TIEE

Teaching Issues and Experiments in Ecology - Volume 1, January 2004

ISSUES – FIGURE SET

Controlled fire, © Konza Prairie LTER, Manhattan, KS {www.konza.ksu.edu/ gallery/hulbert.jpg}

Ecology of Disturbance

Charlene D'Avanzo, School of Natural Sciences
Hampshire College, Amherst, MA, 01002
cdavanzo@hampshire.edu

Figure Set 1: Intermediate Disturbance Hypothesis

Purpose: To illustrate the intermediate disturbance hypothesis with 2 field experiments.
Teaching Approach: "Pairs Share"
Cognitive Skills: (see Bloom's Taxonomy) — comprehension, interpretation, application, analysis
Student Assessment: Take home or in class essay quiz

BACKGROUND

W. Sousa (1979)

In this study, Wayne Sousa tested the intermediate disturbance hypothesis proposed by Connell (1978). In the 70's and 80's ecologists hotly debated factors explaining high diversity in tropical regions and bottom of the deep sea. Popular ideas included: the time hypothesis (older communities are more diverse), the competition hypothesis (in agreeable climates where biological and not physical factors prevail, interspecific competition and niche partitioning results in high diversity), and the environmental stability hypothesis (relatively unchanging physical variables allow more species to exist). Connell questioned all of these and reasoned instead that highest species diversity exists under conditions of intermediate disturbance. He proposed that in recently disturbed communities a few early colonizing species prevail; similarly after a long time diversity is also low, but these few are long-living and competitively dominant organisms. Diversity would therefore be greatest at intermediate points when a variety of species had colonized a habitat but competitive exclusion had not yet taken place.

As Peters (1991) piercingly explains (see Overview) the ecological diversity debates have been plagued by imprecise definitions and inattention to operationalizing hypotheses. One advantage of Connell's Intermediate Disturbance Hypothesis was that it could be experimentally tested as Sousa did in his field study.

Sousa examined effects of wave movement on diversity of organisms living on boulders along beaches in California. In this study Sousa first determined the relationship between boulder size and force required to move them. As expected, small boulders moved often, large ones seldom; when boulders rolled over attached species become damaged or dislodged. Measurement of various sized boulders therefore allowed Sousa to examine a gradient of disturbance frequency and intensity.

Sousa found few species on small boulders; the ones there were opportunistic early colonizers such as sea lettuce (*Ulva*) and barnacles (*Chthamalus*). On the largest boulders species diversity was also low, but in this case a competitively dominant and late colonizing red algae was most abundant (*Gigartina canaliculata*). Highest diversity was seen on the boulders intermediate in size. These rocks supported early and late colonizers and also bare spots.

To measure the force necessary to move boulders of different sizes Sousa pulled boulders with a chain attached to a spring scale; he pulled in the direction of incoming waves and converted the measured dislodging force from kilograms to Newtons (N).

J. Lubchenco (1978)

Jane Lubchenco expanded the research of her mentor, Bob Paine, by looking at effects of the herbivorous snail *Littorina littorea* on diversity of macroalgae on the New England (MA) coast. She studied both tidepools in the upper intertidal zone and rock surfaces lower down.

In the tidepools, Lubchenco first observed that algal diversity could be quite different from pool to pool. Some were dominated by one species (such as the green alga, *Enteromorpha intestinalis*) while others supported 10 or more algal species. Snail density also differed between pools. Lubchenco conducted 2-way choice laboratory studies on food preferences of the snails. *Enteromorpha* was clearly a preferred food while others such as the red alga, *Condrus crispus*, was not.

In the field, Lubchenco manipulated snail density in studies lasting several years. In the tidepools she found that algal species diversity was highest in pools with intermediate snail numbers (about 100-200 m^{-2}). At low snail densities, *Enteromorpha* out competed other seaweeds, and the pools looked emerald green. At high densities the snails consumed all the preferred algae and only the inedible *Chondrus* and encrusting corraline algae remained.

The relationship between snail density and algal diversity was different on the exposed rock faces in the lower intertidal zone. Here diversity decreased with snail density. The snail's food preferences remained the same, but physical disturbance by ice and intense waves limited competition of ephemeral seaweeds like *Enteromorpha*. At low snail densities more than a dozen algae coexisted; seaweeds grew on bare patches and on each other. As their number increased snails ate preferred algae with declines in diversity as a result.

Literature Cited

Connell, J. H. 1978. Diversity in tropical rainforests and coral reefs. Science 199: 1302-1310.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive ability. American Naturalist 112: 23-39.

STUDENT INSTRUCTIONS

To prepare the class for a discussion of disturbance and the intermediate disturbance hypothesis you have data from either of 2 papers. One is Wayne Sousa's 1979 study called "Disturbance in marine intertidal boulder fields: the non-equilibrium maintenance of species diversity" (*Ecology* 60: 1225-1239). The other is Jane Lubchenco's 1978 study. "Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive ability." (*American Naturalist* 112: 23-39) Both focus on the intertidal zone between high and low water on coasts.

In this "pairs-share" you first work on your figure/table by yourself. Use the step one-step two approach you have practiced in class (see footnote below). After this you will pair up with a student who has focused on the other study and the two of you will explain the figures/table to each other in class. When you finish this compare and contrast the studies and make a list of similarities and differences.

Sousa Study

Wayne Sousa tested the intermediate disturbance hypothesis proposed by Connell (1978). In the 70's and '80's ecologists hotly debated factors explaining high diversity in tropical regions and the deep sea. Popular ideas included: the time hypothesis (older communities are more diverse), the competition hypothesis (in agreeable climates where biological and not physical factors prevail, interspecific competition and niche partitioning results in high diversity), and the environmental stability hypothesis (relatively unchanging physical variables allow more species to exist). Connell questioned all of these and reasoned instead that highest species diversity exists under conditions of intermediate disturbance. He proposed that in recently disturbed communities a few early colonizing species prevail; similarly after a long time diversity is also low, but these few are long-living and competitively dominant organisms. Diversity would therefore be greatest at intermediate points when a variety of species had colonized a habitat but competitive exclusion had not yet taken place.

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Lubchenco Study

Jane Lubchenco looked at effects of the herbivorous snail *Littorina littorea* on diversity of macroalgae (seaweed) on the New England (MA) coast. She studied both tidepools in the upper intertidal zone and on surfaces of very large (immovable) rocks lower down in the low intertidal zone. (The intertidal zone is the zone between highest and lowest tides).

The research began from visual observations. In the tidepools, Lubchenco noticed that algal diversity was different from pool to pool. Some were dominated by one species (such as the green alga, *Enteromorpha intestinalis*) while others supported 10 or more seaweed species. Snail density also differed between pools. Lubchenco then conducted 2-way choice laboratory studies on food preferences of the snails. *Enteromorpha* was clearly a preferred food while others such as the red alga, *Condrus crispus* was not.

In the field, Lubchenco manipulated snail density in studies lasting several years. She measured diversity of seaweed in the pools and on the rock surface and compared the relationship between snail density and algal diversity in the two habitats.

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* In step one you first figure out how the figure or table is set up (e.g. what the labels on the axes mean). You also need to have a pretty good idea of the experimental design - how Sousa or Lubchenco set up the experiments - and the hypotheses the scientists address. In step two, you can go on to interpreting the data. For both steps, write down any questions you have.

FIGURES

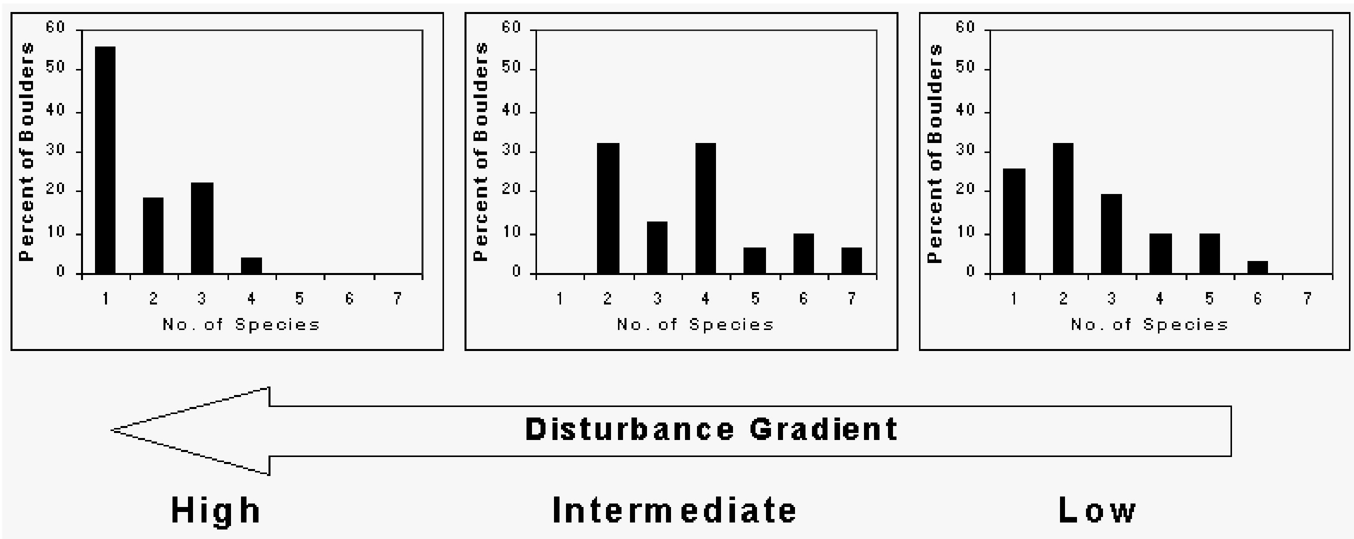

Figure 1A. Degrees of disturbance and species diversity of algae on intertidal boulders in the intertidal zone in Nov. Data are from 6 permanent plots mapped and photographed monthly for 2 years. High disturbance = 42% disturbance frequency per month (less than 49 Newtons), Intermediate = 9% per month (50-294 N), Low = 1% per month (more than 294 N). From W. Sousa. 1979. Disturbance in marine intertidal boulder fields: the non-equilibrium maintenance of species diversity. Ecology 60: 1225-1239.

	Incidence of disturbance		
	Frequent	Intermediate	Seldom
Nov. 1975	1.7 ± 0.18	3.3 ± 0.28	2.5 ± 0.25
May 1976	1.9 ± 0.19	4.3 ± 0.34	3.5 ± 0.26
Oct. 1976	1.9 ± 0.14	3.4 ± 0.4	2.3 ± 0.18
May 1977	1.4 ± 0.16	3.6 ± 0.2	3.2 ± 0.21

Table 1. Species diversity (Average ± Standard Error) of macroalgae on boulders subject to 3 degrees of disturbance. Frequent = rock size requiring less than 49 Newtons (N) to move horizontally, intermediate (50-294 N); seldom (more than 294 N). From W. Sousa. 1979. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. Ecological Monographs 49: 227-254. and I. Valiela. 1995. Marine Ecological Processes, Springer-Verlag, New York.

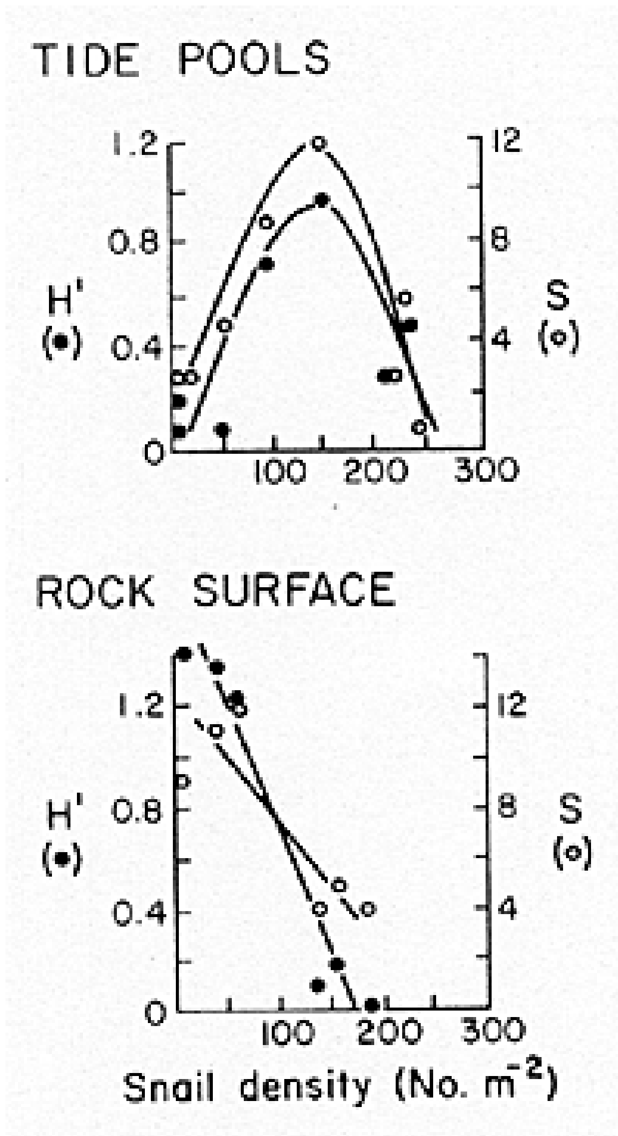

Figure 1B. Effect of density of the herbivorous snail *Littorina littorea* on diversity of algae in tide pools and rock surfaces on the New England coast. H' is the Shannon-Weaver diversity index and S is the number of species. From J. Lubchenco. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive ability. American Naturalist 112: 23-39, and I. Valiela. 1995. Marine Ecological Processes, Springer-Verlag, New York.

FACULTY NOTES

Pairs-share

For this pairs-share approach give half the class the Sousa data and the other half the Lubchenco data (that is, individual student are given - or have access to - one of the data sets). Students first work on the data sets alone. This can be done in class or as a homework assignment. In the next step the "Sousas" talk to each other ("Lubchencos" as well) to make sure everyone understands their data well enough to explain it to someone else. Then allow students to pair up in class: the "Sousas" explain their study to the "Lubchencos" and visa versa. (The directions to students asks them to write down similarities and differences between the two studies which emphasizes the application skill. If students do this be sure do ask for examples from their lists.) Finally, show each data set to the class as a whole and lead a discussion and ask questions.

You can also simply project the data and lead a discussion, or alternatively ask students to think-pair-share and then go into discussion.

Either study will nicely introduce the concept of disturbance to students because the approaches are straightforward and the data quite accessible. In addition, the research does not focus on catastrophes such fires or hurricanes, and therefore students can better appreciate how ecologists define and study disturbance (e.g. that it is not "bad"). Both studies look at disturbance on a small or local scale and could also stimulate a discussion of the importance of scale in ecological thinking.

You might choose to tell students about Connell's ideas concerning the intermediate disturbance hypothesis and ask them to explain how the studies test the hypothesis.

Sousa study

You can use both the figure and table or just one of them. For a quick introduction to disturbance, project only the figure (or table) and lead a discussion.

Discussion questions & topics include:

- Contrast the likely life history characteristics of the most abundance species on boulders that roll over often vs. those that move seldom.

- Describe what typical boulders in the 3 disturbance categories would look like (e.g. the kinds of organisms, other characteristics).

- Sousa measured movement of the rocks with a spring scale. What assumptions did he make using this approach?

- For many years ecologists have debated what is meant by "disturbance". What aspects of disturbance does Sousa look at in his study? (Here you might ask students to list different possible ecological meanings for the term disturbance. These might include catastrophic events such as hurricanes, small-scale events such as tree falls, man-made vs. more natural events, and disturbances caused by organisms including herbivory or diseases)

For practice on data manipulation and presentation ask students to make a figure from the data in the table. They don't necessarily need graph paper for this; they can simply sketch the figure on a piece of paper. You could ask students to sketch the figure on their own first and then compare their figure with efforts of others around them before going into a general discussion. Time allotment for this exercise will depend on the students' familiarity with making figures and with means and standard errors. This exercise emphasizes application and analysis.

Lubchenco study

For a simple discussion you can use both parts of the figure or just the tidepool data (which is most commonly seen in ecology texts). Students may not be familiar with double Y plots and you might want to explain this ahead of time. Most students will also not know the Shannon-Weaver index. To introduce the index ask students how they would measure diversity of species in a place (use a local example); students will likely say that they would count species. Follow this by asking the limitations of a simple species count and lead into a discussion of uneveness of species distributions.

Discussion questions include:

- What are some different ways that ecologists could examine food preferences by snails in the laboratory (experimental designs)?

- Describe the appearance of tidepools with few, some, many snails - if you were standing next to the pools, what would they likely look like?

- Explain the interplay between physical disturbance and competition between algae in the lower intertidal exposed rock zone.

- Why might snails prefer some algae over others?

- Imagine what 300 snails m-2 in a tidepool looks like. Is this a reasonable density for snails in this habitat? Why is this an important question?

Student Assessment: Take home or in class essay quiz.

Use one or more of the questions above as a test question and ask students to write a brief essay.

Evaluating an Issue: How do you know whether it is working?

On-going (also called formative) evaluation of the approaches your are using is critical to the success of student-active teaching. Why try out new ideas if you don't know whether or not they are working? This is a brief overview of formative evaluation. For more information, go to the Formative Evaluation essay in the Teaching Section.

Course Goals:

Formative evaluation only works if you have clearly described your course goals - because the purpose of the evaluation is to assess whether a particular technique is helping students reach these goals. For instance, most of us have "learn important ecological concepts and information" as a course goal. If I reviewed the nitrogen cycle in a class, for evaluation I might ask students to sketch out a nitrogen cycle for a particular habitat or system. Each student could work alone in class. Alternatively, I might ask students to work in groups of 3 and give each group a different situation (e.g. a pond receiving nitrate from septic systems, an organic agricultural field, an agricultural field receiving synthetic fertilizer). The students could draw their flows on a large sheet of paper (or an overhead transparency) and present this to the rest of the class.

The Minute Paper:

Minute papers are very useful evaluative tools. If done well they give you good feedback quickly. Minute papers are done at the end of a class. The students are asked to respond anonymously to a short question that you ask. They take a minute or so to write their response in a 3x5 card or a piece of paper. You collect these and learn from common themes. In the next class it is important that you refer to one or two of these points so that students recognize that their input matters to you. The UW - FLAG site (www.wcer.wisc.edu/nise/cl1/flag/) gives a good deal of information about using minute papers including their limitations, how to phrase your question, step-by-step instructions, modifications, and the theory and research behind their use.