

A model for range expansion of coastal algal species with different dispersal strategies: the case of *Fucus serratus* in northern Spain

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ABSTRACT: A model was used to investigate the nature of the distributional boundary of the brown alga *Fucus serratus* in northern Spain. The model explored the colonisation of a shore by invaders with contrasting dispersal modes: an exponentially bounded mode, as an example of short-range dispersal; an extreme, long-range dispersal mode; and a mixed mode with variable proportions of short- and long-distance dispersers. The organisms were dioecious, had a limited life-span and reproduced only when plants of different sexes were within a short distance. For species with exponentially bounded dispersal and interannual variability in the environment, the model reproduced the basic features of the distribution of *F. serratus*: survival and reproduction beyond the distributional boundary, sharp boundary and displacements of the boundary through time. Species with exclusively long-range dispersal exhibited continually accelerating rates of spread under favourable conditions. However, long-range dispersers might fail to invade or become extinct when exposed to a short series of unfavourable years. Regional abundance is critical for the persistence of local populations. For long-range dispersers, no distinct distributional boundary was recognised. At the opposite extreme, invaders with exponentially bounded dispersal had small and decelerating rates of spread, high resistance to disturbances and distinct distributional boundaries; the persistence of populations mainly relies upon local abundance. Mixed strategies, with most of the propagules having exponentially bounded dispersal and a small fraction having long-range dispersal, appear to be the superior strategy; they combine rapid colonisation rates and high resistance to disturbances. The combination of Allee effects and propagule pressure (i.e. number of propagules arriving at a given locality) explains the differences among dispersal strategies.

KEY WORDS: Allee effect · Dispersal · Environmental variability · *Fucus serratus* · Individual-based model · Invasion · Propagule pressure · Spatially explicit model

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INTRODUCTION

On the shores of northern Spain the coastal communities exhibit a conspicuous change (van den Hoek 1975, Anadón & Niell 1981, Anadón 1983). Algal floras of the north-west have affinities with floras of more northern European latitudes, while floras of the north-east have southern affinities (van den Hoek 1975). Among the species exhibiting an unequal distribution along the shore is *Fucus serratus*. *F. serratus* is a large perennial brown macroalga abundant on moderately

exposed European rocky shores (e.g. Lüning 1990). *F. serratus* has a distinct and sharp boundary. From a more or less intermediate point on the northern shore, it dominates localities to the west and is totally absent from all localities to the east. The transition from zones of abundance to absence is very abrupt. However, experimentation (Arrontes 1993) showed that transplanted specimens of *F. serratus* survive, grow and reproduce beyond the distributional boundary. There is also evidence that the boundary has moved east- and westwards during the 20th century, expanding

and contracting, respectively, the range of the species (Miranda 1931, Fisher-Piette 1957, Anadón 1983). At present, the boundary is moving eastwards, and, thus, *F. serratus* is expanding its range (Arrontes 2002). As in many other marine algae, the large-scale distribution of *F. serratus* may be reasonably well described in terms of thermal tolerances. Coincidence of distributional limits and isotherms of temperatures crucial to some stage of the life history is evident for many species (van den Hoek 1982, Breeman 1988, Cambridge et al. 1990). The location of the boundary might be set by the effects that environmental factors may have on survival, reproduction, growth, or the outcome of interspecific interactions. However, at smaller scales, the precise position of the boundary might be mediated by other processes, in particular dispersal ability (Arrontes 1993, 2002). In the present paper, I use a simulation model to explore whether limited dispersal in *F. serratus* coupled with environmental fluctuations and a gradient in survival along the shore are, together, responsible for survival beyond the boundary, the sharp distributional limit and the displacement of boundaries. This path of inquiry is based on evidence of limited dispersal of *F. serratus* (van den Hoek 1987, Arrontes 2002), the existence of a temperature gradient along the northern shore of Spain (Botas et al. 1990, SATMER 1990), which affects the survival of *F. serratus* embryos (Arrontes 1993), and the interannual variability of the summer upwelling conditions responsible for the temperature gradient (Blanton et al. 1984).

The first models used to investigate the spread of organisms used reaction–diffusion (R–D) equations (Skellam 1951). The simplest R–D models combine a Gaussian spatial distribution of dispersers (the diffusive component) with exponential growth of the spreading population (the reactive component). Skellam's (1951) model appears to be, by far, the most used invasion model, and has successfully described the patterns of expansion for a wide range of species (e.g. Lubina & Levin 1988, Hengeveld 1989, Andow et al. 1990, Levin 1992), though in some situations it can grossly underestimate the rates of spread. With R–D models, range expansion only occurs by recruitment of propagules in the immediate vicinity of the parent population (termed 'neighbourhood diffusion' by Shigesada et al. 1995). The spread is characterised by a distinct population front of constant shape moving across the new habitat (i.e. travelling wave) at a constant speed. R–D models, however, have been criticised on the basis of the limited realism of the underlying assumptions, particularly the dispersal probability function (e.g. Kot et al. 1996), or because they ignore stochastic effects on population growth (Higgins et al. 1996). Dispersal distances of propagules are, in most

cases, leptokurtic rather than Gaussian, and are frequently fitted with negative exponential curves (see Kot et al. 1996 for references). The consideration of exponentially bounded tails in the distribution of propagules also leads to constant-speed travelling-wave solutions (Kot et al. 1996), but with faster rates of range expansion. In some cases, however, the species may exhibit a mixed mode of dispersal, when occasional or rare long-range dispersal events occur. Good examples may be found among marine algae. During calm periods or in average conditions, most propagules settle within a few metres of the adult plants; however, drift currents or very rough seas may transport detached floating algae and propagules over considerable distances, thus seeding distant localities (Anderson & North 1966, Deysher & Norton 1981, Reed et al. 1988, Santelices 1990, Norton 1992). Of course, mixed dispersal strategies are not exclusive to marine algae, and may be observed in a wide variety of organisms (e.g. Hengeveld 1989, Andow et al. 1990, Clark 1998). Shigesada et al. (1995) demonstrated that modifying the R–D model to consider the mixed mode of dispersal (also known as stratified diffusion) may generate continually accelerating rather than linear range expansions.

An alternative to R–D models was used by Kot et al. (1996). They focused on integrodifference equations to re-examine the *Drosophila* dispersal data of Dobzhansky & Wright (1943). Integrodifference equations allow the consideration of very different probability density functions for dispersing propagules. Kot et al. (1996) found that fat-tailed distributions of dispersal distances provided the best fit to the empirical data and predicted a continually accelerating invasion. A similar result was obtained by Clark (1998), who used the same equations and a mixed mode of dispersal, resulting in a fat-tailed distribution, to explain the fast spread of trees at the end of the Pleistocene.

With low numbers of specimens, as is the case for initial stages of invasion, random events may lead to variability in the possible outcomes of the invasion process. Stochastic models are the best choice if we consider that spatial and temporal variability may also affect survival and spread, or that rare long-distance dispersal may generate patchiness in the spread of a population (Lewis & Pacala 2000). Stochastic individual-based models (DeAngelis & Gross 1992, Judson 1994) analyse the fate of every individual in a population through relevant stages of the life cycle. Because the unit of the model, the individual, has an obvious biological and ecological sense, predictions of individual-based models are very intuitive. Spatial and temporal variability in dispersal processes may be incorporated into spatially explicit simulation models (Vance 1984, Dunning et al. 1995). Spatially explicit models specify

the exact position of each individual in the experimental landscape and their interactions with the precise features of the location. The extension of individual-based models to spatially explicit models is easy. Factors relevant for the spread of invading organisms, such as habitat-specific survival, fecundity, or dispersal, and temporal variability in the quality of the habitat may be easily incorporated into these models. Higgins et al. (1996) compared the predictions of a R–D model and a spatially explicit, individual-based simulation model and found important differences between them, the R–D model having a reduced predictive ability.

I used a spatially explicit, individual-based model to explore how different modes of dispersal influenced colonisation along a 1-dimensional shore. The model used random simulations to analyse the fate of every propagule and specimen on the experimental shore. The dispersal strategies analysed were: an exponentially bounded mode, as an example of short-range dispersal; an extreme, long-distance mode; and a mixed mode with variable proportions of short- and long-distance dispersers. In a shore context, exponentially bounded dispersal might be found in non-floating macroalgae with large and heavy propagules (as is the case for *Fucus serratus*) or in brooding benthic invertebrates. In both cases, the density of settled propagules declined exponentially with distance from the parents. A long-distance mode might be associated to invertebrates with planktotrophic larvae. Finally, a mixed mode might occur in macroalgae with large propagules, but in which mature thalli float and survive after detachment (e.g. *Sargassum muticum*). I considered a gradient in survival along the shore and interannual variability in the environment. For expanding species with different dispersal modes, I first evaluated the extent of shore colonisation, including the sensitivity of the invader to unfavourable periods and the ability to invade a shore, and then I described the patterns of colonisation associated to each dispersal mode, including the existence and shape of distributional boundaries.

MATERIALS AND METHODS

Simulation models. The simulated shore is 1-dimensional and consists of 1000 adjacent cells. A total of 20 consecutive cells define 1 locality. The shore may be continuous, with no gaps between adjacent localities, or discontinuous, with gaps between localities. Gaps are groups of cells in which survival of both propagules and adults is 0. For *Fucus serratus* and other intertidal species, gaps might be sandy stretches of shore or very exposed headlands.

The invader is dioecious, with a sex ratio of 1:1, and has a maximum life-span of 5 yr. The population has an age structure. Propagules enter Age Class 0+ when released. Specimens reproduce immediately before completing their first year of life, when they are still in the 0+ class, and always reproduce at the end of each age class. A probability of death is assigned to each age class. Mortality only occurs between reproductive periods. Probability of death in Age Class 5+ (after the fifth reproductive period) is 1. The cell-carrying capacity of 20 specimens is identical for all cells. Density-dependent mortality only occurs in Age Class 0+, before the specimens reach their first reproductive season. No variation in fecundity with age is considered. The number of propagules produced by a female in each reproductive season was fixed at 100. To produce viable propagules at least 1 male and 1 female must be present in the same cell; provided that this assumption is met, all females produce propagules.

An environmental gradient exists along the shore. The major influence of the gradient is on propagule survival to the age of first reproduction and, to a lesser extent, on adult survival. Maximum survival of propagules is highest at the first locality at one end of the shore (hereafter the favourable end) and decreases linearly towards the opposite end (the unfavourable end); in the simulations it is calculated as:

$$PS_i = 0.2 - 0.2(i - 1)/n$$

where PS_i is maximum survival of propagules at locality i , 0.2 is the fixed absolute maximum probability of survival of propagules for all simulations and n is the number of localities forming the shore. Survival of propagules at each cell within a given locality is obtained by multiplying locality survival (PS_i) by a random number between 1 and 0.1 at intervals of 0.1. Thus, no trend of survival exists among cells within each locality, but survival of propagules randomly varies among cells between 1 and 0.1 times the maximum assigned to the locality. Survival of adults along the shore also decreases linearly and is obtained as:

$$AS_{ij} = \text{Max}A_j - 0.15(i - 1)/(n - 1)$$

where AS_{ij} is maximum survival at locality i of Age Class j and $\text{Max}A_j$ is the absolute maximum survival for Age Class j (fixed at 0.8, 0.7, 0.3, 0.2 and 0 for Age Classes 1+ to 5+). Survival of adults does not vary among cells within localities. With these arbitrary survival probabilities for propagules and adults, the observed rate of increase at favourable localities is close to the rate of increase of expanding natural populations of *Fucus serratus* when invading a new locality (Arrontes 2002).

The environment varies from one reproductive period to the next and influences both survival of

Table 1. *Fucus serratus*. (A) Maximum survival of adults at both extreme localities of the shore gradient. For each Age Class and type of year range of values are maximum survival in the most favourable (left) and in the most unfavourable localities (right). (B) Parameters of the Laplace distribution for the 3 exponential dispersal abilities, each of which is the combination of 4 possible dispersal scenarios

(A)	Favourable years	Intermediate years	Unfavourable years
Age 1+	0.80–0.65	0.778–0.611	0.750–0.563
2+	0.70–0.55	0.667–0.500	0.625–0.438
3+	0.30–0.15	0.222–0.056	0.125–0
4+	0.20–0.05	0.111–0	0
5+	0	0	0
(B)	Scale parameter, <i>b</i>	Probability of <i>b</i>	
Long range (D1)	6	0.50	
	2	0.30	
	1.15	0.15	
	0.75	0.05	
Medium range (D2)	3	0.05	
	2	0.40	
	1.15	0.40	
	0.75	0.15	
Short range (D3)	2	0.05	
	1.15	0.40	
	0.75	0.40	
	0.6	0.15	

propagules and adults. An environmental index (E.I.), a number between 0.05 and 1 at 0.05 intervals, is supplied for each reproductive period. For each year, survival of propagules is obtained by multiplication of cell survival by the E.I. assigned to that year. For adults, 3 cases are considered. Case 1 is for favourable years (E.I. ≥ 0.7); in this situation, adult survival is not affected. Case 2 is for intermediate years ($0.3 < \text{E.I.} < 0.7$), and adult mortality ($1 - AS_{ij}$) of Age Class *j* at locality *i* is increased by a factor of 1.11. Case 3 is for unfavourable years (E.I. ≤ 0.3), and adult mortality is increased by a factor of 1.25. Depending on the year, the maximum life-span may be < 5 yr in some (or all) localities (see extreme values in Table 1).

For short-range dispersal, the distance travelled by propagules was approached by a Laplace (double exponential) distribution. The Laplace distribution has the probability density function:

$$f(x) = \frac{\exp\left(-\frac{|x-a|}{b}\right)}{2b} \quad -\infty < x < \infty$$

where *a* is the mean (in this case, number of the cell of origin of the propagule cloud) and *b* is the scale parameter. A small *b* implies that most of the propagules settle in the immediate vicinity of the parent

plants, while a large *b* implies longer distance dispersal. The dispersal model assumes an equal probability of dispersal to both sides of the cell of origin. For each propagule, 4 possible dispersal scenarios were considered in the simulation model. Each scenario simulated different conditions of water movement, from calm waters (smallest *b*) to very rough seas (largest *b*), and, thus, 4 different Laplace functions were considered. A probability was assigned to each of the 4 conditions for dispersal. Three different dispersal abilities simulated short-, medium- and long-range exponential dispersal. Each of them consisted of a set of 4 different dispersal scenarios (see Table 1 for values).

Two additional models considering long-range dispersal were also explored. One of them consisted of a uniform distribution of propagules in cells: irrespective of the origin of the propagule, the probability of settling at a given cell was identical for all cells on the shore. The second was a mixed model: a variable fraction of the propagules in a propagule cloud was considered to follow 1 of the 3 exponential dispersal abilities, while the remaining propagules followed the uniform distribution. The mixed model gives a quasi-exponential distribution of propagules in cells with fat tails.

For most simulations the source of the invaders is a population at the first cell (at the favourable end of the shore) at the carrying capacity, with an exact 1:1 sex ratio and entering their first reproductive period. This population persists during the whole simulation, and, thus, a small but permanent source of propagules exists. It is called the seeding population. Other simulations began with the whole shore colonised at the carrying capacity and/or limited persistence of the seeding population.

An Allee effect is implicit to the model. The Allee effect was defined by Stephens et al. (1999) as: 'a positive relationship between any component of individual fitness and either numbers or density of conspecifics'. The model considers a dioecious species and imposes restrictions on distances between specimens of the 2 genders to reproduce. Failure to settle close enough to conspecifics to allow reproduction in dioecious species is one of the simplest Allee effects. Another manifestation of the Allee effect is demographic stochasticity at low population numbers, which is also included in the model.

A computer program written in Turbo Pascal 7.0 (Borland International) was used to carry out the simulations. A typical simulation run consisted of 1000 reproductive seasons (years). To test for each specific effect, 50 runs were performed. At the beginning of each run, all variables and parameters are set to the original values and the same environmental file is used. The only difference among runs is the survival of propagules within localities, which are recalculated.

The output is the mean progress of the invasion with time (percent of the shore colonised by the invading species \pm 95% confidence interval). See Appendix 1 for operational steps.

Conditions of experimental simulations. The effect that different environmental indexes might have on the extent of range expansion was assessed by exploring how the E.I. influenced the theoretical net reproductive rate (deterministic) of the expanding population at each locality along the experimental shore. It was assumed that propagules do not disperse and that they remain at the parent cell. The net reproductive rate at locality i (R_{0i}) was calculated as:

$$R_{0i} = \sum_j S_{ij}F$$

where S_{ij} is the probability of survival to the j reproductive period (includes both propagule and adult survival) at locality i and F is the number of propagules produced by an individual in each reproductive period. Since a sex ratio of 1:1 was considered, F is half the number of propagules produced per female. A deterministic shore was considered, and, therefore, the cell influence on propagule survival was fixed at 0.55 (average cell effect). For each E.I., R_{0i} and the boundary locality were obtained. The boundary locality was defined as the last locality in which $R_{0i} > 1$. This gives a crude estimation of the average maximum theoretical range expansion for the species in a given constant environment.

Extent of shore colonisation. Three aspects were considered. (1) Maximum range expansion in a favourable environment was examined. The environment had an average E.I. of 0.89 and annual values always >0.5 . The mixed mode considered 50% of the propagules with uniform dispersal and 50% with medium-range exponential dispersal. Shores were continuous or with gap sizes of 5, 10 and 15 cells. (2) The effect of unfavourable periods on the distributional range was examined. At the start of the simulations the shore was completely colonised by the species. Two randomly varying environments were used. The E.I. varied at random between 0.5 and 1 at one of them and between 0.25 and 0.75 at the other. Both environments included 2 distinct periods of 10 seasons, 1 period with very unfavourable (E.I. < 0.15) and another period with very favourable (E.I. > 0.9) conditions. The shore was discontinuous, with a gap size of 5 cells. (3) Probability of invasion failure was considered. The environment had distinct periods of unfavourable and favourable conditions. Uniform dispersal, 3 mixed strategies (with proportions of uniformly dispersed propagules of 0.5, 0.2 and 0.1) and 3 exponential dispersal modes were used. The shore was discontinuous, with a gap size of 5 cells. The founding

population was only kept for the first 25 yr. An invasion failed when the expanding population disappeared from the experimental shore. The number of failed invasions was recorded for 500 runs.

Patterns of colonisation. The pattern of variation of range expansion with time was explored for the exponential mode and several mixed modes with several proportions of uniformly dispersed propagules (from 0.0001 to 0.1). The shore was discontinuous with a gap size of 5 cells, and only the favourable environment was considered. The existence and shape of a distributional boundary was investigated for a continuous shore and the favourable environment. The mixed mode considered proportions of uniformly dispersed propagules of 0.1, 0.01 and 0.001. Simulations were stopped when the total number of specimens on the shore was 25% of the global carrying capacity of the shore. Each simulation consisted of 25 runs. Then, the mean number of specimens at each locality was calculated.

RESULTS

For each E.I., the deterministic net reproductive rate of the population decreased almost linearly along the shore. The theoretical extent of the shore that may be colonised, estimated as the last locality in which $R_{0i} > 1$, exhibited little variation for years with intermediate to large E.I.s: from 75% for an E.I. = 0.35 to 92% for E.I. = 1 (Fig. 1). Only in unfavourable years did the deterministic boundary of the distribution show considerable variations with different E.I.s. None of the localities may be colonised with the lowest E.I. (0.05); 20%, with E.I. = 0.1; and 56%, with E.I. = 0.2.

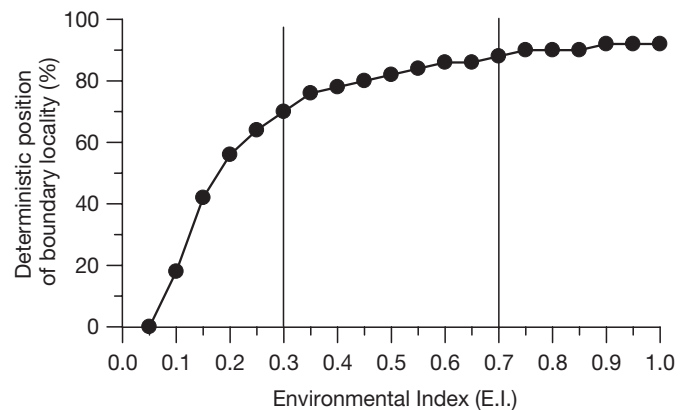


Fig. 1. Theoretical maximum extent of shore colonisation, expressed as the position of the boundary locality, as a function of the environmental index. Vertical lines separate the arbitrary distinction of (from left to right) unfavourable, intermediate and favourable environments

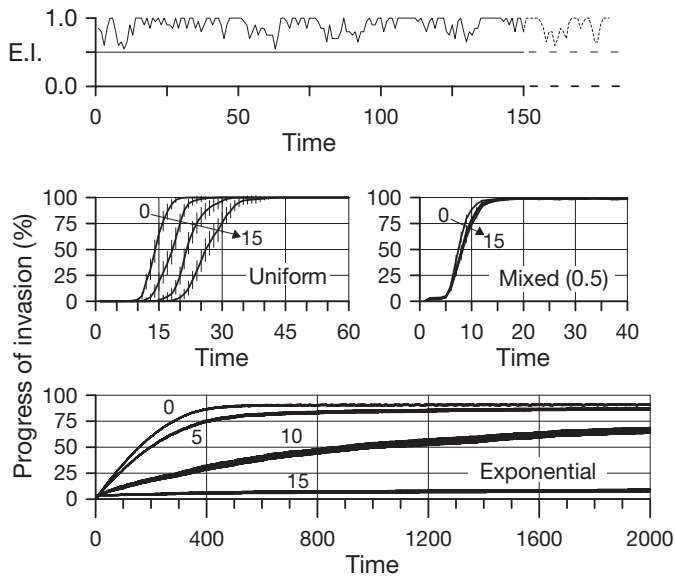


Fig. 2. Spread for the 3 dispersal modes in a favourable environment. The environmental index (E.I.) for the first 150 reproductive seasons is presented in the upper panel. Mixed (0.5) shows uniform dispersal for 50% of propagules and exponential medium-range dispersal for the rest. Numbers are gap sizes of 0 (continuous shore), 5, 10 and 15 cells. Progress of invasion is given as mean percentage of shore colonised. Error bars: $\pm 95\%$ confidence interval ($N = 50$ runs). The thickness of the lines for the exponential mode represents mean $\pm 95\%$ confidence interval

Extent of shore colonisation

Colonisation of a shore under favourable environmental conditions was faster with the mixed dispersal strategy (Fig. 2). No effect of increased gap sizes was observed. Colonisation was a little slower with uniform dispersal, though all localities were occupied after 45 reproductive seasons (years). Spread was slower on shores with larger gap sizes. The whole shore was occupied with uniform and mixed modes of dispersal. With the exponential mode, the spreading population reached an asymptote. Gap size was crucial to determine the extent of the colonisation process. When the shore was continuous, the extent of colonisation was very close to the deterministic boundary of the average E.I. (0.89). With increased gap sizes, a lower asymptote was reached and an increasing significant fraction of the shore remained free of the spreading species.

When simulations were initiated with the whole shore colonised at the carrying capacity, both uniform and mixed modes of dispersal allowed almost complete colonisation of the experimental shore, beyond the deterministic limit. With the exponential mode, however, the expanding species stabilised in a locality near the deterministic distributional limit. Short periods of extreme, unfavourable conditions had contrasting

effects on the 3 dispersal modes (Fig. 3A,B). When the E.I.s fluctuated between 0.5 and 1, both for uniform and mixed dispersal, the expanding species disappeared from the shore, except for the seeding population. Recovery was very fast with the mixed strategy, and took more time and was more unpredictable with the uniform mode. An expanding species with the exponential mode did not disappear from the shore during the period of unfavourable environmental conditions, but recovery was slow, and the species remained well below the theoretical distributional limit

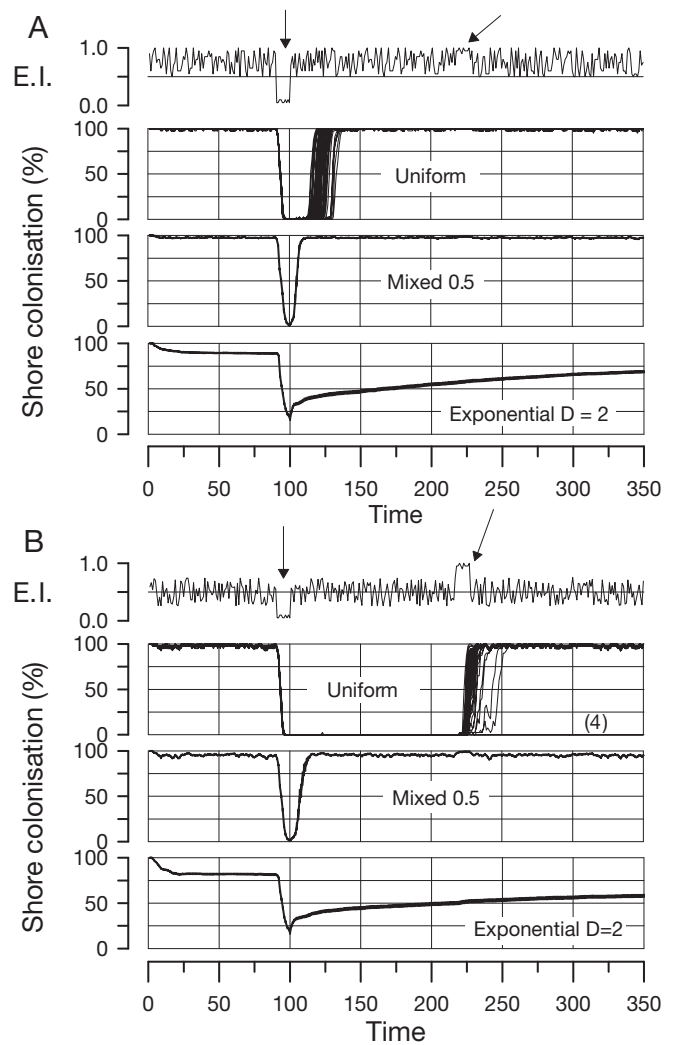


Fig. 3. Effects of short periods of favourable and unfavourable environments on the extent of shore colonisation. Mixed (0.5) as in Fig. 2; exponential ($D = 2$) is a medium-range exponential dispersal: (A) environmental index (E.I.) randomly variable between 0.5 and 1 and (B) E.I. randomly variable between 0.25 and 0.71. For both Panels A and B, the upper graphs represent variation in the E.I. with time. Arrows indicate sequences of extreme E.I.s. For uniform dispersal, lines are individual runs and the number in parentheses represents runs that failed to recolonise. For mixed and exponential dispersal, line thickness as in Fig. 2

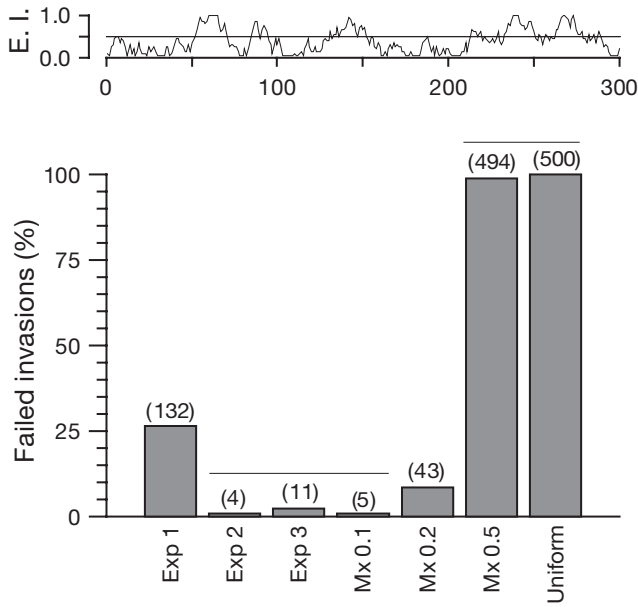


Fig. 4. Percentage of failed invasions, depending on dispersal mode, when the environment is unfavourable (upper panel) and the seeding population is restricted to the first 25 yr (Exp 1 to Exp 3: long- to short-range exponential modes; Mx0.1 to Mx0.5: mixed modes with 10 to 50% of propagules with exponential dispersal, the remaining propagules with medium-range exponential dispersal). Numbers are failed invasions (out of 500 runs). Horizontal lines above bars group dispersal modes that were not statistically significant. Five Chi-squared tests were carried out, and significance was set at a probability of 0.01 to cope with the increase in Type I error due to multiple pairwise comparisons

for a long time. In a fluctuating environment, between $E.I. = 0.25$ and $E.I. = 0.75$, the species with the uniform mode was unable to recolonise after extreme, unfavourable conditions. Only when a short period of favourable conditions occurred did the species expand again. Variability existed among individual runs; in 4 out of 50 runs the species did not recolonise the shore.

When the expanding species was under unfavourable environmental conditions and the founding population was kept for a short time, long-range dispersal modes had the highest probability of failure (Fig. 4). All or most invasions failed for the uniform and mixed 0.5 dispersal modes. The most successful strategies were mid- and short-range exponential dispersal and the mixed model with a 0.1 proportion of uniformly dispersed propagules.

Patterns of colonisation

The rate of colonisation was significantly affected by the fraction of propagules with uniform dispersal (Fig. 5). From a decelerating rate of spread for pure

exponential dispersal, increased rates of spread were observed at increased fractions of propagules with uniform dispersal. With very low fractions (1 in 10 000), no differences between the mixed mode and the pure exponential mode existed (results not presented). Differences in the spread rate became apparent when the fraction with uniform dispersal in the mixed mode was as low as 5 propagules in 10 000. For all the mixed dispersal strategies considered, increase in the colonisation rate was delayed for a variable number of reproductive periods. Irrespective of the fraction of propagules with uniform dispersal, there is a common part in all the colonisation curves. This common part is very small for large fractions of uniformly dispersed propagules (only during a few reproductive periods) and increases for diminishing fractions. Important differences between runs existed for the intermediate mixed dispersal strategies, the mean being a poor descriptor of the progress of spread.

A distinct and sharp boundary was observed for the exponential mode of dispersal (Fig. 6A). Specimens concentrated at the favourable end of the shore, where localities were occupied at the carrying capacity. As a consequence of the environmental gradient, the rate of shore colonisation decreased as spread progressed. A clear decelerating travelling wave can be recognised. For the uniform dispersal mode, the species was present on the whole shore (Fig. 6B). The abundance at each locality decreased linearly towards the unfavourable end. The abundance of the species was proportional to the average survival at each locality

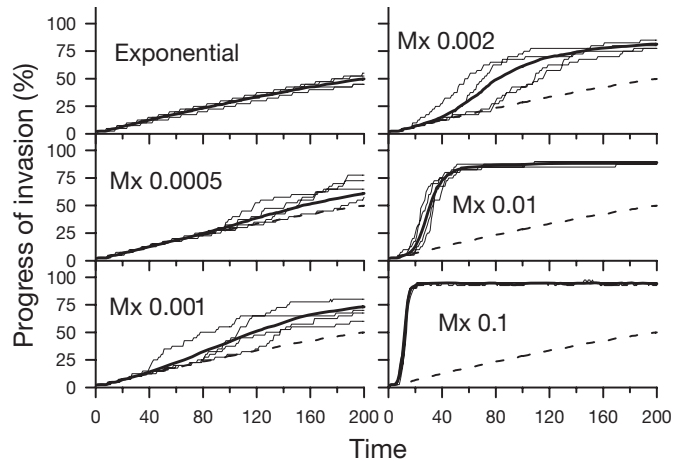


Fig. 5. Effect of the increasing proportion of uniformly dispersed propagules in the mixed model. The thick lines are the means of 50 runs, the thin lines are samples of individual runs and the discontinuous lines are the average range-expansions for the exponential mode. Mx0.0005 to Mx0.1 represent the mixed mode with variable proportions of uniformly dispersed propagules. In all cases, exponential is medium range, environment is favourable and gap size is 5 cells

defined by the shore gradient. During spread, the density of the species increased at all localities, though it was faster at the favourable end of the shore. No boundary at all can be recognised. For the mixed mode, average shore colonisation and boundary were

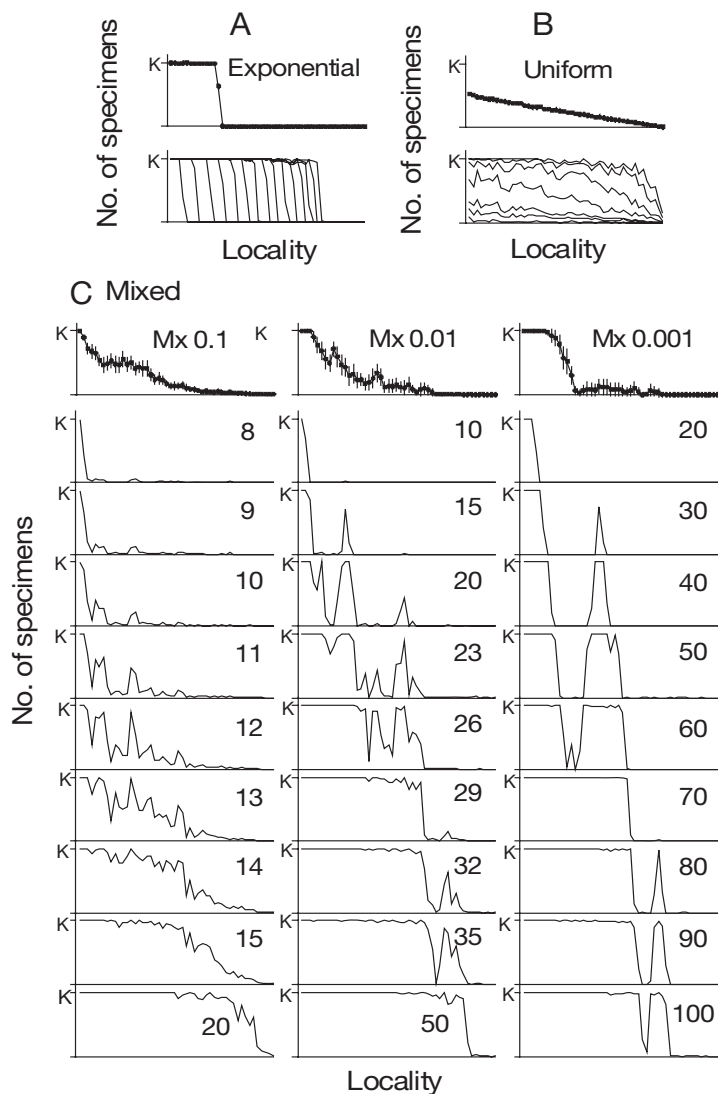


Fig. 6. Boundary shape for different dispersal modes: (A) exponential dispersal—mean abundance of the invader at each locality at an intermediate stage of colonisation, when the global shore is colonised at 25% of the shore-carrying capacity (above) and abundance of the invader along the shore in a single run at 20 yr intervals from time 0 to 300 (below); (B) uniform dispersal—as in (A), times for the single run are 5, 10, 11, 12, 13, 14 and 15; (C) mixed mode with 10 to 0.1% ($Mx0.1$ to $Mx0.001$) of propagules with uniform dispersal—the remaining propagules with medium-range exponential dispersal. The first graph in each column shows mean abundance at intermediate stages of invasion; the graphs below are abundances in a single run at different times (numbers). K is the locality-carrying capacity (summation of all cell-carrying capacities). Error bars as in Fig. 2 (for uniform and exponential modes, the error bars are smaller than symbols)

intermediate between those for exponential and uniform modes and were influenced by the proportion of propagules with uniform dispersal (Fig. 6C). Individual runs showed considerable variation in the extent of shore colonisation, which was caused by the random colonisation of localities separated from the original centre of dispersal. Mean values can be misleading as they do not describe the exact shapes of the boundaries of individual runs. New colonisation nuclei were formed by long-range dispersed propagules. This colonisation was rarer and less predictable, as the proportion of propagules with uniform dispersal decreased. When the proportion is very low (1 in 1000), the spread pattern for some runs might be identical to that under the exponential mode. In other cases, however, single, isolated nuclei might appear at variable distances from the main range of the species. In these cases, colonisation rates increased because the population had several fronts. If the isolated nuclei merged with the main range, then the colonisation rate decreased to initial values, since, again, a single population front existed.

DISCUSSION

The basic features of the distribution of *Fucus serratus* observed in northern Spain and its past distributional changes (Anadón 1983, Lüning 1990, Arrontes 1993) represent only 1 of the multiple solutions of the model. Conditions that mimic the dynamics of *F. serratus* are an exponentially bounded mode of dispersal and some degree of interannual environmental variability. In *F. serratus* only a fraction of the suitable shore is colonised (Arrontes 1993). In most of the simulations, the expanding species with exponential dispersal reached an asymptote well below the deterministic boundary. At any time, the species may survive and reproduce beyond its distributional boundary. Simulations show that environmental fluctuations may cause range contractions in spreading species. For short-range dispersers, recovery of the former range can take a long time. I suggest that distributional changes in *F. serratus* (Miranda 1931, Fisher-Piette 1957, Anadón 1983) might have occurred as rapid range contractions during rare periods of extreme environmental conditions followed by long periods of slow range expansion. Unfortunately, no historical data on upwelling conditions are available.

Spread is faster when some probability of long-distance dispersal exists. However, being an exclusively long-distance disperser may entail problems. With long-range dispersal occurring in a large proportion of the propagules, results show that (1) the spreading population is very sensitive to disturbances and

(2) failure of invasion is more likely. A dilution effect appears to be the main reason. Under unfavourable environmental conditions, a significant fraction of the propagules should be lost to unfavourable localities. The local populations receive a much smaller number of propagules than are produced locally. As a consequence, the realised net reproductive rate of a local population might be considerably below the theoretical rate for a hypothetical closed population (no dispersal). Regional, rather than local, abundance is crucial to predict success in species with long-range dispersal. The size of the global propagule cloud appears to be the limiting factor of spread. Exponentially bounded dispersal is a better strategy to cope with unfavourable environments. Because most of the propagules remain at the parent population or in its vicinity, the realised reproductive rate should be closer to the theoretical rate with no dispersal. Thus, local populations with exponential dispersal modes may cope with harsher environmental conditions before the population starts to decline. The consequence is that the decline is not as severe as with uniform dispersal.

The superior strategy, however, is the mixed dispersal mode, with a very small fraction of long-range dispersers. It combines fast spread with resistance to disturbances. The proportion of propagules with uniform dispersal does not need to be large to generate accelerating range versus time curves; it may be as low as 1%. A small fraction of long-distance dispersers (<1%) may not be enough to severely influence the realised reproductive rate of the local population, but it provides a chance to spread quickly when favourable conditions return. Disproportionate effects of small numbers of long-distance dispersers on the rate of an invasion are well known from theoretical simulations (Goldwasser et al. 1994, Kot et al. 1996). The consideration of long-distance dispersers together with neighbourhood diffusion also allows the interpretation of notorious ecological invasions. Two examples are the expansion of the house finch in North America (Veit & Lewis 1996) and the spread of trees at the end of the Pleistocene (Clark 1998). No equivalent simulation has been done to explain the fast spread of the brown alga *Sargassum muticum* on European shores, but mixed dispersal probably plays an important role. An immense majority of the propagules of *S. muticum* recruit within metres of the parent plants, though detached fertile plants may drift away, seeding distant locations before they are cast ashore (Norton 1977, Deysher & Norton 1981), see similar comments by Kendrick & Walker (1991, 1995) for other *Sargassum* species.

Both pure strategies, long-distance (uniform) and exponential, may be expected to be absent in small and remote favourable sites. For the exponentially

bounded mode, this is obvious, as distances that are too large might be well beyond any realistic probability of the species to reach the site. Van den Hoek (1987) reported the absence of *Fucus serratus* from the Faeroes, a place where the species should be expected. The reason is the limited dispersal ability of the species. The thallus does not float, and the propagules spend a very limited time in the water column. For exclusive long-distance dispersal the reason is different. Propagules may occasionally reach the isolated shore and produce specimens to maturity, but the dilution effect on the propagules produced by the founding population may make replacement highly unlikely, and the population may eventually disappear. A good example is the littoral zone of Rockall, a small rocky cliff 400 km west of the Outer Hebrides (Johannesson 1988). Only invertebrate species lacking planktonic larvae are present as well as macroalgae, most of which are very efficient dispersers at small distances (Anderson & North 1966, Reed et al. 1988, Santelices 1990, Norton 1992).

With exponential dispersal, the model generated sharp boundaries and predicted sequential colonisation of the shore. The distributional limit is not directly generated by physical barriers or physiological incompetence beyond the limit. Boundaries are generated by low probability of arrival of propagules beyond the locality where the species was currently expanding. In most cases, and particularly at the unfavourable end of the shore, a locality is colonised only when the previous locality has already been completely colonised. Because the probability of success in reaching reproductive age decreases along the shore, the boundary moves at a decreasing speed towards the unfavourable end of the gradient. This generates a decelerating travelling wave. At some position on the shore, the chance of 2 propagules of different sex arriving at the same time at the same cell may be too low for a given size of the propagule cloud, and spread stops. This may happen even when a viable population could conceivably be kept at that cell or locality. This appears to be the case for the well-known sharp boundary in the distribution of *Fucus serratus* in northern Spain (see Arrontes 1993, 2002, and references therein). The boundary becomes imprecise when the proportion of uniform dispersers increases in the mixed model. New colonies establish ahead of the main range and eventually coalesce between themselves or with the main range. As the proportion increases, more and more colonies are established and the boundary is lost. Sharpness of the distributional boundary depending on dispersal distance was also found by Lennon et al. (1997) with their metapopulation model (see also Carter & Prince 1981). As predicted by Lennon et al. (1997), consider-

ation of local population dynamics renders spatial distributions with sharper edges.

Most, if not all, of the above results may be explained by a combination of Allee effects and differences in propagule pressure among different dispersal modes, environments and shore types. Allee effects are considered to be responsible for the slow spread rates at the beginning of an invasion or for delays in the commencement of the period of fast expansion (Veit & Lewis 1996), as obtained here for the uniform mode. Allee effects may also introduce critical thresholds of global population size for successful colonisation (Kot et al. 1996). This is the case for the failure of invasion under the uniform mode of dispersal in unfavourable environments. Propagule pressure is considered a good predictor of invasion success (Williamson 1996, Lonsdale 1999). In fact, there is a clear relationship between the size of the inoculum and the success of an invasion for a large number of species (e.g. Green 1997). Many other examples are provided by Williamson (1996). Propagule pressure appears in the model as the number of propagules arriving at a given cell after each reproductive season. Due to the random nature of the simulations, larger numbers of propagules arriving increase the chance of successful colonisation.

The random model used here reproduces results obtained with different models, but with similar life-history traits of the spreading species. The model predicts a travelling wave solution for species with neighbourhood diffusion (exponentially bounded modes) (Skellam 1951, Shigesada et al. 1995, Kot et al. 1996) and accelerating colonisation rates with long-distance dispersal (e.g. Shigesada et al. 1995); it also stresses the importance of a small proportion of propagules with long-distance dispersal (Goldwasser et al. 1994, Clark 1998). Furthermore, the model reveals the sensitivity of long-distance dispersal to environmental harshness due to Allee effects (South & Kenward 2001). Results are consistent with distribution patterns of real species with contrasting dispersal strategies (Johannesson 1988). Predictions in relation to sharpness of the boundaries and survival beyond the edge also agree with results from metapopulation models (Lennon et al. 1997). The main limitation of the model is related to its use with real data or species. The strength of the model relies on its correct parameterisation. Incorporation of real local effects on survival and reproduction and their variation with time may be difficult and requires exhaustive knowledge of the species and their habitats.

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Appendix 1. Steps in the simulation model

The process of invasion of a shore starts by assigning the probability of survival to each cell on the shore. In addition, 1 file of environmental data, with the E.I.s for each reproductive period, has to be provided. The details of the operational steps of the simulation may be summarised as follows:

(1) At the beginning of the simulation for each reproductive period, at each cell where both male and female plants are present, the total amount of propagules is calculated. This is the propagule cloud for each cell. For the first reproductive period of each run, there is only 1 propagule cloud at the first cell of the first locality, the seeding population.

(2) A survival probability is randomly assigned to each propagule at each propagule cloud by generating a random number from a uniform distribution (S , $0 < S \leq 1$). If this random number is larger than the maximum survival probability for that reproductive season (maximum survival multiplied by the E.I. provided by the environmental file), the propagule has no chance to survive at any destination cell and is discarded. A new propagule is considered.

(3) If the propagule has the chance to survive, the destination cell is obtained. If the dispersal mode is uniform, then the destination cell is obtained by randomly sampling a uniform distribution of integers between 1 and 1000. If exponential dispersal is used, 1 out of 4 possible dispersal scenarios is randomly assigned. For this scenario, the destination cell is obtained from its associated Laplace probability density function. Previous to the estimation of the distance travelled, whether the propagule moves to the right or left of the origin cell is randomly assigned. Then, a random number (P , $0 < P \leq 1/2b$, being b the scale parameter) is generated. By transformation of the probability density function, the exact distance travelled by the propagule is

$$x = a + |b \ln(2bP)|, \text{ if the propagule has moved to the right, and}$$

$$x = a - |b \ln(2bP)|, \text{ if the propagule has moved to the left}$$

where a is the cell of origin. By rounding x to the nearest integer the destination cell for the propagule is obtained. This procedure assumes the propagule cloud is exactly in

Appendix 1 (continued)

the middle of the cell. If the destination cell is beyond the shore limits ($x < 1$ or $x > 1000$) or is in a gap, then the propagule is considered as lost and dies. If the mixed dispersal mode is used, whether exponential or uniform dispersal is selected is obtained by generating a random number between 0 and 1. If this number is smaller than the fraction of propagules with exponential dispersal, then the destination cell is obtained as for the exponential mode above. If the random number is larger, the destination cell is obtained as for the uniform distribution.

(4) The survival of the propagule at the destination cell is calculated comparing the S obtained above (Step 2) with the survival assigned to that cell. If the propagule survives, then 1 arrival is scored for that cell and the sex of the future plant is randomly assigned.

(5) After analysing the fate of all propagules of all propagule clouds, the previously resident plants at each cell are aged 1 yr. The survival of each resident plant at each cell to the next reproductive period is randomly assigned by generating a random number between 0 and 1. If this number is smaller than the survival assigned to its age for that year and cell, the plant survives. The number of

vacant spaces for the settled propagules is obtained by subtracting the number of surviving plants to the cell-carrying capacity.

(6) If the number of settled propagules is smaller than the number of vacant spaces, all of them are incorporated into the algal population in the cell. If the number is larger, then a random sample of plants is obtained until the cell-carrying capacity is reached. All the remaining propagules die (a seed bank is not considered).

(7) The number of plants at each locality is obtained from the sum of the plants of all cells of the locality. If the number of plants in a locality exceeds 10% of the carrying capacity for that locality (summation of all cell-carrying capacities), then the locality is considered as colonised. The number and position within the shore of the invaded localities is recorded. In addition, the program keeps records of the number of plants per cell and the sex and age of each plant at each cell.

(8) Simulation of a new reproductive period may start. A typical simulation run is completed after 1000 reproductive periods.

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