Mathematical Model for the Dispersal of the Leaf Beetle, *Diorhabda elongata*, from the Old World Released in the United States for Biological Control of Invasive Saltcedar

TSSWCB Project # 04-15

FINAL REPORT

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EXECUTIVE SUMMARY

The project on biological control of exotic, invasive saltcedar by introduced, host-specific leaf beetles from Asia has become highly successful. The beetles are spreading and rapidly defoliating saltcedars along 100 miles and more along rivers in Nevada, Utah and Colorado, in ways that are expected to increase water supplies, improve wildlife habitat, and augment management programs in various ways. A great need exists for a method of predicting the time of arrival of the beetles and of saltcedar biomass and stand reduction at areas where management practices will need to be adapted to the newly changed ecosystems. This project seeks to use mathematical/statistical models, based on data collected from the field at the beginning of a beetle release along Beals Creek east of Big Spring, Texas over a 4-year period, where the beetles are annually spreading and defoliating saltcedar at a rapidly increasing rate. Data collection began in June 2005, a year after beetles were released in April 2004, while populations were still low, and defoliation had not begun. The study continued for another 3 years through 2007, as the beetles spread for 7 km along the creek. This has been a unique opportunity to document, analyze and model a biological control of weeds project including control insect (beetle) population increase and dispersal rate from the beginning of the introduction.

Since very little information exists on this type of modeling, and much of that only for insect dispersal in annual crops, the strategy was to test some of the most appropriate models, modify them as appropriate, and also to discover the factors that most influenced the rate of dispersal, using data collected weekly or biweekly from the Big Spring release site. The monitoring data was collected with unprecedented detail and scope and could provide the behavioral and ecological explanations that influence beetle dispersal.

During the first year, various on-site physical factors were analyzed and eliminated that might determine the rate and direction of dispersal. Temperature (standard taken at the weather station, at 2-3 m high within the saltcedar trees, and under litter below the trees), humidity, rainfall, wind speed and direction, and solar radiation appeared to have no effect – the only important factors influencing direction of dispersal were availability of green biomass and the spacial distribution of the saltcedar trees, measured in terms of time and distance dispersal of the beetles in the trees from the release point.

The **Okuda model** was discarded early because some of the required parameters could not be obtained and runs of the model using the field data did not resemble the population waves observed at the site. The **Kovalev model** well represented population waves over distance from monthly average counts and could be used to estimate dispersal speed and relative proportion of the area covered month to month. However, the model was completely deterministic and too inflexible to represent the high variability resulting from the many biotic and abiotic factors seen in the field.

The **spatial regression model** acceptably predicted the magnitude of beetle populations and how far they spread during a growing season. This model could accommodate all the data and all the variable characteristics of the insect populations in the natural environment. The model was able to describe generation peaks and dates of occurrence of adults and larvae during the season, in 2005 describing 4 larval generations (2 of them partially overlapping) with peaks from 400 up to 40,000 (averaging 200 to 1800) larvae per 16 m^2 quadrat. Adult populations were up to 25,000 and averaged 100 to 1400, per quadrat and, spread outward in 6 waves over 130 m, that advanced about 40 m per month. During 2006, the populations were greater and dispersal farther. The beetles soon consumed most of the food, forcing them to fly farther and start satellite colonies at ca. 500 m out.

In 2007-2008, the beetles spread up and down Beals Creek for 12 km, including a large satellite population on each end. The beetles spread outward in successive waves of adults, then larvae. Peak adult and larval populations were recorded within 1 km upstream and downstream of the creek nearest the release site/population center. The models accurately represented the populations, outward spreading waves, and speed of dispersal.

INTRODUCTION

Saltcedars (*Tamarix* spp.), exotic small trees or shrubs native in the deserts of Asia and the Mediterranean area, were introduced into the United States beginning in 1823 as ornamentals and later to prevent stream bank erosion. The trees spread rapidly along streams and reservoirs of the western U.S. and since the 1920's have come to dominate the native riparian ecosystems where it is causing one of the worst ecological disasters in the recorded history of this region. The invasion includes all of the rivers in the western half of Texas. The United States Department of Agriculture, Agricultural Research Service (USDA-ARS) located at the Grassland, Soil and Water Research Laboratory, Temple, Texas, began the program on biological control of saltcedar in 1986, led by C. Jack DeLoach. After extensive literature reviews, U.S. surveys, overseas explorations, and risk analyses, the leaf beetle, *Diorhabda elongate*, was collected by DeLoach and his overseas collaborators from Fukang, China and Chilik, Kazakhstan in 1992-1998, brought into the ARS Insect Quarantine Facility at Temple, TX where its host specificity, biology and behavior was further tested and Regulatory Approvals were obtained from USDA-APHIS, USDI-Fish and Wildlife Service and State Departments of Agriculture. In collaboration with other ARS scientists, other USDA and federal agencies, State agencies and University scientists, these beetles were released in outdoor cages at 10 sites in 6 western states during July 1999 and into the open environment at the same sites in May 2001. They have achieved spectacular success in biological control of saltcedar at 4 of 6 sites in NV, UT, CO and WY but were not adapted to more southern climates and did not overwinter or establish at the 4 sites south of the 37th parallel in CA and TX.

The first releases of the Crete beetles were by DeLoach's team in the summer of 2003, at Lake Thomas and Beals Creek in Texas, assisted by Okla Thornton (Colorado River Municipal Water District, Big Spring, TX). Later, Texas Agrilife Research and Extension assisted in establishing and monitoring the beetles in the upper Colorado River watershed near Big Spring (Allen Knutson, Dallas), the Pecos River (Knutson and Mark Muegge), the Canadian River (Gerry Michels, Bushland); the Rio Grande of western Texas (Tyrus Fain, Rio Grande Institute, Marathon, TX and Mark Donet, NRCS, Alpine, TX) and Balmorhea (Donet and Chris Casaday, NRCS, Balmorhea), Matador Wildlife Management Area (Chip Ruthven and Mike Janis, TPWD) and Seymour (Charles Randal and others, USDA-APHIS, Olney, TX).

This modeling project collected data during the growing seasons of 2005, 2006, 2007, and 2008 to pursue the following objectives:

- To use mathematical and statistical models to study the dispersal of *Diorhabda* in the initial stages of colonization in a *Tamarix* community,
- To identify temporal and spatial patterns of the *Diorhabda* dispersal, and to estimate the speed of the dispersal, and
- To identify factors that affect the dispersal of *Diorhabda* in a new area of colonization.

MODELING METHODOLOGIES

Two types of modeling strategies were used to study the dispersal of *Diorhabda* in *Tamarix* communities during the initial establishment stages of the insect in the geographical area where it has been introduced. The first type of methodologies are physically based deterministic models that use the principle of diffusion to represent the movement of insect populations from areas of high population to others of lower population, and the second type are statistical models that combine a deterministic component with a stochastic component. The statistical models are spatial regression models that predict the movement of the insect population using predictor variables such as distance from the release point or from a population focus, and properties of the vegetation and other environmental characteristics of the area being colonized by the insect.

Dispersion of many insects in nature resemble the physical phenomenon of diffusion. This can be represented mathematically by partial differential equations that describe changes of insect population with respect to space and time variables. A key element in those equations is a term equivalent to the diffusion coefficient. Kovalev and Vechernin (1986) developed and applied an Isolated Population Wave (IPW) model that represents a wave movement similar to that followed by fire in a prairie; they used the model to study the dispersion of the ragweed beetle *Zygogramma suturalis* F. which is used to control ragweed *Ambrosia artemisiifolia* L. in Russia. A similar model initially developed by Okudo (1980) was used by Smith, et al. (2001) in forests to study the dispersal of *Anoplophora glabripennis* (Cerambycidae) which is a pest of many hardwood trees like maple and poplar. This second model was designed to be used with marked and recaptured insects but can be adapted to work with the whole insect population if the disappearance coefficient δ is changed to an appearance-disappearance coefficient; such a coefficient can be estimated experimentally in the field and/or laboratory. Another parameter required to adapt the model to work with the entire insect population is the original beetle population n_0 at the beginning of the growing season.

One limitation of the physical models like those described above is the lack of biological explanation for the diffusion coefficient and other parameters, in other words, the physical models are able to describe the dispersal of insects but do not tell us why they disperse or what are the biotic or abiotic factors that move the insect population to colonize an area. The two physical models will be used together with a spatial regression model (Neter, et. al., 1989). Both the diffusion models and the spatial regression model will estimate the insect population variation during the growing season, and estimate how far the insect will reach during each growing season. Another possible use of spatial regression model is to identify biotic or abiotic factors associated with the insect dispersal. The same basic data of counts of eggs, larvae and adults made every week at quadrats along the transects is used for the physical and statistical models.

Additional variables that will be measured at each quadrat or transect point for the statistical model will be saltcedar biomass, under canopy temperature, and solar radiation.

Descriptions of the models follow:

A. Okudo's Diffusion Model
The diffusion model used by Smith, et. al. (2001) was originally developed by Okudo (1980), it has been tested in studies by Shigesada and Kawasaki (1997) and by Turchin (1997). It is based in the following differential equation:

$$\frac{\partial n}{\partial t} = D\left(\frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2}\right) = D\left(\frac{\partial^2 n}{\partial r^2} + \frac{1}{r}\frac{\partial n}{\partial r}\right) \qquad [1]$$

Where n is the number of beetles per unit of area or tree, t is time in weeks, D is the diffusion coefficient, x and y are spatial coordinates. The spatial coordinates can be transformed to radial distance using the expression $r = \sqrt{x^2 + y^2}$

The diffusion coefficient determines the rate at which the beetles move, which may change with the direction of movement, the distribution of saltcedar trees, obstacles in the path of movement, and environmental variables like wind direction and speed, and orientation to the sun angle.

The dispersal of the saltcedar beetle will be studied using the solution of equation [1].

$$n(r,t) = \frac{\delta n_0}{4\pi Dt} \exp\left(-\frac{r^2}{4Dt}\right) \quad [2]$$

Where δ is a coefficient for the appearance-disappearance of beetles, n_0 is the original number of beetles at release time, or an estimate of the beetle population at the beginning of a growing season.

The diffusion and appearance-disappearance coefficients can be estimated using the distribution of beetle abundance through several distances from the release point during a number of weeks. Equation [2] is fitted, $nf(r^2)$, using least squares for each week. Smith, et. al. (2001) counted the number of insects at nine distances in each of the eight weeks.

Another way to estimate the diffusion coefficient and the advance distance were suggested by Karaeiva (1983):

$$D = \frac{r_a^2}{\pi t} \quad [3]$$

$$r_{.98} = 2\sqrt{4Dt} \quad [4]$$

where r_a is the average distance of displacement of the beetles for a week, and $r_{.98}$ is the radius reached by 98% of the original beetle population.

Rearranging equation [3] the average distance of displacement by the beetles can be estimated for each week:

$$r_a = \sqrt{\pi Dt} \quad [5]$$

Smith, et.al. (2001) also used another approach to estimate number of insects at a given distance using the following equation:

$$n(r) = \frac{n_0(8\pi)^{-1/2}(\delta D^3)^{-1/4}}{r^{1/2}} \exp\left(-\frac{r}{(D/\delta)^{1/2}}\right), \quad [6]$$

where $n(r)$ is the total abundance across time at a distance. This equation depends only on distance, and the diffusion and appearance-disappearance coefficients can be estimated from the distribution of abundance at a number of distances; Smith, et. al. (2001) used nine distances.

B. Kovalev's IPW Model

Kovalev and Vechernin (1986) developed an IPW model to study the spread of the ragweed beetle *Zygogramma suturalis* F. (Chrysomelidae) during the control of ragweed *Ambrosia artemisiifolia* L. in the field infested by this weed in Russia. The model is formulated as a diffusion equation as follows:

$$\frac{\partial n}{\partial t} = -\nabla I + f(n), \qquad\qquad [7]$$

where n(r,t) is the insect density, number of insects per m^2 at a given place r at a particular time t; I (r,t) is the vector of insect flux; $f(n)$ is the insect birth rate minus insect death rate per unit time per unit area; and $\nabla = $ gradient $= \partial/\partial r$.

Equation [7] indicates that the change in the number of insects at a given place is equal to the difference between the insects that have migrated to a particular point and the number of insects that have left the same point including the difference in the number of births and deaths at the same place.

The vector I of insect flux is equal to:

$$I = -D\nabla n + B\nabla p , \qquad [8]$$

where D is the coefficient of diffusion which is proportional to the gradient of insect density and describes the movement of insects from high to low density. The second term shows B, the coefficient of food search efficiency proportional to the gradient of plant density, the insects move from places of low plant density to places of high density. Plant density at a given place r and a time t is designated as p(r,t).

The change of plant material available under the influence of insect feeding is given by the equation:

$$\frac{\partial p}{\partial t} = -An , \qquad\qquad [9]$$

where A is the amount of biomass eaten by one insect per unit time. The amount of biomass eaten by the insects in a day in an area unit is equal to the biomass eaten by an insect multiplied by the number of insects in that area unit.

Assuming that the coefficient of diffusion is constant, and replacing equation [8] in [7], the IPW model for the dispersal of the saltcedar beetle can be expressed by the following system of differential equations:

$$\begin{cases} \dfrac{\partial n}{\partial t} = D\Delta n - \nabla(B\nabla p) + f(n) \qquad\qquad [10] \\[3mm] \dfrac{\partial p}{\partial t} = -An , \end{cases}$$

where $\Delta = \dfrac{\partial^2}{\partial x^2} + \dfrac{\partial^2}{\partial y^2}$ is the Laplace operator.

The solution of the equations in [10] yields the speed of the wave in equation [11], the shape of the IPW wave in equation [12], the damage caused to saltcedar by the beetle population in equation [14], and the width of the insect wave in equation [15].

$$V = \sqrt{A.B} \qquad\qquad [11]$$

The speed of the wave depends only on A, the amount of biomass eaten by an individual insect in a day, and B a coefficient of food search efficiency.

$$n(x,t) = \frac{3n_0}{2\cosh^2\left[\frac{1}{2}\sqrt{\frac{E}{D}}(x - x_0 - V_t)\right]} \;, \qquad [12]$$

where n_0 is a critical insect density at which the birth rate is equal to the death rate, it is the point where the following quadratic polynomial intercepts the n axis. Also, one characteristic of the IPW is that the maximum insect density, at the top of the wave, is approximately equal to $3n_0/2$

$$f(n) = -En + \frac{E}{n_0}n^2 \qquad\qquad [13]$$

The coefficient E is the slope of the linear component in equation 13, $x - x_0$ is the distance between the initial position of the wave x_0 and any point in the path of the wave, V_t is the speed of the wave at time t, and cosh is the hyperbolic cosine.

The damage caused to saltcedar by the beetles feeding on it is given by

$$P(x,t)\% = \frac{1}{2}\left\{1 - \tanh\left[\frac{1}{2}\sqrt{\frac{E}{D}}(x - x_0 - Vt)\right]\right\}.100\,, \qquad [14]$$

where tanh is the hyperbolic tangent.

The width of the wave is represented by equation [15]

$$L = 4\sqrt{\dfrac{D}{E}}\,\ln(\sqrt{2}+1)\,, \qquad\qquad [15]$$
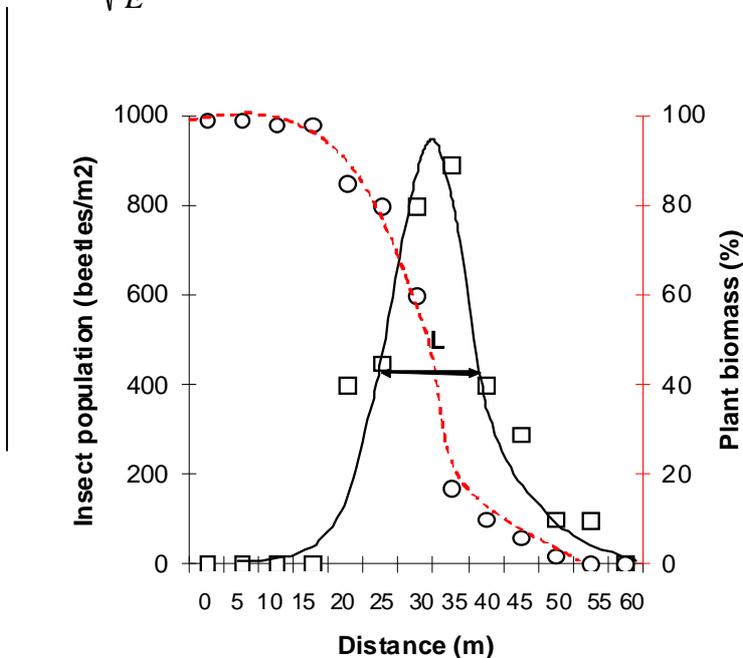

Figure 1. Insect population and plant biomass from field experimental data and IPW model application. (Adapted from Kovalev and Vechernin (1986) in a study of *Zygogramma suturalis* dispersal to control ragweed in Russia.)

Figure 1 shows the experimental data collected and curve calculation of Kovalev and Vechernin (1986) for July 9, 1985, for the beetle population (squares) and plant biomass (circles), and the curves calculated from equations [12] and [14] for the waves of beetles (continuous line) and plant biomass (dotted line) respectively.

Kovalev and Vechernin (1986) used this figure to estimate L from the experimental data, then using equation 15 the ratio E/D can be calculated to be used in equations [12] and [14]. The other parameter *Vt* in equations [12] and [14] can be estimated by plotting several weekly periods and calculating the average distance between peaks of beetle population. An analytical solution of equation [11] was not attempted by Kovalev and Vechernin (1986) for a theoretical wave velocity given the difficulties to estimate the coefficient of food search efficiency B.

C. Spatial Regression Model

The spatial regression model used to study the dispersal of *Diorhabda* is based in the methodology known as LOESS, which is short for Local Regression. It was originally proposed by Cleveland (1979) and further developed by Cleveland and Devlin (1988). Models of this type were used by Steege, et. al. (2003) to study spatial variability and density of trees in the Amazon. Honek, et. al., (2006) employed spatial LOESS regression to study growth patterns of aphids in cereals. Nilsson, et. al. (1997) made ecological studies in

riparian areas using the same spatial regression methodology. Renofalt, et. al. (2005) used LOESS regression to study plant invasiveness in a riparian corridor, using this regression methodology they were able to establish spatial patterns of several plant community characteristics against distance to a river mouth.

The method is a non-parametric technique also known as neighborhood weighted polynomial regression. At each neighborhood in the data set a first or second degree polynomial is fit to a subset of data with explanatory variable values near the point whose response is being estimated. The polynomial is fit using weighted least squares, giving more weight to points near the point whose response is being estimated and less weight to points further away. The value of the regression function for the point is then obtained by evaluating the local polynomial using the explanatory variable values for that data point. One or more explanatory variables can be used. In spatial analysis applications distance with respect to a reference point is the most commonly used explanatory variable. Other variables such as environmental factors, characteristics of vegetation, or time may be included as explanatory variables.

The subsets of data used for each weighted least squares fit in LOESS are determined by a nearest neighbor algorithm. A user-specified input to the procedure called the "bandwidth" or "smoothing parameter" determines how much of the data is used to fit each local polynomial. The smoothing parameter, q, is a number between $(d+1)/n$ and 1, with d denoting the degree of the local polynomial. The value of q is the proportion of data used in each fit. The subset of data used in each weighted least squares fit is comprised of the nq (rounded to the next largest integer) points whose explanatory variables values are closest to the point at which the response is being estimated. q is called the smoothing parameter because it controls the flexibility of the LOESS regression function. Large values of q produce the smoothest functions that wiggle the least in response to fluctuations in the data. The smaller q is, the closer the regression function will conform to the data. Using too small a value of the smoothing parameter is not desirable, however, since the regression function will eventually start to capture the random error in the data. Useful values of the smoothing parameter typically lie in the range 0.25 to 0.5 for most LOESS applications.

The local polynomials fit to each subset of the data (first or second degree) is, either locally linear (in the straight line sense) or locally quadratic. Using a zero degree polynomial turns LOESS into a weighted moving average. Such a simple local model might work well for some situations, but may not always approximate the underlying function well enough. LOESS is based on the ideas that any function can be well approximated in a small neighborhood by a low-order polynomial and that simple models can be fit to data easily.

As mentioned above, the weight function gives the highest weight to the data points nearest the point of estimation and the least weight to the data points that are furthest away. The use of the weights is based on the idea that points near each other in the explanatory variable space are more likely to be related to each other in a simple way than points that are further apart. Following this logic, points that are likely to follow the local model best influence the local model parameter estimates the most. Points that are less likely to actually conform to the local model have less influence on the local model parameter estimates.

The traditional weight function used for LOESS is

$$w(x) = \begin{cases} (1 - |x|^3)^3 & \text{for } |x| < 1 \\ 0 & \text{for } |x| \geq 1 \end{cases}$$

However, any other weight function that satisfies the properties suggested by Cleveland (1979) can be used. The weight for a specific point in any localized subset of data is obtained by evaluating the weight function at the distance between that point and the point of estimation, after scaling the distance so that the maximum absolute distance over all of the points in the subset of data is exactly one.

The smooth parameter is the most important component affecting the quality of the prediction, one way of identifying the appropriate value of the smooth parameter is to examine the residual distribution for its symmetry with respect to zero and homogeneity of variance after using systematically smoothing values between 0.1 and 0.5. Values too low tend to overfit the data, and values too high tend to overrun variability contained in the data.

D. Data Collection for the Models

The sampling scheme for counting larvae and adults of the saltcedar beetle, and for measuring variables that may affect its dispersion change according with whether the insect is just being released or it has been well established in the site for at least one season. In new sites the dispersion can go in any direction, so four radial transects were traced to cover the study area as is shown in Figure 10. Another special situation is where the distribution of saltcedar forms narrow and long bands along a stream, like along Beals Creek only one transect following the direction of the creek was used for sampling. In areas where the insect has been well established for some seasons, the transects will have the orientation of the dispersion fronts. Length of transects and number of sampling points on the transects will be set according with the particular characteristics of the site. Distance between transect sampling points at the beginning of the first season were 10 meters and later were increased due to gaps free of saltcedar. Sampling was carried weekly at each transect point during the growing season. When the beetle dispersion reaches regional levels, like in Lovelock, NV estimates of insect population, the severity of defoliation, and other model input variables need to be estimated by remote sensing and GIS methodologies.

1. The sample unit at every sampling point in the transects was an area of 4 m by 4 m called quadrat. The distance between the edges of sample units was 10 meters initially, and increased to 20, 50 and 100 m as the beetles spread outward. Later, that distance was the result of the distance between trees across gaps without saltcedar.

2. Insect counting will be done in subsample units that are branch sections 1 m long.
Length of branches per quadrat and number of branches per quadrat were estimated to be used for later extrapolations.

3. Saltcedar defoliation was done through visual estimation of the foliage percentage with *Diorhabda* damage.

4. Sampling of environmental variables. Hobo temperature sensors, with data loggers incorporated, were located at approximately 3 m high every other sampling point along the transects in the Beal Creek site to collect air temperature and relative humidity under the canopy. A weather station was used to measure air temperature, solar radiation, relative humidity, wind velocity, wind direction, and precipitation for the entire sampling area. An infrared thermometer was employed to measure canopy temperature at the beginning of the 2005 season.

Sampling along Beals Creek

The above sampling methodology was applied for the insect counts from transects in 2005 and 2006. At the end of the 2006 growing season the beetles started to reach Beals Creek and the sampling became focused on the transect along the creek during the 2007 and 2008 growing seasons. The *Tamarix* community along the creek is continuously distributed for long distances, sometimes longer than one kilometer. After gaps of few meters the tree community continues uniformly for long distances. The high number of trees made impractical to continue using the 16 m^2 quadrat as the sampling unit, and the 9 branches per quadrat as the subsampling units. In the transect along the creek the insect count continued making timed 1-m branch counts on individual *Tamarix* trees spaced about every 25 m. Counts of *Diorhabda* egg masses, three larval instars, and adults were made on at least four 1-m branches (on four sides of the tree) for at least two

minutes. counting additional 1-m branches if four branches can be counted in around one minute.   Time spent counting on a branch was recorded. Counts on several of the 4x4 m quadrats using both couting methods was used to develop conversion factors to transform the timed counts in individual trees to number of beetles per 16 m^2 of saltcedar. Saltcedar foliage condition ratings will be made for the overall tree sampled.

RESULTS

The environmental variables measured along the transects: canopy temperature, under canopy temperature, and relative humidity, as well as weather variables measured at the weather station for the full sampling area: wind velocity, wind direction, solar radiation, air temperature, and precipitation did not show any significant correlation with the different forms of *Diorhabda* population counted during 2005. There was special interest in exploring a possible connection of canopy and under canopy temperatures, as well as wind velocity and direction with the orientation of the dispersal population waves. The canopy temperature and the temperature under it may affect the volatility of plant substances that attract the insects, and the wind velocity and direction could affect the physical movement of adults from tree to tree, but the data did not show evidences of such relationships. In the absence of the mentioned relationships, and observing and measuring the behavior of the beetles along the transects we can say that the dominant factors controlling the direction of *Diorhabda* dispersal in *Tamarix* communities are the availability of green biomass and the spatial distribution of the trees.

The environmental variables above were considered to be used as predictor variables in the spatial regression model to study dispersion; since there was not correlation between those variables and the beetle populations, the only variables used as predictors in the spatial regression model were time and distance from the release point. Time and distance were used in separate models.

 Differences about the implementation of the three models (Okudo, Kovelev, and Spatial Regression) to study the dispersal of *Diorhabda* on *Tamarix* communities became evident very soon after collecting the first sets of data in 2005.

First, was the impossibility of representing insect population waves along the transect distance using the Okudo model. The experimental estimation of the appearance-disappearance parameter of the model was impossible under the open field conditions without using unmarked insects and without having a clue of a numerical value for the starting insect population in the 2005 season. The mathematical estimates of the mentioned parameter, using population values from the data and solving the equation for the unknown parameter, were unsatisfactory. The Okudo model was unable to resemble population waves of the kind suggested by the counts on the transects. There were no further attempts to use this model.

Second, Kovalev's model parameterization and use for representing insect population waves work well but is restricted to selected pieces of data that follow "idealized" population waves. Since the model is completely deterministic, it does not have any flexibility to adapt to the high variability of the beetle populations that result from the interaction of innumerable biotic and abiotic factors. The symmetric waves that result from the cosine hyperbolic component of the model are far from the unpredictable population shapes that occur in the field. The model performs well representing population changes through space in seldom particular sampling dates or sections of a transect that happen to yield well bell shaped changes of population. Waves fit to monthly averages can be used to estimate dispersal speed and relative proportion of area covered from month to month.

Third, the spatial regression model is able to develop population waves to predict magnitude of insect populations and how far they reach during a growing season using all the data collected. Counts from all branches surveyed per quadrat (2005 and 2006) or per tree (2007 and 2008) were used for the prediction.

This way, the prediction is done accounting for all the random variability that is characteristic of insect populations in natural environments.

Description of the uses of spatial regression models and Kovalev's model for the study of *Diorhabda* dispersal in the initial stages of establishment in a geographical area follows.

2005 Growing Season

The large larvae population (addition of 2nd and 3rd instars) in 2005 came from 4 generations of *Diorhabda* as suggested by the LOESS regression model predictions in Figure 2. Every figure from LOESS regression prediction is composed of two graphs A and B. A shows all the data range with the prediction line at the bottom going through the data sector of highest density, and B shows a zoom of A with the prediction line and the 95% confidence interval of the prediction that are dwarfed by the very wide range of the data. There was a first well differentiated generation that went from 25 June to approximately July 23. There are two generations overlapped between 30 July and 27 August, the two peaks on 13 August and 27 August indicate that there were two generations in the mentioned period. Then a fourth generation took place between 27 August and 17 September. The highest population of approximately 1800 large larvae per 16 m^2 of saltcedar occurred in the second generation around the 13th of August. The highest population was between 1500 and 2200 large larvae per 16 m^2 of saltcedar with a 95% confidence.

In the process of dispersing from the release point, the large larvae population described 6 major waves, as it is shown in the predictions done by the spatial regression model in Figure 3 for Transects 1 to 4 combined. The first wave peaked close to 22 m, the second at 40 m, the third at around 52 m where there was the highest number of large larvae for the growing season. At 52 m from the release point there was a population mean of 2800 large larvae per 16 m^2 or a population that was between 2200 and 3500 large larvae per 16 m^2 with a 95% confidence. After reaching this maximum the number of large larvae started to decline, made two additional waves and stopped moving at a distance around 130 m from the release point. The six population waves can be also interpreted as the components of a large wave that peaked at 52 m from the release point.

Predictions of adult population dispersal by the spatial regression model are in Figure 4, for Transects 1 to 4 combined. Across the 130 m distance that was sampled during 2005 the adults also described 6 waves. The population peaked at a mean value of 1400 adults per 16 m^2 of salcedar. The mean at the maximum of the adult population varied between 1100 and 1700 adults per 16 m^2 of saltcedar with a 95% confidence. The peak of adult population took place at 60 m from the release point, 10 m or a quadrat ahead of the large larvae population which always lags behind the adults.

Data of total number of larval density in Transect 2 was used to model dispersal with Kovalev's model. Field data for different sampling periods and predictions for the mean populations of July and August 2005 are shown in Figure 5. Height difference between the two monthly waves indicate higher density of larva population in July than a month later in 2005, but the more extended wave of August suggests that in that month the larval population was covering more saltcedar area than the previous month. Distance between the larval density peak in July and in August indicates that the *Diorhabda* population was dispersing in the *Tamarix* community at an approximate speed of 40 meters per month.

2006 Growing Season

LOESS regression applied to the large larvae population of 2006 was able to differentiate three generations of beetles in Figure 6. Apparently a first generation that grew between the end of May and the beginning of June was missed by the model; a little adjustment of the smoothing parameter may be enough for the model to detect that first generation. The four generations, included the undetected one, have a clear tendency to

have one month duration. The highest population of large larvae, with a mean of 1100 larvae per 16 m^2 of saltcedar, took place in the second generation. After the second generation the population mean goes down to reach a mean close to 700 large larvae per 16 m^2 of saltcedar in the fourth generation.

Dispersal of large larvae in 2006 is modeled with LOESS regression combining Transects 1 to 4 in Figure 7. The dispersal pattern in this year had considerable differences with respect to the previous one. In 2006 the first wave is formed by a population mean of around 1300 large larvae per 16 m^2 of saltcedar, then the average population mean at the peak of the following waves decrease considerably but the extension of the waves cover more saltcedar area than the first population wave. The first high and narrow wave is the result of a large number of larvae originated at the end of the last expansion wave in 2006. That high population consumed the foliage available from a small area of saltcedar relatively fast. It is apparent from Figure 6 that the starting beetle population run into food limitations and for that reason the large larvae numbers decreased and each wave covered more saltcedar area. Starting at 420 m from the release point there is a steep increase of larvae population after a 130 m gap free of saltcedar trees, such increase may be due to a satellite beetle population that started growing in a patch of saltcedar trees at 500 m.

The dispersal pattern of adults in 2006, Figure 8, is similar to the pattern followed by large larvae in the same year. Explanations for the first sharp and narrow wave and for the wave that starts at the end of the distance sampled are the same as for the large larvae.

Two dispersal waves of larval density means from two sampling periods were estimated with Kovalev's model, Figure 9. The two population peaks for the two waves occurred at 140 and 240 m from the release point. The spatial LOESS regression (Figure 7) detected waves for the large larvae population at the same distances. The second wave estimated by Kovalev's is associated with less number of days than the first wave but has a larger larval density and covers more saltcedar area than the first wave. According with Kovalev's estimations, the population shows evidences of increase and expansion to more area from the middle of June to the middle of August. LOESS waves in Figure 7 were showing decrease of population but expansion to more area. We put higher confidence in the LOESS estimates due to the establishment of spatial patterns based in the full data set from the growing season. Using the distance between wave peaks in Figure 9 we can say that the approximate dispersion speed was of 50 m per month. There is a reasonable agreement between mean larval density and dispersion speed in the 2005 and 2006 growing seasons.

The longitudinal prediction of population dispersal employing the regression LOESS model and Kovalev's model are represented in area terms in Figure 10. The defoliation of a saltcedar area of 2 acres in 2005 grew to an area of 17 acres in 2006.

2007 Growing Season

The large larvae population growth through the growing season was modeled with LOESS regression as shown in Figure 11. Every peak is supposed to be associated with a generation, but separating them across time was difficult. Between 2 June and 30 June there is a generation, then between 30 June and 4 August there are 4 overlapped generations, and after 11 August appear to be 2 overlapping generations. The highest number of large larvae, 1600 large larvae per 16 m^2 of saltcedar happened in 7 July.

The generation separation of *Diorhabda* in 2007 was better defined by the temporal distribution of the adult population modeled with LOESS regression in Figure 13. There was a first generation that occurred between 2 June and 30 June, two overlapped generations in the period between 30 June and 28 July, another generation between 28 July and 25 August, and last generation between 1 September and October 13. The different generation peaks did not show large differences, 150 adults per 16 m^2 of saltcedar was the approximate maximum in all generations.

The spatial distribution of the large larvae population modeled with LOESS regression is shown in Figure 12. The highest population waves occurred 500 m west of the origin and 500 m east of the origin. The origin identified as point 0 in Figure 17 is the intersection point between the projection of Transect 4 and Beals Creek. The peak population 500 m east of point zero was close to 1000 large larvae per 16 m^2 of saltcedar, and close to 920 large larvae per 16 m^2 of saltcedar at 500 m west of point zero. There is a decreasing population of large larvae as the sampling points get farther from the transect origin in either direction. The distance range from -2000 m (east) to 2000 m (west) had an abundant presence of large larvae that explains the heavy defoliation depicted on the same transect range on Figure 17. The spatial distribution modeled with LOESS regression for adults in Figure 14 also matches the sectors of heavy defoliation in Figure 17. Both the prediction of large larvae and adults (Figures 12 and 14 respectively) present other two peaks that may be due to satellite populations at 2700 m and 5000 m west. Figure 17 shows sample points with defoliations between 25 and 75% at around 2700 and 5000 m west and 1800 and 2640 east.

2008 Growing Season

Resource limitations in this growing season did not allow sampling with spatial continuity along the Beals Creek transect. The distance intervals showing zero population of large larvae in Figure 15 were not sampled. LOESS modeling in Figure 15 shows a peak of approximately 100 large larvae per 16 m^2 of saltcedar at 1500 m east of the transect origin, and two other peaks of 1700 and 800 large larvae per 16 m^2 of saltcedar at 1000 and 2500 m west of the transect origin.

Residual distribution along distance is a criterion to judge the quality of the dispersal modeling done by the spatial LOESS modeling. Figure 16 shows the residual distribution for large larvae population estimates done in 2007 and 2008. The large cluster of residual dots between -2000 and 2000 m are symmetrical with respect to zero, and the cloud of dots has a reasonable homogeneous variance across the distance. Thus we can say that LOESS estimates are of good quality in 2007. From the two conditions that the residuals from 2008 should meet, the symmetry with respect to zero is good, but the homogeneity of variance is not good, indicating that quality of estimates are highly affected by location, which is a result of the limited sampling performed during 2008.

CONCLUSIONS

Environmental factors such as micrometeorological (under canopy) conditions or weather factors do not affect the dispersion of *Diorhabda* in *Tamarix* communities during the initial stages of establishment, where the dominant movement of the beetles is from one tree to another in the proximity, as long as the environmental factors remain within ranges that do not influence the *Diorhabda* population. Dispersal of *Diorhabda* in the initial stages of colonization of an area is driven largely by the availability of *Tamarix* green foliage and by the spatial distribution of *Tamarix* trees.

Weather factors such as air temperature, wind direction and wind velocity are expected to be mayor factors in later stages of dispersal in large areas. The main way of dispersal in this case is through the establishment of satellite populations in distant areas from the point of original release. Satellite populations are initiated by large groups of adults that probably move with the wind and convective air masses.

The spatial LOESS regression modeling allowed to identify the temporal and spatial patterns of the *Diorhabda* colonization in a new area using the bulk of the data collected. Those patterns were discussed for the four growing seasons of the study.

Modeling of *Diorhabda* dispersal with the Kovalev's model was especially useful to estimate dispersal speed.

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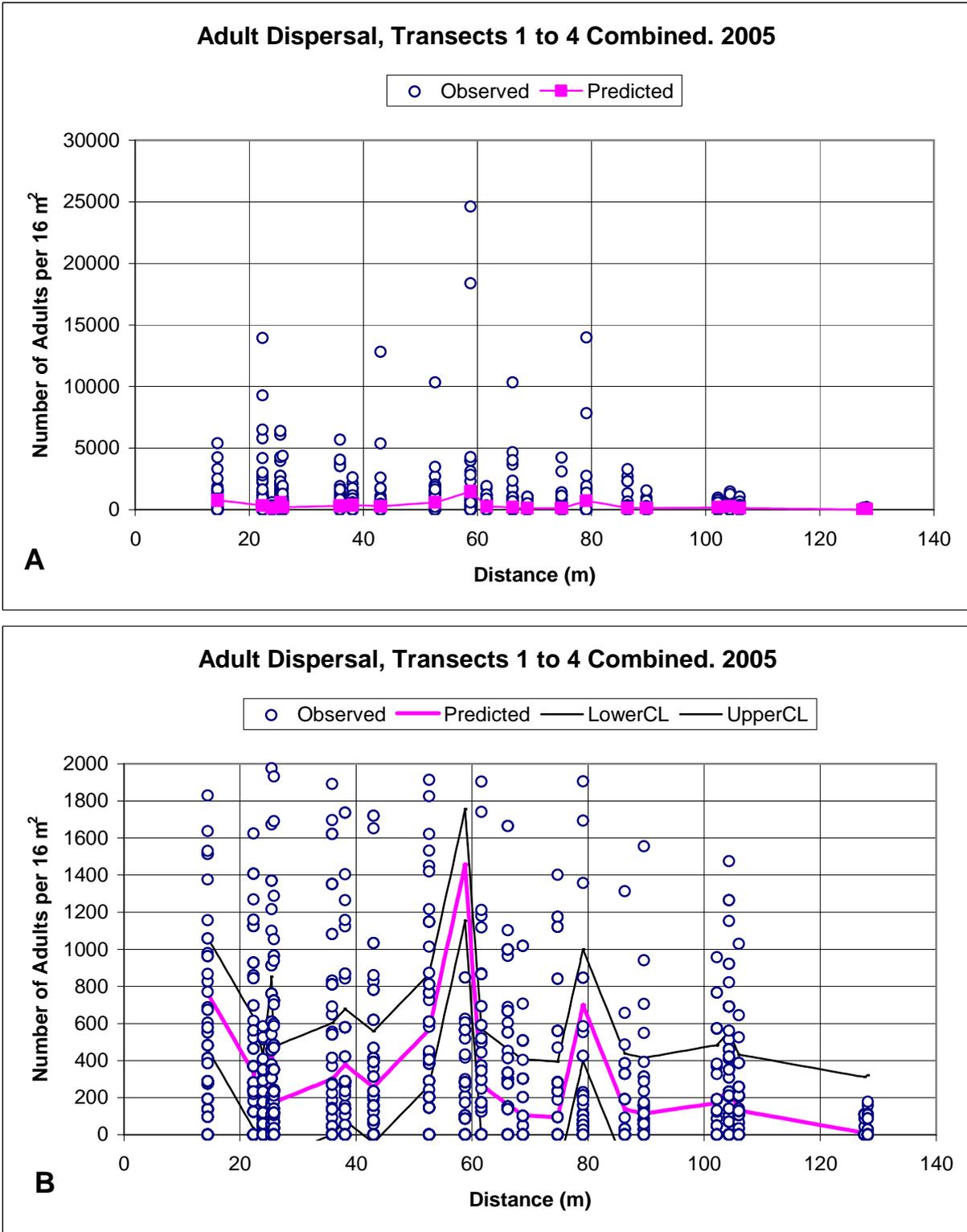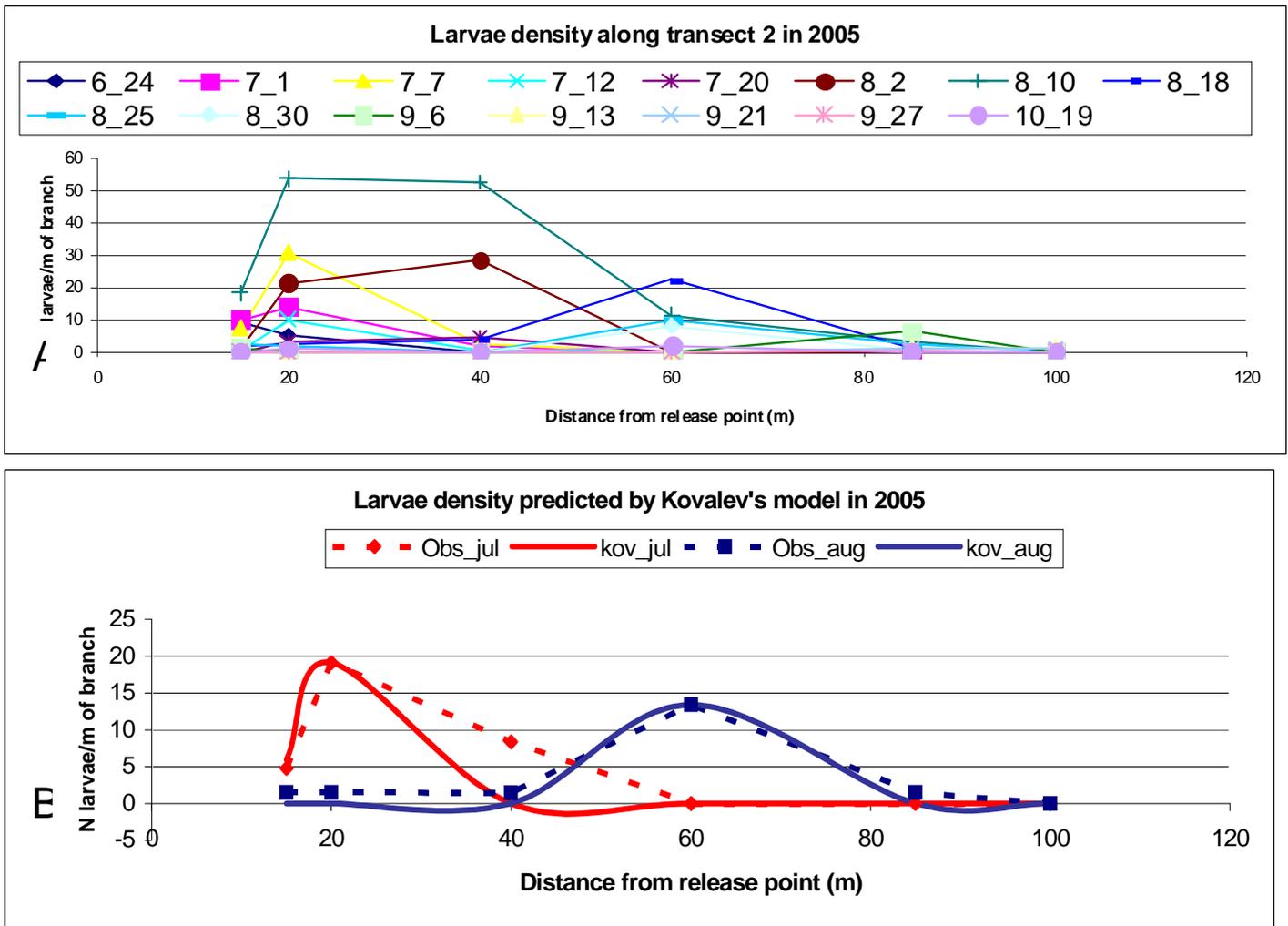
FIGURES
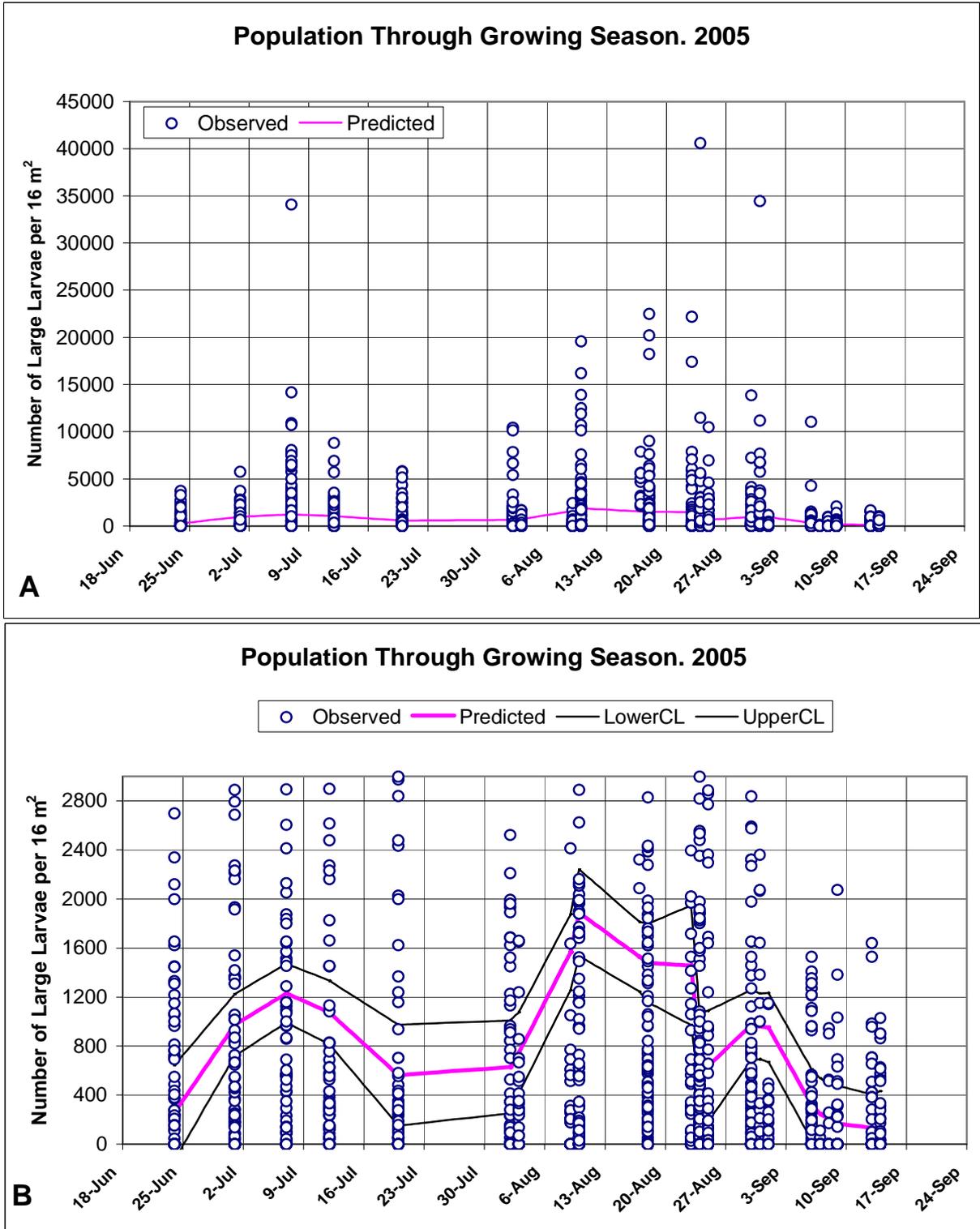
Figure 2. Large larvae, 2005 – population **densities** observed and predicted through the growing season (mean ± 0.95 confidence intervals, Transects 1-4 combined) – **LOESS Regression**, **Higgins Ranch**. A. All data. B. Detail close to prediction lines.
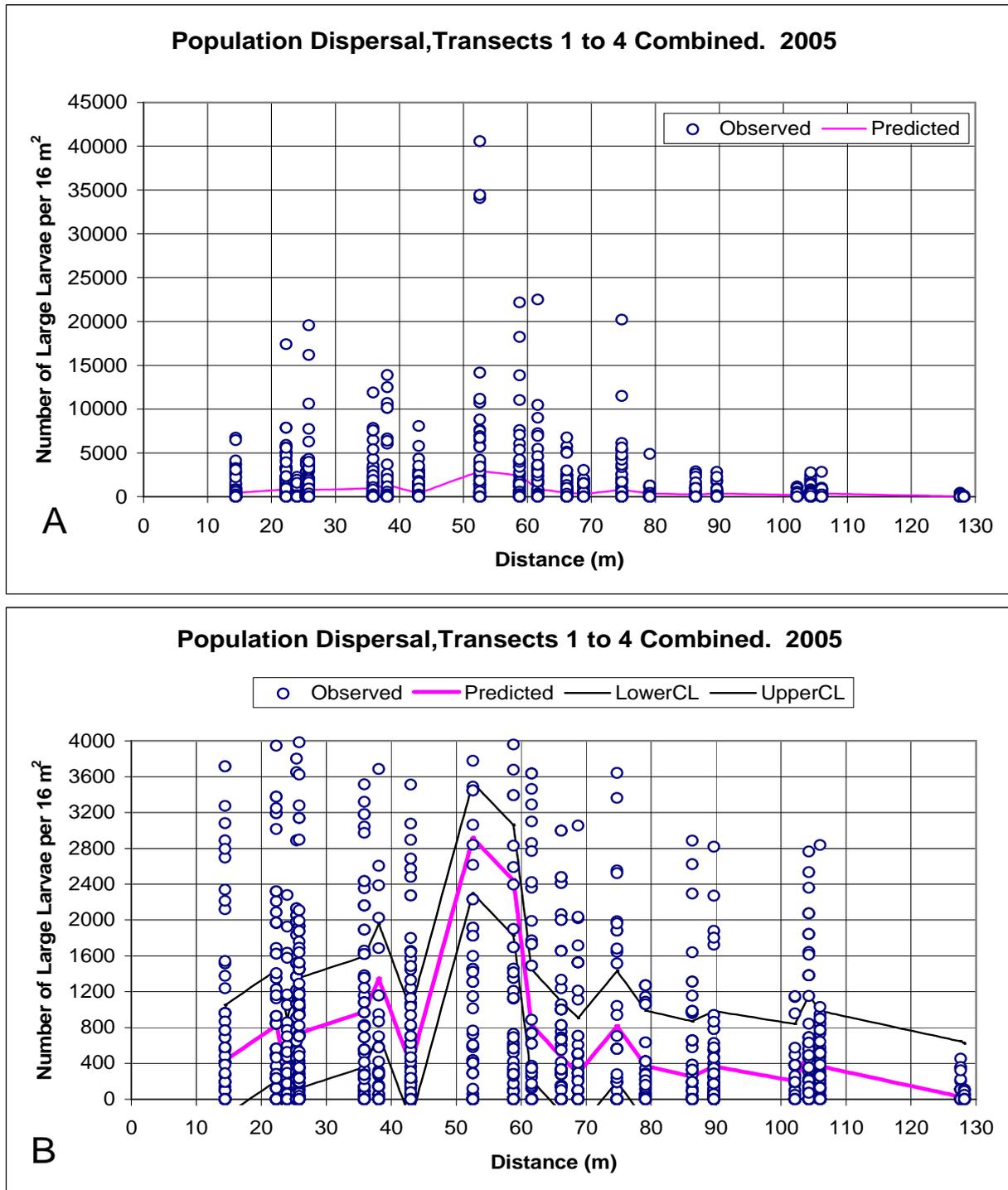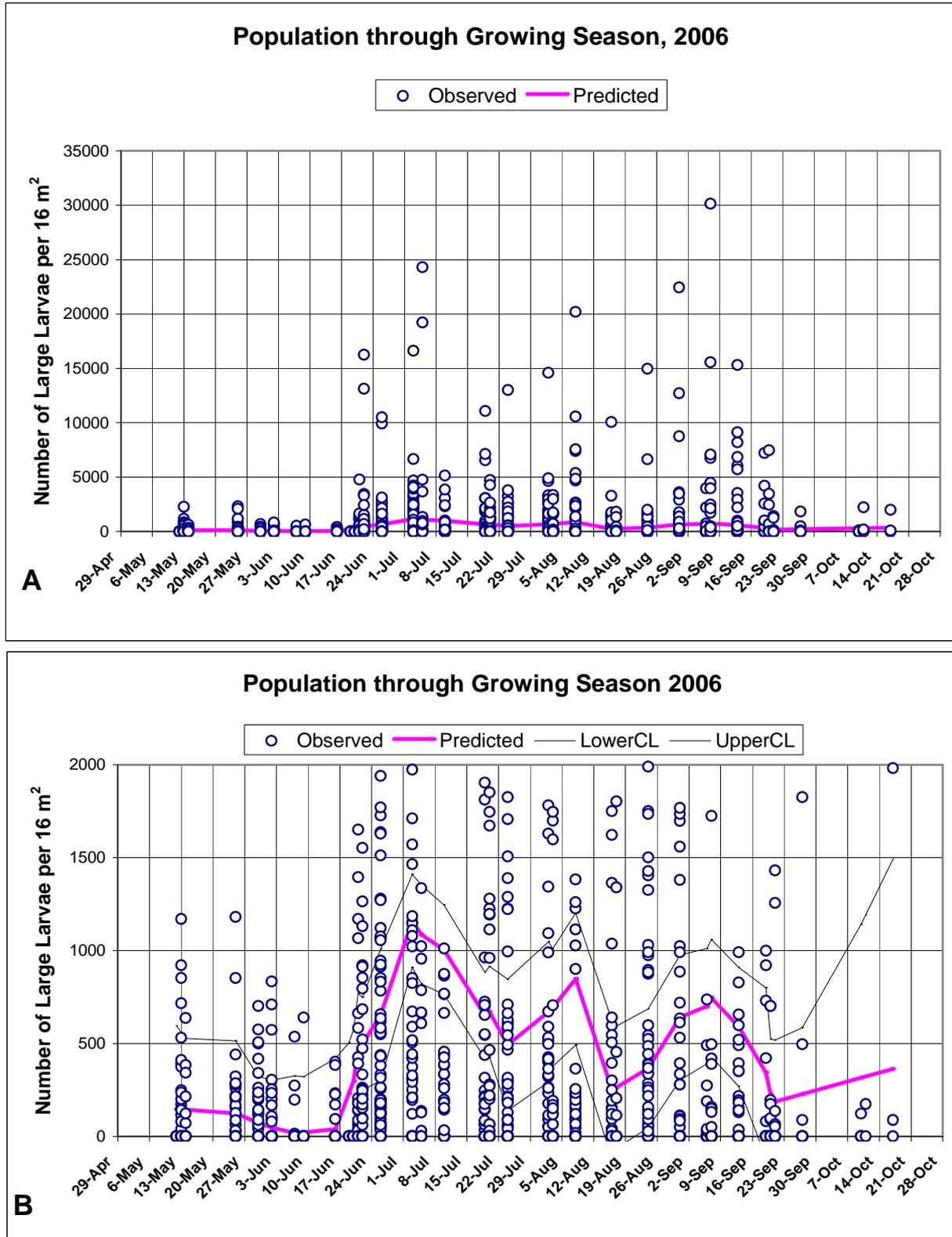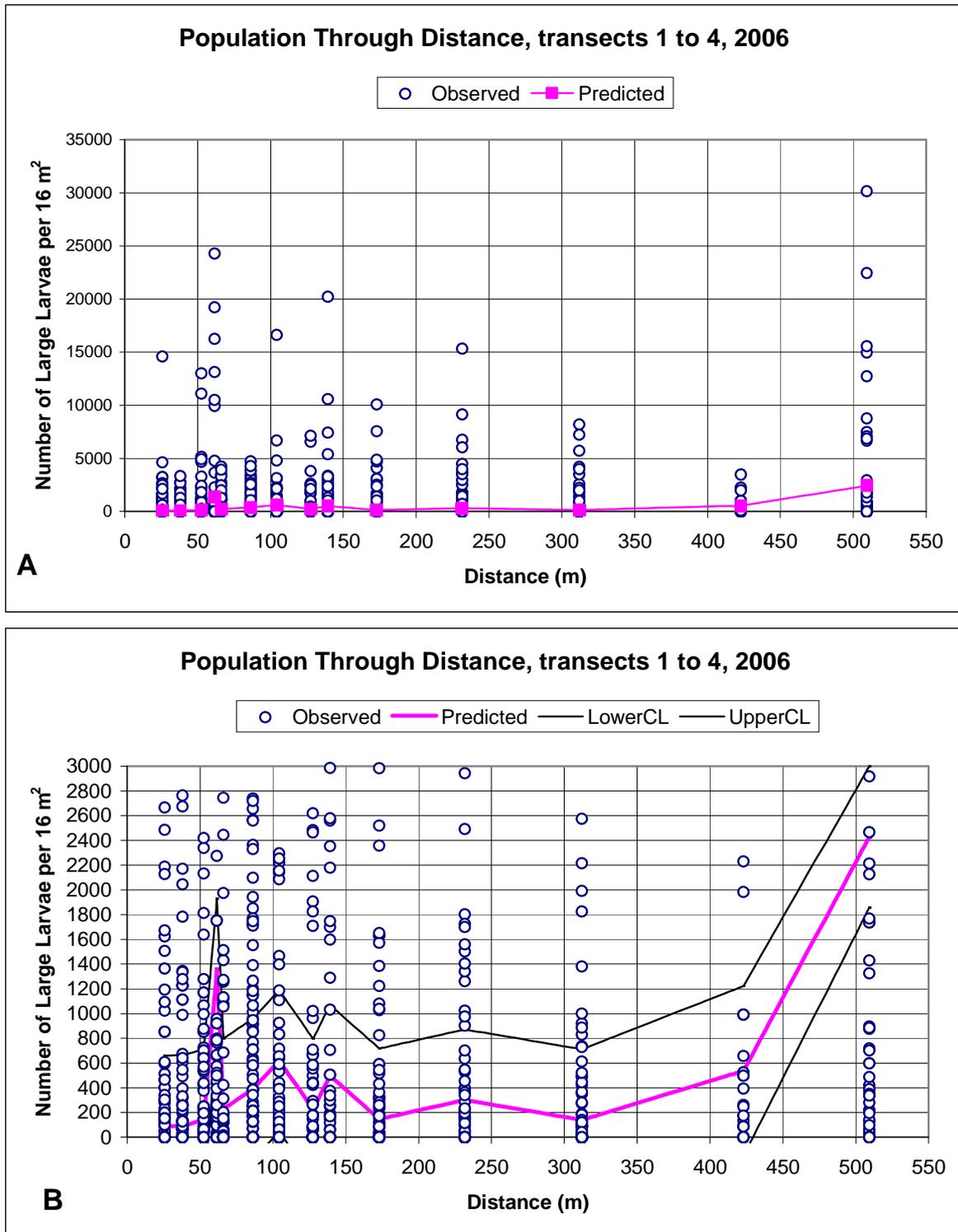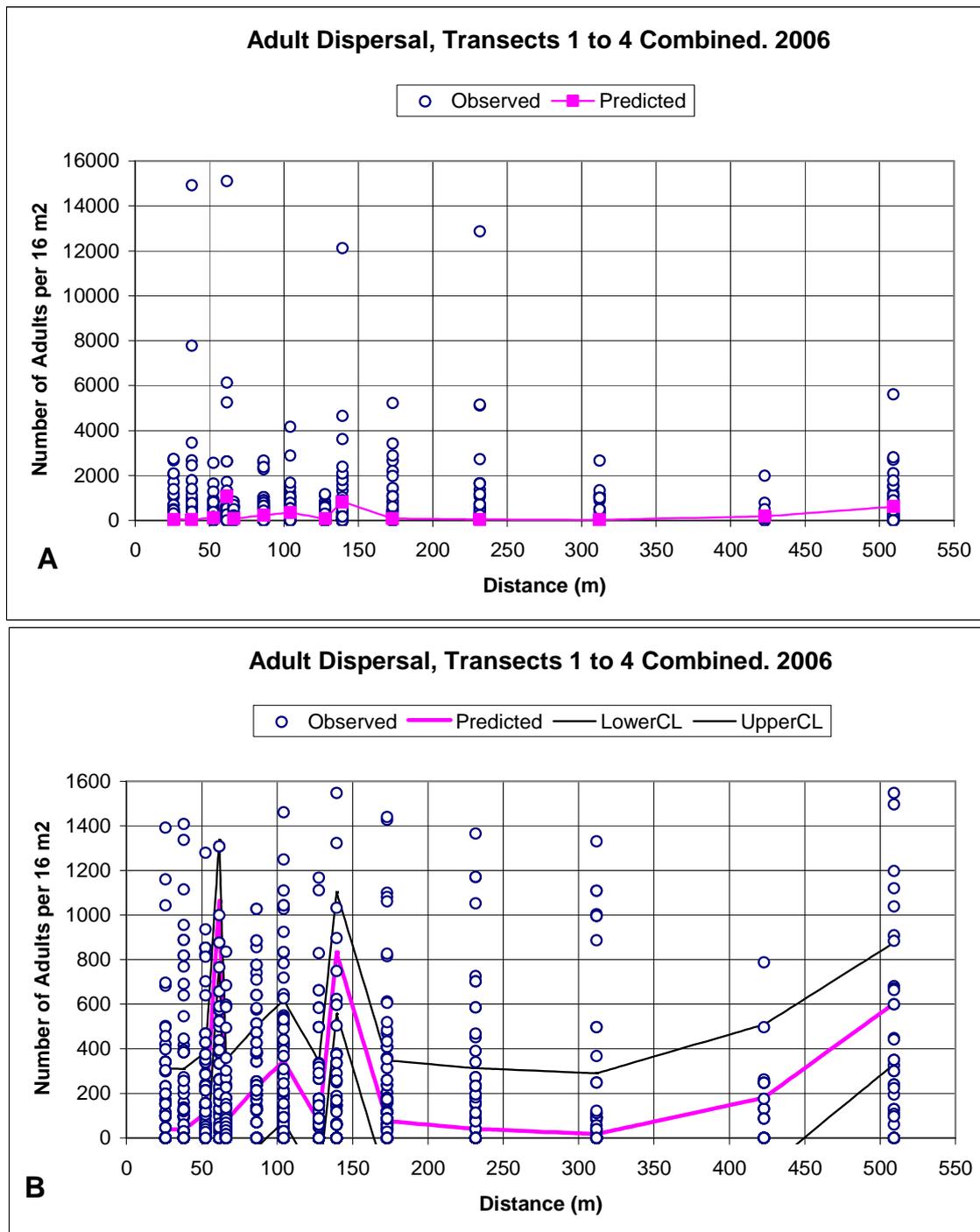
Figure 3. Large Larvae, 2005 – population **dispersal** observed and predicted through the growing season (mean ± 0.95 confidence intervals, Transects 1-4 combined) – **LOESS regression**, **Higgins Ranch**. A. All data, B. Detail close to prediction lines.

Figure 4. Adults, 2005 – population **dispersal** observed and predicted through the growing season (mean $\pm$ 0.95 confidence intervals, Transects 1-4 combined) – **LOESS regression**, **Higgins Ranch**. A.. All data. B. Detail close to prediction lines.

Figure 5. Variation in **larval population density** from 24 June – 19 October **2005**, along Transect 2 at Quadrats 1-7, **Higgins Ranch**. A) Observed density at each ca. weekly count date (mean number larvae per nine 1 m-long branches counted per quadrat), B) Mean density per branch observed and predicted at each quadrat during July or August, by the **Kovalev Model**.
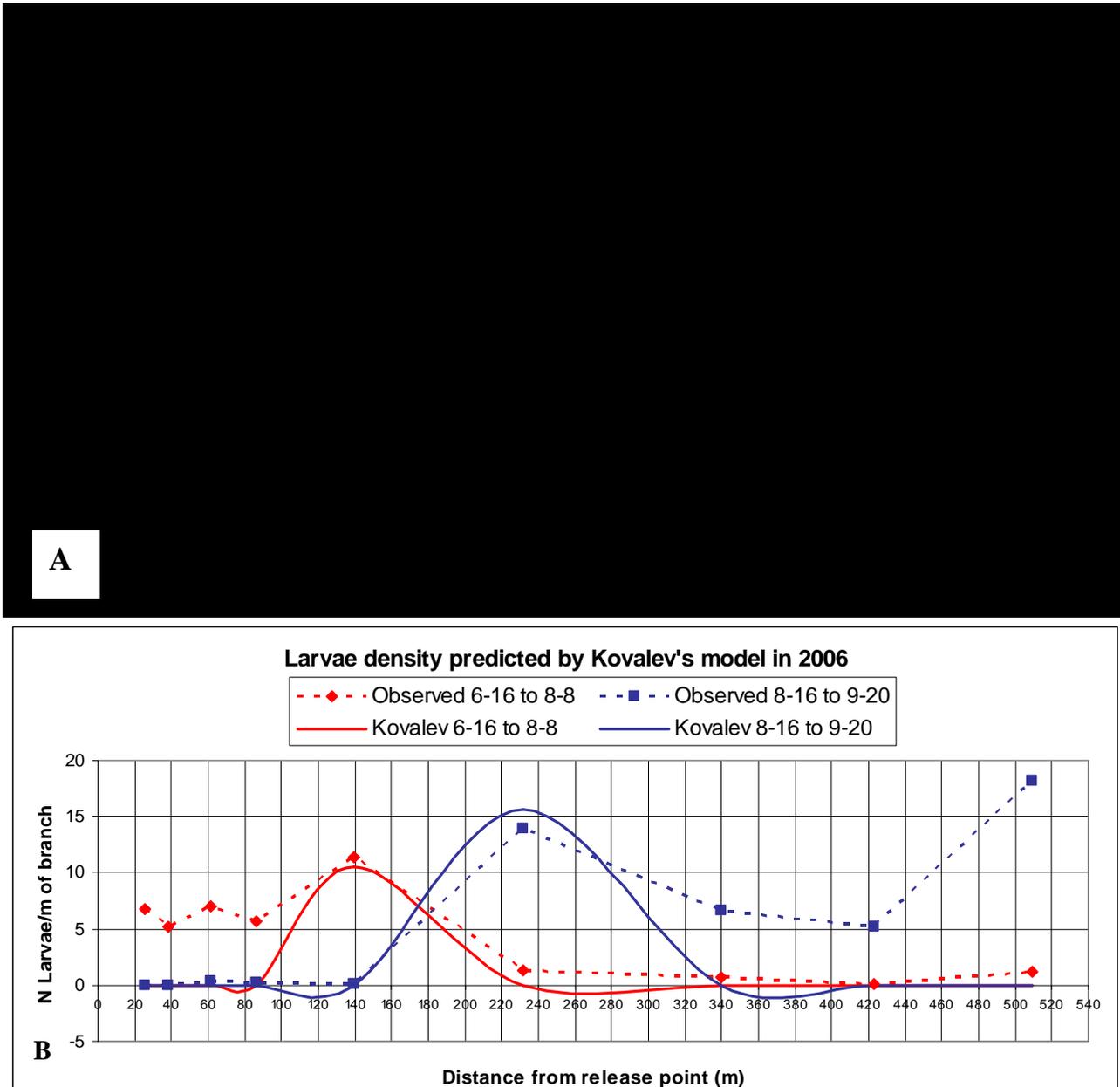
Figure 6. Large larvae, 2006 – population **densities** observed and predicted through the growing season (mean ± 0.95 confidence intervals, Transects 1-4 combined) – **LOESS Regression**, **Higgins Ranch**. A. All data. B. Detail close to prediction lines.

Figure 7. Large larvae, 2006 – population **dispersal** observed and predicted through the growing season (mean ± 0.95 confidence intervals, Transects 1-4 combined) – **LOESS Regression**, **Higgins Ranch**. A. All data. B. Detail close to prediction lines.

Figure 8. Adults, 2006 – population **dispersal** observed and predicted through the growing season (mean $\pm$ 0.95 confidence interval, Transects 1-4 combined) – **LOESS Regression**, **Higgins Ranch**. A. All data. B. Detail close to prediction lines.

A

B

Larvae density predicted by Kovalev's model in 2006

- - ◆ - - Observed 6-16 to 8-8   - - ■ - - Observed 8-16 to 9-20

——— Kovalev 6-16 to 8-8   ——— Kovalev 8-16 to 9-20

N Larvae/m of branch

Distance from release point (m)

Figure 9. Variations in **large larval population density** along **Transect 2** through the growing season, **2006**, **Higgins Ranch** (mean number per nine 1-m long branches per quadrat counted on each date: quadrats added as the beetles dispersed outward and some earlier quadrats omitted that were defoliated and with low beetle populations – see Figure 10A, B). A) Mean number larvae per branch observed on all 11 quadrats on 17 dates (not all counted on all dates), B) Numbers per branch observed and predicted during two periods: 16 June – 8 August and 16 August – 20 September, using the mean population density for each count date during the two periods – by the **Kovalev Model**.
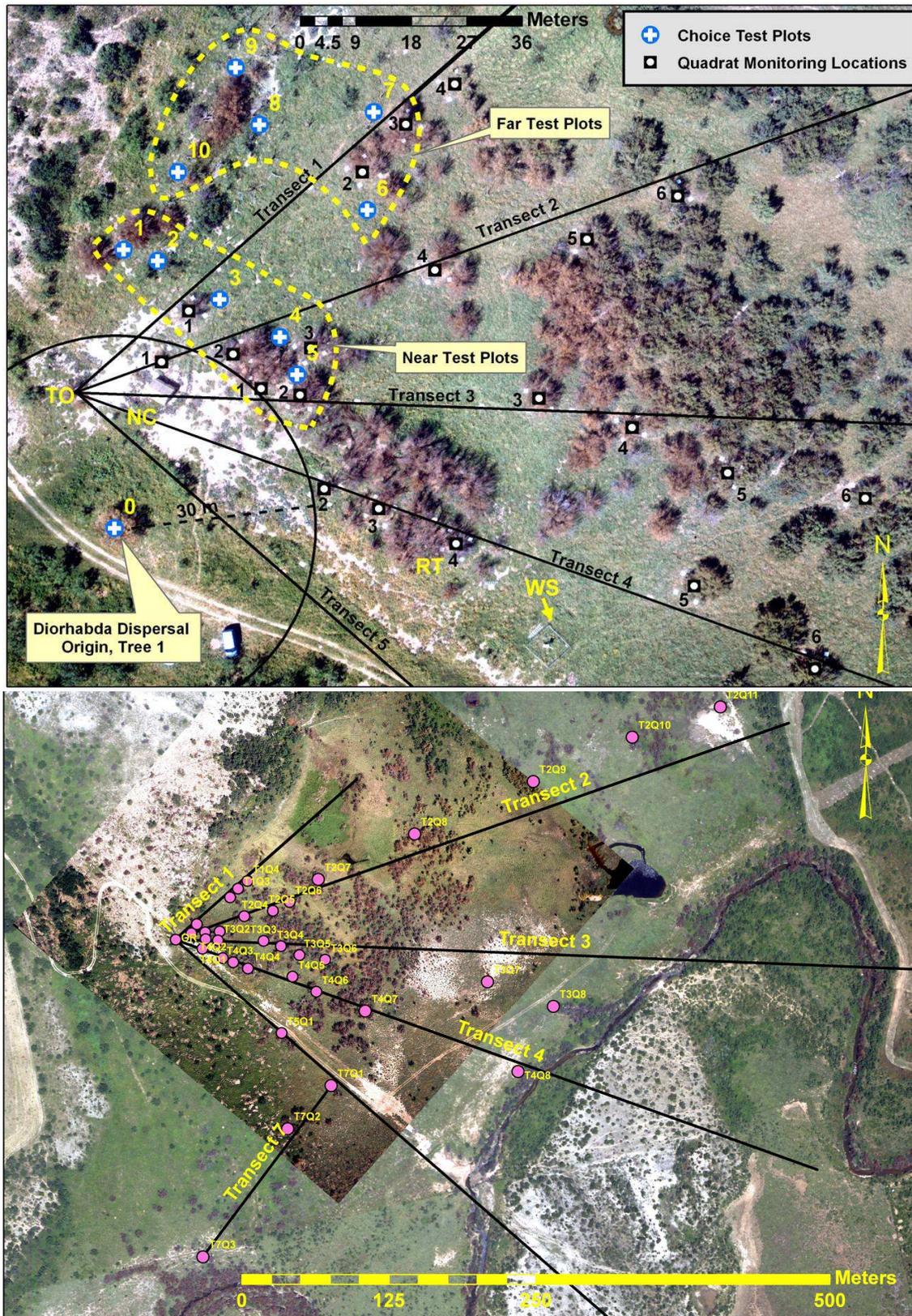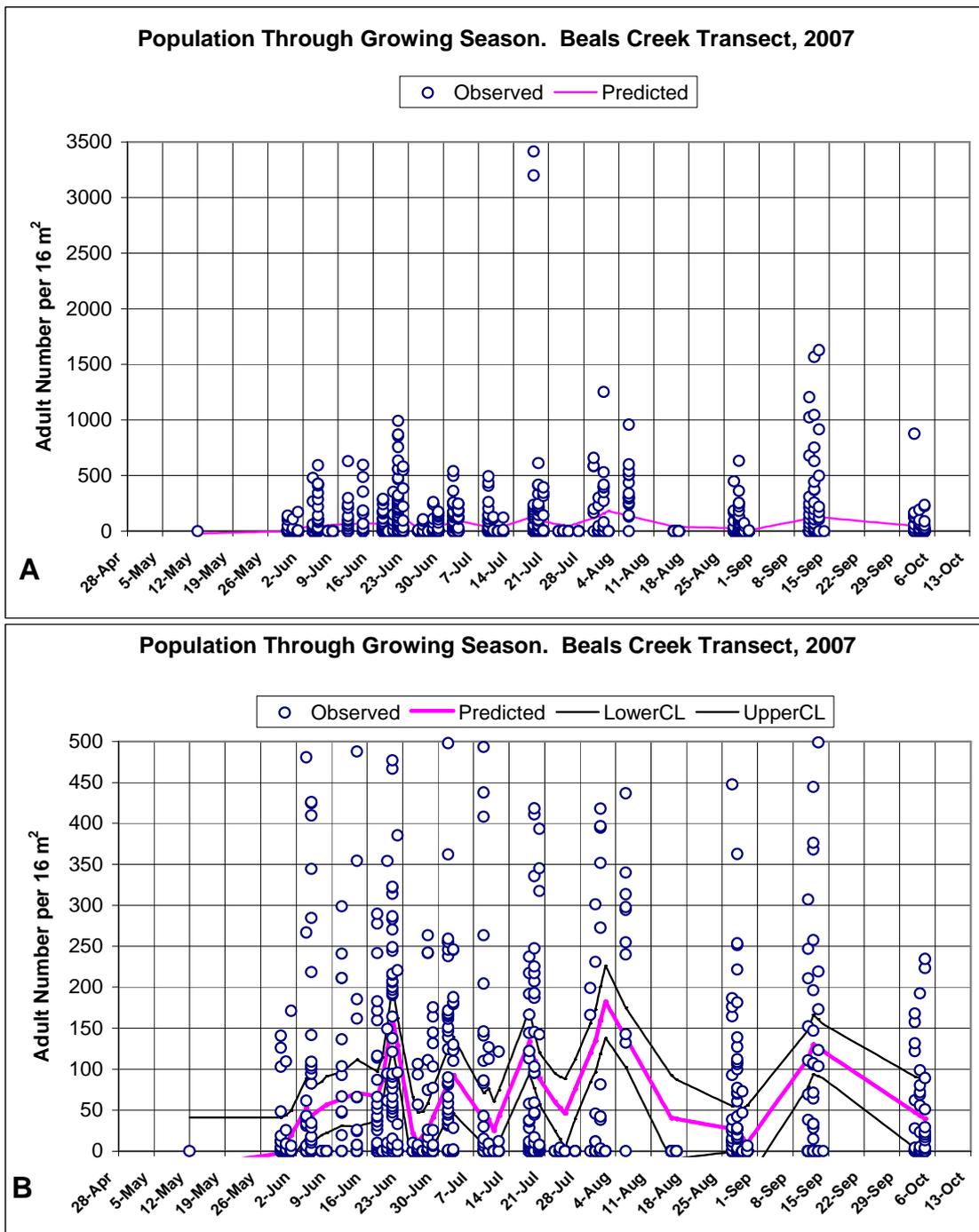
Figure 10. Plot layout of *Diorhabda* (Crete ecotype) open-field, uncaged, host-plant selection test comparing test plants of saltcedar, athel (3-ft tall) and *Frankenia* (8-12 in tall) at each plot or station, monitored weekly June-September; NC=nursery cage, RT=original release tree (beetles did not remain here), WS=weather station, TO=transect origin of large-area transects and sampling Quadrats, and first 2 small trees defoliated (June 2004) and Tree #1=first large tree defoliated (September 2004): A) 2005 test (21 September 2005 photo), B) 2006 test (19 September 2006 photo (aerial photos by James Everitt (USDA-ARS, Remote Sensing Group, Weslaco, TX).
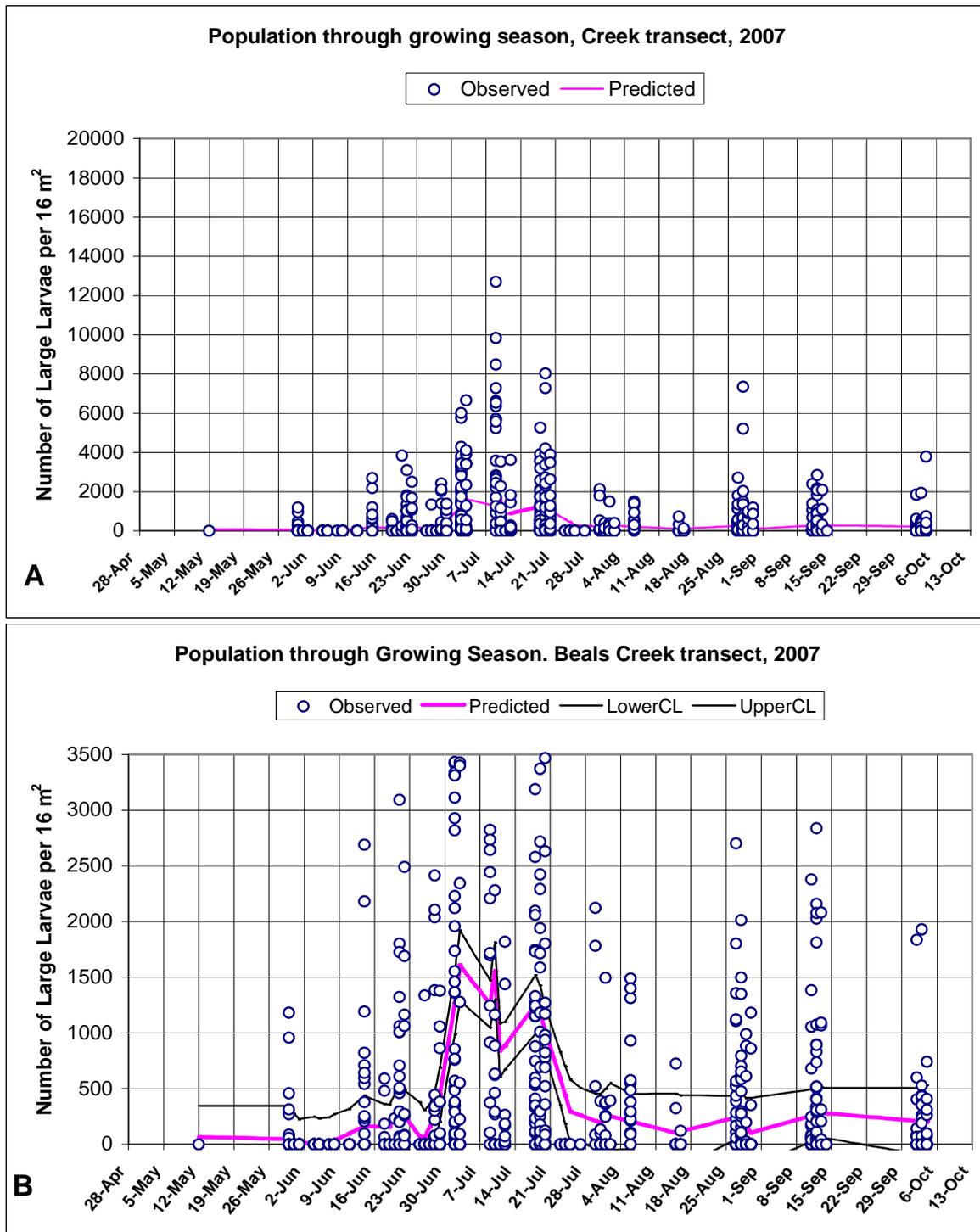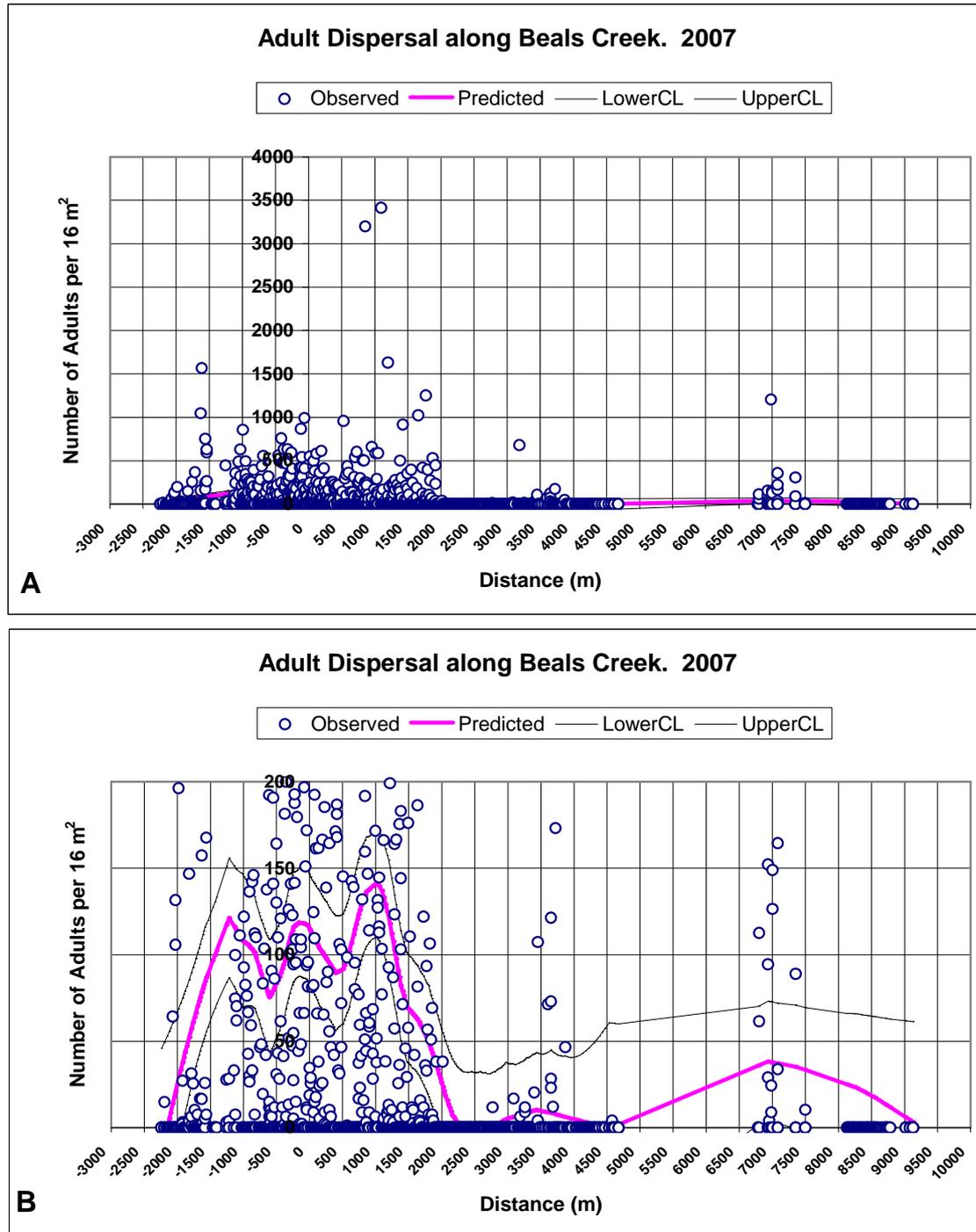
Figure 11. Large larvae, 2007 – population **density** through the growing season (mean $\pm$ 0.95 confidence interval predictions) – **LOESS Regression**, **Beals Creek 12-km long transect**. A. All data. B. Detail close to prediction lines.
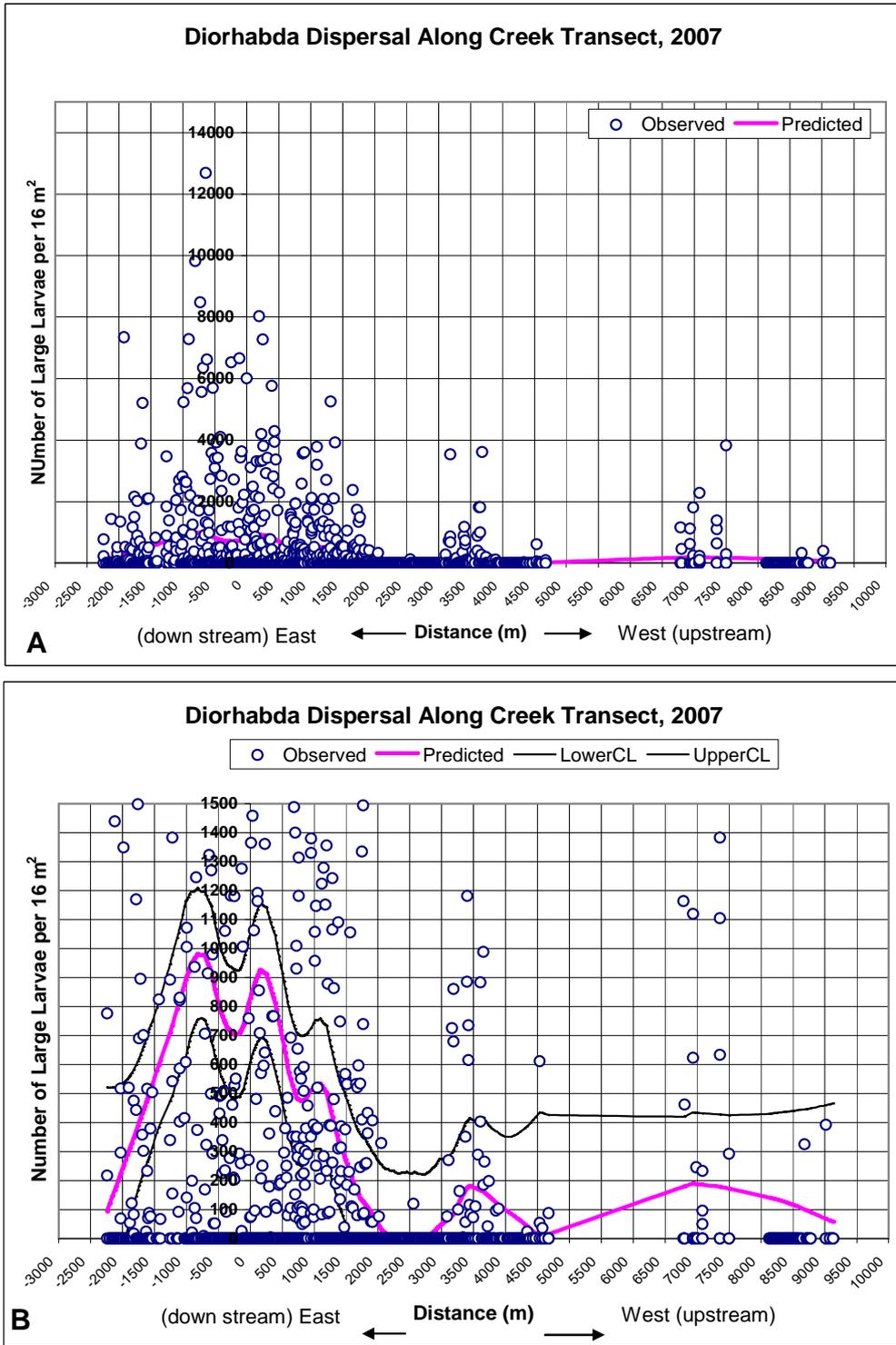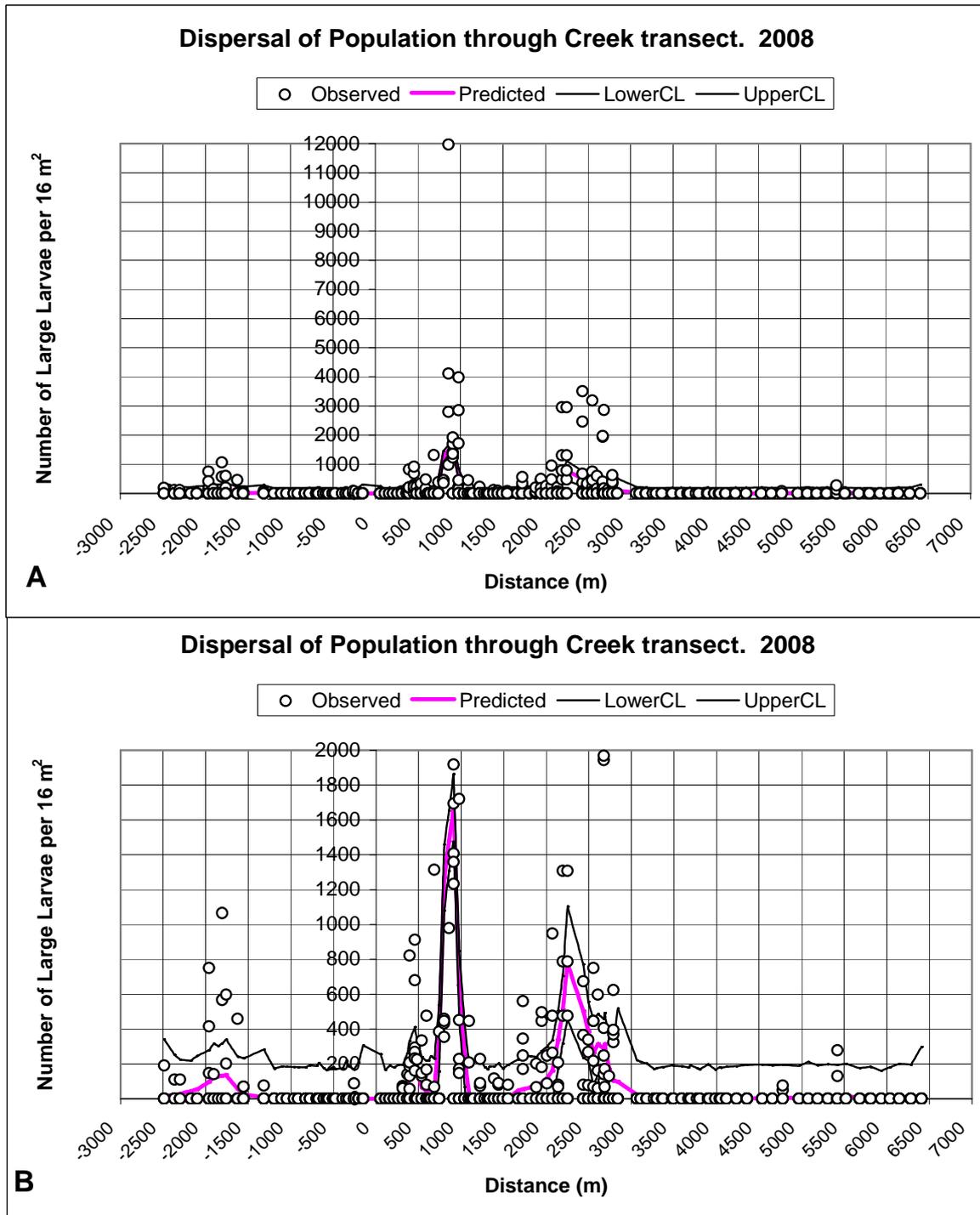
Figure 12. Large larvae, 2007 – population **disperal** through the growing season (mean $\pm$ 0.95 confidence interval predictions) – **LOESS Regression**, **Beals Creek 12-km long transect**. A. All data. B. Detail close to prediction lines.

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Figure 13. Adults, 2007 – population **density** through the growing season (mean $\pm$ 0.95 confidence interval predictions) – **LOESS Regression**, **Beals Creek 12-km long transect**. A. All data. B. Detail close to prediction lines.

Figure 14. Adults, 2007 – population **dispersal** observed and predicted through the growing season (mean ± 0.95 confidence interval predictions) – **LOESS Regression, Beals Creek 12-km long transect**. A. All data. B. Detail close to prediction lines.

Figure 15. Large larvae, 2008 – population **dispersal** through the growing season (mean ±
0.95 confidence interval predictions) – **LOESS Regression**, **Beals Creek 12-km long
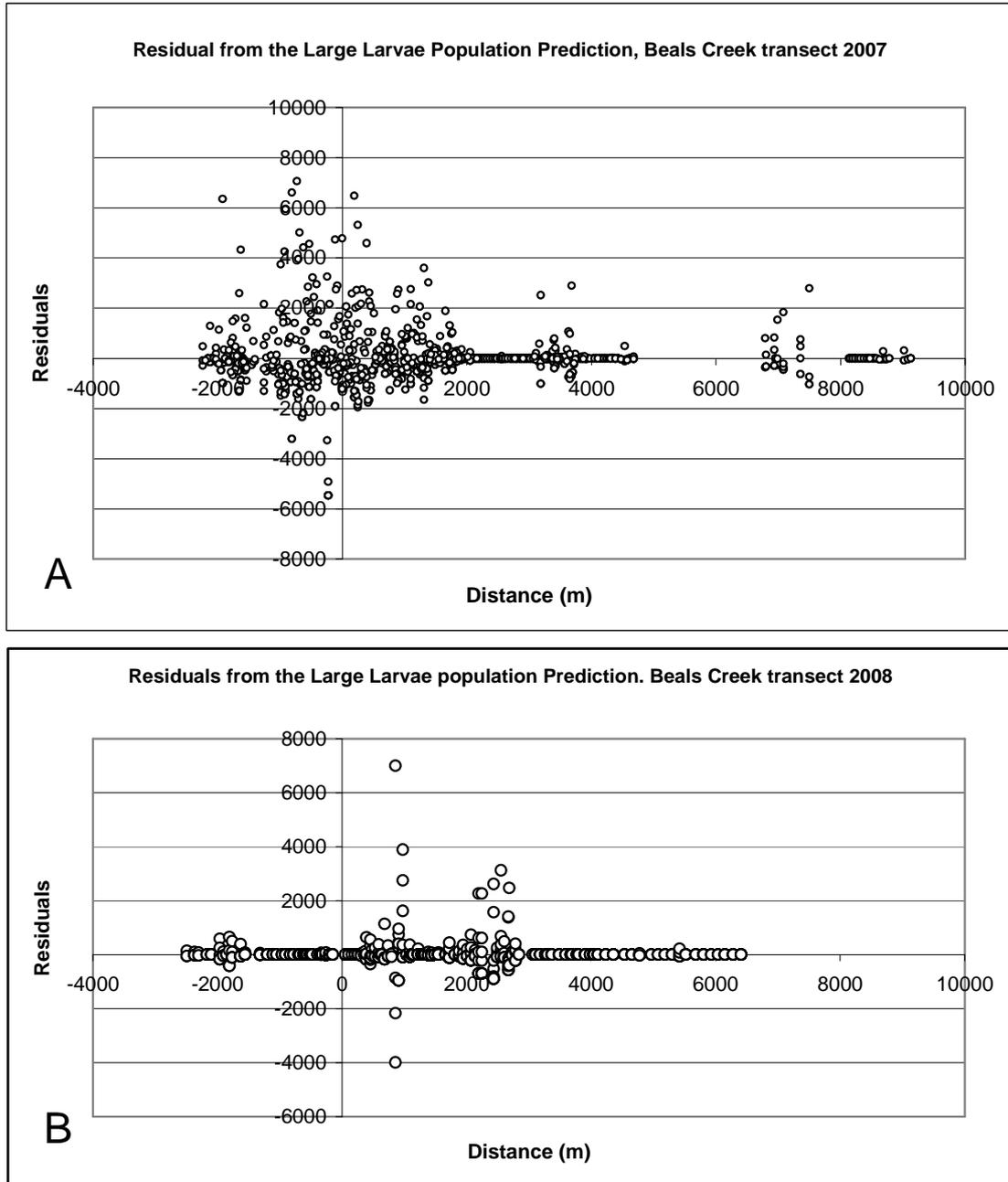transect**. A. All data. B. Detail close to prediction lines.

Residual from the Large Larvae Population Prediction, Beals Creek transect 2007

A

Residuals from the Large Larvae population Prediction. Beals Creek transect 2008

B

Figure 16. Large larvae – residual distributions from prediction – **LOESS Regression**, **Beals Creek, 12-km long transect**. A) 2007, B) 2008.

Figure 17. Distances along the Beals Creek transect and extension of the defoliation in 2007.