

Chapter 5

Mechanism of eelgrass (*Zostera marina* L.) colonization: Patch dynamics
and effect of disturbance

Abstract

The process of re-colonization of bare substrate by eelgrass (*Zostera marina*) was documented using a forty year record of historical photographs of two regions in Massachusetts (West Island, Fairhaven; Wianno Beach, Osterville). The pattern of colonization were similar at subsites within each region: discrete circular patches of eelgrass first appeared on bare areas (via seed dispersal) and grew laterally, and additional new patches appeared each year. On a scale of 1000's of m, eelgrass took 25 and 40 yr respectively to reach peak cover after initial colonization subsequent to the wasting disease. On a smaller scale (100's of m) eelgrass expanded to peak cover 15 yr after at subsites in each area.

On the smaller scale, rates of colonization, and peak eelgrass cover at these and other areas appeared to vary primarily due to differences in lateral bed growth, new bed recruitment, disturbance size, and percent of the substrate disturbed each year by non-catastrophic disturbances. These phenomena could be measured by analyzing photograph sequences, and were incorporated in a computer simulation. Lateral growth rate, bed recruitment rate, percent of the area disturbed, and disturbance size were set in the simulation and validated with values documented in the photograph record.

The simulation agreed well with observed small-scale colonization rates and percent cover at peak abundance at validation sites in each area. Changes in recruitment rate within the model demonstrated that

new bed recruitment was fundamental for rapid colonization. Higher lateral growth rates also shortened the time for eelgrass to reach peak cover, but not to the same degree as recruitment rate. In contrast, both disturbance size and percent area disturbed had much less effect on the time for eelgrass to reach peak abundance. The percent of the habitat disturbed each year primarily affects the percent of the habitat covered by eelgrass at peak abundance. High levels of disturbance explain why eelgrass cover in some areas never exceeds 50% of the available habitat. Disturbance sizes less 10 m^2 had little effect on colonization rates or percent cover at peak abundance, even when 20% or more of the eelgrass cover was removed each year. Changes in disturbance size when disturbances are greater than 100 m^2 , also have little effect on peak cover or time to reach peak cover. Disturbance sizes in the range $10\text{--}100 \text{ m}^2$ can greatly affect the time to reach peak cover, especially when more than 10% of the eelgrass habitat is disturbed each year.

The slower colonization on a large scale (1000's of m) can be explained by stepwise colonization from refuge populations. That is, numerous small subareas showing logistic growth will result in linear expansion on larger scales. The slow large scale dispersion of eelgrass populations, together with catastrophic storms, and in some areas, human disturbance, explain why eelgrass populations took many decades to recover from the wasting disease, and why some areas are still recovering today.

Introduction

Disturbance, patch formation, succession, recruitment, and growth are fundamental processes affecting the abundance in sessile organisms (Pickett and White, 1987; Paine and Levin, 1981). In addition to these factors, analysis of succession and patch dynamics are generally altered or defined by competition and predation among species. Thus, interspecific interactions make it more difficult to study the effects of patch formation and disturbance on the colonization and abundance of a sessile species, especially on a large scale.

Eelgrass (*Zostera marina* L.) meadows are one community where the relation between population growth and disturbance can be studied without complicating effects of predation and competition. This community is ideal for a number of reasons. For most of its range, and in most habitats, eelgrass does not compete for space with other species (Thayer et al., 1984). That is, eelgrass beds exhibit the simplest form of succession: bare substrate colonization >> eelgrass meadow disturbance >> bare substrate. Less than 10% of eelgrass primary production is directly consumed, and eelgrass beds are rarely denuded by herbivores (Jacobs et al., 1979; Nienhuis and Groenendijk, 1986). Consequently, the role of herbivory in eelgrass colonization can be ignored for most sites. Virtually all eelgrass beds were destroyed by a "Wasting Disease" in the early 1930's (Rasmussen, 1977); thus a large-scale natural "experiment" has occurred. Finally, eelgrass beds often show up clearly on aerial photographs, and many areas have been repeated

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surveyed since the late 1930's, hence a large data base exists for analysis. In this paper, I document and model the process of eelgrass colonization at two sites in southeastern Massachusetts (USA), and determine how population growth is affected by different levels of disturbance and rates of population expansion.

Eelgrass life history

Eelgrass is a marine angiosperm that grows subtidally in Northern temperate waters, often forming extensive meadows. All stages in the life cycle of eelgrass including pollination and germination occur underwater. Expansion of existing beds occurs by production of new shoots and recruitment of new seedlings, whereas the colonization of bare areas not adjacent to existing beds almost completely depends on propagation and germination of seeds because uprooted plants float and are usually lost to sea or get cast on shore. Seed production often exceeds many thousands of seeds per square meter (Thayer et al., 1984). Eelgrass seeds are negatively buoyant, and most fall near the beds that produced them (Robertson and Mann, 1984; c.f. Davis, 1985); but some may also be carried by currents or uprooted flowering shoots (Churchill et al., 1978).

Disturbances

Like most regions, nearly all eelgrass populations in Massachusetts were destroyed (Cottam, 1933, 1934; Stevens, 1935; Stevens et al., 1950; Costa, 1987, 1988). One of the most remarkable aspects of the wasting disease was that eelgrass populations took many decades to

recover, and are still expanding in some areas today (Costa, 1987; den Hartog, 1987). Superimposed on this gradual recovery were smaller or localized impacts from natural or human disturbances of various scale. These chronic or periodic disturbances slowed or sometimes "reinitialized" colonization. Human disturbances affecting eelgrass and other seagrass populations include physical removal, toxic pollution, and degradation of water transparency (Cambridge, 1979; Cambridge and McComb, 1984; Orth and Moore, 1983b; Orth et al, 1980; Phillips, 1978; Thayer, et al., 1975). Natural disturbances affecting eelgrass and other seagrasses (besides disease) include catastrophic storms, periodic non-catastrophic storms, sediment transport, ice damage, and grazing pressures (Harlin et al., 1982; Jacobs et al., 1981; Kirkman, 1978; Orth, 1975; Rasmussen, 1977; Robertson and Mann, 1984). On Cape Cod and Buzzards Bay, MA, storms and ice scouring are the principal disturbances affecting the two areas studied here (storm dates and severity are summarized in Costa, 1987).

This study documents recolonization after the wasting disease and analyzes the mechanisms and patterns of colonization based on growth and natural disturbances. In general, there has been little effort to model large-scale seagrass bed growth and recruitment. Many of the techniques used here, such as mapping of seagrass beds using aerial photographs is now routine (e.g. Kirkman, 1977; Harlin and Thorne-Miller, 1982). In addition, small scale (10's of m) patterns of colonization have been studied in transplanted eelgrass (e.g. Fonseca et al. 1979; Kenworthy et al., 1982). What is lacking is a quantification of eelgrass colonization rates at larger scales, especially how they are affected by

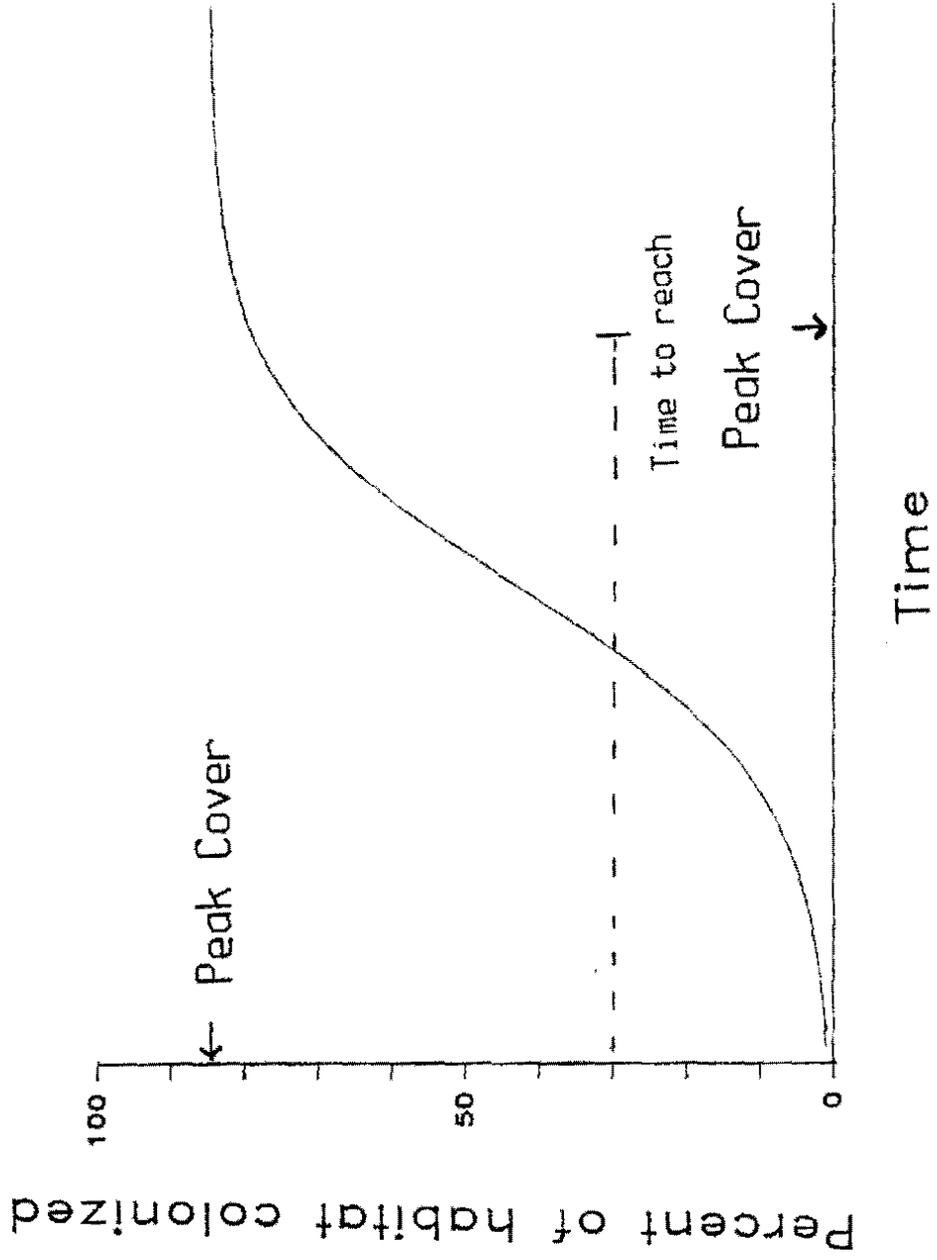
disturbances that remove eelgrass, recruitment rate of new beds, and bed lateral growth.

Abundance or the percent of surfaces covered over time typically follows a logistic curve. A species may not completely cover a habitat either because of competition, disturbance, or suitability of habitat. In this study, the asymptotic portion of the curve is termed percent cover at peak abundance, and the time to reach the asymptotic phase was termed years to peak abundance (Fig. 1).

After the wasting disease, surviving eelgrass populations took 30 to 50 years to recolonize parts of Buzzards Bay and Cape Cod Massachusetts (Costa, 1987). These long colonization periods are due to the fact that initial re-colonization in some areas did not begin until 20 or 30 years after the disease because they were remote from refuge populations. In small areas (less than 20 ha), once colonization began, peak cover would nearly always be reached in less than 20 years, and in some cases, in as few as 5 years.

On high energy coasts, discrete circular beds of eelgrass first appeared, which expanded laterally. Each year new beds were recruited nearby, and they too expanded, and this process continued until peak cover was achieved. There was considerable variation in this colonization process: not only did the time to reach peak cover vary, but some areas had nearly continuous eelgrass cover at peak abundance whereas others had less than 50% of the available substrate covered, even after decades. This variability in colonization patterns appeared to be due to differences in bed recruitment rates, bed lateral growth, disturbance size, and the percent of the habitat disturbed each year.

Figure 1. Hypothetical colonization of an area by vegetation as percent of the area covered over time. In this paper, the asymptotic part of the curve is termed percent cover at peak abundance. The time to reach the asymptote is termed years to peak abundance.



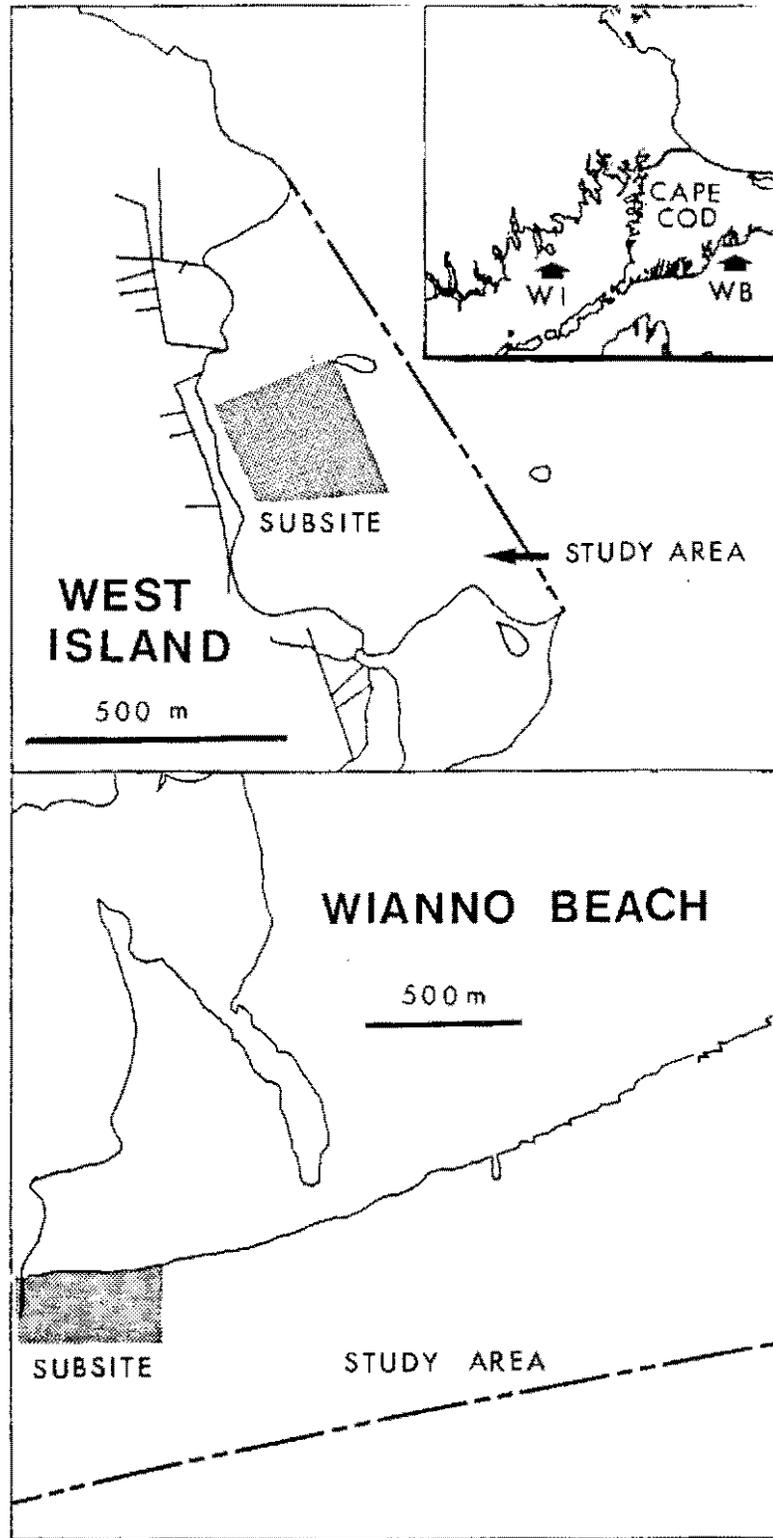
To test how changes in colonization rates depended upon differences in bed lateral growth rate, bed recruitment, and disturbance size and frequency, a graphical simulation (a two-dimensional cellular automata) was developed that incorporated these parameters. Cellular automata are mathematical systems that simulate complex spatial or temporal patterns using lattice matrices of cells whose value or contents are determined by the contents of adjoining cells, based on a set of rules (Cocho et al., 1987; Wolfram, 1984). This type of model is necessary where spatial relationships exist that cannot be evaluated algebraically or through differential calculus. In this case, eelgrass mortality cannot be modeled using classical growth equations because a 10% annual mortality rate results in very different patterns of colonization if the mortality consists of numerous small disturbances or large infrequent ones. Similarly, eelgrass cover expands both by vegetative growth of existing shoots and recruitment of new seedlings, but the relative importance of each phenomenon cannot be distinguished by an analysis of intrinsic growth rates.

Materials and methods

Site description

Two regions typical of moderate to high energy coastlines were studied: 50 ha in East Bay off West Island, Fairhaven, MA, and 150 ha off Wianno Beach, Osterville, MA (Fig. 2). These regions were chosen because aerial surveys were available and eelgrass grows on broad sandy coastal shelves, and patterns of eelgrass distribution are distinct. The Wianno beach site is a more exposed south facing shore and

Figure 2. The site locations in Massachusetts. The areal extent of beds is marked by the dashed line which encloses 50 ha at West Island and 1500 ha at Wianno Beach. The outlined area within each site denotes the subsite (6.5 and 6.2 ha, respectively) in which detailed changes in percent coverage were mapped and for which rates of lateral expansion, disturbance, and recruitment were measured.



experiences more wave and storm action than the West Island site. Ice scouring is more important in East Bay, West Island because it is shallower, and ice accumulation is more prominent in that area.

Both areas have experienced little human activity. The Wianno Beach had extensive groin construction during the 1940's and 1950's, but the eelgrass beds there grow away from shore, and were probably not influenced by changes in sand transport caused by the groins.

Photograph analysis

Data on changing eelgrass abundance was obtained from analyzing sequences of aerial photographs at each site (Costa, 1987; Orth and Moore, 1983b). Photographic coverage was obtained for West Island beginning 1951, and Wianno Beach beginning 1940, with a 1 to 5 year spacing between photographs.

Eelgrass beds are rarely continuous patches of vegetation; instead there are bare areas within beds of varying size. Some of these bare areas are apparent on the photograph, others are below the limit of resolution on the photograph and are measurable only by field observations. Alternatively, eelgrass may occur as numerous discrete patches too small and numerous to digitize. In all these cases, a border was drawn around eelgrass beds or clusters of eelgrass beds on photographs, and the area of each "bed" was measured by digitizing. These bed areas were corrected percent cover by comparing them to a cover scale chart (Costa, 1987).

To map bed positions and calculate areas, a sheet of acetate was placed on the photograph, and the borders of eelgrass beds and notes on

percent cover were recorded. The photograph and overlay were photographed with slide film, and this slide was projected onto coastline maps. The edge of the eelgrass beds were traced onto the maps from the slide image. The eelgrass beds were digitized using mapping software, and stored for later analysis and plotting.

Each of these coastal regions have complex habitat heterogeneities such as sand waves and long-shore currents. No attempt was made to include these features in the model. Photographs showed that the larger coastal regions exhibited asynchronous colonization along different parts of shore, but small parcels of substrate showed relatively uniform and synchronous colonization. Consequently a small subsites in each study area (Fig. 2, West Island subsite = 6.2 ha , Wianno Beach subsite = 6.5 ha) was analyzed for differences growth, recruitment, and disturbance and used to validate the computer model.

Lateral growth of eelgrass was measured by changes in bed area of new discrete eelgrass beds between two consecutive photographs. The beds were treated as circles to calculate radius, and the change in radius between two time periods was divided by the number of growing seasons to obtain bed lateral growth rate (Gr). Only during early stages of eelgrass colonization were individual eelgrass beds sufficiently circular and recognizable for this calculation.

Disturbances may remove pieces of, or entire eelgrass beds. These disturbances occur during all stages of eelgrass colonization, but is easiest to measure during early stages of eelgrass colonization when there are many small discrete beds covering the bottom and the identity and survivorship of individual beds can be followed over time. If there

was only one year between photographs, yearly bed mortality rate (M_Y) was calculated as:

$$(M_Y) = 1 - (N_S - N_0) / N_0,$$

where N_S equals the number of surviving beds, and N_0 is the original number of beds (new beds are ignored). If there is more than one year between photograph pairs, M_Y was calculated from the exponential decay equation:

$$M_Y = 1 - (N_S / N_0)^{(1/Yr)}$$

It was assumed that both disturbances and beds are randomly distributed and independent. Therefore, the percent of the habitat disturbed each year (PHD) also equals M_Y .

Similarly, the yearly recruitment rate of eelgrass (b) can be calculated by counting the number of new beds formed between photograph pairs during early stages of colonization. Because the model required an estimate of bed formation rate produced by existing eelgrass bed area, b was calculated as multiplicative percent increase in bed number each year (rather than from the calculating intrinsic rate of growth of bed number, r) as:

$$b = (N_0 + N_n) / N_0 - 1$$

If more than one year occurred between photographs then:

$$b = ((N_0 + N_n) / N_0)^{(1/Yr)} - 1.$$

Because this estimate of b ignores mortality of newly recruited beds that may have occurred during the interval, the equation was revised as:

$$b' = b - b \times M_Y.$$

Because eelgrass populations do not exist as discrete units in late stages of colonization in the field or model, bed recruitment for

the model (R_b) was defined as the number of new beds produced per 1000 m^2 of initial bed area, or:

$$R_b = (b' * N_0) / (1000 \text{'s of } m^2 \text{ of } N_0).$$

This method may slightly overestimate bed recruitment because it ignores increased eelgrass bed area during the intervals during photograph sequences separated by more than one year. Nonetheless, as shown in the results, this estimate is sufficiently accurate for the operation of the model.

In nature, recruitment is a function of the available seed pool which ultimately is a function of local eelgrass abundance, because eelgrass seeds fall near the beds that produced them (Davis, 1985; Robertson and Mann, 1983; Costa, 1987). In this model the effects of current velocity and direction were ignored, and seeds were randomly dispersed throughout the model area.

Disturbance size was calculated from the mean size of bare areas within eelgrass beds that were at peak abundance. This clearly underestimates disturbance size because existing bare areas are of different age and lateral expansion of bed margins could have taken place. This estimate of disturbance size is a first approximation, and the implications of disturbance size on colonization are discussed below.

Model configuration

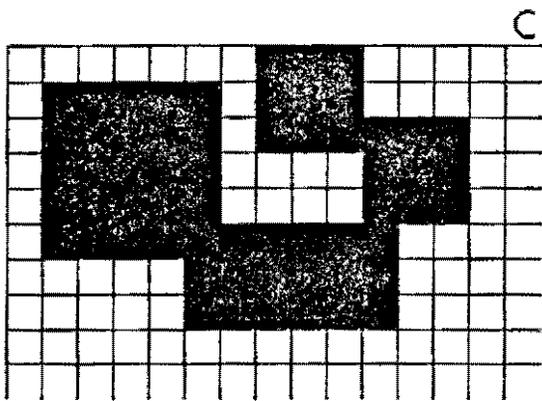
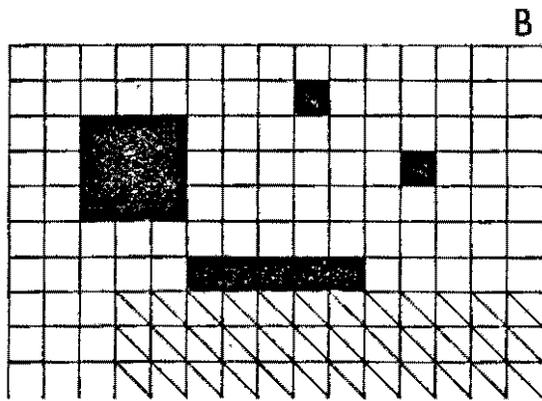
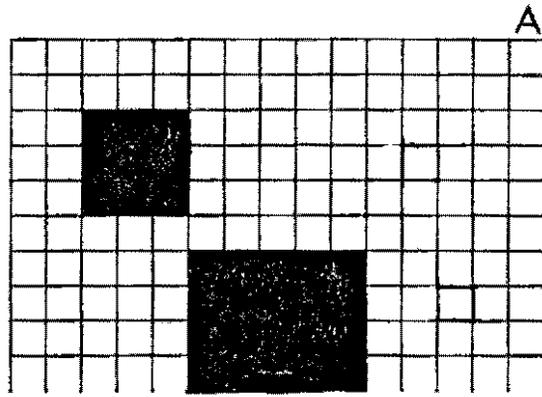
Lateral expansion rate, recruitment rate, disturbance size, and percent of the habitat disturbed were incorporated in a two-dimensional graphical simulation written in TURBO Pascal™ for a microcomputer. The

model was composed of a spatial lattice of 310 x 190 square cells which represented the habitat on which eelgrass grew. Each cell could be empty or contain eelgrass. To eliminate edge effects in the lattice, the habitat was defined as a "wraparound" universe; that is, an expanding bed or disturbance propagating at the edge of this spatial lattice appeared on the other side of the habitat lattice.

The model was initialized (year = 0) with 2% of the model habitat area randomly covered with eelgrass, composed of both 9 cell (3x3 cells) and 1 cell beds. This initial cover was similar to the cover observed at the validation sites after initial colonization. The model ran simulating 30 years of growth and disturbance. During each year in the model: 1) existing beds would expand laterally, 2) disturbances would randomly remove some existing eelgrass, and 3) new beds were recruited (Fig. 3). To validate the model, the four parameters (lateral expansion rate, bed recruitment, disturbance size, and percent area disturbed) were set with values measured from the validation sites, and the resulting colonization curve was compared to actual colonization curve for each site. To test the relative importance of each parameter, on colonization, the simulation was repeated with each of the parameters changed over a wide range of possible values. Since the model includes stochastic events, each 30 year run of the model was repeated four times to obtain a mean and standard error of the percent cover at peak abundance, and the time to reach peak cover.

Lateral expansion of beds in the model was accomplished by cells containing eelgrass "growing into" the adjacent eight cells (Fig 3). If eelgrass grew into a cell that already contained eelgrass, that cell was

Figure 3. A small portion of the habitat lattice in the model. The model underwent 3 phases each year. 'a' shows eelgrass coverage at time t . The model first randomly disturbed areas (b), cross hatched area), removing all eelgrass within the disturbance. Next, new eelgrass beds are recruited (b, new bed). This was followed by vegetative lateral expansion (c) which is now at time $t+1$. The size of each cell varied depending on what lateral expansion rate was desired (refer to text).



not affected. Thus an isolated, undisturbed cell could in subsequent years grow into beds composed of 9, 25, 36, 49, etc. cells. The mean lateral expansion rate of this process can be calculated if each square bed is assumed to be circular with initial radius (r_i) and area = 9, 25, 36, etc. The change in radius between any two years ($r_{(i+1)} - r_i$) equals $2 \times (\text{area}/\pi)^{0.5}$. Because the square root of the area of a square equals the length of a side, then lateral expansion rate = length of square $\times 1.13$. Because of computer memory limitations, lateral expansion rate in the model was adjusted by changing the size of each cell. This changed the absolute size of simulation lattice, but did not affect recruitment rates, percent of the habitat disturbed, or disturbance size, because each of these parameters was determined by cell size.

In nature, many more seeds are produced than either germinate or survive to form new beds. In the model and photograph analysis, new bed recruitment is conceptually equal to a seed being dispersed, germinating, and growing into a new bed. For clarity, I will call this process "new bed dispersal".

New beds were randomly dispersed throughout the area of the model. Like lateral growth, if a new bed "landed" in an empty cell, that cell became filled with eelgrass; if the cell already had eelgrass, it was unaffected. Recruitment would continue until a specific number of "beds" were dispersed (based on the area of existing eelgrass bed area as described above), regardless of whether they landed empty or full cells.

The mean size of large disturbances was measured from photographs with beds near peak eelgrass abundance, and was varied in the model. Disturbances of greatly differing sizes occur naturally, but small patch removal is probably more common. In the model, disturbance size was randomly generated, nearly conforming to a Poisson distribution centered around the mean disturbance size selected, and bounded by 0.2 x and 2.0 x mean disturbance area. This distribution was similar to the size distribution of bare areas at Wianno site. These limits in disturbance size were arbitrarily set to simplify the model, and the robustness of the model with respect to disturbance size are discussed.

The disturbances were randomly placed without respect to previous disturbances. Thus it was possible to have an area disturbed more than once during one year of the model. Disturbances would continue in the habitat lattice of the model until the total area disturbed in that year equaled the disturbance area selected when the model was initialized.

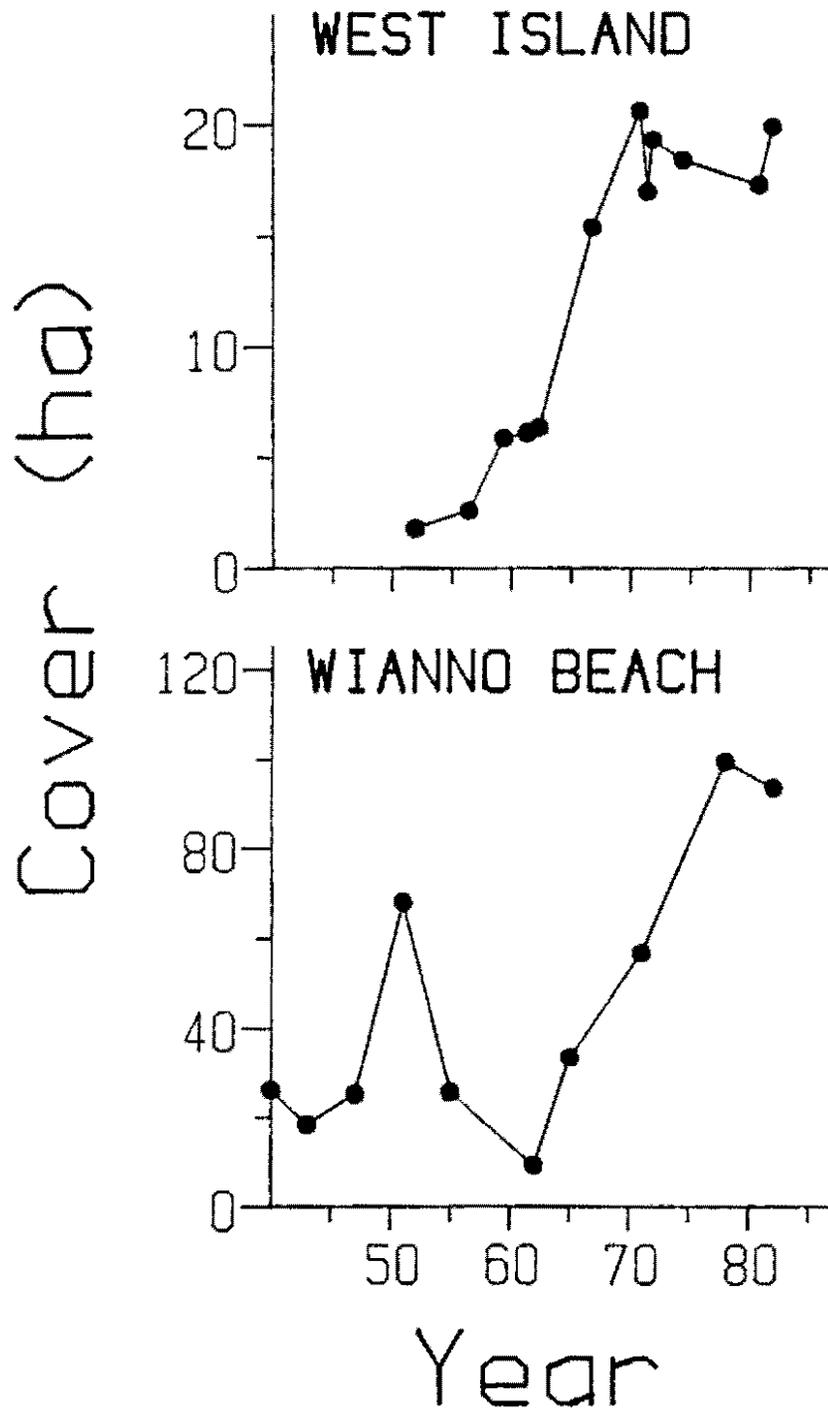
Percent eelgrass cover in the model area was calculated by dividing the number of cells containing eelgrass by the total number of cells times 100. The size of the model lattice habitat area was approximately the same size as the validation sites. At this scale, the distance effects on new bed recruitment colonization were assumed to be unimportant, and were not part of the model. Because of scale effects and because the larger regions have too much habitat heterogeneity, only data from the validation sites could be compared to the model in a meaningful way.

Results

Like other areas in Massachusetts, eelgrass populations took forty years to fully recover in East Cove of West Island, and 45 years to recolonize Wianno Beach (Fig. 4; see also Costa, 1987). Over these regions, periods of areal expansion were nearly linear reaching an asymptotic peak cover. Colonization in both locals was asynchronous and occurred stepwise along each coastline: from east to west at Wianno Beach, and from northern deep parts of East Cove to shallow flats at the south end (data not shown). In particular, East Cove, West Island was characterized by two major phases of expansion: extension of deep beds at the north end of the Cove during 1956-1960, and colonization of shallow areas in the south part of the cove during 1962-1966 (Fig 4, top). Colonization may have been slowed during the mid-1950's in part due to a hurricane. Eelgrass expanded into the shallow nearshore of West Island during the 1960's and 1970's, but large portions of these beds were destroyed during the late 1970's due to severe ice scour and winter storms.

At Wianno Beach, eelgrass showed major expansion between 1948 and 1954, and between 1966 and 1973 (Fig. 4, bottom), and appears to be still expanding today, but at slower rates. This coast is more exposed, and catastrophic storms (hurricanes in 1954, and a hurricane and severe blizzard in 60-61) resulted in the loss 60% of existing eelgrass cover. Eelgrass beds on deeper habitat than at West Island, and ice does not accumulate along Wianno Beach to the same degree. Consequently, losses of eelgrass along Wianno Beach during the late 1970's were nominal.

Figure 4. Historical changes in eelgrass abundance at East Cove, West Island, 1951-1983 (top) and Wianno Beach, 1940-1981 (bottom). Slow eelgrass growth (East Bay) or declines (Wianno Beach) resulted from hurricanes in 1954 and a hurricane-blizzard combination in 1960-61.



Colonization of the validation subsites (Fig. 5) was more rapid than the larger study area (Fig. 4), and at both sites, eelgrass achieved peak abundance 13-15 years after initial colonization. The process of colonization at the two subsites differed in several respects. Eelgrass at the West Island site reached 90% peak cover whereas the Wianno Beach site reached only 77% peak cover. The two validation sites had different rates of lateral expansion, bed recruitment, and size and frequency of non-catastrophic disturbances (Table 1).

When values of each of the parameters modeled were initialized in the model, the simulation results compared well with actual colonization (Fig 5). Also, the spatial pattern of eelgrass cover in the model had a similar appearance as on photographs (Fig. 6). Because the model matched the photographic record well, the model was run through 100's of iterations to determine how changes in lateral bed expansion rate, bed recruitment rate, disturbance size, and percent of the habitat disturbed affected the process of colonization.

For example, recruitment rate was changed, but lateral expansion rate, disturbance size, and percent of the habitat disturbed were kept constant, with values appx. equal to the Wianno Beach validation site. Results from the model (Fig. 7) suggest that at low recruitment rates, it would have taken more 30 years for colonization to reach peak abundance at the Wianno subsite, instead of the 13 years observed. At higher recruitment rates, changes in rate had less effect on years to peak abundance than low recruitment rates, but still reduced the time to reach peak abundance, <8 years for very high rates. The curve is not

TABLE 1. Bed lateral expansion, survivorship, and recruitment at early stages of succession for the two validation sites. Bed numbers for the West Island site during the 61-62 sequence were too merged for bed count calculations, but this was unnecessary because of there was only 1 growing season between photographs and R_b could be calculated directly as number of beds produced per existing bed area. For validation purposes, the model was tested with the 1951-56 data for West Island.

	Wianno Beach	West Island	
Photograph pair sequence:	4/62-10/65	10/51-5/56	4/61-4/62
Growing seasons in sequence:	4	4	1
Initial # of beds (N_0):	128	42	nd
initial bed area (A_i):	1400	75	776
Bed survivorship (N_s):	100	36	nd
New beds recruited (N_n):	113	9	47
Final bed area (A_f):	5850	179	nd
Parameters used in model:			
Bed recruitment/1000 m^2 of N_0 ($=R_b$):	36	49	61
Percent of habitat disturbed per yr (PHD):	6.0	3.2	nd
Mean disturbance size (m^2):	78	≤ 10	nd
Bed lateral expansion rate (m/yr):	0.45	0.29	0.45

Figure 5. Top: Colonization by eelgrass at the West Island subsite (see fig. 2) beginning 1956 (closed squares) compared and results of the 4 runs (mean +/- sd) of the simulation set with the four parameters set as in Table 1. Bottom: Colonization by eelgrass at the Wianno Beach subsite beginning 1962 (closed squares) compared and results of the 4 runs (mean +/- sd) of the simulation set with the four parameters set as in Table 1.

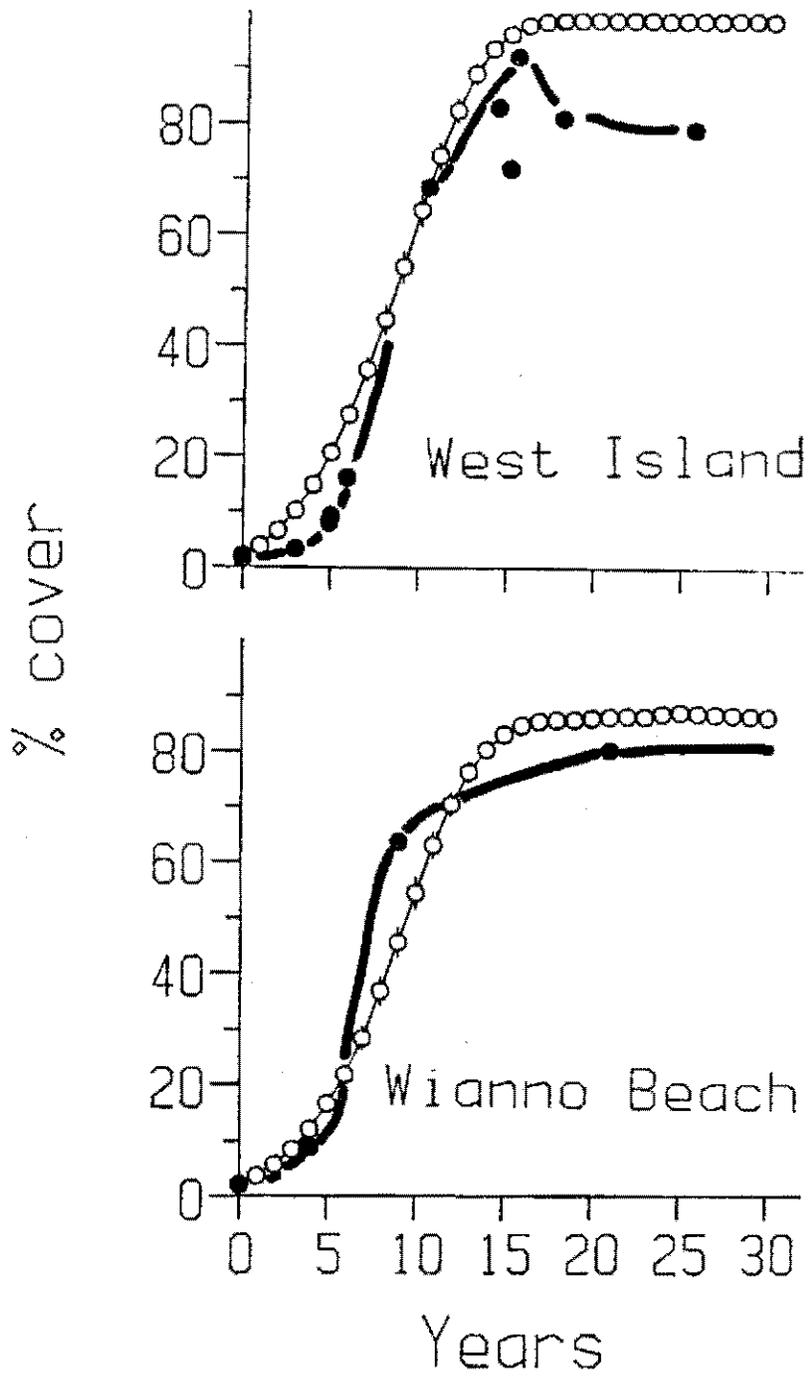


Figure 6. A comparison between a 1.3 ha portion of the model (bottom), and photograph area of equal size (top) at Wianno Beach, on which this model run was based. Both are at 19 years after colonization.

25 m

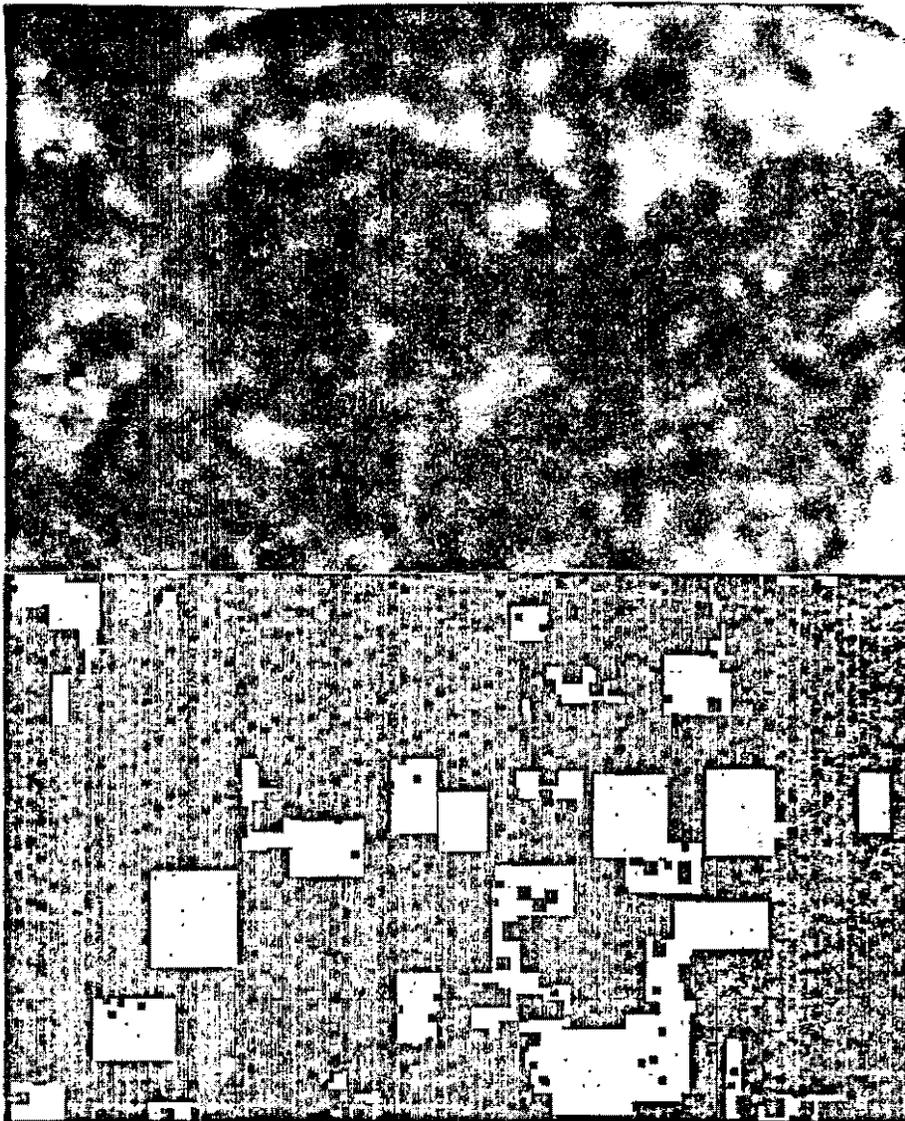
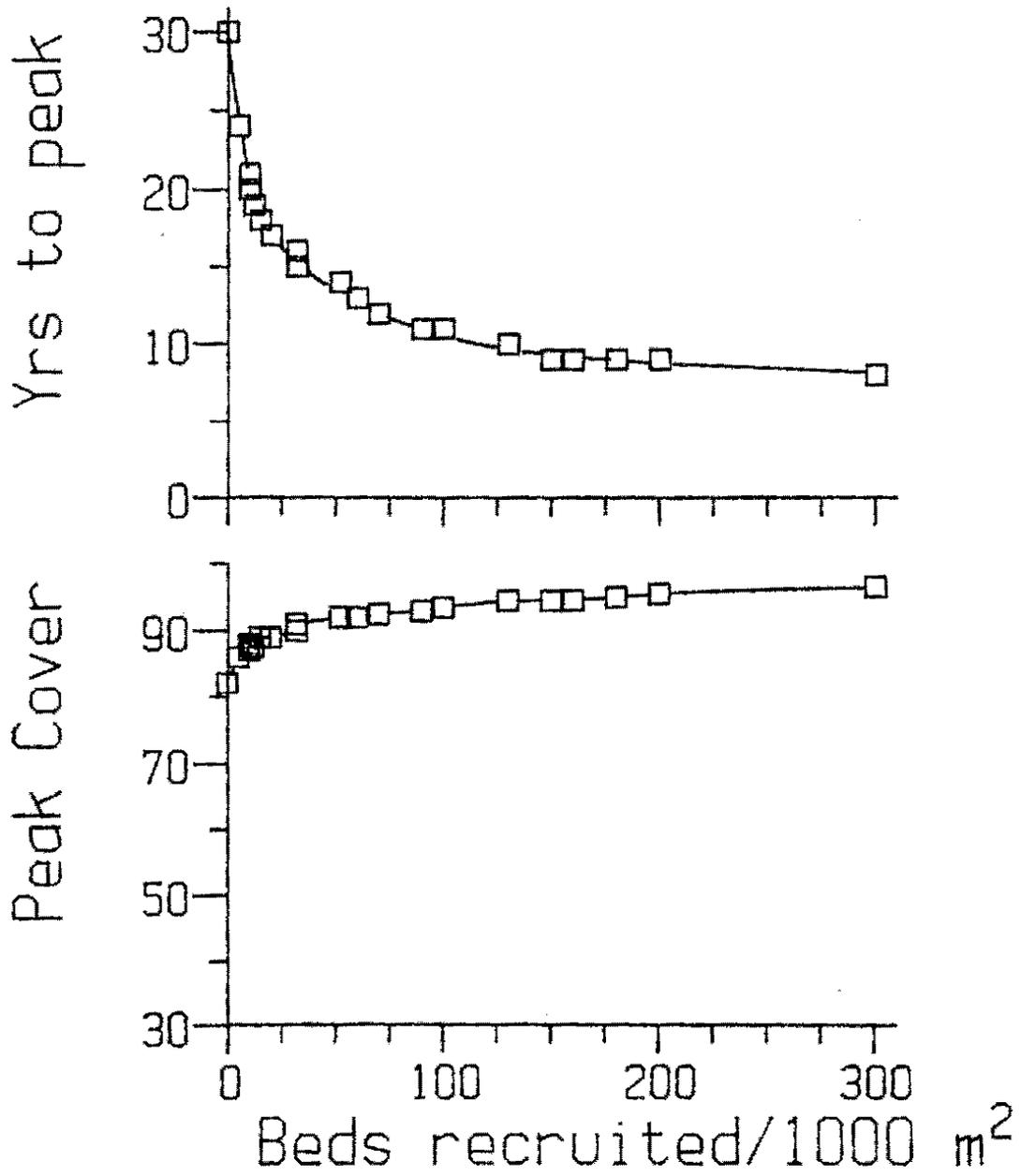


Figure 7. The effect of recruitment rate (# of beds produced per 1000 m⁻² of existing eelgrass) on years to peak abundance (top) and percent cover at peak abundance (bottom). For these runs, percent of the habitat disturbed = 5.0, mean disturbance size = 76.5 m², and lateral expansion rate = 0.45 m yr⁻¹



asymptotic but instead becomes linear with a shallow slope suggesting that if higher recruitment rates are possible, colonization may occur in periods less than 8 years. Increased recruitment rates increased slightly percent cover at peak abundance (from 85 to 93%). The impact of changes in recruitment rate were much less than the effect of changes in disturbance size or percent area disturbed.

Increased lateral expansion, like increased bed recruitment, reduces both peak cover and the number of years to reach peak abundance (Fig. 8). Changes in lateral expansion rate between 0.1 and 0.5 m year resulted in the greatest changes on peak cover and years to peak abundance. Over this interval, colonization time decreased from thirty years to less than fifteen years, and increased percent cover from 73% to more than 90%. Nonetheless, increases in lateral expansion rate had less effect on reducing colonization time than increases in bed recruitment rate.

The percent of the habitat area disturbed each year had a strong effect on peak abundance, but had only a moderate effect on years to reach peak abundance (Fig. 9). The slope of the percent cover curve was linear (Fig. 9, bottom) with a slope of -2.1. Thus, if 10% of an eelgrass habitat is disturbed each year, under the specified rates of bed lateral expansion and bed recruitment, eelgrass cover will never exceed 80% of the bottom. The effect of percent habitat disturbed on years to reach peak cover was less than the effect of changes bed recruitment rates or bed lateral expansion. If 30% of the habitat is disturbed each year, eelgrass will take 30 years to colonize an area

Figure 8. The effect of changes in lateral expansion rate on years to peak abundance (top) and percent cover at peak abundance (bottom). For these runs, recruitment rate = 35 beds/1000 m², disturbance size = 77 m², and percent of habitat disturbed 5%.

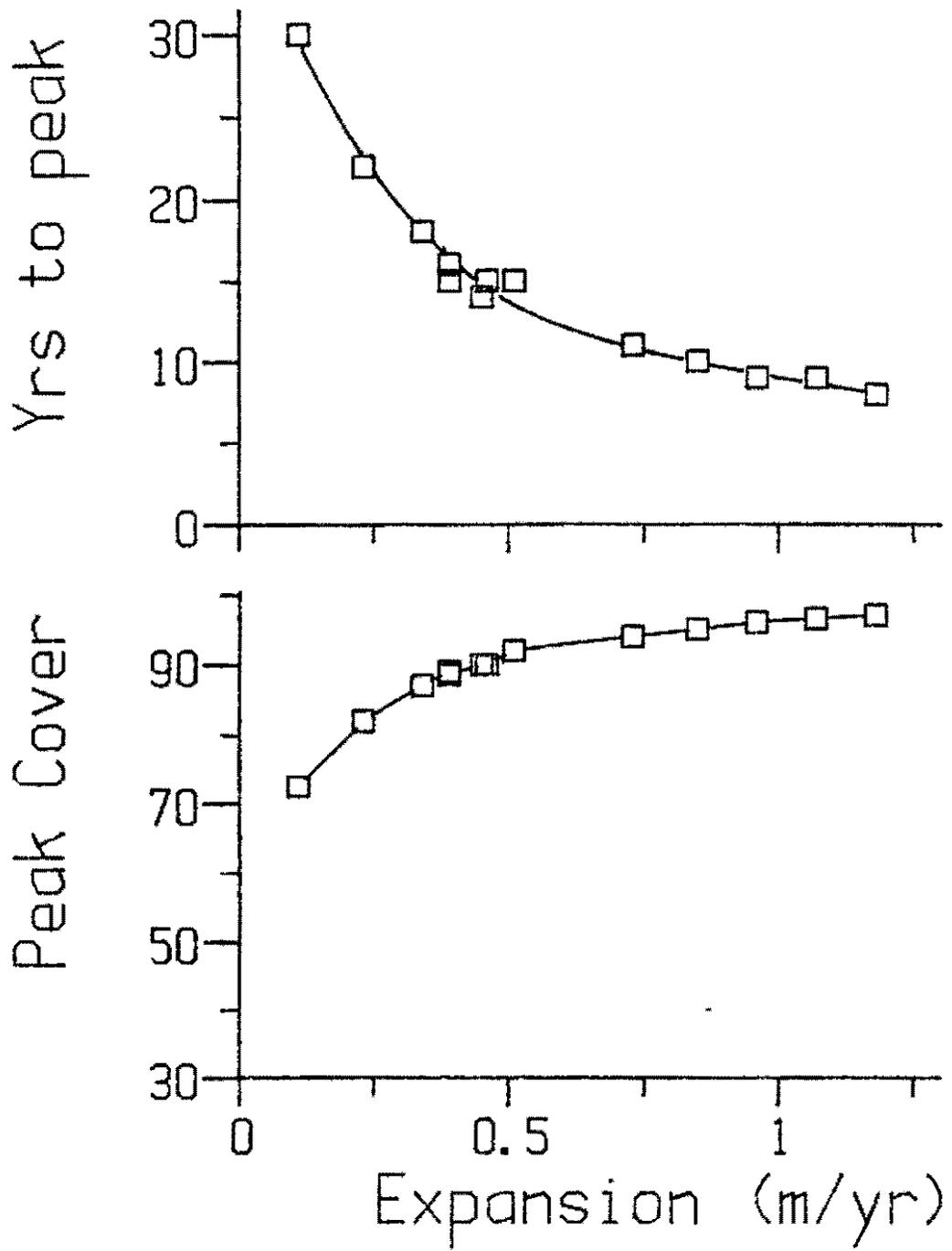
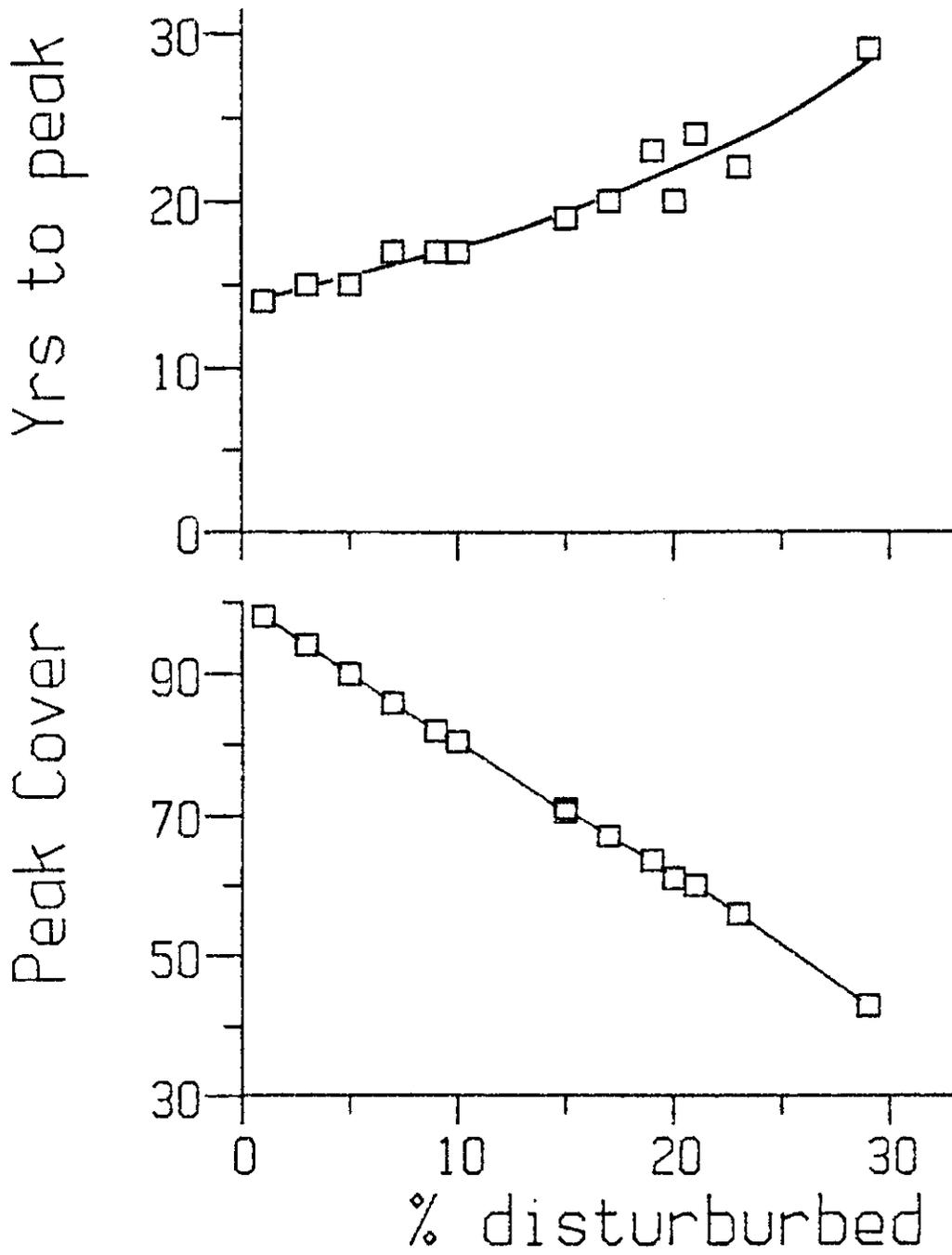


Figure 9. The effect of percent of the habitat area disturbed each year on years to peak abundance (top) and peak abundance (bottom). For these runs, recruitment rate = 35 beds/1000 m², mean disturbance size = 76.5 m², and lateral expansion rate = 0.45 m yr⁻¹



instead of the 14 years required when none of the habitat is disturbed under this set of conditions.

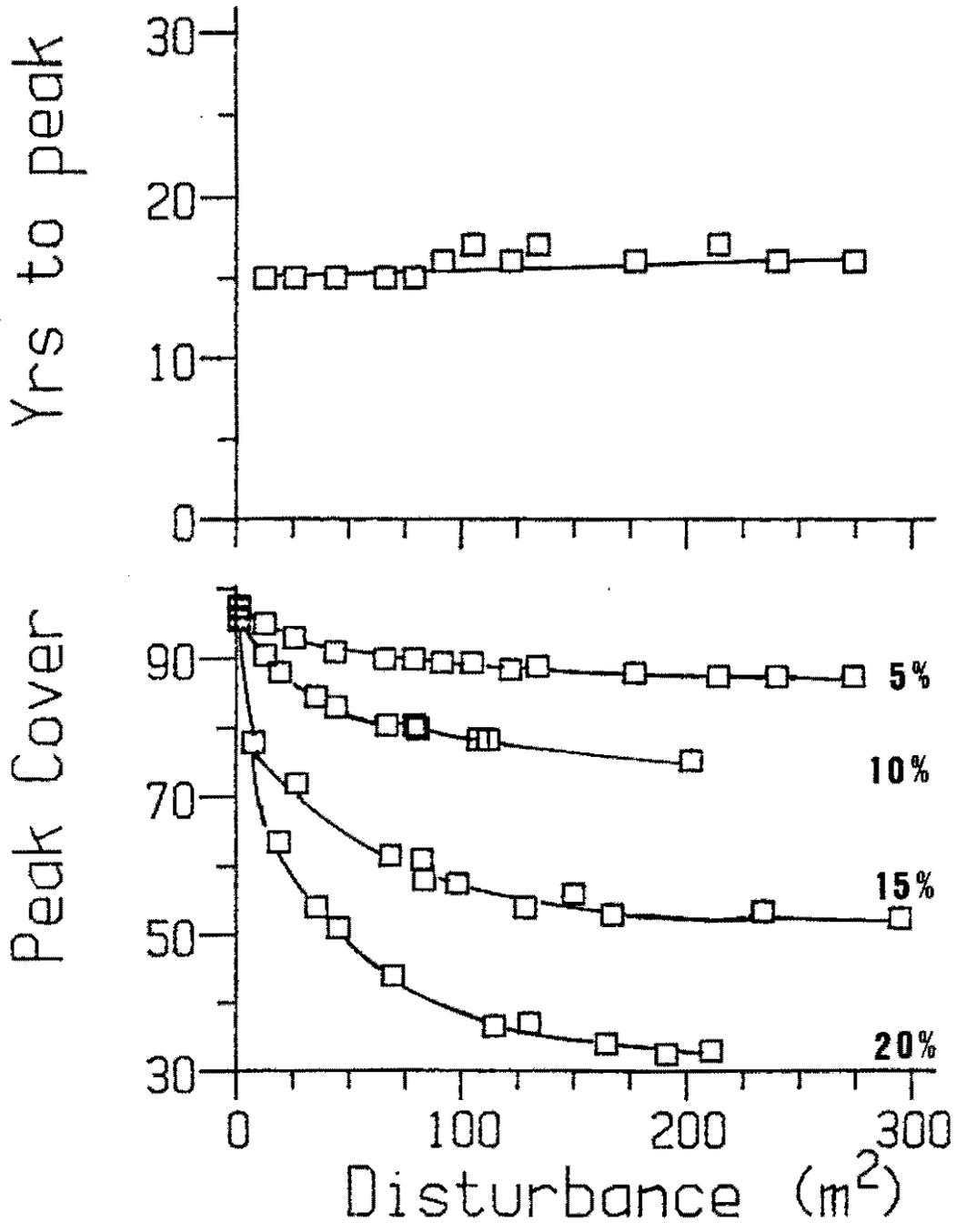
Disturbance size did not affect the time to reach peak abundance at all (Fig. 10), but was an important factor regulating peak cover. The impact of disturbances of 10-100 m² on peak cover depended greatly on the percent of the habitat disturbed (Fig. 10). For example, if mean disturbance size is 80 m² but only 5% of the bottom is disturbed each year, 90 percent of the bottom will be cover by eelgrass when the population reaches peak abundance. In contrast, 80 m² disturbances totalling 20% of the habitat each year will result in eelgrass habitat area that never exceeds 40% cover.

Changes in the size of disturbances for disturbances greater than 100 m², however, had less effect on peak cover, irrespective of percent of the habitat disturbed. Disturbance less than 5 m², had virtually no effect on peak abundance, even if 20% of the habitat was disturbed each year (Fig. 10).

Discussion and conclusions

Overall the model closely fit observed patterns of colonization at each validation subsite. Differences between the model and data from the subsites can be explained in part by uncertainty in the calculated parameters since small changes in some of the parameters. For example, in the model, a 9 % yearly disturbance level and recruitment rate of 80 beds per 1000 m² would give a nearly perfect fit to the Wianno Beach data. Alternatively, some the parameters in the model such as lateral expansion and recruitment rates may change during different periods as

Figure 10. The effect of disturbance size on years to peak abundance (top) and peak cover (bottom). For these runs, recruitment rate = 35 beds (1000 m²)⁻¹, and lateral expansion rate = 0.45 m yr⁻¹. The model was reiterated in both cases for 5%, 10%, 15%, and 20% percent of the habitat area disturbed.



illustrated in Table 1. These differences could be due to changing habitat conditions ("good" and "bad" years, effects of catastrophic storms), or alteration of habitat and facilitation of growth. Because neither lateral expansion or bed recruitment can be easily from photographs during late stages of colonization, field studies over long periods are necessary to answer these questions.

To simplify the model, several assumptions were made which are not necessarily true, but these assumptions probably do not affect the results. For example, bed recruitment rate may not be proportional to bed area in later stages of colonization, but this unimportant because vegetative growth is more important in expanding bed cover at that time. I assumed random dispersion of eelgrass propagules throughout the colonized area of the model, but observations on eelgrass and other passively dispersed seeds show that most seeds fall near their source, and decline exponentially with increasing distance (Sharpe and Fields, 1982; Costa, 1988). This may not be a serious conflict, however, because beyond a certain distance, the 'tail' of an exponential decay curve at great distances may not be statistically significant from a random or uniform distribution of low frequency (Poisson). The distribution of disturbance size probably has little bearing on the model results because disturbance size does not affect peak cover at all, and for many class sizes, has only marginal effects on peak cover.

Bed margin lateral expansion rates used in the model are realistic based on reports in the literature for actively growing beds (Araski, 1980; Fonseca et al., 1979). The highest rates observed in photographs could also be an artifact due to new seedlings that may recruit near the

edge of existing beds; a phenomenon that cannot be resolved from photographs. Functionally, however, this mechanism does not affect the model, because all that was considered is the net expansion of existing beds.

The graphical simulation approach used here is heuristic in many ways. The model used here was based on three well documented phenomena: eelgrass beds expand vegetatively, new beds may recruit from seeds, and eelgrass may be removed by disturbances of various size and frequency. Because this model was based on these concepts, it can operate without any a priori knowledge of the values of any of these parameters. In this case, when values of each parameter (derived from photographic observations) were used the model, they matched well with the real world.

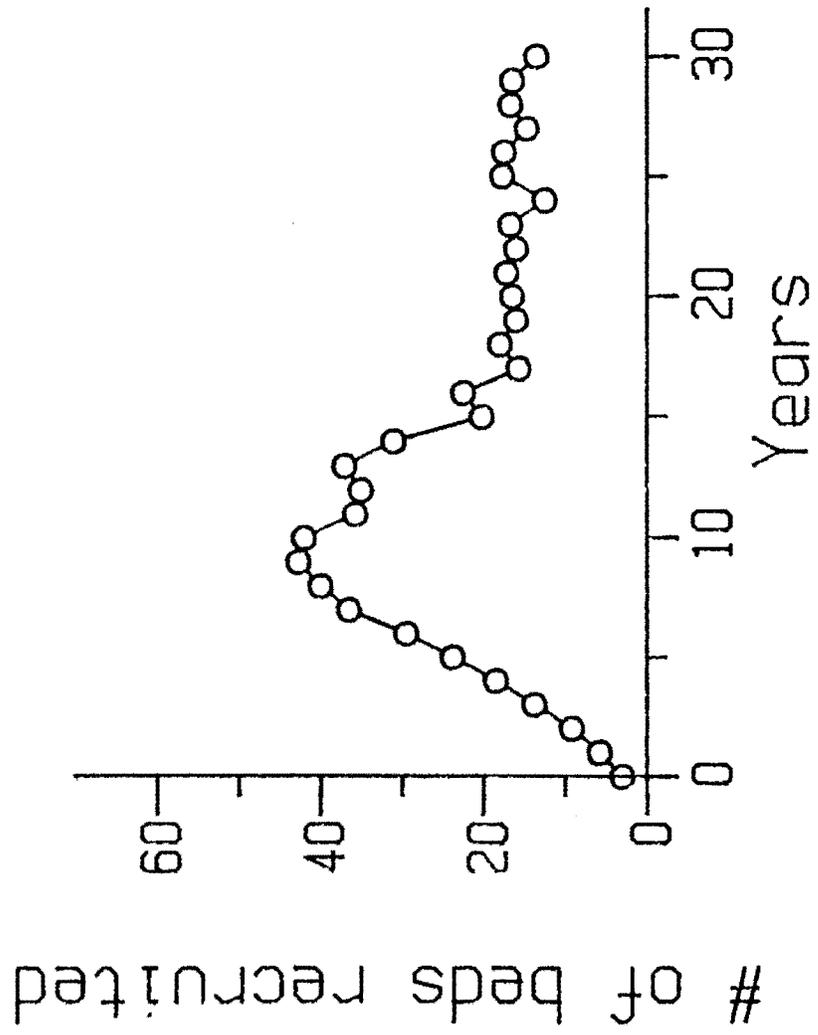
The results of the model suggest that many patterns of colonization observed in the field can be explained by differences in bed lateral expansion rates, new bed recruitment, disturbance size, and per cent of the habitat disturbed each year. For example, a high energy site near Wianno Beach never has ever exceed 40-55% cover, even after many decades. Assuming similar rates of bed recruitment and lateral expansion as the Wianno Beach site, the model results suggest that approximately 20% of the eelgrass habitat is removed each year at this site by large disturbances. At a site in Buzzards Bay (Great Neck, Wareham), peak cover was reached in less than 8 years after initial colonization (Costa, 1987). This phenomenon can only occur if the rates of new bed recruitment were 3 to 4 times higher than observed at Wianno Beach. Thus this model is both heuristic and predictive, and these

hypotheses are testable. This model could also be used to predict eelgrass growth in transplanted areas with known rates of vegetative expansion, recruitment, and disturbance.

The photographic record and model results show that recruitment of new beds greatly enhances the rate of colonization of the area. In the simulation, bed recruitment generally accounted for less than three percent of the cells filled in each year, yet this dispersal could at least halve the time it took to reach peak abundance by vegetative growth alone. Bed recruitment showed its greatest contribution to colonization during midpoint of the colonization when both propagule production and open space are high (Fig.11). The importance of seed dispersal has broad implications because seedlings and seed germination is often the most sensitive stage in a plants life history, and is fundamental for colonizing new habitat. Any disturbance preferentially affecting seedling survival, such as toxic pollutants, or shading effects from enrichment induced algal growth can greatly slow recovery in an area.

The results from the simulation suggest that small disturbances (<5 m²) have little effect on colonization, even when the percent of the habitat disturbed per year is very large (Fig. 8). This suggests that eelgrass beds can accommodate frequent small disturbance such as may occur from animal foraging or shellfishing. This does not mean however that shellfisherman do not have any impact because sizable areas of eelgrass may be removed from heavily fished areas (pers. obser.). Furthermore, shellfishing generates much suspended sediment and releases

Figure 11. Relative contribution of recruitment to colonization during the model run for $R_b=56$, PHD =5.6%, Gr= 0.45 and DS=74.

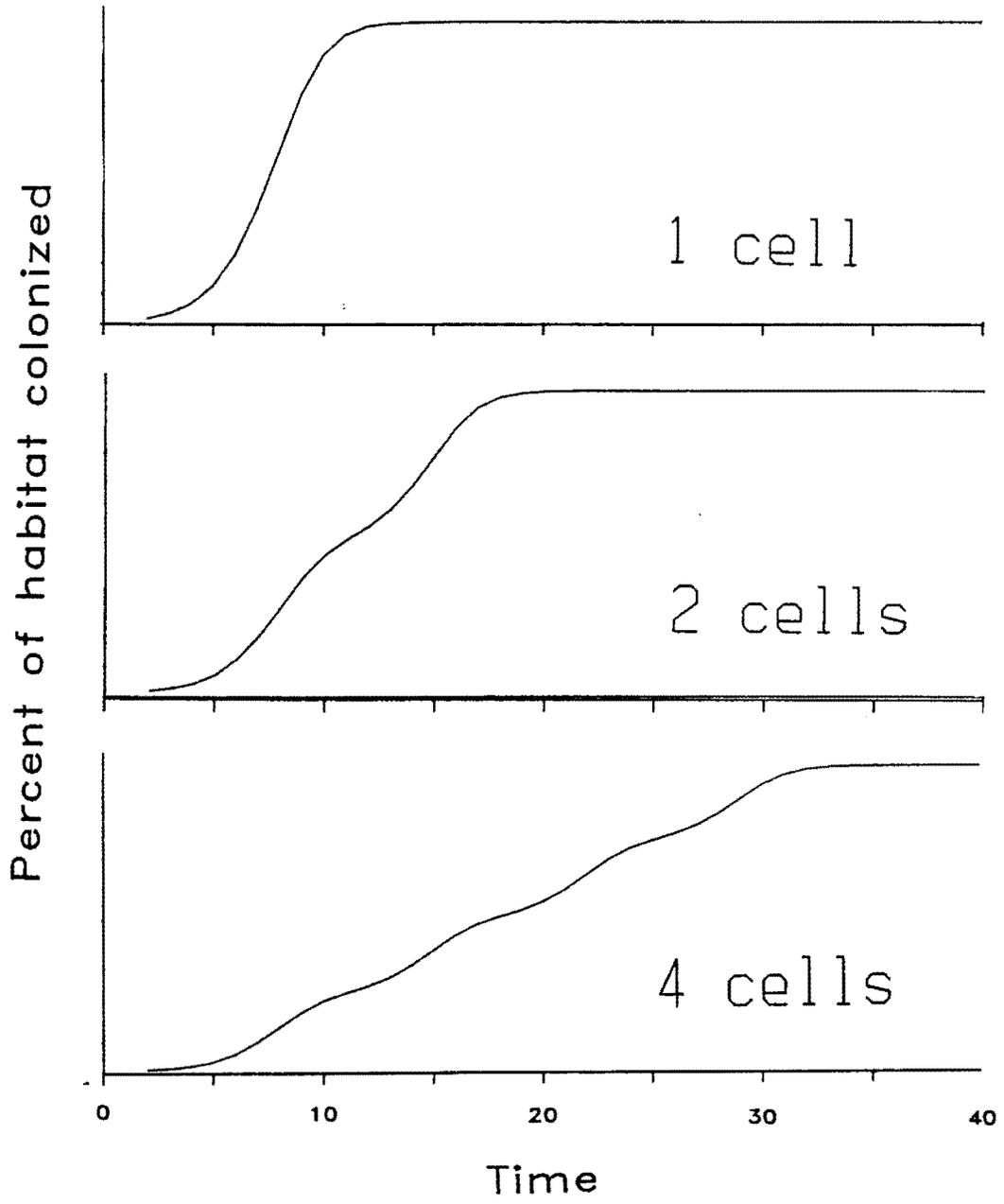


nutrients, both of which will result ultimately decrease light availability, which can lead to loss of eelgrass (see also Costa, 1987).

This model and photograph analysis elucidate the mechanism of colonization, but other patterns of eelgrass colonization such as bed morphology, onset of colonization, and distribution are set by other factors such as large scale disturbances, wave scour, long shore sand transport, sand wave migration, and habitat heterogeneities. Also, the pattern of colonization described here (expanding, recruiting, and merging of distinct beds) is prominent only in more exposed environments, whereas in sheltered shallow bays, eelgrass abundance may show rapid colonization or wide fluctuations in abundance (Costa, 1987). The rapid colonization seen in these shallow protected bays can only be simulated in the model with very high recruitment rates. This may be realistic, however, because beds in these areas are often annuals and show high rates of seed production. In deeper offshore areas, seed production is lower, and seedling survival is also lower because the substrate is unstable. New beds, once established, have higher rates of survival than individual shoots, and this leads to the discrete pattern of colonization observed in exposed areas.

The patterns of colonization modeled here reflect only small scale phenomenon. Colonization of eelgrass over 1000's m is often linear, or shows temporal and spatial stepwise expansion, often set back by catastrophic disturbances (here and Costa, 1987). These results can be explained by the results of another model shown in Fig. 12. In a one "cell" model (a single subsite), a species could show logistic expansion in cover. In an adjoining subsite became colonized only after the first

Figure 12. Comparison of colonization curves of a species with logistic growth in a single cell system (top), in a two cell system (middle) where logistic growth begins in second cell only after 50% cover is achieved in the first cell. The four cell model used the same stepwise colonization process as the two cell module. Increasing designed Relative contribution of recruitment to colonization during the model run for $R_p=56$, PHD =5.6%, Gr= 0.45 and DS=74.



site reached 50% cover, then in a 2 step colonization would occur (2 cell model, Fig 12). By adding more cells, the colonization curve became both increasingly linear, and of longer duration. The onset of colonization depended on the distance of each portion of shore from existing beds (and refuge beds that survived the wasting disease. This phenomenon is visible on many sequences of photographs and explains why eelgrass populations took so many decades to recover from the wasting disease, and why some populations are still expanding today.

Acknowledgments

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