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A theoretical and experimental study of Allee effects

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A THEORETICAL AND EXPERIMENTAL STUDY OF ALLEE EFFECTS

A Dissertation

Presented to

The Faculty of the School of Marine Science

The College of William and Mary in Virginia

In Partial Fulfillment

of the Requirements for the Degree of

Doctor of Philosophy

by

Joanna Gascoigne

2003

APPROVAL SHEET

This dissertation is submitted in partial fulfillment of

the requirements for the degree of

Doctor of Philosophy

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Approved August 2003

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To my family

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ABSTRACT

Allee effects occur when individual fitness suffers at low population size or density. This can lead to reduced population growth rate, which can in turn lead to a critical density below which the population goes extinct. Allee effects are important for conservation and management, but are poorly understood theoretically and in real populations. I examine Allee effects and their population consequences in models and in the field.

Chapter 1 is a review of evidence for Allee effects in marine systems. There is little firm evidence of Allee effects, perhaps for methodological reasons, but there are suggestive observations in broadcast spawners and heavily exploited populations. In theoretical models, Allee effects interact with exploitation to cause non-linear population collapse.

Chapter 2 examines the population consequences of Allee effects in juvenile survival and reproduction using a two-stage matrix model. Critical densities are higher in reproductive Allee effects than in juvenile survival Allee effects, making reproductive Allee effects more severe (higher extinction probability). In terms of the critical Allee effect threshold, reproductive Allee effects are more severe in *r*-selected populations, while juvenile survival Allee effects are more severe in *K*-selected populations. For populations with negative density dependence, there is a maximum critical Allee threshold, above which a population of any density goes extinct. Critical thresholds are reduced (Allee strength) or increased (density) by increases in mortality or time to maturity or decreases in reproductive output. Adding two Allee effects together has unpredictable consequences depending on the life history, while adding negative density dependence makes Allee effects more severe. The *K*-selected life history model often took many time-steps to equilibrate. The *r*-selected model could show stable, large-amplitude oscillations under circumstances not previously reported in the literature.

Chapter 3 presents the results of a field test of Allee effects. In the queen conch *Strombus gigas*, a heavily exploited marine gastropod, mating and egg production are reduced in low-density areas. This could be due to low encounter rates, habitat quality or ontogenetic differences. To distinguish between these hypotheses, mature conch were translocated between high and low density sites. Conch were at equal high density in all enclosures, but high source-site density produced higher reproductive activity. Conch from high-density source sites also had thicker shell lips, indicating that they were older. These data reject the hypothesis of an Allee effect; possibly reproduction is delayed after morphological maturity. In model simulations, a reproductive Allee effect and delayed reproduction could both produce non-linear population collapse.

Chapter 4 sets out a theoretical framework for Allee effects driven by predation. Predators can generate an Allee effect in prey if they have a Type II functional response and the aggregative or numerical response is not Type III (or *vice versa*). A literature review reveals several unrecognised examples of predation-driven Allee effects from the literature, mainly from systems that have been perturbed by exploitation or introduced predators. This mechanism for Allee effects does not arise from the specifics of prey life history, which makes it difficult to predict and prepare for.

A THEORETICAL AND EXPERIMENTAL STUDY OF ALLEE EFFECTS

CHAPTER 1

ALLEE EFFECTS IN MARINE SYSTEMS

ABSTRACT

A population with Allee effects has positive density dependence in fitness or in the population growth rate at low population size or density, which can result in a critical threshold below which the population goes extinct. I argue that Allee effects are intrinsically feasible in marine populations and metapopulations. I model the population consequences of Allee effects and show that increases in mortality interact with critical Allee thresholds, such that an Allee effect with no population consequences at low mortality can drive a population to extinction when mortality is increased. I predict that Allee effects are likely to be most apparent in exploited species, because populations that have been exposed to periods of low population size or density over evolutionary time are likely to have evolved mechanisms to avoid Allee effects, while populations that have been large and stable prior to exploitation may have latent Allee effects. I review empirical evidence for Allee effects in marine populations, and find suggestive observations, particularly for broadcast spawners and exploited fish populations, but little firm evidence. This might be for methodological reasons, i.e. problems with the definition of Allee effects and with demonstration of causal relationships. The population-level consequences of mechanisms for Allee effects in many marine species remain virtually unexplored. I suggest that including Allee effects in models of potentially vulnerable populations is useful, and may be particularly critical for the precautionary management of exploited marine species.

INTRODUCTION

What are Allee effects?

An Allee effect occurs when some component of individual fitness declines as population density or size decreases towards zero (Allee 1938, Stephens *et al.* 1999), resulting in a positively density-dependent relationship. Standard population models assume that fitness increases as density declines (negative density dependence), but there are various processes that can reduce fitness when there is a dearth of conspecifics (e.g. a lack of mating encounters, failure of fertilisation for broadcast spawners or wind pollinated plants, inbreeding depression; see Fowler and Baker 1991 and Stephens *et al.* 1999 for reviews).

If there is an Allee effect in some component of fitness, there may also be a decline in *per capita* population growth rate at low population size or density. If the population growth rate becomes negative, there will be a critical population size or density below which the population cannot sustain itself (Courchamp *et al.* 1999). An Allee effect in some component of fitness (e.g. output of fertilised eggs) may or may not result in a decline in the population growth rate since it may be balanced by negative density dependence in other components of fitness (e.g. survival or growth). Stephens *et al.* (1999) distinguish between *component* Allee effects (positive density dependence in some component of individual fitness) and *demographic* Allee effects (positive density dependence in the *per capita* population growth rate). Component Allee effects may or may not lead to demographic Allee effects. Note that “depensation” can be used to refer to positive density dependence in stock-recruitment relationships (Myers *et al.* 1995), by analogy with compensation (negative density dependence). This is equivalent to a demographic Allee effect.

Component Allee effects can arise from various processes, such as reproductive strategies (Levitan *et al.* 1992, Shepherd and Brown 1993, Kuussaari *et al.* 1998, Petersen and Levitan 2001), predator-prey interactions (Kenward 1978, Calvert *et al.* 1979, Foster and Treherne 1981, Inman and Krebs 1987, Chapter 4) or social systems (Halliday 1980, Clutton-Brock *et al.* 1999, Courchamp *et al.* 2000a, b, Courchamp and Macdonald 2001). Conservation biologists and managers are usually more interested in demographic Allee effects because they ultimately govern extinction or recovery probability of species at low abundance.

Are Allee effects likely in marine systems?

Marine populations have generally been considered to be open with large effective population sizes because most marine taxa have planktonic larvae that spend days to months in the water column and are therefore (in theory) capable of wide dispersal. Allee effects have thus been assumed to be relatively unimportant. However, for many species larvae may be retained locally, which produces relatively closed populations (Jones *et al.* 1999, Swearer *et al.* 1999, Barber *et al.* 2000, Cowan *et al.* 2000), and many species have fragmented or dramatically reduced populations (Myers and Worm 2003), rendering them susceptible to Allee effects.

Allee effects may occur at low population size or low population density. Most marine populations are probably metapopulations with subpopulations connected by larval transport (Lipcius *et al.* 1997, 2001, Crowder *et al.* 2000). Allee effects relating to density (such as encountering conspecifics for reproduction) can still exert an effect on large populations or on metapopulations if population density has declined to low levels. Allee effects dependent on population size are also possible in large populations and metapopulations, if they depend on the size of the local sub-population rather than on the metapopulation as a whole (e.g. predator dilution effects). Local population size and density may interact, as for fertilisation success in broadcast spawning sea urchins, where an effect of density is exacerbated by small population size (Levitan and Young 1995). Allee effects on subpopulation growth rate can also cause metapopulation-level "Allee effects" on a larger spatial scale, with a critical number of sub-populations below which the metapopulation will go extinct (Courchamp *et al.* 2000a). Hence the postulated large size and metapopulation structure of marine populations is not necessarily a protection against Allee effects.

Allee effects and human impacts on marine systems

Populations that are naturally susceptible to Allee effects are under selective pressure to evolve mechanisms to avoid them (e.g. large eggs, long-lived sperm, and aggregation or spawning synchrony in the case of broadcast spawners; Yund 2000). The simplest way of avoiding Allee effects is to maintain a large or dense, and stable population – if the population is never small or at low density, Allee effects never become relevant. Allee effects could still be "latent" in the population, should population size or density be reduced – there is a component Allee effect (a mechanism for an Allee effect) but the population is not small or sparse enough for the mechanism to create a demographic Allee effect.

Top-down predation by humans has become a dominant force in almost every marine ecosystem (Dayton *et al.* 1998, Pauly *et al.* 1998, Jackson *et al.* 2001), even in remote locations and at what is normally considered low levels of fishing intensity (biomass at 95% of unfished levels; Jennings and Polunin 1996). Numerous species have been fished to greatly reduced population levels; in 1994, the FAO considered 25% of the world's exploited marine resources to be "overexploited", "depleted" or "recovering", with another 44% "heavily or fully exploited" (Garcia and Newton 1997), and the assessment of the situation has deteriorated since then (Watson and Pauly 2001, Myers and Worm 2003). Hence, population dynamics at low population size or density have recently become important for marine species in a way that it has not been in "natural" systems through their evolutionary history.

Some marine species have also been severely reduced through disease outbreaks. The causes are frequently anthropogenic, either directly by introduction of diseases into new areas (e.g. the oyster disease agents *Bonamia ostreae* and *Haplosporidium nelsoni*; Ford and Tripp 1996), or indirectly through land use and desertification (e.g. mass mortalities of *Acropora* corals and the Caribbean long-spined sea urchin *Diadema antillarum*; Shinn *et al.* 2000, although this idea is controversial).

It is important to know how exploitation, or other anthropogenic factors that increase mortality, interact with latent or component Allee effects. Exploited or perturbed populations are the logical place to look for empirical evidence of demographic Allee effects in marine systems. I develop a model to examine the interaction between Allee effects, exploitation and critical thresholds quantitatively. I then examine the published evidence for Allee effects in marine populations.

MODEL DESCRIPTION

I used a matrix population model (Caswell 2001) with density-dependent reproduction to examine the interaction between Allee effects, critical thresholds and exploitation. The core of the model is a transition matrix that defines transition probabilities within and between each stage of the life history, as determined by rates of survival, maturation and reproduction. A vector representing the population size at time t is multiplied by the transition matrix (Table 1) to obtain the projected population at time $t+1$, and so on for the desired number of iterations.

This model has two stages (juvenile and adult). Individuals move from juvenile to adult at a rate determined by the time to maturity (τ). Adults reproduce at a *per capita* rate α – in this case this value incorporates the production of embryos and survival up to the juvenile stage. Individuals in each stage have a natural mortality rate M_j (juveniles) and M_a (adults), resulting in survival probabilities e^{-Mj} and e^{-Ma}. This definition of mortality is usual in fisheries science, and has the advantage that different sources of mortality are additive. In addition to natural mortality, adults suffer a fishing mortality rate F, resulting in an overall adult survival probability of $e^{-(Ma+F)}$.

I added density dependence to the model in reproduction only, for simplicity. In Chapter 2 I show that density-dependent reproduction and juvenile mortality have similar qualitative population consequences. Mortality from exploitation may be negatively density-dependent (if fishers aggregate in high density areas) or positively density-dependent or density-independent (if fishers are not completely free to choose a fishing area). Here I assume it is density-independent. The model is appropriate for iteroparous species without a fixed life span; but other life histories can be accommodated by changing the parameters (Table 1; see Chapter 2).

I added density dependence in reproduction as follows:

Per capita reproductive output = $\alpha N_t^{(\delta-1)} / (1 + \beta N_t^{\delta})$ - *Equation 1*

where N_t = adult density at time t, α = maximum reproductive output and β sets the slopes and intersection point of the curves (Table 2).

When $\delta=1$, Equation 1 collapses to $\alpha / (1 + \beta N_t)$, which results in negative density dependence. Increasing δ any amount above 1 adds positive density dependence at low density (a component Allee effect in reproduction). Larger values of δ intensify the Allee effect by shifting the peak reproductive output towards higher densities, while not affecting reproductive output at densities above the peak (Fig. 1). I varied the value of δ

between 1 (no Allee effect) and 5 (a strong Allee effect) (Myers *et al.* 1995; Stoner and Ray-Culp 2000).

Parameter values were set such that the model represented a generalised iteroparous “marine invertebrate” and equilibrated at reasonable population values: adult reproductive output per time-step (embryo production plus larval survival) $\alpha = 1000$, adult mortality per time-step $M_a = 0.5$ resulting in adult survival probability of 0.61 per time-step, juvenile mortality per time-step $M_j = 2$, resulting in juvenile survival probability of 0.14 per time-step, time to maturity $\tau = 3$ time-steps, scaling parameter $\beta = 45$. β was set empirically; biologically, its role is to ensure that the curves look similar at high density, such that the Allee effect only operates at low density. The model was run for 200 time steps, by which time it had reached equilibrium.

With the model I examined the effects of fishing mortality (F) and initial density for different levels of Allee effect (δ) upon equilibrium population size and critical thresholds. I defined the critical threshold in three ways; i) a *critical Allee effect threshold* (critical δ value), above which a population of given density and mortality rate goes extinct, ii) a *critical mortality rate*, above which a population of given density and Allee effect strength goes extinct, and iii) a *critical density threshold*, below which a population with a given Allee effect strength and mortality go extinct.

MODEL RESULTS

Equilibrium population size for an unexploited population is affected very little by the strength of Allee effect, while exploitation without an Allee effect causes an approximate exponential decline in equilibrium population size. The most dramatic effect of exploitation on a population with Allee effects is that there is a critical threshold value of fishing mortality, above which the population crashes abruptly to extinction. Such thresholds have been shown in many models incorporating Allee effects (Gerritsen 1980, Dennis 1989, Quinn *et al.* 1993, Courchamp *et al.* 1999, Boukal and Berec 2002). When I varied the strength of the Allee effect, fishing mortality and the Allee effect interacted, such that populations with stronger Allee effects became extinct under lower levels of fishing mortality, or conversely that as fishing mortality increased, weaker Allee effects drove populations extinct (Fig. 2). Additional fishing mortality caused an exponential decline in the critical Allee effect (the Allee effect which drives a population of given size extinct; Fig. 3). It also caused an exponential increase in critical density thresholds (Fig. 4). The modelling results demonstrate that increased fishing mortality (or any other anthropogenic source of mortality) can activate latent demographic Allee effects by i) reducing population size or density to the Allee threshold and ii) increasing the critical density threshold such that a given component Allee effect has more severe demographic consequences.

EMPIRICAL EVIDENCE

In general, there have been two approaches to the empirical study of Allee effects in marine and terrestrial systems: i) experimental or observational studies on component Allee effects, with the link to population dynamics sometimes made through modelling; and ii) Allee model fitting to empirical data such as reproductive success or population time series where there is large variation in population size. Studies of component Allee effects, or possible mechanisms for Allee effects, can show where there are latent Allee effects in a population. Studies of population time series, however, are looking for demographic Allee effects.

In marine systems, studies of component Allee effects have focused mainly on reproductive success in invertebrates, particularly broadcast spawners. In contrast, studies of demographic Allee effects have focused on searching for evidence of Allee effects in fisheries stock-recruitment data as a possible explanation for the collapse and lack of recovery in exploited fish populations.

Broadcast spawners

Many marine taxa possess a clear-cut mechanism for component Allee effects in their reproductive system: they are sessile or semi-sessile broadcast spawners. Fertilisation success of eggs depends on the concentration of sperm in the water column. The proportion of eggs fertilised declines exponentially with the distance of the female downstream from the nearest male (Fig. 5). At nearest-neighbour distances of less than a metre, models predict that less than 0.1% of eggs will be fertilised under high turbulence (Denny and Shibata 1989), although fertilisation efficiency varies depending on the taxon and the environment (Pennington 1985, Babcock *et al.* 1994).

Numerous marine invertebrate taxa are broadcast spawners (Giese and Kanatani 1987). Most species such as corals, anemones, ascidians and sponges, where the adults are usually sessile, have no other option for sexual reproduction, although they usually also reproduce clonally and may be self-fertile (Carlon 1999). Bivalves, echinoderms and archaeogastropods are also broadcast spawners, despite many being somewhat mobile as adults.

In sea urchins, both density and population size have an effect on fertilisation efficiency, with density being critical in small populations but less so in large ones. There is evidence of a trade off between fertilisation efficiency and competition in several species, implying that there is a positive relationship between density and fertilisation efficiency across the full range of natural densities to the carrying capacity (Levitan *et al.* 1992, Levitan and Young 1995). Research has therefore emphasised the importance of Allee effects in these species.

The relationship between population size, density and fertilisation efficiency do not guarantee a demographic Allee effect or even a component Allee effect in reproductive output. In urchins, competition often results in a smaller mean body size rather than higher mortality, since most echinoderms can shrink as well as grow if resources are scarce (Levitan 1991). In *Diadema antillarum*, the increase in gamete production by larger individuals at low density seems to offset the reduction in fertilisation efficiency, such that individual reproductive output remains broadly comparable across a wide range of densities (Levitan 1991). In addition, many taxa have evolved ecological and physiological mechanisms to avoid sperm limitation, so in natural (non-experimental) systems, it may be more of an evolutionary than an ecological phenomenon (Yund 2000). Moreover, various invertebrates show negatively density-dependent predation mortality at low population densities (Seitz *et al.* 2001), which could offset component Allee effects in reproduction.

The populations of many broadcast spawners have suffered dramatic reductions in density through exploitation. There has been heavy exploitation of sea urchins (Pfister and Bradbury 1996), sea cucumbers (Uthicke and Benzie 2001), Eastern oysters (Hargis 1999), scallops (Murawski *et al.* 2000) and abalone (Guzman del Proo 1992, Tegner *et al.* 1992, Parker *et al.* 1992, Farlinger and Campbell 1992). An anthropogenic origin for the major disease outbreaks in corals and *Diadema antillarum* is controversial but they seem to be unprecedented in recent or even geological history (Lessios *et al.* 1984, Aronson and Precht 2001). Is there evidence that a component Allee effect from broadcast spawning has had demographic consequences in these exploited populations?

There are several examples where populations subjected to exploitation have collapsed rapidly (e.g. abalone: Guzman del Proo 1992, Tegner *et al.* 1992, Parker *et al.* 1992, Farlinger and Campbell 1992; urchins: Lesser and Walker 1998, Kalvass 2000). Others have recovered only slowly from low abundance (e.g. Karlson and Levitan 1990). There is also evidence from the geological record that, within taxa which have a diverse variety of life histories (e.g. corals, gastropods), species with brooding larvae survived better through times of stress, implying that they can recover more easily from episodes of reduced density or population size (Wray 1995). Aronson and Precht (2001) suggested that Allee effects are implicated in the failure of the corals *Acropora palmata* and *A. cervicornis* to recover from the disease and bleaching outbreaks of the 1980s and 1990s. Both species broadcast eggs and sperm, with fertilisation in the water column and planktotrophic larvae. They have been largely replaced on Caribbean reefs for the first time in recent geological history by *Agaricia* and *Porites*, which are by contrast brooding species where eggs are retained by the females during and after fertilisation, hence allowing them to circumvent problems of sperm limitation.

Aside from the effects of decreased population size or density and increased mortality, evolved mechanisms for avoiding sperm limitation may break down at low density. In abalone, a decreasing proportion of reproductive adults participate in reproductive aggregations in heavily fished, low-density populations (Shepherd and Brown 1993). Abalone species have been serially depleted along northeastern Pacific coasts, demonstrating the rapidity with which each population collapsed after the fishery focused on that species (Fig. 6).

Abalone may be unable to support heavy fishing mortality at any density – i.e. the decline in population growth rate may not be density-dependent, as would be required for a demographic Allee effect. To test this, I examined landings of red and pink abalone, which have the longest time series. If I assume that landings are proportional to population size, the ratio of landings at time t+1 to landings at time t is an estimate of the average population growth rate over the year. The relationship between estimated population growth rate and landings is significantly positive (Figs. 7 and 8), suggesting that population growth rate increases with population size. This is suggestive of a demographic Allee effect, though it could also be a function of changes in effort.

Reproduction in non-broadcast spawners

There are few experimental studies on Allee effects in marine systems not related to fertilisation efficiency in broadcast spawners. In general, non-broadcast spawners have been considered too mobile and too behaviourally sophisticated to suffer from reproductive Allee effects, however, there are some exceptions. In queen conch (*Strombus gigas*), a heavily exploited Caribbean gastropod, there is a positive relationship between density and *per capita* reproductive activity at low density (Stoner and Ray-Culp 2000). This has been interpreted as an Allee effect related to the decreasing probability of encountering a mate at low density.

An observational study cannot demonstrate a causal relationship between *per capita* reproductive output and density. There are alternative explanations, such as migration into and away from reproductive aggregations, ontogenetic effects or phenotypic plasticity. This is not to say that Allee effects are not important, but rather, that the evidence for Allee effects in queen conch is indirect (including vulnerability to fishing pressure and failure to recover when fishing is stopped, e.g. in Bermuda and Florida; Berg *et al.* 1992a,b, Glazer 2001; see Chapter 3). Such studies illustrate the difficulty of demonstrating Allee effects in natural populations convincingly.

Several studies have shown that sperm limitation can be an issue at low density, even in mobile animals, particularly when the mechanism for density reduction is fishing, since this also reduces the proportion of older and larger males (Fig. 9). Potential for sperm limitation has been demonstrated in the New Zealand rock lobster (*Jasus edwardsii*), the Caribbean spiny lobster (*Panulirus argus*), and the blue crab (*Callinectes sapidus*), all of which are fished heavily and where large males are targeted. Smaller males and fewer matings result in smaller female clutch sizes and a higher proportion of unfertilised females (MacDiarmid and Butler 1999, Kendall *et al.* 2001, Jivoff, P., Rutgers University Marine Station, pers. comm.).

Sperm limitation in crabs and lobsters may or may not reduce female fitness at low density (i.e. a component Allee effect). These species possess other life-history components that mitigate the impact of component Allee effects at the population level. Rock and spiny lobster have an exceptionally long larval duration (several months; Lipcius and Eggleston 2000), which decouples local recruitment from local reproductive success (Lipcius *et al.* 1997, 2001). The blue crab also has larval mixing on a broad scale and is cannibalistic, such that low adult density may improve juvenile survival (Moksnes *et al.* 1997) and female reproductive output (Lipcius and Stockhausen 2002). Nonetheless, if fishing pressure is substantial across the entire metapopulation, which is likely in these species, demographic Allee effects may occur.

Survival-related Allee effects

Positive density dependence in individual survival also constitutes a component Allee effect. For example, survival due to predation will be positively density-dependent where predators have a Type II functional response (Holling 1959) with a limited aggregative or numerical response (Fig. 10). This is an interesting mechanism in that it is not linked to specific life-history traits such as broadcast spawning (see Chapter 4).

Positive density dependence in survival during some life stage has been demonstrated experimentally in a number of marine species, including queen conch (Marshall 1992, Ray and Stoner 1994), New Zealand rock lobster (Butler *et al.* 1999), Caribbean spiny lobster (Mintz *et al.* 1994), red sea urchins (*Strongylocentrotus franciscanus*; Quinn *et al.* 1993), Pacific salmonids (Wood 1987), soft-shell clams (*Mya arenaria*; Lipcius and Hines 1986), Eastern oysters (*Crassostrea virginica*; Eggleston 1990), marine insects (Foster and Treherne 1981) and zooplankton (Folt 1987); see Seitz *et al.* (2001) for a review for marine bivalves. The survival of one life history stage may be positively related to the density of another; for example, newly settled red sea urchins, Virginia oysters (*Crassostrea virginica*) and mussels (*Mytilus edulis*) survive better under adult canopies (Rowley 1989, Quinn *et al.* 1993, R. Mann, Virginia Institute of Marine Science, pers. comm.), and adult cod feed on the competitors and predators of juvenile cod (Walters and Kitchell 2001). With the exception of red sea urchins (Botsford *et al.* 1993, Quinn *et al.* 1993, Pfister and Bradbury 1996), these results have not yet been linked to demographic Allee effects.

Human "predation" can be a mechanism for creating component Allee effects in survival. An exploitation Allee effect occurs when the *per capita* exploitation rate increases as population size or density decreases. There are, for example, situations where decreasing population size does not result in decreasing population density (e.g. schooling fish, spawning aggregations), and in this case a reduction in population size will not make individuals any harder to catch. Hence if effort is constant, total catch will remain more or less constant, and the proportion of individuals caught (the *per capita* exploitation rate) will increase as population size decreases, creating an Allee effect (= depensatory fishing mortality). Another possibility is for effort to increase as catch per unit effort declines (as is usual, given economic investments in fisheries), so that catches decrease at a lower rate than population size, again resulting in an increase in the *per capita* exploitation rate. Note, however, that these Allee effects will only operate under exploitation; elimination of exploitation also removes the Allee effect. Therefore, exploitation Allee effects will affect the rate at which a population declines under heavy exploitation, but will not affect the rate at which populations recover if exploitation stops, unlike Allee effects intrinsic to species life history or ecology.

Demographic Allee effects

For fish, as for mobile invertebrates, Allee effects were not considered likely to be important, until the failure of several populations to recover from overexploitation after substantial reductions in fishing effort led to a debate about the possibility of recruitment failure and low or negative *per capita* population growth rates at low density (demographic Allee effects). This work has focused on fitting models with and without Allee effects to population size and recruitment data, which is possible only for intensively studied (economically important) species for which such data sets exist. In a database of population size and recruitment for 128 fish stocks, 26 allowed an analysis with high statistical power (>0.95) and there was significant evidence of Allee effects in only three (Myers *et al.* 1995). Myers concluded that Allee effects were not likely to be of widespread importance, and collapses and recovery failures should be attributed to other causes.

The large variance in stock-recruitment data means that Myers's approach may have limited power to detect Allee effects, and the failure to reject a null hypothesis of no

Allee effects might not be an indicator that they are not present (Shelton and Healey 1999, Liermann and Hilborn 1997). In addition, there is often uncertainty about what constitutes a “stock”, which should be a population or sub-population that is more or less reproductively isolated. If the stock considered by managers actually consists of several sub-stocks, the impact of Allee effects and extinctions at the sub-stock level may be masked until the metapopulation reaches a critical point (Frank and Brickman 2000, Courchamp *et al.* 2000a). Conversely, if the “stock” is only part of a much larger open population, recruitment will be decoupled from local individual fitness, even if component Allee effects due to density are important (i.e. component Allee effects will not lead to demographic Allee effects until a critical point is reached across the whole population).

There is indirect evidence for Allee effects in some exploited fish species, particularly gadids (the cod family). An analysis of recovery from exploitation in 90 fish populations showed that 15 years after major declines in stock size, 40% of populations (mainly gadids) showed no recovery, with 48% showing only marginal recovery (Hutchings 2000).

CONCLUSIONS

There is no *a priori* reason for Allee effects to be intrinsically unlikely in marine populations, despite their (possibly) open, metapopulation structure. Furthermore, exploitation and disease have made many marine populations exceptionally vulnerable to Allee effects, which can interact catastrophically with increased mortality. Our analysis of the empirical data on Allee effects in diverse marine species revealed numerous suggestive observations but very little firm evidence. Does this mean that Allee effects can be dismissed as unusual or marginal in marine systems?

The failure to demonstrate Allee effects convincingly in marine populations might in fact be methodological. There is a lack of clear understanding on the part of many ecologists as to the precise definition of Allee effects. Allee effects require a causal relationship between density or population size and either a component of individual fitness (component Allee effects, *sensu* Stephens *et al.* 1999) or the *per capita* population growth rate at low density (demographic Allee effects, *sensu* Stephens *et al.* 1999). Correlations between density and fitness can have various explanations, including mutual dependence on a third variable such as site or age. Showing a causal relationship between two variables is an age-old problem for ecologists, to which I do not have a solution, except to say that clear demonstrations of component Allee effects are likely to require large-scale manipulative experiments, and will therefore be limited to a few taxa.

Given constraints on assessing Allee effects in marine populations, I feel that a promising tactic is to model potentially vulnerable populations with different strengths of Allee effect (e.g. Fig. 2; see Chapter 2). This heuristic approach gives a prediction of the likely consequences of different scenarios if Allee effects are important. This is particularly useful for exploited populations in the context of precautionary management. If Allee effects are strong, spatial considerations become critical. Traditional fisheries management, with control of inputs (effort) or outputs (landings) may not be very successful because it allows fishers to target dense areas and tends to reduce a population to uniform low density. Spatial management, such as permanent no-take reserves, maintains areas of high population density, and should be considered seriously in the management and conservation of species where Allee effects may be a risk.

Where the modelling approach has been applied (Botsford *et al.* 1993, Quinn *et al.* 1993, Pfister and Bradbury 1996) it has demonstrated that Allee effects have major consequences for population dynamics, sustainable exploitation and management. The potential population consequences of mechanisms for component Allee effects remain unexplored in most marine species. I contend that this limits both our ecological understanding and the probable success of conservation for marine species.

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TABLES

Table 1

Transition matrix for the density-independent version of the model; M_j = mortality of juvenile stage, M_a = mortality of adult stage, τ = time to maturity, α = reproductive output of adults.

$e^{-Mj} . (1 - 1/\tau)$	α
$e^{-Mj} . 1/\tau$	e^{-Ma}

Table 2

Transition matrix for density-dependent Allee effect model; δ=Allee effect parameter, α = maximum reproductive output, β = scaling factor, M_j = mortality of juvenile stage, M_a = mortality of adult stage, τ = time to maturity.

$e^{-Mj} . (1 - 1/\tau)$	$\alpha . N_a^{\delta-1} / (1 + \beta N_a^{\delta})$
$e^{-Mj} . 1/\tau$	e^{-Ma}

FIGURES

Fig. 1

The effect of the exponent δ in the density-dependent equation for reproductive output.

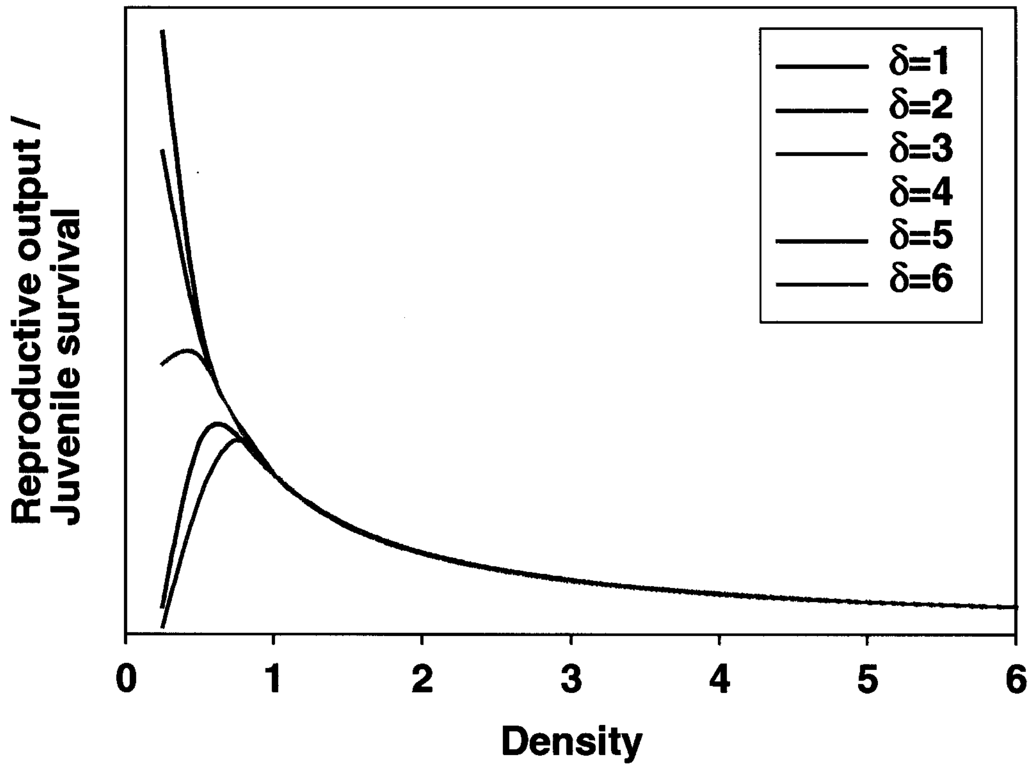


Fig. 2

Fishing mortality and equilibrium population size with varying strength of Allee effect. No Allee effect: $\delta=1$, moderate Allee effect: $\delta=3$, strong Allee effect: $\delta=5$.

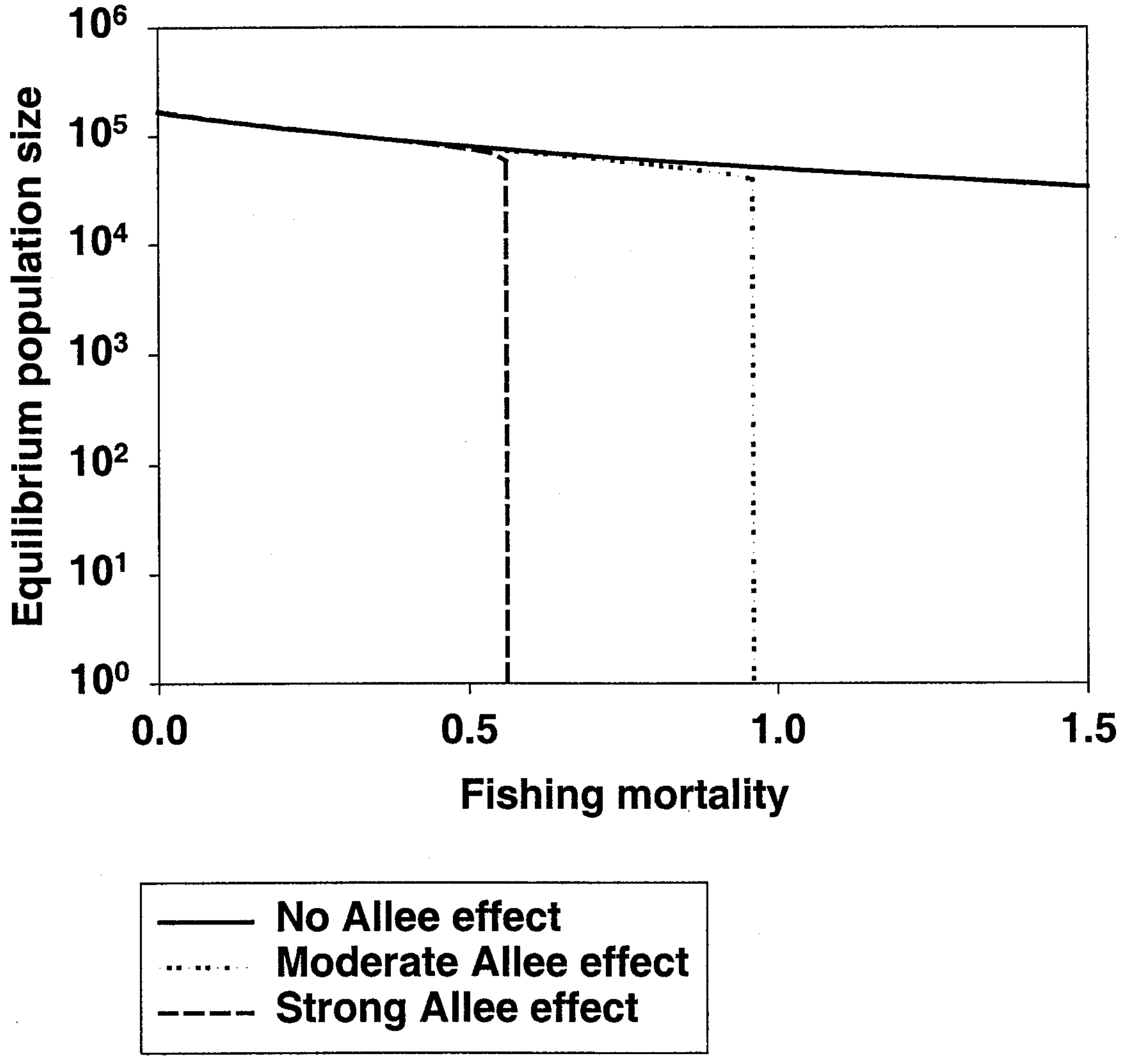


Fig. 3

Relationship between fishing mortality and the strength of Allee effect at which the population goes extinct (critical δ). Mortality causes an exponential decline in the strength of Allee effect that causes extinction.

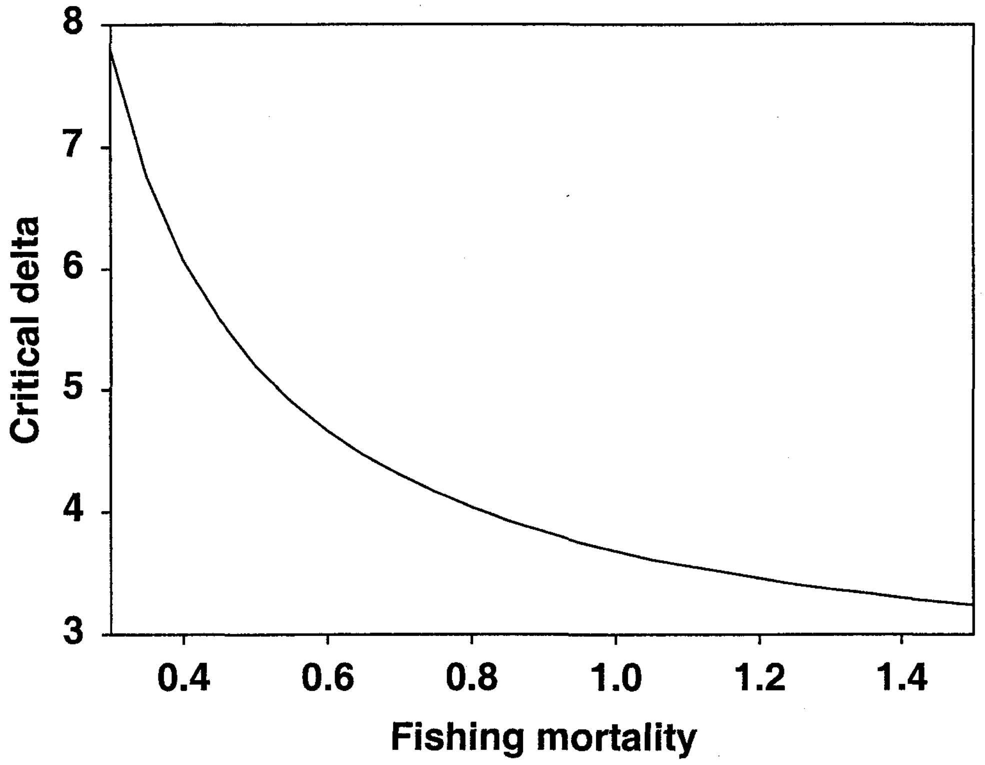


Fig. 4

Relationship between fishing mortality and critical density thresholds for a given strength of Allee effect (in this case, δ=3). Increasing fishing mortality causes an exponential-type increase in the critical density below which the population goes extinct.

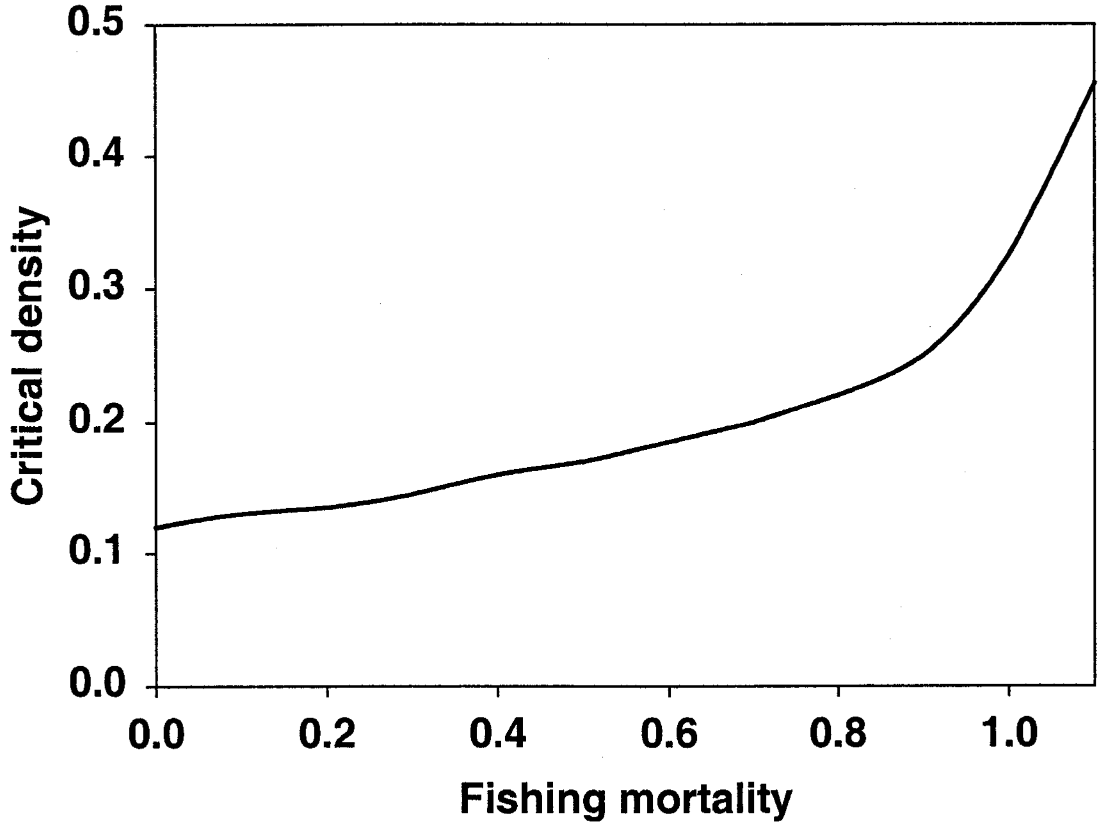


Fig. 5

Fertilisation success in echinoderms, showing a general trend of exponential decline in the proportion of eggs fertilised with distance downstream of the nearest male. Data from Babcock *et al.* 1994 (crown of thorns starfish, *Acanthaster planci*); Levitan *et al.* 1992 (red sea urchin, *Strongylocentrotus franciscanus*); Pennington 1985 (green sea urchin, *S. droebachiensis*); Levitan 1991 (Caribbean long-spined sea urchin, *Diadema antillarum*).

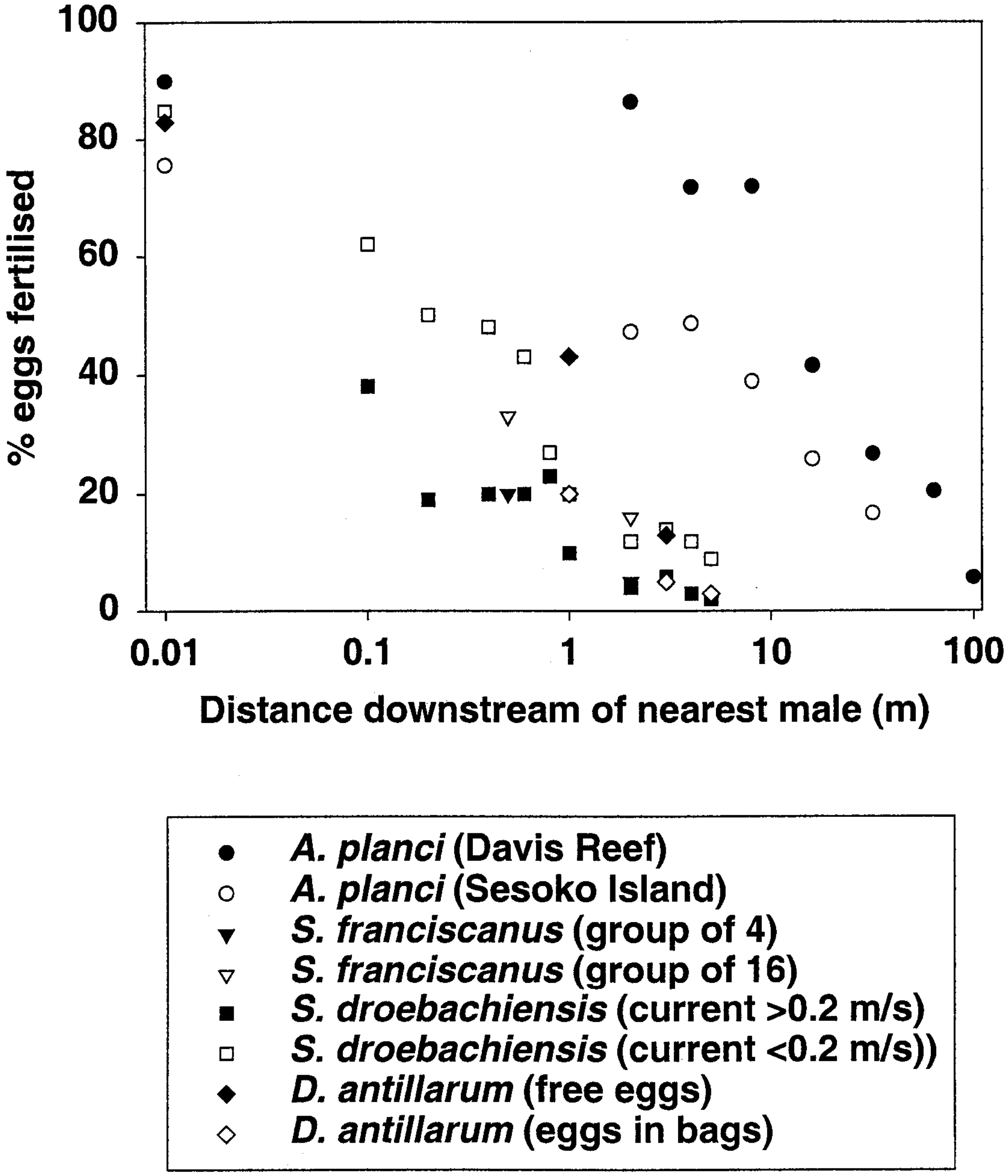


Fig. 6

Population size of abalone species (red abalone *Haliotis rufescens*, pink abalone *H. corrugata*, green abalone *H. fulgens* and black abalone *H. cracherodii*) in California. Note the pattern of serial collapse as the fisheries moves on to each species in turn. Red are the preferred species for the fishery, followed by pink, green and black. Data from Tegner *et al.* 1992, Parker *et al.* 1992.

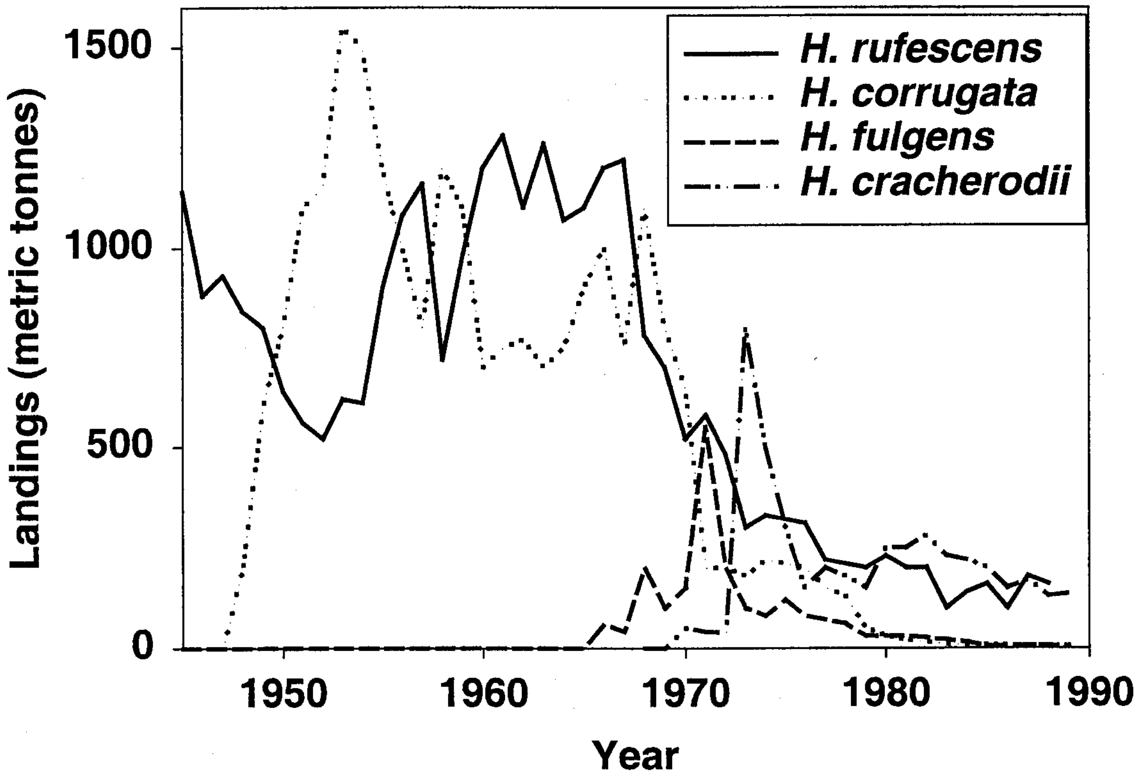


Fig. 7

Mean annual population growth rate of red abalone, on the assumption that landings are proportional to the population size (ratio of landings at time *t*+1 to landings at time *t*) vs. landings in metric tonnes. A positive slope indicates the possibility of an Allee effect, with an Allee threshold (population growth rate = 1) at the population which provides landings of ~1,200 tonnes.

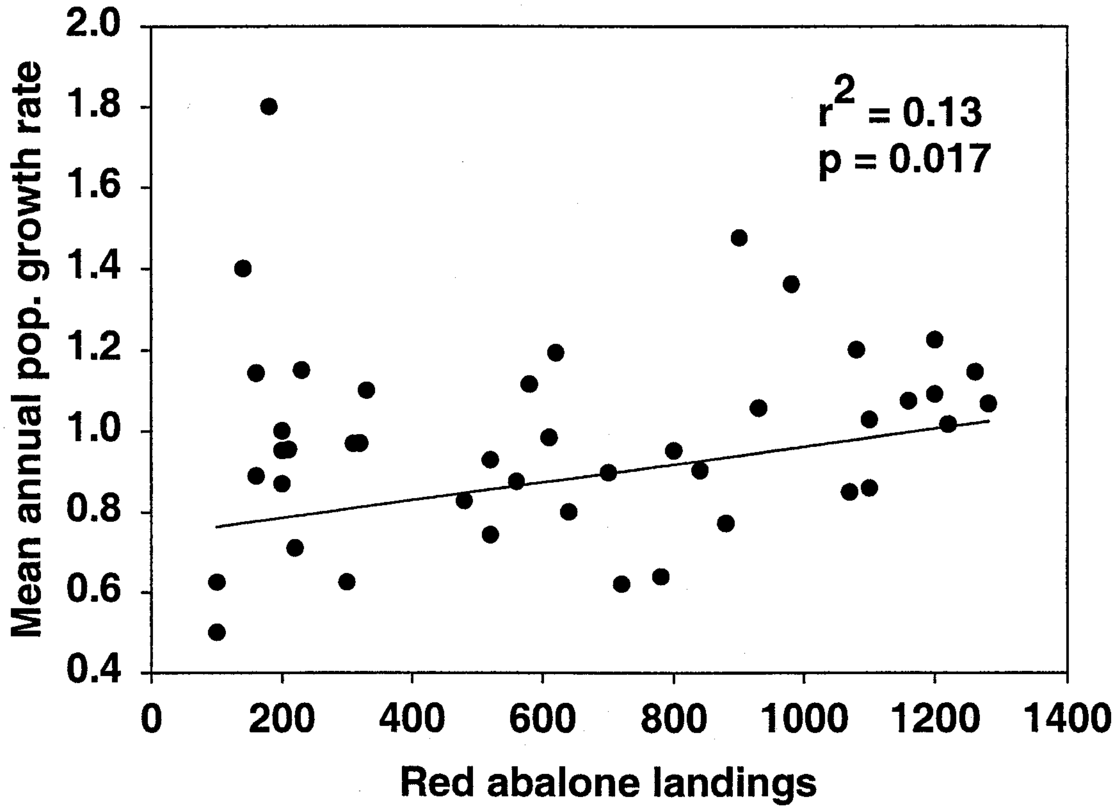


Fig. 8

As Fig. 7 for pink abalone. Again, a positive slope indicates a potential Allee effect with a threshold at landings of ~1,200 tonnes.

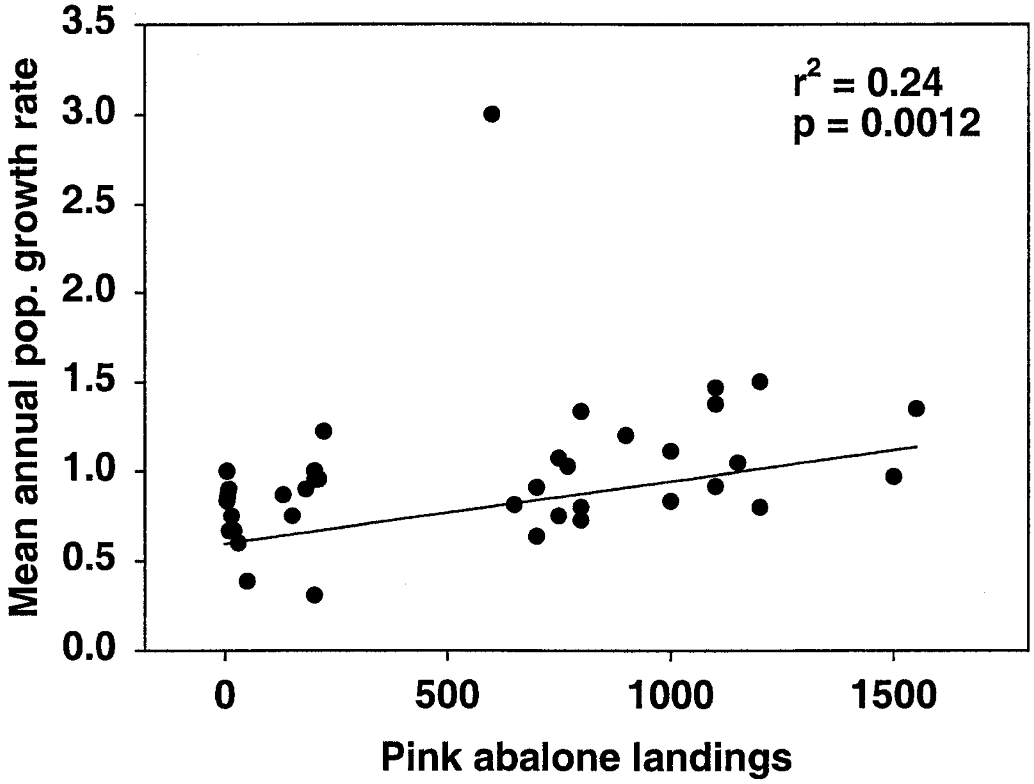


Fig. 9

Age structure of populations with different probabilities of survival (*p*) from one stage to the next. Data from a simple density-independent matrix population model. High *p* (0.7) corresponds to low mortality (i.e. the unfished scenario), while low *p* (0.3) corresponds to high mortality (i.e. the fished scenario). Note that even though all stages have an equal survival probability in each case, the lower survival probability (higher mortality) scenario results in a depletion of older stages relative to younger ones. Hence a fishery that targets all individuals in the population equally still alters the age structure by reducing the proportion of older individuals.

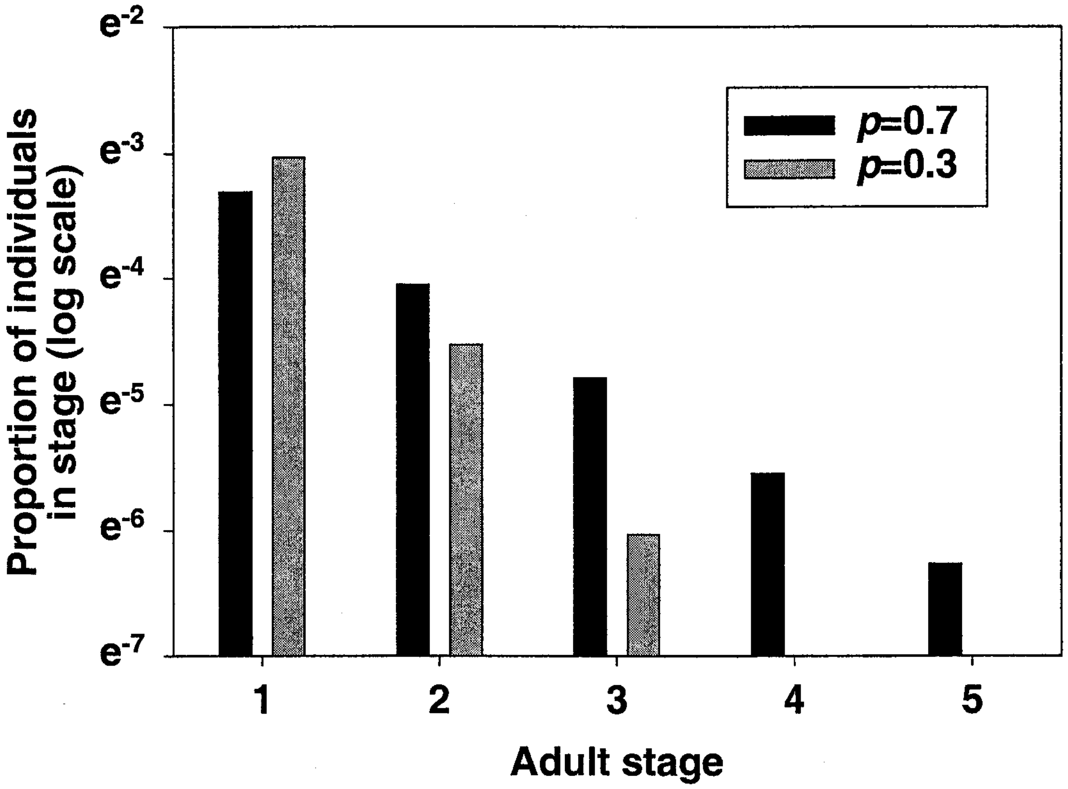
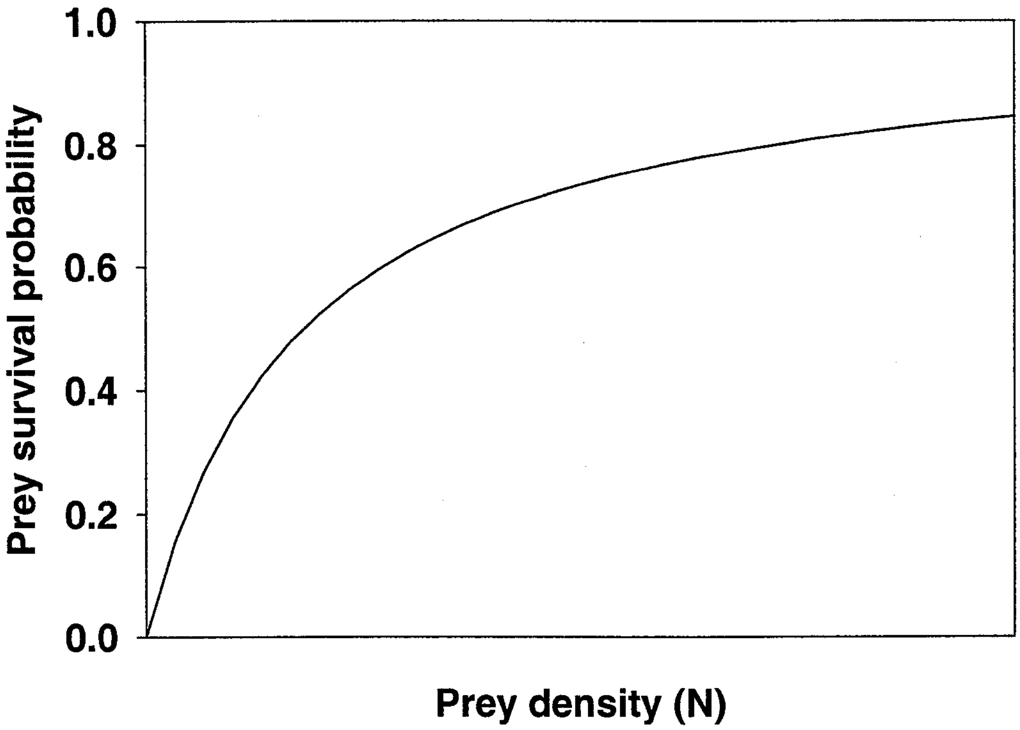


Fig. 10

Prey survival probability due to predation as a function of prey density, where predators have a Type II functional response and constant numbers.



CHAPTER 2

POPULATION CONSEQUENCES OF ALLEE EFFECTS IN REPRODUCTION AND SURVIVAL IN RELATION TO LIFE HISTORY

ABSTRACT

Allee effects (reduced fitness at low density) can occur in different components of the life history, however, there is at present no theoretical framework for comparing different types of Allee effect, or for considering the consequences of several Allee effects simultaneously. I use a simple density-dependent model to i) compare the population consequences of Allee effects in juvenile survival and reproduction, ii) examine the effect of adding two kinds of Allee effect together and iii) examine the impact of vital rates and negative density dependence on Allee dynamics. I measured the severity of the population consequences of an Allee effect by examining critical thresholds at which populations went extinct. I parameterised the model in two ways; "*r*-selected" (high mortality and reproduction, short time to maturity) and "*K*-selected" (low mortality and reproduction, long time to maturity). I found that reproductive Allee effects usually have higher density thresholds than juvenile survival Allee effects, and thus in these terms are usually more severe. This is not surprising given that reproductive Allee effects act on the adult stage, which is nearly always less numerous than the juvenile stage (except for some clonal organisms). In terms of critical Allee effect thresholds (the strength of Allee effect that drives a population with given initial conditions extinct), I found more complex results. For the model with negative density dependence, longer time to maturity increased the severity of juvenile survival Allee effects relative to reproductive Allee effects. In this model, there was a critical strength of Allee effect above which all populations would go extinct regardless of initial density. For the model with no negative density dependence, reproductive Allee effects were more severe for the *r*-selected

parameterisation, while juvenile survival Allee effects were more severe for the *K*-selected parameterisation, even when they both had the same time to maturity. In the density-dependent model, the *K*-selected parameterisation took much longer to equilibrate than the *r*-selected parameterisation, and I suggest that the population consequences of Allee effects will be difficult to detect in these populations because they are unlikely to be at equilibrium, although they will still be present. The population consequences of adding two types of Allee effect together are difficult to predict, and depend on parameter values. Adding a second Allee effect can change extinction thresholds drastically, or can have relatively little effect. I found that adding negative density dependence in the non-Allee stage of the model nearly always had a large effect on extinction thresholds. Density-independent parameters have an exponential-type relationship with critical density thresholds, so that human-induced changes in mortality, growth rates or fecundity could potentially have large impacts on populations with Allee effects. Finally, I found that with the *r*-selected parameterisation, both types of Allee effect can create stable, large-amplitude oscillations with a broader range of population parameters than are reported for this kind of dynamics with Allee effects elsewhere in the literature.

INTRODUCTION

In standard equilibrium population models such as the logistic model, individual fitness is inversely related to population density, resulting in negative density dependence (Gotelli 1998). There are, in contrast, organisms that benefit from the presence of conspecifics at low density (see review by Fowler and Baker 1991). In these instances, fitness declines as population density decreases at low density (positive density dependence) such that *per capita* population growth rate may become negative, causing a threshold below which the population will collapse to extinction (Courchamp *et al.* 1999). Populations with positive density dependence at low density are said to have Allee effects (Allee 1931). Allee effects do not necessarily cause extinction since *per capita* population growth rate can be depressed but still remain positive.

Allee effects can occur in various components of the life history (Stephens *et al.* 1999). Reproductive Allee effects are a commonly cited example, with mechanisms including mate finding (McCarthy 1997, Kuussaari *et al.* 1998, Shepherd and Brown 1993), fertilisation efficiency (Levitan *et al.* 1992, Baker and Tyler 2001, Widen 1993, Groom 1998, Hackney and McGraw 2001) or threshold group size for cooperative breeding (Courchamp *et al.* 2000). Allee effects can also occur in survival. They can be driven by generalist predators (often called the "dilution effect"; Marshall 1992, Gilchrist 1999, Seitz *et al.* 2001, Cuthbert 2002; see Chapter 4), as well as factors such as group defence against predation (wood pigeons - Kenward 1978), exposure protection (monarch butterflies - Anderson and Brower 1996), cooperative hunting (African wild dog -

Courchamp and Macdonald 2001), or if adults enhance juvenile survival by providing physical protection (oyster reefs; red sea urchin – Tegner and Dayton 1977) or preying on their predators (Atlantic cod - Walters and Kitchell 2001).

By extension, there are examples of animals that may have Allee effects in both reproduction and survival. Armoured bivalves tend to suffer heaviest predation at low density (Seitz *et al.* 2001), and are also broadcast spawners. Adult red sea urchins (*Strongylocentrotus franciscanus*), also broadcast spawners, provide protection against predation for juveniles under their spine canopy. Very few studies have considered examples where species may have more than one Allee effect (but see Quinn *et al.*1993).

There are a variety of general (non-species specific) models examining Allee effects in diverse ways (see review of older literature in Dennis 1989). This includes their role in extinction and conservation of rare species and the evolution of reproductive strategies (Gerritsen 1980, Wells *et al.* 1998), their interaction with demographic and environmental stochasticity (Dennis 1989, Møller and Legendre 2001), their interaction with dispersal (Etienne *et al.* 2002) and metapopulation dynamics (Amarasekare 1998, Courchamp *et al.* 2000), their potential to create oscillatory and chaotic population dynamics (Cushing 1994, Schreiber *in press*) and their potential to determine the spatial distribution of species (Hopf and Hopf 1985).

No general modelling study has considered i) whether Allee effects in different components of the life history have different effects on population dynamics and extinction thresholds (e.g. is one more “severe” than another?) or ii) the population effects of different types of Allee effect in combination. In this study, I construct and analyse simple, heuristic models to examine the population consequences of Allee effects in reproduction and juvenile survival, both separately and in combination. I use the models to address the following questions:

- Do Allee effects in different components of the life history have qualitatively and quantitatively different impacts on population dynamics?
- Are the effects of several types of Allee effects additive and symmetrical?
- How are the outcomes of different types of Allee effect affected by life history and negative density dependence?

In this paper, I use the terms “strength” and “severity” of Allee effects to refer to different concepts. In the models, I can set parameter values which determine the “strength” of an Allee effect in terms of the amount of positive density dependence in the model. I measure the “severity” of an Allee effect in terms of the population consequences, i.e. the value of critical extinction thresholds. For example, if two model runs had the same strength of Allee effect (the same parameter value), but went extinct at different densities, the model with the higher critical density would be considered to have more severe Allee effects, since a given strength of Allee effect had more severe consequences.

METHODS

Model description

I used a two-stage Leslie matrix projection model (Caswell 2001) to compare population trajectories with and without Allee effects in reproduction and juvenile survival. I concentrate on juvenile survival for several reasons: i) juveniles tend to have higher mortality than adults, ii) juvenile survival affects only one life history stage, as does reproduction, and thus provides a contrast of Allee effects in Stage I vs. Stage II and iii) focusing on survival in only one model stage simplified analysis and interpretation.

The model is heuristic, and is not intended to predict the dynamics of any particular species or population. I parameterised the model in two different ways, to represent two sets of contrasting life histories, "*r*-selected" and "*K*-selected" (Table 1).

By adapting the model I was able to examine juvenile survival probability and reproductive output in four ways: i) density independent, ii) with negative density dependence only (Model 1), iii) with negative density dependence plus Allee effects (Model 1) and iv) with Allee effects only (Model 2).

In the basic (density-independent) model, individuals move from Stage I ("juvenile") to Stage II ("adult") at a rate determined by the time to maturity (τ). Adults reproduce at a rate α. Individuals in each stage have a density-independent mortality rate (M_j and M_a, resulting in survival probabilities e^{-Mj} and e^{-Ma}). This definition of mortality is usual in fisheries science, and has the advantage that different sources of mortality are additive.

Adults die at a rate determined by M_a, rather than after a predetermined time period. The specifics of the life history can be changed by setting the four basic population parameters; α, M_j, M_a and τ. α has units of individuals, τ has units of time, while M_j and M_a are dimensionless. I did not draw any conclusions from the density-independent model, but it is included here for clarity, as the basis of the Allee effect models (Table 2).

Models 1 and 2 incorporate Allee effects in juvenile survival probability (e^{-M_j}) and reproductive output (α). Density dependence in juvenile survival probability depends on the density of juveniles only, i.e. the model assumes that juvenile and adult stages are either spatially segregated or have different predators. Density dependence in reproductive output depends on the density of adults only.

In Model 1, the model adds negative density dependence at high density as well as Allee effects at low density, so that the model reaches some equilibrium value. I used the following density-dependent equation (Myers *et al.* 1995):

per capita *survival probability* or *reproductive output* $= K \,.\, N_{it}^{(\delta-1)} / (1 + \beta N_{it}^{\delta})$

\- *Equation 1*

where K = density-independent rate (e^{-M_j} for juvenile survival, α for reproduction) and N_{it} = density of stage i at time t; for description of β and δ see below.

When $\delta=1$, the right hand side of Equation 1 collapses to $K / (1 + \beta N_{it})$, providing straightforward negative density dependence. Increasing the value of δ even a fraction above one gives curves with similar negative density dependent behaviour at high density but positive density dependence at low density, which becomes increasingly strong as the value of δ is increased. δ can be considered an index of the strength of the Allee effect (Myers *et al.* 1995). I tested values of δ between 1 and ~6, since this seemed to be a realistic range when this method was used to obtain best fit values of δ from field data for a marine invertebrate (Stoner and Ray-Culp 2000). β sets the slope of the curve relative to values of N and δ. Biologically, β is used to ensure that the curves varied as little as possible from each other at high density, since Allee effects act only at low density. In this heuristic model β was set such that for δ values between 1 and 6 the curves were similar at high density and the model equilibrated at reasonable population values (β=45) (Table 3, Fig. 1). I determined that equilibrium had been reached by plotting and inspecting the trajectory.

In Model 2, I incorporated Allee effects without adding negative density dependence. In this model, the density-dependent equation was as follows:

per capita *survival probability* or *per capita reproductive output* $= K \,.\, \gamma N_{it} / (1 + \gamma N_{it})$

\- *Equation 2*

where K = density-independent rate (e^{-Mj} for juvenile survival, α for reproduction) and N_{it} = density of stage i at time t; for description of γ see below.

Equation 2 is a hyperbolic equation that reaches an asymptote at the density-independent value of reproductive output or juvenile survival, and declines at low density. The rate of decline is set by the value of γ, by assuming that at $N = 1$, the *per capita* survival probability or reproductive output is some proportion y of the density-independent rate (Fig. 2). Substituting into Equation 2:

$y\,K = K\gamma\, /\, (1 + \gamma)$, and hence $\gamma = y\, /\, (1 - y)$.

Thus y can be regarded as an index of the strength of the Allee effect, albeit not one that is directly comparable with δ (since it must be greater than zero and less than one). γ can be calculated from y (Table 4). The advantage of these techniques for modelling Allee effects is that the strength of the Allee effect can be set by the values of δ or y. This allows a more subtle analysis of Allee effect dynamics than a straightforward Allee vs. no-Allee comparison.

Model runs

The model was run in terms of population density rather than population size. I assumed a population area of 10^5 units, so density values are multiplied by 10^5 to get population size (i.e. population size and population density are interchangeable in the results). I started with a vector containing initial population density for juvenile and adult stages. This vector was multiplied iteratively by the appropriate transition matrix (Tables 3 and 4) using Matlab version 6.1 (The MathWorks Inc.).

In Model 1 the population trajectory would eventually equilibrate, with the rate of equilibration depending strongly on parameter values. For each set of parameter values, I inspected the population trajectory and chose an appropriate number (t_{eq}) of time-steps, such that the model was at or near equilibrium by $t = t_{eq}$. The population vector at t_{eq} was assumed to be an equilibrium level (with some exceptions, see below). The model could be run across a range of values for a particular parameter or initial population vector and the population vector at t_{eq} plotted against parameter values to examine the effect of parameters on equilibrium population size.

In Model 2, since there is no negative density dependence, the model does not equilibrate. This made the model more difficult to deal with, since the population size could exceed the capacity of Matlab to deal with large numbers in 50 time-steps or fewer. For this model I set t_{eq} at ~30 time-steps, and visually inspected population trajectories to make sure that the model dynamics had settled down to a constant population growth rate. Instead of equilibrium population, I used "equilibrium" population growth rate (r_{eq}) as a dependent variable. This was calculated as follows:

$$r_{eq} = (\ln N_{teq} - \ln N_{teq-5}) / 5$$

where N_t is the density of either stage at time t (since both stages grow at the same rate).

Critical values (unstable equilibria) correspond to points where $r = 0$, since if $r < 0$ the population declines to extinction, while if $r > 0$ the population grows without bound.

The short trajectories in Model 2 resulted in some limitations; specifically, models with the K parameterisation sometimes took so long to equilibrate that analysis using Model 2 was not possible. I used Model 2 to test the generalities of conclusions drawn using

Model 1, and particularly to tease out the interacting impacts of Allee effects and negative density dependence.

Analysis of equilibria

I looked at model equilibria more directly, by calculating equilibrium equations. For each model, the equation for the equilibrium in terms of δ and the equilibrium population density N_* for the density-dependent stage (juveniles for the juvenile survival Allee effect, adults for the reproductive Allee effect) can be calculated by setting N_{t+1} equal to N_t, or alternatively by calculating the determinant of the matrix $(A - \lambda I)$ where A is the transition matrix (Tables 3 and 4), I is a 2 x 2 identity matrix and $\lambda=1$.

For Model 1, the population is at equilibrium for either type of Allee effect separately when the following equation is satisfied:

$$\beta N_*^{\delta} - K N_*^{\delta-1} + 1 = 0$$

where N_* = equilibrium density of density-dependent stage and K = amalgam of density-independent parameters.

For reproductive Allee effect, $K_{\text{rep}} = (\alpha\, e^{-Mj}\, 1/\tau) / [(1 - e^{-Ma})(1 - e^{-Mj}\,(1 - 1/\tau))]$

For juvenile survival Allee effect, $K_{\text{juv}} = e^{-Mj}\,(1 - 1/\tau)\,(1 - e^{-Ma}) + (\alpha\, e^{-Mj}\, 1/\tau) / (1 - e^{-Ma})$

When τ (time to maturity) = 1, K_{rep} and K_{juv} are identical, i.e. the equilibrium population size of the juvenile stage with juvenile survival Allee effects is equal to the equilibrium population size of the adult stage with reproductive Allee effects.

For Model 2, the equilibrium equations are as follows:

Reproductive Allee effects: $N_* = K / \gamma(\alpha - K)$

where N_* = equilibrium density of density dependent stage, $K = (1 - e^{-Ma})(1 - e^{-Mj}(1 - 1/\tau)) / (e^{-Mj} . 1/\tau)$

Juvenile survival Allee effects: $N_* [(\gamma\, e^{-Mj} / \tau)(\tau + \alpha - 1) - \gamma] = 1$

For both types of Allee effect together, a solution is possible for Model 2:

$$N_{a*} = (1 + \gamma N_{j*} - e^{-Ma} - \gamma N_{j*}e^{-Ma}) / \gamma\, (\gamma N_{j*}e^{-Ma} + \alpha\gamma N_{j*} + e^{-Ma} - \gamma N_{j*} - 1)$$

This solution is also true if N_{j*} and N_{a*} are reversed above.

RESULTS

Dynamics with one Allee effect only

Allee effects in reproduction and juvenile survival show very similar qualitative dynamics, characterised by threshold effects and abrupt population crashes. I use these threshold values as a measure of the severity of an Allee effect in terms of its population consequences. The thresholds can be displayed in several ways; i) as critical values of the Allee parameters (δ, y) for a given set of initial conditions above (δ) or below (y) which the population goes extinct; ii) as critical values of density for a given set of model parameters, below which the population goes extinct; iii) as critical values of some density-independent parameter (e.g. mortality), above which the population goes extinct.

Critical Allee effect thresholds: In Model 1, below a critical value of Allee effect strength for reproductive Allee effects (δ_r) or juvenile survival Allee effects (δ_j), a linear increase in δ causes a gradual (but accelerating) decline in the final population size, but above a critical value, the population crashes to extinction (Fig. 3). For a given set of parameter values, the critical δ value is identical for reproductive Allee effects and juvenile survival Allee effects when $\tau=1$, but lower for juvenile survival Allee effects when $\tau>1$ (Fig. 4). Thus increasing the time to maturity increases the severity of juvenile survival Allee effects relative to reproductive Allee effects, if severity is measured by the Allee effect threshold.

The equivalent phenomenon in Model 2 is an abrupt change in population growth rate from positive to negative as *y* decreases (the Allee effect gets stronger). In this case, reproductive and juvenile survival Allee effects are not equivalent, even when $\tau=1$. The relative importance of juvenile survival and reproductive Allee effects depends on the parameterisation. For the *r* parameterisation (low survival probability, high reproductive output, short time to maturity), reproductive Allee effects are more severe, since they cause population collapse at a collapse at a higher value of *y*, corresponding to weaker Allee effects. For the *K* parameterisation (high survival, low reproductive output, long time to maturity), juvenile survival Allee effects are more severe. This is not simply a function of the value of τ (as in Model 1) since reproductive Allee effects are still more severe in the *r* parameterisation when $\tau=2$ and juvenile survival Allee effects are still more severe in the *K* parameterisation when $\tau=1$ (Figs. 5 and 6).

In Model 1, the critical value of δ_r and δ_j increases with the initial population size over a range of initial population size; however, for a given set of density independent population parameters, the critical δ value reaches a maximum above which the population will always go extinct, regardless of the size of the initial population is (Fig. 7). Model 2 also reaches a point at which there is extinction for all initial densities, but unlike Model 1, this point depends only on the value of density-independent parameters (the balance between reproduction and mortality), rather than the strength of the Allee effect.

Critical density thresholds: In Model 1, for any value of δ_r or δ_j below the maximum critical value, there is a threshold in initial density, such that populations that start off below that density go extinct, while those above that density reach some positive equilibrium. Density dependence in juvenile survival has a stronger proportional depressing effect on the equilibrium population size than density dependence in reproduction, since when the population is extant the equilibrium population size is lower in the juvenile survival model than the reproduction model. On the other hand, this means that critical thresholds are also lower, such that for a given value of δ, the critical density for a population with reproductive Allee effects is greater than the critical density for a population with juvenile survival Allee effects.

Model 2 also has critical density thresholds associated with particular values of y, with critical densities being higher for lower values of y (stronger Allee effects). For the r parameterisation, critical density thresholds are higher for reproductive Allee effects than for juvenile survival Allee effects, i.e. reproductive Allee effects are more severe. For the

K parameterisation, the converse is true; critical density thresholds are higher for juvenile survival Allee effects than reproductive Allee effects, so juvenile survival Allee effects are more severe.

In terms of critical density thresholds, reproductive Allee effects are more severe than juvenile survival Allee effects in Model 1 (i.e. when there is negative density dependence) regardless of parameter values. When there is no negative density dependence (Model 2), the relative severity of the different types of Allee effect, in terms of the critical density thresholds, depends on the life history (Figs. 7 – 9).

Other comments on qualitative dynamics: There is a significant difference in the dynamics of Model 1 with the *r* vs. *K* parameterisation in that the *K* parameterisation takes much longer to equilibrate (~2000 time-steps or more, vs. 5-100 for the *r* parameterisation).

For some combinations of parameter values and initial adult and juvenile density, the *r* parameterisation of Model 1 results in periodic dynamics, with stable, large amplitude oscillations rather than a straightforward equilibrium population size or extinction. The *K* parameterisation does not do this, due to its much longer response time. I discuss the cause of these periodic dynamics in the analysis of equilibria below.

Effect of density-independent parameter values

I examined the relationship between different density-independent parameters (juvenile and adult mortality, maximum reproductive output and time to maturity) and critical thresholds.

For Model 1, both kinds of Allee effect have qualitatively similar responses to changes in juvenile mortality (M_j) and adult mortality (M_a). Critical thresholds of δ decrease as mortality increases with the rate of decline tailing off as mortality increases further. The relationship looks qualitatively like an exponential decline, but I did not find any simple exponential or quadratic function that fits the model results well. For both kinds of Allee effect, juvenile mortality is more important than adult mortality in determining the critical value of δ (Fig. 10).

As with critical values of δ, critical population thresholds change with mortality, increasing as mortality increases. Again, no standard exponential or quadratic function could be fitted to the data. Adult and juvenile mortality have similar quantitative effects on the critical density, but the maximum critical mortality value is lower for juvenile mortality than adult mortality (Figs. 11 and 12).

The relationship between critical values of δ and density and the other population parameters (time to maturity τ and maximum reproductive output α) look similar to the relationships with mortality (an exponential-type decline in critical δ with increases in τ or α, although an exponential relationship does not fit the model values precisely).

Although mortality and reproductive output affect the two kinds of Allee effects equally in Model 1, τ has a stronger effect on populations with juvenile survival Allee effects than with reproductive Allee effects. When τ=1, the critical threshold for juvenile survival and reproductive Allee effects is equal. Increasing τ above one decreases the critical δ threshold for both kinds of Allee effects, but more strongly for juvenile survival Allee effects than reproductive Allee effects, meaning that juvenile survival Allee effects become more severe than reproductive Allee effects in terms of critical δ thresholds (Figs. 13 and 14).

In Model 2, each of the density-independent parameters in isolation has a relatively small effect on model dynamics, which is qualitatively similar to that of Model 1. Eventually, a point is reached at which reproduction can no longer balance mortality, resulting in global extinction. Unlike Model 1, this point is unrelated to the strength of the Allee effect (Figs. 15 and 16).

Adding negative density dependence to Allee effects

It is apparent from the differences in behaviour between Model 1 and Model 2 that negative density dependence has some effect on the qualitative dynamics of populations with Allee effects. The model with both Allee dynamics and negative density dependence (Model 1) has more complex dynamics, and includes a critical strength of Allee effect that results in extinction regardless of initial density. However, the qualitative dynamics outlined above are broadly similar for Models 1 and 2.

There is a large difference in the range of initial conditions in which Models 1 and 2 go extinct, which implies that negative density dependence has a strong quantitative effect on Allee dynamics (e.g. see initial conditions for Figs. 3 and 5). Negative density dependence appears to increase critical density thresholds and decrease critical δ thresholds dramatically. I examined this idea by using Model 1 to add negative density dependence in reproduction to Allee effects in juvenile survival, and *vice versa*.

The effects of adding negative density dependence in one parameter to Allee effects in the other are not symmetrical. For the r parameterisation, negative density dependence in juvenile survival has a very significant effect on the critical δ_r and equilibrium population size for reproductive Allee effects. Although negative density dependence in reproduction has an effect on both critical δ_j and equilibrium population size for juvenile survival Allee effects, it is much more limited (Figs. 17 and 18). For the K parameterisation with $\tau=1$, the situation is reversed, with negative density dependence in reproduction having a greater effect on critical δ and equilibrium population size than negative density dependence in juvenile survival (Figs. 19 and 20).

For the K parameterisation with $\tau=5$, the outcome is more ambiguous, with each kind of density dependence having a comparable proportional effect on critical δ and population size. This is interesting, in that for Allee effects individually both the K parameterisation and increasing τ made juvenile survival Allee effects more severe relative to reproductive Allee effects. However, the effects of the density-independent parameters are non-linear, and in this case, since critical δ for reproductive Allee effects was already higher with the K parameterisation, increasing the value of τ had a proportionately higher effect on reproductive than juvenile survival Allee effects. Thus, the comparisons of the effects of individual population parameters only hold if all other parameters are held equal (Figs. 21 and 22).

Combining both kinds of Allee effect

As with negative density dependence, a combination of two kinds of Allee effects reduces critical values significantly relative to only one Allee effect at a time, for both Model 1 and Model 2. The effects of the two kinds of Allee effect are again not symmetrical, either for equilibrium population size or for critical δ or y values. For the r parameterisation, critical thresholds usually depend more on the value of δ_r than δ_j, while the reverse is true for the K parameterisation. Thus effects cannot be said to be additive – the outcome of changes in parameter values are non-linear so the effect of different combinations is difficult to predict (Tables 5 and 6 and Figs. 23 – 26). Note that Tables 5 and 6 apply to the r parameterisation only – it proved impossible to do the same for the K parameterisation because the model took too long to equilibrate around critical values.

In combination, population persistence depends more on reproductive Allee effects than juvenile survival Allee effects in the r parameterisation, but depends more on juvenile survival than reproductive Allee effects for the K parameterisation (for both models). This is despite the fact that in Model 1, negative density dependence in the juvenile stage combined with reproductive Allee effects is more serious for the r parameterisation, while negative density dependence in the adult stage combined with juvenile survival Allee effects is more serious for the K parameterisation (Figs. 17 – 20). In fact, these two are a corollary of each other; essentially for the *r* parameterisation, a higher value of δ_r than δ_j is more serious, while for the *K* parameterisation, a higher value of δ_j than δ_r is more serious.

Analysis of equilibria

So far I have been concentrating on critical values – the boundaries between areas of parameter space that result in different equilibrium points. These are unstable equilibria, and I can examine these directly by analysing the equilibrium functions themselves. Analysing the equilibria sheds some light on the phenomena discussed above.

For Model 1, the form of the equilibrium equations for each type of Allee effect is shown in Fig. 27. The upper part of each line represents a stable equilibrium, while the lower line is an unstable equilibrium. The stable and unstable lines meet at the maximum critical δ, above which the population goes extinct regardless of initial density. If both stages have initial densities above their respective lower line, the population of each stage goes to the value of the upper line for the given value of δ. If both stages are below their respective lower line, the population goes to extinction. If one stage is below and one is above, the behaviour of the model is unpredictable. Periodic behaviour can happen when one stage is above its unstable equilibrium (i.e. tending to the upper stable equilibrium) while the other stage is below its unstable equilibrium (i.e. tending to extinction). However, it does not fill this entire region of parameter space, nor does it always occur in any part of parameter space under these circumstances (Fig. 28).

Fig. 29 shows the effect of adult mortality on the equilibrium curves for reproductive Allee effects. The other density-independent parameters (M_j, α, τ) look similar, as do the curves for juvenile survival Allee effects.

For Model 2, the equilibrium equation is simpler, with only one solution for any given value of y and density-independent parameters. This solution is an unstable equilibrium corresponding to the critical values. For both types of Allee effect together, the equilibrium curve bisects the N_j/N_a plane, with points to the left and below the curve going to extinction and points above and to the right going to infinity. Changing values of y moves the position of the curve (Fig. 30).

DISCUSSION

Qualitative dynamics

In common with other Allee effect models of different types (differential – Dennis 1989, Quinn *et al.* 1993, Amarasekere 1998, Wells *et al.* 1998, Courchamp *et al.* 1999; delay differential – Cushing 1994; difference – Schreiber *in press*; stochastic – Dennis 1989; Poisson – Gerritsen 1980; spatial and temporal simulation model – Etienne *et al.* 2002), this model confirms that Allee dynamics result in threshold effects. For a given set of parameter values, a model with an Allee effect has a critical population size below which the population does not persist. Conversely, a population of a given size may have a critical strength of Allee effect above which the population will go extinct. This applies equally to Allee effects in reproduction, in juvenile survival and to a combination of both.

I found the same qualitative dynamics with each kind of Allee effect, and by both Allee effects together.

The model with negative density dependence also showed a potential for periodic behaviour (large amplitude oscillations). As with thresholds, I observed periodicity both for reproductive Allee effects and juvenile survival Allee effects, as long as one stage starts above the critical density while one is below (but not in all cases where this is true). Stable, large amplitude oscillations have previously been observed in a model with reproductive Allee effects, where there is a delay in maturation and a narrow fertility window (Cushing 1994), or overcompensatory density dependence (Schreiber *in press*). This model does not have these requirements for periodicity to occur.

Natural systems are more complicated than models, and periodicity is likely to be disrupted by environmental stochasticity, more age classes, recruitment from elsewhere, metapopulation structure etc. Nonetheless, such periodic and chaotic behaviour has been shown to be more important than expected in undermining persistence in simple experimental systems (Belovsky *et al.* 1999), although in models chaotic fluctuations can either increase or decrease extinction probability (Allen *et al.* 1993, Schreiber *in press*). It is important to bear in mind that Allee effects have the potential to create such unstable dynamics.

Which type of Allee effect is worse?

I have considered the severity of an Allee effect in terms of critical thresholds in both density and Allee effect strength. Using the critical density measure, reproductive Allee effects are usually more severe than juvenile survival Allee effects. This is not surprising since reproductive Allee effects are acting on the adult stage, which is nearly always going to be less numerous than the juvenile stage (some clonal organisms excepted). Thus, all else being equal, an Allee effect which acts on a later life history stage, up to the point of first reproduction, will cause a higher critical density than an Allee effect that acts earlier in the life history. An Allee effect that acts only after the point of first reproduction has much greater difficulty in driving a population extinct. I tested this by trying to incorporate Allee effects into adult survival (the bottom right element of the transition matrices shown in Tables 3 and 4), and found that I could not get the Allee effect to drive the population to extinction for any parameter values that I tried.

Using the measure of critical density thresholds, it is possible that an Allee effect is most severe when it acts on the stage which has the highest reproductive value. Reproductive value, which measures the proportional contribution of an individual to future generations from that point on, is usually maximised around or just before the age of first reproduction (Gotelli 1998, Caswell 2001). It is difficult to calculate reproductive value in a density-dependent model, but in the density-independent version of our model, adults have a higher reproductive value than juveniles for both *r* and *K* parameterisations, which would be consistent with this hypothesis.

If I consider severity in terms of critical Allee thresholds, the relative severity of reproductive and juvenile survival Allee effects depends on life history. Essentially, populations with more "*K* selected" life histories (low reproductive rates, low mortality and long time to maturity) are more likely to be affected by juvenile survival Allee effects, while populations with more "*r* selected" life histories (high reproductive rates, high mortality and short time to maturity) are more likely to be affected by reproductive Allee effects. This does not mean that certain species will only have certain types of Allee effect, it just means that a given strength of Allee effect has different population consequences, depending on the life history.

I found very different response times in the model for the *r* vs. *K* parameterisation. While the *r* model equilibrated quickly (nearly always in less than 10 time-steps), the *K* model took several hundred or more time-steps to equilibrate. In real populations, this will have the effect of blurring the population consequences of Allee effects, particularly in combination in demographic and environmental stochasticity. Allee effects can still exist in *K* selected populations, and can still have population consequences, but those consequences might be difficult to observe since such populations are not usually at equilibrium.

Adding Allee effects together

I found that it is difficult to predict the consequence of combining more than one kind of Allee effect. Sometimes the effect of two Allee effects was minimally different from one, sometimes it was drastically worse, although it was never better. Since reproductive and juvenile survival Allee effects had different population consequences depending on the life history, the effect of adding them together was also not symmetrical. Overall, for a population that has two potential sources of Allee effects, I found no convenient rule for combining Allee thresholds, and can only recommend that research concentrates on elucidating the life history. Only when that is known can predictions be made about the impact of multiple Allee effects on population dynamics.

Effect of negative density dependence

It is clear from this study that negative density dependence has strong impacts on the population consequences of Allee effects. This can be seen in the quantitative differences between Models 1 and 2, as well as when negative density dependence was added in the non-Allee stage in Model 1. In both cases, adding negative density dependence made the population consequences of a given Allee effect much worse. Often, adding negative density dependence alone had almost the same impact as adding negative density dependence plus a second Allee effect. It is clear from this model that information about other sources and types of density dependence are important in making predictions about the population consequences of Allee effects.

Effect of human disturbance

Anthropogenic changes to density-independent population rates: I found with this model that there is an exponential-type relationship between the value of density-independent parameters in the model (juvenile and adult mortality, maximum reproductive output and time to maturity) and critical thresholds. Thus relatively small change in density-independent parameters could have large impacts on the value of critical thresholds (increasing critical density thresholds and decreasing critical Allee effect thresholds). Human activities have the potential to alter the value of all these parameters in natural populations, by changing survival, condition and growth rates. I am particularly interested in the effect of mortality, since this is where there is the strongest evidence for human-induced change in many populations. Here I consider the potential effect of direct human intervention in mortality rates through exploitation, in the context of an Allee effect.

Several models conclude that mortality or exploitation increases critical density thresholds for Allee effects (Gerritsen 1980, Dennis 1989, Quinn *et al.* 1993), but not many have looked at the form of the relationship. Gerritsen (1980) describes the relationship between mortality and critical density as "exponential", which is true also in the model in the sense that a linear increase in mortality - defined as *–ln*(survival probability) - results in a monotonic relationship with critical density of increasing slope. However, in this model, a simple exponential model does not fit the data for any of the density-independent parameters, and this appears to be the case with Gerritsen (1980) as well. The relationship may not be easily defined mathematically.

Exploitation can double or more than double adult mortality relative to natural levels, even when it is considered sustainable. The American Fisheries Society recommends that for vulnerable stocks such as long-lived reef fish, management should act conservatively by keeping fishing mortality "at or near natural mortality" i.e. doubling total mortality (Coleman *et al.* 2000). See Table 7 for some examples of estimates of natural and fishing mortality in some exploited populations.

From this model, what are the potential consequences of large increases in mortality rates for a population with Allee effects? Given the "exponential" nature of the relationship, this model suggests that a doubling of total mortality could have a dramatic impact in terms of approaching critical thresholds and thus increasing extinction probability. Recall that with *K*-selected species, the crossing of a critical threshold will not be immediately visible according to this model, but it can nonetheless put the population on a downward trajectory towards extinction. Some *K*-selected exploited species, such as sharks, may be on such a trajectory (Baum *et al.* 2003), although as far as I know no-one has looked for Allee effects in sharks.

Dennis (1989) applied Allee effects to a standard fisheries model, and showed that as harvesting rates (adult mortality) increase, critical population thresholds approach the population size at which maximum sustainable yield (MSY) is obtained. Traditional fisheries management has focussed on trying to maintain biomass at the level which produces MSY (B_{MSY}), since this is the most efficient (biologically speaking), although most modern work on fisheries suggests that this is a risky approach (Hilborn and Walters 1992). If B_{MSY} is also close to the Allee threshold biomass, managing stocks for MSY is even more risky that previously thought.

There are a large variety of mechanisms for Allee effects in exploited marine species, including broadcast spawning (Denny and Shibata 1989, Levitan *et al.* 1992), predation (Wood 1987, Seitz *et al.* 2001), "cultivation effects" (predation by adults on the predators of juveniles; Walters and Kitchell 2001) and the physical protection of juveniles or habitat modification for juveniles by adults (Tegner and Dayton 1977, Quinn *et al.* 1993).

Could Allee effect thresholds provide part of the explanation in some cases for unexpected collapses in fished populations where mortality has been increased to several times natural levels? Evidence for Allee effects (or "depensation" as it is usually referred to in the fisheries literature) in exploited fish stocks is equivocal (Myers *et al.* 1995), however the large variance in stock-recruitment data means that Myers's approach may have limited power to detect Allee effects (Liermann and Hilborn 1997, Shelton and Healey 1999, Hutchings 2000). In addition, there is often uncertainty about what constitutes a "stock", which should be a population or sub-population that is more or less reproductively isolated. If the stock considered by managers actually consists of several sub-stocks, the effects of Allee effects and extinctions at the sub-stock level may be masked until the metapopulation reaches a critical point (Frank and Brickman 2000, Courchamp *et al.* 2000a). I suggest that some expectation of non-linear dynamics, rather than smooth, gradual stock declines under exploitation, should be incorporated as a component of precautionary fisheries management.

<u>Anthropogenic changes to density dependence</u>: Human impacts on natural populations can create Allee effects. For example, fishing tends to act like a Type II predator functional response, causing increasing *per capita* mortality with declining population size (Post *et al.* 2002). Introduced predators can act the same way (Sinclair *et al.* 1998, Chapter 4). Human activities can also alter the strength of Allee effects. For example, a predation-driven Allee effect is affected by the number, species composition and mobility of predators, availability of alternative prey, availability of shelter, spatial heterogeneity etc. (Sinclair and Pech 1996, Murdoch *et al.* 1996). An Allee effect that is driven by some

factor intrinsic to a population (such as reproduction) may also vary. For example, if the Allee effect is mediated by the animal's ability to locate a suitable mate at low density, this might vary by habitat type, habitat fragmentation, water clarity (for visual cues) and pollution (for chemical cues). Anthropogenic changes to ecosystems could make Allee effects stronger (e.g. disrupting mate finding ability) or weaker (e.g. reducing predator populations).

The model with negative density dependence has a maximum critical strength of Allee effect for a given population, above which the population will go extinct regardless of the initial population size. This becomes clear in the equilibrium analysis, since there is a value of δ, above which there is no equilibrium population size except zero. Essentially, the population is being squeezed between the lower, unstable Allee threshold and the carrying capacity. As well as changing the Allee effect threshold, human activities can reduce the carrying capacity, by reducing habitat quality or resource availability, or by fragmenting habitat. Thus while it seems unlikely that a population in its natural state would have evolved under conditions which bring it close to a "maximum critical Allee effect" (Yund 2000) it is not impossible that human pressure could squeeze population equilibria in both directions such that an Allee effect could drive even a large or dense population extinct (Fig. 29).

Resilience in populations and ecosystems

In Fig. 27, the distance between the top and bottom of the equilibrium curve can be thought of as corresponding to the resilience of the population to natural or anthropogenic change. As the critical Allee threshold gets closer to the upper stable equilibrium, the population is less able to recover back to the stable equilibrium from perturbations, hence increasing the value of δ or increasing mortality makes the population less resilient. Resilience is a concept which is usually applied to ecosystems which have shown a propensity for abrupt transitions to alternative stable states, such as rangelands, coral reefs and lakes (Noy-Meir 1975, Scheffer *et al.* 2001). Allee effects may provide a new way to look at mechanisms for resilience and rapid change at the ecosystem as well as the population level.

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TABLES

Table 1

Value of density-independent parameters used in this paper.

Parameter	Symbol	"*r*" parameter values	"*K*" parameter values
Survival probability	e^{-Mj}, e^{-Ma}	0.03 – 0.6	0.78 – 0.99
Maximum reproductive output	α	10 – 150	0.5 – 0.75
Time to maturity	τ	1	1 – 5

Table 2

Density-independent transition matrix (Model 1). e^{-Mj} = juvenile survival probability, e^{-Ma} = adult survival probability, τ = mean time to maturity, α = reproductive output.

$e^{-Mj} . (1 - 1/\tau)$	α
$e^{-Mj} . 1/\tau$	e^{-Ma}

Table 3

Density-dependent transition matrix with Allee effect and negative density dependence (Model 1). δ = Allee effect parameter, β sets slopes and intercepts of curves with different δ values, N_j = juvenile density, N_a = adult density, D_r and D_j are dummy variables that act as switches turning on and off density dependence in juvenile survival and reproduction respectively.

$D_j . e^{-Mj} . (1 - 1/\tau) . N_j^{\delta-1} / (1 + \beta N_j^{\delta}) + (1 - D_j) . e^{-Mj} . (1 - 1/\tau)$	$D_r . \alpha . N_a^{\delta-1} / (1 + \beta N_a^{\delta}) + (1 - D_r) . \alpha$
$D_j . e^{-Mj} . 1/\tau . N_j^{\delta-1} / (1 + \beta N_j^{\delta}) + (1 - D_j) . e^{-Mj} . 1/\tau$	e^{-Ma}

Table 4

Density-dependent transition matrix with Allee effect only (Model 2). γ is a function of y, the Allee effect parameter.

$D_j \,.\, e^{-Mj} \,.\, (1 - 1/\tau) \,.\, \gamma N_j / (1 + \gamma N_j) +$ $(1 - D_j) \,.\, e^{-Mj} \,.\, (1 - 1/\tau)$	$D_r \,.\, \alpha \,.\, \gamma N_a / (1 + \gamma N_a) + (1 - D_r) \,.\, \alpha$
$D_j \,.\, e^{-Mj} \,.\, 1/\tau \,.\, \gamma N_j / (1 + \gamma N_j) +$ $(1 - D_j) \,.\, e^{-Mj} \,.\, 1/\tau$	e^{-Ma}

Table 5

Model 1: Critical values of adult mortality (M_a) for different combinations of Allee effects and negative density dependence, in order of decreasing critical M_a (increasing severity of population consequences of Allee effect), for the *r* parameterisation. The effects of combined density dependence in juvenile survival and reproduction are not symmetrical, even though the effects of each separately are (for these parameter values). Critical M_a depends to some extent on the value of δ_j but much more on the value of δ_r. (Initial conditions are $M_i = 1.5$, $\tau = 1$, $\alpha = 100$, initial population density vector = [10 10].)

δ_r	δ_j	**critical M_a with *r* parameters**
density indep.	4	1.3
4	density indep.	1.3
1	4	0.8
2	2	0.07
2	3	0.05
3	2	0.025
4	1	0.02

Table 6

Model 2: Critical values of y for different combinations of Allee effects, in order of increasing y (increasing severity of population consequences of Allee effect), for the r parameterisation. Where there are two Allee effects, the value of one is fixed and the critical value of the other is shown. A given value of reproductive Allee effect has a stronger effect on critical values of juvenile survival Allee effects than *vice versa*. (Initial conditions are $M_i = M_a = 2$, $\tau = 1$, $\alpha = 10$, initial population density vector = [10 10].)

Reproductive Allee effect?	Juvenile survival Allee effect?	Value of fixed y_r	Value of fixed y_j	Critical y
no	yes	-	-	0.02
yes	yes	0.5	-	0.02
yes	no	-	-	0.18
yes	yes	-	0.5	0.18
yes	yes	-	0.2	0.22
yes	yes	-	0.1	0.26
yes	yes	0.2	-	0.52
yes	yes	0.1	-	extinct for all y

Table 7

Natural mortality and fishing mortality for a variety of exploited species, showing that fishing can cause large increases in the mortality of exploited stages (usually adults).

Stock	**Natural mortality**	**Fishing mortality**	**Reference**
Pink shrimp, *Pandalus borialis*, Kachemak Bay, Alaska	0.4	0.3 [1]	Fu *et al.* 2001(b)
Pink shrimp, northern Barents Sea	0.24	0.2 – 0.39 [1]	Fu *et al.* 2001(b)
Bigmouth sole, *Hippoglossina stomata*, Baja California	0.17	0.52 [2]	Martinez-Munoz and Ortega-Salas 2001
Atlantic cod, *Gadus morhua*, eastern Nova Scotia, pre-1990	0.3	0.5	Fu *et al.* 2001(a)
Southern rock lobster, *Jasus edwardsii*, northwest Tasmania	< 0.1	1 – 1.2	Frusher and Hoenig 2001
Striped bass, *Morone saxatilis*, Lake Gaston, North Carolina, 1997 / 1998	0.16 / 0.12	0.74 / 0.34	Hightower *et al.* 2001
Brown trout, *Salmo trutta*, Lake Songsjoen, Norway	0.31	0.5	Langeland and Pedersen 2000
Western king prawn, *Penaeus latisulcatus*, Gulf St. Vincent, Australia, males / females	1.25 / 1.12	6.1 / 4.9	Xiao and McShane 2000
Red sea urchin, *Strongylocentrotus franciscanus*, northern California	0 – 0.23	0.11 – 1.87	Morgan *et al.* 2000

[1] Considered optimum fishing mortality for maximum sustainable yield

[2] Not a target species; mortality from by-catch

FIGURES

Fig. 1

Effect of δ on curves in Model 1. With β=45, the curves are affected by the value of δ only at low density, as is appropriate for modelling an Allee effect.

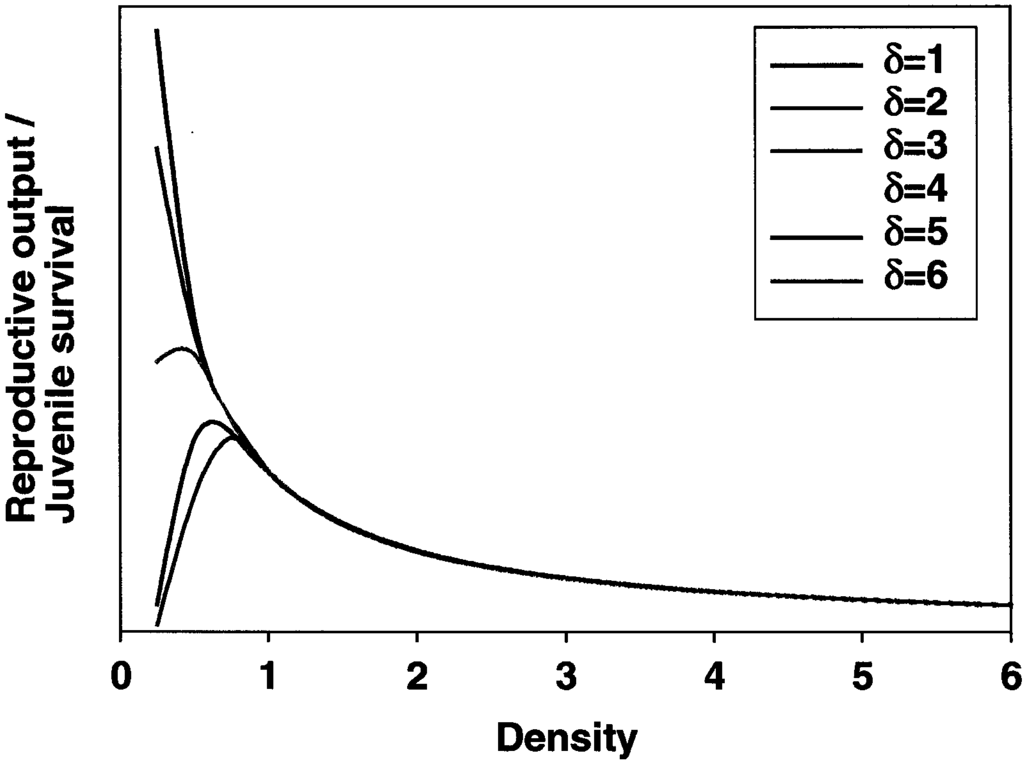


Fig. 2

Effect of *y* on curves in Model 2.

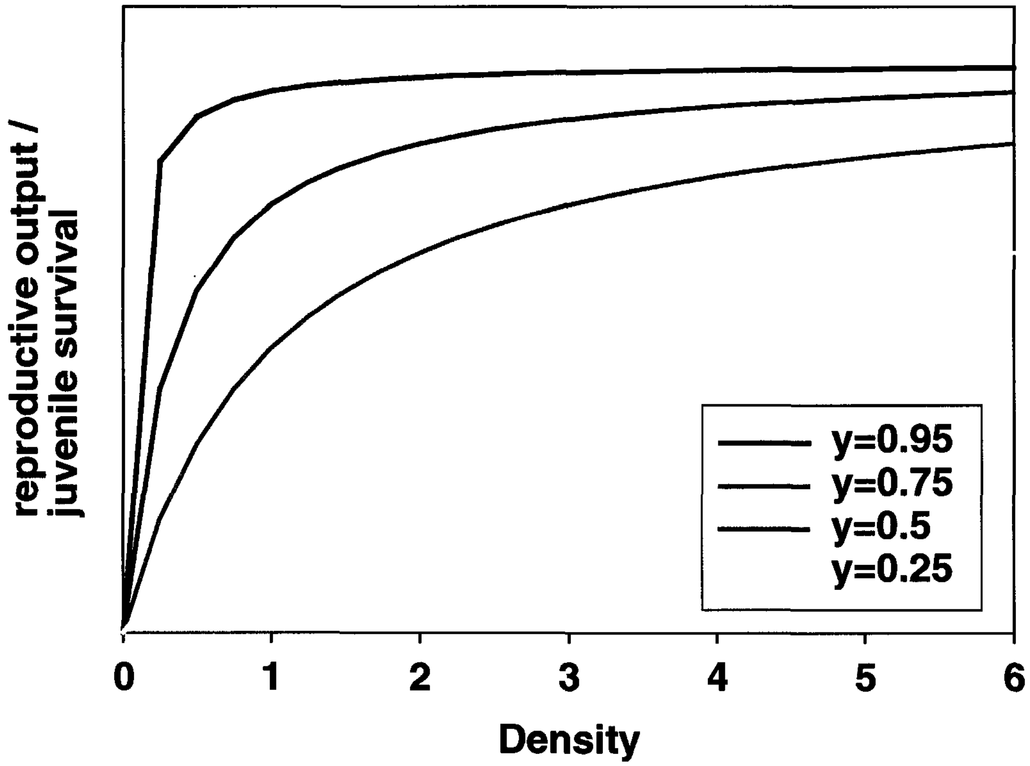


Fig. 3

Model 1: Strength of Allee effect (value of δ) vs. adult population size at equilibrium, for reproductive Allee effects and juvenile survival Allee effects with *r* parameterisation. There is a threshold strength of Allee effect above which a population with a given set of initial conditions goes extinct; for $\tau = 1$ the threshold value is identical for both kinds of Allee effects (initial conditions: $M_j = M_a = 1.5$, $\tau = 1$, $\alpha = 100$, initial density vector = [10 10]).

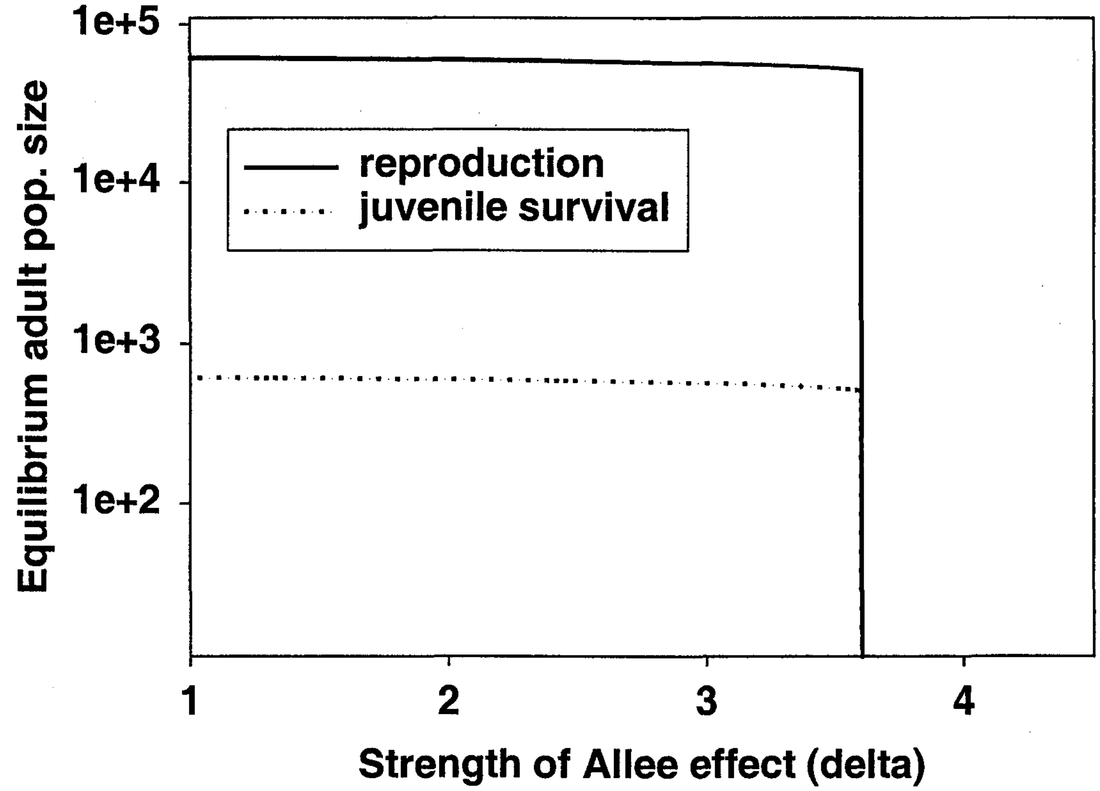


Fig. 4

As Fig. 3, with τ=2. The critical Allee threshold is reduced for both types of Allee effect, but more so for juvenile survival Allee effects.

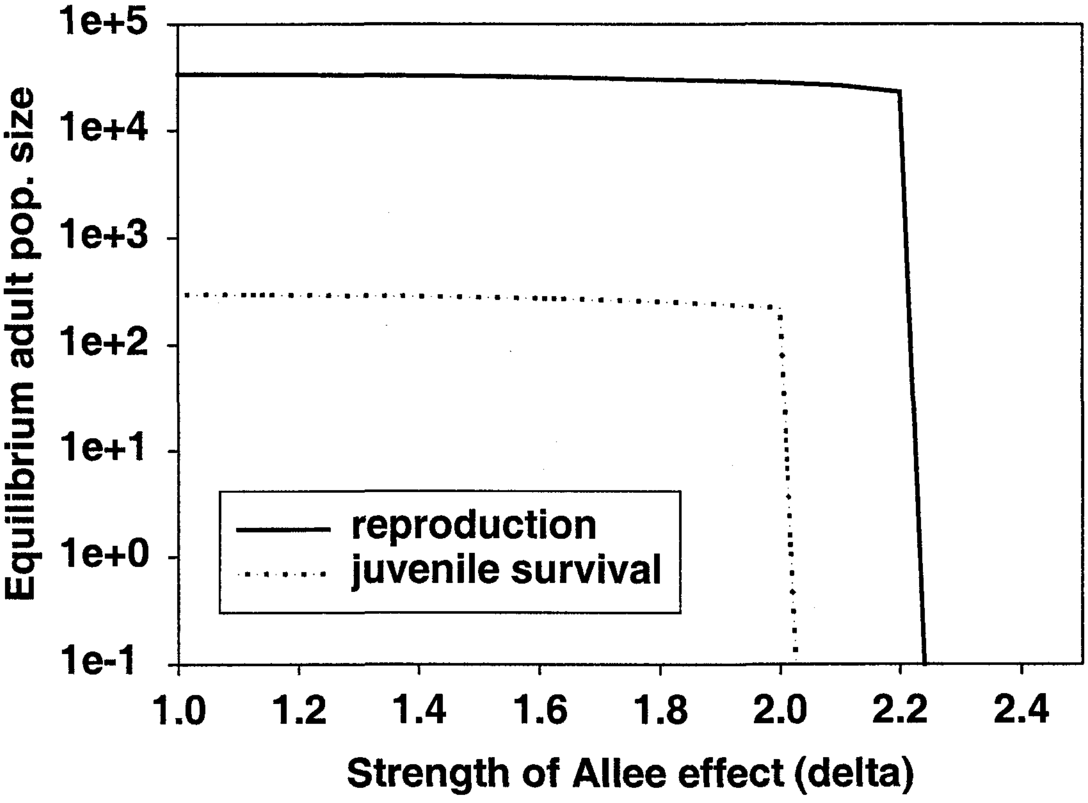


Fig. 5

Model 2: Strength of Allee effect (value of y – lower value of y is a stronger Allee effect) vs. population growth rate (r), for reproductive Allee effects and juvenile survival Allee effects, with r parameterisation. As with Model 1, there is a threshold strength of Allee effect below which a population with a given set of initial conditions goes extinct, indicated by the heavy dashed line at r=0. The threshold is higher for reproductive than for juvenile survival Allee effects, indicating that a given strength of reproductive Allee effects has more serious population consequences than the same strength of juvenile survival Allee effects for these initial conditions ($M_j = M_a = 2, \tau = 1, \alpha = 10$, initial density vector = [10 10]).

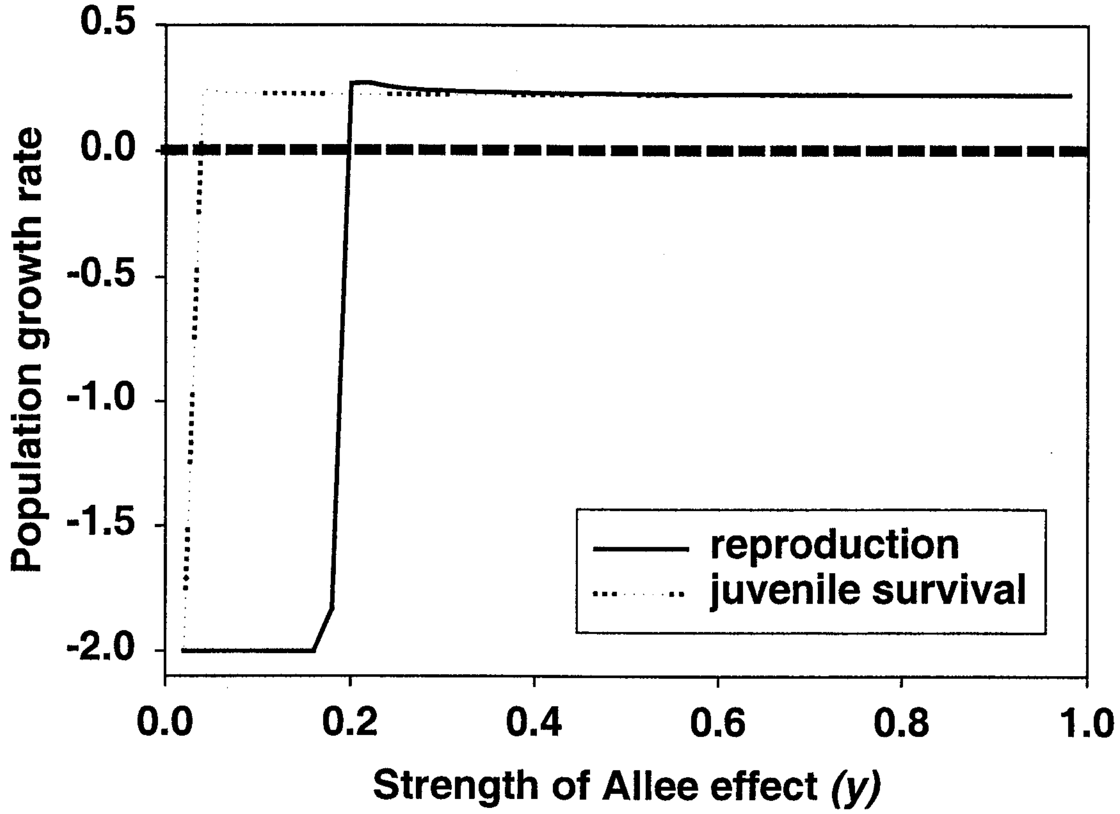


Fig. 6

As Fig. 5, with *K* parameterisation (M_j=0.25, M_a=0.2, α=0.5, τ=5). In this case, juvenile survival Allee effects cause collapse at a higher value of *y* than reproductive Allee effects.

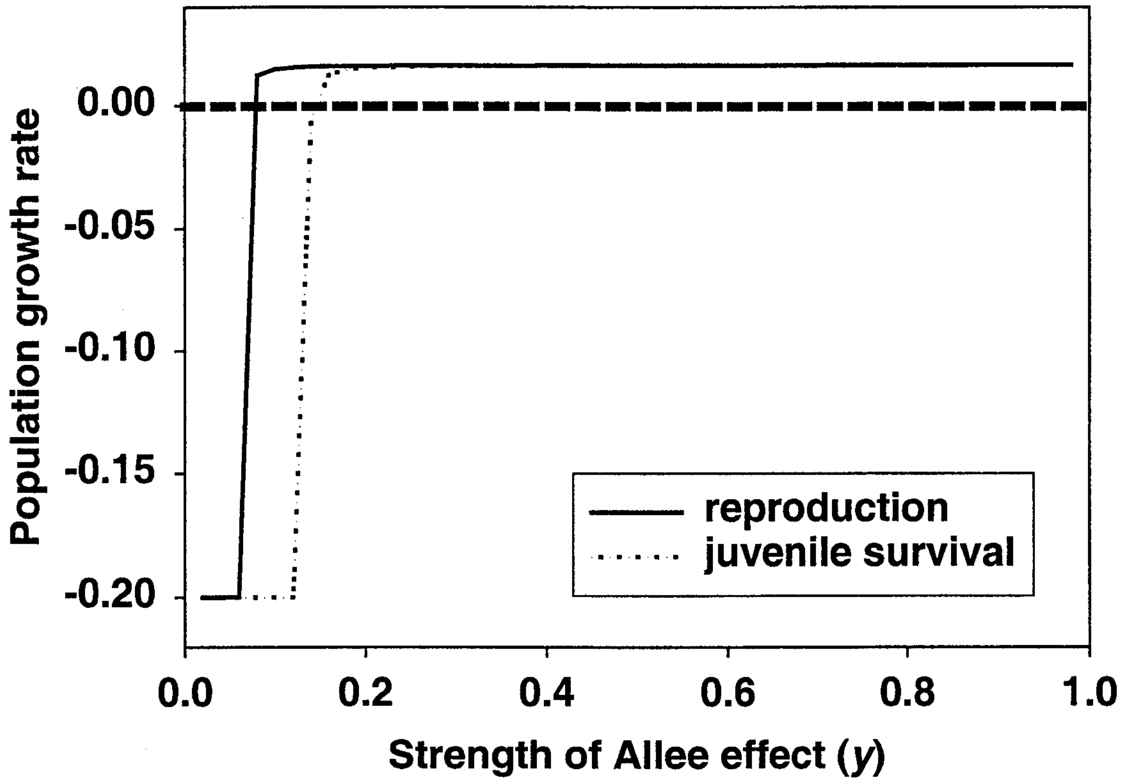


Fig. 7

Model 1: Strength of Allee effect (value of δ) vs. critical adult population density (initial density below which the population collapses to extinction) for reproductive and juvenile survival Allee effects. The maximum critical δ for these parameter values is δ=3.7 for both kinds of Allee effect. For δ<3.7, the relationship between critical density and strength of Allee effect is roughly exponential.

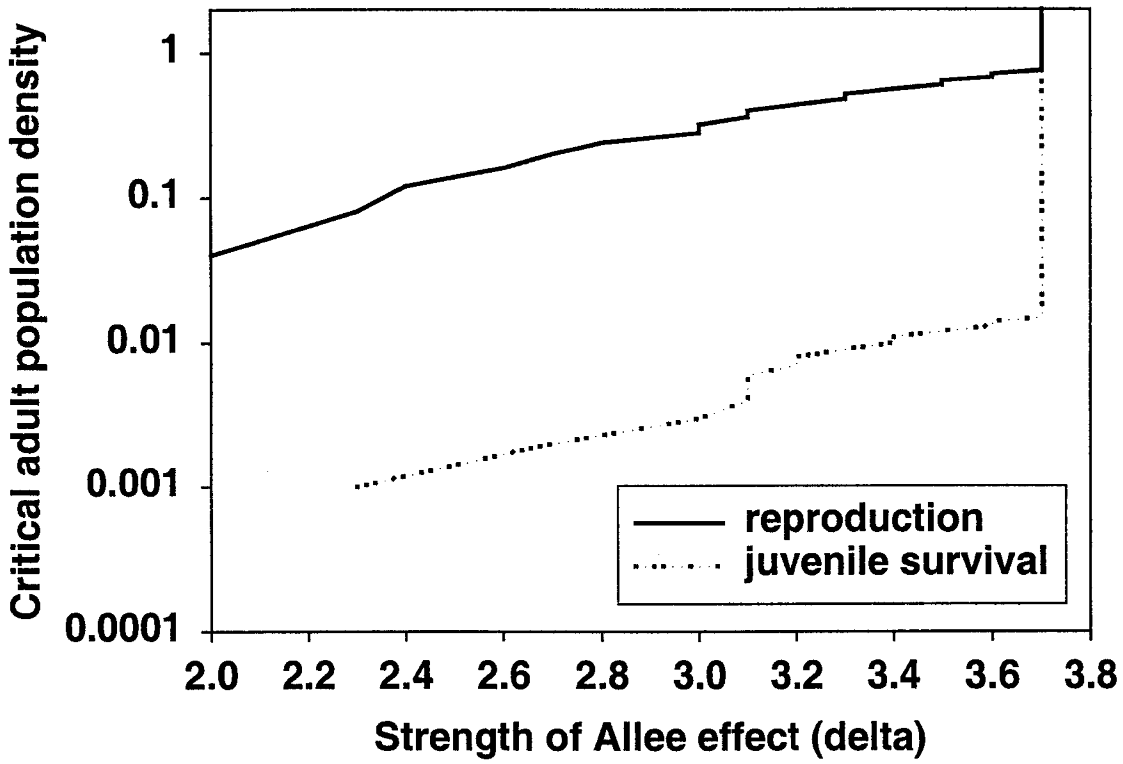


Fig. 8

Model 2: Strength of Allee effect (value of y) vs. critical juvenile population density (initial density below which the population collapses to extinction) for reproductive and juvenile survival Allee effects, with r parameterisation.

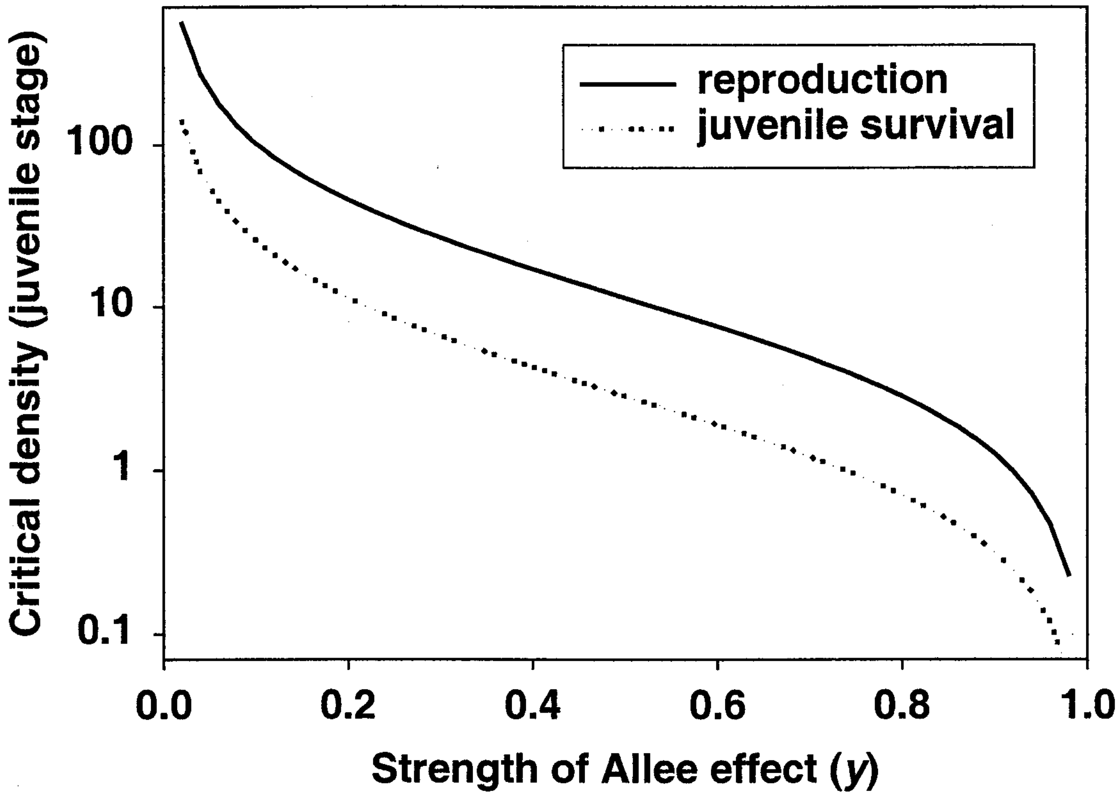


Fig. 9

As Fig. 8, but with *K* parameterisation (M_j=0.2, M_a=0.1, τ=1, α=2). Note that juvenile survival Allee effects are now more severe than reproductive Allee effects in terms of critical density thresholds.

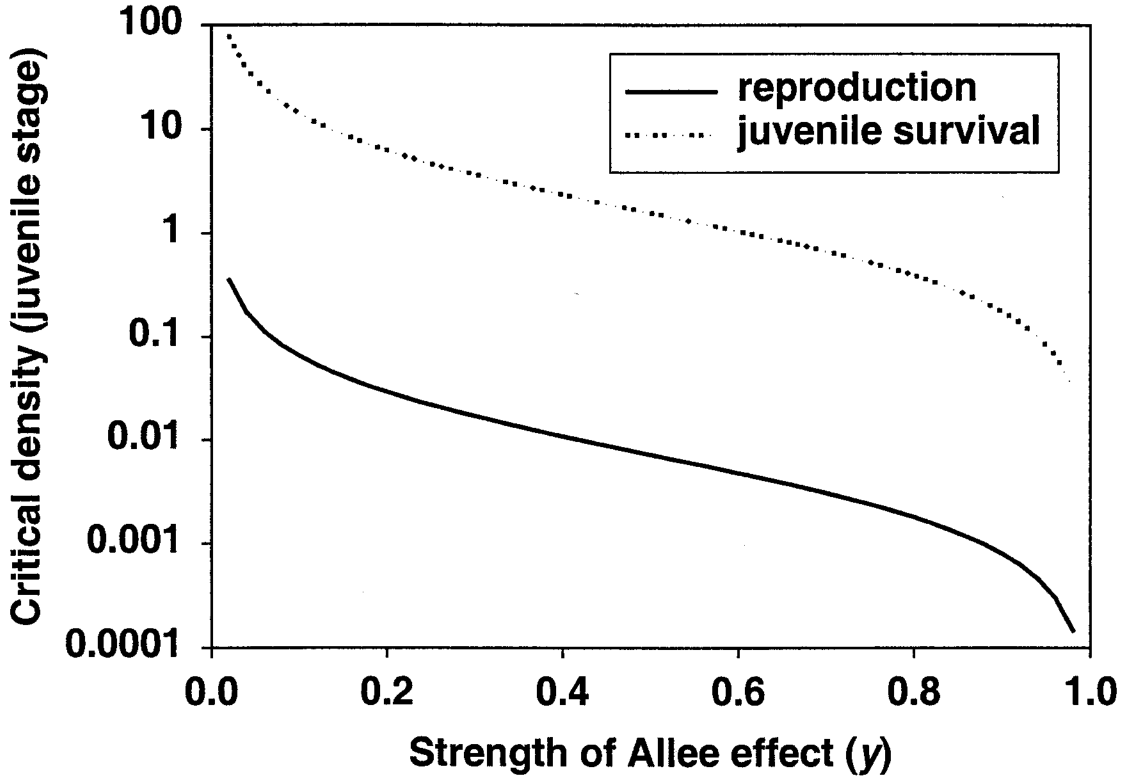


Fig. 10

Model 1: Adult and juvenile mortality vs. max. critical δ. Increasing mortality decreases maximum critical δ, with juvenile mortality having a stronger effect that adult mortality. This qualitative relationship applies for reproductive Allee effects, juvenile survival Allee effects and a combination, although the specific values of δ and M are different. Here initial conditions are as for Figs. 7 and 8, with reproductive Allee effects (δ_r=3).

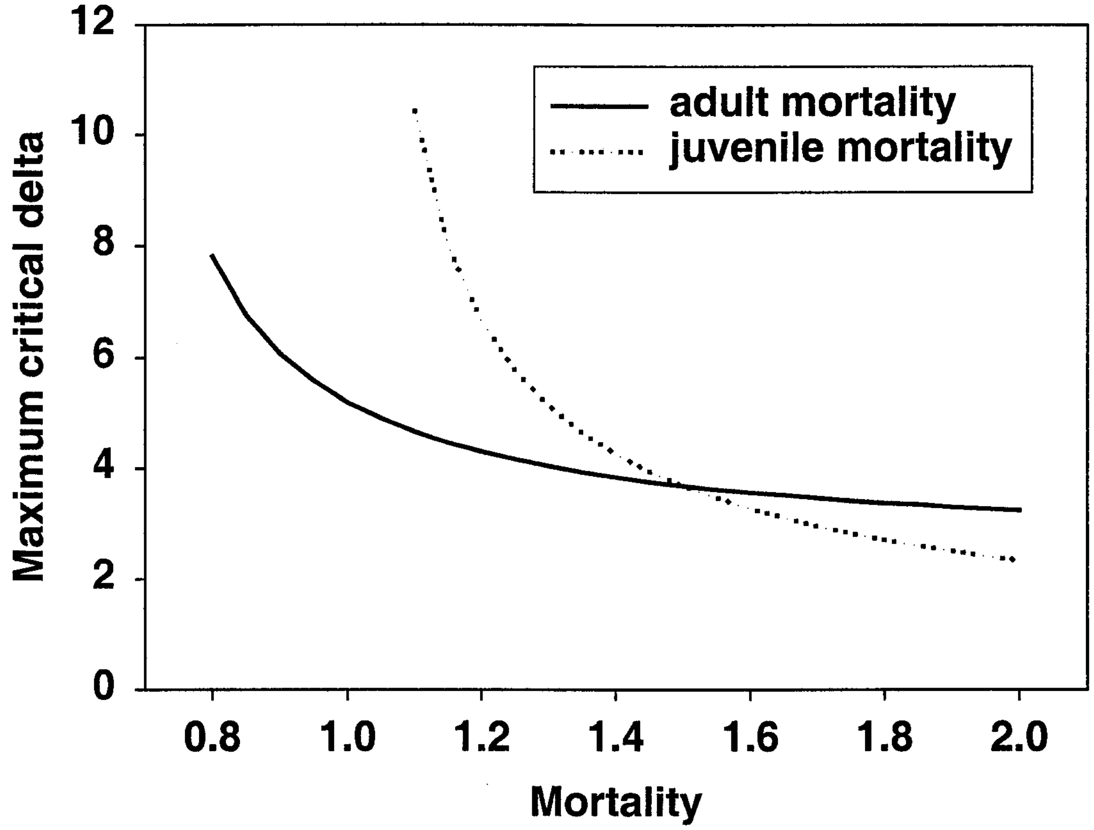


Fig. 11

Model 1: Adult and juvenile mortality vs. critical density for reproductive Allee effect ($\delta_r = 3$). The relationships are similar in shape, with a possible change in slope at intermediate mortality. The curve in each case stops at the maximum critical mortality (extinction at all densities).

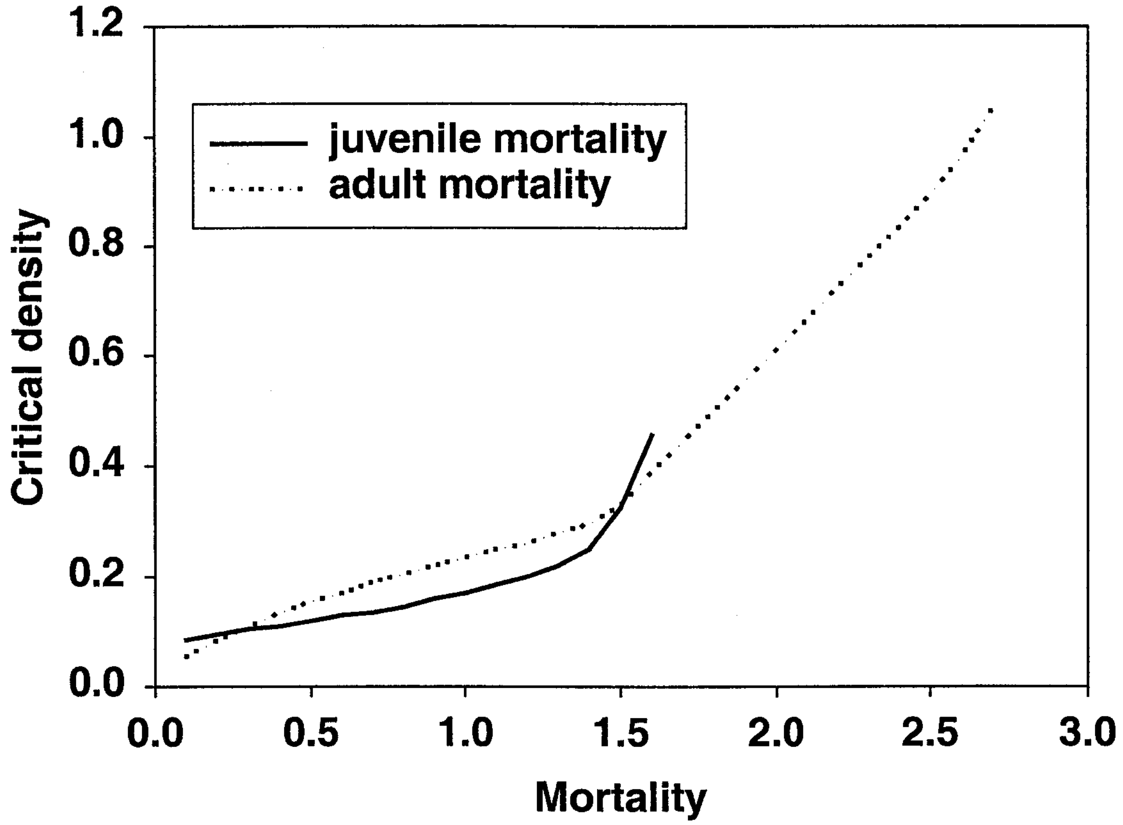


Fig. 12

As Fig. 11, but with juvenile survival Allee effects (δ_j=3).

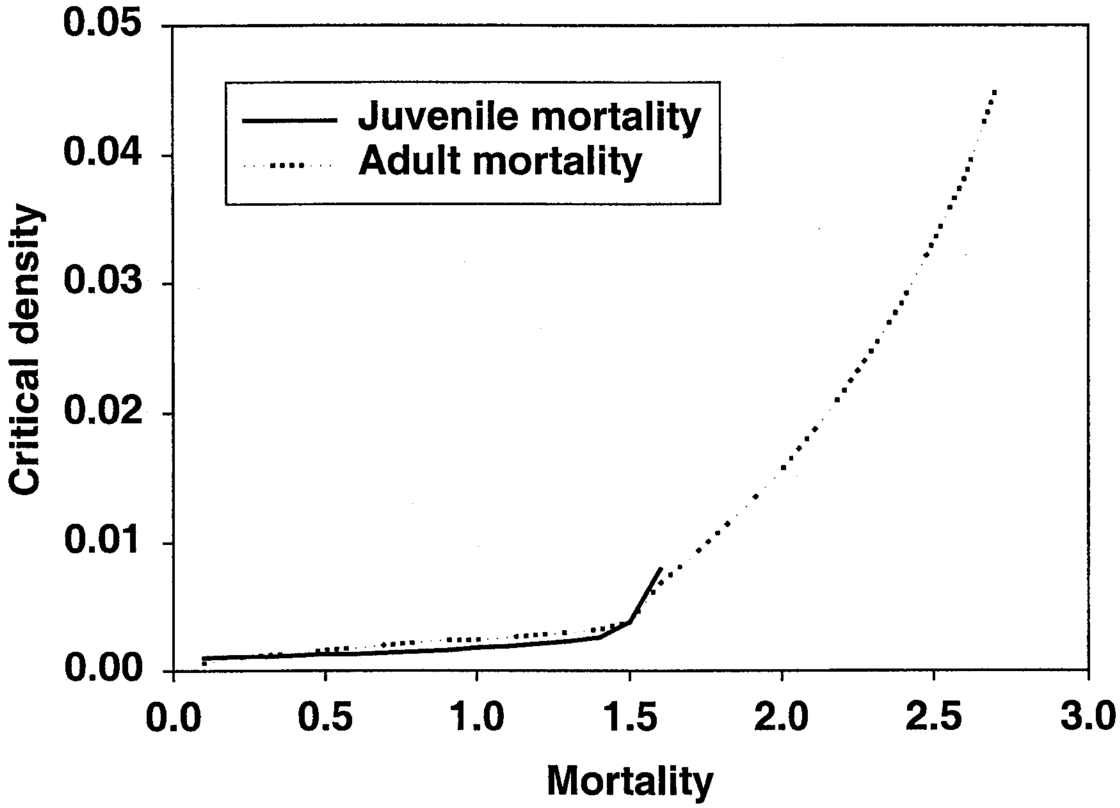


Fig. 13

Model 1: Maximum critical δ as a function of time to maturity (τ).

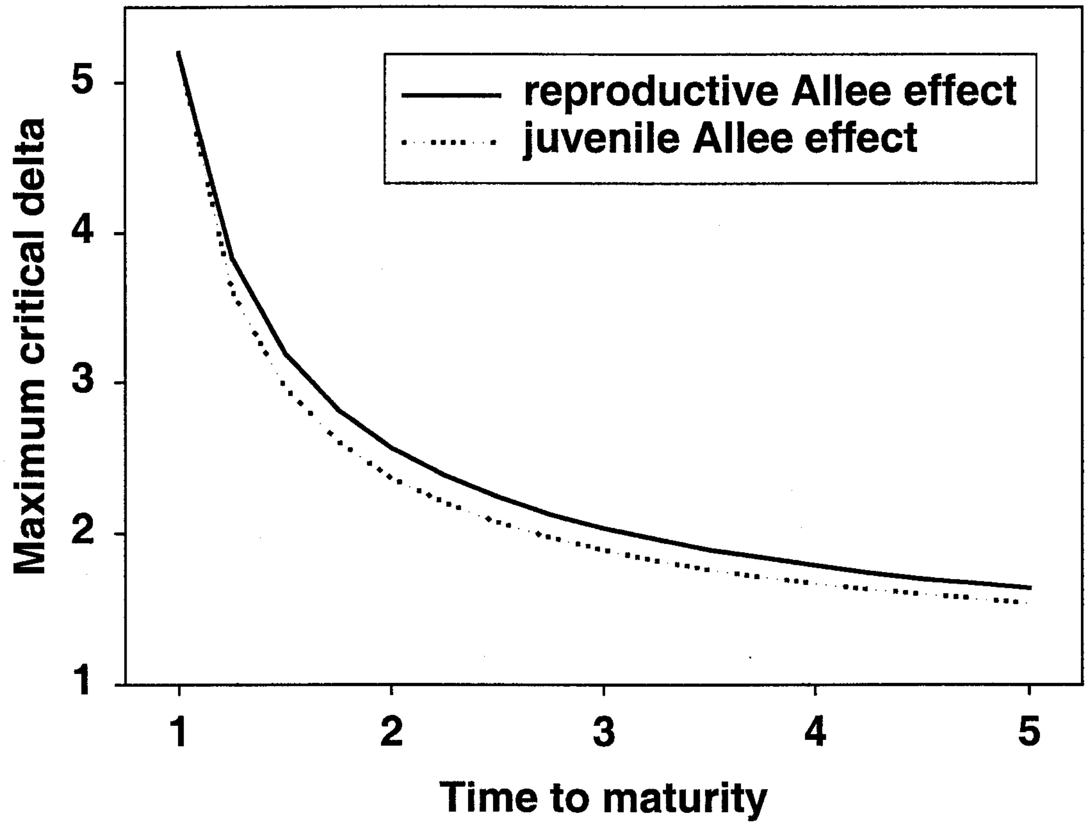


Fig. 14

Model 1: Maximum critical δ as a function of maximum reproductive output (α). Curves for reproductive and juvenile survival Allee effects are identical for τ=1, and very similar for other values of τ.

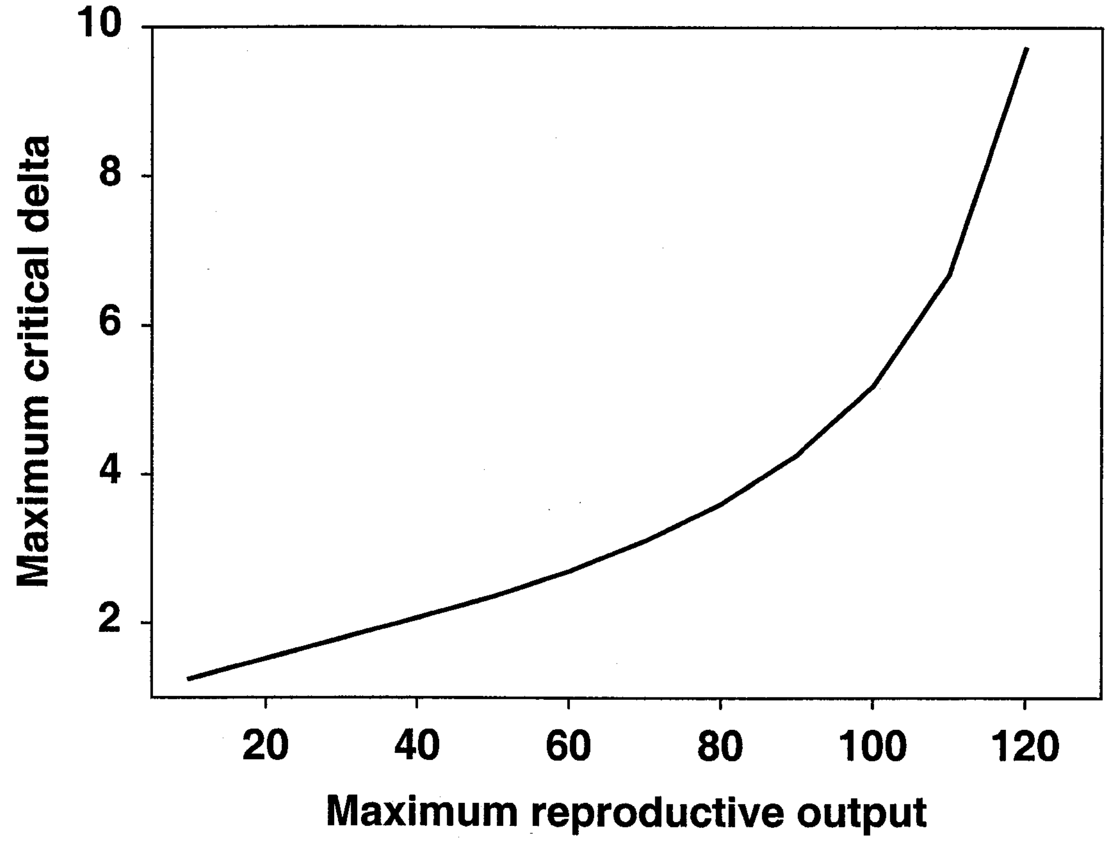


Fig. 15

Model 2: Critical density vs. *y* for various values of adult mortality (other initial conditions as for Fig. 5). Density independent parameters had a more limited impact on Model 2 than Model 1, up to the point were reproduction no longer balanced mortality (global extinction).

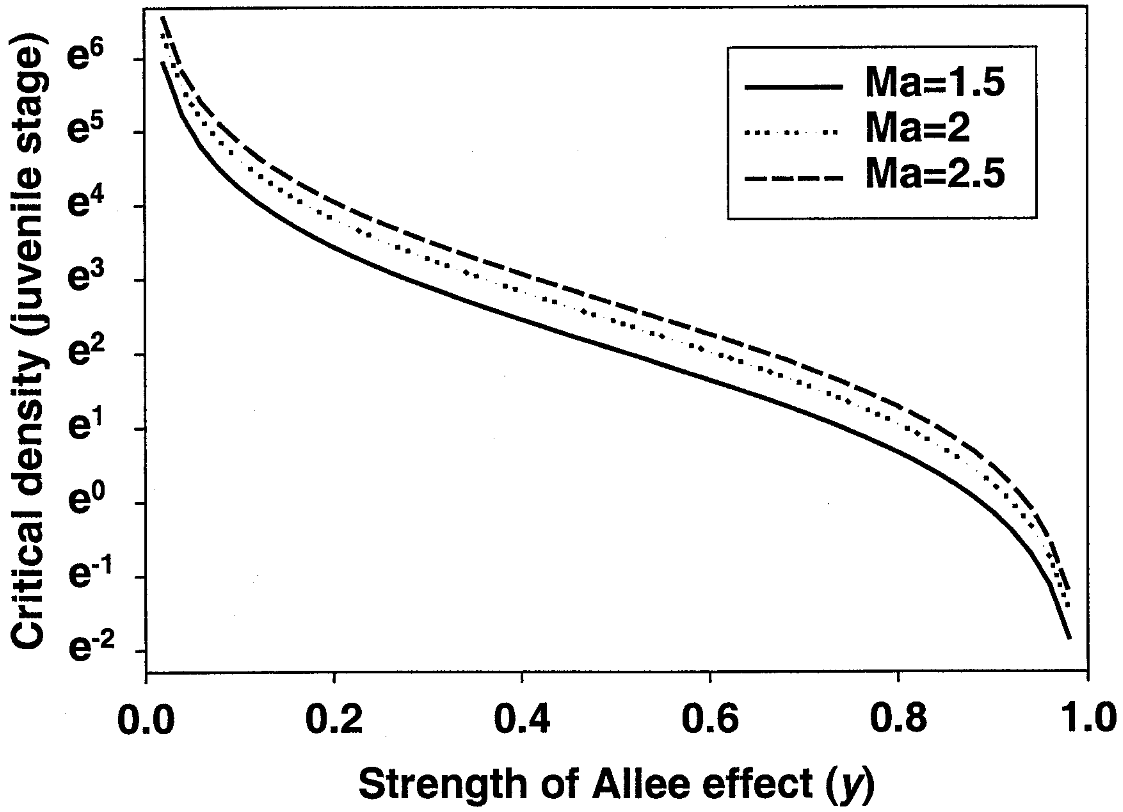


Fig. 16

Model 2: Effect of time to maturity (τ) on critical densities for a given strength of Allee effect. Curves look qualitatively similar for both types of Allee effects and parameterisations; in this case I show juvenile survival Allee effects and *K* parameterisation.

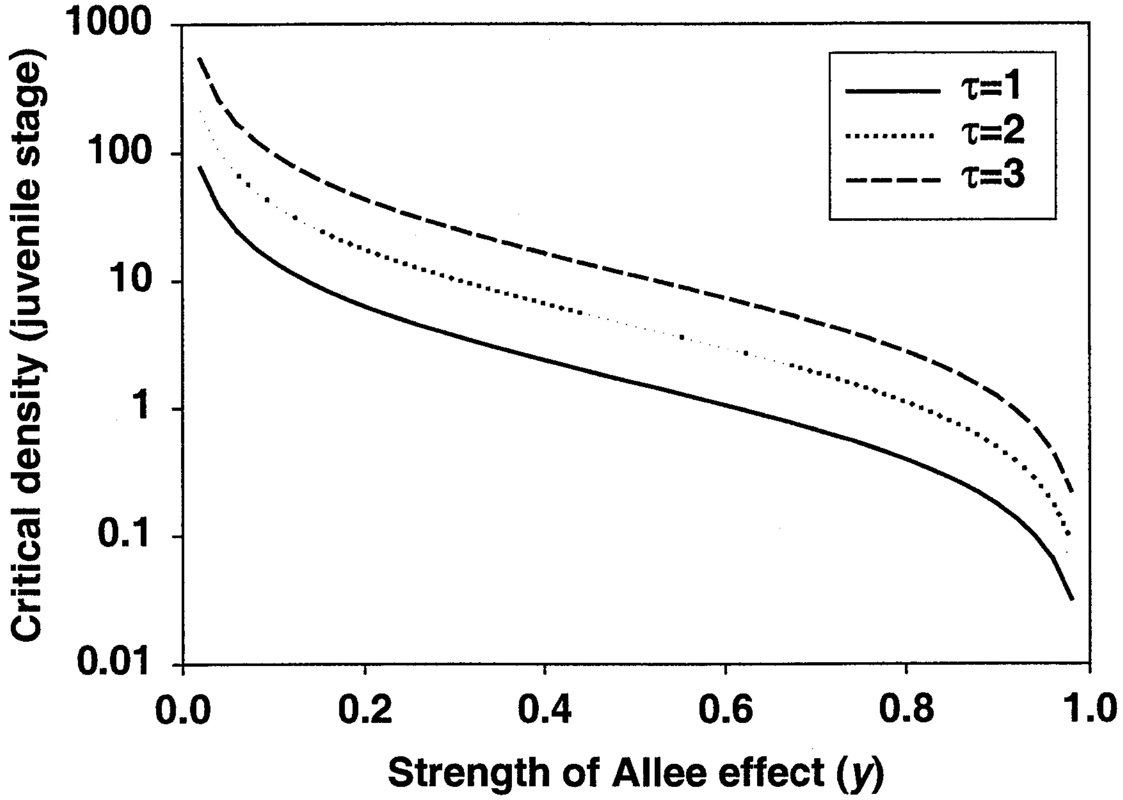


Fig. 17

Model 1: Strength of Allee effect vs. adult equilibrium population size with *r* parameterisation, for i) reproductive Allee effect only; ii) reproductive Allee effect, with negative density dependence in juvenile survival ($\delta_j = 1$), iii) juvenile survival Allee effect only and iv) juvenile survival Allee effect with negative density dependence in reproduction ($\delta_r = 1$). (Initial conditions: M_j=M_a=1.5, α=100, τ=1, initial density vector = [10 10].)

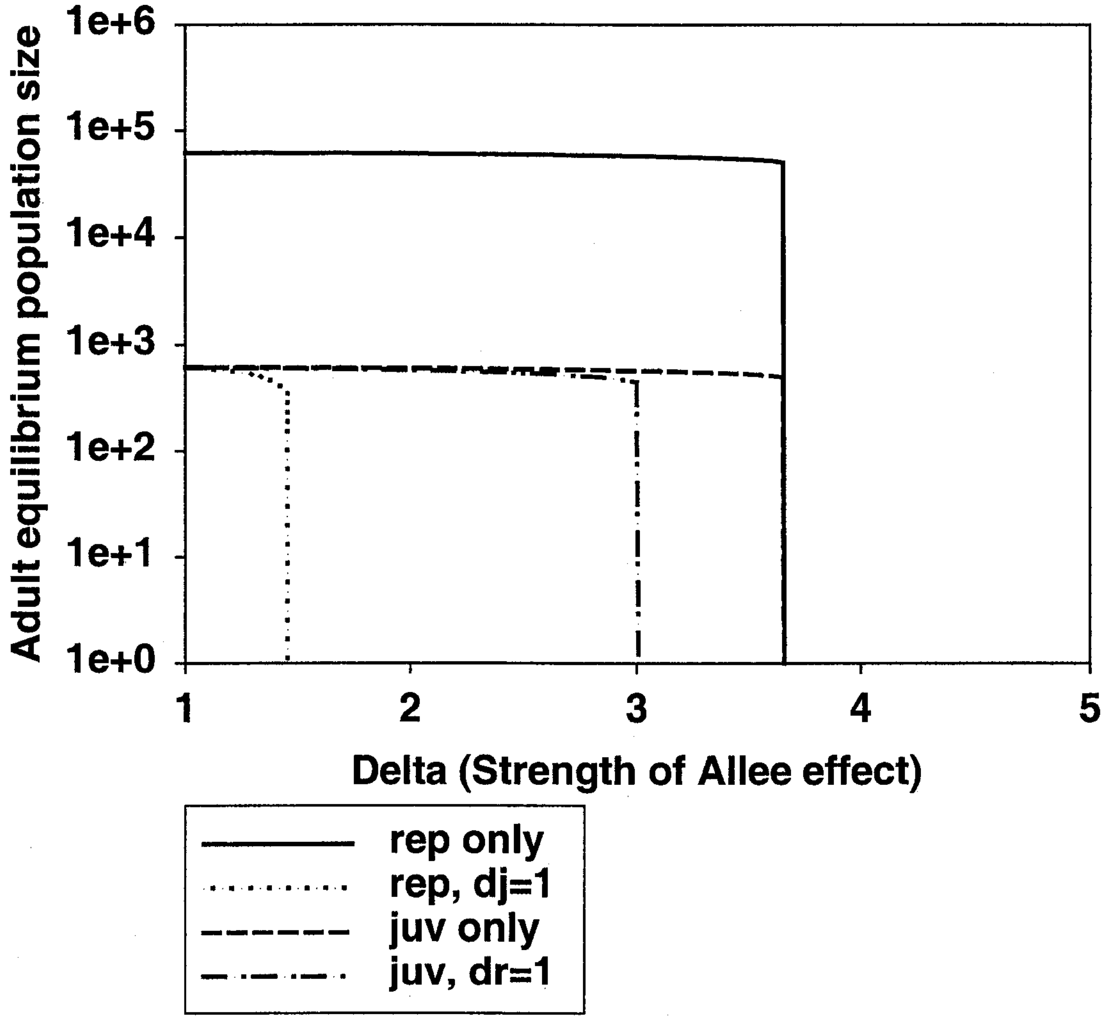


Fig. 18

As Fig. 17, with juvenile rather than adult equilibrium population size.

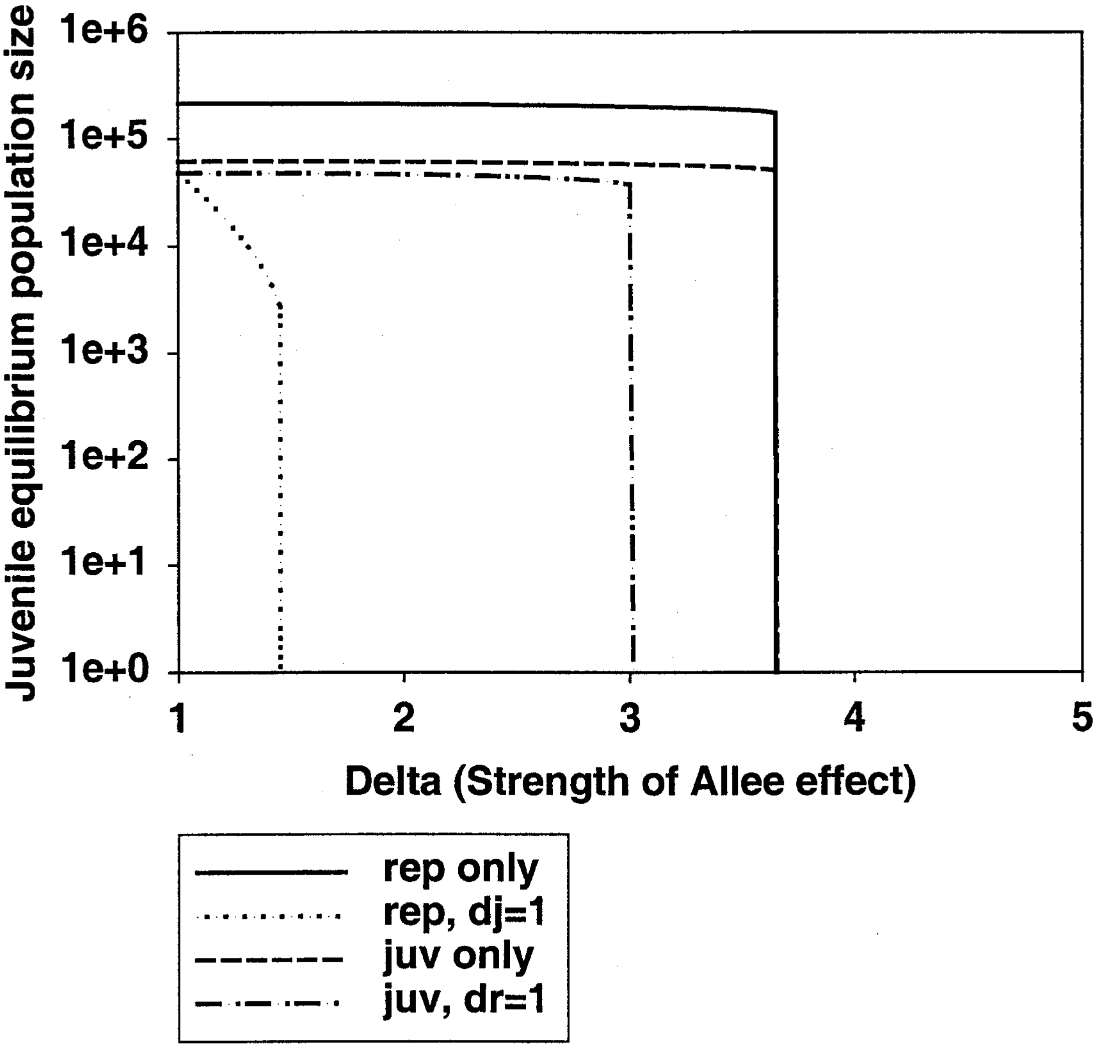


Fig. 19

As Fig. 17, but for *K* parameterisation with τ=1.

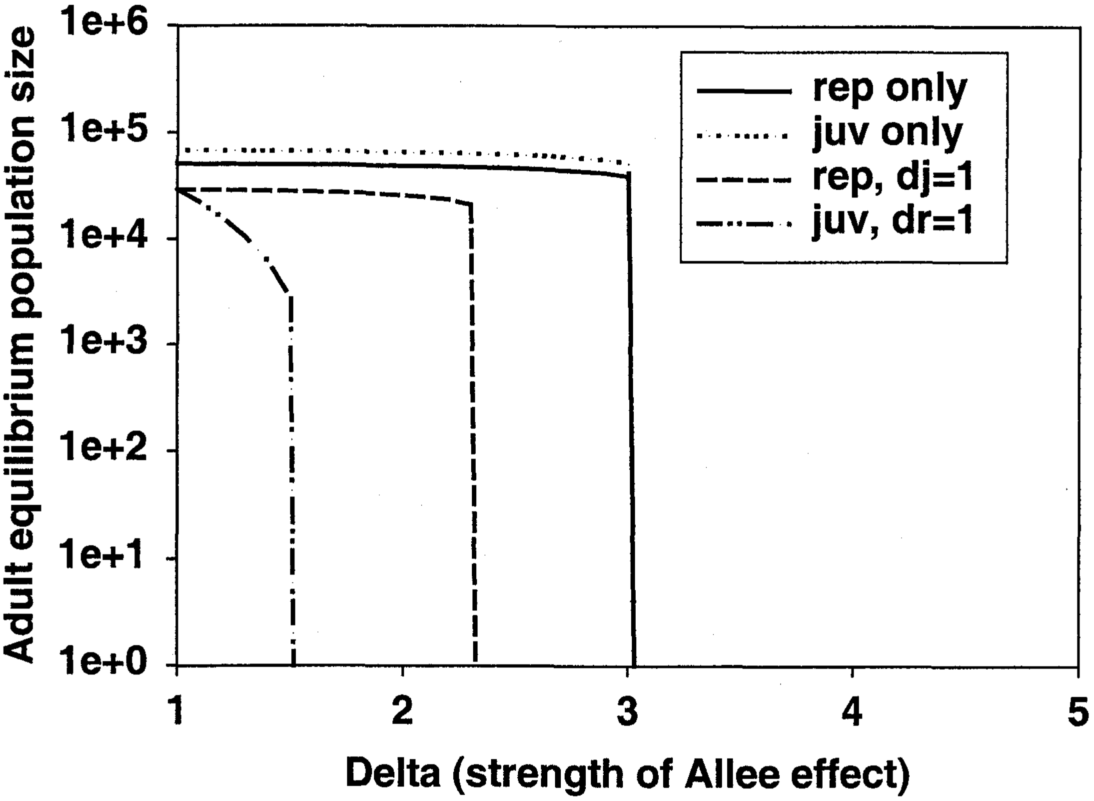


Fig. 20

As Fig. 19, with juvenile equilibrium population size.

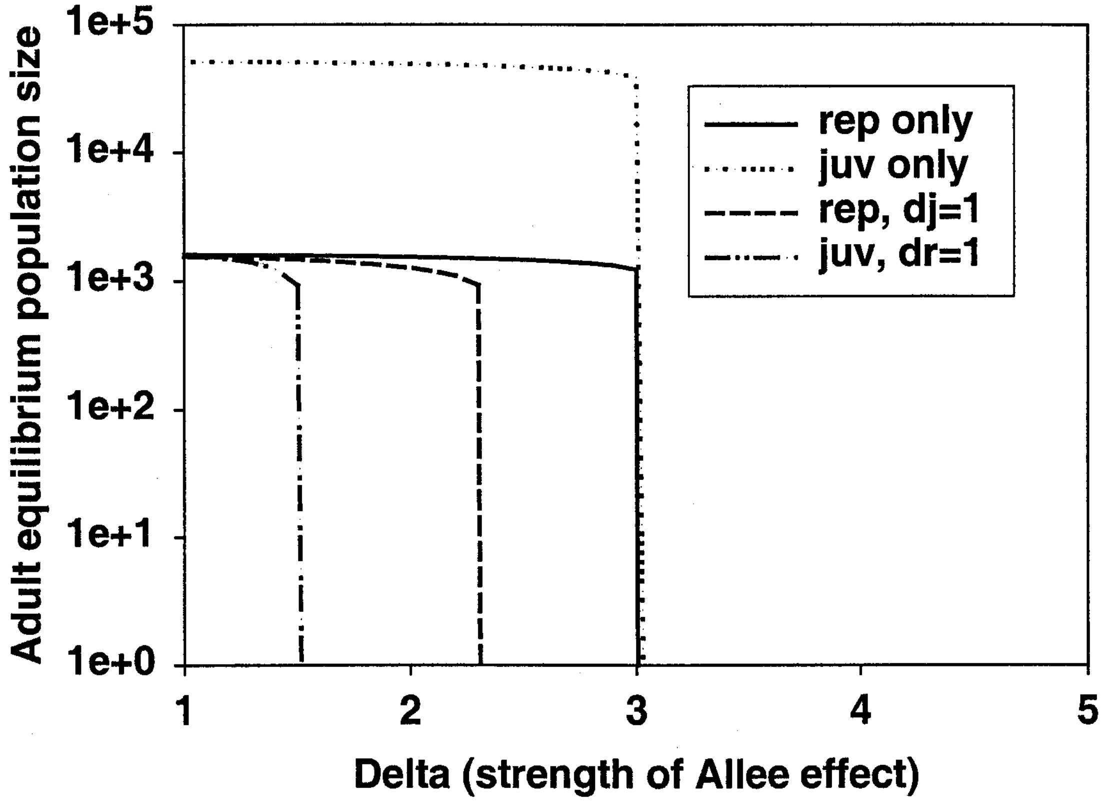


Fig. 21

As Fig. 19, but for *K* parameterisation with τ=5.

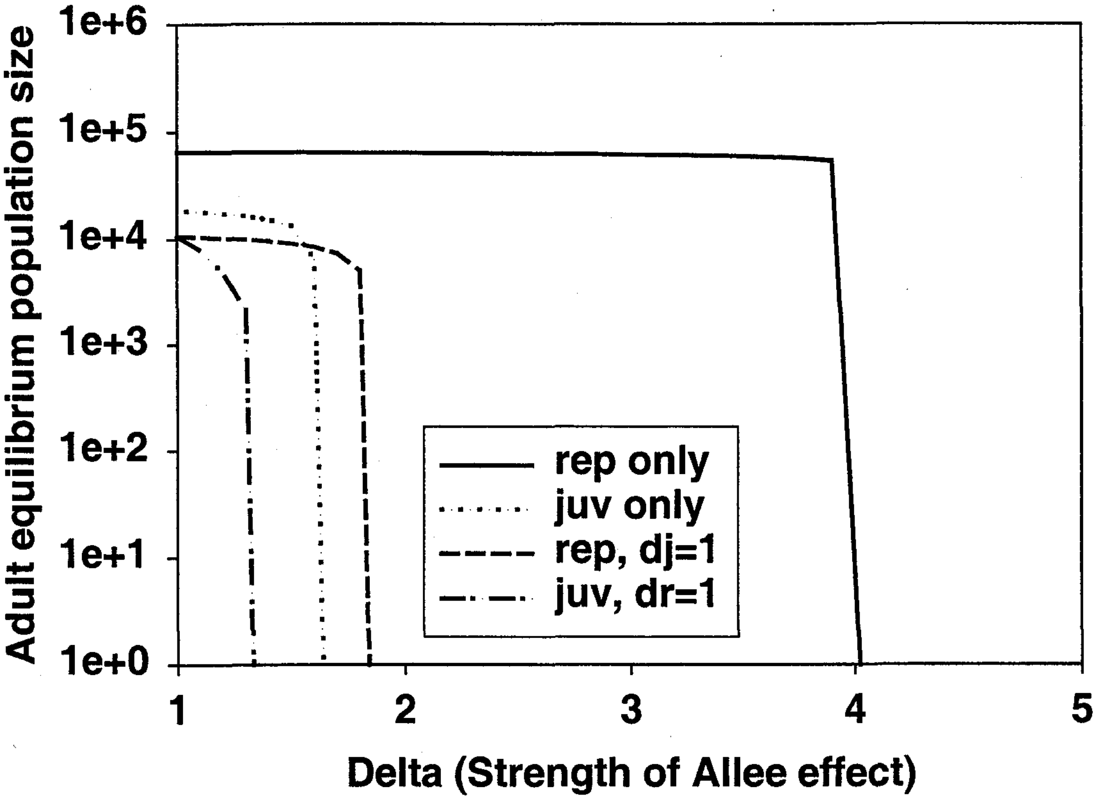


Fig. 22

As Fig. 21, with juvenile equilibrium population size.

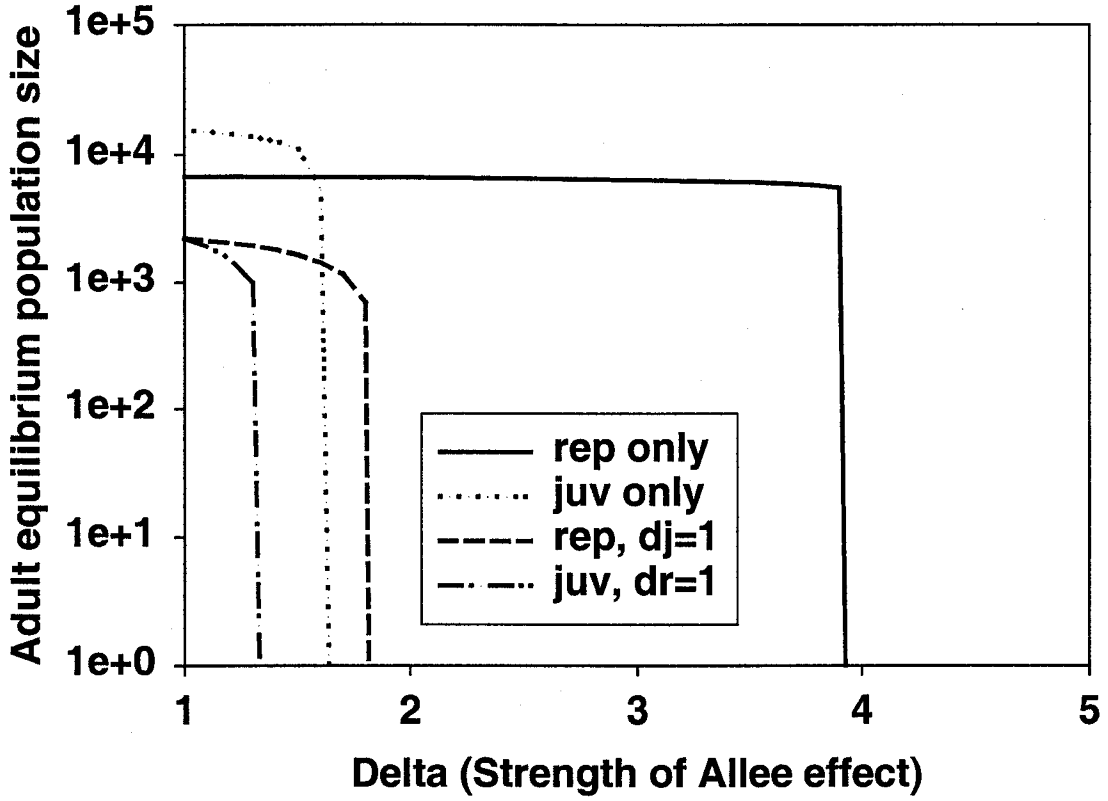


Fig. 23

Model 1: Combined critical values of δ_r and δ_j for *r* parameterisation (M_j=M_a=1.5, α=100, τ=1, initial population vector = [10 10]). Extinction thresholds depend more strongly on reproductive Allee effects (δ_r) than juvenile survival Allee effects (δ_j).

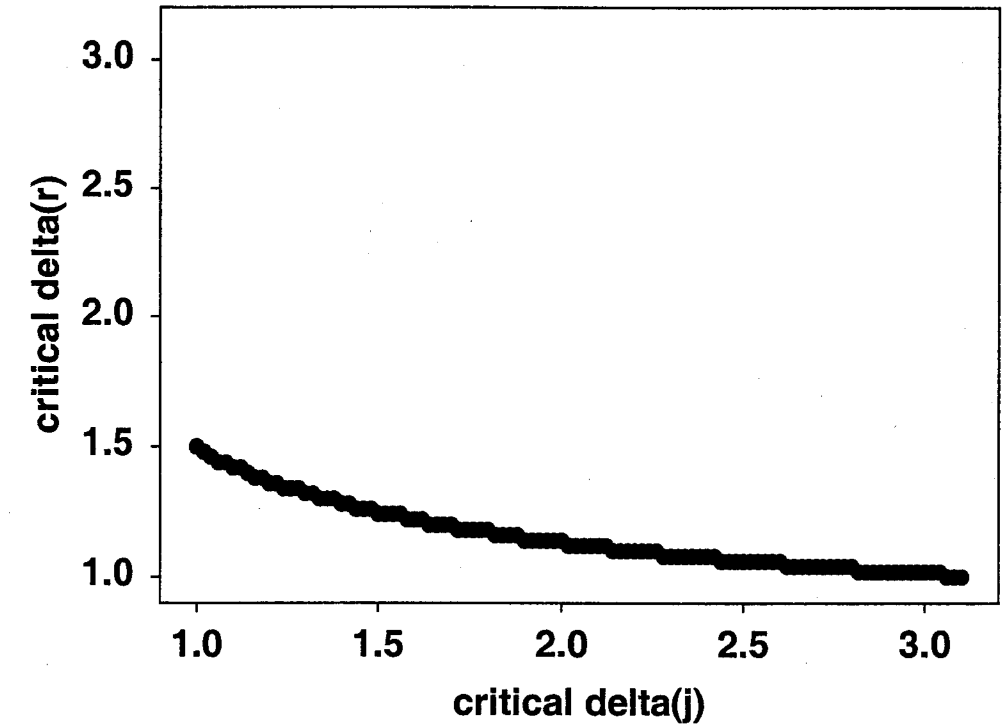


Fig. 24

As Fig. 23, for Model 2 with *r* parameterisation. Again, extinction thresholds depend more strongly on reproductive Allee effects.

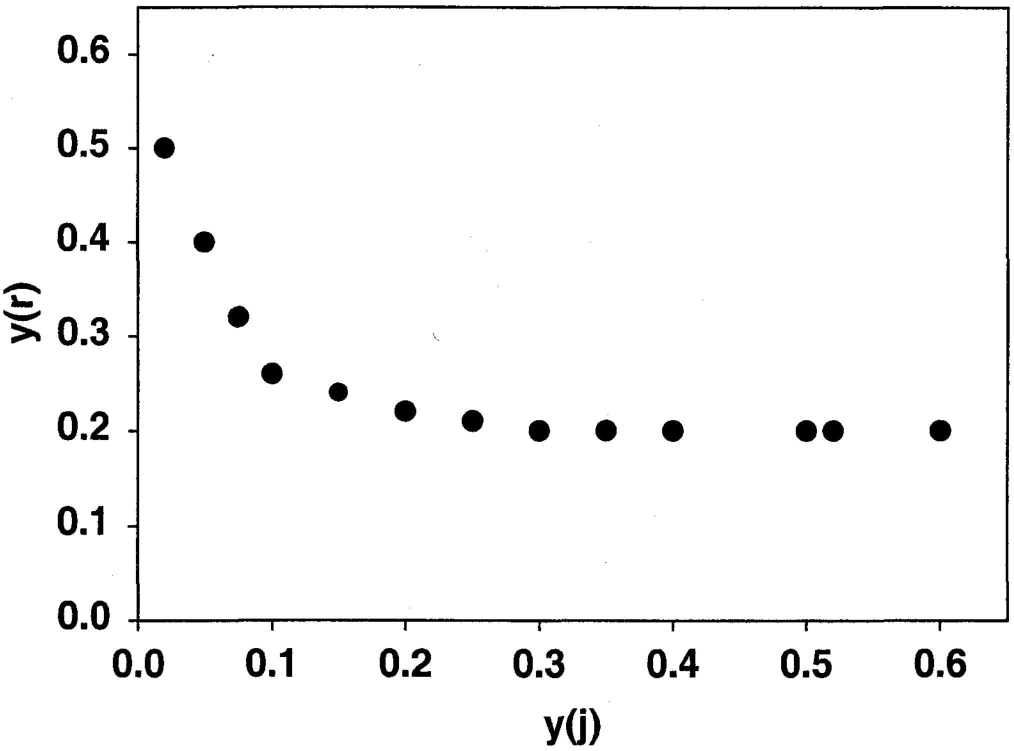


Fig. 25

As Fig. 23, with *K* parameterisation, τ=1. Extinction thresholds now depend more on juvenile survival Allee effects.

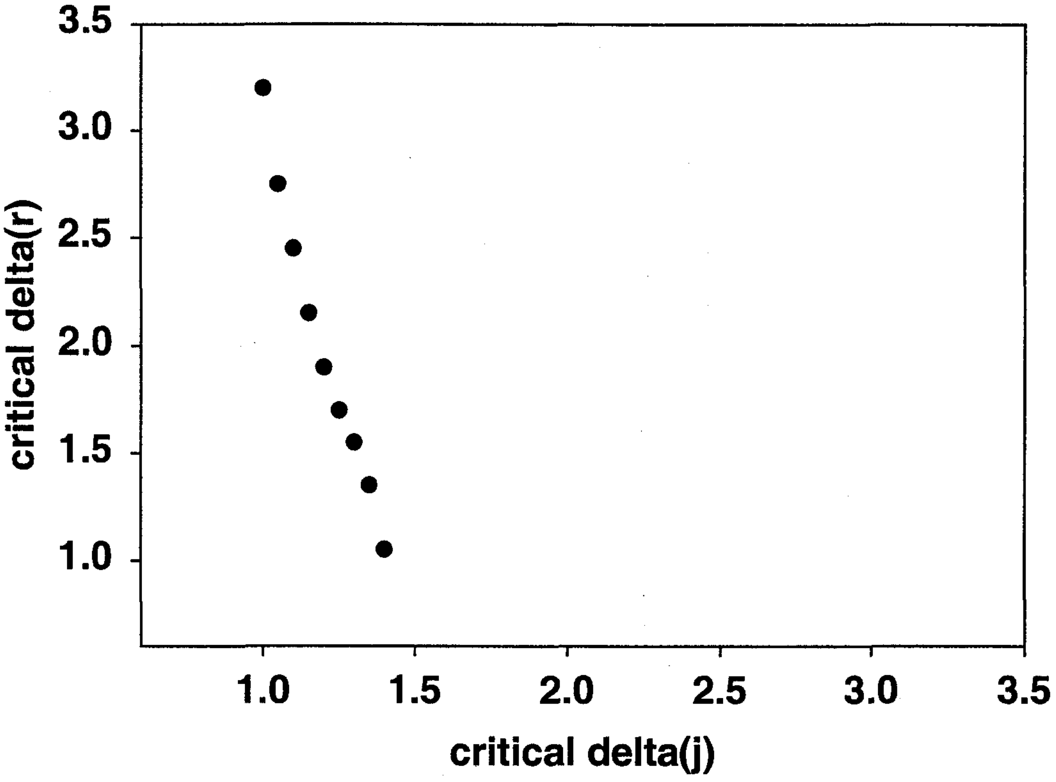


Fig. 26

As Fig. 25, for Model 2 with *K* parameterisation (Mj=0.2, Ma=0.1, τ=2, α=1, initial population vector = [10 10]). In this case, critical thresholds depend to approximately equal extent on reproductive and juvenile survival Allee effects.

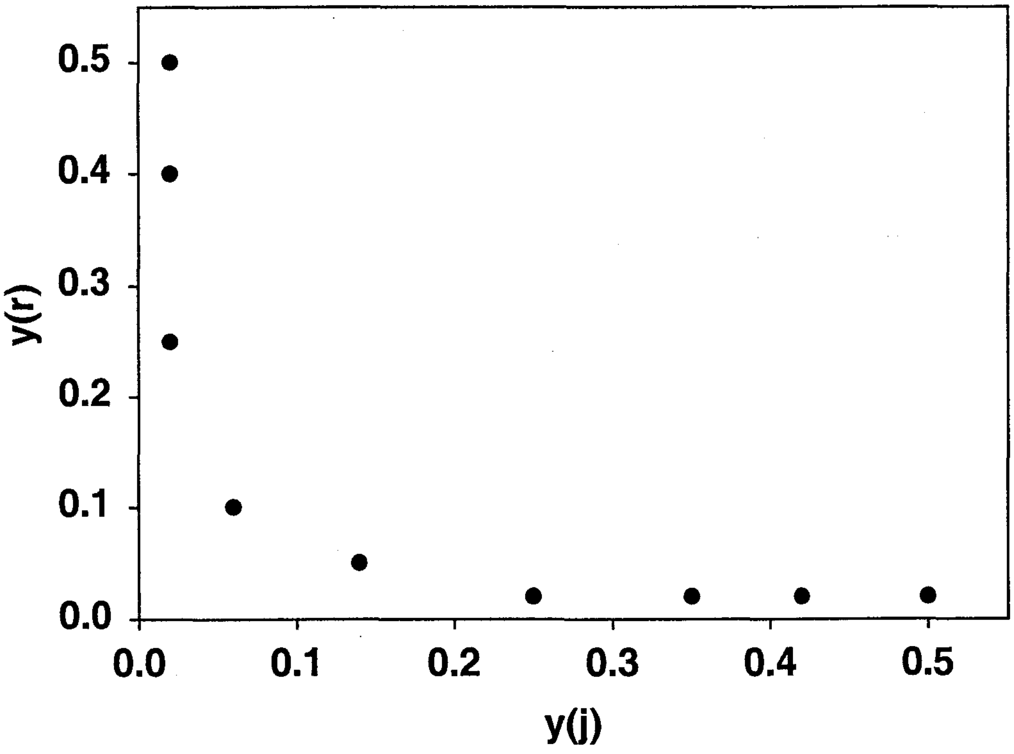


Fig. 27

Model 1: Form of equilibria (in this case for reproductive Allee effects but form is qualitatively the same for juvenile survival Allee effects). For each stage, the upper line represents a stable equilibrium and the lower line is an unstable equilibrium. They meet at the maximum critical δ.

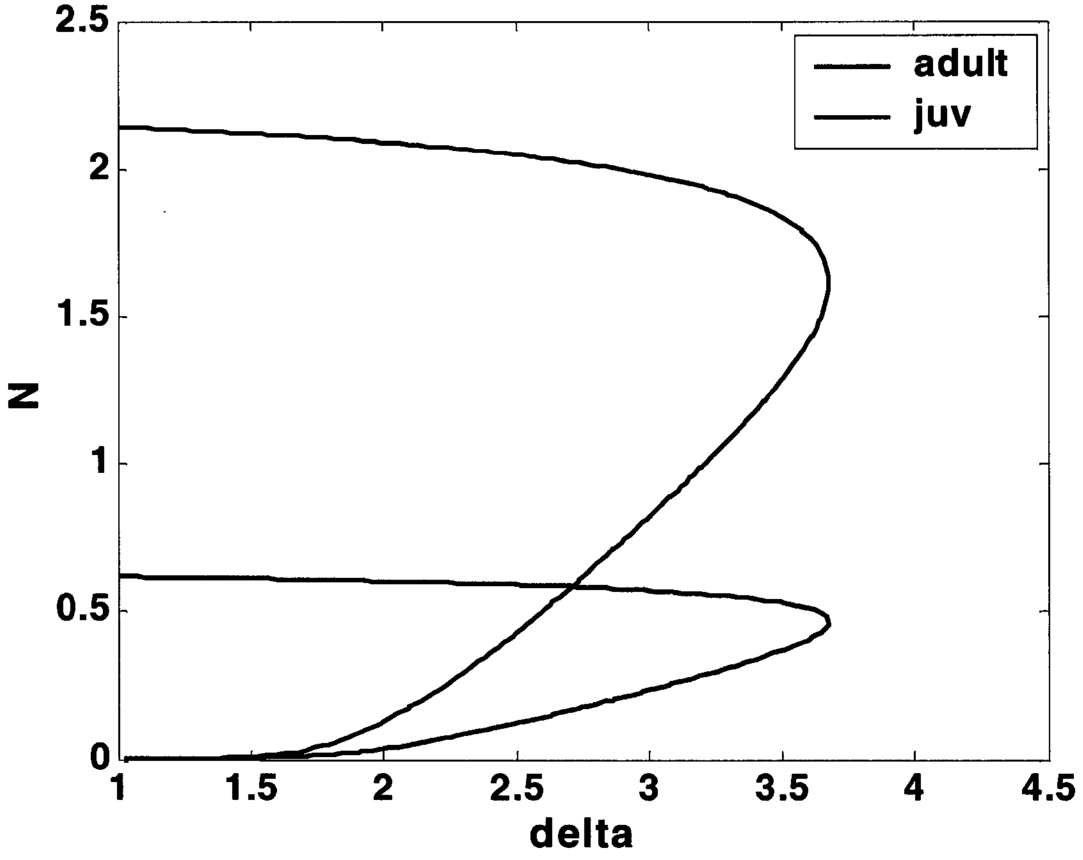


Fig. 28

Model 1: Dynamics with different values of initial juvenile and adult population density (N). Blue curve = adult equilibrium curve, yellow curve = juvenile equilibrium curve. Both stages were started at the same value of N. The area between the lower part of the blue curve and the lower part of the yellow curve represents the area where one stage (in this case juveniles) were tending to extinction, while the other stage (adults) were tending to the upper stable equilibrium. In the red area, populations of size N and Allee effect strength δ remained extant, in the blue area populations went extinct, and the in the green area dynamics were periodic. Periodic dynamics only occur in the area where there is tension between the juvenile and adult equilibria, but do not fill the entire area. In this case I used a reproductive Allee effect with initial conditions $M_j = 0.9$, $M_a = 3$, $\alpha = 100$, $\tau = 1$.

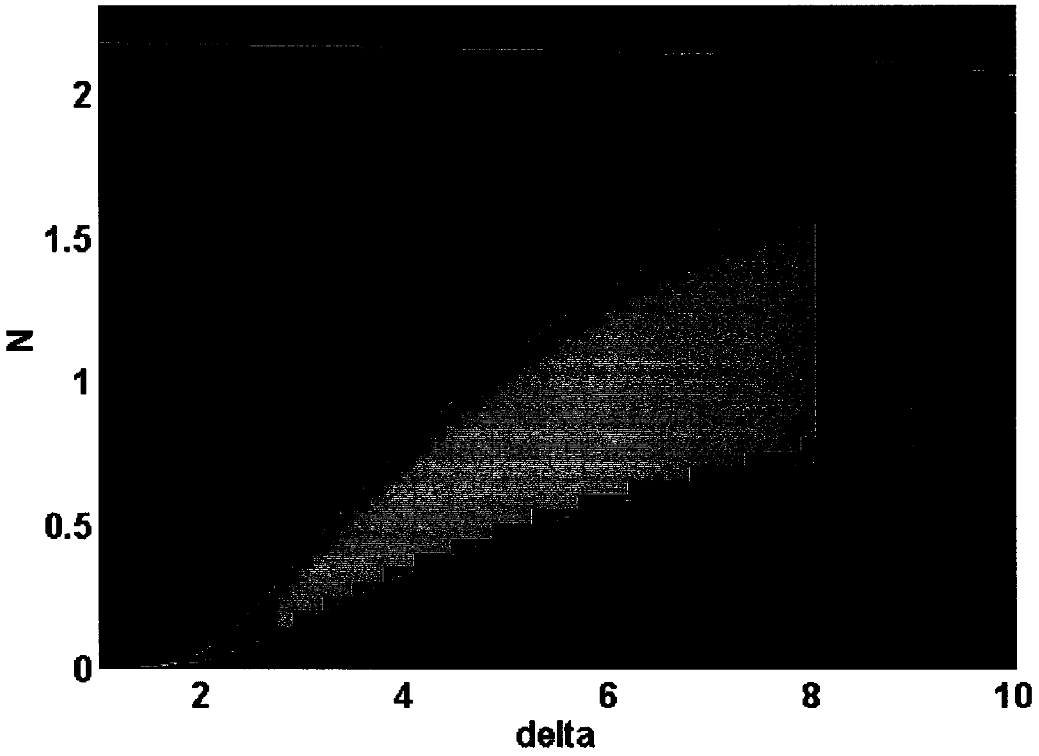


Fig. 29

Model 1: Effect of adult mortality on equilibrium curves (in this case for adult equilibria for reproductive Allee effects, although the form of the curves is the same for both population stages and both types of Allee effect).

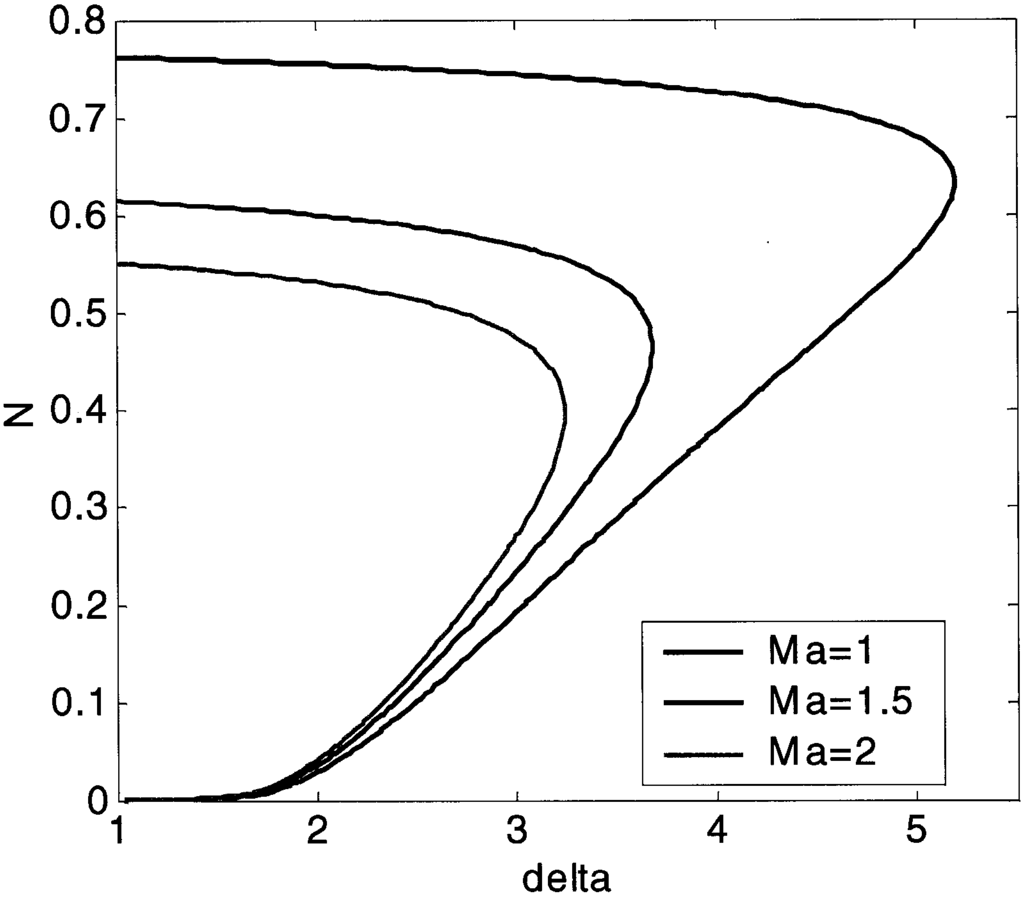
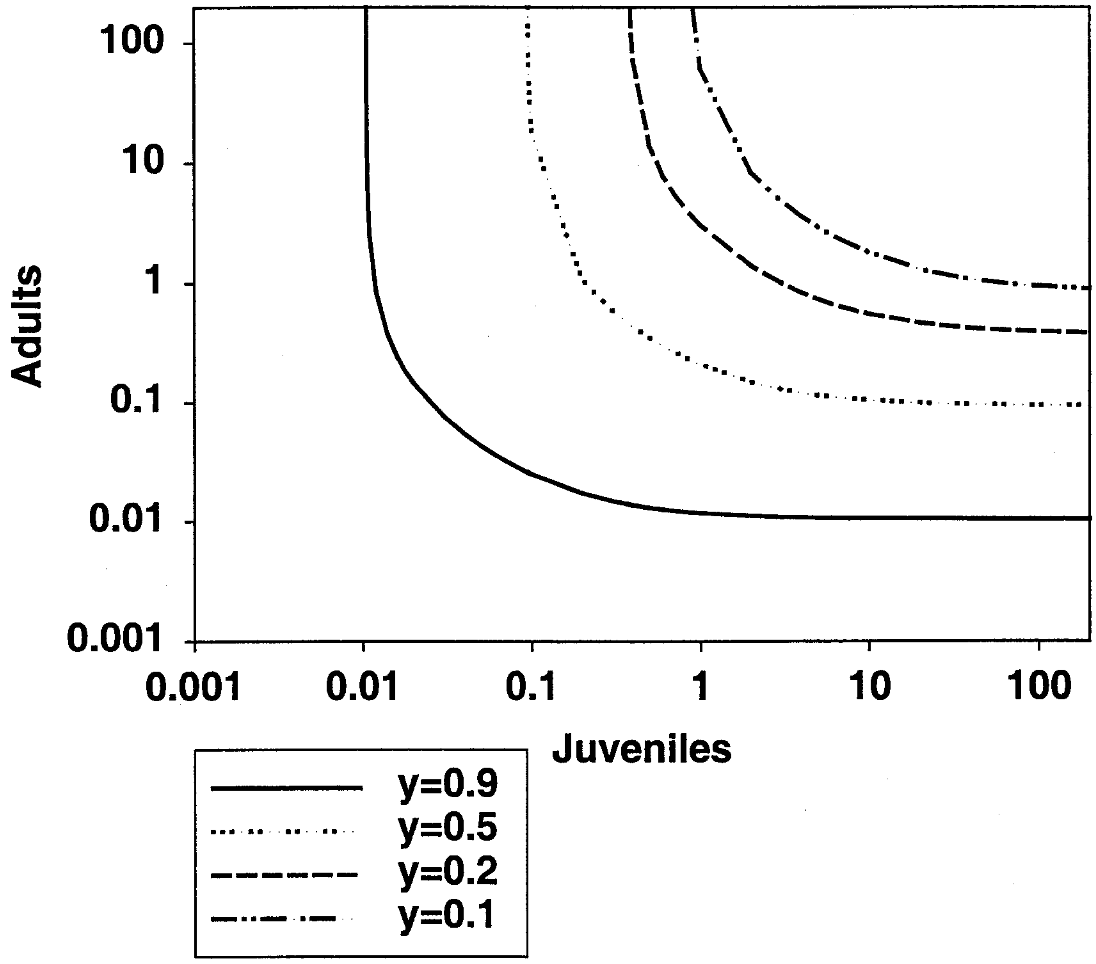


Fig. 30

Model 2: Equilibrium curves for different values of *y* (strength of Allee effect). Initial conditions $M_j = M_a = 2$, $\alpha=70$, $\tau=1$.



CHAPTER 3

ALLEE EFFECTS IN QUEEN CONCH REPRODUCTIVE BEHAVIOUR: FIELD TEST AND THEORETICAL CONSEQUENCES

ABSTRACT

The Allee effect – a reduction in fitness at low population density – can increase extinction probability for exploited or endangered species. In queen conch (*Strombus gigas*), a heavily exploited gastropod, mating and egg production are reduced in low-density areas. This was hypothesised to be due to low encounter rates with suitable mates. Alternative hypotheses include effects of habitat quality or decreased reproductive activity and tendency to aggregate in younger mature conch. To distinguish between these hypotheses, morphologically mature conch were translocated from source sites with ambient conch density either high (~1,000 conch/ha) or low (~20 conch/ha), and kept at high density in enclosures within high- and low-density host sites; reproductive activity was then monitored. I also modelled conch population dynamics under exploitation, a reproductive Allee effect and delayed reproduction. Though conch were at equal high density in all enclosures, high source-site density produced higher reproductive activity. Conch from high-density source sites also had thicker shell lips, indicating that they were older. These data do not support the hypothesis that reduced reproductive activity in low-density areas is due solely to an Allee effect, or to differences in habitat quality. I hypothesise that a high cost of reproduction and low adult mortality have selected for delayed reproduction in maturing conch, which also have less tendency to aggregate, at least in some habitats. In model simulations, both a reproductive Allee effect and delayed reproduction in maturing conch produced non-linear population collapses when fishing mortality was increased to moderate levels, indicating that both an Allee effect and delayed reproduction in queen conch can affect population persistence.

INTRODUCTION

In most equilibrium population models, individual fitness is inversely related to population density (Gotelli 1998); however, in some cases organisms benefit from the presence of conspecifics at low density (see review by Fowler and Baker 1991); e.g. encounters with potential mates (Kuussaari *et al.* 1998), fertilisation efficiency in broadcast spawners (Levitan *et al.* 1992, Baker and Tyler 2001), plant pollination success (Widen 1993, Groom 1998, Hackney and McGraw 2001), vigilance against predators (Kenward 1978) and social structure (Shepherd and Brown 1993, Courchamp *et al.* 2000). In these instances, fitness declines as population density decreases such that *per capita* population growth rate may become negative and local extinction may result (Courchamp *et al.* 1999). Population dynamics of this kind are known as Allee effects (Allee 1931). Allee effects do not necessarily cause extinction since *per capita* population growth rate can be depressed but still remain positive.

Stoner and Ray-Culp (2000) provide field evidence for a reproductively driven Allee effect in the queen conch, *Strombus gigas*, a large, heavily exploited, tropical gastropod. In surveys of a conch population in Exuma Sound, Bahamas, no reproductive activity was observed where adult conch density was less than 50 ha^{-1} (Fig. 1). The presumed mechanism was a reduced encounter rate with suitable mates at low conch densities due to low mobility. Copulation in conch is also more likely in spawning than non-spawning females, providing another positive feedback mechanism that would enhance this effect (Appeldoorn 1988a).

If animals are distributed randomly in space, the probability of encountering a mate in some time period can be estimated from the Poisson probability distribution (McCarthy 1997) as:

$$p = 1 - e^{-mS}$$

where m = mate density and S = search area per unit time. If density of the opposite sex is 25 per ha (= critical conch density below which there is no reproduction, assuming a 1:1 sex ratio; Fig. 1), and with estimated daily movements that cover ~50 m^2 (Stoner and Ray-Culp 2000), a male and female conch have an encounter probability of 0.12 per day, or one encounter with the opposite sex every 8.3 days, on average. This encounter rate is a rough approximation – it would be reduced if some proportion of females are not receptive (females can store sperm for 4-6 weeks; D'Asaro 1965, Weil and Laughlin 1984) or if the sex ratio is biased, which is possible in some areas (see below), but increased if mate searching is non-random; in fact, males may follow female tracks (Stoner and Ray-Culp 2000). However, if encounter rate is the only issue, it is surprising that no reproduction was observed in these areas. Although it is difficult to discover individuals in the act of reproduction at these low densities, mating can last several hours (Reed 1995, pers. obs.) and egg masses persist several days before hatching and for some time as egg-mass remnants (Stoner *et al.* 1992), such that some form of reproductive activity should be evident.

The lack of observations of reproductive behaviour may be explained by alternative mechanisms that are not Allee effects, but which may be associated with low population density. Adult conch migrate between feeding and reproductive sites seasonally, at least in deep water (Stoner and Sandt 1992). Hence, conch might migrate between high-density spawning grounds, where environmental triggers for reproduction (e.g., for larval transport) are present, and low-density feeding areas, where reproductive activity is minimal. Alternatively, both density and reproductive activity could be associated with site-specific habitat quality or ontogenetic changes. During maturation, conch are progressively migrating from shallower nursery grounds to deeper adult habitats (Randall 1964, pers. obs.). Conch mature a few months after developing a flared lip on the shell (Appeldoorn 1988b), when the shell is at least 5 mm thick (Egan 1985). However, newly morphologically mature conch may become functionally mature gradually, and these newly mature conch might be at low population density compared to their more reproductively active counterparts due to ontogenetic migration, low adult mortality and the associated accumulation of conch in adult habitats.

It is therefore uncertain whether the lack of reproductive activity at low conch density is due solely to an encounter-rate mediated Allee effect. The issue is of practical importance because the queen conch is heavily exploited and in decline throughout most of its range (Berg and Olsen 1989). Understanding the mechanisms underlying spatial patterns of adult aggregation and reproductive activity may be important for effective conservation and restoration.

More generally, this is of interest because the other mechanisms are not strictly Allee effects. Although they predict a correlation between low density and low *per capita* reproductive output, the decline in fitness is not caused by low density, but by another factor (e.g. habitat quality, reproductive status) which is correlated with both density and reproductive output. This is important in trying to predict the population consequences of the ongoing “experiment” in fishing conch to low density throughout much of their range. In general, observations of low reproductive activity or low population growth rates coincident with low population densities in any species cannot be presumed to reflect Allee effects. Conservation strategies devised for Allee effects and disregarding other explanations may be less effective. I therefore examined the mechanisms and patterns associated with Allee effects in the queen conch as a model system for investigating Allee effects in heavily exploited species.

I designed a manipulative field experiment to test whether an Allee effect due to low encounter rate was the sole mechanism for the lack of queen conch reproduction at low population density, and if not, to distinguish between competing mechanisms (Table 1). First, I selected sites of high (>>50 per ha) and low (<50 per ha) adult conch density to meet the density criteria for an Allee effect (Stoner and Ray-Culp 2000). I then transplanted mature conch between sites of high and low population density, with controls, placing the conch in enclosures at high density. The conch were deemed to be mature when they had a shell lip thicker than 5 mm (Egan 1985). Although I could not employ low-density enclosures because they would have had to have been 2000 m^2 to enclose a minimum of 10 conch, the use of high-density enclosures, along with other corroborating data (see below) permitted us to distinguish between several alternative hypotheses (Table 1).

If the observed pattern of low reproductive activity in conch (Stoner and Ray-Culp 2000) was indeed due purely to an Allee effect mediated by reduced encounter rates with potential mates, I would expect equally high reproductive activity in all enclosures, regardless of treatment, since conch inside all the enclosures would be at high density. This was therefore our null hypothesis (Table 1: H_0). An effect of host-site density (high reproductive activity in conch transplanted *to* high-density sites) would imply that these sites have an environmental trigger for reproduction that attracts reproductive conch, and which the low-density sites lack (Table 1: H_{A1}). An effect of source-site density (high reproductive activity in conch transplanted *from* high-density sites) would be explained by a site-mediated factor that controls both reproductive activity and density, such as site-specific differences in conch age, growth, condition (habitat quality), or reproductive status (e.g., if conch migrate between reproductive (high-density) and feeding (low-density) sites; Table 1: H_{A2-4}).

To distinguish site-specific differences that might control conch density and reproduction, as well as to ensure that all conch used in the experiment were reproductively competent, I assessed shell morphology, conch condition, and reproductive status at each site (Stoner and Sandt 1992, Stoner and Schwarte 1994). If conch were migrating freely between sites (Table 1: H_{A2}), I expected no significant morphological differences between sites. If there were site-specific reproductive output controlled by differences in habitat quality (Table 1: H_{A4}), I would expect differences in conch condition index and in the allocation of resources to reproductive and somatic tissue.

Finally, I developed a stage-based matrix population model (Caswell 2000) for queen conch to estimate the population-level consequences of Allee and non-Allee mechanisms underlying the patterns in reproductive activity.

METHODS

Site characteristics and surveys

I conducted the experiments at four sites near Lee Stocking Island, Exuma Cays, Bahamas (Fig. 2). Two sites had high densities of mature conch (Rainbow Gardens: 1,140 per ha, Bock Cay: 963 per ha) and two sites had low densities (Children's Bay Cay (CBC): 19.1 per ha, Shark Rock: 21.2 per ha). Low density was defined as less than 50 mature conch per ha, the proposed lower limit for reproductive activity (Fig. 1; Stoner and Ray-Culp 2000). Shark Rock had a total conch density of 127 per ha, but most were immature; the other three sites only had mature conch. I measured conch density in 25 m x 1 m transects (Rainbow) or circles of radius 10 m, covering a total area of not less than 1,000 m^2. The habitat at all four sites was moderately dense seagrass with strong tidal currents. Shark Rock and CBC ranged in depth from 2-4 m, Rainbow 3.5-4 m, and Bock 7-9 m. I surveyed the low-density sites extensively while searching for mature conch, and observed no evidence of reproductive activity (e.g., mating, egg masses). Mating was very commonly observed at the high-density sites, but only quantified at Bock Cay, where 11 out of 121 animals (9.1%) were engaged in reproductive activity during the survey. Levels of reproductive activity at Rainbow were similar.

Experimental design

I collected 64 conch haphazardly from each site and randomly allocated them to one of four groups: two control treatments and two translocation treatments. Conch were tagged and placed in an enclosure either back at the same site (control) or translocated to a paired site (Rainbow-CBC, Bock-Shark). Each enclosure (6 m diam., 28.3 m^2 area) contained 16 conch, yielding a conch density of 5,654 per ha. Enclosures were made of 20-25 cm Vexar strips supported by PVC, and retained most of the conch while not visibly altering the habitat. I conducted the experiment twice, once from 22-31 July 2001 (Experiment I) and again from 2-14 August 2001 (Experiment II). Procedures were similar in both experiments.

While the experiment was running, I checked enclosures daily or twice daily, using either snorkel or SCUBA, and recorded the tag numbers of conch involved in reproductive activity (Stoner and Ray-Culp 2000), which included: (i) copulation (a pair of conch lined up with the front of the male shell covering the back of the female shell, male extending the penis into the female mantle cavity) and (ii) pairing (a pair of conch lined up as for copulation but without the male penis extended). I also recorded the number of conch in each cage so that results would not be biased by escape from the enclosures, although the escape rate was low (an average of ~2 from each cage during each experiment). No external conch ever broke into the enclosures.

I checked enclosures at the Rainbow-CBC site pair 14 times during Experiment I and 17 times during Experiment II, and at the Bock-Shark site pair 7 times during Experiment I and 9 times during Experiment II. I calculated a reproductive index (number of matings (pairing or copulation) per observation per conch) for each enclosure so that results could be compared across all enclosures, sites and experiments.

Morphological data

At the end of Experiment II, I haphazardly collected four conch from each enclosure (i.e. N=16 for each site), determined their gender, and measured their shell features (length, weight and lip thickness). I assessed their condition using the ratios of flesh wet weight:shell length (Ray and Stoner 1995, Stoner and Sandt 1991) and flesh wet weight:shell weight. I froze and subsequently dissected and weighed gonad samples to estimate allocation of resources to reproductive vs. somatic tissue (ratio of gonad wet weight to flesh wet weight). I used gonad colour as an indicator of reproductive status in males (orange = producing sperm; Reed 1995).

Data analysis

<u>Reproductive activity</u>: Reproductive index (RI) was calculated as follows:

$$RI = \frac{\text{observed copulations and pairings}}{\text{mean no. conch in enclosure} \times \text{no. observations on enclosure}}$$

In an analysis of variance model, RI was the dependent variable, and Source site and Host site were fixed factors. To account for the effect of location (= system) and experimental period, I included System and Time as fixed factors with two levels corresponding to the two pairs of sites (system 1 = Rainbow / Children's Bay Cay; system 2 = Bock Cay / Shark Rock) and the two experimental periods.

Since mating activity was recorded by conch tag number, I also had a record of individual matings. I was therefore able to determine if the pattern of matings was driven by a few active individuals, and if there was evidence for mate choice. I compared the distribution of matings in each of the 32 enclosures (4 replicates x 4 sites x 2 experiments) to a Poisson distribution, using a X^2 test, to assess whether the distribution of mating activity among individuals was random, uniform (a higher number of individuals involved in fewer mating each), or clumped (a few individuals accounting for most of the matings) (Zar 1999). In 8 cases, X^2 could not be calculated because there were too few matings in the enclosure.

To test whether there were significant changes in reproductive activity over the course of the experiment, I divided each experiment into two week-long periods. I tested the distribution of mating against a Poisson distribution to check if it was random, and then compared the mean rate of matings in the two time periods using a X^2 test (Zar 1999). In this case, I had to combine replicate enclosures and experiments to have an adequate sample size, and even then only 4 of 8 site pairs could be analysed.

Sex ratio: I compared the sex ratio of the subsample from each site using a binomial distribution with $p = 0.5$, which would be expected for a random sample of a 1:1 sex ratio. I also compared individual sites and high vs. low density sites using X^2 tests.

Morphological data: I analysed morphological measurements (shell length and weight, lip thickness, flesh weight:shell weight ratio, and gonad weight:flesh weight ratio) using an analysis of variance model with Source density, System and Sex as fixed factors. I used Student-Newman-Keuls (SNK) pairwise comparisons to compare levels of a factor within each level of another factor when there were interaction effects (Underwood 1997).

Modelling

I used a population matrix projection model (Caswell 2000) with density-dependent reproduction to compare population trajectories with and without Allee effects, and with delayed functional maturity. The model has a juvenile stage and a series of adult stages (Fig. 3, Table 3). Individuals move through the stages at each time step (= 1 yr), spending a fixed number of years as a juvenile (J1: Fig. 3, T_i: Table 3) and one year each in adult stages 1 and 2. Individuals accumulate in adult stage 3, dying at a rate determined by adult mortality and exploitation of adult stage 3 (Table 3). Hence, the model is appropriate for long-lived iteroparous species. Reproduction is negatively density dependent across all densities except in the Allee model, where it is positively density dependent at low density, with the strength of positive density dependence being fixed by the Allee factor δ (Myers *et al.* 1995, Stoner and Ray-Culp 2000).

The equation for density-dependent reproduction used in the model is as follows (Table 3):

reproductive output at time $t = \alpha N_{At}{}^{\delta-1}/(1 + \beta N_{At}{}^{\delta})$

where N_{At} is the density of the adult stage at time t and α is the maximum reproductive output without Allee effects; for description of δ and β see below.

The exponent δ is an index of the Allee effect (Myers *et al.* 1995). For simple negative density-dependent reproduction, $\delta=1$. In this case the reproduction equation collapses to $\alpha/1+\beta N_{At}$, where reproductive output tends to a maximum of α as N_A tends to 0, and tends to 0 as N_A gets large. Increasing δ gives a curve that looks similar at high values of N_A but causes it to drop back to 0 as N_A tends to 0, as would an Allee effect (Fig. 4).

Parameter β sets the slope of the curve. In this heuristic model β was set such that the slope was over appropriate values of N_A, so that the model equilibrated at reasonable population values ($\alpha=1000$, $\beta=0.01$).

I ran the model in four ways (Table 3):

- Model "null1": All adult stages reproduce ($D=1$), all adult stages are fished ($F_1=F_2$), and there are no Allee effects ($\delta=1$).
- Model "null2": Only adults in stage 3 reproduce ($D=0$), only adults in stage 3 are fished ($F_1=0$), no Allee effects ($\delta=1$).
- Model "rep": Only adults in stage 3 reproduce, but all adults are fished, no Allee effects.

- Model "Allee": All adults reproduce and are fished (as in null1), but reproduction is subject to different strengths of Allee effect ($\delta=1$ – no Allee effect; $\delta=3$ – intermediate Allee effect; $\delta=5$ – strong Allee effect).

Unlike the other models, the Allee model took N_A in values of density rather than population size, necessitating a change in parameterisation ($\beta=45$). In the Allee model, all adult stages reproduce and $F_1=F_2$, as in model null1. Because of the differences in model structure and parameters, it is not directly comparable to the straightforward negative density-dependent models. I therefore examined the influence of Allee effects by comparing $\beta=3$ (intermediate Allee effect) and $\delta=5$ (strong Allee effect) (Stoner and Ray-Culp 2000) with $\delta=1$ (null model of no Allee effect).

The models were run for 200 time steps, by which time they had all reached an equilibrium population size for each stage. They were run over a range of F values, and the equilibrium adult population size plotted against F. The initial population size did not affect the equilibrium population size for models 'null1', 'null2' and 'rep'. All runs were started with 1000 individuals in each stage ($N_A=3000$). In the case of the Allee model, the area of each stage was set at 1000 units and the density of each stage at 1 (giving the same initial population size). The initial density affected the equilibrium population size, but did not alter the dynamics significantly (i.e. the value of F at which the models reached extinction).

RESULTS

In all analyses of variance, variances were either not significantly heterogeneous (Levene's test), or the null hypothesis for the *F* test was rejected at an α value lower than that used to test for homogeneity of variance (Underwood 1997). Hence, transformations were not required.

Matings and reproductive index

Mating activity in each enclosure for the two experiments is shown in Table 2.

The interaction effect between Source site density and Host site density was significant (ANOVA, $P = 0.017$), precluding singular conclusions about the main effects. When analysed within treatment combinations (SNK tests, $\alpha = 0.05$), the reproductive index (RI) was higher for conch from high-density source sites than for conch from low-density source sites, irrespective of host site (Fig. 5). In addition, the RI for conch from high-density source sites returned to high-density host sites was higher than the RI for conch translocated to low-density host sites. The RI values of conch translocated from low-density source sites did not differ, irrespective of host-site density.

There was also a significant System x Host site density interaction effect (ANOVA, $P = 0.042$), because the effect of Host site density was only significant (SNK tests, $\alpha = 0.05$) in one of the systems (Rainbow / Children's Bay Cay). Hence, the strongest effect upon the RI was that of Source site density, such that all enclosures with conch from Source sites with high conch densities had high values of the RI, and all those with conch from Source sites with low conch densities had lower values of the RI (Fig. 5).

Out of the 24 enclosures for which X^2 could be calculated, only three had a distribution of mating activity between individuals that differed significantly from random, and these three were more uniform than random (i.e., more individuals participating in fewer matings). The results were therefore not due to a few active individuals, and there was little evidence for mate choice or any other mechanism that would create a non-random distribution of matings.

When replicates and experiments were combined, none of the Source site x Host site combinations had a distribution of individual matings different from random (X^2 test, $\alpha = 0.05$). When the data were divided into two week-long time periods there were no significant differences in the rate of mating activity between the first and second halves of the experiments for the four site pairs that could be tested (X^2 test, $\alpha = 0.05$).

Sex ratio

Conch from one high-density source site (Bock Cay) had a significantly male-biased sex ratio (X^2 test, $P = 0.038$). The other high-density site (Rainbow) had a slight but non-significant male bias. Overall, the conch from high-density source sites had a male-biased sex ratio (X^2 test, $P = 0.021$), whereas conch from low-density sites did not (X^2 test, $P = 0.298$). Sex ratios of conch from high- and low-density sites differed significantly (X^2 test, $P = 0.037$).

Shell morphology and reproductive anatomy

Conch from high-density source sites had significantly thicker lips (ANOVA, $P < 0.0005$) and shorter shells (ANOVA, $P = 0.003$) than conch from low-density source sites (Fig. 6); there were no significant differences in shell weight (ANOVA, $P = 0.452$). The sexes did not differ significantly in shell characteristics (ANOVA, $P = 0.260$ (lip), 0.051 (length), 0.536 (weight)). The main reproductive structures were fully developed in all conch (males: verge, prostate gland, testes; females: ovary, uterus). The gonads of all males were orange, indicating that they were producing sperm (Reed 1995). N = 16 for all sites except Rainbow where N = 14.

Condition and resource allocation to reproduction

The two variants of condition index (flesh weight:shell weight ratio, flesh weight:shell length ratio) gave similar results. There was a significant interaction effect between Source site density and System (ANOVA, $P = 0.004$, $P = 0.01$) and Source site density and Sex (ANOVA, $P = 0.018$, $P = 0.007$). Flesh weight:shell length ratio also had a significant System x Sex interaction (ANOVA, $P = 0.047$). When analysed within treatment combinations (SNK tests, $\alpha = 0.05$), conch from one low-density site (Shark Rock) were in significantly better condition than conch from the other three sites according to both indices (Fig. 7). There were no significant differences in the ratio of gonad to somatic tissue by source density, site or sex, and no interaction effects (ANOVA, $P >> 0.05$ for all effects).

Modelling

In negative density-dependent models (Fig. 8: null1 and null2, Fig. 9: $\delta=1$) equilibrium population size declined in a log-linear fashion with increasing mortality from exploitation (F). By contrast, equilibrium population size under either delayed reproduction (Fig. 8: rep) or Allee effects (Fig. 9: $\delta=3$ and $\delta=5$) declined in a log-linear manner with increasing F at low values of F, but then rapidly collapsed to extinction at moderate values of F. In the case of the Allee models (Fig. 9), increasing the value of δ did not affect the dynamics at low values of F, but it reduced the critical value at which the population collapsed to extinction. A strong Allee effect (Fig. 9: $\delta=5$) and heavy exploitation prior to the age of maturity (Fig. 8: rep) had comparable, drastic effects on extinction probability under exploitation.

DISCUSSION

The major finding of this investigation is that the lack of reproductive activity in queen conch at low population density could be due not just to an attenuation in encounter rate with potential mates (i.e. a classic Allee effect – Stoner and Ray-Culp 2000), but also to other processes associated with low population density. A diminished encounter rate at low density may have a significant effect on reproduction in conch. Although reproductive activity was never observed in the low-density sites in the field (Stoner and Ray-Culp 2000, this study), there was some reproductive activity in conch from the low-density sites when translocated into the high density enclosures (Fig. 5). However, the significant differences in reproductive activity of conch held in various experimental treatments at high density indicate that there are additional significant processes acting on reproductive activity that compound the Allee effect in encounter rates (Table 1). The decline in reproductive activity associated with low adult conch density also seems to involve more subtle mechanisms related to age and reproductive behaviour.

The findings also indicate that an observed correlation between density or population size and some measure of fitness cannot be used exclusively as evidence for an Allee effect, which implies a causal relationship between population density and fitness (Courchamp *et al.* 1999, Stephens *et al.* 1999). Density and fitness may be related to a third causal factor, so that although mean fitness may decline in areas of low population density, it may nonetheless not be an Allee effect. A correlation between density and some measure of fitness has been used in many empirical studies of Allee effects to infer a causal relationship (e.g., Lamont *et al.* 1993, Shepherd and Brown 1993, Clutton-Brock *et al.* 1999, Stoner and Ray-Culp 2000). In many cases, experimental tests of Allee effects are impractical (e.g. for protected species), but this study shows that the results of observational studies need to be interpreted with care.

I should note that this study was carried out in a different habitat to that of Stoner and Ray-Culp (2000), although in the same geographical location. They reported very little reproductive activity in conch populations in shallow seagrass beds, and concentrated on conch in deeper (>10 m) sand habitats. In contrast, in surveys for appropriate sites for this experiment, I found the highest densities of conch and rates of reproductive activity in the two high density seagrass sites (Rainbow and Bock Cay), and therefore decided to focus on this environment. It is therefore possible that the results of Stoner and Ray-Culp have a different explanation to our results.

Our findings did not support the hypothesis that the reduction in queen conch reproductive activity (at least in these seagrass beds) was due exclusively to an Allee effect mediated by a reduced encounter rate at low population density. Various alternative hypotheses exist (Table 1). Two factors argue against the hypothesis that habitat quality in the low-density sites was poor (Table 1: H_{A4}); (1) condition indices at low-density sites were comparable to high-density sites or higher and (2) the periodic occurrence of high densities of juveniles at both the low density sites (Marshall 1992, Ray and Stoner 1995, pers. obs.). Morphological differences between conch at the different sites allowed us to reject the hypothesis of free migration between high- and low-density sites (Table 1: H_{A2}).

Morphological differences could be ontogenetic, or could arise as a response to differential predation. There is some evidence that juvenile conch respond to predation by thickening shells, since hatchery reared conch have thinner shells and higher mortality from predation (Ray *et al.* 1994). However, there is no evidence for this in adults. The main adult predators are tulip snails (*Fasciolaria tulipa*), nurse sharks (*Ginglymostoma cirratum*) and rays of various species, of which only the shark and rays crush the shells. These predators are wide ranging and I saw no evidence for differences in their density between the sites. The most likely explanation for the morphological differences between high and low-density sites is that the adult conch at the low-density sites were younger (Stoner and Schwarte 1994) and not all as functionally mature (Egan 1985). A difference in the ages of morphological and functional maturity has been observed in the queen conch (Egan 1985) and other gastropods (e.g., abalone; Shepherd and Brown 1993), which tend to allocate an increasing proportion of resources to reproduction as they age (Yonge and Thompson 1976), or in other invertebrates such as lobsters and crabs (Lipcius 1985).

Late maturity will evolve in species with deterministic growth if reproduction is costly for future reproductive output or survival and if mortality is low (Roff 1992, Bulmer 1994). There is no direct information about the cost of reproduction in queen conch relative to their size. However, females produce several large egg masses over the course of a reproductive season, each containing ~400,000 eggs (Stoner *et al.* 1992), while males produce apyrene (anucleate) sperm as well as DNA-bearing sperm. (The increase in sperm volume through the production of apyrene sperm is thought to play a role in sperm competition; Silberglied *et al.* 1984; Wedell 2001). Both sperm and eggs are energy rich (Reed 1995). There is also a cost to aggregation, at least in juveniles (Stoner and Ray 1993). Therefore it is possible that reproduction is energetically costly in queen conch relative to other gastropods.

Delayed functional maturity is an integral, evolved life-history component. Allee effects, in contrast, are either selectively neutral, if conditions of low density rarely or never occur, or function as the cost component of a cost-benefit trade-off if they are a corollary of some trait that improves fitness at intermediate or high density. I therefore presumed that delayed functional maturity and Allee effects might have different effects on the population dynamics. Although simulated populations in the delayed maturity model and the Allee model fared worse than those in the null models, both the delayed functional maturity model (model “rep” in Fig. 8) and the Allee effect model (models “δ=3” and “δ=5” in Fig. 9) affected population dynamics in a strikingly similar way, increasing vulnerability to exploitation and causing extinction at significantly lower values of mortality than the null models. Both exhibited threshold effects, with a rapid decline in the equilibrium population size to extinction above a critical value or small critical range of additional mortality. If anything, the effects of exploitation before the age of functional maturity were more severe than even the most severe Allee effects.

From the perspective of queen conch conservation, our results are potentially disturbing since the basis of management in many areas, including the Bahamas, is a ban on the exploitation of conch until they have reached morphological maturity, as indicated by the presence of a “well-formed” flaring lip. Our experimental findings suggest that young adult queen conch, which are legally exploited, may not be functionally mature even at lip thickness values up to 11 mm (Fig. 6). Hence, a large fraction of the population of queen conch may be subject to exploitation before reproducing. This situation was modelled as the “rep” treatment in our simulations, with delayed reproduction and immediate exploitation of adults that do not reproduce. In this case, moderate levels of fishing mortality led to non-linear collapses in equilibrium population size, indicating that this species may be much more vulnerable to exploitation and population collapse than previously thought. In fact, population collapses have been common in heavily exploited queen conch populations (Berg and Olsen 1989). Moreover, the likelihood of restoration success may be diminished substantially by a combination of Allee effects and delayed functional maturity.

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TABLES

Table 1

Expected level of reproductive activity from each translocation given alternative mechanisms associated with low population density. All conch were at high density in enclosures. There were four treatments: (1) conch from high density source sites translocated to enclosures in low density host sites (high-low); (2) control: conch from high density source sites put back into enclosures at the same site (high-high); (3) conch from low density source sites translocated to high density host sites (low-high) and (4) control (low-low).

	Allee effect?	Mechanism	Translocation (Source site density – Host site density)			
			high-high	high-low	low-high	low-low
H_0	Yes	Encounter rate	**high**	**high**	**high**	**high**
H_{A1}	No	Environmental trigger for reproduction	**high**	**low**	**high**	**low**
H_{A2}	No	Seasonal reproductive migration into spawning sites	**high**	**high**	**low**	**low**
H_{A3}	No	Functionally mature conch in high density areas; immature in low density areas	**high**	**high**	**low**	**low**
H_{A4}	No	Poor condition in low density areas	**high**	**high**	**low**	**low**

Table 2

Incidents of mating (copulation and pairing) in each treatment for the two experiments. Note that for logistical reasons the CBC-Rainbow system was checked more frequency during each experiment so that higher numbers of observed matings in that system reflect this. I calculated the reproductive index as an estimate of reproductive activity which is unbiased by numbers of checks as well as by the few escapes.

Source site	**Host site**	**Matings Experiment I**	**Matings Experiment II**
CBC	CBC	3	0
CBC	Rainbow	2	6
Rainbow	Rainbow	16	25
Rainbow	CBC	4	2
Shark Rock	Shark Rock	3	2
Shark Rock	Bock Cay	2	0
Bock Cay	Bock Cay	7	8
Bock Cay	Shark Rock	3	11

Table 3

Generalised transition matrix for population model. T_i=time to physiological maturity (time spent as juvenile), M_i=juvenile mortality, M_a=adult mortality, F_1=mortality due to exploitation in adult stages 1 and 2, F_2=mortality due to exploitation in adult stage 3, N_{At}=total number of adults at time *t* and α, β and δ are parameters for the density dependent equation. The parameter D fixes delayed reproduction (D=0, adult stages 1 and 2 do not reproduce) vs. immediate reproduction (D=1, all adult stages reproduce). Values of T_i, M_i and M_a were fixed to be approximately appropriate for queen conch, although since the model is heuristic and comparative, and values were equal across all models, they do not affect the results. In the case presented here, T_i=3, M_i=2 and M_a=0.5.

	Juvenile	**Adult 1**	**Adult 2**	**Adult 3**
Juvenile	$(1-1/T_i) \cdot e^{-Mi}$	$\frac{D \cdot \alpha N_{At}^{(\delta-1)}}{1+\beta N_{At}^{\delta}}$	$\frac{D \cdot \alpha N_{At}^{(\delta-1)}}{1+\beta N_{At}^{\delta}}$	$\frac{\alpha N_{At}^{(\delta-1)}}{1+\beta N_{At}^{\delta}}$
Adult 1	$1/T_i \cdot e^{-1/2(Mi+Ma+F1)}$	0	0	0
Adult 2	0	$e^{-(Ma+F1)}$	0	0
Adult 3	0	0	$e^{-1/2(2Ma+F1+F2)}$	$e^{-(Ma+F2)}$

FIGURES

Fig. 1

Relationship between *per capita* reproductive activity and adult queen conch density in the Exuma Cays, Bahamas (adapted from Stoner and Ray-Culp 2000).

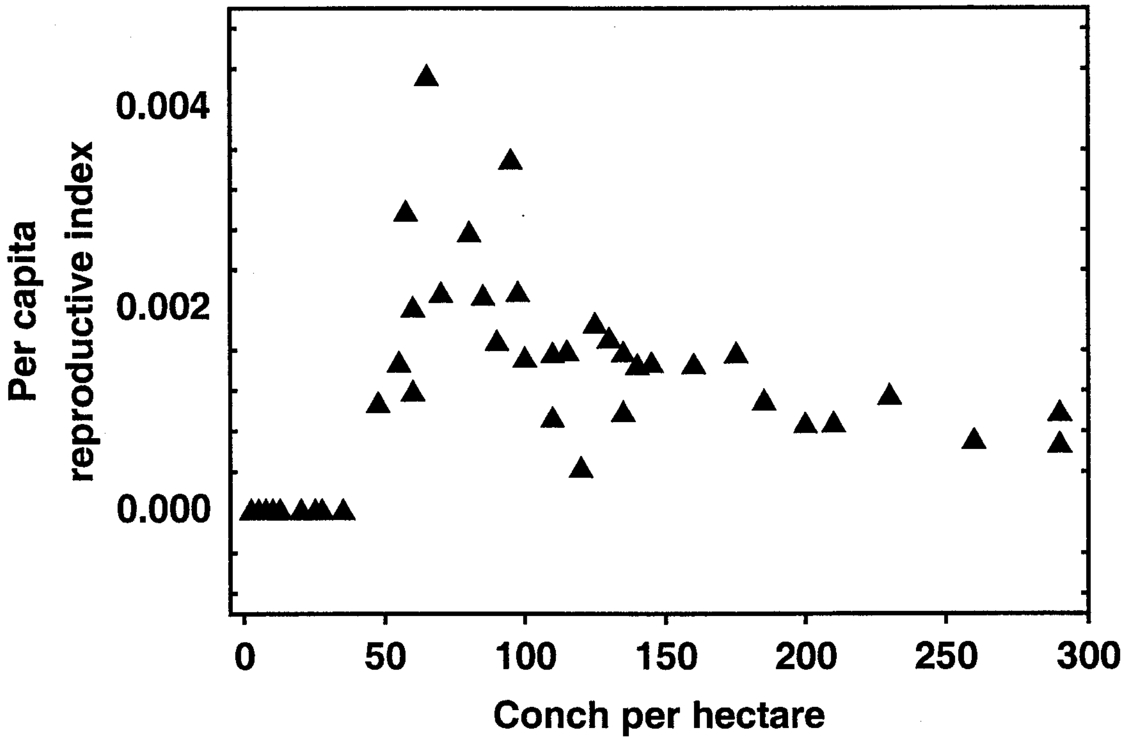


Fig. 2

Map of sites in the Exuma Cays, Bahamas.

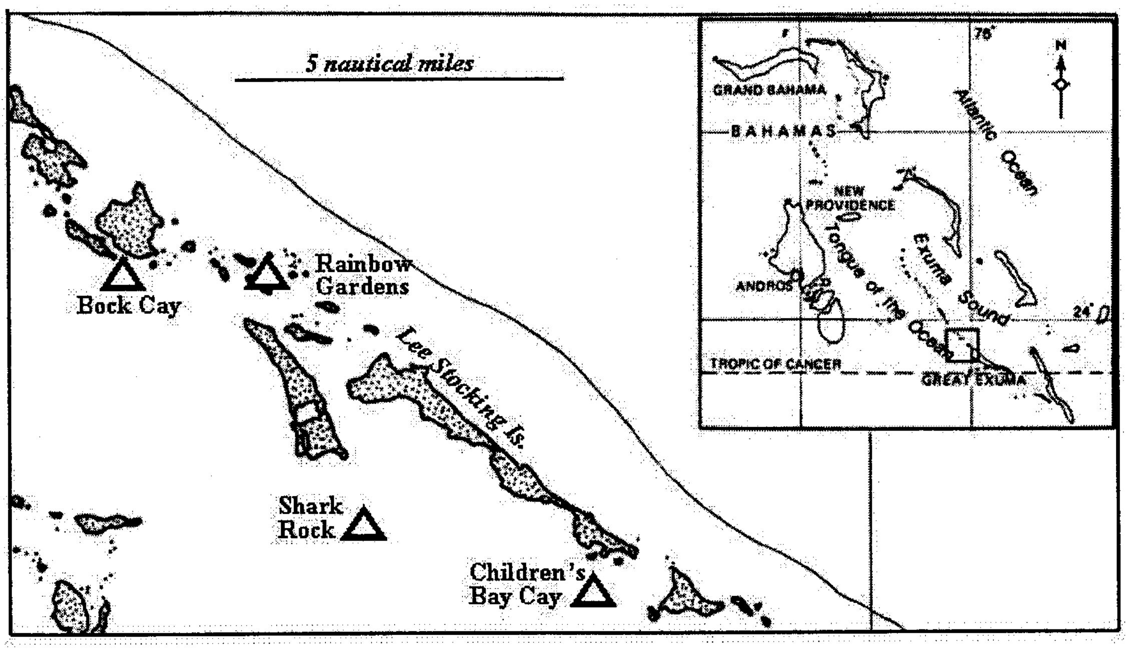


Fig. 3

Life-cycle diagram for the queen conch population matrix projection model. The life cycle is composed of a juvenile stage (J1), and three adult stages (A1-A3). The transition probabilities (*S*) reflect growth and survival to the next stage (Table 3), including retention of some fraction of juveniles in the juvenile stage ($S_{J1\text{-}J1}$) and adults in the last adult stage (A_3). Reproductive contributions of each adult stage are indicated as F_1 to F_3.

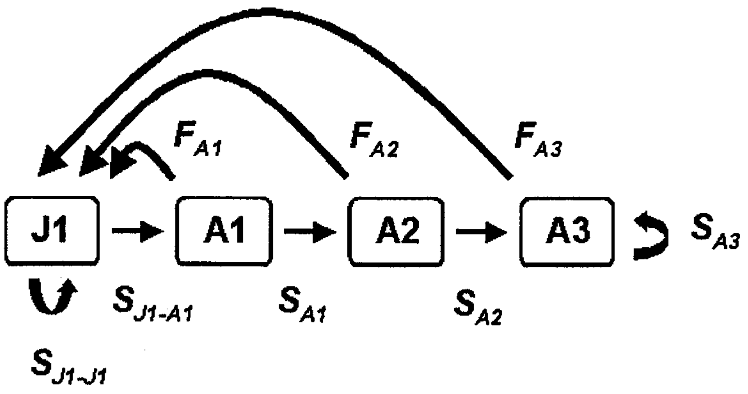


Fig. 4

The effect of the exponent δ in the density-dependent equation for reproductive output.

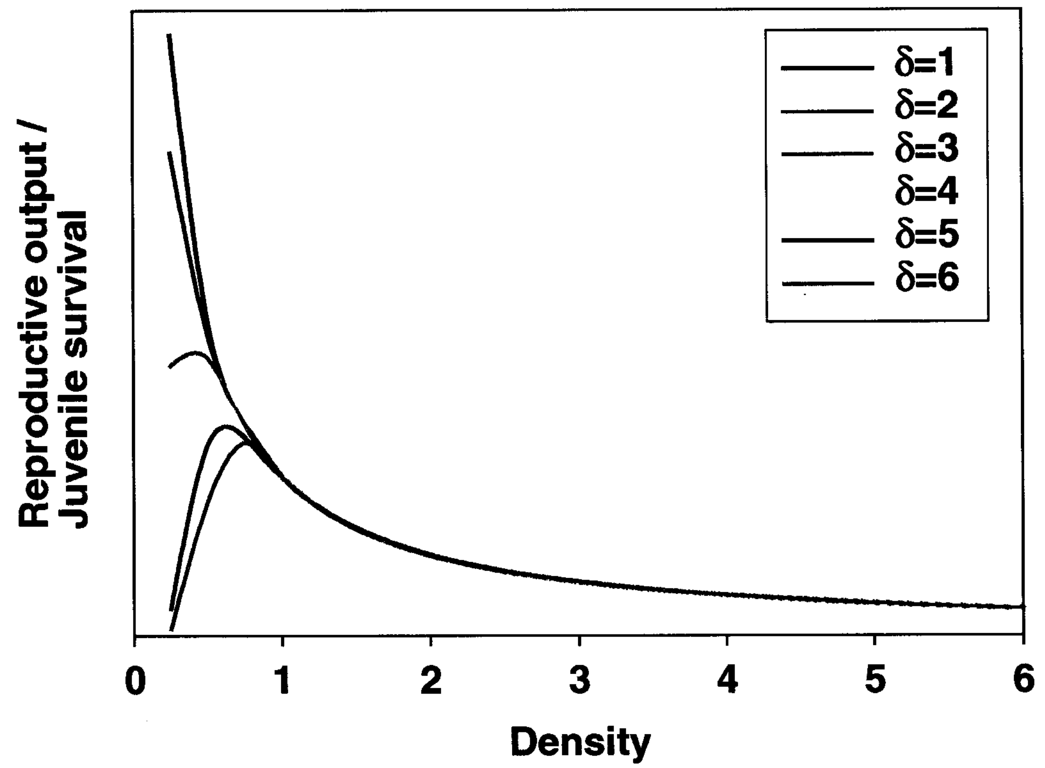


Fig. 5

Mean reproductive indices for each combination of Source site density and Host site density. Treatment combinations that did not differ significantly (Student-Newman-Keuls pairwise comparisons) share the same letter. Error bars are one standard deviation.

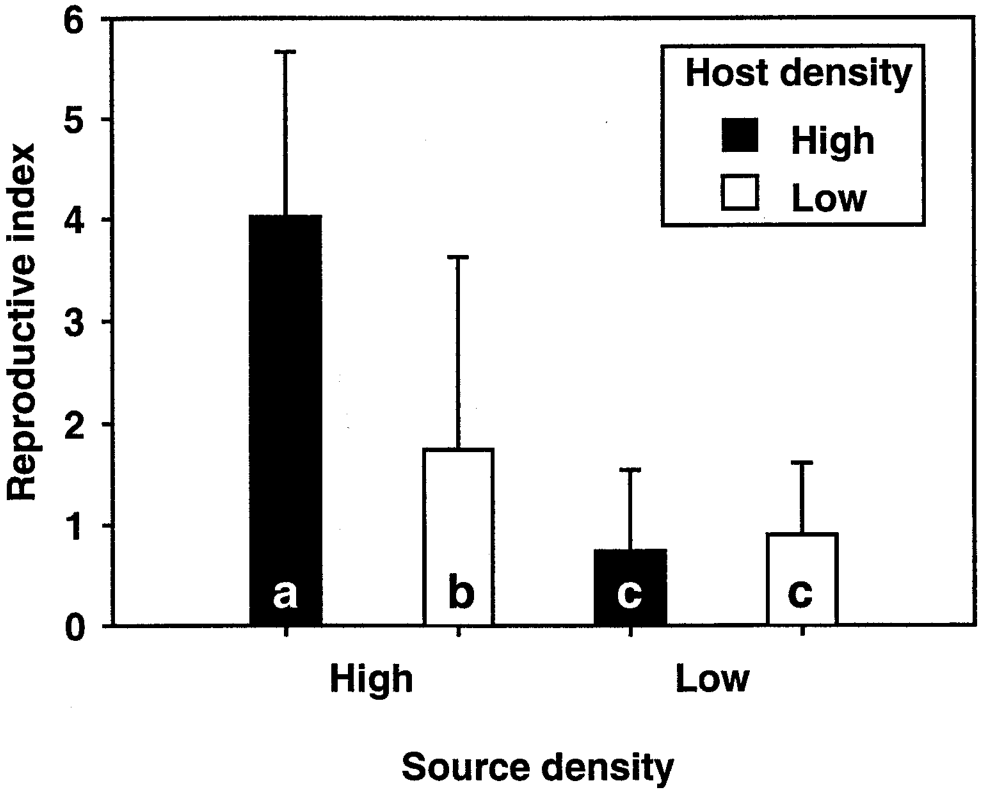


Fig. 6

Lip thickness (mm) and shell length (cm) for subsampled conch from high and low density sites.

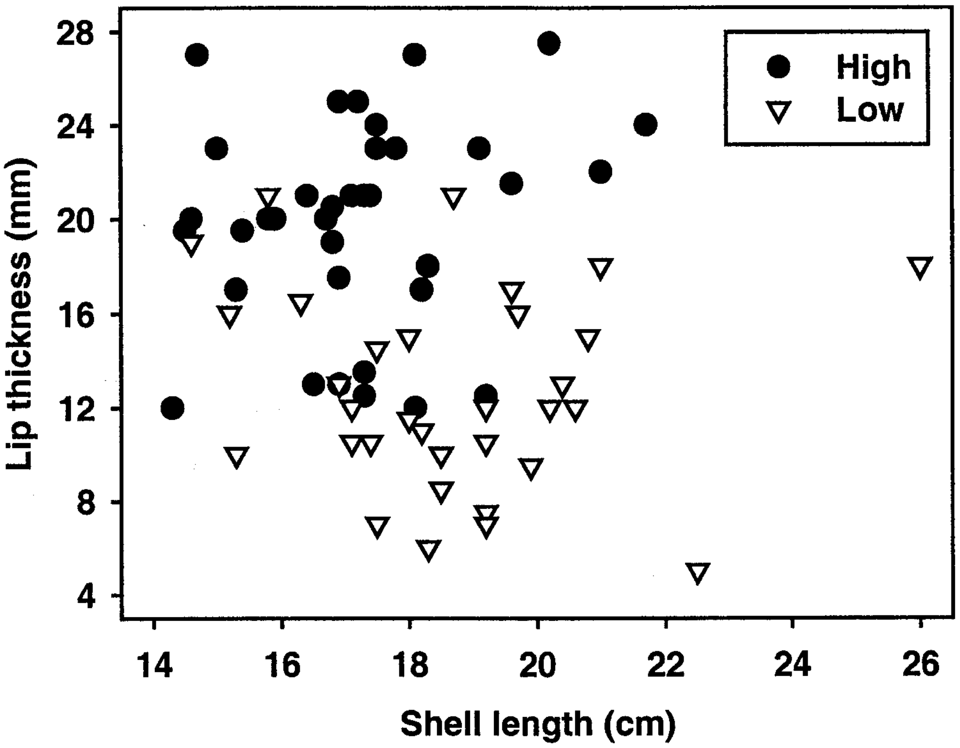


Fig. 7

Ratio of flesh wet weight (g) to shell weight (g) (condition index), by site and sex. Sites B and R are high density sites, sites C and S are low density sites.

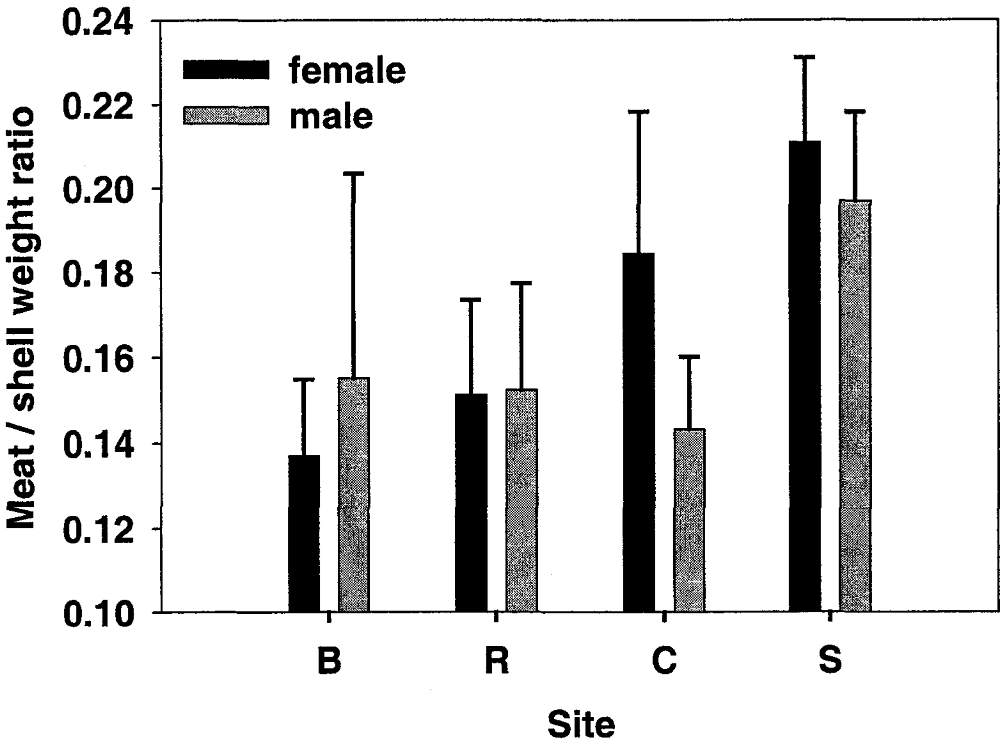


Fig. 8

Equilibrium adult population size vs. exploitation mortality (F) in model runs (see Appendix). In model null1 all adults reproduce and all adults are exploited; in model null2, adult stages 1 and 2 do not reproduce and are not exploited; in model rep, adult stages 1 and 2 do not reproduce but are exploited (delayed functional maturity model). The model is heuristic and only comparative values of population size and F are meaningful.

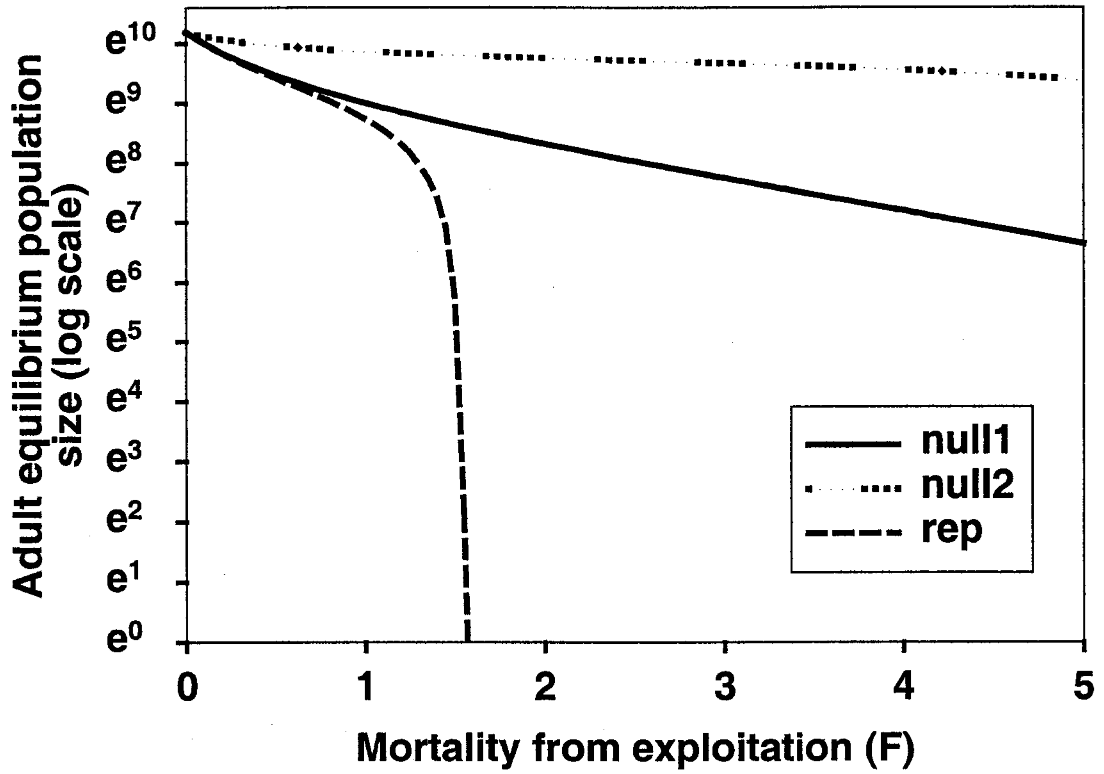
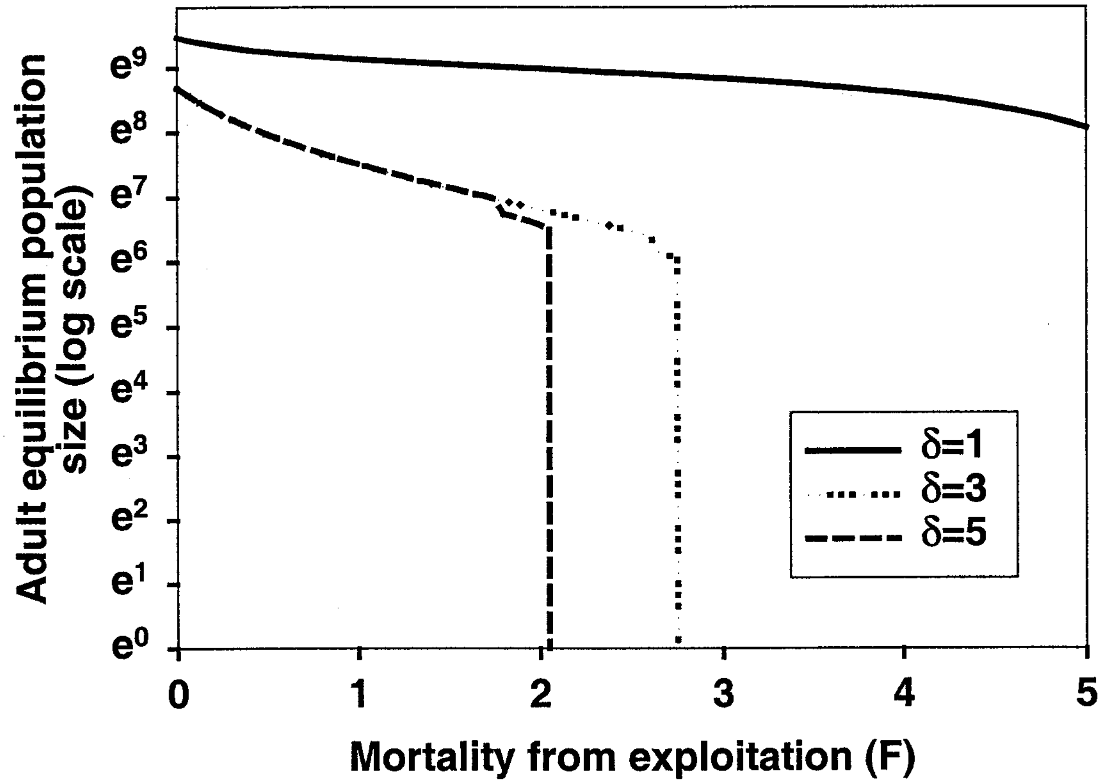


Fig. 9

Equilibrium adult population size vs. exploitation mortality (F) in Allee model runs (see Appendix). Allee models are similar to model null1 (see Fig. 8) but with an Allee effect in reproduction at low density. The value of δ indicates the strength of the Allee effect; δ=1 – no Allee effect; δ=3 - intermediate effect, δ=5 - strong effect (Stoner and Ray-Culp 2000). The model is heuristic and only comparative values of population size and F are meaningful.



CHAPTER 4

PREDATOR-DRIVEN ALLEE EFFECTS: THEORETICAL FRAMEWORK AND EMPIRICAL EVIDENCE

ABSTRACT

An Allee effect is positive density dependence in individual fitness at low density, and may result in thresholds below which populations are not viable. It is well known that some types of predator-prey interactions are unstable; this is partly because predators can cause Allee effects in prey populations. I use a series of simple heuristic models to develop a theoretical framework for predator-driven Allee effects. Predators can create an Allee effect if they have a Type II functional response without a Type III aggregative or numerical response, or *vice versa*. In addition, predation must be the main driver of prey dynamics, and prey must have little spatial or temporal refuge from predation. I present several unrecognised examples of predation-driven Allee effects from the literature, the majority of which come from systems that have been perturbed by exploitation or introduced predators. Unlike most mechanisms for Allee effects studied to date, this mechanism does not arise from the specifics of prey life history, but from a general ecological process, which makes it difficult for managers to predict and prepare for.

INTRODUCTION

The Allee effect

In classical steady-state population models such as the logistic model, the *per capita* population growth rate is highest at low population size or density (negative density dependence). However, individual fitness can be compromised at low density, such that *per capita* population growth rate may be reduced at low population size or density (positive density dependence). If the population growth rate declines below replacement levels, this can result in a critical threshold below which the population will become extinct (Courchamp *et al.* 1999, Stephens and Sutherland 1999). This positive density dependence at low population size or density is termed an Allee effect, after the pioneering ecologist Warder Clyde Allee (Allee 1931). An Allee effect can be a function of population size or density (or both), depending on the mechanism.

A key feature of an Allee effect is positive density dependence in the *per capita* population growth rate *at low density*, rather than at any other point in the relationship between population growth rate and population density. From a conservation perspective, this is the most critical consequence of an Allee effect - its potential to drive a population to extinction by reducing *per capita* population growth rate to negative values as density declines to low levels.

Above, I frame conceptual mechanisms for the Allee effect in terms of individual fitness, but define the Allee effect in terms of population growth rate. Numerous density-dependent and density-independent factors affect fitness; population growth rate will therefore not always react predictably to changes in one component of fitness with density. Hence, any particular *component* Allee effect (positive density dependence in one component of fitness such as reproductive output) will not inevitably produce a *demographic* Allee effect (positive density dependence in the population growth rate; *sensu* Stephens *et al.* 1999; see Levitan 1991 for an example). Whether a component Allee effect creates a demographic Allee effect depends on the trade-offs between positive and negative density dependence due to various component effects. Thus, a component Allee effect will create a demographic Allee effect and drive a population to extinction only if that component of fitness is an important control of population dynamics at low density.

Component Allee effects: reproduction vs. survival

Individual fitness has, broadly, two components that can interact with population density: reproductive output and survival probability. Though reproductive output (which includes fecundity, reproductive lifespan and age at maturity) and survival probability will typically vary with habitat features, age and life-history stage, each may also have various density-dependent relationships in different traits or stages.

Empirical studies of Allee effects have largely focused on positive density dependence in reproductive output, such as cooperative breeding in mammals (Clutton-Brock *et al.* 1999, Courchamp and Macdonald 2001), broadcast spawning in marine invertebrates (Levitan 1991, Levitan and Young 1995, Baker and Tyler 2001), pollination in plants (Lamont *et al.* 1993, Widén 1993, Hackney and McGraw 2001) and mating in species with low mobility or small home ranges (Kuussaari *et al.* 1998, Stoner and Ray-Culp 2000). Allee effects driven by reproduction are consequently fairly well accepted in the literature, and in some cases reproduction has become part of the definition of an Allee effect (e.g. Pulliam and Dunning 1997). The focus on specific reproductive traits that are likely to provide mechanisms for Allee effects has left many conservation biologists with the idea that Allee effects are generally confined to species with a limited range of life histories. Here I focus on Allee effects in survival probability caused by predation. This is a more general ecological mechanism that may be applicable over a range of species with different life history traits.

The predator functional response and the Allee effect

In a predator-prey relationship, predators react to prey density in three interrelated ways:

1. Individual predators change their feeding rates in response to changes in prey density (the functional response);

2. Predators aggregate at patches of high prey density (the aggregative response);

3. Predator population size varies as a function of prey availability (the numerical response).

The predator functional response is often seen by modellers as a simple mechanism for creating an Allee effect (Scheiber *in press*, Frank and Brickman 2001). Conversely, it is often overlooked as a mechanism by empiricists and conservation biologists. In this paper I lay out the theoretical basis for Allee effects driven by predator functional response.

Using simple, heuristic models, I show how some types of predator functional response create an Allee effect, while other types do not. I also show that the functional response interacts with the numerical and aggregative response, and what combinations of each can create an Allee effect. I then use this theoretical foundation as a basis for a search for examples of predation-driven Allee effects in the empirical literature.

MODELS

Functional response model

The functional response defines the rate of prey consumption for a given number or density of predators, as a function of prey density (Holling 1959). The *per capita* functional response can also be interpreted (given appropriate parameterisation) as the probability of a prey individual being consumed by a predator as a function of prey density, and is calculated by dividing the functional response by the prey density. A prey individual's probability of *not* being consumed (prey survival probability) is (1 – the *per capita* functional response).

After the pioneering work of Holling (1959), predator-prey theory traditionally defines three types of functional response: linear (Type I or Lotka-Volterra), hyperbolic (Type II) and sigmoid (Type III). Other types of functional response are possible; these characteristically alter predator-prey dynamics only at high density (Arditi 1982, Crawley 1992, Sabelis 1992) or they incorporate aggregative and numerical responses (ratio-dependent functional responses; Arditi and Ginzburg 1989, Hanski 1991), which I discuss separately. The functional response may also be defined in terms of the overall or mean functional response of a predator guild, which can also be measured and defined as Type I, Type II, Type III etc. (Seitz *et al.* 2001). For the purposes of this heuristic model it does not make any difference whether I regard the predators as one species or several, as long as their overall responses can be defined.

Type I (linear) functional response: In a Type I functional response, prey consumption rate per predator initially increases linearly with prey density, before reaching a maximum. The Type I functional response is considered a realistic model mainly for passive predators such as filter feeders and web-spinning spiders, although it may be more widespread (Arditi 1982).

I model a Type I functional response as follows (Fig. 1A):

$$y = \alpha N \qquad \text{for } N < N_{\text{crit}}$$

$$y = \alpha N_{\text{crit}} \qquad \text{for } N > N_{\text{crit}}$$

where y = rate of prey consumption per predator, N = prey density, N_{crit} = prey density where predator consumption rate reaches maximum, α = coefficient.

Corresponding prey survival probability for a given density of predators, as a result of predation with a Type I functional response (assuming appropriate coefficient γ such that $0 \leq p \leq 1$; Fig. 1B):

$$p = 1 - \gamma \qquad \text{for } N < N_{\text{crit}}$$

$$p = 1 - (\gamma N_{\text{crit}} / N) \quad \text{for } N > N_{\text{crit}}$$

Type II (hyperbolic) functional response: In a Type II functional response, predator feeding rate rises hyperbolically to an asymptote as prey density increases. This is probably the most common type of functional response found in field studies, for a large range of vertebrate, invertebrate and herbivore-plant predator-prey systems (Arditi 1982, Begon *et al.* 1996).

I model a Type II functional response as follows (simplified from Holling 1959; Fig. 1C):

$$y = \alpha N / (1+\beta N)$$

Corresponding prey survival probability for a given density of predators, as a result of predation with a Type II functional response (with appropriate parameterisation; Fig. 1D):

$$p = 1 - [1 / (1 + \gamma N)]$$

Type III (sigmoid) functional response: A Type III functional response is similar to a Type II for high prey densities, but the slope of the curve is maximised at intermediate rather than low prey density. This can arise from "prey switching", whereby predators with more than one prey species target only the more abundant species.

A Type III functional response can be modelled as follows (Fig. 1E):

$$y = \frac{\alpha N^2}{1 + \beta N^2}$$

Corresponding prey survival probability for a given density of predators, as a result of predation with a Type III functional response (Fig. 1F):

$p = 1 - [N / (1 + \gamma N^2)]$

Functional and aggregative response model

Next I consider the net effect of a Type II functional response with various forms of aggregative response. The functional response model above assumes a linear aggregative response, i.e. that predator numbers per prey are constant across the full range of prey density. However, I can incorporate other aggregative responses into the model in exactly an analogous way a functional response: i) constant predator numbers (no aggregative response); ii) constant predator to prey ratio, i.e. a linear (Type I) aggregative response; iii) asymptotic (Type II) aggregative response; and iv) sigmoid (Type III) aggregative response. The total probability that a prey individual will be killed by a predator is the *per capita* functional response (the probability that an individual predator will kill that prey individual as a function of prey density) multiplied by the number of predators encountered by that prey individual as a function of prey density (the *per capita* aggregative response).

Corresponding prey survival probability (p) with a Type II functional response and the various aggregative responses are:

Constant predator numbers (no aggregative response): $p = 1 - 1 / N(1 + \gamma N)$

Linear numerical response: $p = 1 - 1 / (1 + \gamma N)$

"Type II" numerical response: $p = 1 - 1 / (1 + \delta N)(1 + \gamma N)$

"Type III" numerical response: $p = 1 - N / [(1 + \delta N^2)(1 + \gamma N)]$

where δ is the coefficient for the aggregative response and γ is the coefficient of the functional response.

Fig. 2. shows prey survival probability as a function of prey density with a Type II functional response and the above types of numerical response.

Adding predator density to the functional response model

I can also extend the functional response model to look at prey survival probability as a function of both prey and predator density. Prey encounter probability (p(enc)) as a function of predator density can be modelled as a simple hyperbolic curve:

$p(\text{enc}) = \delta P / (1 + \delta P)$ where P = predator density

The *per capita* functional response (in this case, a Type II functional response) is the probability that an individual prey will be consumed if it encounters a predator as a function of prey density ($p(\text{con}|\text{enc})$):

$p(\text{con}|\text{enc}) = \delta / 1 + \gamma N$ where N = prey density

The total probability of a prey individual being consumed by a predator is the product of the probability that the prey individual will encounter a predator and the probability that the prey will be consumed if it is encountered:

$p(\mathrm{con}) = p(\mathrm{con}|\mathrm{enc}) \, . \, p(\mathrm{enc})$

with corresponding prey survival probability (Fig. 3):

$1 - p(\mathrm{con}|\mathrm{enc}) \, . \, p(\mathrm{enc}) = 1 - \delta\gamma P \, / \, (1 + \delta P)(1 + \gamma N)$

MODEL RESULTS

Functional response model

For an Allee effect, prey survival probability should be positively density dependent at the low density end of the range, all the way to the origin. Positive density dependence in prey survival probability is indicated by a positive slope in the relationship between prey survival probability and prey density (Figs. 1B, 1D and 1F).

The Type I functional response is positively density dependent above N_{crit}, but density independent below N_{crit}. Hence this functional response does not cause an Allee effect (Fig. 1B).

For a Type II functional response, the slope of the curve is positive across the entire range of prey density, and the slope is steepest close to the origin. Hence (all else being equal), prey fitness due to predation is always positively density dependent with a Type II functional response. Furthermore, fitness declines most strongly with density when density is low. Hence the Type II functional response has the potential to create a deterministic Allee effect in prey population dynamics (Fig. 1D).

Like a Type I functional response, a Type III functional response results in positive density dependence in prey fitness at high prey density but not at low prey density. In fact, prey fitness increases as density declines at low density. This means that a Type III response can potentially keep prey at a low stable equilibrium corresponding to the minimum in the graph above (sometimes called a "predator pit"). Therefore, this functional response does not have the potential, *a priori*, to create an Allee effect (Fig. 1F).

Functional and aggregative response model

The Allee effect generated by a Type II functional response is cancelled out by a Type III aggregative response. However, with other types of functional response, or with constant predator density, the Allee effect is maintained (Fig. 2). This also applies in reverse; a Type II aggregative or numerical response can create an Allee effect that is mitigated by a Type III functional response, but maintained by other types of functional response. A Type II functional response with constant predator numbers creates the strongest Allee effect, followed by a Type II response with a Type I aggregative response, followed by two Type II responses.

Adding predator density to the functional response model

Prey survival probability depends mainly on predator density (*P*) at low prey density, and mainly on prey density (*N*) at high predator density (Fig. 3). The true relative importance of prey and predator density depends to some extent on the coefficients (here set to be equal), but this model implies that dynamics at low prey density will be dominated by changes in predator numbers rather than prey numbers, i.e. the aggregative or numerical rather than the functional response. Thus the shape and strength of the numerical or aggregative response is likely to be important in determining the strength of the predator-driven Allee effect.

DISCUSSION

Functional response and the Allee effect

The Type II functional response shows strong positive density dependence at low population density (Fig. 1D; Hassell and May 1973, Murdoch 1973, Hassell 1978). Hence the Type II functional response can create a component Allee effect in predation mortality. Other functional response curves are either negatively density dependent or density independent at low prey density, and will therefore not cause an Allee effect. However, depending on the prey density range over which the Type I and Type III functional responses operate, they may suppress prey to low density or population size where a population may be vulnerable to extinction due to environmental or demographic stochasticity (a "predator pit"). There is an ongoing debate about whether demographic stochasticity should be considered an Allee effect – it is not a density dependent process *per se*, but the extinction probability associated with it is density dependent (Lande 1998, Dennis 2002, Levitan and McGovern *in press*). If so, all three main types of functional response have the potential to cause Allee effects. However, in this paper I focus on deterministic Allee effects, which can be caused only by a Type II functional response.

Predator-prey models incorporating a Type II functional response normally have unstable prey dynamics (Hassell and May 1973, Murdoch 1973, May 1974, Oaten and Murdoch 1975, Hassell 1978, Crawley 1992) and can cause critical population or patch size effects in prey (Sinclair *et al.* 1998, Cantrell *et al.* 2001). However, the association between functional response and Allee effects in prey is rarely made in empirical studies, the predator-prey literature and general ecological texts. Conversely, some modelling studies suggest a Type II predator functional response as one of the simplest mechanisms for generating an Allee effect (e.g. Schreiber *in press*). I would like to make the link between conservation biologists working on Allee effects, and the extensive predator-prey modelling literature. From a conservation perspective, it is critical to realise that predation has the potential to create an Allee effect in prey dynamics, without recourse to specific traits in the prey life history.

Numerical or aggregative response

A Type III predator aggregative or numerical response has the potential to eliminate the Allee effect caused by a Type II functional response (Fig. 2). Likewise, a Type III functional response can stabilise dynamics with a Type II aggregative or numerical response. However, if either response is Type II, and neither is Type III, a component Allee effect in prey mortality from predation is the result. (Constant predator numbers regardless of prey density, in combination with a Type I functional response, or conversely constant predators per prey with a constant predator feeding rate regardless of prey density would also create an Allee effect. The former might be relevant, for example, in sessile filter feeders such as corals, but I don't consider it further here.)

Given the importance of predator density at low prey density (Fig. 3), the form of the aggregative or numerical response is likely to be very important in determining the presence and strength of a predator-driven Allee effect. Unfortunately, the form of the aggregative or numerical response is rarely, if ever, quantified in empirical studies. Presumably, a Type III aggregative response would result when predators actively avoid areas of low prey density as well as actively seeking out areas of high prey density, and would be unlikely where predators interfere with each other, are territorial or agonistic (Roger and Hassell 1974, Perkins-Visser *et al.* 1996, Rohner and Krebs 1998, Clark *et al.* 1999). A Type III numerical response would result if predators suffered elevated levels or mortality or reproductive failure below a critical prey density, and would be less likely in predators with alternative prey.

Our model is very simplified, notably in that it focuses on an aggregative rather than a numerical response for predators. Aggregative and numerical responses operate on different time-scales, and predators may have both, with each taking a different form. The relative strengths of the functional, aggregative and numerical response is also likely to be important in determining the presence and strength of an Allee effect. A weak Type III aggregative response may not be enough to stabilise prey dynamics with a very strong Type II functional response (and *vice versa*). However, the model gives a useful overview of where predator-driven Allee effects are likely to occur. Since the shape and strength of responses are variable in space and time (Morgan *et al.* 1987, Hanski 1991, Fauchauld *et al.* 2000, Johnstone and Norris 2000) and difficult to measure, a more complicated model may not be justified.

The conclusions from this model correspond well to those from more specific predator-prey models. In a Lotka-Volterra predator-prey system (linear functional response), aggregation is generally destabilising unless it is accelerating, i.e. there are disproportionate numbers of predators in dense patches (Murdoch and Stewart-Oaten 1989). This corresponds to a Type III aggregative response. In a review of predator-prey models, Murdoch (1994) concludes that the stabilising effect of predator aggregation in systems with overlapping generations is open to question. This makes sense since the form of the response (i.e. the specifics of a given model) is critical to prey dynamics.

Prey distribution

Prey can have three types of distribution: random, uniform and clumped. For a random distribution, functional and aggregative responses are both relevant. As the distribution becomes more uniform, there is less scope for an aggregative response, so a functional response-driven Allee effect potentially becomes more important. As the distribution becomes more clumped, a higher proportion of prey is living at high density, so the functional response becomes less relevant and the aggregative response more important. An Allee effect driven by a Type II aggregative or numerical response might be possible in this situation. For extremely aggregated distributions (such as schooling fish), predators can respond to prey population size or density both within aggregations and between aggregations. I don't consider this possibility further here, except to note that the situation for highly aggregated prey is potentially complicated.

Other factors that may eliminate Allee effects

Prey population size: Perhaps the simplest mechanism for dealing with the Allee effect is prey population size; if the prey population is large or dense, and stable, it is never in the part of the curve where Allee effects are important. Instead it is likely to be regulated by other density-dependent factors such as intraspecific competition. The Allee effect could still be "latent" in the prey population, and could manifest itself if population size or density were reduced (e.g. through overexploitation or habitat loss). This predator avoidance strategy is sometimes called the "dilution effect" (Inman and Krebs 1987).

Spatial heterogeneity: The literature on the effect of spatial heterogeneity on predator-prey relationships is substantial (Hassell 1984, Comins and Hassell 1987, Kareiva 1987, Latto and Hassell 1988, Taylor 1990, Hawkins *et al.* 1993, Murdoch 1994, Cosner *et al.* 1999, Takagi 1999, McCauley *et al.* 2000), and can only be summarised briefly here. In general, spatial heterogeneity in predator or prey distribution is a stabilising force, although there are exceptions (Kareiva 1987, see below).

It was recognised early on that a spatial refuge from predation can stabilise predator-prey systems (Gause 1934, Connell 1970, Hassell 1978, Murdoch *et al.* 1996 and references therein), although field experiments have yielded equivocal results (Murdoch *et al.* 1996). A Type II functional response with a fixed number of prey in a spatial refuge will cross the x-axis to the right of the origin (Fig. 4). In terms of prey dynamics this yields results that are generally indistinguishable from a Type III functional response, with a stable prey equilibrium at low density, depending on refuge size and dispersal rates. In models, refuges can stabilise populations if they protect either a fixed proportion of the prey population or a fixed number of prey, depending on the predator-prey model (Hassell 1978, Murdoch *et al.* 1996), with their effectiveness depending mainly on the rates of prey dispersal between the refuge and vulnerable habitats (Takagi 1999).

A prey metapopulation structure (prey subpopulations connected by dispersal) also seems to reduce the likelihood of an Allee effect in models (Taylor 1990, de Roos *et al.* 1998, Hanski 1999, Frank and Brickman 2000, 2001) and in practice (McCauley *et al.* 2000, but see also Murdoch *et al.* 1996). The crucial characteristic for metapopulation stability is that the dynamics of prey subpopulations are not synchronous, such that individual subpopulations which have declined to low density and are suffering from the Allee effect have a high probability of being "rescued" (brought back above the critical Allee threshold) by immigration from neighbouring patches that are at high density (Taylor 1990, McCauley *et al.* 2000). However, a metapopulation can also suffer an "Allee effect" in that it may require a critical number of subpopulations to remain viable, so populations with a metapopulation structure are certainly not immune from threshold effects analogous to Allee effects (Courchamp *et al.* 2000, Frank and Brickman 2000, 2001).

Habitat fragmentation and the attendant population subdivision may be either beneficial or detrimental to the metapopulation. McCauley *et al.* (2000) showed that a series of connected prey subpopulations in fragmented habitats had more stable dynamics than a homogeneous environment. Habitat fragmentation can also disrupt a predator aggregative response and effectively turn a metapopulation into a series of separate populations, both of which make the Allee effect more likely to lead the metapopulation to extinction (Kareiva 1987). Thus the scale of fragmentation relative to the scale of the prey and predator populations and the dispersal abilities of the prey are critical for patchiness to provide protection from the Allee effect.

Theoretical framework

There is a set of characteristics that are necessary for a predator-prey system to be susceptible to predator-driven Allee effects.

1. A Type II predator functional or aggregative/numerical response, without a Type III response in the other.

2. Predation must be a key driver of prey dynamics. In this model, our dependent variable is prey survival due to predation. This is only one component of fitness. If predation is not the major constraint on survival, positive density dependence in this component may not translate into positive density dependence in the population growth rate – a demographic Allee effect.

3. No spatial or temporal refuge from predation for prey.

How likely are these conditions to be met in natural systems? The Type II functional response seems to be the most common (Arditi 1982, Begon *et al.* 1996) for generalist and specialist predators (Murdoch 1969, Murdoch and Oaten 1975, Katz 1985, Sinclair *et* *al.* 1998, Johnstone and Norris 2000). Generalist predators, or even predators with two main prey species, need not show any numerical or aggregative response to a given prey species (Katz 1985, Cappuccino 1987, Sinclair *et al.* 1998).

In addition, prey as well as predator life history plays a role in determining the functional response. Some predator avoidance strategies, such as crypsis and refuges, are more effective at low density, and predators on prey with these strategies are likely to have a Type III functional response. The same predators on prey species with passive, non-density dependent predation avoidance strategies such as armouring, spines or aposematic colouring are likely to have a Type II functional response (Cappuccino 1987, Rangeley and Kramer 1998, Jeschke and Tollrian 2000, Seitz *et al.* 2001). Many of these prey species may take advantage of positive density dependence and use weight of numbers as an anti-predator strategy (the dilution effect).

I have also discussed other mechanisms that mitigate Allee effects or their consequences in these systems. In fact, given that the predator-prey systems I observe in natural systems are stable in evolutionary time, it is unlikely that prey have come under frequent serious threat of extinction from predator-driven Allee effects. It therefore seems likely that most natural predator-prey systems have some (or several) stabilising mechanisms that reduce or eliminate predator-driven Allee effects, even if the stabilising mechanism remains unexplained (Murdoch *et al.* 1996). Thus a fourth criterion for predator-driven Allee effects is probably that the system is perturbed in some way.

Empirical evidence for predator-driven Allee effects

I searched the literature for examples of predator-driven Allee effects. I looked for both component Allee effects in survival and demographic Allee effects. In order to show a predation-driven component Allee effect, I need to find data that show that prey in sparse or small populations have higher mortality than in dense or large populations and that this increase in mortality at low density is due to predation. To show a predation-driven demographic Allee effect I need to show that predation causes a lower population growth rate or higher extinction risk for small or sparse populations.

Hence I required data on predation rates, prey dynamics and (if possible) predator functional response across a range of prey densities. I reviewed over 100 published predator-prey studies. I did not find enough information to do a true meta-analysis, since in most papers data were not available across a large enough range of prey densities to decide whether an Allee effect was operating or not. I simply searched for examples of studies that show, or strongly suggest, predator-driven Allee effects. These are discussed below according to the type of evidence that they provide. Interestingly, none of the papers discussed below, which provide evidence for predation-driven Allee effects, mention the phrase "Allee effect" anywhere.

1. Critical population size below which the prey goes extinct due to predation.

Sinclair *et al.* (1998) present a clear example of a predator-driven demographic Allee effect in a study of small populations of Australian native marsupials suffering predation due to introduced predators. Under predation, black-footed rock wallabies (*Petrogale* *lateralis*) had a threshold population size of 5-10 below which population went extinct. When foxes were removed there was no such threshold and populations stabilised. Sinclair and Pech (1996) also give an example of a wildebeest (*Connochaetes taurinus*) population that is periodically cut off from the larger population by flooding and extirpated by lions (*Panthera leo*), while the larger population is stable.

2. *Higher* per capita *predation rate as population size decreases to low density, with demographic consequences*

Sinclair *et al.* (1998) have two examples of accelerating population decline due to predation; the eastern barred bandicoot (*Perameles gunnii*) and the quokka (*Setonix brachyurus*), where *per capita* predation rates increased as population size declined. Reintroduced populations all eventually went extinct due to predation. Analysis of predation rates indicates an Allee threshold (switch from negative to positive population growth rate) of about 100-150 animals for the quokka.

Seabird colonies are a good example of large population size and density as a predator avoidance strategy. Several species suffer higher *per capita* predation rates in smaller colonies (Gilchrist 1999 and references therein, Cuthbert 2002). Cuthbert (2002) showed that larger colonies of Hutton's and sooty shearwaters (*Puffinus huttoni, P. griseus*) are thriving, with low predation rates, while mortality increases exponentially as colony size decreases. Small colonies suffer high predation rates and are declining, with some colonies having already gone extinct. Again, introduced predators are implicated (feral pigs, *Sus scrofa*, and stoats, *Mustela erminea*), with pigs reducing colony size below the

Allee threshold for Type II predation by stoats. Stoats are limited by over-winter survival and territoriality, which overrides any numerical response to shearwater numbers. In this case, the Allee threshold for stoat predation appears to be around 600 breeding pairs. Likewise, small, sparse thick-billed murre (*Uria lomvia*) colonies experience higher predation rates from gulls than large, dense colonies, and the latter are increasing in size while the former are declining. Smaller, sparser colonies were reduced from higher density by hunting (Gilchrist 1999).

Predatory mergansers (*Mergus merganser*) take a higher proportion of migratory salmon in years when the population is smaller (Wood 1987). Human "predators" have also been shown to have a Type II functional response and a limited numerical response in commercial, recreational and artisanal fisheries (Peterman 1980, Rose and Kulka 1999, Post *et al.* 2002). Due to fish aggregative behaviour and fishers' knowledge, fish do not usually become more difficult to catch as population size declines, and catchability may increase. Numerical and aggregative responses are limited by i) travel time, ii) investment in expensive equipment, iii) economics, which dictates that prices rise with rarity and iv) reduced expectations of catches as stocks decline (the "sliding baseline" phenomenon). Thus fishing can cause a "predation"-driven Allee effect in fish stocks, which can lead to stock collapses (Rose and Kulka 1999, Post *et al.* 2002).

(There has been a great deal of discussion of demographic Allee effects, or "depensation", in the fisheries literature (e.g. Myers *et al.* 1995, Frank and Brickman 2000, 2001). Generally, the emphasis is not on the mechanism for Allee effects, but rather whether they might explain the fact that stocks reduced to low density by overexploitation often fail to recover as fast as demographic theory predicts. Since exploitation rates ("predation" by humans) have usually been reduced in such stocks by cuts in quota or fishing moratoria, the above argument does not apply to this situation.)

3. *Type II predation holds prey at low density with low or negative population growth rate, or results in the extirpation of a population.*

The demographic consequences of Type II predation can be difficult to distinguish from the consequences of Type III predation if the latter leads to population decline to a low density "predator pit" or extinction from other consequences of small population size (demographic stochasticity, inbreeding depression, etc.). It is not clear that this is an Allee effect *per se*, so I only admit the above scenario as evidence of predator-driven Allee effects when the predator functional response is known to be Type II. I also need evidence that predation has increasingly severe effects on the prey population as density declines.

Blue crabs (*Callinectes sapidus*) have a Type II functional response to the soft-shelled clam (*Mya arenaria*) in mud, but a Type III response in sand (Lipcius and Hines 1986, Eggleston *et al.* 1992, Seitz *et al.* 2001). Their aggregative response is limited by agonism (Perkins-Visser *et al.* 1996, Clark *et al.* 1999). In Chesapeake Bay, *Mya* settles in both habitats and is abundant in sand year round, but declines to extinction in mud each summer due to blue crab predation (Eggleston *et al.* 1992, Seitz *et al.* 2001). The baltic clam (*Macoma balthica*), on the other hand, persists in both habitats and is usually more abundant in mud than sand, despite being the main prey item for blue crabs. Crabs show a Type III functional response to this species in both habitats. Hence *Mya* seems to suffer a predator-driven Allee effect in mud habitats, although not in sand; this is a good example where the overall system is stabilised by a habitat refuge and metapopulation dynamics.

Predation is the main factor dictating the survival of juvenile abalone, *Haliotis* spp. (Shepherd 1997, Mayfield and Branch 2000, Rogers-Bennett and Pearse 2001). In south Australia, predation by the wrasse *Notolabrus tetricus* is the main source of natural mortality for the population. *Notolabrus* is a generalist predator with a Type II functional response on abalone (Shepherd and Clarkson 2001). In South Africa, rock lobsters play the same role, particularly since a commercial fishery for sea urchins has removed a spatial refuge for juvenile abalone under the urchin spine canopy (Mayfield and Branch 2000). Hence a predator-driven Allee effect is a hypothesis for the fishing-induced collapse of many abalone stocks worldwide (Shepherd *et al.* 1992), although reproductive Allee effects (Shepherd and Brown 1993, see Chapter 1) and the short scale of larval dispersal (Tegner 1993) may also be important.

CONCLUSIONS

Predator-driven Allee effects in disturbed ecosystems

The requirements for a predator-driven Allee effect can easily be met in predator-prey systems. However, there are several common mechanisms by which prey may avoid an Allee effect (and there are likely to be others, some as yet untested; Murdoch *et al.* 1996). There are, of course, other complexities that can be added to our simple conceptual model. Functional and aggregative response in a given predator-prey system can vary with prey and predator size (Eggleston 1990a,b), predator sex (Eggleston 1990b), temperature (Eggleston 1990c), habitat (Lipcius and Hines 1986, Eggleston *et al.* 1992, Johnstone and Norris 2000), predator density (Arditi and Ginzburg 1989), the presence of other prey species (Chesson 1989) and the spatial scale of data collection (Morgan *et al.* 1987, Hanski 1991, Ives *et al.* 1993, Fauchauld and Erikstad 2002), among other things. And all predator-prey relationships obviously take place in a multispecies context, as one component of many interactions within and between trophic levels, and as part of a variable and stochastic physical environment. It is not unreasonable to assume that some stabilising mechanism will operate in most predator-prey relationships in natural systems, given that they must have been, to an extent, stable in evolutionary time.

Despite these various complicating factors, I believe that predator-driven Allee effects are potentially relevant. Humans are disrupting most natural ecosystems, and are potentially removing many of the stabilising factors in predator prey relationships. It is striking that in more than two-thirds of the empirical examples that I present above, human intervention is important in the system. Furthermore, in the examples where it is not important, the overall system is stable despite Allee effects. In the other examples, the original population size of the prey has been drastically reduced by fishing, hunting or introduced predators, such that stabilising factors have been removed and the predator-driven Allee effect comes into operation.

I suggest that most types of anthropogenic disturbances to natural systems have the potential to destabilise natural predator-prey interactions and create an Allee effect in prey populations, including i) reduction in population size, ii) habitat insularisation and fragmentation, iii) large scale disturbance and iv) enhancement of generalist predators.

Reduction in population size: Perhaps the most straightforward impact that humans have had on many species is a large decrease in their population size. A large, dense population is a defence against predation in itself. Prey species for whom the dilution effect is the main defence are likely to have predators which show a Type II functional response, since the prey probably have density-independent rather than negatively density-dependent anti-predator strategies (Jeschke and Tollrian 2000, Seitz *et al.* 2001). Good examples might be seabird colonies, large ungulates and non-cryptic invertebrates – not species that have traditionally been considered likely candidates for Allee effects.

Generally, top predators have been most affected by reduction in population size, thus reducing the impact of predation on the prey population even if the prey population is also being reduced in size (a human-induced "numerical response"). However, this doesn't apply if the top predator in the system is humans, as it is in exploited ecosystems. I have discussed above how (for example) fishers act as Type II predators with limited numerical or aggregative response (Post *et al.* 2002). Thus increasing rates of population decline with decreasing population size, and thresholds below which populations collapse abruptly should be considered plausible trajectories for exploited populations, rather than an outcome that takes conservationists and managers by surprise.

Habitat fragmentation and isolation: By contrast with marine systems, which suffer most from straightforward exploitation, the most critical conservation issue in terrestrial systems is insularisation of populations through the loss and fragmentation of natural habitat (Myers 1997). As I discuss above, prey subpopulations may suffer Allee effects but the overall metapopulation can nonetheless be stable, due to dispersal between subpopulations (Taylor 1990, de Roos *et al.* 1998, Hanski 1999, McCauley *et al.* 2000, Frank and Brickman 2000, 2001). For stability, the metapopulation system may require a spatial scale much larger than that of both predator and prey organisms (Kareiva and Wennergren 1995). Thus, fragmentation and insularisation has the potential to disrupt metapopulation structure and isolate individual subpopulations, which then have the potential to suffer from Allee effects (e.g. Kareiva 1987).

A potential example of predator-driven Allee effects mediated by habitat fragmentation is the situation where habitat fragments are in a matrix of human-altered habitat such as agricultural land. Generalist predators may "commute" into habitat patches from the surrounding matrix. Nonetheless, their population size is regulated by resources from the matrix rather than the habitat patches (i.e. they have no numerical response to prey in the habitat fragments). Under these circumstances, predation rates in a given patch are strongly related to patch size (or, more specifically, perimeter:area ratio; Angelstam 1986, Pasitschniak-Arts and Messier 1995). Models of this process show that a Type II functional response leads to a critical patch size below which prey go extinct – i.e. an Allee effect in prey (Cantrell *et al.* 2001).

Allee effects are not necessarily apparent in the dynamics of spatially structured populations unless data are collected at the spatial scale of the subpopulation rather than the metapopulation (Frank and Brickman 2000, 2001). Even then, the demographic consequences of component Allee effects due to predation will be eliminated by immigration while the metapopulation structure is intact. Even a small amount of connectivity between subpopulations may be sufficient to reduce extinction risk for each subpopulation significantly (Hill *et al.* 2002), so conservationists are likely to miss seeing potential Allee effects until the subpopulation is isolated, by which time it may be too late.

Large-scale disturbance: The definition of "large-scale" is relative to the scale of the prey population or metapopulation; such disturbances could include pollution, disease and climate change. Evidence for the destabilisation of predator-prey interactions by such large-scale disturbances is hard to find, but climate change has been shown to affect predator tendency to switch between prey types (functional response; Chown and Smith 1993), predator numerical response (Mckone *et al.* 1998), prey reaction to predators (Awmack *et al.* 1997) and prey trade-offs between microhabitat use and predation risk (Martin 2001).

A particularly important large-scale impact in aquatic systems is nutrient enrichment. In model ecosystems, enrichment can destabilise predator-prey interactions by increasing prey carrying capacity and thus reducing the strength of competitive negative density dependence in prey relative to positive density dependence caused by predation – the so-called "paradox of enrichment" (McCauley and Murdoch 1990, Persson *et al.* 2001). Essentially, this is another case of revealing latent predator-induced Allee effects in the system, by shifting the Allee threshold to a higher prey population density. Evidence for this in practice is equivocal (McCauley and Murdoch 1990, Persson *et al.* 2001).

However, the idea of predator-driven Allee effects in vulnerable prey species might help to clarify some of the ecosystem changes associated with eutrophication (Persson *et al.* 2001).

Introduced species: Several of the examples discussed above involve introduced generalist predators, which have wreaked havoc on indigenous faunas worldwide (Drake *et al.* 1989). In our examples, introduced predators act in concert with hunting and habitat destruction, which reduce populations below the Allee threshold. In reality, predation rates from introduced predators have often driven vulnerable prey to extinction in a density-independent manner. However, there may sometimes be a threshold population size above which prey can resist introduced predators (Sinclair *et al.* 1998, Gilchrist 1999, Cuthbert 2002).

Predicting predator-driven Allee effects in evolutionary time

One of the conclusions that I emphasise in this paper is that Allee effects do not necessarily arise as a consequence of specific life history characteristics of a given species. Instead, they arise naturally out of general ecological processes such as predation. However, the life history of the prey population should still to some extent be a predictor of the likelihood of Allee effects in general. It is an old idea that species evolve in response to historic population densities (MacArthur 1962, Mueller 1997). Species whose populations are naturally small or sparse (either chronically or periodically) should therefore evolve some resistance to Allee effects, which might manifest itself in the life history (low mortality, bet-hedging) or the ecology (density dependent anti-predation strategies, high dispersal rates).

On the other hand, populations of prey species that are naturally large and stable may not be resistant to becoming rare. So Allee effects of any kind should (paradoxically) be intrinsically more likely in populations that are "naturally" (in the absence of direct or indirect human intervention) large and stable, because they have not had the opportunity to evolve any resistance to rarity, whether that be low density or small population size. This argument is related to the old argument about *r*- vs. *K*- selection (MacArthur 1962). Certainly so-called *K*-selected species with naturally stable populations and low intrinsic rates of population increase might be expected to suffer from Allee effects if their populations are reduced, whether it results from predation or other factors. However, many of the examples presented above are from species that are not considered strongly *K*-selected (e.g. various fish species, marine molluscs, colonial seabirds), so the idea of "resistance to rarity" is broader than the idea of *K*-selection. The idea is supported empirically by selection experiments on *Drosophila melanogaster*, where populations raised at consistent high density show a reduction in population growth rate at low density (Mueller 1997). Note also that the models presented in Chapter 2 indicate that Allee effects will be hard to find in the field in *K*-selected species.

The argument can be extended to predator-prey systems in the sense that predators on large, stable prey populations are not under strong selection pressure for prey switching, while prey in large stable populations are not under strong selection pressure for developing (for example) spatial refuges from predation or other density-dependent predator avoidance tactics. Thus predator-prey systems that have not historically experienced low prey density may lack behavioural or ecological mechanisms to avoid a predator-driven Allee effect. There is, as far as I know, no empirical evidence for or against this idea.

Final thoughts

Perhaps due to their name, Allee effects have until recently been treated in the ecological literature almost as a curiosity (Dennis 2002). Our hope in writing this paper is twofold. Firstly, I would like to encourage those who work empirically on Allee effects to look beyond systems such as broadcast spawners and cooperative breeders. Allee effects need not be driven by peculiarities in a species life history, but rather are a general statement of positive density dependence in prey dynamics at low density that can therefore be generated by general ecological processes such as predation. Secondly, I am trying to integrate some of the large body of theory on positive density dependence and stability in ecological interactions into work on Allee effects and practical conservation.

Predator-driven Allee effects are not quite the same conceptually as "standard" Allee effects driven by some feature of prey life history, in that they are not an intrinsic part of prey dynamics that are inevitable in all prey populations. A prey species may suffer predation-induced Allee effects in some places or times but not others (for example, predator-driven prey cycles could be regarded as temporary predator-driven Allee effects). I do not want to overstate the case for predator-driven Allee effects; not all, or even most, predator-prey systems are likely to suffer from Allee effects, and anthropogenic change may often reduce rather than increase predation pressure (Tomiatojc *et al.* 1984, Dayton *et al.* 1998, Laurance *et al.* 2002). Nonetheless, predator-driven Allee effects provide an extinction mechanism that is potentially applicable in scenarios in which conservationists are involved: heavily impacted or exploited populations, or populations in fragmented habitats, for example.

Allee effects due to factors such as broadcast spawning or cooperative breeding are, in principle, relatively easy to predict. Unfortunately, this is not the case with predator-driven Allee effects. However, if predation by generalist predators is important in driving prey population dynamics ecologists might be able to infer that an Allee effect is a risk if the system is disrupted by exploitation or habitat loss. In general, I believe that, to apply the precautionary principle, conservation biologists should expect non-linear and threshold effects in exploited or degraded populations.

Finally, predator-driven Allee effects may provide a new concept (or at least, a new view on an old concept) that is helpful in clarifying issues such as ecosystem response to anthropogenic disturbance (pollution, eutrophication, fragmentation). Ecosystems can be regarded (to some extent) as a series of interconnected predator-prey relationships with different types of stabilising factors; and in fact such a modelling framework may not be invalid even in systems which are on the face of it much more complicated (Murdoch *et al.* 2002). Some systems, such as rangelands, lakes and coral reefs, have shown abrupt transitions to alternative stable states, with predation by herbivores or fish as important mediating factors (Noy-Meir 1975, Scheffer *et al.* 2001). Allee effects predict thresholds and non-linear population dynamics and may provide a link between population, predator-prey and ecosystem dynamics in these cases.

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FIGURES

Fig. 1

The three major types of functional response, and the corresponding prey survival probability curve. The Type I functional response (Fig. 1A) and Type III functional response (Fig. 1E) create prey survival curves which are positively density dependent only at high density (Figs. 1B, 1F). The Type II functional response (Fig. 1C) creates a survival curve with maximum positive density dependence at low density, i.e. an Allee effect (Fig. 1D).

Fig. 1A

Type I functional response

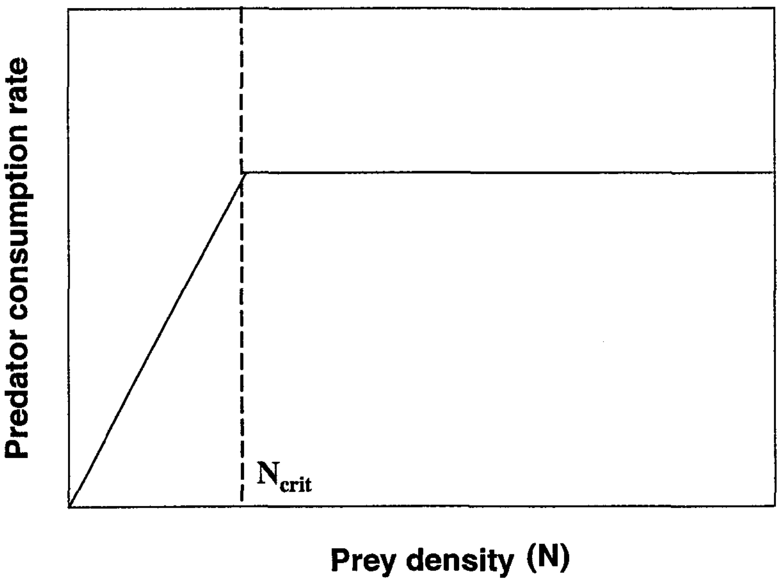


Fig. 1B

Prey survival probability as a result of predation with a Type I functional response.

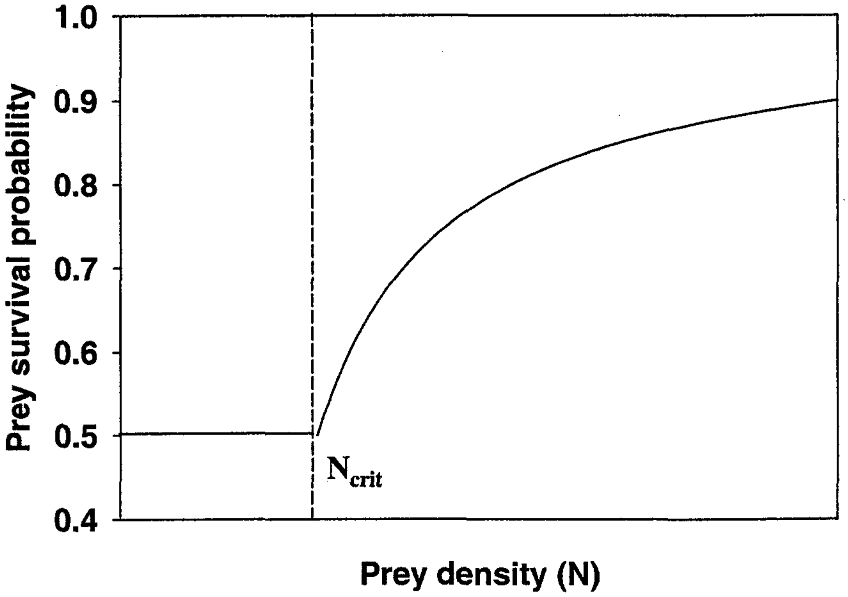


Fig. 1C

Type II functional response.

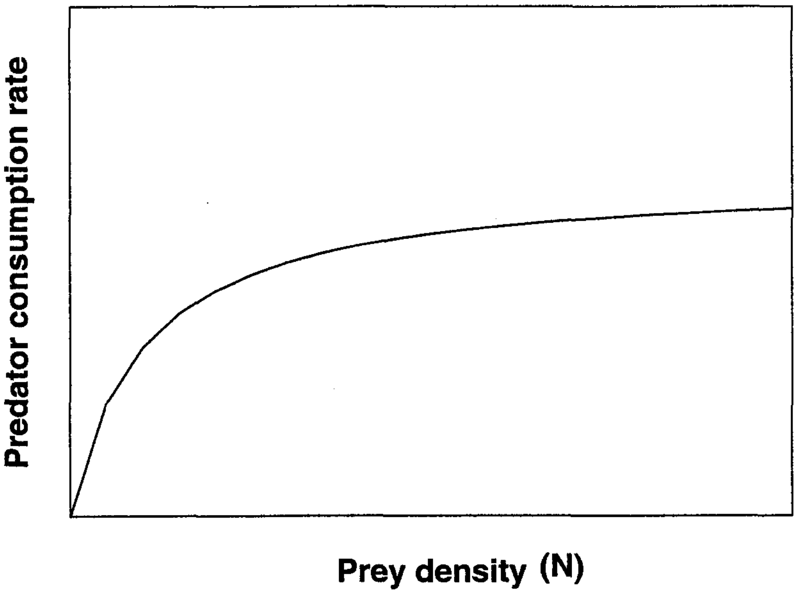


Fig. 1D

Prey survival probability with a Type II functional response.

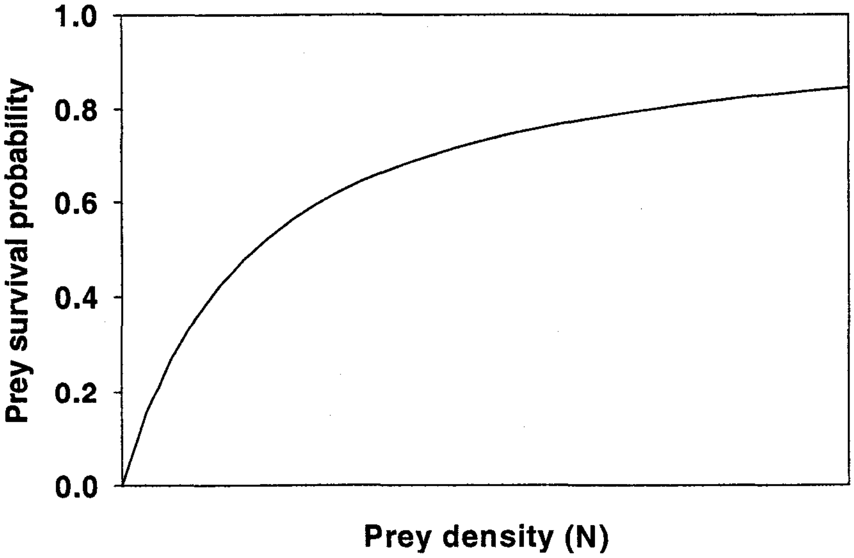


Fig. 1E

Type III functional response.

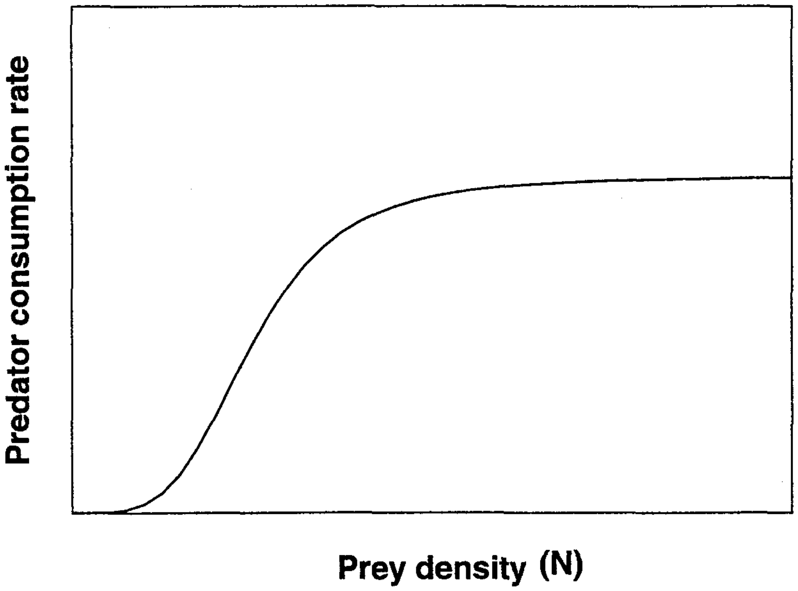


Fig. 1F

Prey survival probability with a Type III functional response.

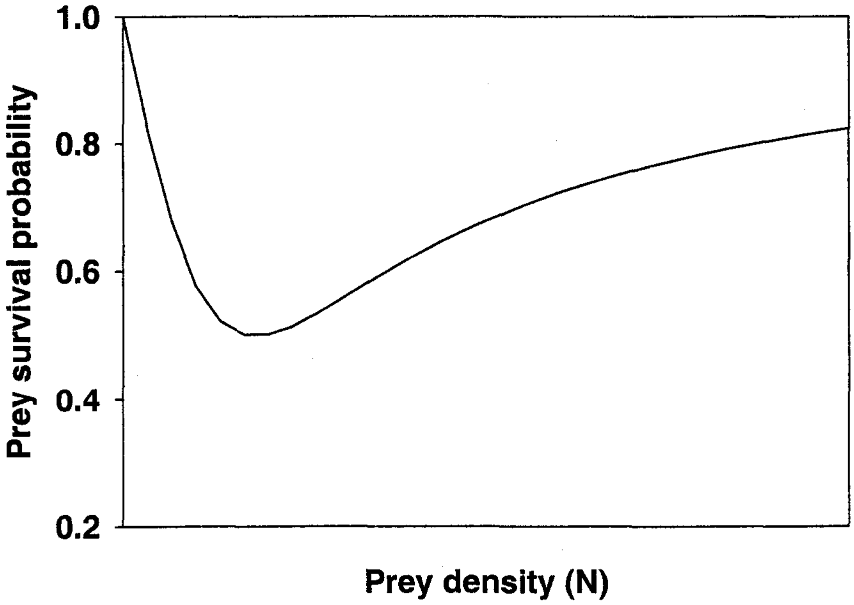


Fig. 2

Different types of numerical / aggregative response combined with a Type II functional response ($\delta = \gamma = 1$).

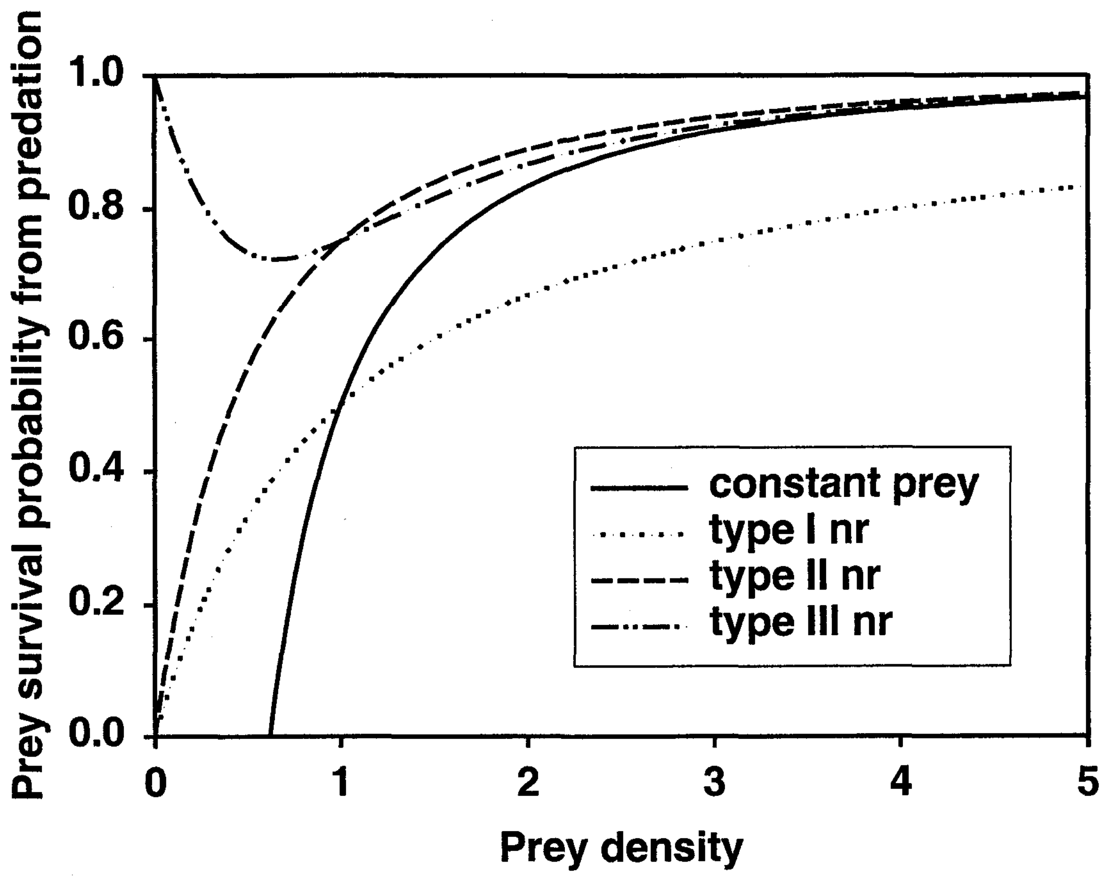


Fig. 3

Contours of equal prey survival probability as a function of prey numbers (*N*) and predator numbers (*P*) ($\delta = \gamma = 1$).

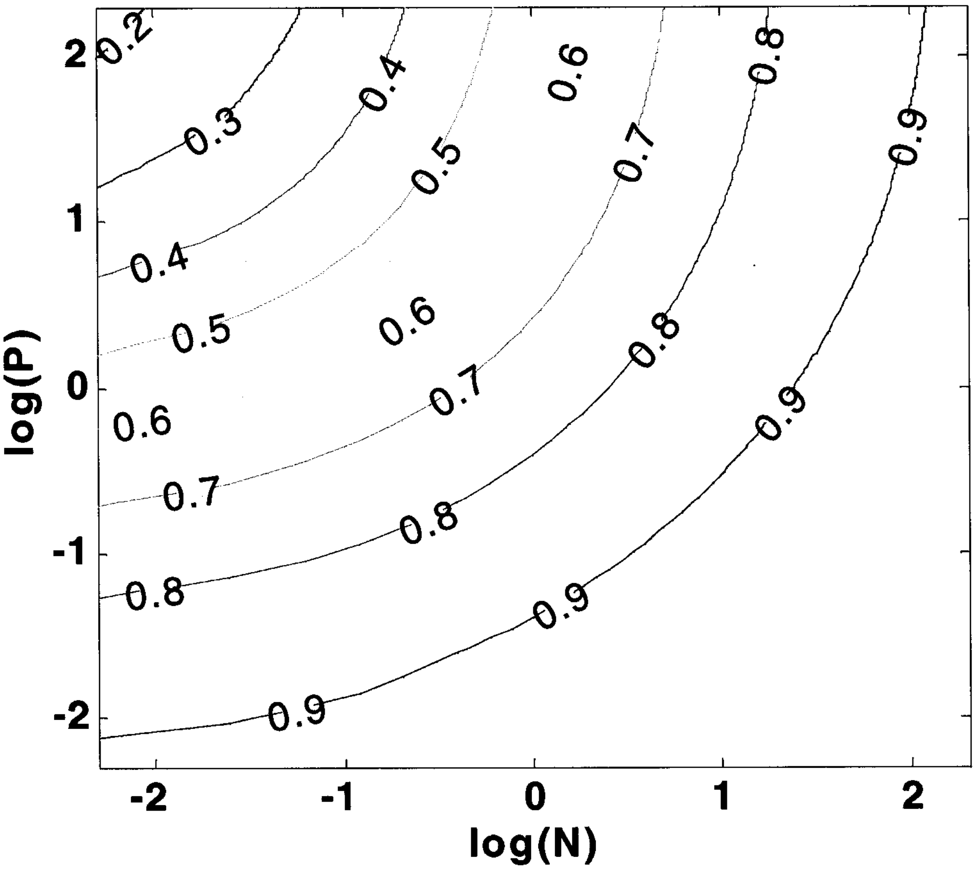
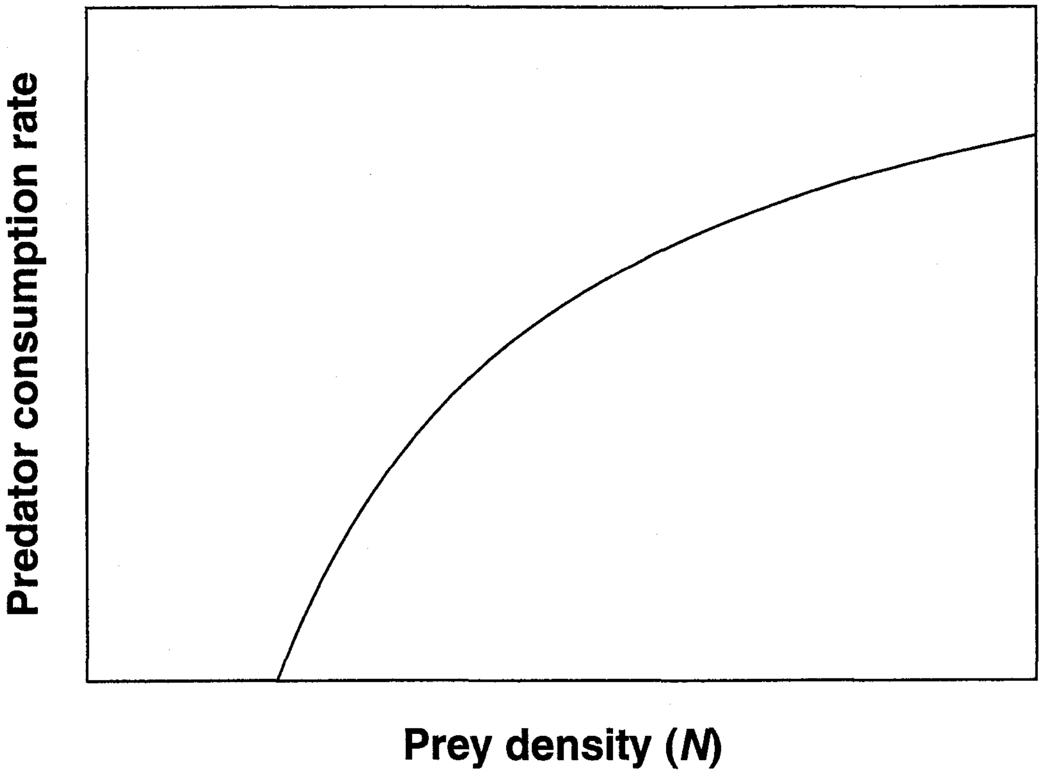


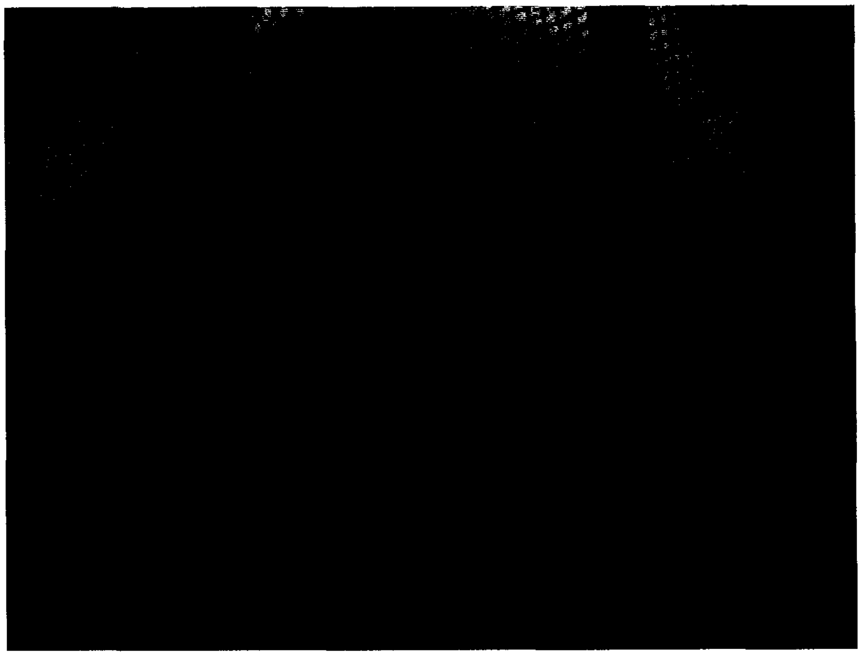
Fig. 4

A Type II functional response with a spatial refuge.



VITA

JOANNA CLARE GASCOIGNE



I was born on May 4th 1971, in Leamington Spa, England, but brought up in St. Andrews, Scotland, where I went to secondary school at Madras College. I started at Corpus Christi College, Cambridge, in 1990 and graduated in 1993 with a degree in Zoology. In 1994 I completed an M.Phil. in Environment and Development at the University of Cambridge. After a year in Brussels and four years working for a fisheries consultancy in England, I came to Virginia in July 1999 to start a PhD at the School of Marine Science, College of William and Mary.