The Mathematics Behind Biological Invasions
Project Ideas

1. **Invasible species and habitats** The conventional wisdom among ecologists holds that

    - species that are able to live in a wide variety of habitats (*habitat generalists*) are more likely to be invaders than species with very specific habitat requirements (*habitat specialists*);
    - habitat specialists are able to outcompete habitat generalists in the habitat for which they are specialized;
    - disturbed or fragmented habitats are more invasible than "pristine" habitats.

    In a recent manuscript, Marvier et al. (*Risk Analysis*, in press) formulated a patch-occupancy metapopulation model to examine the relationship between these observations. The model has three species (two habitat specialists and one habitat generalist) and three types of habitat (one for each of the specialists and uninhabitable habitat). Their analysis showed that, in this model, habitat loss, habitat fragmentation, and habitat disturbance all tended to favor the generalist species over the specialists. There are a number of ways that this model could be improved/generalized. The objective of this project is to pick one of these improvements, and to see how the results of the Marvier model change (if at all).

2. **Resource fluctuation and invasibility** Davis, Grime and Thompson [*J. Anim. Ecol.* (2000) 88:528-534; see also Davis and Pelsor *Ecol. Lett.* (2001) 4:421-428] claim to have formulated "a new theory in which fluctuation in resource availability is identified as the key factor controlling invasibility, the susceptibility of an environment to invasion by non-resident species." They claim that "the theory is mechanistic and quantitative in nature leading to a variety of testable predictions." Yet in the paper, there is not a single equation. Can you covert their verbal "theory of fluctuating resource availability" into a mathematical model?

3. **Allee effects in a predator invasion** Allee effects can arise in mathematical models in surprising ways. In a recent paper, Neubert, Kot and Lewis [*Proc. Roy. Soc. Lond. B.* (2000) 267:1603-1610] studied the wave of advance of a predator into a fluctuating prey population. For certain parameters, the model has two attractors: one without predators and one at which both species co-exist. This creates an Allee effect for the predator. Since the invasion speed formulae they derived do not hold in the presence of an Allee effect, they did not calculate wave speeds for these parameters. Can you?

4. **Re-invasion of Otters to California's Costs** One example of a biological invasion is the spread of a re-invading sea otter species off the coast of California. It was thought to be extinct until a relict population was found off Point Sur in 1914. Under protection from hunting it grew and spread spatially, and now it calls much of the west coast of North America its home. Details on the early spatial spread are given in the attached table and figure. Most of the sea otter activity occurs within 1 km of the coast, and so the spread can thought to be linear (up and down the coast).

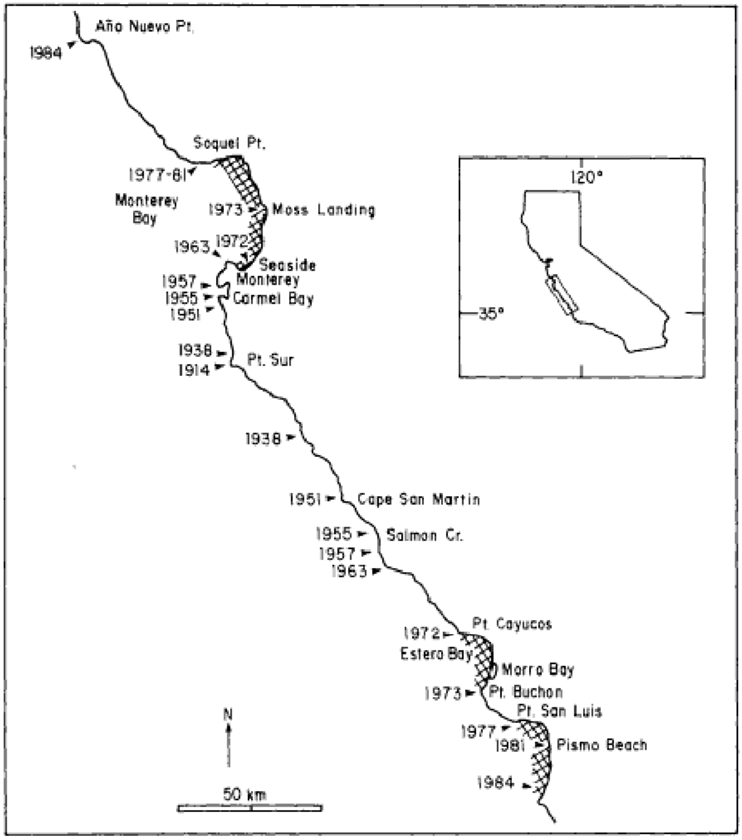

FIG. 1.—Expansion of the range of the California sea otter along the central California coast. Only representative locations of the position of the range boundaries are shown. Point Sur is the traditional location of the division of the range into northern and southern halves. *Crosshatching*, the approximate location of sandy or soft-bottom habitats. Data are taken from table 1. (Map after Wild and Ames 1974.)

RANGE EXPANSION OF SEA OTTERS

TABLE I

RANGE EXPANSION AND POPULATION SIZE OF THE CALIFORNIA SEA OTTER ALONG THE CALIFORNIA COAST (IN km)

Year	Extent of Range Increase: North	Extent of Range Increase: South	Estimated Total Range	Population Size
1914	?	?	(11)	(50)
1938	11	(21)	43	310
1947	8	23	74	530
1950	2	13	89	660
1955	3	16	108	800
1957	11	6	125	880
1959	6	6	137	1050
1963	5	10	152	1190
1966	0	6	158	1260
1969	6	13	177	1390
1972	0	15	192	1530
1973	23	29	244	1720
1974	6	5	255	1730
1975	8	0	263	?
1976	10	6	279	1789
1977	8	6	293	?
1978	0	0	293	?
1979	0	6	299	(1443)
1980	0	13	312	?
1982	0	0	312	1338
1983	26	15	353	1226
1984	0	0	353	1203
1986	?	?	?	1400

NOTE.—The extent of the range is determined by the linear distance along the coastline between the outermost main raft of otters at the population boundaries. Point Sur was used as the location of the division between the northern and southern populations. The total estimated population size was based on aerial and shore counts. Parentheses indicate that the estimate was considered unreliable; a question mark means that no estimate was made.

SOURCES.—E. Ebert, pers. comm.; Riedman and Estes, MS; Estes, unpubl. data.

Plot the distance spread versus time in northward and southward directions. Also plot the total range radius versus time. Discuss why spread may be different in north and southward directions. Come up with a mathematical model for the spread process. You may want to research into the life history of sea otters and consider stage structure so as to make your model realistic.

5. **Zebra mussel invasion of the Great Lakes** The spread of zebra mussels across the eastern North American landscape has been closely monitored since their initial North American discovery in 1988. Range expansion quickly occurred throughout commercially navigable waters, but overland dispersal to inland lakes has been slower. The first US inland lake colonization occurred in 1991 in northeast Indiana, and by December 1997 only 56 inland lakes were colonized in Michigan (37 lakes) Indiana (12 lakes), Wisconsin (6 lakes) and Illinois (1 lake). Although many potential mechanisms for dispersal exist, the overland transport of recreational boats is widely believed to be the primary vector for zebra mussel dispersal into inland lakes.

   The paper by Bossenbroek et al. (2001) models the spread of zebra mussel using "production constrained gravity models". Read the paper. How do these models work? Create your own gravity model for a system of 100 inland lakes (you decide the configuration and sizes of the lakes). Try both the deterministic and stochastic formulations, and program a simulation of the model. How much variability is present in the stochastic version? How sensitive is spread rate (number of newly infected lakes per year) to lake size, to distances between lakes, and to other factors?

6. **Escape of farmed Atlantic Salmon** By the end of this decade, world-wide production of farmed salmon is estimated to reach 2,000,000 metric tons and almost all farmed salmon production takes place in sheltered areas of the coastal zone. Escaped salmon may live in the wild and/or hybridize with wild fish. In the case of farmed Atlantic salmon on the west coast of Canada, escaped populations of farmed Atlantic salmon may be living in the wild. The review article by Milweski is a good place to start reading about impacts of salmon aquaculture on the coastal environment.

   Assuming that the Atlantic salmon population dynamics include an Allee effect (depensation), use a model to estimate the rate of release from farms that would be required to allow for establishment of a reproducing wild population. Start with a nonspatial model, then proceed to a spatial model where the salmon farms are point sources distributed in space, and the salmon move spatially.

7. **Comparison of spread rate estimates** Models for population spread need dispersal kernels. Kot *et al.* (1996) included the dispersal kernels into integrodifference models to assess the effect of the shape of the kernel on spread rates. These kernels were based on R. A. J. Taylor's (*Ecological Entomology* 1978 volume 3, pages 63-70) summary of Dobzhansky and Wright (1943) measurements of the dispersal of genetically marked *Drosophila* from a point source.

   Kot *et al.* (1996) found that when the dispersal kernels were put into an integro-difference model with Beverton-Holt dynamics, spread rates were very sensitive to the precise shape of the dispersal kernel.

   In this project, you are asked to use the empirical estimator and furthest-forward estimators (covered in class) to calculate the spread rates.

   Start by going over your class notes, the Kot *et al.* (1996) paper and the methods for calculating empirical and furthest-forward estimators. Create a program to calculate the spread rate for an integrodifference model, given R_0 and the dispersal kernel k. Extend this to include the empirical estimator, which requires R_0 and the measured dispersal distances $x_1, \ldots, x_N$. Use the dispersal distances measured by Dobzhansky and Wright. Compare the spread rate prediction from the empirical estimator with the prediction in Kot *et al.*. Bootstrap your dispersal distance data to get a range of different spread rates, and using this method, construct a 95 per cent confidence interval on the spread rate.

   Next calculate the spread rate using the furthest-forward estimator, and some of the kernels used in Kot *et al.*. How do the estimates differ? Compare and contrast the different estimators.

8. **Modeling spatial competition using PDE/IDE models** Two different questions, one more technical and one more biological:

   (1) numerically, under what parameter ranges does the linearization give the correct spread rate? It turns out that the linearization does not always give the correct spread rate (this can be seen numerically, but technical details of the proof are given in Spreading speed and linear determinacy for two-species competition models J. Math. Biol. 45, 219-233 2002).

   (2) can the competition model be extended and modified to describe invasion of brook trout into bull trout habitat? Here the growth rate of each species is temperature dependent (bull are endangered and prefer cold), and there tends to be a temperature trend along a stream (from cold up high to warmer down low). The result should be an invasion that stalls and then forms a cline.