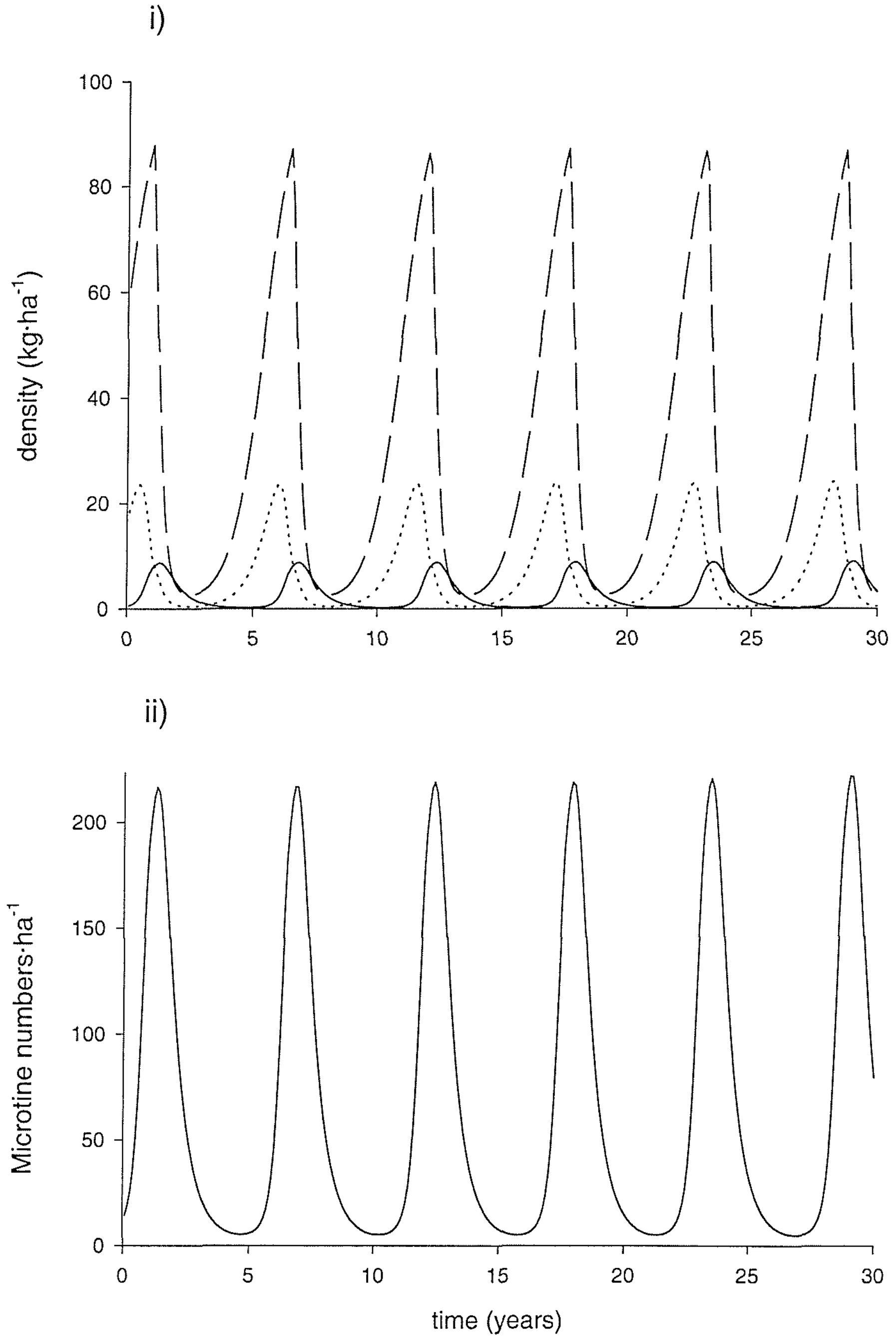


Figure 5.2 An example of the predicted microtine dynamics generated using the optimal foraging model (eqn 5.1 to 5.3) and median values of the three variable parameters (r_i = 1.7, q_i = 0.8 and e_1 = 0.36) when K_i = 100, h_i = 0.016, e_2 = 0.04, d = 1.7. Solid line shows microtine density, broken line non-preferred prey density and dotted line preferred prey density i) a comparison of predator and prey densities expressed as kg·ha^{-1} , ii) Corresponding cyclic microtine population densities expressed as the number of individuals per hectare assuming microtine weight = 0.04 kg.

Many of the parameter combinations given in Table 5.5 matched four of the five criteria for realistic cycles (maximum density, minimum density, maximum to minimum ratio and period of cycles). The general trend exhibited by the time series plot (Figure 5.2 ii), when all four criteria were met, was visually similar to comparable empirical results. Characteristically, there was a rapid increase in the microtine population followed by rapid decrease, there then followed an extended low-density phase before the cycle was repeated. The decrease did not correspond to a catastrophic crash, however, being as smooth as the corresponding increase. We will go on to show how introducing a toxicity threshold into the model can satisfy the requirement for a crash (Section 5.4.1).

As a measure of the success of their model, Hanski & Korpimäki (1995) plotted the cycle amplitude (maximum to minimum ratio density) against cycle period. Empirical data has shown that as cycle period increases, so too does the maximum to minimum density ratio (Hentonnen, *et al.*, 1985; Hanski *et al.*, 1991; Hanski & Korpimäki 1995). We also obtained a positive correlation between cycle period and maximum to minimum ratio with our model (Figure 5.3) using the parameter combinations given in Table 5.5. However, in Table 5.5 where minimum density was less than 1 we assumed it took the value of 1. This assumption consequently reduced the range of the ratio displayed in the graph.

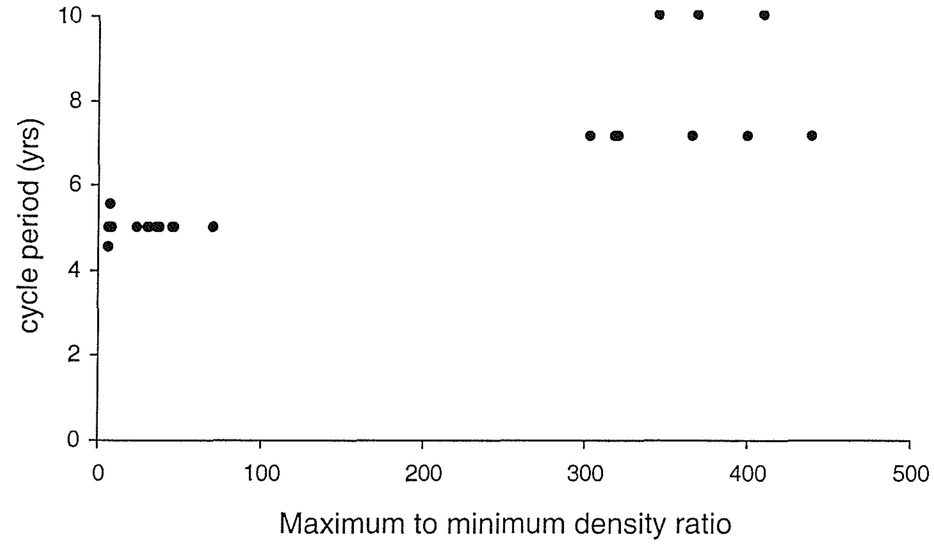


Figure 5.3 The ratio of maximum density to minimum density plotted against the length of the cycle period for simulated microtine populations. Plotted results are those obtained from the parameter combinations given in Table 5.5.

5.4 MODIFICATIONS TO THE KŘIVAN MODEL

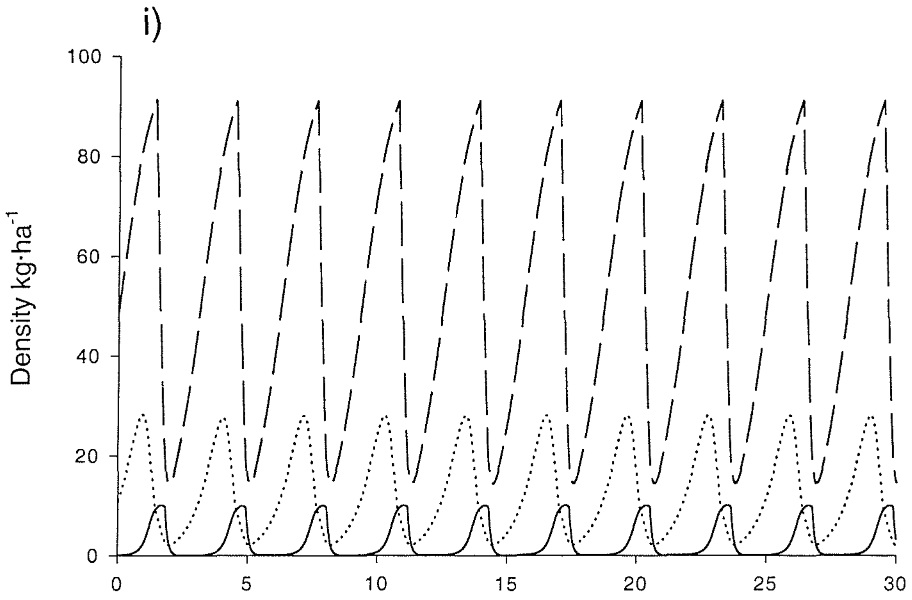
5.4.1 Increased microtine mortality when a toxic threshold is met - the toxic prey model

In the original model described above, the reduced palatability of the non-preferred prey type was only expressed in the net energy parameter, e_2. The energy obtained by microtine rodents consuming only the non-preferred prey type was insufficient to enable further reproduction. Only four out of the five model criteria were met and the population decline did not constitute a collapse (see Table 5.5).

We therefore decided to extend the original Křivan model to include a direct toxicity effect on the microtine rodents. We adjusted the original model by introducing a pulse of toxin from the non-preferred plant type. The adjustment was modelled as outlined below. Once the density of the non-preferred prey type drops below a given toxic threshold the microtine mortality rate significantly increases (we set $d = 1.7\ \text{yr}^{-1}$ above the toxic threshold, $d = 10\ \text{yr}^{-1}$ below the toxic threshold). Once the non-preferred prey population recovers sufficiently, so that its density is above the toxic threshold the microtine mortality rate returns to its original value ($d = 1.7\ \text{yr}^{-1}$). This switch in mortality therefore represents the toxic pulse as described by Jensen & Doncaster (1999). Increasing mortality rate to a very high level represents the periodic production of toxins by the non-preferred prey type that consequently results in the death of most microtine individuals that consume it.

The effects of employing a toxic threshold on the population dynamics are shown in Figure 5.4 and Figure 5.5. To produce Figure 5.4, the value of the toxic threshold was set at a level that was related to the critical threshold value. Setting the toxic threshold as a function of the critical threshold enabled us to fix the position of the toxic threshold in relation to the critical threshold, regardless of what values were used for the parameters. In this instance, toxic threshold = critical threshold × 2. Introducing the toxic threshold improved the fit of the microtine dynamics with respect to the number of criteria met. The interval between population crashes decreased from 5 years to 3 years. The maximum and minimum densities were still within the confines of the empirical criteria, and so too was the maximum to minimum ratio. Interestingly, the depletion of the toxic prey plant did not occur to the same extent in the toxic threshold version of the model as it did in the original model. This is seen in the comparison of Figure 5.2 and Figure 5.4. The toxic prey therefore benefited from the toxicity.

Introducing the toxic threshold did affect the rate at which the population decreased. The adjustment to the model resulted in a microtine population crash as also described by Jensen & Doncaster (1999) in their verbal explanation of the PLTP hypothesis. Not only was the rate of population decrease considerably greater than the rate of increase there was also a stationary phase at the peak of the cycles, as also detailed by Jensen & Doncaster (see Figure 5.5). Consequently, this alteration resulted in all five empirical criteria being met rather than just the four as observed with the original Krivan model (compare Figure 5.2 and Figure 5.4).



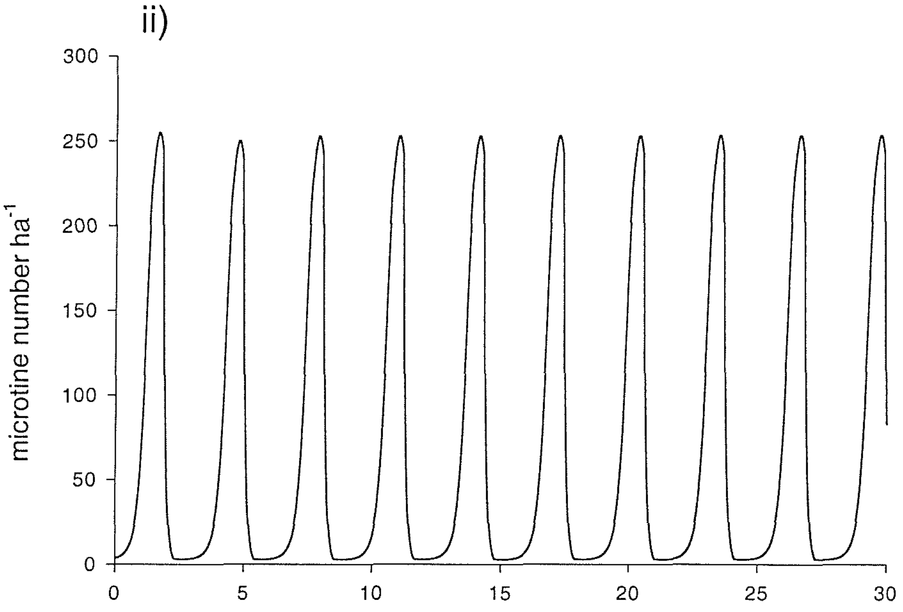


Figure 5.4 An example of the predicted microtine dynamics generated using the optimal foraging model (eqn 5.1 to 5.3) with a toxic threshold equal to the critical threshold × 2, the toxic prey model. Once the density of the non-preferred prey type drops below the toxic threshold the microtine mortality rate increases from 1.7 to 10 yr^{-1}, other parameter values are the same as those used in Figure 5.2. Solid line shows microtine density, hashed line toxic prey density and dotted line preferred prey density i) a comparison of predator and prey densities expressed as $kg{\cdot}ha^{-1}$, ii) Corresponding cyclic microtine population densities expressed as the number of individuals per hectare assuming microtine weight = 0.04 kg.

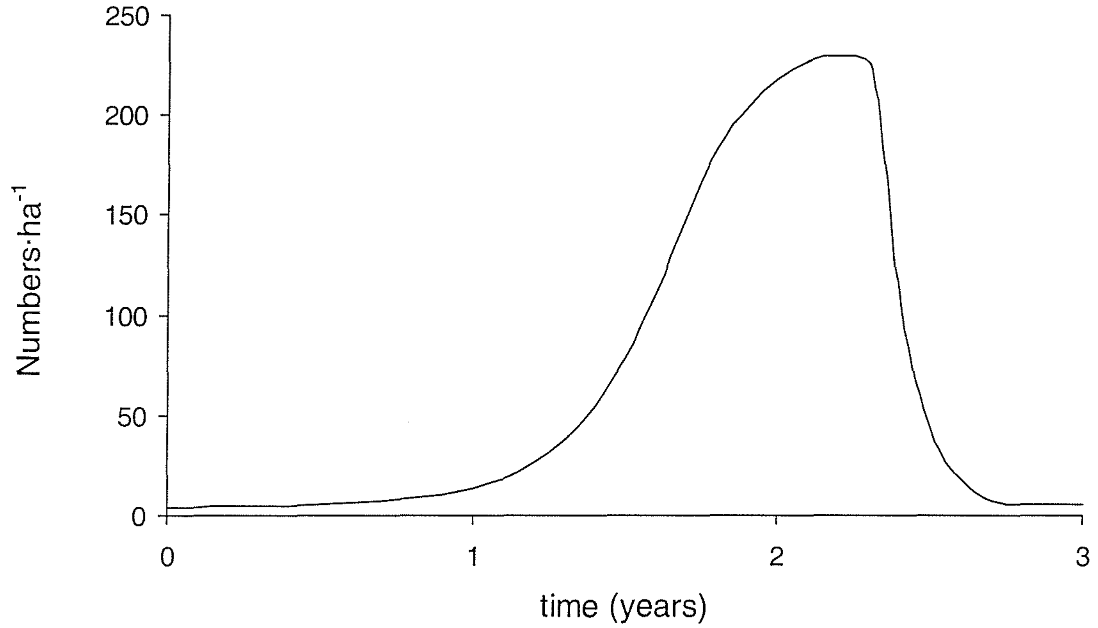


Figure 5.5 An example of a single microtine cycle taken Figure 5.4 generated using the optimal foraging model (eqn 5.1 to 5.3) with a toxic threshold equal to the critical threshold × 2, the toxic prey model. This figure concurs exactly with Figure 1 in Plesner-Jensen & Doncaster (1999) which describes their verbal model. The lethal effects of the toxins cause the crash in microtine numbers once the toxic threshold has been met.

5.4.2 Continual toxin production by non-preferred plant type

To compare the effects of periodic toxin production to those of continual toxin production the original model was adapted in such a way that once the critical preferred prey threshold was met the mortality rate of the microtine rodents consuming the non-preferred prey immediately increased. This version of the model therefore represented a microtine-two plant species model whereby the non-preferred prey type is always toxic and not periodically toxic unlike the model in Section 5.4.1.

This modification altered the dynamics of both the prey and the predator species. Using the same parameter values that were employed to generate cyclic populations in Figure 5.2, and with an increase in d from 1.7 to 10 yr^{-1} whenever the toxic plant species was included in the diet, resulted in none of the criteria being met. The resulting populations converged to a single stationary value. Dynamics of this kind are described by a stable focus (as also described and observed in Chapter 2)

If the level of toxicity was reduced so that there was an increase in d from 1.7 to 2 yr^{-1} then stable limit cycles once more prevailed. However, although cycles were evident, only 2 of the five criteria were met. The corresponding time series plot is shown in Figure 5.6.

Introducing the continual toxicity effect ($d = 2\ yr^{-1}$) reduced the maximum density of microtine rodents from over 200 per hectare to just over 100 per hectare, which was still within the confines of our maximum density criteria. The alteration to toxicity also increased the minimum density when compared to Figure 5.2. The comparison showed that when additional mortality was included, the preferred prey species was above the critical threshold for relatively longer than it was when there was not additional toxic mortality. This enabled the microtine population to recover at higher densities than those observed in Figure 5.2

The minimum microtine density given by the parameters used to generate Figure 5.2 was approximately 5 $ind{\cdot}ha^{-1}$, whereas the minimum density given by the parameters used to generate Figure 5.6 was 30 ind·ha^{-1}. The alteration to the model therefore increased the minimum microtine density to a level that no longer met the minimum density criteria (< 25 ind·ha^{-1}). The extent of the toxic prey species recovery was not as great in Figure 5.6 as in Figure 5.2 as the period between cycles was shorter; consequently resulting in less re-growth.

The maximum to minimum ratio was lower than the ratio value set in the criteria, though still within the confines of empirical results reported by Hanski *et al.* (1991). Although the model with continual toxin production did not mirror empirical microtine density data any more closely than the original model, it did result in an increase in the frequency of microtine cycles. The period of cycles decreased from 5 years to 4 years when mortality was varied in direct accordance to microtine diet.

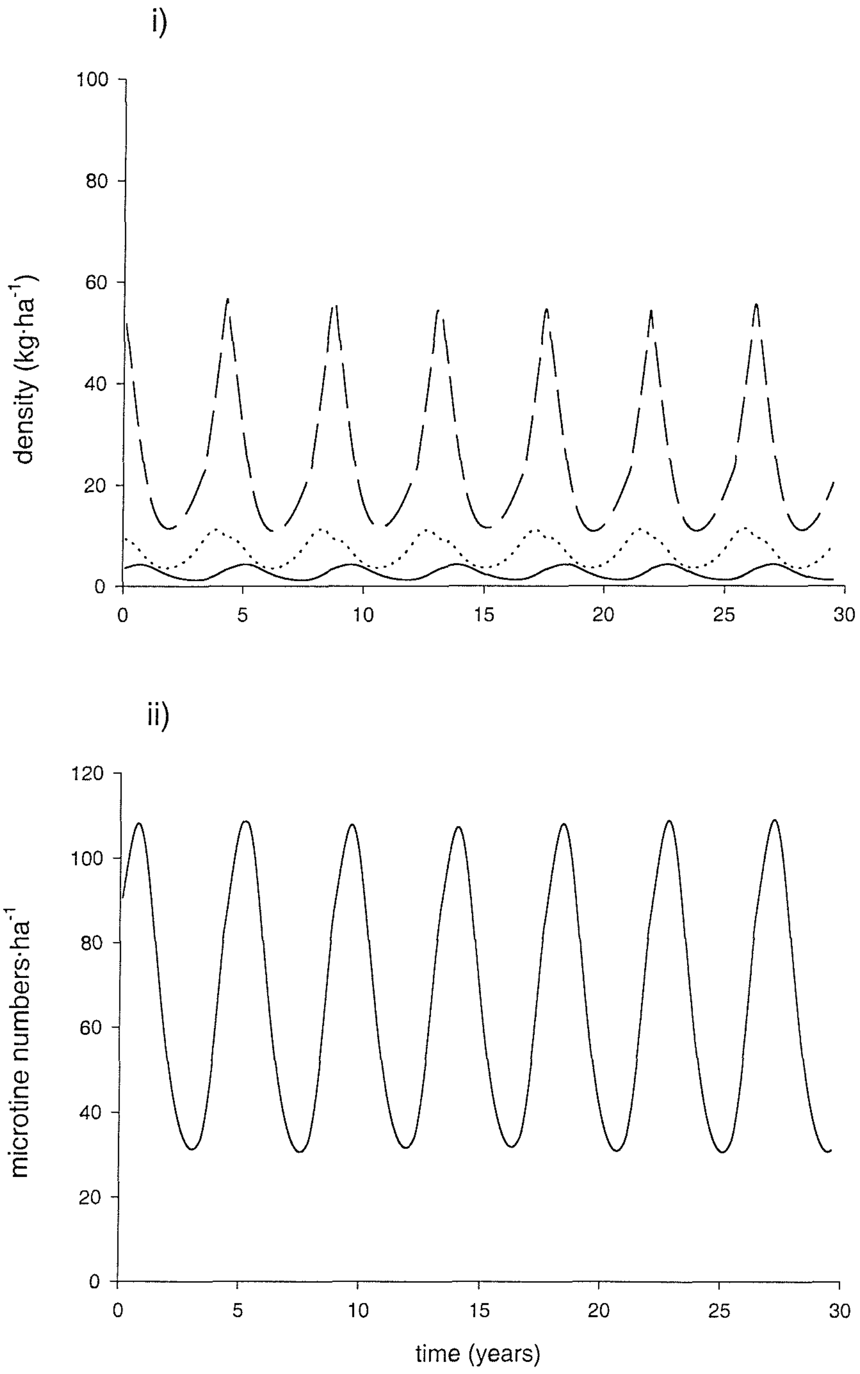


Figure 5.6 An example of the predicted microtine dynamics generated using the optimal foraging model (eqn 5.1 to 5.3) with variable mortality rate. The microtine mortality when the preferred prey type is the only prey eaten $d = 1.7$ yr^{-1}, mortality when the toxic prey type is included in the diet, $d = 2.0$ yr^{-1}, other parameter values are the same as those used in Figure 5.2. Solid line shows microtine density, hashed line toxic prey density and dotted line preferred prey density i) a comparison of predator and prey densities expressed as kg·ha^{-1}, ii) Corresponding cyclic microtine population densities expressed as the number of individuals per hectare assuming microtine weight = 0.04 kg.

5.4.3 Prey species with equal net energy gain and no toxicity

The driving force behind the PLTP hypothesis is the over consumption of a preferred prey type, which leads to the inclusion of a toxic non-preferred prey type in the diet of microtine rodents. It is the production of the lethal toxin by the non-preferred prey type that alters the microtine population dynamics. Therefore, if the alternative prey type were no longer toxic, or no less preferred than the first prey type then we expect the dynamics of the system to be altered in such away that the model output no longer mirrors empirical results. We modelled the extreme of this alternative system by setting $e_1 = e_2$ with no toxin production i.e. the net energy gain obtained by the microtine rodent was equal for both prey types. An example of the resulting time series plot is displayed in Figure 5.7.

Setting $e_1 = e_2$ strongly influenced microtine dynamics. The population dynamics can be compared between Figure 5.2 ($e_1 = 0.36$, $e_2 = 0.04$) and Figure 5.7 ($e_1 = 0.36$, $e_2 = 0.36$). With the parameter values used in Figure 5.2 four of the five empirically derived criteria were met. If only the value of e_2 is altered so that $e_1 = e_2$ only one of the five criteria is met. The maximum density increased almost four-fold (209 ind·ha^{-1}to 756 ind·ha^{-1}), whereas the minimum density decreased to almost zero which was, however, still within the confines of the minimum density criteria. Due to the increase in maximum density and the decrease in minimum density the maximum to minimum density ratio was more than double the criteria value. The period of the cycles was also reduced from one in every 5 years (as seen in Figure 5.2) to one in every 10 years (as seen in Figure 5.7). Consequently, it was only the minimum density criteria that was met when $e_1 = e_2$.

Not only was the frequency of the cycles reduced when $e_1 = e_2$ but also the general shape of the population peaks. The increasing phase of the population peak was very steep, whereas the decreasing phase was comparatively shallower (as seen in Figure 5.7) the exact opposite of what is detailed in the PLTP hypothesis.

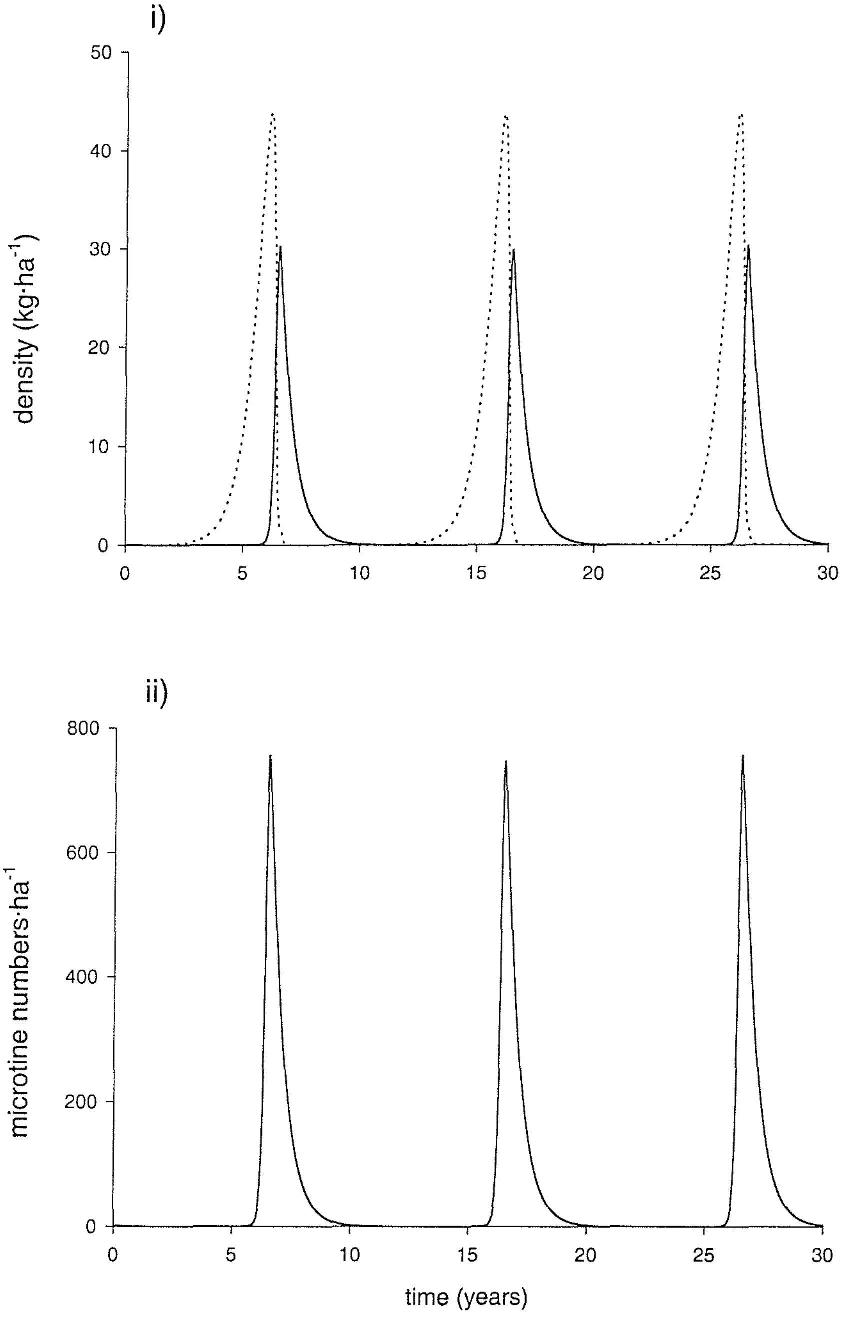


Figure 5.7 An example of the predicted microtine dynamics generated using the optimal foraging model (eqn 5.1 to 5.3) when the two prey types have equal net energy gain with respect to microtine predators ($e_1 = e_2$). Other parameter values are the same as those used in Figure 5.2. The solid line shows microtine density. The dotted line shows prey density. Both prey species follow the trajectory of the dotted line. i) a comparison of predator and prey densities expressed as kg·ha^{-1}, ii) Corresponding cyclic microtine population densities expressed as the number of individuals per hectare assuming microtine weight = 0.04 kg.

5.5 AN ALTERNATIVE MODEL

The coupled predator-prey dynamics of the Holling-Tanner model have been shown to generate periodic cycling with certain parameter combinations (e.g. see Renshaw, 1995; Gragnani, 1997; Renshaw, 1999). The Holling-Tanner model has also been used successfully to model cyclic empirical populations (e.g. Tanner, 1975; Wollkind *et al.*, 1988). A description of the Holling-Tanner model and the corresponding parameters are given in Appendix 2.1. As already discussed, the Křivan (1996) optimal foraging model has the same prey dynamics as the Holling-Tanner model though it is adapted to allow for two prey types. Its predator dynamics are slightly different, with prey consumption contributing to birth-rate in the Křivan model and to death rate in the Holling-Tanner model. We decided to test the two-prey Křivan model against the simpler one-prey Holling-Tanner model. This would provide a check on the significance of including a second prey type.

The equilibrium conditions of both the Holling-Tanner and Křivan models are characterised by smaller prey densities in the presence of larger predator populations when prey are abundant, but larger prey densities with larger predator populations when prey are scarce. This is the effect of inverse density-dependence on consumption, which results from a constant handling time, h, of each prey, s, by the predator, added to the search time for each prey. In the Holling-Tanner model, predators mutually interfere with each others' net recruitment rate, since the per capita recruitment of predators declines with predator density, though predator density has no effect on per capita intake.

The Holling-Tanner model has six parameter combinations. Values attached to each of these parameters are outlined below:

1. **The prey carrying capacity, K.** Using the same parameter assumptions as detailed in Section 5.3.1 we estimate K to be 100 $\text{kg}\cdot\text{ha}^{-1}$.
2. **The intrinsic rate of prey increase, r.** Using the same parameter assumptions as before and the analysis of the optimal foraging model we estimate r to be 1.7 $\text{kg}\cdot\text{kg}^{-1}\cdot\text{yr}^{-1}$.

3. **Predator search efficiency, q.** Using the same parameter assumptions as before and the analysis of the optimal foraging model we estimate q to be 0.8 ha·yr^{-1}·kg^{-1}.
4. **Predator handling time, h.** Using the same parameter assumptions as detailed in Section 5.3.1 we estimate h to be 0.016 yr.
5. **The intrinsic rate of predator increase, a.** Hanski *et al.* (1993) and Hanski & Korpimäki (1995) estimate the intrinsic rate of increase in microtine rodents to differ between summer and winter months. Using empirical data sets from western Finland they estimated maximal rates of increase for summer and winter months, they gave $r_{summer} = 5.4$ kg·kg^{-1}·yr^{-1} and $r_{winter} = 2.7$ kg·kg^{-1}·yr^{-1}.
6. **Density of prey to sustain one predator; b.** This parameter represents the density of s renewing prey that just sustains one predator and that enables it to replaces itself with a single offspring when it dies. As no data were available to estimate b, a range of values were explored $b = 0.01$ - 1000 kg·ha^{-1}.

Analysis of the Holling-Tanner model with the parameter values outlined above showed that regardless of the value taken by b, the microtine and the plant species both converged to an equilibrium point. For no combinations of the ranges of parameter values detailed previously did we observe a cyclic equilibrium. We were, however, able to produce a cyclic population when the values of q and h were increased and r and a were decreased beyond the ranges detailed; though the resulting plots did not mirror empirical microtine data. Therefore the Holling-Tanner model (with one prey species) did not represent cyclic microtine populations as successfully as the Křivan model (with two-prey species). However, variations of the one-predator one-prey Holling-Tanner model have been used to successfully model cyclic microtine populations where the microtine species has been modelled as the prey (e.g. see Hanski *et al.*, 1991; Hanski *et al.*, 1993; Hanski & Korpimäki, 1995).

A variation on this same analysis was carried out using the Křivan model, by setting the parameter e_2 to zero. Setting $e_2 = 0$ meant that the microtine predators would be modelled to no longer consume any of the non-preferred prey type. Simulations under these conditions reproduced cyclic populations that did meet four of the five criteria. The criteria not matched was the rapid population collapse following peak densities. However a value of e_2 just above zero ($e_2 = 0.01$) produced cyclic populations that no longer met any of the five criteria.

5.6 DISCUSSION

The aim of this chapter was firstly to model the series of events proposed in the microtine PLTP hypothesis as described by Jensen & Doncaster (1999). Secondly, we wished to evaluate the PLTP model by comparison to alternative models. By using Křivan's (1996) model of an optimally foraging predator of two prey species we were able to introduce a non-preferred prey type into the microtine diet. Using parameter values generated from field data it was shown that the model was capable of producing cyclic populations. Further analysis of parameter values resulted in oscillating population densities that matched certain standard criteria generated from empirical data. The inclusion of periodic toxin production in the original model resulted in all five criteria being met.

5.6.1 Parameter specificity and the effect on simulated microtine dynamics

The microtine population dynamics predicted from the optimal foraging model were compared against five empirically derived criteria: maximum density, minimum density, maximum to minimum density ratio, cycle periodicity and population collapse. This enabled us to gauge the success of the model and identify the parameter values that fitted the empirical data most closely. We suggest that future hypothesises and model output values be tested against these criteria in order to ascertain similarities between theoretical and empirical data.

Analysis of the full range of parameters derived from empirical experimental data collected from the literature produced various kinds of population dynamics when used in the model. Not only were limit cycles observed but also stable nodes and stable focuses, in some instances irregular dynamics appeared to be evident. These forms of population dynamics have been noted by other authors studying similar microtine models (e.g. Batzli, 1983; Hanski *et al.*, 1993, Hanski & Korpimäki, 1995), and have also been identified in time series data from natural population (e.g. Turchin & Taylor, 1992). Initial sensitivity analysis allowed us to focus on limited ranges of values that produced aspects of cycling populations. This facilitated further more detailed investigation into the effect of certain parameter combinations on population dynamics.

Not only did we assess the success of the model in terms of the five criteria but we also sought other similarities between the model outputs and observed population dynamics. A characteristic of cyclic microtine populations studied in the field is the presence of a relatively long low phase between consecutive population peaks. Where microtine predators have been modelled as the driving force behind microtine cycles, the long low phase has not successfully been replicated (e.g. Hanski *et al.*, 1993, Hanski & Korpimäki, 1995). However, in the analysis of our model we were able to replicate low phases between population peaks. Jensen & Doncaster (1999) hypothesise that the long low phase is caused by the toxin effect. At this point in the cycle the local population contributes minimally to the next generation. Instead, recruitment from outside the immediate system (from lower latitudes and altitudes) re-seeds the population. Our numerical analysis has not simulated recruitment from outside, but we obtained a long low phase even without it.

Both Turchin & Batzli (2000) and Hanski *et al.* (1993) recorded that a reduction in the carrying capacity of prey reduces the amplitude and the period of oscillations. A further reduction eventually results in stability. Analyses of our model with the parameter values used in this study have also shown a similar result.

Microtine rodents experience greater longevity at higher altitudes and latitudes (Innes & Millar, 1990). Typically the period between cycles also increases at higher altitudes and latitudes (Mackin-Rogalska & Nabaglo, 1990; Hanski *et al.*, 1991). In this study the natural mortality rate of the microtine rodents in the model was represented by the parameter, *d*. If the average life span of microtine is increased in the original model (by decreasing the value of *d*) the period between cycles increases. A positive correlation was found between cycle length and the ratio of maximum to minimum ratio density. A similar correlation has been found in empirical data collected from populations at numerous field stations (Hansson, 1988, Henttonen, *et al.*, 1985; Hanski *et al.*, 1991). Consequently, we were able to reproduce not only general microtine cycles but also other dynamical properties observed in field populations.

Interestingly, the number of offspring produced per year also increases at higher altitudes and latitudes (Innes & Millar, 1990). Increasing the net energy conversion factor of the preferred prey type (e_1) in the model, however, increased the frequency of cycles, whereas the cycle frequency has been shown to decrease in empirical populations at higher altitudes and latitudes (Hanski *et al.*, 1991; Mackin-Rogalska & Nabago, 1990).

Although the intrinsic rate of prey increase that we used appears high at $1.7\mathrm{kg}\cdot\mathrm{kg}^{-1}\cdot\mathrm{yr}^{-1}$, plant species utilised by microtine rodents re-grow rapidly after defoliation. The rapid re-growth of some prey species is achieved by the utilisation of stored energy reserves (Smirnov & Tokmakova, 1971). *E. vaginatum* has an exceptionally high above-ground phytomass in winter (Andreev *et al.*, 1972). However, the primary production of the tundra region varies quite strongly from year to year (Wielgolaski, 1971). The length of the growing season decreases as altitude and latitude increase (Laine & Henttonen, 1983), with the highest biomass production at the lowest latitudes (Wielgolaski, 1971). This has led Selås (1997) to suggest that the increase in the period between cycles at greater altitudes and latitudes could be explained by the increased length of time required by plants to recover from grazing. We have found in our model that a decreased prey intrinsic rate of increase, r_i, decreases the number of cycles, in accordance with field data.

Oscillations in microtine rodent population densities disappear once lower latitudes have been reached (Akçakaya, 1992). Our model did produce stable dynamics when the search rate parameter was reduced sufficiently. If at lower latitudes plant species were more abundant, we would expect the microtine-searching rate to reduce accordingly. There is evidence for an increase in the available standing crop at lower latitudes and altitudes (Moen, 1990; Jedrzejewski & Jedrzejewski 1996). The model therefore suggests that the observed stability at lower altitudes could be related to reduced search rate.

The analysis of the optimal foraging model predicts not only cyclic microtine populations but also cyclic prey populations. Microtine rodents can greatly effect vegetation during single peak years (Moen, 1990). Laine & Henttonen (1983) and Oksanen & Ericson (1987) observed a degree of synchronous cycling between microtine density and a range of botanical variables. Jedrzejewski & Jedrzejewski (1996) observed a correlation between rodent density and the standing crop of ground vegetation as well as the net productivity of ground vegetation. Laine & Henttonen (1983) showed a positive correlation between flower production in year t and rodent density in year $t + 1$ in 10 plant species including a *Salix* sp. a *Vaccinium* sp. and *E. n. hermaphroditum*. Moen (1990) did not find any depletion in plant species density in a microtine enclosure experiment. However, density censuses were only taken for a maximum of 55 days, which might be insufficient to reveal the effect.

5.6.2 Adaptations and variations to the model

The original Křivan model, with no periodic toxin production, simulated population dynamics that met four of the five empirically set criteria; the criteria not met was the catastrophic population collapse. To replicate periodic toxin production by the non-preferred plant type, as described in the original PLTP hypothesis, we introduced a toxic threshold into the original model. The production of the toxin was dependent upon the density of the non-preferred plant type. When the density of the non-preferred prey type was below the toxic threshold the toxin was produced and consequently microtine mortality increased. Adapting the model by adding a toxic pulse resulted in all five of the empirically derived criteria being met, including the catastrophic population collapse. This is consistent with observational field data (e.g. Laine & Henttonen, 1983; Hanski *et al.*, 1993; Hanski & Henttonen, 1996; Turchin *et al.*, 2000). In our toxic threshold model as in the PLTP hypothesis, the rapid collapse of microtine numbers is a direct attribute of periodic lethal toxin production.

Although a toxic pulse was included in the toxic threshold model, the net conversion factor e_2 was still set at a value close to zero. In the PLTP hypothesis the non-preferred plant type is described as having two lines of defence against over grazing, the periodic production of toxins and the continual accumulation of chemicals that act as feeding deterrents or digestibility reducers (Jensen & Doncaster, 1999). It has been shown that certain phenolic plant compounds function as reproductive inhibitors in certain microtine species (Berger, *et al.*, 1977). Therefore the assumption of a low net conversion factor at all times when microtine consume the non-preferred plant type coincides with the original hypothesis.

Due to the periodic production of a lethal toxin the density of the non-preferred plant type did not drop as low in the toxic threshold version of the model as it did in the original model. If this translates into a higher survival of individuals that produce toxins, compared to others in the same population that do not, we would expect selection to favour toxin production.

To compare the effect of periodic toxin production by the non-preferred plant type to that of continual toxin production, we again adapted the original model. In this version of the model the mortality of individuals increased immediately once microtine rodents switched diets to the non-preferred prey type. The increase in mortality represented the switch to a plant that continually produced toxins. Freeland (1974) originally suggested this mechanism was responsible for driving microtine cycles. However, Batzli & Pitelka (1975), could find no supporting evidence for Freeland's theory. We too could find no evidence supporting this hypothesis. When continual rather than periodic toxin production was modelled the number of criteria met by the model dropped to two. We also note that resistance to the toxin should develop in the microtine population if the population as a whole was subjected continually to the toxin for sufficient generations. With continual toxin production the period of cycle peaks was one in every 10 years (see Figure 5.7). Interestingly, this mirrors the frequency of snowshoe hare (*Lepus americanus*) cycles in the tundra regions of North America (see Keith, 1983).

By simply setting $e_1 = e_2$, we were able to model a system whereby both plant species were equally nutritionally attractive to the microtine rodents. The resulting simulations showed that under these circumstances none of the empirically derived criteria were met.

It was found that when the non-preferred prey type was excluded from the diet of microtine rodents ($e_2 = 0$) in the original Křivan model, cyclic dynamics still prevailed. Four of the five criteria were met, though this was not the case once the value of e_2 was increased marginally. The one criteria not met was the rapid collapse in the microtine population. Although in essence the result indicates that a single prey model can represent cyclic microtine populations almost as successfully as a two-prey model, evolutionary aspect not included in the model favour the two species model. It is rare for a predator species to depend entirely on a single prey species, typically a predator evolves to exploit more than one species to enable it to maximise net energy intake in a fluctuating environment. It has also been shown that microtine rodents prey on more than one plant species (Hansson, 1971; Stenseth *et al.*, 1977; Batzli & Pitelka, 1983; Rodgers & Lewis, 1985; Moen, 1990). However, the five criteria were not met when the original Holling-Tanner model was tested.

5.6.3 Empirical behaviour not met by the model

The models used did not always replicate all the empirical evidence detailed in the literature. The majority of parameters generated from the literature in this chapter have concerned only vole populations, though even among vole species (*Microtus* sp. and *Clethrionomys* sp.) the different behaviours may influence their population dynamics (Stenseth, 1988). Turchin *et al.* (2000) suggest that a single driving mechanism is unlikely to provide a 'universal' explanation of all cyclic microtine dynamics. They go on to suggest that the mechanisms behind cyclic vole populations and cyclic lemming populations are different. However, the behaviour of vole and lemming species cannot necessarily be predicted at a generic taxonomic level. Not only are there striking differences in the diets of different lemming species (e.g. Batzli & Pitelka, 1983) but brown lemmings (*Lemmus sibiricus*) cycles have been shown to be more similar to voles cycles than to Norway lemming (*Lemmus lemmus*) cycles (Oksanen & Oksanen, 1981). Although we have concentrated on seeking parameters for voles, many of the corresponding parameters for lemmings obtained from the literature are comparable. Lemmings are mainly moss-eaters. The re-growth of moss is slow following depletion (Callaghan, *et al.*, 1978; Turchin & Batzli, 2000), and parameter estimates of primary production may therefore require alteration to model realistic prey increase in a purely lemming-prey model.

Although the PLTP hypothesis has been proposed as the driving force behind cycling microtine populations, the other hypothesis outlined in Section 5.2.1 may also contribute to the microtine cycles observed in the field. The degree of influence would depend on amongst other things location, species, weather, and on the relative abundance of microtine rodents, food species, and predators. Some or all of these factors may explain the inconsistency between field data sets. However, Haukioja *et al.* (1983) have explored various complementary and exclusive alternatives and have concluded that plant availability and grazing resistance is crucial to the cycling dynamics of herbivores.

A future extension to the model could involve inclusion of immigration and emigration. The present model considers no direct age structure, and recruitment is assumed to be included in the rate of population renewal. A metapopulation model would introduce direct immigration and emigration both of which are important factors in determining microtine population levels in surrounding habitats under the PLTP hypothesis (see Figure 5.1).

The microtine population peaks generated in this study were uniform and regular because our analysis was deterministic, and so did not accommodate variations seen in empirical time series data (e.g. see Laine & Henettonen, 1983; Hanski, *et al.*, 1993). Typical empirical data depicts microtine populations that cycle with some degree of stochasticity. Maximum and minimum densities vary between peaks, with a variable rate of population increase and decrease between seasons. Some of these differences may be due to inter-specific competition (Henttonen *et al.*, 1977). There are two ways in which the model could be adjusted to fit the empirical data more closely:

1. **The introduction of more parameters**. The present model is a predator two-prey model in one of its simplest forms. It does not include microtine or plant age structure, variation in parameters due to seasonal effects, evolutionary factors, or any degree of microtine predation, all of which have been hypothesised to influence population dynamics (e.g. see Andersson & Jonasson, 1986). Although these could be added, differential equation models with increasing numbers of parameters present results that are increasingly more difficult to interpret (Batzli, 1988; Caswell, 1988; Stenseth, 1993).
2. **The introduction of stochasticity**. Stochastic models have parameter values that are defined by a probability distribution, so that one parameter takes many values and can be sensitive to initial or previous conditions (Hilborn & Mangel, 1997).

While stochastic simulations provide added realism, in general they are best used after the underlying processes have been thoroughly analysed with 'analytical' models of the sort we have used here. This is because the analytical models tend to be more generic in their applications than the simulations.

5.6.4 Conclusions

In summary we have used the framework of the Jensen & Doncaster (1999) verbal PLTP hypothesis to successfully simulated cyclic microtine populations. By applying an optimal foraging model (Křivan, 1996) and parameter values extracted from the literature we were able to assess the suitability of the model and deduce the influence each parameter had on the simulated population dynamics. By adapting the model to include a toxic threshold we were able to model the periodic production of a lethal toxin by the non-preferred prey type. This enabled simulated output to match all criteria derived from field data, including a catastrophic population collapse. Interestingly, the limit cycles generated by the one-predator one-prey PF model in Chapter 2 also predicted a rapid collapse in the density of predators under a prey influx regime (see Figure 2.5).

Verbal hypothesis based on empirical data tend to be complex, consequently mathematical formulation may not occur (Hestbeck, 1988). We have, however, taken a relatively complex data-driven inductive hypothesis and used a simple predator-prey population model with empirically derived parameter values to successfully rationalise the original PLTP verbal hypothesis.

Although there are problems with deterministic modelling of the kind used in this study as highlighted above they can, however, be used to provide an insight into the likely explanations of observed patterns (Murray, 1993). Deterministic models are therefore essential to enable the increased understanding of ecological processes (Nisbet & Gurney, 1982; Hilborn & Mangel, 1997). Population models need not duplicate every detail of the real world, and no single model should be expected to settle an issue completely (Caswell, 1988). Unless we know the consequences of simple assumptions between grazers and plant interactions we are in no position to interpret the complex dynamical processes observed in the field (Crawley, 1983). We have not intended the model to give a detailed representation of microtine dynamics, but rather our intention has been to give a representation of the effects of the PLTP hypothesis. Although there are weak areas in the model, the simulated output still presented us with theoretical data that were matched by empirical evidence. In 1993 Hanski *et al.*, stated that apart from their simulations no other hypothesis about microtine cycles has been formulated as a quantitative model and been tested with field data. Since then Hanski & Korpimäki, (1995) and Turchin & Batzli (2000) have also formulated models and using empirically derived parameter values successfully tested them against field data. Our study can now be added to that list.

As Jensen & Doncaster (1999) highlight, experimental investigations are required to fully test the predictions of the PLTP hypothesis, and to determine whether lethal plant toxins produced by a non-preferred plant type do influence microtine densities. The results obtained by such experimental investigations will provide more accurate parameter estimates for the models analysed in this chapter. Once these experiments have been conducted the model can be re-tested and used with more confidence using more realistic inputs. Microtine rodents are important pest species in horticulture and forestry (Myllymäki, 1977a), lemmings have been known to consume all over-wintering plant biomass (Brunnel, *et al.*, 1975). Field voles may also transmit human diseases (Stenseth *et al.*, 1977). Successful simulation modelling may help not only to resolve the problem of what drives microtine cycles, which in itself is one of the most keenly researched area of modern ecology, but also to understand better how to control or to conserve microtine species.

6 GENERAL DISCUSSION

The research presented in this thesis has investigated the relationship between recruitment and population persistence in open and closed systems. This has been carried out using a variety of techniques including mathematical stability analysis (Chapter 2), spatial analysis (Chapter 3), simulation modelling (Chapter 3), statistical modelling (Chapters 3 and 4), and the evaluation of alternative models (Chapter 5). Techniques have been developed to suit the model organisms studied i.e. barnacles (Chapter 3 & 4) and microtine rodents (Chapter 5). Chapter 2 was based on a purely theoretical framework though conclusions derived from this chapter have implications for all animal and plant species. Results are discussed at length at the end of each chapter; consequently in this General Discussion I will focus only on direct comparisons between chapters and on common themes that run through the whole thesis. I start with a brief summary of each chapter before comparing concepts raised throughout the thesis. Finally, I discuss the limitations of the studies along with suggestions for future work.

6.1 SUMMARY OF RESULTS

We began by modelling a system in which a consumer population was subsidised by a prey influx (Chapter 2). As expected, an increasing value of prey influx increased stabilising mechanisms. In contrast under prey outflux limit cycles were no longer sustained in the system, instead there was a large region on the predator-prey phase plane in which both populations collapsed to zero. We contrasted our results to those of Rosenzweig's 'paradox of enrichment' in which an increase in prey stock stabilises the system. The prey flux model is a type of open system, in so far as its dynamics depend on the influx of prey from outside the system. Its outcomes are similar to those of other open system models involving an influx of consumers (rather than prey), which also stabilise the system.

In Chapters 3 and 4 we studied empirical dynamics of a typical open system using barnacles as model consumers, in this case consumers of free space, or colonists. The position and number of barnacle settlers was shown to depend directly on the presence of conspecifics as well as the availability of free-space. This recruitment behaviour was attributed to the immobility of adults, requiring them to settle within a penis length of a conspecific in order to reproduce. Two barnacle species were studied: *Chthamalus montagui*, which can self-fertilise, and *Semibalanus balanoides*, which cannot. Conspecific-conspecific attraction was shown to be evident in at least one age class for both species and suggested the possibility of geometric population growth. It was shown empirically that within certain populations the number of adult barnacles does increase geometrically. Geometric growth is typically described as a characteristic of populations in closed systems, whereas we observed it in an open system. We went on to discus the implications for population persistence. A simulation model and MLE techniques were used alongside field data to determine the potential effect that a limited penis length and territorial repulsion can have on the spatial arrangements of barnacle populations. The barnacles were consumers of a single resource: space.

In Chapter 5 we examined the dynamics of a consumer population with two alternative prey populations and observed that the degree of resource depletion can lead to unstable microtine dynamics. The toxic prey hypothesis for vole cycles (Jensen & Doncaster, 1999) was qualified using a model of an optimally foraging predator of two prey. Parameter values for the model were obtained from the literature. Model outputs were compared to empirically set criteria for accepting apparent cycles as reflecting real microtine cycles. An adaptation of the original model to include a toxic threshold allowed all 5 criteria to be met. The periodic production of the microtine toxin was shown to be instrumental in enabling the model to match all criteria.

6.2 THE CONSEQUENCE OF RECRUITMENT BEHAVIOUR TO POPULATION PERSISTENCE IN OPEN AND CLOSED SYSTEMS

6.2.1 Predator-prey systems

Predator-prey models have become a firmly established theoretical tool, used by population biologists to describe and investigate a whole range of biological interactions between consumers and their resource (e.g. Maynard Smith, 1973; Tanner, 1975; Hassell, 1976; Wollkind *et al.*, 1988; Hanski, 1993; Křivan, 1996). By modelling these simple systems biologists can examine the effects of different components and their interactions (Begon *et al.*, 1990). In this thesis two variations of the Lotka-Volterra model have been adapted in order to meet the aims of specific chapters. The dynamics of the models have been investigated under differing regimes and the effects on population persistence discussed. The two models used were not intended as a precise representation of predator-prey population dynamics, but rather as tools for studying the dynamical interactions between predators and their prey and the consequences these interaction have for local persistence of the consumer populations.

Predator-prey models did not feature directly in the barnacle chapters. However, the consumption of free space by barnacles, as observed in Chapters 3 and 4, is conceptually analogous to the consumption of prey by predators. The empirical results that we obtained on barnacle recruitment dynamics are consistent with the standard analytical model for a population growth rate given by:

$$\frac{dN_i}{dt} = r \cdot S_i \cdot N_i - d \cdot N_i \tag{6.1}$$

where recruitment per capita of N_i barnacles to patch i is proportional to available resource S_i, and loss per capita is constant on average. With free-space as the limiting resource, eqn 6.1 corresponds to Levins's (1969) classical metapopulation model (Doncaster, 2000). Doncaster (2000) has shown that whether the limiting resource is occupied (as in a metapopulation model) or consumed (as in a predator-prey model) the same basic continuous-time model applies to the rate of change of the consumer at all scales from the individual to the metapopulation level. However, unlike predator-prey models the limiting resource (available space) cannot independently self-replicate in the metapopulation equivalent. This means that in the application of eqn 6.1 to a metapopulation, there is no coupled resource equation with independent renewal of the limiting resource, as there is in the application to predator-prey dynamcis.

Equation 6.1 describes geometric growth of a given resource abundance (i.e. constant per capita rate of renewal), which is logistic if the resource has a carrying capacity. In our application to barnacles the carrying capacity, K_i, is the total free-space, so the amount of the resource can be described by:

$$S_i = K_i - N_i . \tag{6.2}$$

Putting eqn 6.2 into eqn 6.1 gives the classical metapopulation model of Levins (1969) as described in Chapter 1. In the standard use of this model, geometric growth results from self-replication of the N_i residents. In our use of the model, geometric growth results from mutual attraction of adults recruiting from outside the system.

In our representation of barnacles as a metapopulation, we are describing a one-dimensional system because the resource of space is either free or occupied by consumers. There can be no cycling of consumers and resource because the two are not independent of each other. In contrast, where we have applied variations of eqn 6.1 to predators in predator-prey models (Chapters 2 and 5) we frequently obtain limit cycles from the coupled dynamics of independent renewing predators and prey.

Microtine rodents are an exemplary example of organisms that cycle in nature (see Chapter 5). Barnacle populations can also display limit cycles. If the growth rate of the barnacle population is large relative to death rate, then this additional growth also consumes the available resource, thereby interfering with recruitment. This can prevent a stable equilibrium and can cause limit cycles in the number of barnacles when analysed against time (Roughgarden *et al.*, 1985; Bence & Nisbet, 1989).

6.2.2 System openness

A population can be described as being closed if recruitment rate depends on the size of the local population. A population occurring in an open system is characterised by recruitment that is independent of the local population (Roughgarden & Iwasa, 1986; Bence & Nisbet, 1989). Clearly the issue of whether a population can be considered open is a question of scale, since everything becomes closed on a global scale (Johnson, 2000). However, migrants to an area of marine substrate or shore-line can land anywhere: migration is not across a perimeter, but from the water column, and consequently the shore-line system can not be made more closed by enlarging its area (Roughgarden *et al.*, 1985).

In two of the chapters the model systems were closed, at least for consumers (Chapter 2 & 5), and in the remaining two the systems were open (Chapter 3 & 4). Although the terrestrial systems studied were closed, both were dependent upon recruitment to supplement numbers at low population densities. In the prey flux model it was the prey species only that entered the system and prevented the predator population from being driven to extinction. We likened this to the rescue effect as described by Brown & Kodric-Brown (1977). The influx of prey species in the prey flux model is not a rescue effect per se. The rescue effect occurs at the regional level; it is typically used to describe the influx of consumers onto a resource. Consequently, much research has been carried out into populations subject to the rescue effect at the metapopulation level (see Hanski, 1999 and references therein). With the prey flux model the influx of prey (detailed in Chapter 2) occurs in a system that is closed for the predator. The influx is confined only to the limiting resource (i.e. the prey population). Jensen & Doncaster (1999) detail the importance of immigration in their verbal description of the toxic prey hypothesis for vole cycles. However, the toxic prey model does not require immigration to reproduce all five characteristic features of microtine cycles. Interestingly, the prey flux model, does give cyclic predator-prey densities under certain conditions of prey influx. Within these cycles the rate of predator decrease was greater than predator increase, reflecting a predator population collapse as also seen and described with microtine populations in Chapter 5.

Both the terrestrial systems studied (Chapters 2 and 5) had geometric rates population increase. Geometric growth is characteristic of self-replication in a closed system, whereas arithmetic growth is characteristic of a steady recruitment influx to an open system. Barnacles are an exemplary model organism occurring in an open marine system (Roughgarden *et al.*, 1985), and yet they show geometric rather than arithmetic growth. We hypothesised that this was due to their immobility and the constant requirement to settle within a penis length of neighbours in order to ensure reproductive success. We tested this hypothesis with empirical manipulations of barnacle populations.

The primary aim for each of the barnacle studies was to assess the influence on population size of a spatial constraint on reproduction. Alternative approaches were used in each of Chapters 3 and 4, but similar conclusions were drawn from both studies.

The experimental design of Chapter 3 tested the hypothesis that settlement was proportional to adult density; recruitment rates measured in Chapter 4 supported this hypothesis. The experimental design of Chapter 4 tested the magnitude of conspecific attraction; spatial patterns described in Chapter 3 supported this hypothesis (see also Wethey, 1984a). The combination of results and the interpretation of the data from both chapters gave strong evidence of geometric population increase, in at least one barnacle species. We then developed a simulation model to describe the geometric population growth of sessile marine organisms in open systems with just two parameters.

6.2.3 The Allee effect

The Allee effect (Allee, 1931) applies to individuals in a population which have a disproportionately low rate of recruitment when their own density is low (Begon *et al.*, 1990). Its numerical effect is inverse density-dependent, since birth rate per capita declines with decreasing density. The Allee effect is typically attributed directly to the inability to find mates at low population densities (Courchamp *et al.*, 1999). However, any mechanism that can lead to a positive relationship between a component of individual fitness and either the number or density of conspecifics can be termed a mechanism of the Allee effect (Stephens & Sutherland, 1999). The importance of this dynamic process in ecology has been under-appreciated (Courchamp *et al.*, 1999).

The Allee effect has been described and modelled in this thesis. The consequence of the Allee effect to a predator-prey system was explored in our prey flux model. Incorporating Allee effects into models of population dynamics leads to important observations with regard to persistence (Stephens & Sutherland, 1999). In the prey flux model the Allee effect was expressed in a net outflux of prey, which reduced recruitment rate of prey at low prey densities. It was shown that even if the prey outflux was minimal the consequences to both the predator and the prey population was usually instability, and that this ultimately resulted in extinction. We then went on to highlight the dangers of harvesting a population at low densities, which in turn can increase Allee effects and extinction probabilities. This research supports the findings of others (e.g. Alvarez, 1998; Courchamp *et al.*, 1999; Stephens & Sutherland, 1999). Its novelty is in the modelling of an Allee effect on the prey as opposed to the focal species - the consumer.

In contrast to the above models, the fitness of an individual barnacle is increased if the density of conspecifics is high. Far from interfering with each other's growth, competitors facilitate reproductive opportunities. Obligate cross-fertilisers must depend on being a penis length from a neighbour to successfully reproduce. At low population densities the fecundity of individuals is also low due to the reduction in mating opportunities. The consequence of population density on overall barnacle fitness can be likened to the Allee effect (Wethey, 1984a). The selective advantage to individuals who are able to locate conspecifics will inevitably be high. Both analyses on *S. balanoides* and *C. montagui* populations revealed that at all densities individuals selectively settled not only in aggregated patterns with regards conspecifics but also preferentially next to adults where free-space was not limiting. We attributed much of the observed gregarious behaviour to the relationship between the barnacle penis length, settlement position in relation to conspecifics and the consequence this has to reproductive success. Barnacles reduce the repercussions of the Allee effect by actively seeking conspecifics at the larval stage; the result is a sessile aggregated adult population.

The direct consequences of an Allee effect were not included in our quantification of the microtine toxic prey model. However, the density of microtines within the simulated populations did drop to levels as low as 2 $\mathrm{ind{\cdot}ha^{-1}}$. At this density the number of potential mates will limit the reproductive success of microtine individuals, and thereby increase the length of the low phase after the population crash. Any subsequent influx of conspecifics from outside the immediate system will help to cancel this Allee effect, though neither of these mechanisms was included in our model. Immigration of individuals into the patch not only prevents direct population extinction but also increases the fecundity of individuals already in the population, therefore alleviating the Allee effect.

6.2.4 Population extinction

Extinction, or the absence of persistence, is a phenomenon that is notoriously difficult to document convincingly (Walde, 1994). Throughout this thesis we noted the relative proximity of populations to deterministic extinction under certain conditions.

In the prey flux model we have shown how even a modest off-take of a prey may provoke the extinction of both prey and predators especially when the density of individuals is already low. Deterministic extinction is approached by reducing the recruitment of prey, or by the presence of an Allee effect. Studies conducted on bird populations have shown that population size is the major factor influencing the likelihood of extinction, with small populations being the most vulnerable (Bellamy *et al.*, 1996). However, the relationship between population size and extinction probability is not as clear in plants as it is in animals (Schemske *et al.,* 1994).

The minimum amount of a suitable limiting resource required for a population to persist is known as the extinction threshold (Lande, 1987). There have been very few attempts to place actual numbers on the threshold population sizes below which extinction is either assured or highly probable (Raup, 1984). Extinction thresholds have only been applied to closed systems, as in open systems the constant influx of recruits from outside the system can re-seed an otherwise doomed population (Pagel & Paine, 1996). In our prey flux model the extinction threshold for predators was observed when $\sigma = 1$, the threshold prey density for which the predator population is greater than the prey carrying capacity.

A possible model that could be used to represent the dynamics of barnacle populations was detailed in Chapter 4 (Figure 4.21). At high resource densities barnacle populations follow closed system dynamics whereas at low densities they follow open system dynamics. What are the consequences for population persistence using this model? Barnacle larvae can travel many kilometres from their release site (Farell *et al.*, 1991; Bertness *et al.*, 1996). Therefore if a population reaches extinction even over a relatively large area it eventually will be re-seeded due to the influx of new recruits from distant shores. In this model there is no true extinction threshold. However, theoretical models of open systems can possess extinction thresholds if the recruitment influx is so slow that the equilibrium density of consumers is less than a single individual (Doncaster, 2000).

The alternative is to consider barnacle populations that only follow closed system dynamics. Section 4.1 and Figure 4.2 detailed the difference between open and closed populations and highlighted the presence of extinction thresholds only in closed populations. So how can we apply this classical model to our barnacle populations? As already discussed an analogy can be drawn between predator-prey systems and barnacle populations, with the 'predatory' barnacles 'consuming' space. In the classical closed system model the extinction threshold is met when the carrying capacity of the environment is reduced so that that the prey isocline no longer intersects the predator isocline. In our barnacle version of the classical closed system model the extinction threshold exists where the density of the barnacles is such that all individuals are exactly a penis length from a neighbour. A reduction in barnacle density results in neighbours being more than a penis length apart. Therefore it is the predator isocline that moves (as the barnacle density varies with recruitment) and the carrying capacity that remains stationary as depicted in Figure 6.1.

In reality of course, individuals are not regulary spaced apart. Thus while the average seperation may be more than a penis length, so long as any two barnacles are less than this distance apart, the population can persist. Our model cannot accommodate this within-patch heterogeneity so it predicts extinction at density S_2^* in Figure 6.1. In fact the predator isocline should bend towards the origin at low N^* (as shown in Figure 4.21) to accommodate this residual population. This is the kind of isocline that would be produced by expanded exponential growth, e.g. changing eqn 6.1 to the local population equivalent (eqn 1.9, Chapter 1):

$$\frac{dN_i}{dt} = r \cdot S_i \cdot N_i^{1-m} - d \cdot N_i \qquad (6.3)$$

where m is slightly greater than zero.

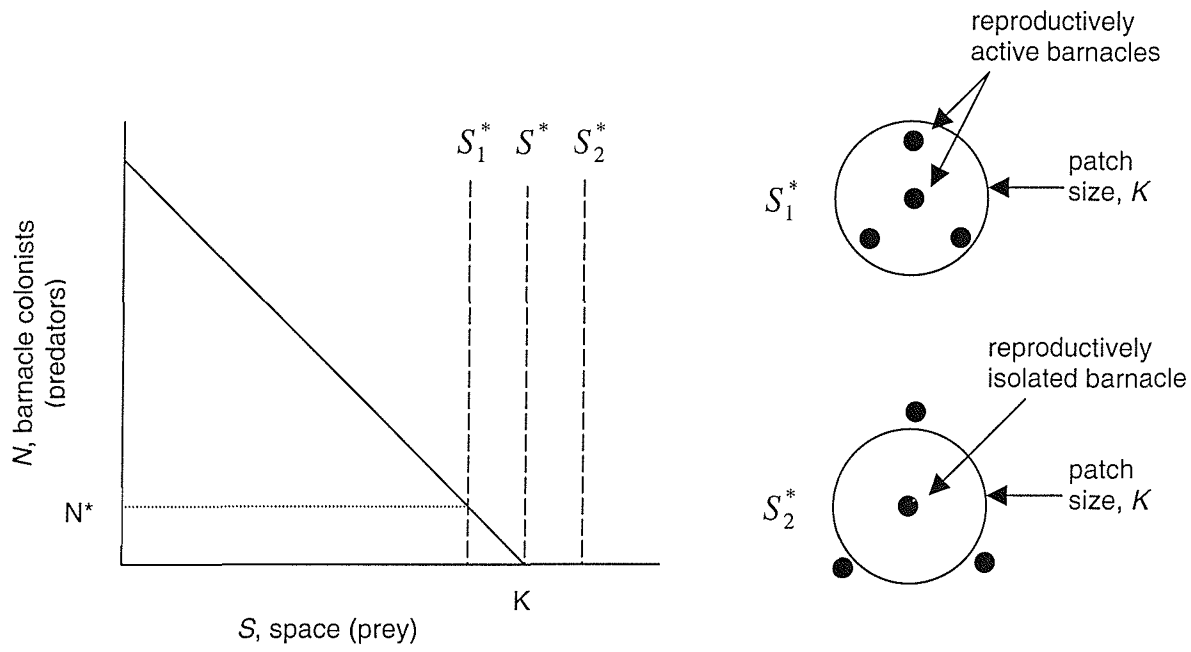


Figure 6.1 The existence of an extinction threshold in barnacle populations. When the density of barnacles is at S_1^* the individuals are sufficiently close enough to conspecifics to allow for cross fertilisation (barnacles are represented by shaded circles and the maximum distance for cross fertilisation by the clear circle), consequently there is individual persistence. When the density of barnacles is at S_2^* the distance to a conspecific is greater than the length of a barnacle's penis; consequently individuals are unable reproduce. An extinction threshold exists when the density of barnacles is at S^*, at this density a penis length exactly separates barnacles.

In all chapters we have either modelled or recorded populations with low densities, though we have shown how changes in resource availability can increase densities. At low densities, however, stochastic processes heighten the threat of population extinction. Demographic stochasticity results from irregularities in birth and death processes operating on an individual basis, and they are important principally in small populations (Lande, 1988; Wissel & Zaschke, 1994). Environmental stochasticity results from the temporally varying environment acting on the population (see Stephan & Wissel, 1999 and references therein). Environmental stochasticity includes abiotic factors (e.g. the weather) and the biotic impact of other populations (e.g. predators, competition, resources) (Simberloff, 1988). In both barnacle and microtine rodent populations the stochasticity of environmental conditions are known to be factors influencing both individual and population persistence. Microtine populations can be depleted by the weather (Shelford, 1943), predators (Klemola *et al.*, 1997) and the reduction of resources (Hansson, 1977), barnacle populations can also be depleted by predators (Hughes & Drewett, 1985; Burrows *et al.*, 1999), exposure (Bertness *et al.*, 1991) and the weather, in the form of desiccation (Ware & Hartnoll, 1996). These stochastic processes need to be considered when translating the theoretical model output into real population equivalents. Future work should therefore include simulations to measure the effect of stochastic extinctions in one or other part of the systems.

6.3 SPECIES MANAGEMENT

Minimising species extinction probabilities is the most appropriate goal for conservation purposes (Diamond, 1976), and is at the root of most fundamental questions in ecology (Strong, 1990). Conservationists are typically concerned with preventing extinction events. Consequently, they are interested in minimum viable populations (Shaffer, 1981). The minimum viable population is the minimum number of individuals within a population that are able to persist over a given period of time with a certain probability. The objectives of biological control programmes and pest eradication techniques are intuitively the reverse to those set by conservationists; the probability of local population extinction is required to be maximised. Biological control depends upon simple density-dependent processes, with the majority of programs relying upon predator-prey or parasitoid-host interactions (Luck, 1990). Throughout this thesis we have commented on the measures required to sustain or eradicate certain populations. Beneficiaries of our research should therefore include the ecological and policy-making communities.

The results from our prey flux model have implications for both conservation and pest management. We hypothesis that a rescuing influx to conserve an endangered population, or an outflux to eliminate a pest, may have more effect if they are applied to the limiting resource rather than to the resource consumer of focal interest itself. However, small-scale experimental research in both the laboratory and the field would be needed before a full-scale program is conducted at a level that would make these programs economically viable.

Microtine rodents are considered an important pest species in horticulture and forestry (Myllymäki, 1977a). Barnacles are an important constituent of marine fouling communities and are of considerable economic importance (Stubbings, 1975). Therefore, in certain circumstances there is considerable interest in controlling both of these species. We have shown that the removal of adult barnacles will limit settler numbers over subsequent settlement seasons. The use of anti-fouling paints not only prevents barnacle cyprids settling and therefore reduces population density but also limits the potential carrying capacity of the surface it is applied to. If the density of barnacle is limited so that individuals are more than a penis length apart then an extinction threshold will prevail. Preventing all barnacles settling within a penis length of conspecifics would be hard to implement, however. Alternatively, if a barnacle species is to be conserved the relationship of settlement rate to conspecific density could be used. In areas where populations are subject to extinction, transplanting populations on plates from areas with an abundance of barnacle would encourage further settlement. For *S. balanoides* the local density of transplanted individuals would be the primary factor to consider in such re-seeding program and not the absolute number as seen in our MLE settlement simulation model with and without peripheral adults.

Researchers have shown that toxic pulses help prevent toxin resistance developing in rodent species (e.g. Greaves, 1986); we have also shown that the periodic production of a toxin not only results in a long low-density phase but also a catastrophic population collapse once populations reach high densities. A continual supply of a toxin was not able to recreate this behaviour.

6.4 LIMITATIONS OF THE STUDY

Certain limitations have been considered in the discussions at the end of each chapter. Here we highlight some of the more fundamental points raised, and discuss them in more detail. Both the modelling and the experimental research have their own distinct limitations; consequently each is discussed individually.

6.4.1 Modelling limitations

Chapter 2 and Chapter 5 investigated predator-prey dynamics using purely deterministic models based on differential equations. The use and role of deterministic models in population ecology was briefly highlighted in Chapter 5. Deterministic models are considered by some as being too simplistic since they do not incorporate any environmental or demographic stochasticity (see Renshaw, 1995), though simplistic models can be applied to a grid in order to model heterogeneous environments (Doncaster, 2000). Deterministic models do, however, consider either explicitly or implicitly the average values of what is being modelled (Stenseth, 1993), and can be more useful than stochastic models for obtaining theoretical results for period length, lag times etc. (Renshaw, 1995). Both deterministic and stochastic models have important roles to play in the understanding of biological systems (Renshaw, 1995), though all models are descriptive and differ only in the degree of resolution and the degree of complexity with which they are observed (Brown, 1993). May (1973) states that models should be constructed with the aim of providing a conceptual framework for the discussion of broad classes of phenomena. Deterministic models do allow central themes and parameters to be explored, analysed and investigated, they also allow the user to understand underlying biological processes and to suggest possible lines of future theoretical and experimental investigation. Unless we know the consequences of simple assumptions and interactions, which can be deduced from deterministic models, we are in no position to interpret the complex data we obtain from the field (Crawley, 1983).

In Chapter 2 the equilibrium conditions of our prey flux model were initially investigated using analytical mathematical techniques. In Chapter 5 we relied solely on model simulations or numerical evidence to characterise the behaviour of the system under varying parameter values. Simulation is a useful tool enabling a model to be investigated without the user getting too bogged down in the technical details of more formal mathematical methods, or for models that are too complex for pure mathematical investigation (Brown, 1993). It should always be recommended, however, that a general theory can only be developed using pure mathematical analysis (Brown, 1993), as was conducted in Chapter 2. We did not need to investigate the pure mathematical behaviour of the model used in Chapter 5 as it has been documented elsewhere (see Křivan, 1996; Křivan & Sikder, 1999). Both mathematical evaluation and numerical techniques are essential in understanding the overall dynamics of a single theoretical model. Without a conceptual mathematical framework simulated data is worthless, whilst conceptual theory is useless if it is never tested against empirical data. Understanding how theory fits into the larger context of ecology requires an appreciation of the problems that theoretical models attempt to solve (Caswell, 1988). Therefore the first step made by a theoretical population biologist should be to rigorously analyse any model mathematically first, then assess the competence of the model with extensive simulations using realistic parameter values. Finally, the predictions of the model can be tested in field or lab experiments. Simulations usually precede experiments, as they are cheaper to run.

Our prey flux model was developed in a non-dimensional form to enable the full dynamics of the model to be investigated in the simplest form. The model was, however, similar to Rosenzweig's 'paradox of enrichment' model, which has been tested against empirical systems (see Chapter 2).

In Chapter 5 parameter values were sought from the extensive literature to enable direct comparisons to be made between the simulated data and empirically derived data also detailed in the literature. However, we did have difficulty finding certain critical parameter values. Microtine rodents have been found to cycle over a range of northerly latitudes. Even though the plants we used as prey species occur in all locations that microtine rodents are found to cycle (see Jensen & Doncaster, 1999), the carrying capacities and growth rates vary tremendously not only between latitudes and altitudes but also between ecosystems and localities (e.g. Chepurko, 1971; Kjelvik 1973; Kallio, 1975; Bliss, 1973). Plant parameters were variable in the literature but some microtine parameters were non-existent and had to be estimated using various indirect approaches. Where indirect estimates were used, broad ranges of values were explored and the resulting dynamics documented.

6.4.2 Experimental limitations

Conceptual ideas were tested with experiments in Chapters 3 and 4. Although barnacles are considered an exemplary model organism to study recruitment processes (Wethey, 1984a; Roughgarden *et al.*, 1985; Hyder, 1999), there are two primary problems associated with their use. These problems stem from areas of barnacle biology and ecology not fully understood i.e. larval transport processes, and the relationship between settlement and recruitment numbers.

The transport of barnacle larvae via tidal and wind driven processes (e.g. Hawkins & Harnoll, 1982; Gaines & Bertness, 1992) is difficult to measure. Although we do not directly relate or model the passive barnacle transport processes in this thesis these processes do control the initial numbers of arrivals to each of the locations. Once the barnacles have arrived active settlement behaviour prevails, and determines the final distribution and abundance of individuals.

The relationship between settlement and recruitment is one that directly effects the results of the barnacle chapters. Settlement describes those barnacles, which have attached to a surface after habitat selection, whereas recruitment describes those that have survived settlement and have become part of the breeding adult population (Connell, 1985; Caffey, 1995). The number of individuals counted at each location was referred to as settlement numbers throughout the thesis. Although we sampled at most twice a week this is still too infrequent to assess true settlement numbers (Minchinton & Scheibling, 1993b). The majority of settlement mortality occurs during the first day of attachment in *Balanus glandula* (Gosselin & Qian, 1996), with significant differences found between estimates of settlement taken at 1.3 and 2 days in *S. balanoides* (Minchinton & Scheibling, 1993b). Consequently, mortality after initial settlement may have modified both numbers and spatial patterns. In some studies, however, recruitment has been shown to be a good estimate of settlement up to 3 months post-settlement (Sutherland, 1990). As counts were all made with the same frequency within a study, results could still be compared between locations.

Not only would increasing the frequency of observations increase the accuracy of settlement counts it would also enable more points to be plotted on both the cumulative settlement and adult population graphs. This would allow a more detailed analysis of the rate of population increase. Increasing the frequency of settlement counts was not possible logistically in this study, due to time and financial constraints. The study locations selected and monitored were geographically close. The locations that we were able to use were also restricted due to time and financial constraints and the suitability of locations in terms of barnacle abundance. Consequently, we were only able to make general conclusions concerning the barnacle populations inside the study locations, though we have no reason to suspect that other populations behave differently.

As detailed in Chapters 3 and 4 barnacle cyprids primarily depend on the presence of conspecifics and the availability of free-space in their selection of a settlement site. There is an array of other secondary settlement cues that ultimately dictate where a cyprid will permanently attach itself. Although uniform substrate at approximately the same tidal height was selected at all locations other factors will have varied i.e. the growth of micro and macro algae, the chemical composition and the colour of the substrate, desiccation rates etc. Consequently, these factors may have been, to some extent confounded within the results. The only way in which these factors could be kept consistent would be to carry out experiments using laboratory populations. Experiments carried out in the field will always be subject to more inconsistencies when compared to those carried out in laboratories under controlled conditions, whether it be the result of predation, weather, interference by humans, location, or time and financial constraints. However, the behaviour of laboratory populations do not always coincide with the observations made of natural marine populations (e.g. see Anderson, 1996; Thompson *et al.*, 1998; O'Riordan *et al.*, 1999). For the questions that we were posing about recruitment behaviour, it is difficult to imagine a laboratory experiment on a suitable scale that could provide useful answers.

Predation and the effect of grazers (e.g. limpets) may have influenced both settlement counts and spatial patterns. Although limpets were removed at the beginning of the settlement season they eventually re-colonised the areas they were removed from. Where present, predatory dog whelks were never found on treatment patches, though we could not observe the patches once they were submerged. Experiments into the effect of predation on barnacle recruitment behaviour could be conducted by placing cages around treatment patches to prevent predation (as detailed below).

6.5 FUTURE WORK

In this thesis we have used both modelling and experimental approaches to determine the effect of differing recruitment regimes on population persistence. Here we suggest future work that could extend the conclusions drawn from the current studies.

6.5.1 Prey flux model

Future work in this area should concentrate on testing the model predictions using experimental systems.

The prey flux model predicted that under prey influx predator populations would be stable whereas a prey outflux would result in prey followed by predator extinction. These predictions could be investigated experimentally by the manipulation of predator-prey populations in contained systems. Much of the experimental work designed to test the validity of Rosenzweig's paradox of enrichment model has focused on the effect of resource enhancement on phytoplankton communities in enclosures (e.g. Hessen & Nilssen, 1986; McCauley & Murdoch, 1987, 1990). We suggest that a similar system be used to test the predictions of the prey flux model. However, we note that to study equilibrium dynamics involves the collection of data over many generation of the organism studied (Nisbet & Gurney, 1982).

It would be useful to test the relative efficiencies of pest control by harvesting the pest directly and by harvesting its resource. We predict that the latter may result in complete elimination before the former.

6.5.2 Barnacle settlement

Future work in this area should concentrate on (1) the role of predation and the rate of mortality; (2) the effect of location; (3) further development of the barnacle simulation model; and (4) the manipulation of settlement patches to investigate further the role of conspecific-conspecific separation during settlement.

By using a combination of caged and uncaged treatment patches and continual photograph analyse we would be able to ascertain the effect predators have on barnacle settlement numbers and spatial patterns. By running the experiments over consecutive years using the same treatment patches and the newly developed digital photography techniques, density-dependent mortality analysis could be carried out. Currently the role of density-dependent processes in barnacle populations is unclear (e.g. see Connell, 1985; Minchinton & Scheibling, 1991; Gosselin & Qian, 1996).

Tremendous variation was recorded in settlement numbers at each of the locations used. If similar experiments were carried out at other locations over a larger geographical scale we would not have to limit our conclusions to a small stretch of coastline along the south coast of England.

The barnacle simulation model did nothing more than simulate random settlement restricted by two fixed values (maximum and minimum distance to a neighbouring conspecific). The model could be developed to match more closely the observed decrease in density towards the edge of the treatment patch. This could be carried out by introducing a probability index into the simulation in place of the maximum and minimum distances. The analysis of density-dependent mortality could also be incorporated into the model in order to evaluate its role in barnacle recruitment dynamics.

The last suggestion for further work in this study involves habitat manipulation. By using an anti-fouling paint the substratum could be adapted so that barnacles are forced to settle a set distance away from conspecifics. This distance could be varied within replicates. If the length of the penis is the primary factor determining settlement and spatial patterns we hypothesis that cyprids will only settle where paint-free islands (big enough for only one barnacle) are within approximately 25 mm of a conspecific. An investigation of this type would help clarify the role of extinction thresholds in barnacle populations as detailed in Figure 6.1.

6.5.3 Toxic prey model

Future work in this area should concentrate on (1) the introduction of stochastic parameters into the model; (2) the introduction of a parallel system to model microtine populations in surrounding areas; (3) confirmation of the identity of toxic plant species; and (4) the experimental manipulations of microtine rodents and their prey at northerly latitudes in order to obtain accurate parameter values for the toxic prey model.

The advantages of stochastic models over deterministic models have been discussed at length earlier; the possible effect stochasticity would have on the toxic prey model has also been raised in Chapter 5 therefore neither issue will be repeated here.

Jensen & Doncaster (1999) not only describe the effect of periodic toxin production on local microtine populations but they also detail the effect on surrounding populations (see also Figure 5.1). The dynamics of the populations in the surrounding lowland areas have influential consequence to those populations displaying the effects of toxins, since they can act as both a source and a sink to the cycling microtine populations. The development of a parallel model to represent the surrounding populations to run along side the toxic prey model would allow further comparisons to be made between model output and empirically derived data sets.

Also highlighted by Jensen & Doncaster (1999) is the need to ascertain whether the plant suspects identified do indeed produce a wound-induced toxin, before the hypothesis can be generally accepted. They also detail possible experimental approaches designed to test the hypothesis. These experimental manipulations would also lend themselves to answering questions with regard to the accuracy of the parameter values used in our toxic prey model. We therefore suggest that this experimental work be conducted in order to answer both lines of enquiry.

6.6 FINAL COMMENT

The mathematical models used in this thesis have never been intended to supplant reality, but rather to analyse concepts and to distinguish between alternative processes. They have informed the experiments and simulations within this thesis. The combination of theory and empiricism is essential in the quest to fully understand ecological systems (Nisbet & Gurney, 1982; Hilborn & Mangel, 1997). The work of theoreticians and empiricists is too often separated (Hall, 1988; Hansson, 1988, Caswell, 1988; Lomnicki, 1988). We have shown by our research that theory can direct empirical work and that empirical work can help quantify theory. The amalgamation of both approaches has provided a powerful tool with which we were able to study population persistence. This in turn enables us to understand more fully the organisation and processes of nature.

7 APPENDICES

7.1 APPENDIX 2.1 - Scaling the prey flux model (PF)

Consider a population of S prey and N predators (m^{-2} or equivalent units), with rates (hr^{1}):

$$\frac{\mathrm{d}S}{\mathrm{d}t} = r \cdot (F + S) \cdot \left(1 - \frac{S}{K}\right) - \frac{q \cdot S \cdot N}{1 + q \cdot h \cdot S} \tag{A2.1}$$

$$\frac{\mathrm{d}N}{\mathrm{d}t} = a \cdot \frac{q \cdot N}{1 + q \cdot h \cdot S} \cdot (S - b) \tag{A2.2}$$

For the prey rate eqn A2.1, parameter r is a constant describing the average rate of prey births per capita (hr^{-1}) in a pristine environment (the intrinsic rate); F is a constant describing the average number of prey immigrants (m^{-2}) for positive values, or emigrants for negative values, at the given rate r; K is the carrying capacity of the prey (m^{-2}), at which births and migration reduce to zero; q is a constant describing the predator's average searching rate for prey ($\mathrm{m}^{2}\mathrm{hr}^{-1}$). Therefore, $1/(q \cdot S)$ is the average time taken by a predator to find each prey (hr); h is the handling time for each encountered prey (hr), and $h + 1/(q \cdot S)$ is therefore the total time between consecutive prey. The reciprocal of this total time is the rate of prey consumption per predator (hr^{-1}), or the predator's functional response: $q \cdot S/(1 + q \cdot h \cdot S)$.

For the coupled predator rate eqn A2.2, a is a conversion ratio of consumed prey into viable predator offspring; b is the density of prey (m^{-2}) that just sustains one predator (m^{-2}), and replaces it with a single offspring when it dies. The parameter b is thus the marginal subsistence demand for prey.

The normalised eqns 2.1 and 2.2 in the text are obtained from the following scaling of parameters:

$$\tau = r \cdot t, \quad s = \frac{S}{K}, \quad n = \frac{N}{K \cdot h \cdot r}, \quad \overset{\bullet}{s} = \frac{\mathrm{d}s}{\mathrm{d}\tau}, \quad \overset{\bullet}{n} = \frac{\mathrm{d}n}{\mathrm{d}\tau},$$

$$D = \frac{F}{K}, \quad D' = \frac{1}{q \cdot h \cdot K}, \quad v = \frac{a}{r \cdot h}, \quad \sigma = \frac{b}{K},$$

The predator functional response given in the PF (eqn A2.1) is also found in the classical Holling-Tanner model (Tanner, 1975):

$$\frac{\mathrm{d}S}{\mathrm{d}t} = S \cdot r \cdot \left(1 - \frac{S}{K}\right) - \frac{q \cdot S \cdot N}{1 + q \cdot h \cdot S} \tag{A2.3}$$

$$\frac{\mathrm{d}N}{\mathrm{d}t} = a \cdot N \cdot \left(1 - \frac{b \cdot N}{S}\right) \tag{A2.4}$$

As the functional response of the Holling-Tanner model is identical to that of the PF model the humped prey isocline is conserved. However, in the Holling-Tanner model the per capita recruitment of predators declines with predator density eqn A2.4. The Holling-Tanner model can therefore be considered as a 'ratio-dependent' model (see Chapter 1 for a full explanation of ratio-dependence). The outcome is a predator isocline with a positive slope similar to that given by Leslie's predator-prey equations for an open system shown in Figure 1.9 and Figure 1.10. Equation A2.4 is an appropriate rate equation for modelling predators that mutually interfere with each other's birth rate unlike PF and Rosenzweig's model

Since its introduction the mathematical dynamics of Holling-Tanner type models have been extensively studied (e.g. see Wollkind *et al.*, 1988; Gragnani, 1997). The Holling-Tanner model has also been used to successfully model real populations (Tanner, 1975; Wollkind *et al.*, 1988; Hanski *et al.*, 1991).

7.2 APPENDIX 2.2 - Linear stability analysis of the prey flux model

On a phase plane of n against s given by eqns 2.3 and 2.4, we require the boundaries of prey density between node, stable focus, and unstable focus. Let f_s describe eqn 2.1 for $\dot{s}$ and f_n describe eqn 2.2 for $\dot{n}$. If s^*, n^* are the equilibrium values of s and n given by eqs 2.3 and 2.4a, the local behaviour of s and n close to the stationary point is governed by the Jacobian matrix:

$$J = \left.\begin{bmatrix} \dfrac{\partial f_s}{\partial s} & \dfrac{\partial f_s}{\partial n} \\ \dfrac{\partial f_n}{\partial s} & \dfrac{\partial f_n}{\partial n} \end{bmatrix}\right|_{\substack{s=s^* \\ n=n^*}} = \begin{bmatrix} \dfrac{\sigma^2 \cdot (1 - D - D' - 2\sigma) - D \cdot D'}{\sigma \cdot (D' + \sigma)} & \dfrac{-\sigma}{D' + \sigma} \\ \dfrac{\nu \cdot (D + \sigma) \cdot (1 - \sigma)}{\sigma} & 0 \end{bmatrix} \qquad \text{(A2.5)}$$

The matrix J has eigenvalues given by $\lambda = 0.5 \cdot \left\{ \mathrm{tr}J \pm \sqrt{(\mathrm{tr}J)^2 - 4 \cdot \det J} \right\}$, where tr$J$ is the trace of J and det$J$ is the determinant of J (e.g. Murray, 1993). Both eigenvalues having negative real parts and imaginary parts generates a stable focus, towards which predator and prey densities spiral; one or both eigenvalues having a positive or zero real part generates an unstable focus, from which predator and prey densities diverge. It follows that the boundary of a stable focus with an unstable focus is given by the solution to tr$J = 0$ for which also det$J > 0$. Thus the lower stability boundary of region **C** in Figure 2.3 is obtained by solving:

$$\sigma^2 \cdot (1 - D - D' - 2\sigma) - D \cdot D' = 0 \qquad \text{(A2.6)}$$

for the condition that $\sigma > -D$.

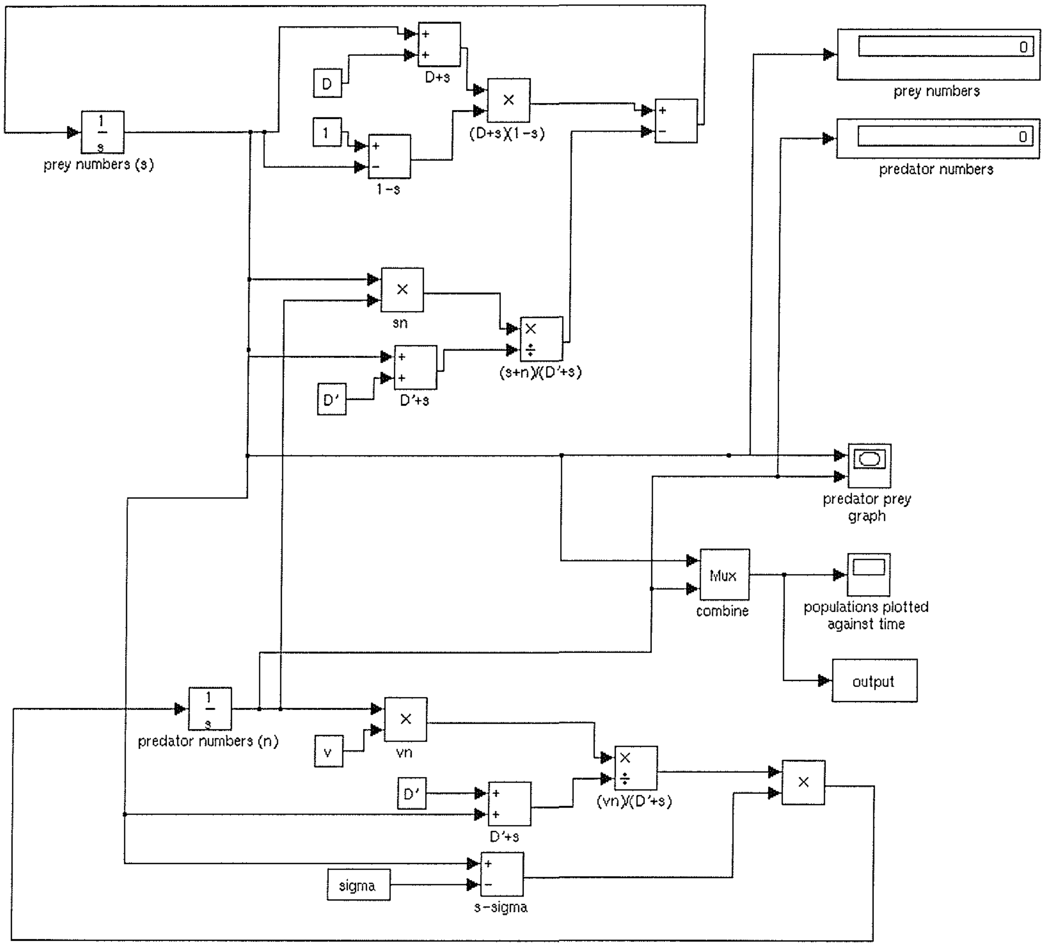
Both eigenvalues having negative real parts and no imaginary part generates a stable node, in which predator and prey densities adjust directly to an equilibrium point. It follows that the boundary of a stable focus with a stable node is given by the solution to

$(\mathrm{tr}J)^2$ - $4\cdot\det J = 0$ for which also $\mathrm{tr}J < 0$ and $\det J > 0$. Thus the upper stability boundary of region **C** in Figure 2.3 is obtained by solving:

$$\left[\frac{\sigma^2\cdot(1-D-D'-2\sigma)-D\cdot D'}{\sigma\cdot(D'+\sigma)}\right]^2-4\cdot\left[\frac{\nu\cdot(D+\sigma)\cdot(1-\sigma)}{D'+\sigma}\right]=0 \qquad \text{(A2.7)}$$

for the conditions that $\sigma^2\cdot(1-D-D'-2\sigma)-D\cdot D'<0$ and $\sigma > -D$.

7.3 APPENDIX 2.3 - Prey flux model built in Matlab: simulink



7.4 APPENDIX 3.1 - A lexicon of terminology used in the barnacle chapters

0+ adult – 0 to 1 year old adults which can be distinguished from juveniles by the clear formation of individual shell compartments and a change in colour (see Section 4.3.5).

Annulus – Concentric rings with an increasing diameter of 15 mm within a treatment patch (see Section 3.3.4).

Areas – Similar stretches along a recruitment shore containing identical sets of treatment patches (see Section 3.3.2).

b – A power function characterising population growth on a continuum between arithmetic and geometric growth (see Section 4.3.5).

Background density – The assessment of natural population densities (either high or low) before the preparation of treatment patches (see Section 4.4.1).

Carrying capacity- The maximum number of barnacles a treatment patch can sustain (see Section 4.2).

Central group – See remnant adults.

Cohort – Barnacles that have recruited to a population in a single settlement season.

Cyprid – The non-feeding specialist settlement stage of the barnacle life cycle.

DAT – Days after treatment patch was prepared (see Figure 4.7).

Free space – Substratum within the treatment patch not occupied by the remnant adults or settlers.

Juveniles – The developmental period in a barnacle life cycle between the spat and the 0+ adult stages.

Locations – The field study site where the experimental manipulations were carried out either along the south coast of England or around the Isle of Wight (see Section 3.3.2).

Maximum inter-individual distance – The distance between conspecifics relating to barnacle penis length (see Section 3.3.6).

Minimum inter-individual distance – The distance between conspecifics relating to barnacle territorial repulsion (see Section 3.3.6).

MLE – Maximum likelihood estimate (see Section 3.3.6).

Peripheral adults – The background adult population immediately outside the prepared treatment patch within the 150-165 mm annulus (see Section 3.3.6).

Recruitment – The supply of barnacles to a location which, ultimately become part of the adult breeding population.

Recruitment shore – Sites within a location that were identified as having either high or low-recruitment in comparison to other shores within a location (see Section 3.3.2).

Remnant adults – The adult barnacles left at the centre of treatment patches that constitute the treatment (see Section 3.3.2).

Replicate – Multiples of a single treatment within a location, recruitment shore or area (see Section 3.3.2).

Settlement – Individuals which have attached to a surface after habitat selection (cf. recruitment).

Settlement plate – Terracotta tiles deployed at locations used in the 1999 *S. balanoides* study to give an independent assessment of recruitment rates (see Section 3.3.2).

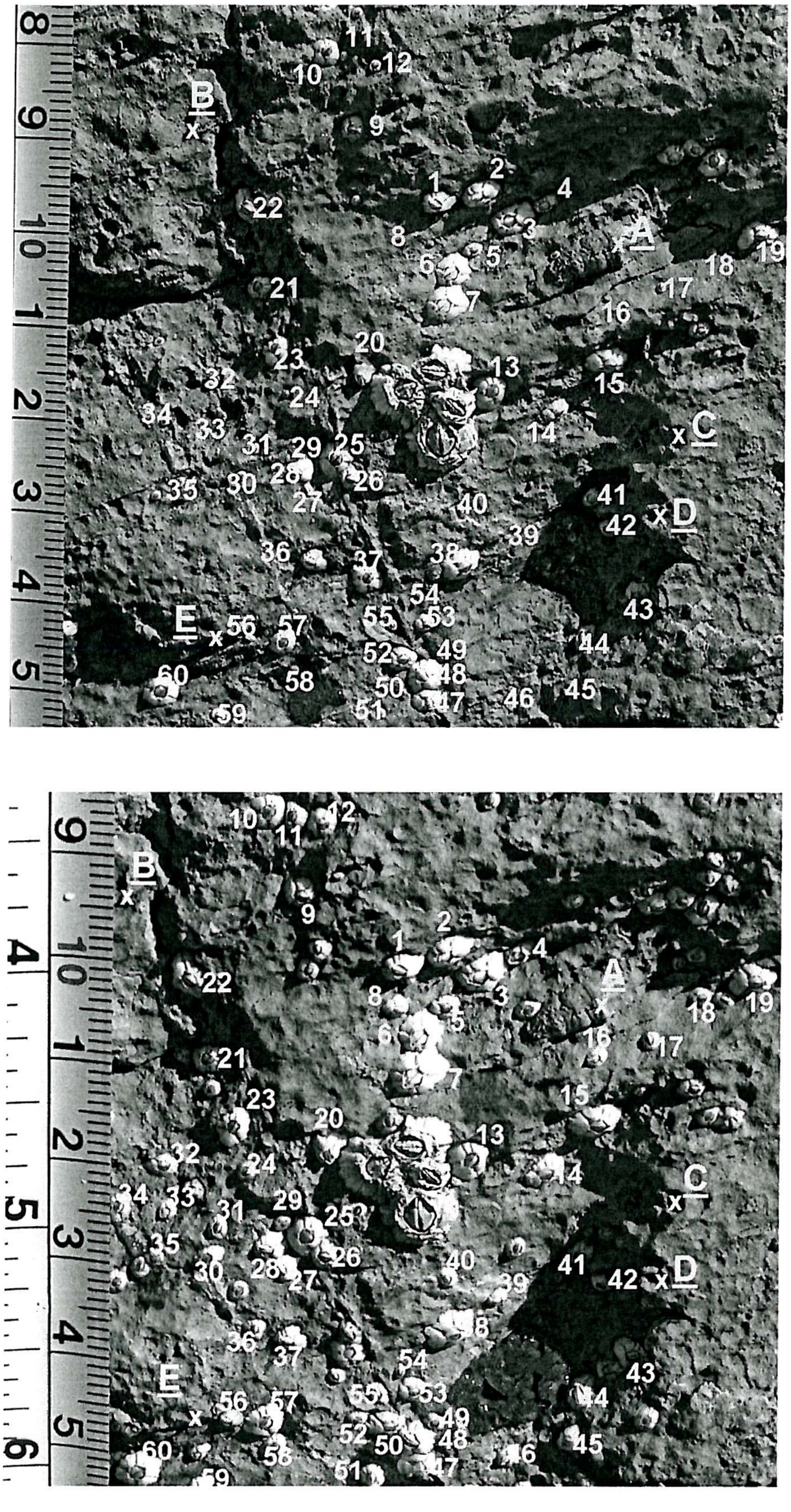
Settlement season – The period of time for which cyprids of a certain barnacle species arrive at a location.

Spat – A newly metamorphosed barnacle.

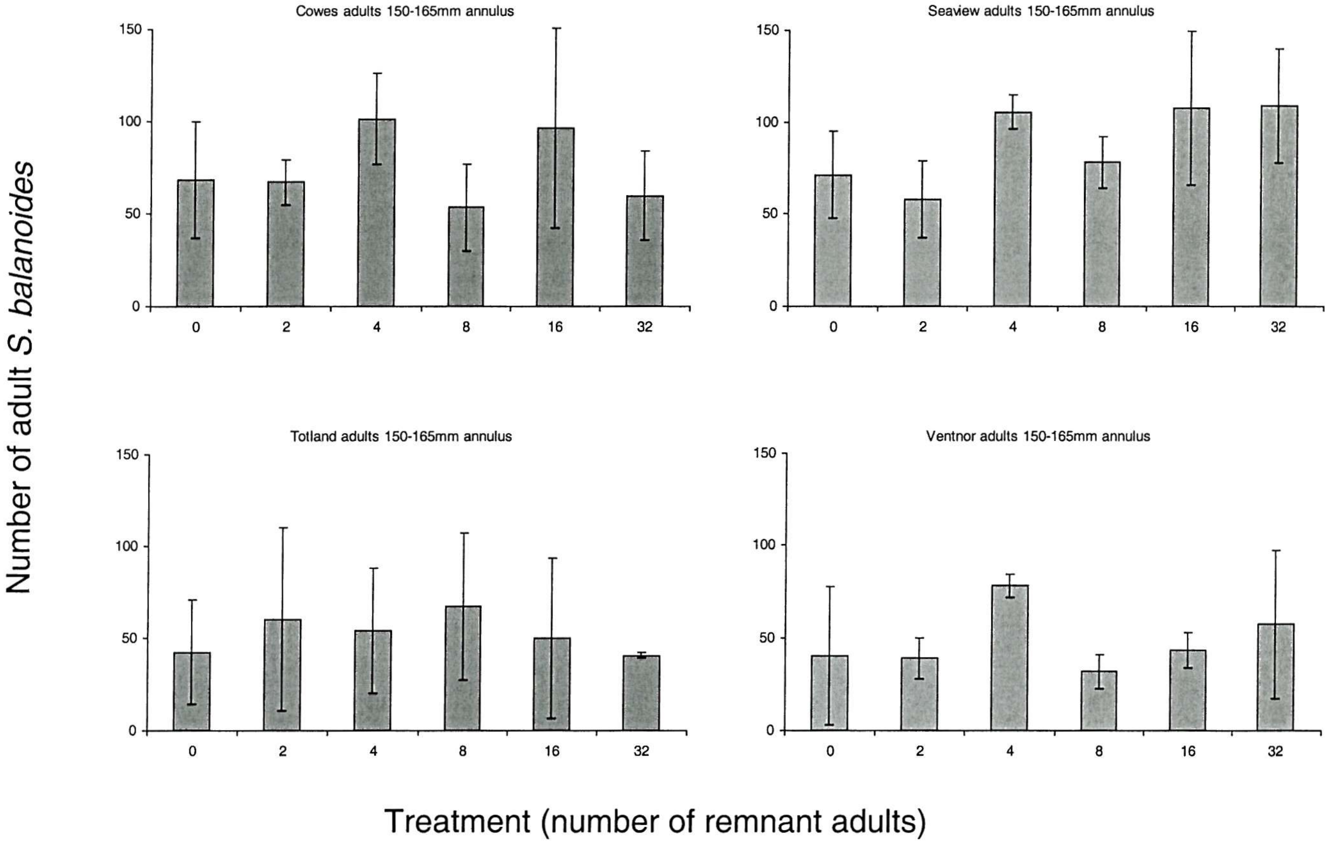
Treatment – The number of adults left as the central adult remnant group (see Section 3.3.2).

Treatment patches – The cleared substrate and the central remnant adult group (see Section 3.3.2).

7.5 APPENDIX 3.2 -The position of 60 barnacles in the same treatment patch photographed at a 10 week interval

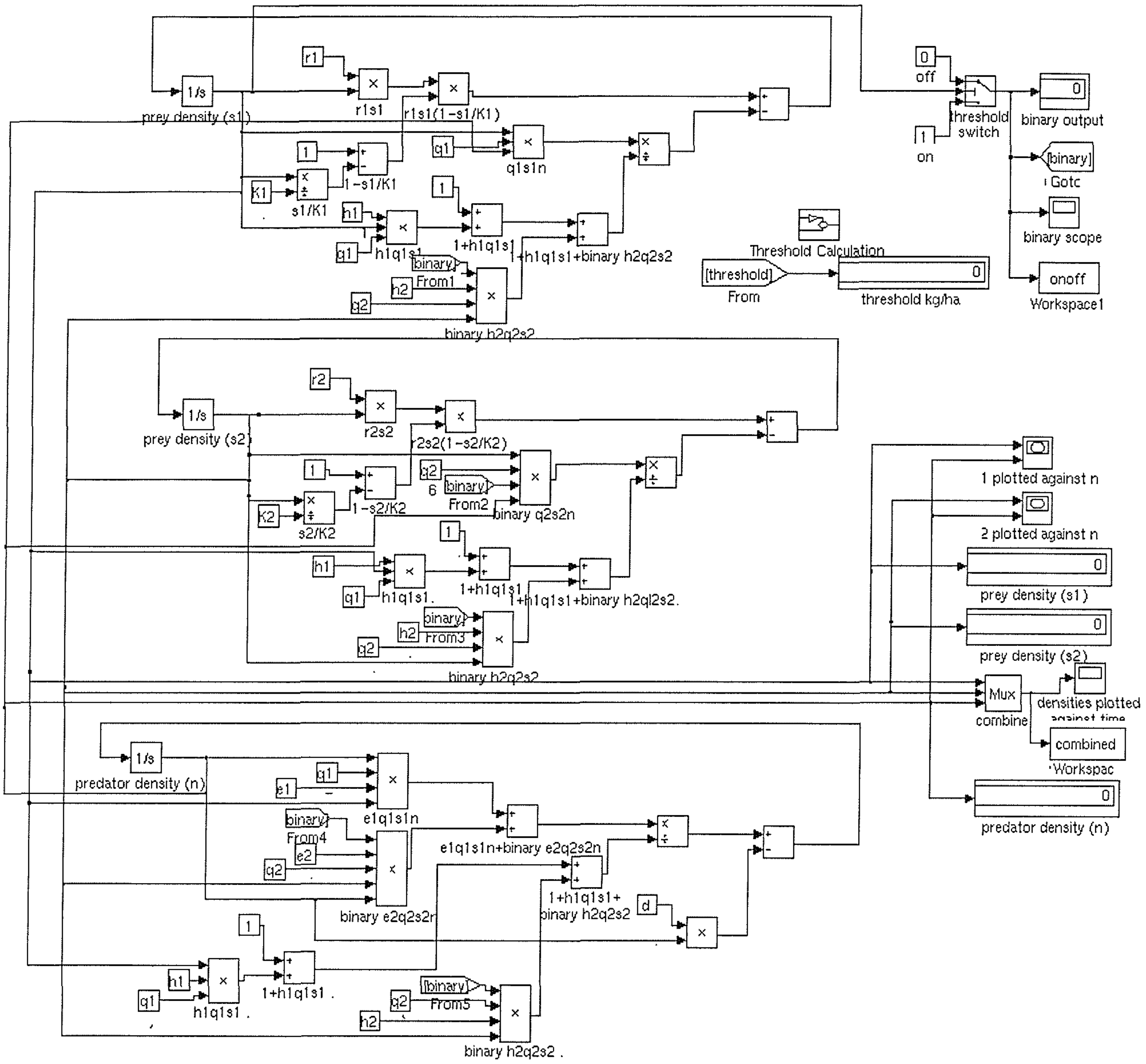


7.6 APPENDIX 3.3 - The number of adult conspecifics in the 150 - 165 mm annulus

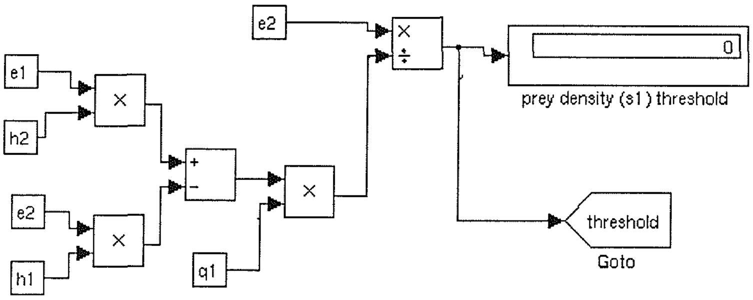


The number of adult conspecifics in the 150 - 165 mm annulus at each of the locations used in the 1999 *S. balanoides* study. Error bars = 95% confidence intervals from 3 replicates.

7.7 APPENDIX 5.1 - Křivan (1996) optimal foraging model built in Matlab: simulink



Threshold calculation



7.8 APPENDIX 5.2 - A complete range of vole and plant parameter values derived from the literature

PREY (PLANT) PARAMETERS

Growth per year, prefered prey (*Salix*) (Carrying capacity = 100)

r_1 (kg·kg^{-1}·ha^{-1})		**Reference:**
0.244	above ground net accumulation *S. pulchra* (USSR)	Kallio, 1975
0.331	above ground net accumulation *S. glauca* (USSR)	Kallio, 1975
3.7	vascular plant ground vegetation (Finland)	Kallio, 1975
6.76	*S. lapponum* leaves and shoots	Kjelvik, 1973
7	Salix growth in Norway	Kallio, 1975
13.26-19.33	above ground *S.lapponum* (DW)	Kjelvik, 1973

Growth per year, less preferred prey (*Ericaceous*) (Carrying capacity = 100)

r_2 (kg·kg^{-1}·ha^{-1})		
0.27	min woody green plants in dry meadow (Norway)	Kallio, 1975
0.4	woody leaves and shoots	Bliss, 1973; Kallio, 1975
0.5	*V.uliginosum* standing crop, Sweeden (not wood)	Kallio, 1975
0.7-3.5	Vascular plants ground vegetation (Finland)	Kallio, 1975
0.8	*E. hermaphroditum* standing crop, Sweeden (not wood)	Kallio, 1975
31.4	max woody green plants in Betula forest (Norway)	Kallio, 1975

Carrying capacity prefered prey

K_1 (kg·ha^{-1})		
9	above ground *S. reticulata* (green parts)	Wielgolaski &Rosswall, 1971
104	above ground *S. lanata* (green parts)	Chepurko, 1971
113	Salix alpine meadow (2 sp)	Chepurko, 1971
230	Salix reticulata all green alpine meadow	Chepurko, 1971
248	above ground *S. reticulata* (all above ground)	Wielgolaski &Rosswall, 1971
1404	above ground *S. lanata* (all above ground)	Wielgolaski &Rosswall, 1971

Carrying capacity less preferred prey

K_2 (kg·ha^{-1})		
49	total above ground DW *V.myrtillus* in Finland (in birch forest)	Kallio, 1975
97	above ground *V. uliginosum* (green parts)	Wielgolaski &Rosswall, 1971
109	*V. uliginosum* leaves (alpine meadow)	Chepurko, 1971
129	*E. hermaphroditium* (dwarf shrub tundra)	Chepurko, 1971
130	*V. uliginosum* standing crop	Flower & Ellis, 1973
130	standing crop of *V.uliginosum* in Sweeden	Kallio, 1975
131	above ground *V. myrtillus*	Wielgolaski &Rosswall, 1971
131	*V. myrtillus* leaves (alpine meadow)	Chepurko, 1971
150	*V. myrtillus all* green parts (dwarf shrub tundra)	Wielgolaski &Rosswall, 1971
309	total above ground DW *V.uliginosum* in Finland (in birch forest)	Kallio, 1975
685	*V. uliginosum* all green (alpine meadow)	Chepurko, 1971
710	standing crop of *E. hermaphroditum* in Sweeden	Kallio, 1975
782	above ground *V. uliginosum* (all above ground)	Wielgolaski &Rosswall, 1971
1070	above ground *V. myrtillus* (all above ground)	Wielgolaski &Rosswall, 1971
1374	total above ground *E. hermaphroditum* in Finland (in a birch forest)	Kallio, 1975

Other prey related parameters gathered from the literature.

Salix sp. 150000 shoots/ha	Kjelvik, 1973; Bliss, 1973
10000 kg·ha^{-1}·yr^{-1}regrowyh of gramanoids	Turchin & Batzli, 2000
Salix shoot average weight 1.28 g	Lundberg, 1988
23.64 Kj·g^{-1} energy in *E. hermaphroditum*	Kallio, 1975
30-50 individuals·ha^{-1} optimal no. for plant community	Smirnov & Tokmakova, 1971
2-3 Kcal·g^{-1} in grasses	Stenseth, *et al.*, 1977
3.8-6.2 g·m^{-1} of *Vaccinium myrtillus* stems and leaves	Hansson, 1974
425 cal·g^{-1}.day^{-1} digestible energy tundra monocots	Batzli & Cole, 1979
above ground annaul production was 13-28 g·m^{2}	Bliss & Kerik, 1973
V. ulignosum 2% of species consumption of the Khibini mountains	Chepurko, 1971
Salix 4.6% of species consumption of the Khibini mountains	Chepurko, 1971
Total annual production (inc. below ground) 500kg·ha^{-1}	Chepurko, 1971
Salix polaris is the most productive dwarf shrub in tundra (4.6-31.6 g·m$^{2-1}$.yr^{-1})	see Rosswall & Heal, 1975
Peak above above ground biomass at Barrow ranges from 60-100 g·m^{2}	see Rosswall & Heal, 1975
Salix pulchra above ground net accumulation 2.44 g·m$^{2-1}$.yr^{-1}	see Rosswall & Heal, 1975
Salix glauca above ground net accumulation 3.31 g·m$^{2-1}$.yr^{-1}	see Rosswall & Heal, 1975
E. hermaphroditum % frequency = 45-100%, Kevo, Finland	Kallio, 1975
E. hermaphroditum % Cover = 4.42-20%, Kevo, Finland	Kallio, 1975
V.uliginosum % frequency = 2-66%, Kevo, Finland	Kallio, 1975
V.uliginosum % cover = 0.1-4%, Kevo, Finland	Kallio, 1975
Biomass of ground vegetation at Kevo is 375-755 g·m^{2}	Kallio, 1975
year leaves and stems *V. uliginosum* 7.2 g·m^{2}	Kallio, 1975
2 years leaves and stems *E. hermaphroditum* 23.1 g·m^{2}	Kallio, 1975
vascular plant biomass 500-800 g·m^{2}, Hardangervidda, Norway	Rosswall & Heal, 1975
2g/m2/day primary production above ground primary production, Norway	Rosswall & Heal, 1975
Biomass above ground green parts range 5-48 g·m^{2}	see Rosswall & Heal, 1975
E. hermaphroditium leaves 129kg·ha^{-1}	see Rosswall & Heal, 1975
primary production can vary from 3-97 g·m$^{2-1}$.yr^{-1}	See Wielgolaski, 1971
Norway above ground green living biomass 11-115 g·m$^{2-1}$	Wielgolaski, 1971
Norway above ground green primary biomass increase 9-74 g·m$^{2-1}$.yr^{-1}	Wielgolaski, 1971

PREDATOR (VOLE) PARAMETERS

Predator mortality rate

d (yr^{1})		
6	Average life span for male *Microtus agrestis*	Myllymaki, 1977a
2	Average life span for female *Microtus agrestis*	Myllymaki, 1977a
1.7	Average life span for *Microtus agrestis*	Macdonald & Barrett, 1993
0.84	Longest life span for *Microtus agrestis*	Myllymaki, 1977a
0.8	Max life span for *Microtus agrestis*	Innes & Miller, 1994
0.67	Max life span for *Clethrionomys glaredus*	Macdonald & Barrett, 1993
0.5	Max life span for *Microtus agrestis*	Macdonald & Barrett, 1993

Predator handling time

h (yr)		
0.02	Cropping/chewing rate of *M. pennsylvanicus* on a monocot. (dry weight)	Belovsky, 1986
0.04	Cropping/chewing rate of *M. pennsylvanicus* on a dicot. (dry weight)	Belovsky, 1986

As no direct data were available for both predator search efficiency (q_i), and net energy gain from each prey species (e_i) estimates had to be obtained via the combination of various parameter values (see Section 5.3.1).

Predator search efficency

q_i (ha·kg^{-1}·yr^{-1})

Yearly home range (ha)

0.01-0.1	*M. agrestis*	Macdonald & Barrett, 1993
0.03-0.1	*C. rufocanus*	Macdonald & Barrett, 1993
0.05-0.73	*C. glaredus*	Macdonald & Barrett, 1993
0.1-2	*C. rutlius*	Macdonald & Barrett, 1993
0.18-0.36	*Microtus sp.*	Brown, 1966
0.5-1.0	*Clethrionomys* sp.	Brown, 1966

Yearly consumption (kg)

6.3	*C. glaredus*	Lundberg, 1988

Net energy gain from prey

e_i (kg·yr·kg^{-1}·yr^{-1})

Weight of vole (kg)

0.011-0.030	*C. rufocanus*	Oksanen & Oksanen, 1981
0.012-0.040	*C. glaredus* in Sweeden	Hannson, 1992
0.014-0.040	*M. agrestis*	Macdonald & Barrett, 1993
0.015-0.040	*C. rutlius*	Macdonald & Barrett, 1993
0.015-0.050	*C. rufocanus*	Macdonald & Barrett, 1993
0.017-0.074	*M. agrestis* in Sweeden	Hannson, 1992
0.025-0.030	*M. agrestis*	Hannson, 1971
0.025-0.062	*M. oeconomus*	Macdonald & Barrett, 1993
0.032-0.046	*C. rufocanus* (males)	Andersson & Jonasson, 1986
0.040	*M. agrestis* average	Gross *et al.*, 1993

Number of newborn a year for each female

8-42	*M. agrestis*	Macdonald & Barrett, 1993
10	*M. agrestis*	Rosswall & Heal, 1975
16-20	*C. glaredus*	Macdonald & Barrett, 1993
21-34	*M. agrestis*	Myllymaki, 1977a

Other predator related parameters gathered from the literature.

231min day feeding time *Microtus pennsylvanicus*	Belovsky & Slade, 1986
48400 kj·yr^{-1} consumption by a *M. oeconomus*	Kallio, 1975
693-1115 Kcal·g^{-1}·day^{-1} ingested energy for *M. californicus*	Batzli & Cole, 1979
18.307-0.431 Kcal·g^{-1}·day^{-1} required for voles	Grodzinski, *et al.*, 1977
13295 Kj·yr^{-1} required by voles	Grodzinski, *et al.*, 1977
3.6 Kcal·day^{-1} must be assimilated for growth	Stenseth, Hansson *et al.*, 1977
10% cost of growth of daily energy consumption (*M. agrestis*)	Stenseth, Hansson *et al.*, 1977
10% cost of growth of daily energy consumption (*M. agrestis*)	Stenseth, Hansson *et al.*, 1977
35% extra required for reproduction	Stenseth, Hansson *et al.*, 1977
21-57% of the vole population killed by predators	Norrdahl, 1998
5.23 g biomass available to bank voles 0.6g utilized in 180 min	Lundberg, 1988
121 Kj·m^{-1}·yr^{-1} energy gained by root voles	Kallio, 1975
231 min·day^{-1} max feeding time in *M. pennsylvanicus*	Schmitz *et al.*, 1997
11.388 kg·yr^{-1} max digestive capacity	Schmitz *et al.*, 1997
200 plants gnawed by *M. oeconomus* each day	Smirnov & Tokmakova, 1971
6.49 - 9.3 Kcal·day^{-1}	Stenseth, Hansson *et al.*, 1977

3.6 Kcal·day^{-1} must be assimilated	Stenseth, Hansson *et al.*, 1977
reproductive females require 3.3 times energy (*M. agrestis*)	Myllymaki, 1977a
2-3 Kcal·g^{-1}·dw^{-1} in grasses	Stenseth, *et al.*, 1977
18.307-0.431 Kcal·day^{-1} required for voles	Grodzinski, *et al.*, 1997
430min·day^{-1} active *M. pennsylvanicus*	Belovsky & Slade, 1986
86-61.2% neonatal mortality in *M. californicus*	Lidicker, 1979
47-202 mg·g^{-1}·day^{-1} ingested matter for *M. ochrogaster*	Batzli & Cole, 1979
157-254 mg·g^{-1}·day^{-1} ingested matter for *M. californicus*	Batzli & Cole, 1979
214-886 cal^{-1}·g^{-1}·day^{-1} ingested energy for *M. ochrogaster*	Batzli & Cole, 1979
693-1115 cal^{-1}·g^{-1}·day^{-1} ingested energy for *M. californicus*	Batzli & Cole, 1979
564-1053 intake cal^{-1}·g^{-1}·day^{-1} in *M. ochrogaster*	Batzli & Cole, 1979
0.012 g/min of willow shoots eaten by *C. glaredus*	Gross *et al.*, 1993
827 cal^{-1}·g^{-1}·day^{-1} ingested tundra monocots	Batzli & Cole, 1979
425 cal^{-1}·g^{-1}·day^{-1} digestible energy tundra monocots	Batzli & Cole, 1979
8.84-9.63 Kj·g^{-1}·dw^{-1} *M. pennsylvanicus* food eaten	Belovsky, 1986
28%, 25% and 18% of total activity spent outside the nest	Grodzinski, *et al.*, 1997
Mean weight of *C. glaredus* at birth = 1.6-2.0 g	Koskella, *et al.*, 1998
Weight of new born *M. epiroticus* range 2.085g-2.38g	Yoccoz, *et al.*, 1993 Appendix
M. abbreviatus weight at birth = 3.5g	Yoccoz, *et al.*, 1993 Appendix
M. arvalis weight at birth = 1.8-2g	Yoccoz, *et al.*, 1993 Appendix
M. californicus weight at birth = 2.8g	Yoccoz, *et al.*, 1993 Appendix
M breweri weight at birth = 3.5g	Yoccoz, *et al.*, 1993 Appendix
M ochrogaster weight at birth = 3.1g	Yoccoz, *et al.*, 1993 Appendix
C glarelus weight at birth = 1.8g	Yoccoz, *et al.*, 1993 Appendix
M pennsylvanicus weight at birth = 2.35g	Yoccoz, *et al.*, 1993 Appendix
C. rutilus weight at birth = 2.95g	Yoccoz, *et al.*, 1993 Appendix
M. socialis weight at birth = 2.0g	Yoccoz, *et al.*, 1993 Appendix

7.9 APPENDIX 5.3 The effect of altering parameter values with the Křivan model

When K_i = 100 kg·ha^{-1}, h_i = 0.016 yr, d = 1.7 kg·kg^{-1}·yr^{-1}then:

r_i kg·kg^{-1}·ha^{-1}	q_i ha·kg^{-1}·yr^{-1}	e_1 kg·kg^{-1}	e_2 kg·kg^{-1}	Threshold kg·ha^{-1}	Max no.·ha^{-1}	Min no.·ha^{-1}	Ratio max:min	peaks Frequency (yr)	No. criteria met
2	0.6	0.32	0.02	6.9	stable	focus.		na	0
2	0.6	0.32	0.04	14.9	195.5	31.8	6.1	4.5	***
2	0.6	0.32	0.06	24.0	365.4	5.5	66.9	5.0	****
2	0.6	0.36	0.02	6.1	stable	focus.			0
2	0.6	0.36	0.04	13.0	196.7	31.4	6.3	4.5	***
2	0.6	0.36	0.06	20.8	385.9	4.5	86.7	5.0	***
2	0.6	0.4	0.02	5.5	stable	focus.			0
2	0.6	0.4	0.04	11.6	202.4	29.6	6.8	4.5	***
2	0.6	0.4	0.06	18.4	405.2	3.5	116.6	5.5	*
2	0.8	0.32	0.02	5.2	82.0	47.5	1.7	3.8	**
2	0.8	0.32	0.04	11.2	221.2	9.3	23.7	5.0	****
2	0.8	0.32	0.06	18.0	434.0	0.5	434.0	6.3	*
2	0.8	0.36	0.02	4.6	83.2	47.0	1.8	3.8	**
2	0.8	0.36	0.04	9.8	236.9	7.7	30.8	5.0	****
2	0.8	0.36	0.06	15.6	465.0	0.3	465.0	6.2	**
2	0.8	0.4	0.02	4.1	137.5	82.4	1.7	3.6	**
2	0.8	0.4	0.04	8.7	245.9	6.8	35.9	5.0	****
2	0.8	0.4	0.06	13.8	486.7	0.3	486.7	7.1	*
2	1.0	0.32	0.02	4.2	68.5	38.0	1.8	3.8	**
2	1.0	0.32	0.04	8.9	365.6	0.3	365.6	7.1	*
2	1.0	0.32	0.06	14.4	484.3	0.0	484.3	8.3	*
2	1.0	0.36	0.02	3.7	68.1	38.0	1.8	3.8	*
2	1.0	0.36	0.04	7.8	400.2	0.2	400.2	7.1	*
2	1.0	0.36	0.06	12.5	510.7	0.0	510.7	8.3	*
2	1.0	0.4	0.02	3.3	67.5	38.2	1.8	3.8	*
2	1.0	0.4	0.04	6.9	438.8	0.1	438.8	7.1	*
2	1.0	0.4	0.06	11.0	548.3	0.0	548.3	8.3	**

r_i kg·kg^{-1}·ha^{-1}	q_i ha·kg^{-1}·yr^{-1}	e_1 kg·kg^{-1}	e_2 kg·kg^{-1}	Threshold kg·ha^{-1}	Max no.·ha^{-1}	Min no.·ha^{-1}	Ratio max:min	peaks Frequency (yr)	No. criteria met
1.7	0.6	0.32	0.02	6.9	stable	focus.	.	.	0
1.7	0.6	0.32	0.04	14.9	172.4	25.6	6.7	5.0	***
1.7	0.6	0.32	0.06	24.0	341.3	3.2	106.1	5.6	***
1.7	0.6	0.36	0.02	6.1	stable	focus.	.	.	0
1.7	0.6	0.36	0.04	13.0	177.5	24.0	7.4	5.0	***
1.7	0.6	0.36	0.06	20.8	364.0	2.4	149.5	6.3	*
1.7	0.6	0.4	0.02	5.5	stable	focus.	.	.	0
1.7	0.6	0.4	0.04	11.6	175.8	24.5	7.2	5.0	***
1.7	0.6	0.4	0.06	18.4	374.8	2.2	169.4	5.6	*
1.7	0.8	0.32	0.02	5.2	71.9	38.9	1.8	4.2	**
1.7	0.8	0.32	0.04	11.2	203.1	6.5	31.5	5.0	****
1.7	0.8	0.32	0.06	18.0	405.2	0.2	405.2	7.1	*
1.7	0.8	0.36	0.02	4.6	72.4	38.8	1.9	4.2	*
1.7	0.8	0.36	0.04	9.8	209.6	5.8	36.2	5.0	****
1.7	0.8	0.36	0.06	15.6	432.2	0.2	432.2	7.1	*
1.7	0.8	0.4	0.02	4.1	72.1	40.2	1.8	3.8	*
1.7	0.8	0.4	0.04	8.7	215.4	5.6	38.2	5.0	****
1.7	0.8	0.4	0.06	13.8	458.2	0.1	458.2	7.1	*
1.7	1	0.32	0.02	4.2	59.0	31.8	1.9	4.2	*
1.7	1	0.32	0.04	8.9	302.5	0.3	302.5	7.1	***
1.7	1	0.32	0.06	14.4	460.0	0.0	460.0	10.0	*
1.7	1	0.36	0.02	3.7	59.3	31.4	1.9	4.2	*
1.7	1	0.36	0.04	7.8	317.9	0.2	317.9	7.1	***
1.7	1	0.36	0.06	12.5	491.5	0.0	491.5	10.0	***
1.7	1	0.4	0.02	3.3	58.4	31.8	1.8	4.2	*
1.7	1	0.4	0.04	6.9	320.7	0.2	320.7	7.1	***
1.7	1	0.4	0.06	11.0	505.1	0.0	505.1	10.0	*

r_i kg·kg^{-1}·ha^{-1}	q_i ha·kg^{-1}·yr^{-1}	e_1 kg·kg^{-1}	e_2 kg·kg^{-1}	Threshold kg·ha^{-1}	Max no.·ha^{-1}	Min no.·ha^{-1}	Ratio max:min	peaks Frequency (yr)	No. criteria met
1.5	0.6	0.32	0.02	6.9	stable	focus.	.	.	0
1.5	0.6	0.32	0.04	14.9	158.9	21.0	7.6	5.0	***
1.5	0.6	0.32	0.06	24.0	325.9	2.1	158.2	6.3	**
1.5	0.6	0.36	0.02	6.1	stable	focus.	.	.	0
1.5	0.6	0.36	0.04	13.0	160.1	20.6	7.8	5.6	**
1.5	0.6	0.36	0.06	20.8	338.9	1.8	192.3	6.3	*
1.5	0.6	0.4	0.02	5.5	stable	focus.	.	.	0
1.5	0.6	0.4	0.04	11.6	163.8	19.4	8.4	5.0	***
1.5	0.6	0.4	0.06	18.4	367.7	1.2	315.6	7.1	*
1.5	0.8	0.32	0.02	5.2	65.1	33.5	1.9	4.2	*
1.5	0.8	0.32	0.04	11.2	198.8	4.2	46.9	6.3	***
1.5	0.8	0.32	0.06	18.0	401.2	0.1	401.2	8.3	*
1.5	0.8	0.36	0.02	4.6	63.9	33.9	1.9	4.5	*
1.5	0.8	0.36	0.04	9.8	214.8	3.0	70.5	5.0	****
1.5	0.8	0.36	0.06	15.6	440.8	0.0	440.8	8.3	*
1.5	0.8	0.4	0.02	4.1	64.6	33.7	1.9	4.5	*
1.5	0.8	0.4	0.04	8.7	197.0	4.3	46.0	5.0	****
1.5	0.8	0.4	0.06	13.8	467.7	0.0	467.7	8.3	*
1.5	1	0.32	0.02	4.2	53.0	27.4	1.9	4.5	*
1.5	1	0.32	0.04	8.9	344.8	0.0	344.8	10.0	**
1.5	1	0.32	0.06	14.4	461.8	0.0	461.8	12.5	*
1.5	1	0.36	0.02	3.7	52.3	27.7	1.9	4.5	*
1.5	1	0.36	0.04	7.8	369.3	0.0	369.3	10.0	**
1.5	1	0.36	0.06	12.5	490.7	0.0	490.7	12.5	*
1.5	1	0.4	0.02	3.3	51.9	27.2	1.9	5.0	*
1.5	1	0.4	0.04	6.9	409.8	0.0	409.8	10.0	*
1.5	1	0.4	0.06	11.0	500.6	0.0	500.6	12.5	*

When $K_i = 100$ kg·ha^{-1}, $q_i = 0.8$ ha·kg^{-1}·yr^{-1}, $d = 1.7$ kg·kg^{-1}·yr^{-1} then:

r_i kg·kg^{-1}·ha^{-1}	h_i yr	e_1 kg·kg^{-1}	e_2 kg·kg^{-1}	Threshold kg·ha^{-1}	Max no.·ha^{-1}	Min no.·ha^{-1}	Ratio max:min	peaks Frequency (yr)	No. criteria met
2	0.01	0.32	0.02	8.3	95.5	47.6	2.0	4.5	**
2	0.01	0.32	0.04	17.9	275.1	3.8	72.0	5.0	****
2	0.01	0.32	0.06	28.8	388.8	0.8	388.8	6.3	**
2	0.01	0.36	0.02	7.4	95.5	48.1	2.0	4.5	**
2	0.01	0.36	0.04	15.6	293.9	2.9	99.7	5.0	****
2	0.01	0.36	0.06	25.0	410.4	0.6	410.4	6.3	*
2	0.01	0.4	0.02	6.6	95.7	47.2	2.0	4.5	**
2	0.01	0.4	0.04	13.9	311.2	2.4	130.6	5.6	***
2	0.01	0.4	0.06	22.1	430.6	0.5	430.6	6.3	*
2	0.016	0.32	0.02	5.2	71.9	38.9	1.8	4.2	**
2	0.016	0.32	0.04	11.2	203.1	6.5	31.5	5.0	****
2	0.016	0.32	0.06	18.0	405.2	0.2	405.2	7.1	*
2	0.016	0.36	0.02	4.6	72.4	38.8	1.9	4.2	**
2	0.016	0.36	0.04	9.8	209.6	5.8	36.2	5.0	****
2	0.016	0.36	0.06	15.6	432.2	0.2	432.2	7.1	*
2	0.016	0.4	0.02	4.1	72.1	40.2	1.8	3.8	**
2	0.016	0.4	0.04	8.7	215.4	5.6	38.2	5.0	****
2	0.016	0.4	0.06	13.8	458.2	0.1	458.2	7.1	*
2	0.022	0.32	0.02	3.8	111.9	35.6	3.1	3.8	**
2	0.022	0.32	0.04	8.1	114.4	52.8	2.2	7.1	*
2	0.022	0.32	0.06	13.1	461.8	0.4	461.8	7.1	*
2	0.022	0.36	0.02	3.3	111.4	35.3	3.2	4.2	**
2	0.022	0.36	0.04	7.1	112.6	54.9	2.0	7.1	*
2	0.022	0.36	0.06	11.4	490.0	0.3	490.0	8.3	*
2	0.022	0.4	0.02	3.0	109.6	35.8	3.1	3.8	**
2	0.022	0.4	0.04	6.3	112.6	52.4	2.2	7.1	*
2	0.022	0.4	0.06	10.0	533.6	0.1	533.6	8.3	*

When $h_i = 0.016$ yr, $q_i = 0.8$ ha·kg^{-1}·yr^{-1}, $d = 1.7$ kg·kg^{-1}·yr^{-1} (where Ki = § then K_1 = 104, K_2 = 130), then:

r_i kg·kg^{-1}·ha^{-1}	K_i kg·ha^{-1}	e_1 kg·kg^{-1}	e_2 kg·kg^{-1}	Threshold kg·ha^{-1}	Max no.·ha^{-1}	Min no.·ha^{-1}	Ratio max:min	peaks Frequency (yr)	No. criteria Met
2	100	0.32	0.02	5.2	82.0	47.5	1.7	3.8	**
2	100	0.32	0.04	11.2	221.2	9.3	23.7	5.0	****
2	100	0.32	0.06	18.0	434.0	0.5	434.0	6.3	*
2	100	0.36	0.02	4.6	83.2	47.0	1.8	3.8	**
2	100	0.36	0.04	9.8	236.9	7.7	30.8	5.0	****
2	100	0.36	0.06	15.6	465.0	0.3	465.0	6.3	*
2	100	0.4	0.02	4.1	137.5	82.4	1.7	3.6	**
2	100	0.4	0.04	8.7	245.9	6.8	35.9	5.0	****
2	100	0.4	0.04	8.7	245.9	6.8	35.9	5.0	****
2	150	0.32	0.02	5.2	86.8	48.2	1.8	3.8	**
2	150	0.32	0.04	11.2	659.0	0.0	659.0	8.3	*
2	150	0.32	0.06	18.0	735.5	0.0	735.5	8.3	*
2	150	0.36	0.02	4.6	85.6	48.4	1.8	3.8	*
2	150	0.36	0.04	9.8	710.7	0.0	710.7	10.0	*
2	150	0.36	0.06	15.6	760.8	0.0	760.8	10.0	*
2	150	0.4	0.02	4.1	643.8	0.0	643.8	8.3	*
2	150	0.4	0.04	8.7	735.6	0.0	735.6	10.0	*
2	150	0.4	0.06	13.8	804.9	0.0	804.9	10.0	*
2	§	0.32	0.02	5.2	83.9	47.0	1.8	4.2	*
2	§	0.32	0.04	11.2	303.6	3.1	96.8	5.6	***
2	§	0.32	0.06	18.0	501.7	0.2	501.7	7.1	*
2	§	0.36	0.02	4.6	83.7	47.0	1.8	2.9	*
2	§	0.36	0.04	9.8	334.5	2.1	156.5	6.3	**
2	§	0.36	0.06	15.6	534.3	0.1	534.3	7.1	*
2	§	0.4	0.02	4.1	83.5	48.2	1.7	3.6	**
2	§	0.4	0.04	8.7	363.3	1.4	264.7	6.3	*
2	§	0.4	0.04	13.8	562.8	0.1	562.8	8.3	*

When K_i = 100 kg·ha^{-1}, r_i = 2 kg·kg^{-1}·yr^{-1}, h_i = 0.016 yr then:

q_i ha·kg^{-1}·yr^{-1}	d kg·kg^{-1}·yr^{-1}	e_1 kg·kg^{-1}	e_2 kg·kg^{-1}	Threshold kg·ha^{-1}	Max no.·ha^{-1}	Min no.·ha^{-1}	Ratio max:min	peaks Frequency (yr)	No. criteria met
0.8	2.4	0.32	0.02	5.2	110.9	31.8	3.5	3.3	**
0.8	2.4	0.32	0.04	11.2	98.0	60.8	1.6	.	0
0.8	2.4	0.32	0.06	18.0	262.0	5.6	46.4	4.5	****
0.8	2.4	0.36	0.02	4.6	115.9	29.7	3.9	3.3	**
0.8	2.4	0.36	0.04	9.8	96.7	61.6	1.6	.	*
0.8	2.4	0.36	0.06	15.6	289.8	4.0	73.0	4.5	****
0.8	2.4	0.4	0.02	4.1	117.0	30.2	3.9	3.1	**
0.8	2.4	0.4	0.04	8.7	98.4	59.9	1.6	.	*
0.8	2.4	0.4	0.04	13.8	314.9	2.8	113.4	5.0	****
0.8	1.7	0.32	0.02	5.2	82.0	47.5	1.7	3.8	*
0.8	1.7	0.32	0.04	11.2	221.2	9.3	23.7	5.0	****
0.8	1.7	0.32	0.06	18.0	434.0	0.5	434.0	6.3	*
0.8	1.7	0.36	0.02	4.6	83.2	47.0	1.8	3.8	*
0.8	1.7	0.36	0.04	9.8	236.9	7.7	30.8	5.0	***
0.8	1.7	0.36	0.06	15.6	465.0	0.3	465.0	6.3	*
0.8	1.7	0.4	0.02	4.1	137.5	82.4	1.7	3.6	*
0.8	1.7	0.4	0.04	8.7	245.9	6.8	35.9	5.0	****
0.8	1.7	0.4	0.04	8.7	245.9	6.8	35.9	5.0	****
0.8	1	0.32	0.02	5.2	123.9	33.6	3.7	6.3	*
0.8	1	0.32	0.04	11.2	457.7	0.3	457.7	10.0	*
0.8	1	0.32	0.06	18.0	556.7	0.1	556.7	12.5	*
0.8	1	0.36	0.02	4.6	311.5	2.3	137.8	8.3	**
0.8	1	0.36	0.04	9.8	486.3	0.2	486.3	10.0	*
0.8	1	0.36	0.06	15.6	583.8	0.1	583.8	12.5	*
0.8	1	0.4	0.02	4.1	122.7	34.8	3.5	6.3	**
0.8	1	0.4	0.04	8.7	521.9	0.1	521.9	12.5	*
0.8	1	0.4	0.04	13.8	617.6	0.1	617.6	12.5	*

8 REFERENCES

Abrams, P.A. (1994). The fallacies of "ratio-dependent" predation. *Ecology.* **75**. 1842-1850.

Abrams, P.A. and Walters, C.J. (1996). Invulnerable prey and the paradox of enrichment. *Ecology.* **77**. 1125-1133.

Akçakaya, H.R. (1992). Population cycles of mammals: evidence for a ratio-dependent predation hypothesis. *Ecological Monographs.* **62**. 119-142.

Akçakaya, H.R., Arditi, R. and Ginzburg, L.R. (1995). Ratio-dependent predation: an abstract that works. *Ecology.* **76**. 995-1004.

Allee, W.C. (1931). *Animal Aggregations. A Study in General Sociology.* University of Chicago Press, Chicago.

Alvarez, L.H.R. (1998). Optimal harvesting under stochastic fluctuations and critical depensation. *Mathematical Biosciences.* **152**. 63-85.

Amarasekare, P. (1998a). Allee effects in metapopulation dynamics. *American Naturalist.* **152**. 298-303.

Amarasekare, P. (1998b). Interactions between local dynamics and dispersal: insights from single species models. *Theoretical Population Biology.* **53**. 44-59.

Anderson, M.J. (1996). A chemical cue induces settlement of Sydney rock oysters, *Saccostrea commercialis* in the laboratory and in the field. *Biological Bulletin.* **190**. 350-358.

Anderson, M.J. and Underwood, A.J. (1994). Effect of substratum on the recruitment and development of an intertidal estuarine fouling assemblage. *Journal of Experimental Marine Biology and Ecology.* **184**. 217-236.

Anderson, R.M. and May, R.M. (1991). *Infectious diseases of humans.* Oxford University Press, Oxford.

Andersson, M. and Jonasson, S. (1986). Rodent cycles in relation to food resources on an alpine heath. *Oikos.* **46**. 93-106.

Andreev, V.N., Galaktionova, T.F., Zakharova, V.I. and Neustrueva, A.I. (1971). Methods of estimation of seasonal changes in above-ground phytomass of herbs. In: *Biological Production of Tundra.* Proceedings of the International Biological Programme (IBP) Tundra Biome, Leningrad, USSR. F.E. Wielgolaski, and T.H. Rosswall, (eds.). Tundra Biome Steering Committee. p. 102-110.

Angerbjörn, A., Tannerfeldt, M. and Erlinge, S. (1999). Predator-prey relationships: arctic foxes and lemmings. *Journal of Animal Ecology.* **68**. 34-49.

Arditi, R. and Ginzburg, L. (1989). Coupling in predator-prey dynamics: ratio-dependence. *Journal of Theoretical Biology.* **139**. 311- 326.

Arditi, R. and Saiah, H. (1992). Empirical evidence of the role of heterogeneity in ratio-dependent consumption. *Ecology.* **73**. 1544 -1551.

Asmussen, M. (1979). Density-dependent selection. II. The Allee effect. *American Naturalist.* **114**. 796-809.

Aviles, L. and Tufino, P. (1998). Colony size and individual fitness in the social spider *Anelosimus eximius. American Naturalist.* **152**. 403-418.

Barne, J.H., Robson, C.F., Kaznowska, J.P., Doody, N.L., Davidson, N.C. and Buck, A.L. (1996). *Coast and seas of the United Kingdom, Region 10. South-West England: Seaton to the Roseland Peninsula.* Joint Nature Conservation Committee.

Barnes, D.J., Crisp, D.J. and Powell, H.T. (1951). Observations on the orientation of some species of barnacles. *Journal of Animal Ecology.* **20**. 227-241.

Barnes, H. and Barnes, M. (1958). Further observations on self-fertilization in *Chthamalus* sp. *Ecology.* **39**. 550.

Barnes, H. and Barnes, M. (1968). Egg numbers, metabolic efficiency of egg production and fecundity: local and regional variations in a number of common barnacles. *Journal of the Marine Biological Association of the United Kingdom.* **32**. 107-128.

Barnes, H. and Crisp, D.J. (1956). Evidence of self-fertilization in certain species of barnacles. *Journal of the Marine Biological Association of the United Kingdom.* **35**. 631-639.

Barnes, H., Crisp, D.J. and Powell, H.T. (1952). Observations on the orientation of some species of barnacles. *Journal of Animal Ecology.* **20**. 227-241.

Barnes, M. (1992). The reproductive periods and condition of the penis in several species of common Cirripedes. *Oceanography and Marine Biology.* **30**. 483-525.

Barnett, B.E. and Crisp, D.J. (1979). Laboratory studies of gregarious settlement in *Balanus balanoides* and *Elminius modestus* in relation to competition between these species. *Journal of the Marine Biological Association of the United Kingdom.* **59**. 581-590.

Bassindale, R. (1964). British barnacles. *Linnean Society of London Synopses British Fauna.* No. 14.

Batzli, G.O. (1983). Responses of arctic rodent populations to nutritional factors. *Oikos.* **40**. 396-406.

Batzli, G.O. (1986). Nutritional ecology of the California vole: effects of food quality on reproduction. *Ecology.* **67**. 406-412.

Batzli, G.O. (1988). The role of nutrition and carrying capacity in models of small rodent population dynamics. *Oikos.* **52**. 224-226.

Batzli, G.O. and Cole, F.R. (1979). Nutritional ecology of microtine rodents: digestibility of forage. *Journal of Mammalogy.* **60**. 740-750.

Batzli, G.O. and Pitelka, F.A. (1971). Condition and diet of cycling populations of the California vole, *Microtus californicus. Journal of Mammalogy.* **52**. 141-163.

Batzli, G.O. and Pitelka, F.A. (1975). Vole cycles: test of another hypothesis. *American Naturalist.* **109**. 482-487.

Bayliss, D.E. (1993). Spatial distribution of *Balanus amphitrite* and *Elminius adelaidae* on mangrove pneumatophores. *Marine Biology.* **116**. 251-256.

Beddington, J.R. (1975). Mutual interference between parasites or predators and its effect on searching efficiency. *Journal of Animal Ecology.* **44**. 331-340.

Beddington, J.R., Free, C.A. and Lawton, J.H. (1976). Concepts of stability and resilience in predator-prey models. *Journal of Animal Ecology.* **45**. 791 -816.

Begon, M., Harper, J.L. and Townsend, C.R. (1990). *Ecology: Individuals, Populations and Communities.* Blackwell Scientific Publishing, Oxford.

Bellamy, P.E., Hinsley, S.A. and Newton, I. (1996). Local extinctions and recolonisations of passerine bird populations in small woods. *Oecologia.* **108**. 64-71.

Bellows, T.S. (1981). The descriptive properties of some models for density dependence. *Journal of Animal Ecology.* **50**. 139-156.

Belovsky, G.E. (1986). Optimal foraging and community structure: implications for a guild of generalist grassland herbivores. *Oecologia.* **70**. 35-52.

Bence, J.R. and Nisbet, R.M. (1989). Space-limited recruitment in open systems: the importance of time delays. *Ecology*. **70**. 1434-1441.

Bengtsson, J. (1989). Interspecific competition increases extinction rate in a metapopulation system. *Nature*. **340**. 713-715.

Berger, P.J., Negus, N.C., Sanders, E.H. and Gardner, P.D. (1981). Chemical triggering of reproduction in *Microtus montanus*. *Science*. **214**. 69-70.

Berger, P.J., Sanders, E.H., Gardner, P.D. and Negus, N.C. (1977). Phenolic plant compounds functioning as reproductive inhibitors in *Microtus montanus*. *Science*. **195**. 575-577.

Berryman, A. (1992). The origins and evolution of predator-prey theory. *Ecology*. **73**. 1530 -1535.

Berryman, A.A. (1995). Population cycles: a critique of the maternal and allometric hypotheses. *Journal of Animal Ecology*. **64**. 290-293.

Bertness, M.D. (1989). Intraspecific competition and facilitation in a northern acorn barnacle population. *Ecology*. **70**. 257-268.

Bertness, M.D., Gaines, S.D., Stephens, E.G. and Yund, P.O. (1992). Components of recruitment in populations of the acorn barnacle *Semibalanus balanoides* (Linnaeus). *Journal of Experimental Marine Biology and Ecology*. **156**. 199-215.

Bertness, M.D., Gaines, S.D. and Wahle, R.A. (1996). Wind-driven settlement patterns in the acorn barnacle *Semibalanus balanoides*. *Marine Ecology Progress Series*. **137**. 103-110.

Bertness, M.D., Gaines, S.D. and Yeh, S.M. (1998). Making mountains out of barnacles: the dynamics of acorn barnacle hummocking. *Ecology*. **79**. 1382-1394.

Bird, E. (1997). *The Shaping of the Isle of Wight: with an excursion guide.* Crowell Press, Wiltshire.

Blacksmith, R.E. (1958). Nearest-neighbour distance measurements for the estimation of animal populations. *Ecology.* **39**. 147-150.

Bliss, L.C. and Kerik, J. (1973). Primary production of plant communities of the Truelove Lowland, Devon Island Canada - rock outcrops. In: *Primary Production and Production Processes, in the Tundra Biome*. Proceedings of the International Biological Programme (IBP), Dublin. L.C. Bliss and F.E. Wielgolaski, (eds.). Tundra Biome Steering Committee. p. 27-36.

Bliss, L.C. and Wielgolaski, F.E. (1973). *Primary Production and Production Processes, in the Tundra Biome*. Proceedings of the International Biological Programme (IBP), Dublin. L.C. Bliss and F.E. Wielgolaski, (eds.). Tundra Biome Steering Committee.

Blower, S.M. and Roughgarden, J. (1989). Parasites detect host spatial pattern and density - a field experimental analysis. *Oecologia.* **78**. 138-141.

Boorman, S.A. and Levitt, P.R. (1973). Group selection on the boundary of a stable population. *Theoretical Population Biology.* **4**. 85-128.

Bradshaw, A.D. (1983). The reconstruction of ecosystems. *Journal of Applied Ecology.* **20**. 1-17.

Brown, L.E. (1966). Home range and movement of small mammals. *Symposium of the Zoological Society of London.* 18. 111-142.

Brown, D. and Rothery, P. (1993). *Models in Biology: Mathematics, Statistics, and Computing.* John Wiley and Sons Ltd.

Brown, J.H. and Kodric-Brown, A. (1977). Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology.* **58**. 445-449.

Brunnel, F.L., Maclean, S.F. and Brown, J. (1975). Barrow, Alaska, USA. In: *Structure and Function of Tundra Ecosystems.* T. Rosswall and O. W. Heal (eds.). Sundt & Co Offset, Stockholm. p 73-124.

Bulmer, M. (1994). *Theoretical Evolutionary Ecology.* Sinauer Association Inc, Sunderland, Massachusets.

Burke, R.D. (1986). Pheromones and the gregarious settlement of marine invertebrate larvae. *Bulletin of Marine Science.* **39**. 323-331.

Burkey, T.V. (1989). Extinction in nature reserves: the effects of fragmentation and the importance of migration between reserve fragments. *Oikos.* **55**. 75- 81.

Burkey, T.V. (1999). Extinction in fragmented habitats predicted from stochastic birth-death processes with density dependence. *Journal of Theoretical Biology.* **199**. 395-406.

Burrows, M.T., Hawkins, S.J. and Southward, A.J. (1992). A comparison of reproduction in co-occurring chthamalid barnacles, *Chthamalus stellatus* (Poli) and *Chthamalus montagui* Southward. *Journal of Experimental Marine Biology and Ecology.* 160. 229-249.

Burrows, M.T., Kawai, K. and Hughes, R.N. (1999a). Foraging by mobile predators on a rocky shore: underwater TV observations of movements of blenies *Lipophrys pholis* and crabs *Carcinus maenas. Marine Ecology Progress Series.* **187**. 237-250.

Burrows, M.T., Hawkins, S.J. and Southward, A.J. (1999b). Larval development of the intertidal barnacles *Chthamalus stellatus* and *Chthamalus montagui. Journal of the Marine Biological Association of the United Kingdom.* **79**. 93-101.

Butman, C.A., Grassle, J.P. and Webb, C.M. (1988). Substrate choices made by marine larvae settling in still water and in flume flow. *Nature.* **333**. 771-773.

Caffey, H.M. (1982). No effect of naturally-occurring rock types on settlement or survival in the intertidal barnacle, *Tesseropora Rosea* (Krauss). *Journal of Experimental Marine Biological and Ecology.* **63**. 119-132.

Caffey, H.M. (1985). Temporal and spatial variation in the settlement and recruitment of intertidal barnacles. *Ecological Monographs.* **55**. 313-332.

Caley, M.J., Carr, M.H., Hixon, M.A., Hughes, T.P., Jones, G.P. and Menge, B.A. (1996). Recruitment and the local dynamics of open marine populations. *Annual Review of Ecological Systematics.* **27**. 477-500.

Callaghan, T.V., Collins, N.J. and Callaghan, C.H. (1978). Photosynthesis, growth and reproduction of *Hylocomium splendens* and *Polytrichum commune* in Swedish Lapland. Strategies of growth and population dynamics of tundra plants 4. *Oikos.* **31**. 73-88.

Caswell, H. (1978). A general formula for the sensitivity of population growth rate to changes in life history parameters. *Theoretical Population Biology.* **14**. 215-230.

Caswell, H. (1988). Theory and models in ecology: A different perspective. *Ecological Modelling.* **43**. 33-44.

Chabot, R. and Bourget, E. (1988). Influence of substratum heterogeneity and settled barnacle density on the settlement of cypris larvae. *Marine Biology.* **97**. 45-56.

Chepurko, N.L. (1971). The biological productivity and the cycle of nitrogen and ash elements in the dwarf shrub tundra ecosystem of the Khibini mountains (Kola Peninsula). . In: *Biological Production of Tundra.* Proceedings of the International Biological Programme (IBP) Tundra Biome, Leningrad, USSR. F.E. Wielgolaski, and T.H. Rosswall, (eds.). Tundra Biome Steering Committee. p 236-248.

Chesson, P. (1998). Recruitment limitation: a theoretical perspective. *Australian Journal of Ecology.* **23**. 234-240.

Chitty, D. (1960). Population processes in the vole and their relevance to general theory. *Canadian Journal of Zoology.* **38**. 98-113.

Chitty, D. (1967). The natural selection of self regulatory behaviour in animal populations. *Proceedings of the Ecological Society of Australia.* **2**. 51-78.

Chitty, D. (1971). The natural selection of self-regulatory behaviour in animal populations. In: *Natural Regulation of Animal Populations.* I. A. McLaren (ed.). Lieber-Atherton Inc. p.136-170.

Chitty, D. and Phillips, E. (1966). Seasonal changes in survival in mixed populations of two species of vole. *Journal of Animal Ecology.* **35**. 311-331.

Christian, J.J. and Davis, D.E. (1964). Endocrines, behaviour, and population. *Science.* **146**. 1550-1560.

Clarke, P.J. and Evans, F.C. (1954). Distance to nearest neighbour as a measure of spatial relationship in populations. *Ecology.* **35**. 445-453.

Connell, J.H. (1959). An experimental analysis of interspecific competition in natural populations of intertidal barnacles. *Proceedings of the XVth International Congress of Zoology, London.* **3**. 290-293.

Connell, J.H. (1961). Effects of competition, predation by *Thais lapillus* and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecological Monographs.* **31**. 61-104.

Connell, J.H. (1985). The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *Journal of Experimental Marine Biology and Ecology.* **93**. 11-45.

Connell, J.H. and Sousa, W.P. (1983). On the evidence needed to judge ecological stability or persistence. *American Naturalist.* **121**. 789-824.

Courchamp, F., Clutton-Brock, T. and Grenfell, B. (1999). Inverse density dependence and the Allee effect. *Trends in Ecology and Evolution.* **14**. 405-410.

Crawley, M. (1975). The numerical responses of insect predators to changes in prey density. *Journal of Animal Ecology.* **44**. 877- 892.

Crawley, M.J. (1983). *Herbivory: The Dynamics of Animal-Plant Interactions.* Blackwell Scientific Publications, Oxford.

Crisp, D. (1961). Territorial behaviour in barnacle settlements. *Journal of Experimental Biology.* **38**. 429-446.

Crisp, D.J. (1955). The behaviour of cyprids in relation to water movement over a surface. *Journal of Experimental biology.* **32**. 569-590.

Crisp, D.J. (1959). Factors influencing the time of breeding of *Balanus balanoides. Oikos.* **10**. 275-289.

Crisp, D.J. (1960). Mobility of barnacles. *Nature.* **188**. 1208-1209.

Crisp, D.J. (1962). The planktonic stages of the cirripedia *Balanus balanoides* (L.) and *Balanus balanus* (L.) from north temperate waters. *Crustaceana.* **3**. 207-221.

Crisp, D.J. (1964). An assessment of plankton grazing by barnacles. *British Ecological Society Symposium.* **4**. 251-264.

Crisp, D.J. (1974). Factors influencing the settlement of marine invertebrate larvae. In: *Chemoreception in marine organisms.* P.T. Grant and A.N. Mackie, (eds.). Academic Press, London. p. 177-265.

Crisp, D.J. (1990). Field experiments on the settlement, orientation and habitat choice of *Chthamalus fragilis* (Darwin). *Biofouling*. **2**. 131-136.

Crisp, D.J. and Barnes, H. (1954). The orientation and distribution of barnacles at settlement with particular reference to surface contour. *Journal of Animal Ecology*. **23**. 142-162.

Crisp, D.J. and Meadows, P.S. (1963). Absorbed layers: the stimulus to settlement in barnacles. *Proceedings of the Royal Society London B*. **158**. 364-387.

Crisp, D.J., Southward, A.J. and Southward, E.C. (1981). On the distribution of the intertidal barnacles *Chthamalus stellatus*, *Chthamalus montagui* and *Euraphia depressa*. *Journal of the Marine Biological Association of the United Kingdom*. **61**. 359-380.

Crone, E.E. (1997). Delayed density dependence and the stability of interacting populations and subpopulations. *Theoretical Population Biology*. **51**. 67- 76.

Davis, A.R. and Campbell, D.J. (1996). Two levels of spacing and limits to local population density for settled larvae of the ascidian *Clavelina moluccensis*: a nearest neighbour analysis. *Oecologia*. **108**. 701-707.

DeAngelis, D.L., Mulholland, P.J., Palumbo, A.V., Steinman, A.D., Huston, M.A. and Elwood, J.W. (1989). Nutrient dynamics and food-web stability. *Annual Review of Ecology and Systematics*. **20**. 71-95.

Dempster, J.P. (1983). The natural control of populations of butterflies and moths. *Biological reviews*. **58**. 461-481.

Diamond, J.M. (1976). Island biogeography and conservation: strategy and limitations. *Science*. **193**. 1027-1029.

Diffendorfer, J.E. (1998). Testing models of source-sink dynamics and balanced dispersal. *Oikos*. **81**. 417-433.

Doak, D.F. and Mills, L.S. (1994). A useful role for theory in conservation. *Ecology.* **75**. 615-626.

Dobson, F.S. (1995). Regulation of population size: evidence from Colombian ground squirrels. *Oecologia.* **102**. 44-51.

Doherty, P.J. (1982). Some effects of density on the juveniles of two species of tropical, territorial damselfish. *Journal of Experimental Marine Biology and Ecology.* **65**. 249-261.

Doncaster, C.P. (1999). A useful phenomenological difference between exploitation and interference in the distribution of ideal free predators. *Journal of Animal Ecology.* **68**. 836-838.

Doncaster, C.P. (2000). Extension of ideal free resource use to breeding populations and metapopulations. *Oikos.* 24-36.

Doncaster, C.P. and Gustafsson, L. (1999). Density dependence in resource exploitation: empirical test of Levins' metapopulation model. *Ecology Letters.* **2**. 44-51.

Doncaster, C.P., Micol, T. and Jensen, S.P. (1996). Determining minimum habitat requirements in theory and practice. *Oikos.* **75**. 335- 339.

Donnelly, K.P. (1978). Simulations to determine the variance and edge effect of total nearest-neighbour distance. In: *Simulation methods in Archaeology.* I.R. Hodder (ed.). Cambridge University Press, Cambridge.

Doyle, R.W. (1975). Settlement of planktonic larvae: a theory of habitat selection in varying environments. *American Naturalist.* **109**. 113-126.

Edwards, A.W.F. (1972). *Likelihood: an Account of the Statistical Concept of Likelihood and its Application to Scientific Inference.* Cambridge University Press, Cambridge.

Elton, C. (1924). Periodic fluctuations in the numbers of animals: their causes and effects. *British Journal of Experimental Biology.* **2**. 119-163.

Erlinge, S.G. (1987). Predation and noncyclicity in a microtine population in southern Sweden. *Oikos.* **50**. 347-352.

Etienne, R.S. and Heesterbeek, J.A.P. (2000). On optimal size and number of reserves for metapopulation persistence. *Journal of Theoretical Biology.* **203**. 33-50.

Fairweather, P.G. (1988). Movements of intertidal whelks (*Morulamargin alba* and *Thais orbita*) in relation to availability of prey and shelter. *Marine Biology.* **100**. 63-68.

Farrell, T.M., Bracher, D. and Roughgarden, J. (1991). Cross-shelf transport causes recruitment to intertidal populations in central California. *American Society of Limnology and Oceanography.* **36**. 279-288.

Flower-Ellis (1973). Growth and morphology in the evergreen dwarf shrubs *Empetrum hermaphroditum* and *Andromeda polifolia* at Stordalen. In: *Primary Production and Production Processes, in the Tundra Biome*. Proceedings of the International Biological Programme (IBP), Dublin. L.C. Bliss and F.E. Wielgolaski, (eds.). Tundra Biome Steering Committee. p. 123-136.

Foster, B.A. (1971). Desiccation as a factor in the intertidal zonation of barnacles. *Marine Biology.* **8**. 12-29.

Freeland, W.J. (1974). Vole cycles: another hypothesis. *American Naturalist.* **108**. 238-245.

Fretwell, S.D. and Lucas, H.L.J. (1970). On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheretica.* **19**. 16-36.

Gaines, S., Brown, S. and Roughgarden, J. (1985). Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, *Balanus glandula. Oecologia.* **67**. 267-272.

Gaines, S. and Roughgarden, J. (1985). Larval settlement rate: A leading determinant of structure in an ecological community of the marine intertidal zone. *Proceedings of the Natural Academy of Science, USA.* **82**. 3707-3711.

Gaines, S.D. and Bertness, M. (1993). The dynamics of juvenile dispersal: why field ecologists must integrate. *Ecology.* **74**. 2430-2435.

Gerritsen, J. (1980). Sex and parthenogenesis in sparse populations. *American Naturalist.* **115**. 718-742.

Gilpin, M.E. (1972). Enriched predator-prey systems: theoretical stability. *Science.* **177**. 902-904.

Gilwicz, J. (1988). The role of dispersal in models of small rodent population dynamics. *Oikos.* **52**. 219-221.

Ginzburg, L. and Akçakaya, H. (1992). Consequences of ratio-dependent predation for steady state properties of ecosystems. *Ecology.* **73**. 1536 -1543.

Gleeson, S.K. (1994). Density dependence is better than ratio dependence. *Ecology.* **75**. 1834-1835.

Goodman, D. (1996). The demography of chance extinctions. In: *Viable Populations for Conservation.* M. E. Soule (ed.). Cambridge University press, Cambridge. p.11-34.

Gosselin, L.A. and Qian, P.Y. (1996). Early post-settlement mortality of an intertidal barnacle: a critical period for survival. *Marine Ecology Progress Series.* **135**. 69-75.

Gotelli, N. (1991). Metapopulation models: the rescue effect, the propagule rain, and the core-satellite hypothesis. *American Naturalist.* **138**. 768-776.

Gotelli, N.J. and Kelley, W.G. (1993). A general model of metapopulation dynamics. *Oikos.* **68**. 36-44.

Gragnani, A. (1997). Bifurcation analysis of two predator-prey models. *Applied Mathematics and Computation.* **85**. 97-108.

Greaves, J.H. (1986). Managing resistance to rodenticides. In: *Pesticide Resistance: Strategies for Management.* National Academic Press, Washington D.C. p. 236-244.

Grimm, V. (1999). Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future. *Ecological Modelling.* **115**. 129-148.

Grodzinski, W., Makomaska, M., Tertil, R. and Weiner, J. (1977). Bioenergetics and total impact of vole populations. *Oikos.* **29**. 494-510.

Groombridge, B. (1992). *Global Biodiversity: status of the earth's living resources.* Chapman & Hall, London.

Gross, J.E., Shipley, L.A., Hobbs, T.N., Spalinger, D.E. and Wunder, B.A. (1993). Functional responses of herbivores in food-concentrated patches: tests of a mechanistic model. *Ecology.* **74**. 778-791.

Gustafsson, T.O., Andersson, C.B. and Nyholm, N.E.I. (1983). Comparisons of sensitivity to social suppression of sexual maturation in captive male bank voles, *Clethrionomys glareolus*, originating from populations with different degrees of cyclicity. *Oikos*. **41**. 250-254.

Gyllenberg, M. and Hemminki, J. (1999). Allee effects can both conserve and create spatially heterogeneity in population densities. *Theoretical Population Biology*. **56**. 231-242.

Gyllenberg, M., Osipov, A.V. and Soderbacka, G. (1996). Bifurcation analysis of a metapopulation model with source sinks. *Journal of Nonlinear Science*. **6**. 329-366.

Hairston, N.G. (1994). An unsolved problem: population cycles. In: *Vertebrate Zoology: an experimental field approach*. Cambridge University Press, Cambridge. p.177-184.

Hall, C.A.S. (1988). What constitutes a good model and by whose criteria. *Ecological Modelling*. **43**. 125-127.

Hanski, I. (1982). Dynamics of the regional distribution: the core and satellite species hypothesis. *Oikos*. **38**. 210-221.

Hanski, I. (1991). Single-species metapopulation dynamics: concepts, models and observations. *Biological Journal of the Linnean Society*. **42**. 17-38.

Hanski, I. (1992). Inferences from ecological incidence functions. *American Naturalist*. **139**. 657-662.

Hanski, I. (1994b). Patch-occupancy dynamics in fragmented landscapes. *Trends in Ecology and Evolution*. **9**. 131 -135.

Hanski, I. (1994b). A practical model of metapopulation dynamics. *Journal of Animal Ecology*. **63**. 151- 162.

Hanski, I. (1998). Metapopulation dynamics. *Nature*. **396**. 41-49.

Hanski, I. (1999). *Metapopulation Ecology.* Oxford University Press, Oxford.

Hanski, I. and Gilpin, M.E. (1997). *Metapopulation Biology: ecology, genetics, and evolution.* Academic Press, London.

Hanski, I. and Gyllenberg, M. (1993). Two general metapopulation models and the core-satellite species hypothesis. *American Naturalist.* **142**. 17-41.

Hanski, I., Hansson, L. and Henttonen, H. (1991). Specialist predators, generalist predators, and the microtine rodent cycle. *Journal of Animal Ecology.* **60**. 353-367.

Hanski, I. and Henttonen, H. (1996). Predation on competing rodent species: a simple explanation of complex patterns. *Journal of Animal Ecology.* **65**. 220-232.

Hanski, I. and Korpimäki, E. (1995). Microtine rodent dynamics in northern Europe: parameterized models for the predator-prey interaction. *Ecology.* **76**. 840-850.

Hanski, I., Moilanen, A. and Gyllenberg, M. (1996). Minimum viable metapopulation size. *American Naturalist.* **147**. 527 -541.

Hanski, I., Turchin, P., Korpimäki, E. and Henttonen, H. (1993). Population oscillations of boreal rodents: regulation by mustelid predators leads to chaos. *Nature.* **364**. 232-235.

Hansson, L. (1971). Small rodent food, feeding and population dynamics: a comparison between granivorous and herbivorous species in Scandinavia. *Oikos.* **22**. 183-198.

Hansson, L. (1974). Small mammal productivity and consumption in spruce forest and reforestation in south Sweden. *Oikos.* **25**. 153-156.

Hansson, L. (1979). Food as a limiting factor for small rodent numbers. *Oecologia.* **37**. 297-314.

Hansson, L. (1988). Empiricism and modelling in small rodent research: how to partition efforts. *Oikos.* **52**. 150-155.

Hansson, L. (1992). Fitness and life history correlates of weight variations in small mammals. *Oikos.* **64**. 479-484.

Hansson, L. and Henttonen, H. (1985). Gradients in density variations of small rodents: the importance of latitude and snow cover. *Oecologia.* **67**. 394-402.

Harrison, S. (1991). Local extinction in a metapopulation context: an empirical evaluation. *Biological Journal of the Linnean Society.* **42**. 73 -88.

Hassell, M. (1975). Density-dependence in single-species populations. *Journal of Animal Ecology.* **144**. 283-295.

Hassell, M., Lawton, J. and May, R. (1976). Patterns of dynamical behaviour in single-species populations. *Journal of Animal Ecology.* **45**. 471- 486.

Hassell, M. and Varley , G. (1969). New inductive population model for insect parasites and its bearing on biological control. *Nature.* **223**. 1133 -1137.

Hassell, M.P. (1985). Insect natural enemies as regulatory factors. *Journal of Animal Ecology.* **54**. 323-334.

Hassell, M.P. (1987). Detecting regulation in patchily distributed animal populations. *Journal of Animal Ecology.* **56**. 705-713.

Hassell, M.P. and May, R.M. (1974). Aggregation in predators and insect parasites and its effect on stability. *Journal of Animal Ecology.* **43**. 567-594.

Hastings, A. (1990). Spatial heterogeneity and ecological models. *Ecology.* **71**. 426-428.

Hastings, A. and Harrison, S. (1994). Metapopulation dynamics and genetics. *Annual Review of Ecological Systems.* **25**. 167-188.

Haukioja, E., Kapiainen, K., Niemela, P. and Tuomi, J. (1983). Plant availability hypothesis and other explanations of herbivore cycles: complementary or exclusive alternatives? *Oikos.* **40**. 419-432.

Hawkins, S.J. (1983). Interactions of *Patella* and macroalgae with settling *Semibalanus balanoides* (L.). *Journal of Experimental Marine Biology and Ecology.* **71**. 55-72.

Hawkins, S.J. and Hartnoll, R.G. (1982). Settlement patterns of *Semibalanus balanoides* (L.) in the Isle of Man (1977-1981). *Journal of Experimental Marine Biology and Ecology.* **62**. 271-283.

Hayward, P., Nelson-Smith, T. and Shields, C. (1996). *Collins Pocket Guide. Sea Shores of Britain and Northern Europe.* Harper Collins, London.

Heikkila, J., Below, A. and Hanski, I. (1994). Synchronous dynamics of microtine rodent populations on islands in Lake Inari in northern Fennoscandia: evidence for regulation by mustelid predators. *Oikos.* **70**. 245-252.

Henettonen, H., Oksanen, T., Jortikka, A. and Haukisalmi, V. (1987). How much do weasels shape microtine cycles in the northern Fennoscandian taiga? *Oikos.* **50**. 353-365.

Henttonen, H., McGuire, A.D. and Hansson, L. (1985). Comparisons of amplitudes and spectral analyses of density variations in long-term data sets of *Clethrionomys* species. *Annales Zoologici Fennici.* **3**. 221-227.

Herbert, R. (in prep). Studies on the distribution, reproductive biology and general ecology of Lusitanian invertebrate species approaching their geographical limits on rocky shores along the central south coast of England. Ph.D. thesis, University of Southampton.

Hessen, D.O. and Nilssen, J.P. (1986). From phytoplankton to detritus and bacteria: the effects of short-term nutrient and fish perturbations in a eutrophic lake. *Archiv fur Hydrobiologie*. **105**. 273-284.

Hestbeck, J. (1982). Population regulation of cyclic mammals: the social fence hypothesis. *Oikos*. **39**. 157-163.

Hestbeck, J.B. (1988). Population regulation of cyclic mammals: a model of the social fence hypothesis. *Oikos*. **52**. 156-168.

Hilborn, R. and Mangel, M. (1997). *The Ecological Detective*. Princeton University Press, Princeton.

Hills, J.M. and Thomason, J.C. (1996). A multi-scale analysis of settlement density and pattern dynamics of the barnacle *Semibalanus balanoides*. *Marine Ecology Progress Series*. **138**. 103-115.

Hoffman, D.L. (1989). Settlement and recruitment patterns of a pedunculate barnacle. *Pollicipes polymerus* Sowerby, off La Jolla, California. *Journal of Experimental Marine Biology and Ecology*. **125**. 83-98.

Holling, C.S. (1959). Some characteristics of simple types of predation and parasitism. *Canadian Journal of Entomology*. **91**. 385-398.

Holling, C.S. (1965). The functional response of predators to prey density and its own role in mimicry and population regulation. *Memoirs of the Entomological Society of Canada*. **45**. 3-60.

Holm, E.R. (1990). Effects of density-dependence mortality on the relationship between recruitment and larval settlement. *Marine Ecology Progress Series*. **60**. 141-146.

Holyoak, M. and Lawler, S.P. (1996). The role of dispersal in predator-prey metapopulation dynamics. *Journal of Animal Ecology.* **65**. 652.

Holyoak, M. and Ray, C. (1999). A roadmap for metapopulation research. *Ecology Letters.* **2**. 273-275.

Hughes, R.N. and Drewett, D. (1985). A comparison of the foraging behaviour of dogwhelks, *Nucella lapillus* (L.), feeding on barnacles or mussels on the shore. *Journal of Molluscan Studies.* **51**. 73-77.

Hughes, R.N. and Griffiths, C.L. (1988). Self-thinning in barnacles and mussels: the geometry of packing. *American Naturalist.* **132**. 484-491.

Hughes, T.P. (1984). Population dynamics based on individual size rather than age: a general model with a coral reef example. *American Naturalist.* **123**. 778-795.

Hui, E. and Moyse, J. (1982). Settlement of *Elminius modestus* cyprids in contact with adult barnacles in the field. *Journal of the Marine Biological Association of the United Kingdom.* **62**. 447-482.

Huxel, G. (1999). On the influence of food quality in consumer-resource interactions. *Ecology Letters.* **2**. 256-261.

Hyder, K. (1999). Barnacle demography: a matrix modelling approach. Ph.D. thesis, University of Southampton.

Inchausti, P. and Ginzburg, L.R. (1998). Small mammal cycles in northern Europe: patterns and evidence for a maternal effect hypothesis. *Journal of Animal Ecology.* **67**. 180-194.

Innes, D.G.L. and Millar, J.S. (1990). Numbers of litters, litter size and survival in two species of microtine at two elevations. *Holarctic Ecology.* **13**. 207-216.

Innes, D.G.L. and Millar, J.S. (1994). Life histories of *Clethrionomys* and *Microtus* (Microtinae). *Mammal Review.* **24**. 179-207.

Irving, L. (1972). *Arctic Life of Birds and Mammals Including Man.* Springer-Verlag, New York.

Ives, A.R. and Settle, W.H. (1997). Metapopulation dynamics and pest control in agricultural systems. *American Naturalist.* **149**. 220-246.

Iwasa, Y. and Roughgarden, J. (1986). Interspecific competition among metapopulations with space-limited subpopulations. *Theoretical Population Biology.* **30**. 194-214.

Jannett, F.G. (1987). The density-dependent formation of extended maternal families of the montane vole, *Microtus montanus nanus. Behavioral Ecology and Sociobiology.* **3**. 245-263.

Järvinen, A. (1987). Microtine cycles and plant production: what is cause and effect. *Oikos.* **49**. 352-357.

Jarvis, J.U.M., Bennett, N.C. and Spinks, A.C. (1998). Food availability and foraging by wild colonies of Damaraland mole-rats (*Cryptomys damarensis*): implications for sociality. *Oecologia.* **113**. 290-298.

Jedrzejewski, W. and Jedrzejewski, B. (1996). Rodent cycles in relation to biomass of ground vegetation and predation. *Acta Theriologica.* **41**. 1-34.

Jensen, A.L. and Ball, R.C. (1970). Variation in the availability of food as a cause of fluctuations in predator and prey population densities. *Ecology.* **51**. 517-520.

Jensen, S.P. and Doncaster, C.P. (1999). Lethal toxins in non-preferred foods: how plant chemical defences can drive microtine cycles. *Journal of Theoretical Biology.* **199**. 63-85.

Johnson, L.E. and Strathmann, R.R. (1989). Settling barnacle larvae avoid substrata previously occupied by a mobile predator. *Journal of Experimental Marine Biology and Ecology.* **128**. 87-103.

Johnson, M. (2000). A re-evaluation of density-dependent population cycles in open systems. *American Naturalist.* **155**. 36-45.

Kallio, P. (1975). Kevo, Finland. In: *Structure and Function of Tundra Ecosystems. Ecological Bulletin.* T. Rosswall and O. W. Heal (eds.). Swedish Natural Science Research Council, Stockholm. p.193-223.

Keith, L.B. (1983). Role of food in hare population cycles. *Oikos.* **40**. 385-395.

Kendall, M.A., Bowman, R.S. and Williamson, P. (1982). Settlement patterns, density and stability in the barnacle *Balanus balanoides. Netherlands Journal of Sea Research.* **16**. 119-126.

Kendall, M.A., Bowmann, R.S., Williamson, P. and Lewis, J.R. (1985). Annual variation in the recruitment of *Semibalanus balanoides* on the North Yorkshire coast 1969-1981. *Journal of the Marine Biology Association of the United Kingdom.* **65**. 1009-1030.

Kenward, R. (1978). Hawks and doves: attack success and selection in Goshawk flights at Wood Pigeons. *Journal of Animal Ecology.* **47**. 449-460.

Kjelvik, S. (1973). Biomass and production in a willow thicket and a sub-Alpine birch forest, Hardangervidda, Norway. In: *Primary Production and Production Processes, in the Tundra Biome.* Proceedings of the International Biological Programme (IBP), Dublin. L.C. Bliss and F.E. Wielgolaski, (eds.). Tundra Biome Steering Committee. p. 115-122.

Klemola, T., Koivula, M., Korpimäki, E. and Norrdahl, K. (1997). Small mustelid predation slows population growth of *Microtus* voles: a predator reduction experiment. *Journal of Animal Ecology.* **66**. 607-614.

Klepal, W. (1987). A review of the comparative anatomy of the males in Cirripedes. *Oceanography Marine Biology Annual Review.* **25**. 285-351.

Klepal, W., Barnes, H. and Munn, E.A. (1972). The morphology and histology of the Cirripede penis. *Journal of Experimental Marine Biology and Ecology.* **10**. 243-265.

Knight-Jones, E.W. (1953). Laboratory experiments on gregariousness during settlement in *Balanus balanoides* and other barnacles. *Journal of Experimental Biology.* **30**. 584-599.

Knight-Jones, E.W. and Stevenson, J.P. (1950). Gregariousness during settlement in the barnacle *Elminius modestus* Darwin. *Journal of the Marine Biological Association of the United Kingdom.* **29**. 281-297.

Kokko, H. and Ebenhard, T. (1996). Measuring the strength of demographic stochasticity. *Journal of Theoretical Biology.* **183**. 169- 178.

Korpimäki, E. (1986). Predation causing synchronous decline phases in microtine and shrew populations in western Finland. *Oikos.* **46**. 124-127.

Korpimäki, E., Norrdahl, K. and Valkama, J. (1994). Reproductive investments under fluctuating predation risk: microtine rodents and small mustelids. *Evolutionary Ecology.* **8**. 357-368.

Koskela, E., Jonsson, P., Hartikainen, T. and Mappes, T. (1998). Limitation of reproductive success by food availability and litter size in the bank vole, *Clethrionomys glareolus. Proceedings of the Royal Society, London B.* **265**. 1129-1134.

Krebs, C.J. (1970). Microtus population biology: behavioural changes associated with the population cycle in *M. ochrogaster* and *M. Pennsylvanicus. Ecology.* **51**. 34-52.

Krebs, C.J. (1989). Methods for spatial maps. In: *Ecological Methodology.* Harper and Row, New York.

Krebs, C.J. (1994). *Ecology: the experimental analysis of distribution and abundance.* Harper Collins, New York.

Krebs, C.J., Gaines, M.S., Keller, B.L., Myers, J.H. and Tamarin, R.H. (1973). Population cycles in small rodents. *Science.* **179**. 35-41.

Kretschmar, M., Nisbet, R.M. and McCauley, E. (1993). A predator-prey model for zooplankton grazing on competing algal populations. *Theoretical Population Biology.* **44**. 32-66.

Křivan, V. (1996). Optimal foraging and predator-prey dynamics. *Theoretical Population Biology.* **49**. 265-290.

Křivan, V. and Sikder, A. (1999). Optimal foraging and predator-prey dynamics, II. *Theoretical Population Biology.* **55**. 111-126.

Kuussaari, M., Saccheri, I., Camara, M. and Hanski, I. (1998). Allee effect and population dynamics in the Glanville fritillary butterfly. *Oikos.* **82**. 384-392.

Laine, K. and Henttonen, H. (1983). The role of plant production in microtine cycles in northern Fennoscandia. *Oikos.* **40**. 407-418.

Lambin, X. (1994). Natal philopatry, competition for resources, and breeding avoidance in Towsend'd voles (*Microtus townsendii*). *Ecology.* **75**. 224-235.

Lamont, B.B., Klinkhammer, P.G.L. and Witkowski, E.T.F. (1993). Population fragmentation may reduce fertility to zero in *Banksia goodii*: a demonstration of the Allee effect. *Oecologia.* **94**. 446-450.

Lande, R. (1987). Extinction thresholds in demographic models of territorial populations. *American Naturalist.* **130**. 624 -635.

Lande, R. (1988). Genetics and demography in biological conservation. *Science.* **241**. 1455 -1460.

Lande, R. (1993). Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist.* **142**. 911-927.

Lande, R., Engen, S. and Saether, B.E. (1994). Optimal harvesting, economic discounting and extinction risk in fluctuating populations. *Nature.* **372**. 88-90.

Larman, V.N. and Gabbott, P.A. (1975). Settlement of cyprid larvae of *Balanus balanoides* and *Elminius modestus* induced by extracts of adult barnacles and other marine animals. *Journal of the Marine Biology Association of the United Kingdom.* **55**. 183-190.

Lawton, J.H. (1994). Population dynamic principles. *Philosophical Transactions of the Royal Society London, Series B.* **344**. 61-68.

Le Tournex, F. and Bourget, E. (1992). Hydrodynamics and behaviour: transport processes in marine invertebrate larvae. *Trends in Ecology and Evolution.* **7**. 288-289.

Leibold, M. (1989). Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *American Naturalist.* **134**. 922-949.

Leigh, E.G. (1981). The average lifetime of a population in a varying environment. *Journal of Theoretical Biology.* **90**. 213-239.

Leslie, P.H. (1948). Some further notes on the use of matrices in population mathematics. *Biometrika.* **35**. 213-245.

Levins, R. (1969). Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin Entomological Society of America.* **15**. 237- 240.

Levins, R. (1970). Extinction. In: *Lectures on Mathematics: Some Mathematical Questions in Biology.* The American Mathematical Society, Rhode Island. p.75 - 107.

Lewis, M.A. and Kareiva, P. (1993). Allee dynamics and the spread of invading organisms. *Theoretical Population Biology.* **43**. 141-158.

Lidicker, W.Z. (1979). Analysis of two freely-growing enclosed populations of the California vole. *Journal of Mammalogy.* **60**. 447-466.

Lindroth, R.L. and Batzli, G.O. (1984). Food habitats of the meadow vole (*Microtus pennsylvanicus*) in bluegrass and prairie habitats. *Journal of Mammalogy.* **65**. 600-606.

Lloyd, M. (1967). Mean crowding. *Journal of Animal Ecology.* **36**. 1-29.

Lomnicki, A. (1988). The place of modelling in ecology. *Oikos.* **52**. 139-142.

Lotka, A.J. (1925). *Elements of Physical Biology.* Williams and Wilkins, Baltimore.

Lotka, A.J. (1932). The growth of mixed populations: two species competing for a common food supply. *Journal of the Washington Academy of Sciences.* **22**. 461-469.

Lucas, M.I., Walker, G., Holland, D.L. and Crisp, D.J. (1979). An energy budget for the free-swimming and metamorphosing larvae of *Balanus balanoides* (Crustacea: Cirripedia). *Marine Biology.* **55**. 221-229.

Luck, R.F. (1990). Evaluation of natural enemies for biological control: a behavioural approach. *Trends in Ecology and Evolution.* **5**. 196-199.

Luckinbill, L.S. (1974). The effects of space and enrichment on a predator-prey system. *Ecology*. **55**. 1142-1147.

Lundberg, A. (1979). Residency, migration and compromise: adaptations to nest-site scarcity and food specialization in three Fennoscandian owl species. *Oecologia*. **41**. 273-281.

Lundberg, P. (1988). Functional response of a small mammalian herbivore: the disc equation revisited. *Journal of Animal Ecology*. **57**. 999-1006.

Lundberg, P. and Fryxell, J.M. (1995). Expected population density versus productivity in ratio-dependent and prey-dependent models. *American Naturalist*. **146**. 153-161.

MacArthur, R.H. and Wilson, E.O. (1967). *The Theory of Island Biogeography*. Princeton University Press, Princeton.

Macdonald, D. and Barrett, P. (1993). *Collins Field Guide. Mammals of Britain and Europe*. Harper Collins, London.

Mackin-Rogalska, R. and Nabago, L. (1990). Geographical variation in cyclic periodicity and synchrony in the common vole, *Microtus arvalis*. *Oikos*. **59**. 343-348.

Malthus, T.R. (1798). *An Essay on the Principles of Populations*. Johnson, London.

Marcström, V., Kenward, R.E. and Engren, E. (1988). The impact of predation on boreal teraonids during vole cycles: an experimental study. *Journal of Animal Ecology*. **57**. 859-872.

May, R., Hassell , M., Anderson, R. and Tonkyn , D. (1981). Density dependence in host-parasitoid models. *Journal of Animal Ecology*. **50**. 855 -865.

May, R.M. (1972). Limit cycles in predator-prey communities. *Science.* **177**. 900-902.

May, R.M. (1973). *Stability and Complexity in Model Ecosystems.* University Press, Princeton.

May, R.M. (1976). Simple mathematical models with very complicated dynamics. *Nature.* **261**. 459-467.

May, R.M. (1981). *Theoretical Ecology: principles and applications.* Blackwell Scientific Publications, Oxford.

May, R.M. (1991). The role of ecological theory in planning reintroduction of endangered species. *Symposium of the Zoological Society, London.* **62**. 145-163.

May, R.M. (1999). Crash test for real. *Nature.* **398**. 371-372.

May, R.M. and Oster, G.F. (1976). Bifurcations and dynamic complexity in simple ecological models. *American Naturalist.* **110**. 573-599.

Maynard Smith, J. and M, S. (1973). The stability of predator-prey systems. *Ecology.* **54**. 384- 391.

Maynard-Smith, J. (1974). *Models in Ecology.* Cambridge University Press, Cambridge.

McAllister, C.D., LeBrasseur, R.J. and Parsons, T.R. (1972). Stability of enriched aquatic ecosystems. *Science.* **175**. 562-564.

McCarthy, M.A. (1997). The Allee effect, finding mates and theoretical models. *Ecological Modelling.* **103**. 99-102.

McCarthy, M.A., Ginzburg, L.R. and Akçakaya, H.R. (1995). Predator interference across trophic chains. *Ecology.* **76**. 1310-1319.

McCauley, E. and Murdoch, W.M. (1987). Cyclic and stable populations: plankton as a paradigm. *American Naturalist.* **129**. 98-121.

McCauley, E. and Murdoch, W.M. (1990). Predator-prey dynamics in environments rich and poor in nutrients. *Nature.* **343**. 455-457.

McCauley, E., Nisbet, R.M., Murdoch, W.W., deRoos, A.M. and Gurney, W.S.C. (1999). Large-amplitude cycles of *Daphnia* and its algal prey in enriched environments. *Nature.* **402**. 653-656.

McCauley, E., Wilson, W.G. and deRoos, A.M. (1993). Dynamics of age structured and spatially structured predator-prey interactions: individual based models and population level formulations. *American Naturalist.* **142**. 412-442.

McGlade, J. (1999). *Advanced Ecological Theory: principles and applications.* Blackwell Science Ltd, Oxford.

McShea, W.J. and Madison, D.M. (1984). Communal nesting by reproductively active females in a spring population of *Microtus pennsylvanicus. Canadian Journal of Zoology.* **62**. 344-346.

Menge, B.A. (2000). Recruitment vs. post-recruitment processes as determinants of barnacle population abundance. *Ecological Monographs.* **70**. 265-288.

Middleton, D.A.J. and Nisbet, R.M. (1997). Population persistence time: estimates, models and mechanisms. *Ecological Applications.* **7**. 107-117.

Miller, K.M. and Carefoot, T.H. (1989). The role of spatial and size refuges in the interaction between juvenile barnacles and grazing limpets. *Journal of Experimental Marine Biology and Ecology.* 134. 157-174.

Milton, P. (1983). Biology of littoral blenniid fishes on the coast of south-west England. *Journal of the Marine Biological Association of the United Kingdom.* **63**. 223-237.

Minchinton, T.E. (1995). Demographic consequences of variation in recruitment and conspecific cover to populations of sessile marine invertebrates. Ph.D. thesis, University of Sydney.

Minchinton, T.E. and Scheibling, R.E. (1991). The influence of larval supply and settlement on the population structure of barnacles. *Ecology.* **72**. 1867-1879.

Minchinton, T.E. and Scheibling, R.E. (1993a). Free space availability and larval substratum selection as determinants of barnacle population structure in developing rocky intertidal community. *Marine Ecology Progress Series.* **95**. 233-244.

Minchinton, T.E. and Scheibling, R.E. (1993b). Variations in sampling procedure and frequency affect estimates of recruitment of barnacles. *Marine Ecology Progress Series.* **99**. 83-88.

Miron, G., Boudreau, B. and Bourget, E. (1999). Intertidal barnacle distribution: a case study using multiple working hypotheses. *Marine Ecology Progress Series.* **189**. 205-219.

Moen, J. (1990). Summer grazing by voles and lemmings upon subarctic snow-bed and tall herb meadow vegetation - an enclosure experiment. *Holarctic Ecology.* **13**. 316-324.

Moore, H.B. (1934). The biology of Balanus balanoides. I. Growth rate and its relation to size, season and tidal level.. *Journal of the Marine Biological Association of the United Kingdom.* **19**, 851-868.

Moore, H.B. (1935). The biology of *Balanus balanoides* III. the soft parts. *Journal of the Marine Biological Association of the United Kingdom.* **20**. 263-277.

Moran, P.A.P. (1952). The statistical analysis of game-bird records. *Journal of Animal Ecology.* **21**. 152-158.

Moyse, J. and Hui, E. (1981). Avoidance by *Balanus balanoides* cyprids of settlement on conspecific adults. *Journal of the Marine Biological Association of the United Kingdom.* **61**. 449-460.

Murdoch, W.W. (1971). The developmental response of predators to changes in prey density. *Ecology.* **52**. 132-137.

Murdock, G.R. and Currey, J.D. (1978). Strength and design of the shell of the two ecologically distinct barnacles *Balanus balanus* and *Semibalanus* (Balanus) *balanoides* (Cirripedia). *Biological Bulletin.* **155**. 169-192.

Murray, J.D. (1993). *Mathematical Biology.* Springer-Verlag, Berlin.

Myers, R.A., Barrowman, N.J., Hutchings, J.A. and Rosenberg, A.A. (1995). Population dynamics of exploited fish stocks at low population levels. *Science.* **269**. 1106-1108.

Myerscough, M.R., Darwen, M.J. and Hogarth, W.L. (1996). Stability, persistence and structural stability in a classical predator-prey model. *Ecological Modelling.* **89**. 31-42.

Myllymaki, A. (1977a). Demographic mechanisms in the fluctuating populations of the field vole *Microtus agrestis. Oikos.* **29**. 468-493.

Myllymaki, A. (1977b). Intraspecific competition and home range dynamics in the field vole *Microtus agrestis. Oikos.* **29**. 553-569.

Myrberget, S. (1973). Geographical synchronism of cycles of small rodents in Norway. *Oikos.* **24**. 220-224.

Myrberget, S. (1986). A note on cycles in plant production and microtine populations. *Oikos.* **46**. 264-267.

Nee, S. (1994). How populations persist. *Nature.* **367**. 123-124.

Nicholson, A.J. (1958). Dynamics of insect populations. *Annual Review of Entomology.* **3**. 107-136.

Nicholson, A.J. and Bailey, V.A. (1935). The balance of animal populations. *Proceedings of the Zoological Society of London.* **3**. 293-299.

Nisbet, R.M., de Roos, A.M., Wilson, W.G. and Snyder, R.E. (1998). Discrete consumers, small scale resource heterogeneity, and population stability. *Ecology Letters.* **1**. 34-37.

Nisbet, R.M. and Gurney, W.S.C. (1982). *Modelling Fluctuating Populations.* John Wiley and Sons, Chichester.

Norrdahl, K. and Korpimäki, E. (1998). Does mobility or sex of voles affect risk of predation by mammalian predators? *Ecology.* **79**(1). 226-232.

Oksanen, L. and Ericson, L. (1987). Dynamics of tundra and taiga populations of herbaceous plants in relation to the Tihomirov-Fretwell and Kalela-Tast hypotheses. *Oikos.* **50**. 381-388.

Oksanen, L., Oksanen, T., Lukkari, A. and Siren, S. (1987). The role of phenol-based inducible defence in the interaction between tundra populations of the vole *Clethrionomys rufocanus* and the dwarf shrub *Vaccinium myrtillus. Oikos.* **50**. 371-380.

Oksanen, L.O. and Oksanen, T. (1981). Lemmings (*Lemmus lemmus*) and grey-sided voles (*Clethrionomys rufocanus*) in interaction with their resources and predators on Finnmarlsvidda, northern Norway. *Reports from the Kevo Subarctic Research Station.* **17**. 7-31.

Oreskes, N., Shrader-Frechette, K. and Belitz, K. (1994). Verification, validation and confirmation of numerical models on the earth sciences. *Science.* **263**. 641-646.

O'Riordan, R.M., Myers, A.A. and Cross, T.F. (1995). The reproductive cycles of *Chthamalus stellatus* (Poli) and *C. montagui* Southward in south-western Ireland. *Journal of Experimental Marine Biology and Ecology.* **190**. 17-38.

O'Riordan, R.M., Myers, A.A., McGrath, D., Delany, J. and Power, A.M. (1999). The sizes at settlement in natural populations of the cyprids of *Chthamalus montagui* and *C. stellatus*. *Journal of the Marine Biological Association of the United Kingdom.* **79**. 365-366.

Pagel, M. and Payne, J.H. (1996). How migration affects estimation of extinction threshold. *Oikos.* **76**. 323-329.

Pascual, M.A. and Kareiva, P. (1996). Predicting the outcome of competition using experimental data: maximum likelihood and Bayesian approaches. *Ecology.* **77**. 337-349.

Pearl, L. and Reed, L.J. (1920). The rate of growth of the population of the United States since 1790 and its mathematical representation. *Proceedings of the National Academy of Science.* **6**. 275-288.

Pielou, E.C. (1960). A single mechanism to account for regular, random and aggregated populations. *Journal of Ecology.* **48**. 575-584.

Pielou, E.C. (1962). The use of plant-to-neighbour distances for the detection of competition. *Journal of Ecology.* **50**. 357-367.

Pielou, E.C. (1969). *An Introduction to Mathematical Ecology.* Wiley, New York.

Pimm, S.L., Jones, H.L. and Diamond, J. (1988). On the risk of extinction. *American Naturalist.* **132**. 757-785.

Pineda, J. (1994). Spatial and temporal patterns in barnacle settlement rate along a southern California rocky shore. *Marine Ecology Progress Series.* **107**. 125-138.

Pitelka, F.A. (1973). Cyclic patterns in lemming populations near Barrow, Alaska. In: *Alaska Arctic Tundra*. E. Britton (ed.). Arctic Institute of North America, Washington. p.199-215.

Possingham, H.P., Tuljapurkar, S., Roughgarden, J. and Wilks, M. (1994). Population cycling in space-limited organisms subject to density-dependent predation. *American Naturalist*. **143**(4). 563-582.

Power, A.M., Piyapattanakorn, S., O'Riordan, R.M., Iyengar, A., Myers, A., Hawkins, S.J., Delany, J., McGrath, D., and Maclean, N. (1999). Verification of cyprid size as a tool in the identification of two European species of *Chthamalus* barnacles using mtDNA-RFLP analysis. *Marine Ecological Progress Series*. **191**. 251-256.

Putman, R.J. and Wratten, S.D. (1984). *Principles in Ecology*. Croomhelm, London.

Raimondi, P.T. (1988). Settlement cues and determination of the vertical limit of an intertidal barnacle. *Ecology*. **69**. 400-407.

Raimondi, P.T. (1990). Patterns, mechanisms, consequences of variability in settlement and recruitment of an intertidal barnacle. *Ecological Monographs*. **60**. 283-309.

Rainbow, P.S. (1984). An introduction into the biology of British barnacles. *Field Studies*. **6**. 1-51.

Raup, D.M. (1984). Death of Species. In: *Extinctions*. M. H. Nitecki (ed.). University of Chicago Press, Chicago.

Remmert, H. (1980). *Arctic Animal Ecology*. Springer-Verlag, Berlin.

Renshaw, E. (1995). *Modelling Biological Populations in Space and Time*. Cambridge University Press, Cambridge.

Riebesell, J.F. (1974). Paradox of enrichment in competitive systems. *Ecology.* **55**. 183-187.

Ripley, B.D. (1985). Analyses of nest spacings. In: *Statistics in Ornithology.* B.J.T. Morgan and P. M. North (eds.). Springer, Berlin Heidelberg, New York. p.151-158.

Rittschof, D., Branscomb, E.S. and Costlow, J.D. (1984). Settlement and behaviour in relation to flow and surface in larval barnacles, *Balanus amphitrite* (Darwin). *Journal of Experimental Marine Biology and Ecology.* **82**. 131-146.

Rodd, H.F. and Boonstra, R. (1988). Effect of adult meadow voles, *Microtus pennsylvanicus*, on young conspecifics in field populations. *Journal of Animal Ecology.* **57**. 755-770.

Rodgers, A.R. and Lewis, M.C. (1985). Diet selection in Arctic lemmings (*Lemmus sibericus* and *Dicrostonyx groenlandicus)*: food preferences. *Canadian Journal of Zoology.* **63**. 1161-1173.

Rosenzweig, M.L. (1969). Why the prey curve has a hump. *American Naturalist.* **103**. 81-87.

Rosenzweig, M.L. (1971). Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science.* **171**. 385-387.

Rosswall, T. and Heal, O.W. (1975). *Structure and Function of Tundra Ecosystems.* Sundt & Co Offset, Stockholm.

Roughgarden, J., Gaines, S. and Iwasa, Y. (1984). Dynamics and evolution of marine populations with pelagic larval dispersal. In: *Exploitation of Marine Communities.* R. M. May (ed.). Springer-Verlag, New York. p.111-128.

Roughgarden, J., Gaines, S.D. and Pacala, S.W. (1987). Supply side ecology: The role of physical transport processes. In: *Organisation of communities: past and present*. J. H. R. Gee and P. S. Giller (eds.). p.491-518.

Roughgarden, J. and Iwasa, Y. (1986). Dynamics of a metapopulation with space-limited subpopulations. *Theoretical population biology*. **29**. 235-261.

Roughgarden, J., Iwasa, Y. and Baxter, C. (1985). Demographic theory for an open marine population with space-limited recruitment. *Ecology*. **66**. 54-67.

Rousi, M., Tahvanainen, J., Henttonen, H. and Uotila, I. (1993). Effects of shading and fertilization on resistance of winter dormant birch (*Betula pendula*) to voles and hares. *Ecology*. **74**. 30-38.

Royama, T. (1981). Evaluation of mortality factors in insect life table analysis. *Ecological Monographs*. **543**. 429-462.

Ruxton, G.D. and Gurney, W.S.C. (1992). The interpretation of tests for ratio-dependence. *Oikos*. **65**. 334-335.

Salman, S.D. (1982). Seasonal and short-term variations in abundance of barnacle larvae near the south-west of the Isle of Man. *Estuarine, Coastal and Shelf Science*. **15**. 241-253.

Sanders, E.H., Gardner, P.D., Berger, P.J. and Negus, N.C. (1981). 6-Methoxybenzoxazolinone: A plant derivative that stimulates reproduction in *Microtus montanus*. *Science*. **214**. 67-69.

Sanford, E., Bermudez, D., Bertness, M.D. and Gaines, S.D. (1994). Flow, food supply and acorn barnacle population dynamics. *Marine Ecology Progress Series*. **104**. 49-62.

Sarnelle, O. (1994). Inferring process from pattern: tropic level abundances and imbedded interactions. *Ecology*. **75**. 1835-1841.

Satchell, E.R. and Farrell, T.M. (1993). Effects of settlement density on spatial arrangement in four intertidal barnacles. *Marine Biology.* **116**. 241-245.

Scheffer, M. and De Boer, R.J. (1995). Implications of spatial heterogeneity for the paradox of enrichment. *Ecology.* **76**. 2270-2277.

Scheltema, R.S. (1971). Long-distance dispersal by planktonic larvae of shoal-water marine benthic invertebrates among central Pacific islands. *Bulletin of Marine Science.* **39**. 241-256.

Schemske, D.W., Husband, B.C., Ruckelshaus, M.H., Goodwille, C., Parker, I.M. and Bishop, J.G. (1994). Evaluating approaches to the conservation of rare and endangered plants. *Ecology.* **73**. 584-606.

Schmitz, O.J., Beckerman, A.P. and Litman, S. (1997). Functional responses of adaptive consumers and community stability with emphasis on the dynamics of plant-herbivore systems. *Evolutionary Ecology.* **11**. 773-784.

Schoener, T.W. (1991). Extinction and the nature of the metapopulation: a case study. *Acta Ecologica.* **12**. 53-75.

Schwinning, S. and Parsons, A.J. (1996). Analysis of the coexistence mechanisms for grasses and legumes in grazing systems. *Journal of Ecology.* **84**. 799-813.

Selås, V. (1997). Cyclic population fluctuations of herbivores as an effect of cyclic seed cropping of plants: the mast depression hypothesis. *Oikos.* **80**. 257-268.

Shaffer, M.L. (1981). Minimum population sizes for species conservation. *Biological Conservation.* **31**. 131-134.

Shanks, A.L. (1986). Tidal periodicity in the daily settlement of intertidal barnacle larvae and an hypothesised mechanism for the cross-shelf transport of cyprids. *Biological Bulletin.* **170**. 429-440.

Shanks, A.L. and Wright, W.G. (1986). Adding teeth to wave action: the destructive effects of wave-borne rocks on intertidal organisms. *Oikos.* **69**. 420-428.

Shelford, V.E. (1943). The abundance of the collard lemming (*Dicrostonyx groenlandicus* (tr) var. *Richardsoni* mer.) in the Churchill area, 1929 to 1940. *Ecology.* **24**. 472-484.

Shkedy, Y. and Roughgarden, J. (1997). Barnacle recruitment and population dynamics predicted from coastal upwelling. *Oikos.* **80**. 487-498.

Shkedy, Y., Safriel, U.N. and Keasar, T. (1995). Life-history of *Balanus amphitrite* and *Chthamalus stellatus* recruits to settlement panels in the Mediterranean coast of Israel. *Israel Journal of Zoology.* **41**. 147-161.

Sih, A., Crowley, P., McPeek, M., Petranka, J. and Strohmeier, K. (1985). Predation, competition, and prey communities: A review of field experiments. *Annual Review of Ecology and Systematics.* **16**. 269-311.

Simberloff, D. (1988). The contribution of population and community biology to conservation science. *Annual Review of Ecology and Systematics.* **19**. 473-511.

Sinclair, A.R.E. and Pech, R.B. (1996). Density dependence, stochasticity, compensation and predator regulation. *Oikos.* **75**. 164-173.

Sinclair, D.F. (1985). On tests of spatial randomness using mean nearest neighbour distance. *Ecology.* **66**. 1084-1085.

Smirnov, V.S. and Tokmakova, S.G. (1971). Influence of consumers on natural phytoceois production variation. In: *Biological Production of Tundra.* Proceedings of the International Biological Programme (IBP) Tundra Biome, Leningrad, USSR. F.E. Wielgolaski, and T.H. Rosswall, (eds.). Tundra Biome Steering Committee. p 122-127.

Smith, A.T. and Peacock, M.M. (1990). Conspecific attraction and the determination of metapopulation colonization rates. *Conservation Biology.* **40**. 320-323.

Sokal, R.R. and Rohlf, F.J. (1994). *Biometry.* W.H. Freeman and Company, New York.

Sonesson, M. and Callaghan, T.V. (1991). Strategies of survival in plants of the Fennoscandian tundra. *Arctic.* **44**. 95-105.

Southwood, A.J. (1976). On the taxonomic status and distribution of *Chthamalus stellatus* (Cirripedia) in the north-east Atlantic region with a key to the common intertidal barnacles of Britain. *Journal of the Marine Biological Association of the United Kingdom.* **56**. 1007-1028.

Stenseth, N.C. (1988). The social fence hypothesis: a critique. *Oikos.* **52**. 169-177.

Stenseth, N.C. (1993). Mathematical models for terrestrial populations. In: *Human Impact on Self-Recruiting Populations.* The Kongsvoll Symposium. G. Sundnes (ed.). Tapir Publishing, Trondheim. p.263-263.

Stenseth, N.C. and Antonsen, J. (1988). Density dependence and the microtine cycles II. A discrete time model for a synchronously reproducing population. *Oikos.* **52**. 207-211.

Stenseth, N.C., Bondrup-Nielsen, S. and Ims, R.A. (1988). A population dynamics model for *Clethrionomys*: sexual maturation, spacing behaviour and dispersal. *Oikos.* **52**. 186-193.

Stenseth, N.C., Hansson, L., Myllymaki, A., Andersson, M. and Katila, J. (1977). General models for the population dynamics of the field vole *Microtus agrestis* in central Scandinavia. *Oikos.* **29**. 616-642.

Stenseth, N.C. and Ims, R.A. (1993). *The Biology of Lemmings.* Academic Press, New York.

Stephan, T. and Wissel, C. (1999). The extinction risk of a population exploiting a resource. *Ecological Modelling*. **115**. 217-225.

Stephens, D.W. and Krebs, J.R. (1986). *Foraging Theory.* Princeton University Press, Princeton.

Stephens, P.A. and Sutherland, W.J. (1999). Consequences of the Allee effect for behaviour, ecology and conservation. *Trends in Ecology and Evolution.* **14**. 401-405.

Stow, C.A., Carpenter, S.R. and Cottingham, K.L. (1995). Resource vs. ratio-dependent consumer-resource models: A Bayesian perspective. *Ecology.* **76**. 1986-1990.

Strong, D.R. (1990). Realistic models of persistence. *Ecology.* **71**. 421.

Stubbings, H.G. (1975). *Balanus balanoides.* Liverpool University Press, Liverpool.

Sutherland, J.P. (1990). Recruitment regulates demographic variation in a tropical intertidal barnacle. *Ecology.* **71**. 955-973.

Sutherland, W.J. (1996). *From Individual Behaviour to Population Ecology.* Oxford University Press, Liverpool.

Tahvanainen, J., Nimela, P. and Henttonen, H. (1991). Chemical aspects of herbivory in boreal forest feeding by small rodents, hares and cerides. In: *Plant Defences against Mammalian Herbivory.* T. Palo and C. Robbins (eds.). CRC Press, Boca Raton, FL. p.115-131.

Tanner, J.T. (1975). The stability and intrinsic growth rates of prey and predator populations. *Ecology.* **56**. 855-867.

Tast, J. and Kalela, O. (1971). Comparisons between rodent cycles and plant production in Finnish Lapland. *Annales Academiae Scientiarum Fennicae. Series A, IV. Biology.* **186**. 1-14.

Thompson, R.C., Norton, T.A. and Hawkins, S.J. (1998). The influence of epilithic microbial films on the settlement of *Semibalanus balanoides* cyprids - a comparison between laboratory and field experiments. *Hydrobiologia.* **375/376**. 203-216.

Tinbergen, L. (1960). The natural control of insects in pinewoods. I. Factors influencing the intensity of predation by songbirds. *Archives Neerlandaises de Zoologie.* **13**. 265-343.

Turchin, P. (1993). Chaos and stability in rodent population dynamics: evidence from nonlinear time series analysis. *Oikos.* **68**. 167-172.

Turchin, P. and Batzli, G.O. (2000 in press). Availability of food and the population dynamics of arvicoline rodents. *Ecology.*

Turchin, P., Oksanen, L., Ekerholm, P., Oksanen, T. and Henttonen, H. (2000). Are lemmings prey or predators? *Nature.* **405**. 562-565.

Uchmanski, J. (1999). What promotes persistence of a single population: an individual-based model. *Ecological Modelling.* **115**. 227-241.

Veilleux, B.G. (1979). An analysis of the predatory interaction between *Paramecium* and *Didinium. Journal of Animal Ecology.* **48**. 787-803.

Verboom, J., Schotman, A., Opdam, P. and Metz, J.A.J. (1991). European nuthatch metapopulations in fragmented agricultural landscape. *Oikos.* **61**. 149-156.

Verhulst, P.F. (1888). Notice sur la loi que la population suit dans san accroiscement. *Correspondance Mathematique et Phsique.* **10**. 113-121.

Volterra, V. (1926). Fluctuations in the abundance of a species considered mathematically. *Nature.* **118**. 558-560.

Walde, S.J. (1994). Immigration and the dynamics of a predator-prey interaction in biological control. *Journal of Animal Ecology.* **63**. 337-346.

Wang, G., Liang, X. and Wang, F. (1999). The competitive dynamics of populations subject to an Allee effect. *Ecological Modelling.* **124**. 183-192.

Ware, F.J. and Hartnoll, R.G. (1996). Desiccation tolerance of the barnacle *Semibalanus balanoides* (L) in relation to shore height (Cirripedia, Thoracica). *Crustaceana.* **96**. 321-329.

Watson, A. (1956). Ecological notes on the Lemmings *Lemmus trimucronatus* and *Dicrostonyx groenlandicus* in Baffin Island. *Journal of Animal Ecology.* **25**. 289-302.

Way, M. and Banks, C. (1967). Intra-specific mechanisms in relation to the natural regulation of numbers of *Aphis fabae*. *Annals of Applied Biology.* **59**. 189-205.

Wells, H., Strauss, E.G., Rutter, M.A. and Wells, P.H. (1998). Mate location, population growth and species extinction. *Biological Conservation.* **86**. 317-324.

Wells, H., Wells, P.H. and Rogers, S.H. (1990). The importance of overwinter aggregation for the reproductive success of monarch butterflies (*Danaus plexippus* L.). *Journal of Theoretical Biology.* **147**. 115-131.

Wethey, D.S. (1983). Intrapopulation variation in growth of sessile organisms: natural populations of the intertidal barnacle *Balanus balanoides*. *Oikos.* **40**. 14-23.

Wethey, D.S. (1984a). Effects of crowding on fecundity in barnacles: *Semibalanus (Balanus) balanoides, Balanus glandula,* and *Chthamalus dalli*. *Canadian Journal of Zoology.* **62**. 1788-1795.

Wethey, D.S. (1984b). Spatial pattern in barnacle settlement: day to day changes during the settlement season. *Journal of the Marine Biology Association of the United Kingdom.* **64**. 687-698.

Wielgolaski, F.E. (1971). Vegetation types and primary production in Tundra. In: *Biological Production of Tundra*. Proceedings of the International Biological Programme (IBP) Tundra Biome, Leningrad, USSR. F.E. Wielgolaski, and T.H. Rosswall, (eds.). Tundra Biome Steering Committee. p 9-34.

Wielgolaski, F.E. and Rosswall, T.H. (1971). *Biological Production of Tundra*. Proceedings of the International Biological Programme (IBP) Tundra Biome, Leningrad, USSR. F.E. Wielgolaski, and T.H. Rosswall, (eds.). Tundra Biome Steering Committee.

Wissel, C. and Zaschke, S.H. (1994). Stochastic birth and death processes describing minimum viable populations. *Ecological Modelling*. **75-76**. 193-201.

Wollkind, D.J., Collings, J.B. and Logan, J.A. (1988). Metastability in a temperature-dependent model system for predator-prey mite outbreak interactions on fruit trees. *Bulletin of Mathematical Biology*. **50**. 379-409.

Wolff, J.O. (1992). Parents suppress reproduction and stimulate dispersal in opposite-sex juvenile white-footed mice. *Nature*. **359**. 409-410.

Wolff, J.O. (1997). Population regulation in mammals: an evolutionary perspective. *Journal of Animal Ecology*. **66**. 1-13.

Wu, R.S.S. (1980). The effects of crowding on the energetics of the barnacle *Balanus glandula* Darwin. *Canadian Journal of Zoology*. **58**. 566-599.

Wu, R.S.S. (1981). The effect of aggregation on the breeding in the barnacle *Balanus-glandula* Darwin. *Canadian Journal of Zoology*. **59**. 890-892.

Yodzis, P. and Innes, S. (1992). Body size and consumer-resource dynamics. *American Naturalist*. **139**. 1151-1175.

Yule, A.B. and Crisp, D.J. (1983). Adhesion of cypris larvae of the barnacle *Balanus balanoides* to clean arthropodin treated surfaces. *Journal of the Marine Biological Association of the United Kingdom.* **63**. 261-271.

Yule, A.B. and Walker, G. (1985). Settlement of *Balanus balanoides* - the effect of cyprid antennular secretion. *Journal of the Marine Biological Association of the United Kingdom.* **65**. 707-712.