Please analyze the attached data for density dependence as described below and then work through the EcoBeaker™ lab on the effects of a Keystone Predator in a marine ecosystem.

**Introduction:**

George Varley and his colleagues at Oxford University in England wanted to find out what caused population fluctuations in the winter moth, *Operophtera brumata*, feeding on oak trees, *Quercus robur*, in Wytham Woods near Oxford. They censused oak trees as shown in Figure 7.1 (from Varley *et al.*, 1973) in order to count the numbers in different life history stages and create a life table. The moth is reproductively active in early winter (hence its name) with males flying actively in November to find large, wingless females as they climb the trunks of oak trees. The females are basically large egg sacks and the winged males mate with them as they climb the trees to lay their eggs on twigs that will carry the new leaves the following spring. These leaves are the larval food.

**Data Observations:**

Observations by George Varley and his colleagues found that there were 4.39 live adult females/m² climbing the trees in November and that each female laid 150 eggs on the bark of oak trees. In spring, there were 96.4 full-
grown larvae/m² and that of these, 6.2/m² were killed by a fly parasitoid, 2.6/m² were killed by other parasites, and 4.6/m² were infected and killed by a microsporidian parasite. From these numbers they determined how many pupae were formed. It was easy to see that 13.4/m² of the pupae were killed by a parasitic wasp, but it was not easy to measure how many were eaten by predators. So predator mortality was estimated from the information gathered. Finally, 7.5 adult females/m² were found climbing the trees in the following November.

From these data, Varley and his colleagues produced the life table shown in Table 7.2 (also from Varley et al., 1973). The research team then went on to collect a further 19 years of data, and these data shown below provide the basis for your exercise in detecting density-dependent mortality factors.

Using the following data, we would like you to determine which mortality factors show the strongest density-dependent regulation of population size (from Varley et al., 1973, Table F) (Data are in this linked spreadsheet).

| Year | stage | 1   | 2   | 3   | 4   | 5   | 6   | 7   | 8   | 9   | 10  | 11  | 12  | 13  | 14  | 15  | 16  | 17  | 18  | 19  |
|------|-------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
|      | k₁    | 1.59| 0.56| 1.14| 1.33| 0.24| 1.16| 0.83| 0.48| 0.83| 1.15| 1.21| 0.91| 1.09| 0.85| 0.66| 0.52| 1.42| 1.20| 1.19|
|      | k₂    | 0.07| 0.01| 0.00| 0.03| 0.01| 0.04| 0.03| 0.02| 0.07| 0.10| 0.02| 0.02| 0.02| 0.01| 0.01| 0.01| 0.01| 0.01| 0.01|
|      | k₃    | 0.05| 0.05| 0.04| 0.06| 0.04| 0.02| 0.05| 0.04| 0.02| 0.03| 0.03| 0.03| 0.01| 0.01| 0.01| 0.01| 0.03| 0.03| 0.03|
|      | k₄    | 0.69| 0.77| 0.75| 0.34| 0.73| 0.65| 0.47| 0.79| 0.82| 0.66| 0.72| 0.22| 0.40| 0.74| 0.87| 0.86| 0.50| 0.48|
|      | k₅    | 0.29| 0.10| 0.03| 0.16| 0.07| 0.09| 0.28| 0.20| 0.16| 0.15| 0.45| 0.08| 0.06| 0.12| 0.14| 0.13| 0.33| ---| ---|

Note: In the linked data sheet, estimates of the missing data have been added to make it easier for you to use Excel (it is important to note that Excel is not a reliable program to use for data analysis – we use it because it is readily available and illustrates the methods we are emphasizing).

To do this we would like you to do the following:

1. Enter the data vertically as shown in the attached Excel sheet (do not enter zero for missing data points) and calculate \( K_{total} \) values for each year (sum each \( k_x \) value).

2. Draw a graph using the graph wizard of each \( k_x \)-value and \( K_{total} \) (y-axis) plotted against time (year) on the x-axis. Which \( k_x \) values do you think are most responsible for overall mortality?
(3) Using the “Tools” menu select “data analysis” and then “regression” and use linear regressions to regress each $k_x$ value as the dependent variable against $K_{total}$ values as the independent variable across all 19 years. This will give you 6 separate analyses.

For each analysis do the following once you have selected “regression”:

**Input Y:** enter the range for your $k_x$ values (including the column title) e.g. $B$1:$B$20 (the $ just means that you have fixed that cell and it won’t change - this is the range of data from cell B1 to cell B20 in the B column and rows 1 to 20).

**Input X:** e.g. $H$1:$H$20 (if $K_{total}$ is in column H).

**Check the labels box:** (this indicates that you have included the column headings)

**Output options:** indicate where you want the regression analysis to be placed (e.g. if you enter A23 the analysis will start at cell A23 in the top left hand corner)

**Residuals:** check the “line fit plots” option (this will automatically plot a graph of the data and the regression as a series of predicted points).

This analysis will tell you which mortality factors have a significant density dependent association with total mortality. From the summary output you need the R square value, and from the ANOVA table you need the F and significance of F values (these tell you whether the regression was significant - any significance value less than 0.05 is significant (very low probability (less than 5%) that they are the same), and lastly you need the coefficients for the intercept on the y-axis and the slope (b) which is the coefficient under the intercept (its P-value will be the same as the ANOVA “Significance F” value).

For each of these 6 regressions, make a summary table that gives the comparison (e.g. $k_1$ against $K_{total}$), then the $R^2$, intercept, regression coefficient (slope or b), F, and Significance F (P-value).

(4) In the same way as for (3) above, plot each $k_x$ value against the logarithm of the density of the stage on which the mortality acted. To do this you will need to calculate these densities using the log larvae data. For example, $k_1$ was the mortality that acted on the eggs and so the actual density was (log larvae + $k_1$). Similarly you should appreciate that $k_2$ acted on log larvae, but $k_3$ acted on (log larvae - $k_2$), and $k_4$ acted on (log larvae-(k_2+k_3)), etc.

When you have completed these regressions, make a summary table as in (3) of the regression statistics.
(5) Using the two tables from (3) and (4) write up your conclusions about what mortality factors \( (k_x) \) were responsible for density dependent mortality and density-dependent regulation of this population of winter moths.

References:

**Fig. 7.1** Adult female winter moth are counted in moth traps on the tree trunks, their larvae are counted in the caterpillar trays into which they fall when prepupal. Larvae of the parasite *Cyzicus* are counted by dissection of the fallen caterpillars. Adults of *Cyzicus* and of *Craticheumon* are counted on emergence from the soil into the parasite traps. From Varley (1971).
Food web structure and the effects of a keystone predator as described in lecture 20.

Work through the “EcoBeaker” student workbook for “Keystone Predator” and while you do this keep in mind that the processes of both competition and predation and their influence on community structure are at work!

More information about EcoBeaker software is available at the SimBiotic Software website at:
http://www.simbio.com/

EcoBeaker™: Keystone Predator (101)

This laboratory recreates the famous experiments of Paine and colleagues in the Pacific Northwest with the sea star Pisaster (and 8 other marine intertidal species). Students do transplant experiments to figure out competitive relationships and sample gut contents to construct a food web. Next they use their data to predict what will happen when each predator is removed from the system. Finally, they do the removal experiments and compare their results with their predictions. This is a great introductory lab in that it explores basic ecological concepts and although it is not difficult, it asks students to think critically, synthesizing experimental data to make predictions. It also provides a nice foundation for discussions of the important roles that different species can play in a community.

PRIMARY CONCEPTS: food-webs; community structure; competition; keystone species