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## The Roles of Dispersal and Predation in Determining the Seedling Recruitment Patterns of a *Zostera marina* System

Stephen R. Manley

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The Roles of Dispersal and Predation in  
Determining the Seedling Recruitment Patterns  
of a *Zostera marina* System

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A Thesis

Presented to

The Faculty of the School of Marine Science  
The College of William and Mary in Virginia

In Partial Fulfillment  
of the Requirements for the Degree of  
Master of Science

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by


Stephen R. Manley

2014

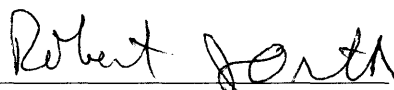
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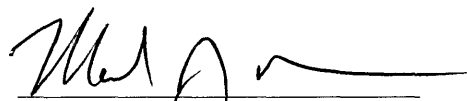
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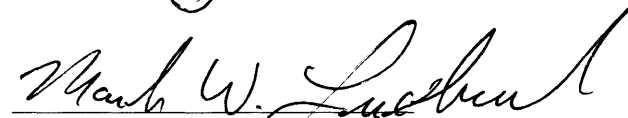
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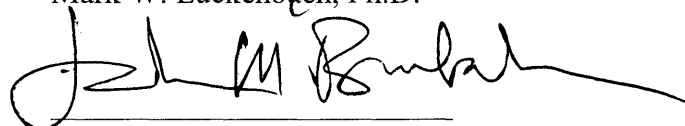
  
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## ABSTRACT

Seed dispersal and seed predation are two important processes in the early life history of plants. The interaction between these two processes influences the population recruitment from a parent plant. These mechanisms have been studied extensively in terrestrial plants and have resulted in various models to describe plant recruitment (e.g. Janzen-Connell, Hubbell, McCanny). However, seed dispersal and predation may also influence the population recruitment of marine angiosperms, such as *Zostera marina* (eelgrass). The objectives of this study were to determine: 1.) the patterns of seed dispersal as a function of distance from the seed source, 2.) the predation pressure on seeds within and outside the parent bed, 3.) the distribution of seedlings as a function of distance from the parent bed, and to test if this distribution corresponds to the seed dispersal and predation pressure, and 4.) how the observed patterns compare with simulated seedling establishment using a model developed by Nathan and Casagrandi (2004).

Seed densities were highest within, and adjacent to, vegetated areas. However, some seeds were found up to 320m from the closest seed source. Seed predation was random throughout the study area; there was no significant difference in predation pressure between vegetated and unvegetated areas. Seedling densities in the spring of 2014 were highly correlated with seed densities found in the previous year, which also suggests that seed predation has a limited impact on population recruitment. The high reproductive output of *Z. marina* as well as the random distribution of seed predators in both vegetated and unvegetated areas may explain how many seeds are able to escape predation.

These results are consistent with the invariant survival model, first described by McCanny, which states that seed predation has no spatial trend. Therefore, a majority of the dispersed seeds remain close to the parent bed, while a small portion of seeds disperse farther from the source. This is the first study of marine angiosperms to address seedling recruitment as a function of dispersal and predation from a parent source and has important implications in recovery and restoration of these systems following disturbances.



The Roles of Dispersal and Predation in Determining the Seedling  
Recruitment Patterns of a *Zostera marina* System

## INTRODUCTION

A number of key processes are involved in successful plant recruitment, including seed dispersal, seed and seedling predation, the availability of “safe sites”, and inter- and intraspecific competition. (Nathan and Casagrandi 2004). Seed dispersal, in particular, can strongly influence the spatial distribution of seedling recruitment and can reduce predation and competition between seeds, seedlings and adult plants, thereby maximizing the offspring’s chance of survival (Howe and Smallwood 1982; Nathan and Muller-Landau 2000). Many plant species have developed a variety of mechanisms that allow their seeds to travel long distances away from the parent plant, and utilize multiple abiotic and biotic vectors to disperse seeds (Nathan 2006).

Seed survivorship is another important process in the early life history of plants, and is influenced by multiple processes, such as the availability of microhabitats, competition, and predation (Nathan and Casagrandi 2004). The interaction between seed dispersal and survival as a function of distance from the parent plant, ultimately determines the seedling recruitment patterns (Nathan and Casagrandi 2004). Seeds that disperse near the parent plant are more likely to encounter conditions favorable to survival, but often have to contend with density dependent seed predation, as a high density of seeds is more likely to attract granivores (Janzen 1970). If the rate of density dependent predation is extremely high, the seeds adjacent to the parent will not survive, despite the presence of favorable conditions for germination, and the likelihood of survival will increase with increasing distance from the parent (Janzen 1970). Therefore, the highest seedling recruitment will occur at an intermediate distance from the parent plant (Janzen 1970; Connell 1971) (Fig. 1a). If the rate of density dependent predation is not high enough to remove all of the seeds closest to the seed source, seedling recruitment will be highest close to the parent, as the seeds are limited more by

dispersal than by predation (Hubbell 1980) (Fig. 1c). In rare cases, the seed survivorship and seed dispersal may change at the same rates, which results in constant seedling establishment rates (Fig. 1b). In some systems, density dependent seed predation may not occur (McCanny 1985), and seed survivorship is a constant value, because predation is random across all distances (Fig. 1d). An alternative model that can happen in the absence of density dependent predation occurs when seed survivorship is highest close to the parent plant, because the seeds are adapted to highly specific microhabitats (McCanny 1985) (Fig. 1e). While all of these recruitment patterns have been shown to occur in terrestrial plants (Nathan and Casagrandi 2004), these models have not been tested in marine plants.

*Zostera marina* (eelgrass) is a marine angiosperm found in temperate regions throughout the northern hemisphere with a high potential for sexual reproduction and seed dispersal (Moore and Short 2006; Kendrick et al. 2012). There are three major abiotic mechanisms involved in seed dispersal: seeds falling to the sediment near the parent plant; individual seeds rafting short distances ( $10^1$  to  $10^2$  m) via gas bubbles (Churchill *et al.* 1985), and; rafting of whole reproductive shoots ( $10^3$  or greater) (Harwell and Orth 2002). Using these varied mechanisms, *Z. marina* has the capacity to disperse seeds within the bed or hundreds of kilometers from the parent plant (Harwell and Orth 2002; Källström *et al.* 2008). *Z. marina* seeds have the ability to disperse over long distances, yet there is very little secondary dispersal, as the seeds settle rapidly and are quickly buried (Orth *et al.* 1994; Blackburn and Orth 2012). While rapid burial is advantageous, burial deep into the sediments has been shown to prevent successful recruitment (Morita *et al.* 2007; Jarvis and Moore 2014). A majority of the seeds released inside of a bed travel less than 5 m from the source (Ruckelshaus 1996). Therefore, the final distribution of seeds may ultimately depend upon the relative frequency with which these varied dispersal mechanisms occur. A recent study using data from the annual, long-term aerial survey of *Z. marina* distribution and abundance in the Chesapeake Bay (Orth *et al.* 2013) found that a majority of new growth occurred within 90 m from the edge of

established *Z. marina* beds and this was hypothesized to be recruitment from seeds (Wilcox, *et al.* unpublished), suggesting that seed recruitment, and thus population growth, decreases with increasing distance from the parent plant.

Once a seed has been successfully dispersed from a parent plant, it must pass through a number of physical and biological ‘sieves’ (Harper 1977) before it recruits into the adult population and can contribute to population growth. These sieves may become more porous with increasing distance from their parent beds. Predation is one process that could contribute to significant seed loss, may vary with seed density and habitat, and would be dependent on the predator’s mobility and capability of detecting seeds when they are buried. Studies have shown a number of fish and invertebrate species found within and outside established *Zostera marina* beds capable of consuming seeds (Wigand and Churchill 1988; Fishman and Orth 1996). Predation may also be responsible for some secondary seed dispersal, as viable seeds are able to pass through some predators, but it is unknown how frequently this may occur (Sumoski and Orth 2012).

While studies have examined seed dispersal and seed predation in *Z. marina*, none have investigated the interaction between dispersal, predation, and the resulting seedling recruitment pattern. The objectives of this study were to determine: 1.) the patterns of seed dispersal as a function of distance from the seed source, 2.) the predation pressure on seeds within and outside the parent bed, 3.) the distribution of seedlings as a function of distance from the parent bed, and to test if this distribution corresponds to the seed dispersal and predation pressure, and 4.) how the observed patterns compare with simulated seedling establishment using a model developed by Nathan and Casagrandi (2004).

## METHODS

### *Study Site*

Seed dispersal and predation experiments were conducted in a *Zostera marina* meadow in Hog Island Bay, a coastal bay on the Delmarva Peninsula, Virginia, USA (37° 25' 2.548" N, 75° 43' 18.635" W) (Fig. 2). Hog Island Bay is part of the Virginia Coast Reserve Long Term Ecological Research Site. This bay had been vegetated prior to the 1930's, when a pandemic resulted in the extirpation of *Z. marina* in this region. Hog Island Bay remained unvegetated until 2006 when a *Z. marina* restoration project was initiated with seeds and continued through 2008 (Orth *et al.* 2012; McGlathery *et al.* 2012). From these initial plantings, the bed has expanded to cover approximately 182.8 hectares in 2012 (Orth *et al.* 2013). This bed is relatively isolated from other *Z. marina* meadows in the region; approximately 8 km from the nearest bed, and separated by marsh islands and a deep channel (Orth *et al.* 2012)

Surveys of adults and seedlings as well as the seed dispersal and seed predation experiments described below were conducted along four pairs of 400 m long by 1 m wide transects, which originated near the boundaries of the bed. This boundary was determined from aerial photography taken in 2012, and each pair of transects were positioned such that they transitioned from the edge of meadow into the unvegetated region. All transects were established in a north-south direction, as this is the predominant direction of tidal flow in this area of Hog Island Bay (J. Rheuban, unpubl. data). Two pairs were located at the north and two at the south end of this bed, and 100 m separated each pair of transects (Fig. 2). Poor visibility resulted in a lack of data along one of the transects, and that transect was removed during the analyses.

### *Seed Production*

Reproductive potential was estimated in May 2013 by assessing the number of reproductive shoots per area and the number of seeds per reproductive shoot within the bed. A minimum of eight 0.17 m<sup>2</sup> cores were haphazardly taken at twenty randomly selected sites throughout the bed. The number of vegetative and reproductive shoots was counted in each core. If no reproductive shoots were found after eight cores were taken, additional cores were taken until at least two cores with reproductive shoots were recorded. A minimum of fifteen reproductive shoots were collected at each site, and the number of seeds per spathe and the number of spathes per shoot were recorded. Seed production at each site was calculated from the number of reproductive shoots m<sup>-2</sup> multiplied by the number of estimated seeds per shoot.

### *Seed, Seedling and Adult Distribution*

Seed distribution was assessed in both the parent bed and outside of the bed. Seeds were sampled in June 2013, immediately following the release and dispersal of all seeds from the parent plants. Eleven of the random sites inside the meadow used to determine seed production were sampled for the presence of dispersed seeds, using sediment cores taken via suction sample. A bar was added near the end of the core to ensure a constant, shallow depth, as viable seeds generally do not occur deep in the sediments (Morita *et al.* 2007; Jarvis and Moore 2014). Thirty random suction cores were taken before the 1 mm mesh collection bag was emptied, and the contents were treated as a single sample. Two of these pooled samples were taken per site, for a total of sixty cores per site.

The same suction sampling method was used along the previously described transects (Fig. 2). All transects were sampled every twenty meters for the first 200 meters, and then every forty meters for an additional 200 meters, for a total of 400 meters per transect. At each site, thirty suction cores were taken per sample perpendicular to each transect, and the thirty cores per site were treated as a single sample. All samples were sieved and the number of seeds, seed coats, and

spathes were recorded in each sample. The seed density survey was completed immediately after seed release and seeds are typically buried rapidly (*Orth et al.* 1994).

The number of seedlings and the percent cover of adult plants were surveyed in May 2013, and April 2014. Divers swam along each transect and recorded the total number of seedlings and percent cover of adult plants every ten meters. Extremely poor visibility prevented divers from recording these data from one of the transects that was not used in the subsequent analyses.

### *Seed Predation*

The spatial distribution of seed predation was measured through the use of predation units. Each unit consisted of a small (10 cm long x 3 cm wide) wooden board containing eight seeds that were secured using insect pins (Size 0). The boards were then anchored to the substrate with metal rebar and large staples. The predation units were placed along the same transects used in the previous studies. However, the transects were extended an additional 100 meters into the bed, in order to compare the amount of seed predation well inside and outside of the *Z. marina* meadow. One seed board was placed every twenty meters for the first 300 meters, and then every forty meters for an additional 160 meters, for a total of 460 meters per transect. The units were deployed August 2013. While this time period is approximately two months after the *Z. marina* seed dispersal event in June, the predator suite in Hog Island Bay is consistent throughout the summer months (R. J. Orth, unpubl. data). The units were deployed and collected after a period of twenty four hours. As dispersed seeds settle and are buried rapidly (*Orth et al.* 1994; Blackburn and Orth 2012), a time period of only 24 hours was considered appropriate. Upon retrieval, the boards were assessed to determine if any pinned seeds were partially or fully eaten.

Laboratory trials were also completed to determine the most likely seed predators, as well as the effectiveness of the seed board method. Four fish species, *Spheroeroides maculatus* (Northern puffer), *Chilomycterus schoepfi* (Striped

burrfish), *Leiostomus xanthurus* (Spot croaker), and *Orthopristis chrysoptera* (Pigfish) as well as the decapod crustacean *Callinectes sapidus* (Blue crab) were collected and placed in 30 gallon aquaria. All of these species are commonly found in the summer months in the Hog Island Bay region. As *C. sapidus* is cannibalistic, a total of four crabs were placed in two separate tanks, while all of the fish were placed in single aquaria by species. The animals were allowed to acclimate for three days and then starved for two days. After the starvation period, a single seed board, created according to the methods previously described, was placed in each aquarium. Unlike the field trials, the seed boards were allowed to remain in the tanks up to five days.

### *Statistical Analysis*

As the true edge of the *Z. marina* bed varied with each transect, it was necessary to numerically define the edge of the meadow. The percent cover of adult plants recorded in 2013 was used to define the edge of the bed by creating an accumulation curve as one moved towards the bed along the transect. The edge of the bed was defined when the percent cover of adult plants doubled within a ten meter span. Each transect was then offset according to the location of the edge. All subsequent analyses were performed according to this edge of bed definition and transect offset.

In order to compare the continuous seedling establishment data to the seed dispersal and predation discrete sampling data, it was also necessary to bin all of the data into forty meter bins and the averages of each distance bin were then compared by distance. The average number of seeds and 2014 seedlings and the percent of seeds eaten during the predation assays were also compared against each other using these forty meter bins. Linear regressions were performed on all of these comparisons. Lastly, a Levene's Test for equality of variance between the forty meter bins was performed on the seed dispersal and 2014 seedling recruitment data.



A spatial autocorrelation test using the Global Moran's I index was used to determine if there was a spatial pattern in the data, as well as determine if there was significant clustering or dispersal of similar values. This test was performed across all transects on the seed dispersal, seed predation, and 2014 seedling recruitment data using the Arc GIS 10.1 spatial statistics toolset. The Euclidean distance coupled with the inverse distance concept was used on all three datasets. The threshold distance was the length of the transects (400 m for seed dispersal and 2014 seedling recruitment, 500 m for seed predation). Row standardization was because data points were already arranged into a pattern along the transects.

### *Theoretical vs. Observed Seedling Establishment*

To elucidate mechanisms controlling our observed seedling recruitment pattern, theoretical survival and subsequent establishment were predicted using the model of Nathan and Casagrandi (2004) under a range of conditions. This model creates a dispersal kernel from seed production and uses it as an input for establishment. It also considers natural mortality and density dependent seed mortality by predation as two separate terms. Their simplified model is as follows:

$$\frac{dS(\rho, t)}{dt} = \phi(\rho) - \omega(S(\rho, t)) - \eta(S(\rho, t), \rho)$$

The density of seeds on the ground ( $S$ ) at a specific distance ( $\rho$ ) over time ( $t$ ) is calculated by subtracting the loss of seeds due to predation ( $\eta$ ) and to other sources of mortality ( $\omega$ ) from the dispersal kernel ( $\phi$ ). The dispersal kernel is the seed density in relation to the distance ( $\rho$ ) from the source, which is calculated with a negative exponential function using the number of seeds that are produced ( $\alpha$ ) and the mean travel distance of the seeds ( $D$ ). Seed mortality is governed by the natural mortality rate ( $\mu$ ), as well as predator activity. Predator activity is the result of the number of predators in the system ( $B$ ), the mean distance the predators are located from the seed source ( $q$ ), the predator searching rate ( $a$ ), and

the handling time of the seeds ( $T_h$ ) by predators. The full model can then be written as:

$$\frac{dS(\rho, t)}{dt} = \frac{2\alpha}{\pi D^2} \exp\left(-\frac{2\rho}{D}\right) - \mu S(\rho, t) - \frac{2B}{\pi q^2} \exp\left(-\frac{2\rho}{q}\right) \frac{aS(\rho, t)}{1 + aT_h S(\rho, t)}$$

In order to calculate theoretical seed dispersal, seed predation, and seedling establishment curves, we followed Nathan and Casagrandi's approach (2004). First we calculated the seed dispersal curve by applying the natural mortality rate over the dispersal kernel ( $\phi/\omega$ ). We then set the left side of this equation to zero, to find the corresponding seed density at equilibrium. This equilibrium condition describes the density of potential seed recruits over distance ( $\bar{S}(\rho)$ ); i.e., the seedling establishment curve (Nathan and Casagrandi 2004). To create the seed survival curve ( $\bar{P}$ ) we used the values at equilibrium to determine the number of seeds that survived predation by calculating the proportion of seeds escaping predation at each given distance ( $\bar{P}(\rho) = \mu\bar{S}(\rho)/\phi(\rho)$ ).

Seed input into the system ( $\alpha=3,000$  seeds/m<sup>2</sup>), was determined from the values found in the seed production survey. Mortality not due to predation ( $\mu = 0.75$ ), the predator searching rate ( $a=25$ ), and handling time by predators ( $T_h=0.005$ ) were estimated based on our understanding of seed dynamics and personal observations. These values were kept constant through all runs of the models. A sensitivity analysis was performed on the mean dispersal distance of the seeds, in order to replicate our dispersal kernel. We found that an average seed dispersal distance of 130 m closely resembled the distribution of seeds in our data.

Due to the diversity of possible seed predators in the system, we ran the model under various conditions. We fixed seed dispersal ( $D=130$ m) and ran the model by increasing the mean foraging distance of predators ( $q$ ) from 5 to 100,000 m, which helped to determine the predation intensity thresholds that would result in different establishment curves. Two mean predator distances were chosen based on these results; a short distance from the source ( $q=50$  m), and a much longer distance ( $q=500$  m). The 500 m distance was greater than the mean

seed dispersal distance ( $D=130\text{m}$ ) but small enough to affect seedling recruitment patterns. Additionally, the number of predators in the system ( $B$ ) was modified to obtain similar ratios of predation pressure per area in a high predator population (60:1) and low predator population (6:1) scenario.

## RESULTS

### *Seed Production*

The average number of seeds produced across all sites (mean  $\pm$  SE) was  $2,796 \pm 259 \text{ m}^{-2}$  (n=19). The average number of reproductive shoots per  $\text{m}^2$  ( $38 \pm 4$ ) was also highly variable. In contrast, the number of spathes per shoot ( $10 \pm 0.4$ ) and number of seeds within each spathe ( $8 \pm 0.1$ ) were not as variable.

### *Seed, Seedling and Adult Plant Distribution*

There was a significant spatial effect on seed and seedling densities ( $p < 0.01$ ), and sites with similar numbers of seeds and seedlings were clustered together ( $z = 18.45$ ,  $z = 29.73$  respectively). The highest seed and seedling densities were found within, or near, vegetated areas (Fig.2). In contrast to seed dispersal and seedling recruitment, there was no spatial autocorrelation in the percent of seeds eaten during the predation assays ( $p = 0.31$ ).

Seeds and seedlings were found along the entirety of the transects, but the mean density of seeds and seedling recruits decreased with increasing distance from inside the bed (Fig. 3). In addition, when grouped into forty meter bins, the average density of seeds and seedlings were highly correlated ( $r^2 = 0.91$ ) (Fig. 4). The density of seeds and seedlings were more variable within vegetated areas, and the variability decreased with increasing distance from the center of the bed. This trend was a result of higher densities within vegetated areas; the variance of seeds was equal within vegetated areas and the variance of seedlings was equal up to 160 m beyond the edge of the bed (Appendix A). However, the unequal variance outside of the bed was due to low densities of seeds and seedlings.

### *Seed Predation*

The average percent of seeds eaten during predation assays showed no spatial trend, both inside and outside the bed, across all forty meter distance bins (Fig. 5). However, predation rate inside of the bed was more variable. In addition, predation rate was not correlated with seed densities or seedling establishment densities.

In the laboratory trials only *Callinectes sapidus* removed and consumed all seeds. While the seeds were eaten within 24 hours in one aquarium, *C. sapidus* in the other aquarium did not eat any seeds until the fourth day. Additionally, *C. sapidus* in the second aquarium were observed actively foraging through sand for alternative food sources, which underscores their role as a generalist predator. *Chilomycterus schoepfi* consumed a single seed within hours of the introduction of the seed board. However, the remaining seeds were never eaten. The other fish species (*Spheroeroides maculatus*, *Leiostomus xanthurus*, and *Orthopristis chrysoptera*) did not consume any seeds.

### *Theoretical Seedling Establishment*

Four scenarios were generated using our data and the model created by Nathan and Casagrandi (2004). The first two scenarios (Fig. 6a,b) would occur if the average distance between the seed predators and seed source is small (50m). This results in an intermediate seedling recruitment maximum, as seed survivorship suddenly increases near the seed source. The magnitude of the seedling establishment maximum is dependent on the number of predators in the system; smaller numbers of predators (Fig. 6b) allow for a higher seedling recruitment maximum when compared to a system with more numerous predators (Fig. 6a).

The other two models would occur in systems where the average distance between the predators and seed source is greater than the mean dispersal distance (Fig. 6c,d). In these models, the seedling establishment is highest near the seed source and decrease with increasing distance. The number of predators in the

system appears to have a greater impact on seed survivorship close to the seed source; systems with more predators (Fig. 6c) have significantly lower survival rates near the parent bed when compared to systems with fewer predators (Fig. 6d).

## DISCUSSION

### *Population Recruitment Model*

The results of the twenty four hour predation assays show that there was no relation between seed grazing and distance from bed edge, and the distribution of predation events was spatially random. The random distribution of predation events suggests that predators in this system are highly mobile, and are not always associated with *Zostera marina*. Additionally, the high correlation between seeds and seedlings, and not predation (Fig. 4), suggests that seed predators are not attracted to areas of high seed densities.

While the constant rate of predation suggests the absence of density dependent predation, it is also possible that seed predators are overwhelmed by the sudden influx of seeds from *Zostera marina*. The predation rate can appear to be constant across all distances if the plant is highly fecund (Nathan and Casagrandi 2004). The Hog Island Bay *Z. marina* bed has a high reproductive potential ( $2,796 \pm 259$  seeds/m<sup>2</sup>), which may overwhelm predators, allowing many of the seeds near the adult plants to escape density dependent predation. Additionally, many predators in the Hog Island Bay system are not exclusively granivorous and are not restricted to seagrass but forage over both unvegetated bottom as well *Z. marina* beds, albeit they are generally more abundant in seagrass (Orth and Heck 1980). While fish such as *Chilomycterus schoepfi* were able to eat seeds from the predation units in the laboratory trials, the major predators in this system appear to be decapods which are both omnivorous and generalists, such as *Callinectes sapidus*. Therefore, these predators may consume fewer seeds than exclusively granivorous animals. Finally, the high correlation between seeds and seedlings indicates that secondary dispersal, either physically (Orth *et al.* 1994) or biologically (Sumoski and Orth 2012) mediated, does not significantly alter seedling recruitment patterns. Therefore, predation does not

appear to significantly impact *Z. marina* seedling recruitment in the Hog Island Bay system.

These predation patterns are consistent with the invariant survival model (McCanny 1985) (Fig. 1d,8). While this strategy is often regarded as a transition between plants that experience seed predation and those that do not, it can occur in systems with granivores, if predator satiation is very high across all distances (Nathan and Casagrandi 2004). While this pattern has been shown to occur in a limited number of terrestrial plant species (McCanny 1985, McCanny and Cavers 1987, Notman *et al.* 1996), it is also considered to be the null hypothesis when testing if seed dispersal confers an advantage to the parent plant (Howe and Smallwood 1982). Therefore, if *Zostera marina* does in fact follow the invariant survival model, predation may not play a significant role in determining the spatial distribution of seedlings.

While predation does not appear to significantly affect seedling recruitment patterns in Hog Island Bay, other processes may still impact seed survival and seedling establishment. Seed and seedling densities were more similar near the bed edge when compared to the difference in densities found within vegetated areas (Fig. 3). This suggests that it may be advantageous for seeds to disperse into unvegetated areas, but still remain close to the parent bed. In this region, seedling survival is often limited by sediment disturbance, which is most severe during winter storm events (Marion and Orth 2012). The close proximity of adult plants can attenuate wave energy and stabilize sediments (Hansen and Reidenbach 2012). This positive feedback can occur within the parent bed as well, but seedlings under the adult canopy may not be able to successfully compete for light (Olesen 1999). The lack of competition, coupled with the reduction in sediment resuspension, may explain why seeds at the bed edge appear to have a higher rate of survival.

A second explanation for this pattern may be seed burial by infauna. Infauna have been shown to bury seeds rapidly and sometimes to depths that prevent successful recruitment (Valdemarsen *et al.* 2011; Blackburn and Orth



2013). Infauna are generally more abundant in vegetated areas (Orth 1977) which could result in a higher proportion of deeply buried seeds in vegetated areas, preventing successful seedling recruitment.

If the close proximity of adult plants to the dispersed seeds does increase the chances of survival, then the McCanny model may be a more appropriate model. This model occurs when seed survival is highest near the parent plant because density dependent predation does not have a significant impact on seedling establishment, and the environmental conditions near the parent plant are more favorable for seedling survival (Nathan and Casagrandi 2004). However, our data show the lowest survival rate was within vegetated areas (Fig 3). Therefore, while adult plants may be able to protect seeds from storm events, it is unknown how important this effect is to seedling establishment patterns on a system-wide scale. Further investigation into the role that parent plants may play in mitigating the deleterious effects of sediment resuspension is needed in order to determine if the McCanny model is more appropriate. Additionally, as this was the first study to investigate population recruitment models for a marine angiosperm, and *Z. marina* inhabits a variety of systems across broad latitudinal and longitudinal gradients, it is unknown if other populations of *Z. marina* have similar dispersal, predation, and recruitment patterns. This study was completed in only one year; multi-year sampling may be necessary in order to confirm if these dispersal, predation, and recruitment patterns are temporally consistent.

#### *Theoretical Implications*

The four theoretical scenarios generated using Nathan and Casagrandi's model (2004) underscore the importance of predator location and population size to plant population recruitment models. If predators are mostly located close to the seed source, significant predation within and near the parent bed is likely to occur (Fig. 6a,b), but if predators are located far from the seed source, seedling establishment will be highest near the seed source (Fig. 6c,d). The full model of our data (Fig. 7) is more similar to the scenarios that assume a long distance between seed predators and the seed source (Fig. 6c,d), as seedling establishment

was highest within vegetated areas. Of these two models, our data appear to be more similar to the model with fewer total predators (Fig. 6d), as the seed survivorship curve is more similar to the invariant survival model. Interestingly, the model with higher predator density (Fig. 6c) is very similar to the Hubbell model (Fig. 1c). The Hubbell model occurs when density dependent predation occurs near the seed source, but the high reproductive potential of the parent plant allows for many of the seeds to survive, and the highest seedling establishment is near the adult plant. This suggests that density dependent seed predation could occur in the Hog Island Bay system if there are large numbers of seed predators. The population of *Callinectes sapidus*, one of the most important predators in this system, was significantly lower in 2013 (R. J. Orth, unpubl. data). Therefore, in years with a higher abundance of *C. sapidus*, seed predation may become more important in determining the seedling recruitment patterns of *Zostera marina* in Hog Island Bay.

#### *Implications for Recovery and Restoration*

Our data on seed densities and seedling recruitment suggests that on a system-wide scale, a majority of seeds appear to remain and successfully establish within, or near, the parent population (Fig. 7), which is consistent with many studies on terrestrial seed dispersal (Nathan and Casagrandi 2004). The occurrence of a majority of seeds inside the parent bed has important implications for recovery dynamics following disturbances that may result in loss of the adult plants. Plus et al. (2003) and Greve et al. (2005) observed rapid recovery of *Zostera marina* beds that had died back from severe anoxic events in France and Denmark, respectively, primarily from seeds. Moore and Jarvis (2010) also recorded rapid recovery from seeds of *Z. marina* beds in the United States that died back from temperature induced stress. Lee et al. (2007) noted recovery of *Z. marina* beds from seeds in Korea, after the adult plants had died from a red tide. Rapid recovery from seeds following disturbance has been observed in other systems as well, such as temperate grasslands (Lavorel 1999). Thus the presence

of seeds in a seed bank (Orth et al 2000) is of fundamental importance to the natural recovery of beds during disturbance events.

Seagrass restoration efforts have been ongoing since the 1970s although there has been a significant increase in the last two decades with most projects utilizing adult plants in small plots (Paling et al 2009; van Katwijk unpublished). As seagrasses are clonal plants and spread laterally via rhizome elongation many projects account for spread via vegetative propagation (Leschen *et al.* 2009) and do not take into account sexual propagation and the production and subsequent seed dispersal characteristics to enhance the spread of planted plots. Rhizome elongation rates depend on individual species and range from mm to  $\text{m yr}^{-1}$  (Duarte et al. 2006). However, seed dispersal distances can be m to  $\text{km yr}^{-1}$  (Kendrick et al. 2012). The average rhizome elongation rate for *Zostera marina* is  $26 \text{ cm yr}^{-1}$  while seed dispersal distances depend on how seeds are dispersed but ranges from cm to km (Orth et al. 1994; Harwell and Orth 2002; Kendrick et al. 2012). Thus, understanding seed dispersal characteristics and dispersal distances of species used in restoration projects can influence the spatial arrangement and size of individual plots to maximize spread and filling in between plots. Our data on seed dispersal distances from an established bed offers additional evidence that the rapid success of a large-scale seed based *Z. marina* restoration in Virginia, USA, was, in part, due to the restoration design. Seeds were planted in forty two 0.4 ha plots in 2001 and 2002, many that were placed 100 m from each other (Orth *et al* 2012). By 2010, areas between these plots had completely filled in with *Z. marina*. Without seeds, rhizome elongation alone would take over a century to infill these plots, yet this occurred in less than a decade. Our data showing seed abundances from the Hog Island Bay bed occurring predominantly within 200 m of the edge offer direct evidence on how seeds facilitated the rapid infilling and that the original design of that project could have placed plots 200 m from each other and would have achieved similar results.

### *Conclusions*

Seed dispersal, and not predation, appears to predominantly determine the spatial distribution of *Zostera marina* seedlings in the Hog Island Bay system. While *Z. marina* has the capacity to disperse seeds hundreds of kilometers from a parent plant, the majority of seed dispersal and subsequent seedling recruitment occurs near the source. This population recruitment strategy may be the result of the high reproductive potential of *Zostera marina* and a lack of specific seed predators, which allows seeds to escape density dependent predation (Orth et al. 2003). As seeds most likely do not experience density dependent predation in this system, seedling recruitment is highest within, and near, the parent bed. The absence of density dependent seed predation has important implications for restoration efforts, and supports the observations of bed expansion from the edge in nearby Chesapeake Bay populations, as well as the hypothesis that this growth was primarily due to recruitment from seeds (Wilcox, *et al.* unpublished). The high reproductive potential, coupled with the patterns of seed dispersal, seed predation, and seedling recruitment, provide *Z. marina* the capacity to quickly recover from disturbance events as well as expand the bed edge into areas that historically supported populations of *Z. marina*.

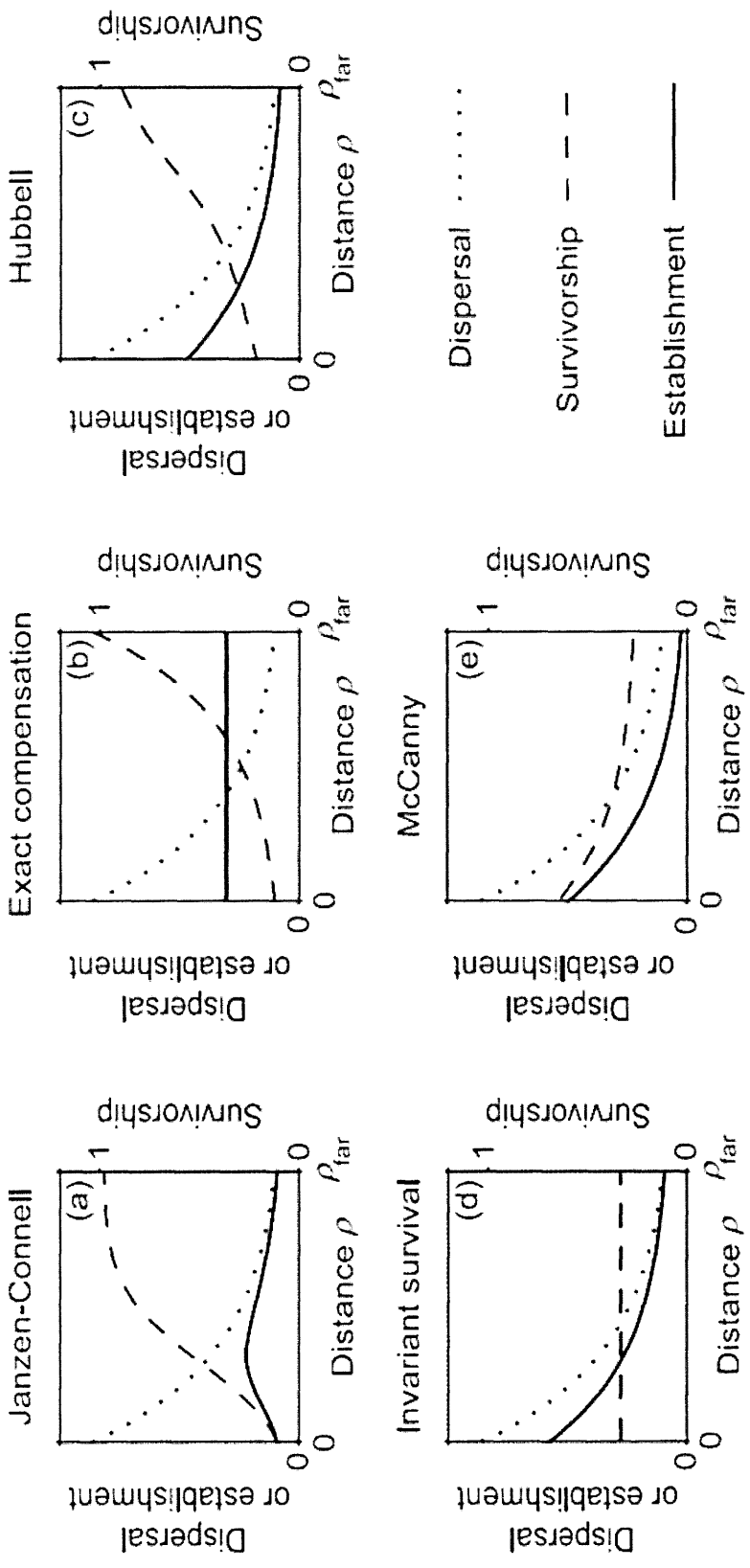


Figure 1: A reproduction of McCanny's five population recruitment models that use seed dispersal and seed survival to describe seedling establishment (1985). The models are: (a) Janzen-Connell, (b) Exact Compensation, (c) Hubbell, (d) Invariant Survival, and (e) McCanny. Reprinted with permission from Nathan and Casagrandi (2004).

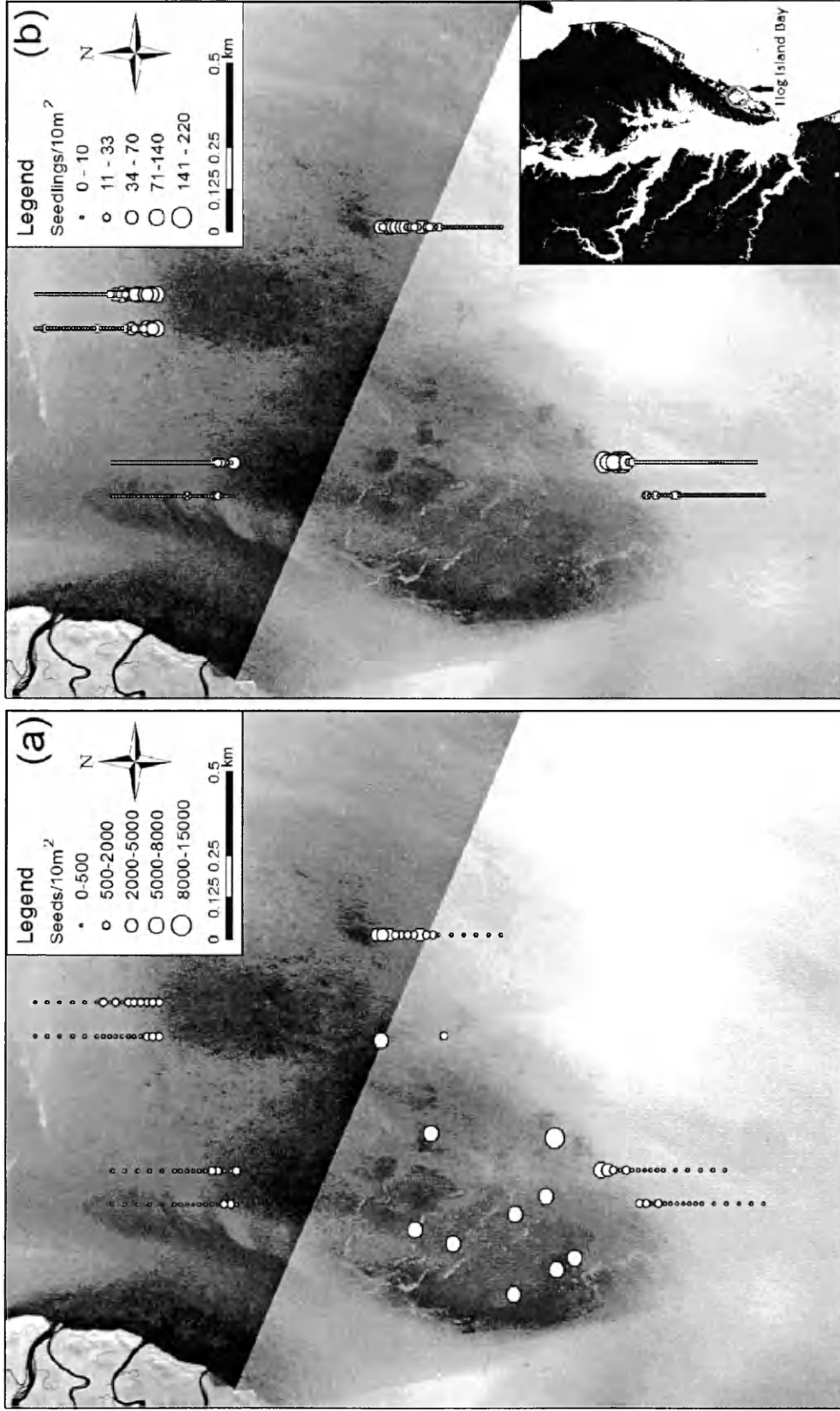


Figure 2: A map of the *Zostera marina* bed in Hog Island Bay with (a) the density of seeds/10m<sup>2</sup> and (b) seedlings/10m<sup>2</sup> across all sites. Each black dot represents a single site, and the size of the dot indicates the relative proportion of seeds or seedling densities found at that site.

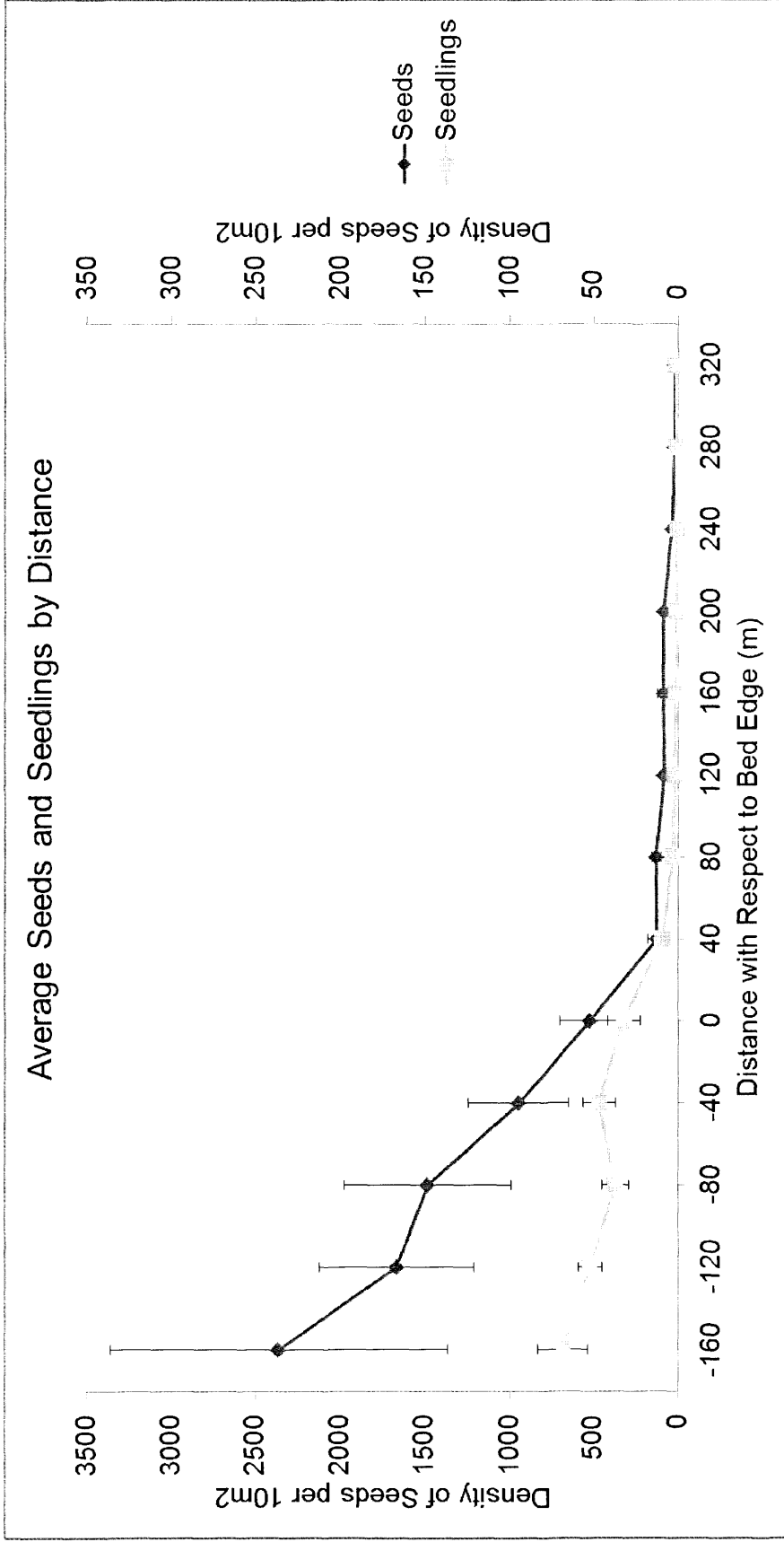


Figure 3: The average density of seeds/10m<sup>2</sup> on the left axis and the density of seedlings/10m<sup>2</sup> on the right axis across all transects. The data were aligned according to the edge of bed in each transect, and the data were grouped into bins of 40 m. Standard error bars within each bin are also shown.

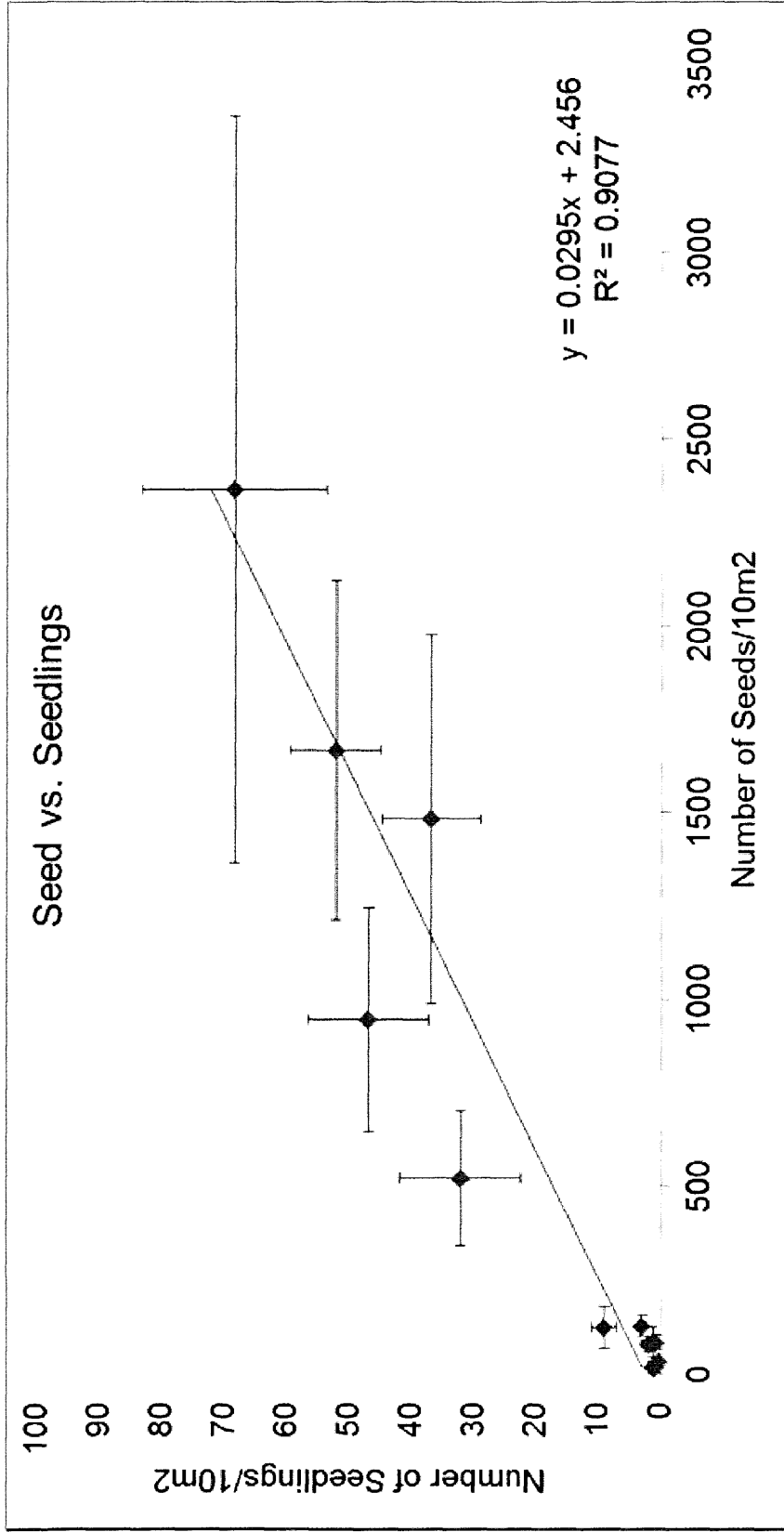


Figure 4: The correlation between the average densities by distance of seeds and seedlings. A linear regression line and equation is shown in each panel. Standard error is also shown.



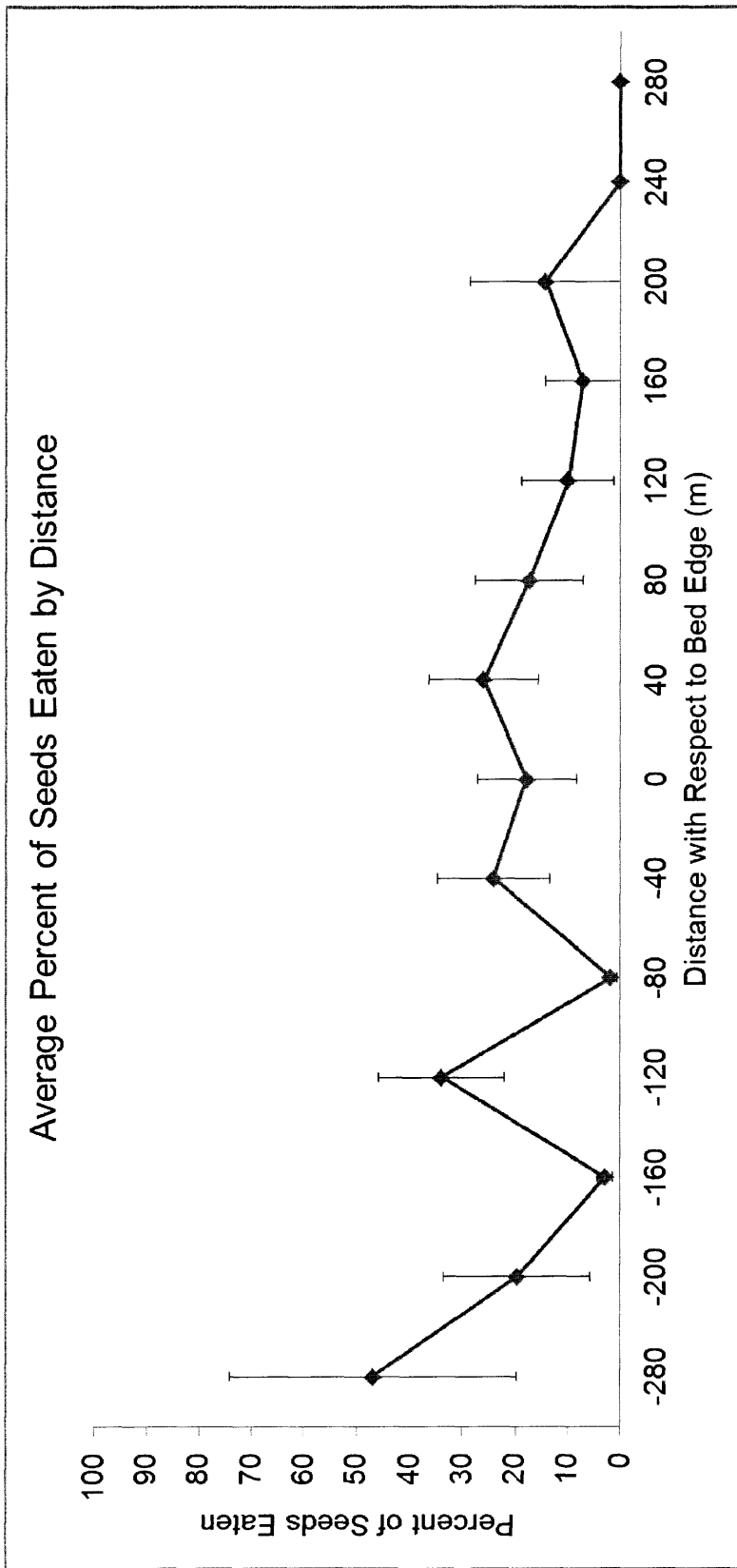


Figure 5: The average percent of seeds eaten during the predation assays. The data are grouped into 40 m bins, and the bars show the standard error within each bin.

Figure 6: The four scenarios generated using the model first described by Nathan and Casagrandi (2004). Seed dispersal and establishment are on the left axis and seed survivorship is on the right axis. The average seed dispersal is held constant while the average distance of predators from seed source ( $q$ ) and the number of predators in the system ( $B$ ) vary. The scenarios are: (a) short distance between predators and seed source with a 60:1 density, (b) short distance between predators and seed source with a 6:1 density, (c) long distance between predators and seed source with a 60:1 density, and (d) long distance between predators and seed source with a 6:1 density.

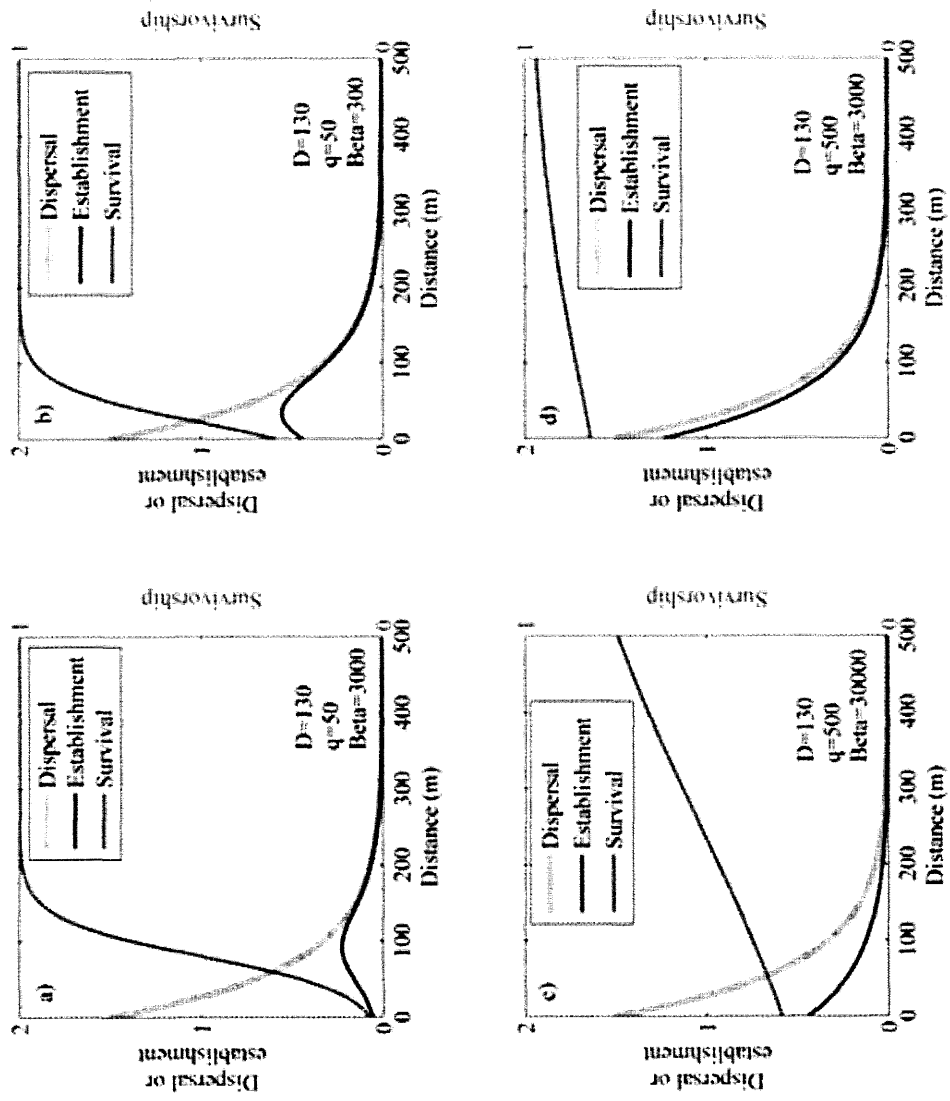


Figure 6

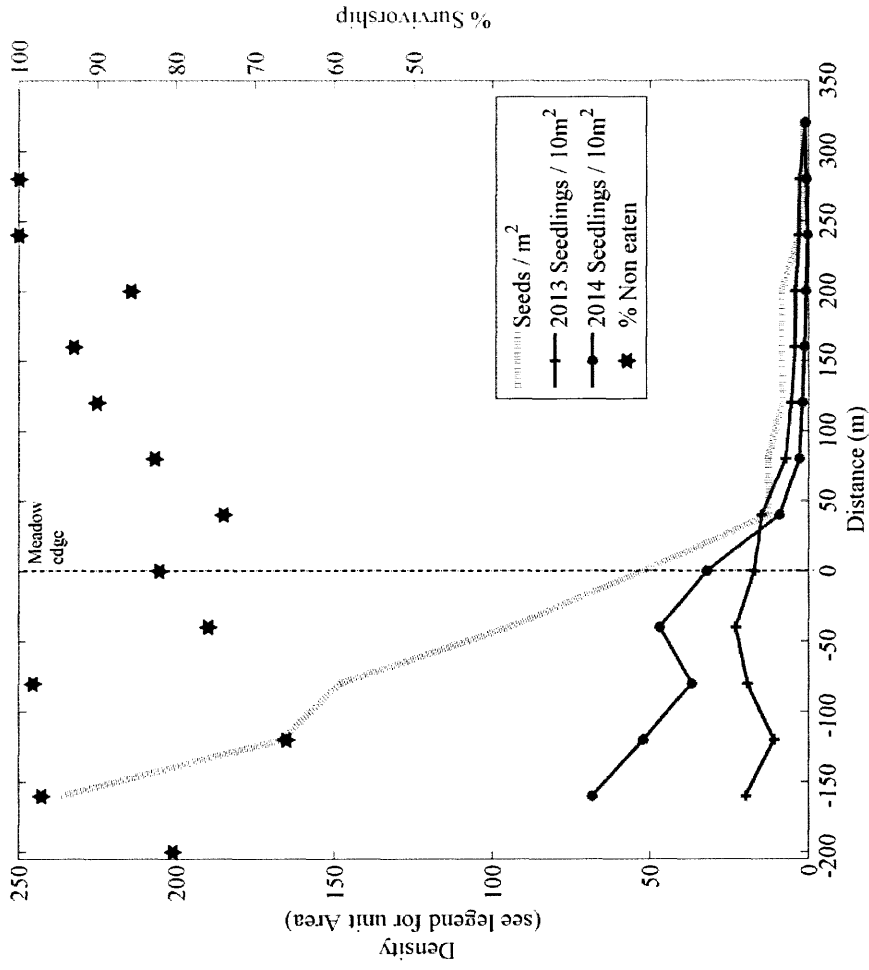


Figure 7: All data compiled into a single model. Seed densities from 2013 and seedling densities from 2013 and 2014 are on the left axis. Seed escape from predation is on the right axis. The dashed line indicates the edge of the bed. All data are grouped into the 40 m bins.

## **Appendix A**

Figure A: The distribution of Levene's statistics of the density of seeds (A. 1) and 2014 seedlings (A. 2) found all sites. The bold line denotes the median Levene's statistic within each 40 m bin. The box encloses the 25<sup>th</sup> and 75<sup>th</sup> percentile and the dashed lines show the range. Open circles are outliers.

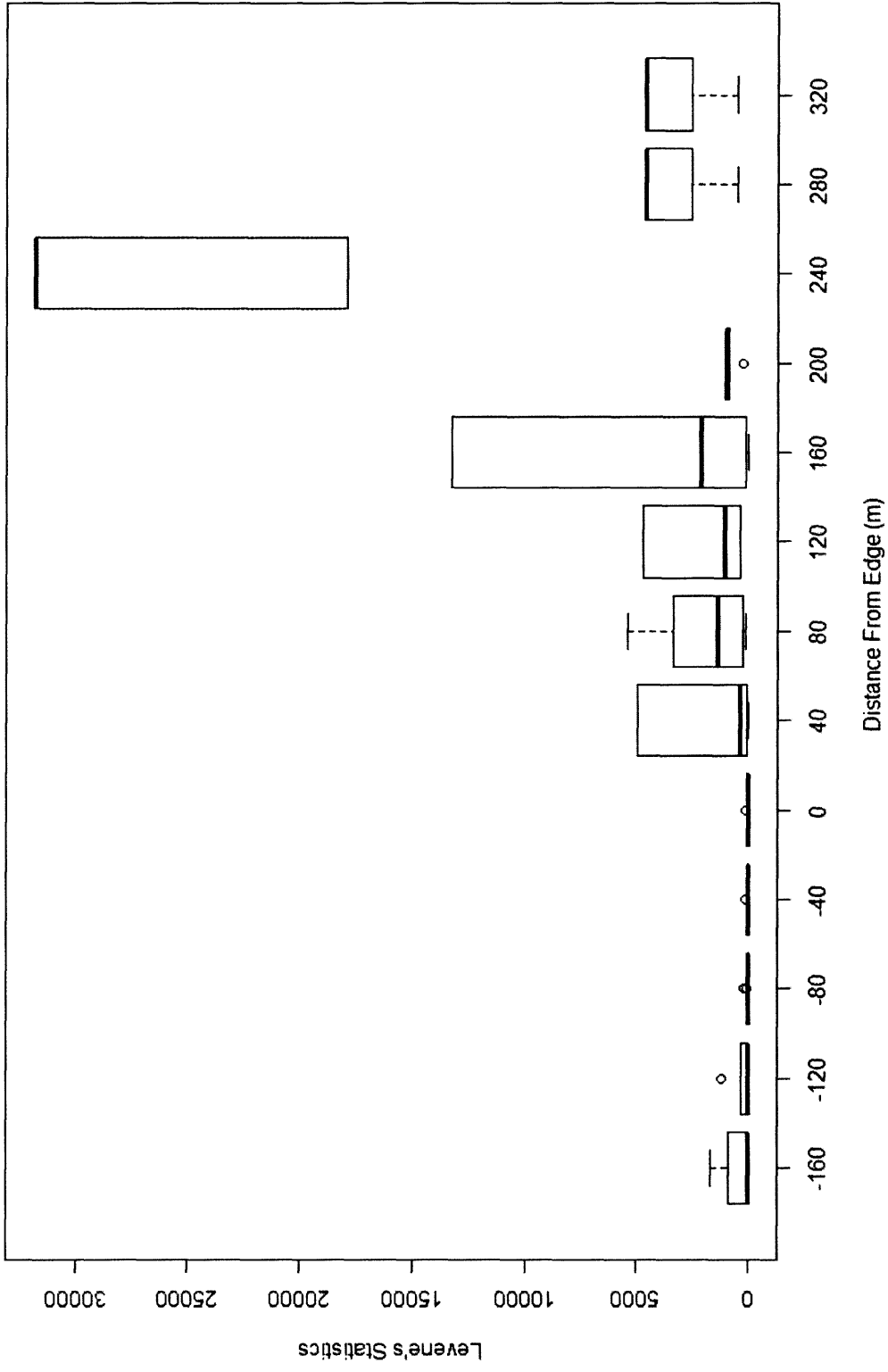


Figure A. 1

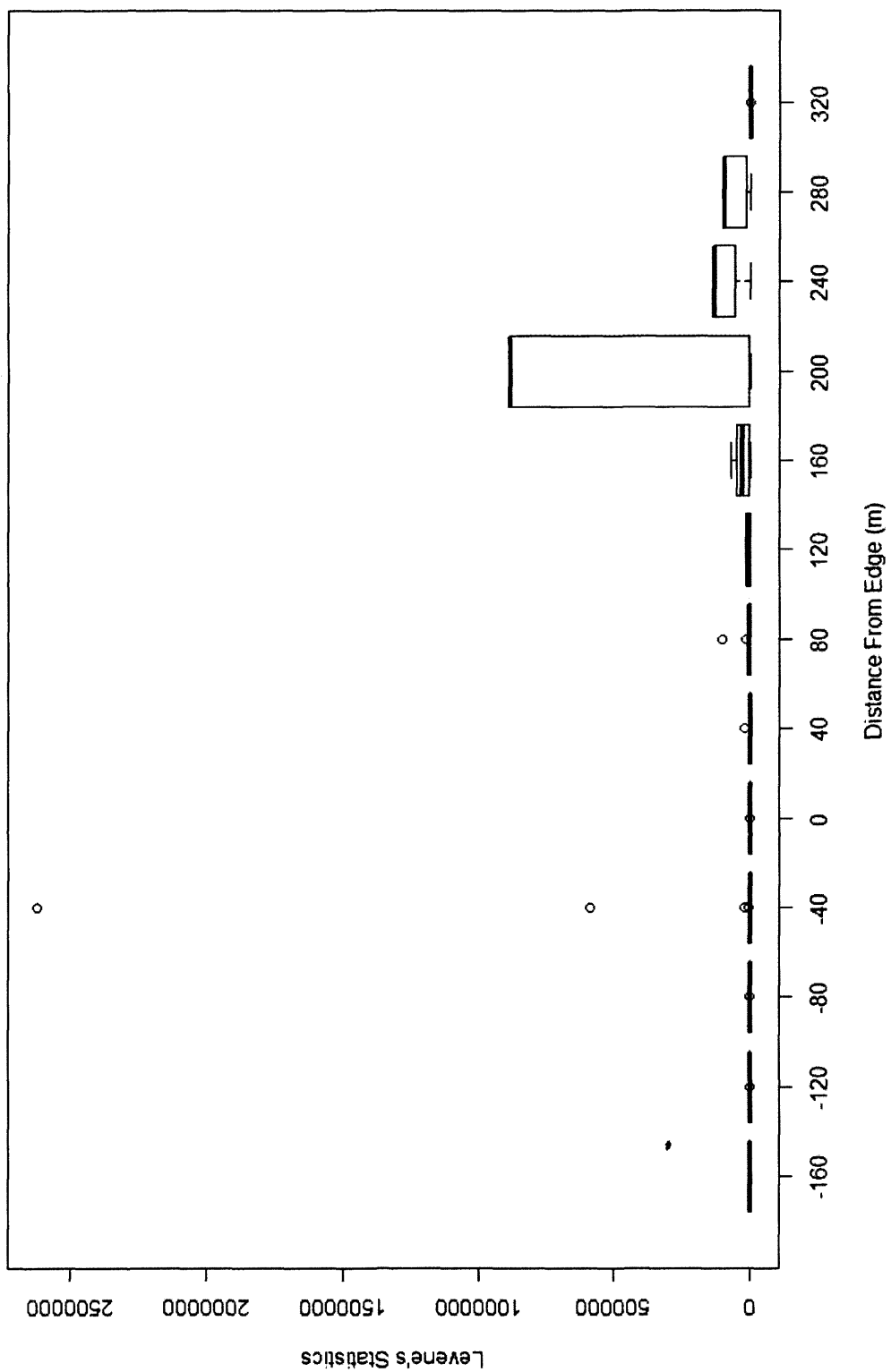


Figure A. 2

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