Reports

Disaster, Catastrophe, and Local Persistence of the Sea Palm *Postelsia palmaeformis*

Abstract. *Two components of natural disturbance, its local intensity and frequency beyond a threshold level, limit a marine benthic alga to wave-swept shores. Transplant experiments indicate that the limited distribution is not due to physiological restriction. Instead, it requires predictable annual disturbance of moderate intensity for local persistence.*

Few if any naturally occurring populations are immune to disruptions of variable magnitude and cause, implying that spatially local, nonequilibrium conditions are characteristic rather than exceptional (*1*). That broad category of species utilizing, probably depending upon, and certainly characterizing spatiotemporal irregularities in critical resources have long been termed fugitive (*2*). Understanding their dynamics and the dynamics of the biotope in which they occur has generated mathematical focus (*3*) and recent interest in specific colonization or resource holding strategies (*4*). It is becoming increasingly certain that either selective removal of competitively dominant species or generalized disturbance drives these systems because, in the absence of such disruptions, they tend toward equilibrium conditions (*5*). Models of disturbance-mediated systems indicate that rate of resource release, its timing, spatial scale, magnitude, and periodicity are major parameters (*6*). Harper (*7*) has developed a convincing argument that ecologically significant catastrophes (defined as infrequent extreme events destroying large portions of a population) and disasters (disruptive influences of more local scale and greater relative frequency) should be distinguished when evaluating the organism-environment relationship. Although these categories are obviously portions of a disturbance continuum, they can generate varying genetic consequences, with some species evolving a dependency on disasters but being incapable of an adaptive response when the ratio of disturbance interval to generation time is too great.

The detailed relationship between a fugitive, the brown alga *Postelsia palmaeformis* Ruprecht, and specific characteristics of its disturbance regime is presented here. The sea palm characterizes shore environments of high wave energy (*8*) and disturbance rates (*9*). Its enigmatic role as a competitively capable annual species is known (*10*). The plant lives within the domain of the outer coast mussel *Mytilus californianus*, the competitive dominant in the system (*11*). *Postelsia* can overgrow and eventually remove individual mussels; however, it inevitably loses space, the primary limiting resource, to mussel populations encroaching from the side. Therefore it requires an extrinsic factor, the shearing force of waves, to remove mussels and renew the resource. Conversely, *Postelsia* is not found in protected areas of minimal wave action, and disappears from the flora as one progresses down wave exposure gradients (*12*). The macroscopic sporophyte first appears on suitable surfaces in February or March, grows rapidly, and is sexually competent by midsummer. Meiospores are dripped during low-tide intervals onto the adjacent rocks. These develop into microscopic male and female gametophytes. Propagules of both phases are of limited dispersal ability (*13*). Eventually the sporophyte is shredded by wave action or pulled from the rock surface, carrying with it those organisms overgrown during the previous summer.

An analysis of the disturbance regime from June 1968 to June 1978, characteristic of 26 sites (total area, 2291 m^2) on Tatoosh Island (48°24′N, 124°43′W), on the outer coast of Washington State is given in Table 1. Disturbance at each site is expressed as the percentage of a mussel bed of known area removed annually during the interval of maximal disruption, November to April, and therefore measures the rate at which space is potentially provided to *Postelsia* and other organisms. The limiting resource is presented as patches that vary greatly, from site to site, in size (area) and rate of generation (*9*). The abundance of *Postelsia* is also known at each site, and ranges from absent over long periods (maximum observation, 11 years) to predictably present. I have divided these sites into four categories according to disturbance intensity (low, < 3 percent per year; high, > 3 percent per year) and the presence or absence of *Postelsia*. *Postelsia* is absent at all sites characterized by low resource provisioning, as indicated by infrequent disturbance and small initial (< 1000 cm^2) patch size. It is generally present at sites exposed to severe wave action (*8*), and hence mussel removal. However, there are areas of high disturbances lacking *Postelsia*, areas that show no apparent or consistent differences in wave intensity, or substrate aspect, orientation, and composition when compared with neighboring sites harboring the species. Comparisons of mean disturbance rates indicate no differences between high disturbance sites with and without *Postelsia* (Mann-Whitney U test, $P = .32$). However, when the between-year variation in disturbance is measured as the coefficient of variation, significant differences are apparent between the same categories (Mann-Whitney U test, $P = .0026$). The result suggests that a sequence of relatively benign years associated with infrequent high disturbance levels, yielding both high annual mean disturbance values and a relatively high coefficient of variation is unsuitable to *Postelsia*. By this criterion *Postelsia* is

Table 1. Disturbance rate of the mussel bed at Tatoosh Island, and its intrinsic between-year variability. Sites with both low disturbance rates and *Postelsia* do not exist naturally. The summed number of annual disturbance estimates for a specific disturbance condition generates the number of site-years. Abbreviation: C.V., coefficient of variation.

Site condition	Number of sites	Site-years	Area examined (m^2)	Disturbance	
				Mean rate	Mean C.V.
Low disturbance					
Without *Postelsia*	3	29	393.1	1.7	165
High disturbance					
Without *Postelsia*	16	142	1278.1	7.4	207
With *Postelsia*	7	59	619.4	7.7	151

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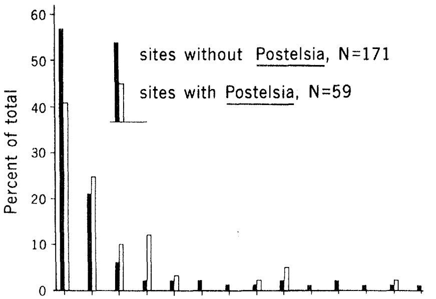

Fig. 1. The disturbance profiles at Tatoosh Island of areas potentially occupiable by *Postelsia*.

unable to invade and persist in areas occasionally devastated by catastrophes. In contrast, more regular (more predictable) disturbances, disasters in Harper's terminology, are conducive to maintenance of long-term populations when these disruptions occur above some threshold level.

The regional characteristics of sites with and without *Postelsia* are shown in Fig. 1. Although these disturbance profiles are not distinguishable statistically (Kolmogorov-Smirnov test, $P > .05$), they indicate the direction of difference between the two areas; those sites with *Postelsia* have more disturbance in the categories of 1 to 5, 6 to 10, 11 to 15, and 16 to 20 percent per year than do those lacking sea palms, and less in the 0 percent. The pattern, that is, the relative proportions of disturbance in these five categories is distinct ($\chi^2 = 11.45$, $P < .001$). Further, assuming that low intensity disturbance (≤ 5 percent per year) is unimportant, because the patches are too small, their rate of formation is too infrequent, or small patches cannot be adequately sampled, I have calculated the mean interval between disturbances only ≥ 6 percent per year. These are distinct (2.36 years with *Postelsia*, 3.77 years without; t-test, $P < .02$) and again suggest that the magnitude and frequency of disturbance are important environmental parameters.

Postelsia can be established experimentally on a variety of intertidal ledges (*14*), and will persist there for at least two natural generations. The inadequate annual replacement at sites both well beyond (10 to 500 m) the limited dispersal range (*13*) and characterized by catastrophic disturbance regimes is shown in Fig. 2. Additional data are given from sites of infrequent, but unquantified disturbance history, and believed to be of marginal quality in that *Postelsia* seems incapable of maintaining long-term populations there. These successfully established populations are dwindling to local extinction (Fig. 2), and are doing so in the absence of predictable winter disturbance. Thus their usual absence from such habitats does not seem to be due to physiological restrictions.

The ultimate causes of these disappearances are found in the nature of the biological interactions between *Postelsia* and adjacent species. *Mytilus californianus* generally outcompetes it, encroaching from the patch perimeter at a mean rate of 19.7 cm/year (*15*). Benthic grazers, especially the chiton *Katharina tunicata*, consume it. *Postelsia* escapes by living higher in the intertidal than the maximum, sustained chiton density (75 per square meter), and by growing rapidly from April to June, thereby becoming too large to be consumed. A more insidious problem is presented by the articulated coralline algae *Corallina vancouveriensis*. This species' presence is facilitated by grazing (*16*); therefore, it is a conspicuous member of the understory community associated with *Postelsia*. Small *Postelsia* sporophytes settle on it and grow, but rapidly exceed the strength of the articulated joints in these high-energy environments. When the joint ruptures, these epiphytic *Postelsia* drift away; *Corallina* has the capacity to recover rapidly.

The dynamics of *Postelsia* provide little relief from these stresses, and the patches of invadable new substrate generated each fall and winter by death of the adult plant (individuals > 25 cm tall) are too small to sustain the local population for more than a few years (Fig. 2) in the absence of predictable disturbance. For instance, if all the adult plants were uniformly spaced and characterized by holdfast areas of an uncrowded individual (83 cm^2, standard deviation (S.D.) = 19.5, $N = 40$), maximal adult density would be 121 per square meter. However, Dayton (*10*) has demonstrated that the plants are tightly aggregated, in practice meaning that mean adult holdfast area is greatly reduced. Measures of the number of stipes per communal holdfast give a mean of 3.6 adult plants per 106 cm^2 (S.D. = 50, $N = 23$) of substratum. Such holdfasts in dense stands in typical habitat cover about 38 percent of the resource's surface. The interstices between these are occupied by other species, most of which exert a negative influence on *Postelsia*'s reestablishment. Adult densities above which the population could be self-sustaining due to self-generated resource renewal are theoretically possible, but are never observed in nature, perhaps a result of shading by adult plants of sporelings or interplant interference in a turbulent environment. Populations that dwindle to densities less than 20 to 30 per square meter may be incapable of repopulating that site.

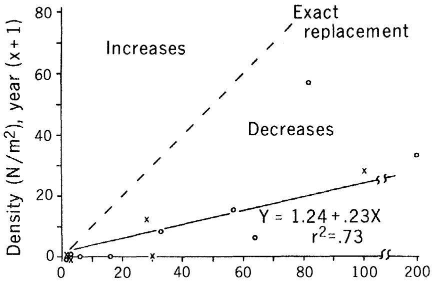

Fig. 2. The site-specific pattern of between-year replacement in *Postelsia* in transplant (O) and selected natural sites (X). Local extinction will occur in the absence of disturbance, or when the adult density falls below about 25 plants per square meter.

Most of the wave-generated disturbance of Tatoosh mussel beds occurs during the November to April interval (*9*). Sporogenic plants are present at least through December, permitting some reseeding. Patches that form later than mid-January are not invaded until subsequent years, if ever. Further, *Postelsia* growth is seasonal whereas mussel encroachment and *Corallina* development are continuous. Predictable disturbance, renewing a necessary resource, must occur at both a sufficient rate and probably above some threshold size distribution for *Postelsia* to occupy sites continually. Infrequent, albeit large-scale disturbances to the mussel community, such as catastrophes, contribute little to *Postelsia*'s long-term persistence, or local distribution, and the species appears to contain no specific adaptation to utilize these extreme environmental events (*17*).

R. T. PAINE

Department of Zoology,
University of Washington,
Seattle 98195

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13. I have repeated Dayton's (*10*) demonstration of a limited dispersal distance of spores released from an attached sporophyte. When the adult plants exist as a point source, dispersal is limited to acceptable sites within a radius of 1.5 m.
14. I have "transplanted" *Postelsia* by cutting off the distal third of sporogenic plants, securing six in a hardware cloth mesh, and attaching this to rock substratum at least 0.3 m^2, freshly scraped clean of mussels or other epifauna or flora. Immature sporophytes appeared in five-sixths of the treatments in September 1975 at Tatoosh, and 14/14 initiated in September 1977. Two of the former populations are still in existence (August 1978) as are all of the latter.
15. The average rate of encroachment of *Mytilus californianus* was determined by measuring rate of movement into small ($\leq$ 100 cm^2, N = 44), intermediate (< 3500 cm^2, N = 78), and large (> 3500 cm^2, N = 11) experimental sites.
16. Corallinaceous algae generally typify areas subject to intense grazing pressure [R. T. Paine and R. L. Vadas, *Limnol. Oceanogr.* **14**, 710 (1969); P. J. Vine, *Mar. Biol.* **24**, 131 (1974)].
17. I thank M. Slatkin, J. F. Quinn, and P. D. Boersma for constructive advice, the U.S. Coast Guard for permission to conduct research on Tatoosh. Supported by NSF grant OCE 77-26901.

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2-Deoxy-D-Glucose Maps Movement-Specific Nervous Activity in the Second Visual Ganglion of *Drosophila*

Abstract. *Adult* Drosophila *were fed with tritium-labeled deoxyglucose prior to a 5-hour period of visual stimulation. A flickering disk of light and a moving grating were presented to the left and right eyes, respectively. Autoradiography revealed enhanced labeling solely in that part of the second optic ganglion (medulla) whose visual field was stimulated by movement.*

2-Deoxy-D-glucose (DG) is believed to be transported to and taken up by nerve cells through the same mechanisms as its structural analog, glucose, which is the major fuel for nervous tissue. Nerve cells with high physiological activity require rapid adenosine triphosphate synthesis to restore electrochemical gradients and take up more glucose, or, when offered, labeled deoxyglucose. After phosphorylation, the first step of glycolysis, DG-phosphate is not metabolized further and thus tends to accumulate preferentially in physiologically active cells.

Although this method of "activity staining," developed by Sokoloff and his colleagues (*1*), has not yet, to our knowledge, been demonstrated to be effective at the level of individual neurons, it has been successfully applied by several scientists to map nervous activity in various areas of the vertebrate brain under various conditions of stimulation (*2*). In a series of qualitative experiments we found that the method is effective in an invertebrate nervous system and can provide functional information in *Drosophila* yet inaccessible by electrophysiological techniques (*3*).

A 3- to 7-day-old female *Drosophila* that had been starved in an empty vial at 19° to 21°C for 24 to 36 hours was etherized briefly in order to be attached to a small brass rod which could be mounted either in the stimulus set-up or, by a special clamp, in a cryostat microtome (South London Electrical Equipment). The fly's head was immobilized by cementing it to the body. The flicker stimulus was generated on the left eye and the movement stimulus on the right eye (Fig. 1). The patterns were presented to the fly through two microscope objectives. This optical procedure (*4*, *5*) effectively prevents stray light from reaching receptors that are not directly stimulated.

At the beginning and halfway through the 5-hour stimulation period, the fly was offered a drop of 0.3 mM aqueous solution of tritiated DG (*6*) from the tip of a syringe and was allowed to drink to satiation. In this way each fly (weight, 1 mg) took up about 2 to 5 μCi of label. Although the precise concentration of label in the hemolymph was not known it certainly was higher by two to three orders of magnitude than that in similar experiments on vertebrates (*2*). At the end of the stimulation period, fly and holder were, under red light, immersed in a drop of embedding medium (OCT) and quickly frozen in melting nitrogen ("slush"). At −25°C, 12-μm-thick sections were cut with a knife cooled by acetone-CO$_2$ ice and picked up on −25°C slides. These were transferred to a freeze-dryer (Balzers BA-3) and kept below −50°C at 10^{-4} to 10^{-3} torr for 2 hours. The dry sections were carefully inspected, and any protruding elements like chitin, cement, or doubly layered pieces of tissue were removed before they were brought into close contact with slides coated with stripping film (Kodak AR-10). The sandwich of section and film between the two slides was clamped together with pressure at about

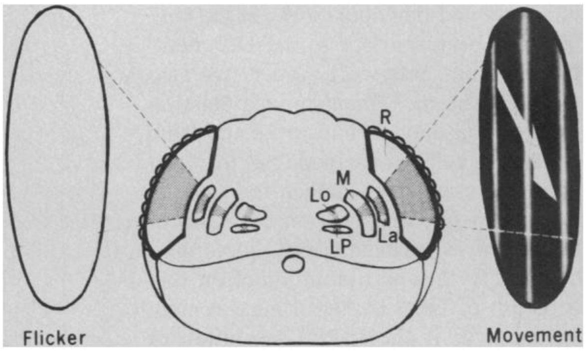

Fig. 1. Visual stimulus. The right eye was exposed to a moving sine-wave grating (angular diameter, 70°; mean luminance, $\bar{I}$ = 1500 cd/m^2; pattern contrast, $\Delta I/\bar{I}$ = 0.40; spatial period, 20°; constant speed, 26° sec^{-1} from anterior to posterior). The left eye was exposed to a homogeneous disk of temporally modulated light. Luminance and sinusoidal modulation (depth and frequency) of the flicker stimulus were adjusted so that the light signals received by individual receptors on either eye were similar. (On the right eye, however, movement induced phase differences in the signals to neighboring receptors.) In the schematic horizontal cut through a *Drosophila* head, the stimulated portions of the retina (*R*) and the optic ganglia lamina (*La*), medulla (*M*), lobula (*Lo*), and lobula plate (*LP*) are stippled.

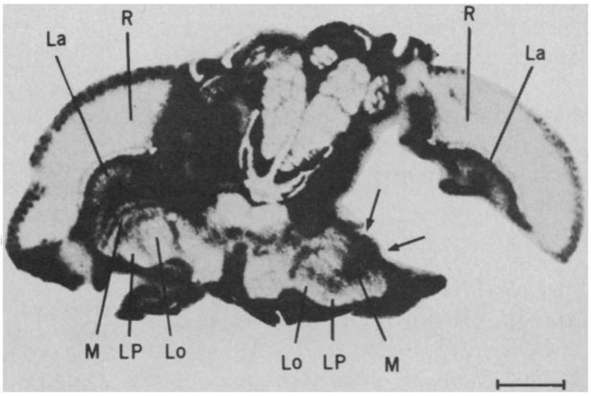

Fig. 2. Autoradiograph of a nearly horizontal section through the head of a *Drosophila* fed with [^{3}H]deoxyglucose. Hemolymph spaces are heavily labeled. The retina and optic ganglia are recognizable (compare with Fig. 1). The movement-stimulated part of the right medulla is strongly labeled (arrows). Scale marker, 100 μm. Note for comparison that one ocular dominance hypercolumn of the monkey visual cortex [770 μm (*2*)] would cover the entire section.

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