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Coastal Uplift and Mortality of Intertidal Organisms Caused by the September 1985 Mexico Earthquakes

PAUL BODIN AND TERRIE KLINGER

Coastal uplift associated with the great Mexican earthquake of 19 September 1985 and its principal aftershock produced widespread mortality of intertidal organisms along the coast of the states of Michoacán and Guerrero, Mexico. Measurements of the vertical extent of mortality at ten sites provided estimates of the magnitude of the vertical component of deformation along the coast. Within the affected area, uplift ranged from about 12 centimeters to about 1 meter, and no subsidence was observed. The observations are consistent with models of the tectonic deformation that results from buried slip on a shallow-dipping underthrust fault.

THE MEXICAN EARTHQUAKES OF 19 and 21 September 1985 (surface wave magnitudes 8.1 and 7.5, respectively) ruptured a portion of the northeastward dipping thrust fault lying between the Cocos Plate and the North American Plate under Mexico. Preliminary aftershock locations indicated that the combined rupture zone was about 240 km long and 70 km wide, was elongated parallel to the trench axis but was landward of the trench, and was below the shoreline of the coasts of Michoacán and Guerrero, Mexico (*1*) (Fig. 1). The vertical component of tectonic deformation associated with the rupture produced a static offset in land level relative to mean sea level.

In the absence of sea level gauges in the rupture area, we surveyed the vertical distribution of intertidal organisms to document local deformation (*2*). Zonation of intertidal species is determined by biotic and abiotic factors that are ultimately related to tidal cycles (*3, 4*). In the high intertidal zone, duration of emergence may determine the upper limit of a sessile species' range because of desiccation and temperature stress. Significant uplift will therefore induce mortality among sessile species whose upper limits are determined by duration of emergence at low tide. Subsidence will introduce previously supralittoral substratum into the littoral zone, where it will be rapidly colonized by algae. The extent of either the resultant mortality or colonization will reflect the magnitude of the local vertical component of tectonic deformation. Darwin (*5*) used such evidence to infer uplift caused by the Chilean earthquake of 1835, and other investigators (*6*) have done so more recently.

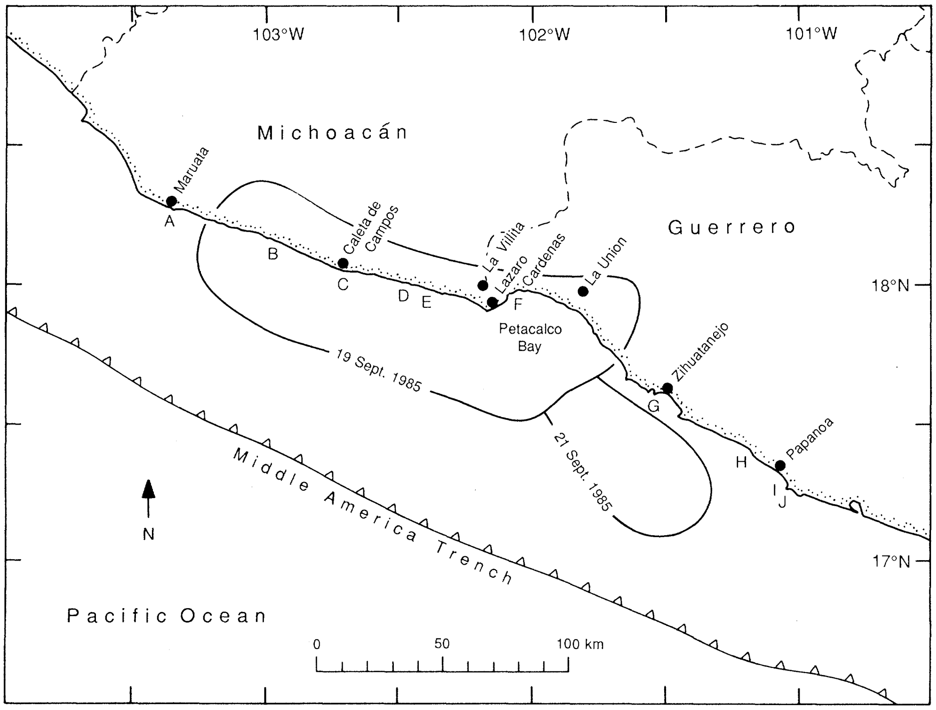

Fig. 1. The coast of the states of Michoacán and northern Guerrero, Mexico. The preliminary aftershock zones of the earthquakes of 19 and 21 September 1985, are outlined (*1*). Sites at which the intertidal organisms were surveyed are indicated by the letters A through J. The Cocos Plate forms the floor of the Pacific Ocean southwest of the Middle America Trench and is being thrust northeast under the North American Plate at the trench axis. The depth of the fault beneath the shoreline is about 20 to 25 kilometers (*1*).

A 6-day survey indicated that uplift had caused mortality among intertidal organisms, and evidence of this was widespread throughout the epicentral region. Uplift-induced mortality was most obvious among macroalgae, both because algae were dominant space-holders in the intertidal and mortality was not always readily apparent in shelled invertebrates. Coralline algae were particularly good indicators of mortality because they discolored rapidly after death (*7*). The preearthquake vertical range of some algal species exceeded the magnitude of uplift; thus both living and dead specimens could be found at each site. The vertical distance between these uppermost living and dead specimens was measured for certain species at ten sites (Fig. 1, A–J) (*8*). This measurement gives an estimate of the vertical extent of mortality (VEM), and represents the difference in a species' upper intertidal limit before and after uplift.

Measurements of the algal mortality that resulted from coastal uplift associated with the earthquakes are shown in Table 1. The northernmost site, Maruata, showed no large-scale mortality and is therefore considered to lie beyond the uplifted zone. Farther south, there was evidence of widespread mortality among both the crustose corallines (Fig. 2a) and the articulated corallines (Fig. 2b), as well as among species of *Gracilaria, Ralfsia, Padina, Chaetomorpha*, and *Cladophora*. The VEM exceeded 60 cm at Caleta de Campos (site C) and decreased north and south of this site. The VEM was smallest at the southern sites (sites F–J), where most values were less than 25 cm. We were unable to determine the southern boundary of the

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P. Bodin, Institute of Geophysics and Planetary Physics, University of California, San Diego, La Jolla, CA 92093.
T. Klinger, Scripps Institution of Oceanography, University of California, San Diego.

uplifted zone since mortality was observed at the southernmost site visited. No evidence of subsidence was seen at any coastal site within the rupture zone.

Variation was observed in the VEM of the crustose corallines from three different habitats at Caleta de Campos (sites C_1, C_2, and C_3 in Table 1 and Fig. 2). However, the VEM of the articulated corallines from two of the three habitats (C_1 and C_2) did not vary substantially. The largest VEM of crustose corallines in the three habitats surveyed at Caleta de Campos (C_2) is comparable with that of articulated corallines from both C_1 and C_2. Apparently there are factors independent of uplift that can reduce the measured VEM of crustose corallines. Therefore, in the absence of confirming evidence, the VEM of the crustose corallines could be regarded as a lower bound on the amount of uplift. However, the consistency of the measurements at most sites indicates that the magnitude of uplift is generally well represented by the VEM.

These data constitute a conservative estimate of the absolute magnitude of vertical displacement associated with the earthquakes. Alternative explanations of the observed intertidal mortality can be discounted. Seasonal changes in species distribution and abundance, or a series of daytime extreme low tides cannot account for the observed mortality. Mortality from these causes would be expected to have occurred at Maruata as well as at the other sites, and none was observed there.

Our findings are consistent with preliminary interpretations of accelerograms of the earthquakes that were recorded at five locations above the rupture zones (*1*) and that indicate about 90 cm of uplift at Caleta de Campos, with less uplift at La Villita and La Union (*9*).

Our observations can be explained by models of the elastic deformation of the earth resulting from buried slip on shallow-dipping thrust faults (*10, 11*) that have been elaborated with data from several previous large buried thrust earthquakes (*6, 12*). Models show a region of surficial uplift directly above the rupture plane; near the down-dip limit of rupture is a hinge line, and an area of subsidence occurs farther inland. Subsequent to a large earthquake, aseismic after-slip may occur down-dip of the coseismic rupture zone, causing gradual uplift in the vicinity of the original hinge line and subsided area.

Distance to the hinge line has a first-order effect on the amount of coseismic uplift. The decreasing uplift from sites C to F may result primarily from this effect. However, other factors may also contribute to the observed pattern. Uplift due to the 19 September earthquake (most likely sites A–G) is not directly comparable with uplift resulting from the 21 September earthquake (most likely sites G–J) because the source mechanisms and locations of the two earthquakes differed. Other processes that may affect the distribution of observed uplift include variable coseismic slip, differences in rheologic properties, and variable dip angles of the subduction thrust fault depending on location along the Michoacán and Guerrero coast (*13*).

The region of greatest observed uplift is marked by flights of uplifted marine terraces (*14*), which are often associated with long-term coastal uplift in a subduction setting and may represent residual uplift resulting from periodic large earthquakes on the underlying megathrust (*11, 15*). In addition, active subsidiary faults in the upper plate might be involved in producing long-term uplift (*16*). Because we did not observe surface faulting and because the ground accelerations recorded in the epicentral area are generally low (*1, 17*), the influence of subsidiary faulting in the production of the raised marine terraces in Michoacán is probably negligible.

Our observations have limited power to resolve the timing of the uplift. Because our measurements agree closely with the accelerograph record at Caleta de Campos, it is likely that most of the observed uplift at this site occurred coseismically. However, it is possible that the uplift observed at sites closer to the hinge line (that is, along the Guerrero coast) may have occurred as a result of early postseismic readjustments.

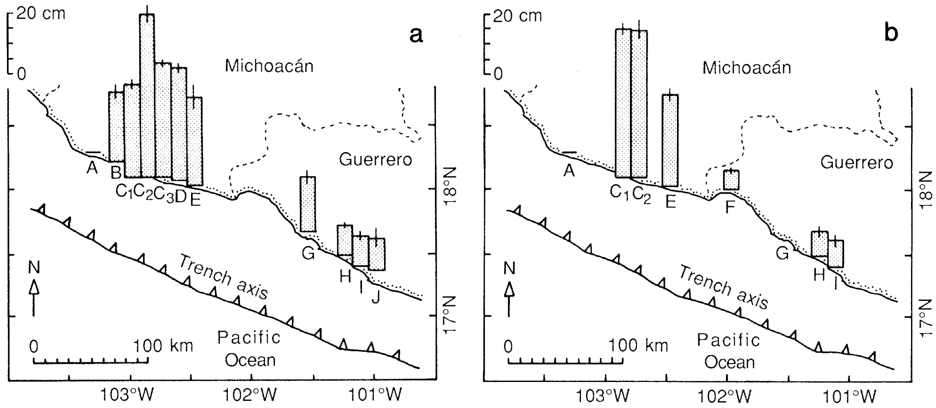

Fig. 2. The VEM along the Michoacán-Guerrero coast for (a) the crustose corallines and (b) the articulated corallines. Stippled bars represent the median value of three replicate measurements. Vertical lines at the top of the bars represent the range of observations. Values from the different habitats at site C are shown as stippled bars with a common base.

Table 1. Measurements of the vertical extent of mortality (VEM) at ten sites along the Michoacán-Guerrero shoreline. Site identification letters refer to locations shown in Figs. 1 and 2. At Caleta de Campos, three habitats that differed in exposure to wave action and in substrate orientation were surveyed. These sites are denoted by subscripts on the site identification letter: C_1 was on the exposed (seaward facing) portion of a mole, C_2 was on the protected side of the mole, and C_3 was from a nearby sea-cliff fronted by a sandy beach. For each organism, the range of three replicate observations is shown (*8*).

Site	Place name	VEM (cm)		
		Crustose corallines	Articulated corallines	*Gracilaria* sp.
A	Maruata	0	0	0
B	K105	50–60		
C_1	Caleta de Campos	57–61	95–100	
C_2	Caleta de Campos	100–113	90–102	
C_3	Caleta de Campos	75–80		
D	K39	75–85		
E	Las Penas	50–66	56–63	
F	Las Penitas		11–15	
G	Zihuatanejo	30–40		25–40
H	La Barrita	19–23	14–20	
I	Playas de Papanoa	17–24	15–22	19–23
J	Puerto Escondido	18–28		

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Transition State Analogs as Ligands for Affinity Purification of Juvenile Hormone Esterase

YEHIA A. I. ABDEL-AAL* AND BRUCE D. HAMMOCK

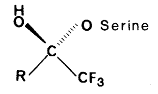
Insect juvenile hormones are metabolized in numerous species of caterpillars by low abundance, highly specific esterases. Because of their role in regulating and possibly disrupting juvenile hormone titer and thus insect metamorphosis, they are of interest to developmental biologists as well as scientists interested in selective insect control. However, the enzymes have defied attempts to purify and characterize them. Juvenile hormone esterase activity can be inhibited by a variety of 3-substituted 1,1,1-trifluoropropanone sulfides. These apparent transition state analogs were used as ligands and eluting agents to purify juvenile hormone esterase from four insect species from 500-fold to over 1000-fold in high yield. After elution from the affinity column, the enzymes were radiolabeled with paraoxon and analyzed by electrophoresis, and the results demonstrate a high degree of purity. Transition state analogs may be useful for the affinity purification of other enzymes.

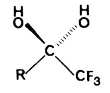
IN HOLOMETABOLOUS INSECTS A PRECIPITOUS decline in the titer of juvenile hormone (see structure in Fig. 1) initiates a series of developmental changes resulting in metamorphosis to a pupal and then to an adult stage. In the lepidopterous species studied, it appears that this reduction in hormone titer is due to a decreased rate of biosynthesis as well as a dramatic increase in highly active and specific enzymes that hydrolyze the methyl ester of juvenile hormone (*1*). There has been interest in purification of these regulatory enzymes for a number of years as probes for the further understanding of insect metamorphosis and as a target for molecular approaches to the control of destructive insect pests. Since the maximum concentration of juvenile hormone esterase in the blood is in the low micromolar range (*2*), and since insect blood is difficult to obtain in large amounts, the isolated enzyme was never obtained in sufficient amounts for characterization. No attempts have been made to purify the enzyme from the key pests in the *Heliothis* complex or from strains of the silk moth *Bombyx mori*, which is widely used by developmental biologists.

The development of powerful and selective inhibitors for juvenile hormone esterase has proved useful for investigating both the biochemistry and the biological role of the enzyme. For instance, selective inhibition of juvenile hormone esterase results in maintenance of juvenile hormone titers and the production of giant larvae (*3*). Among these inhibitors have been trifluoromethyl ketones (*4, 5*), some of which exhibit slow tight-binding kinetics and react almost stoichiometrically with the target enzyme (*2, 6*).

The inhibitory mechanism proposed for these compounds is based on Pauling's idea (*7*) that a compound which even vaguely mimics a transition state should bind tightly to the enzyme. As increasingly powerful enzyme inhibitors such as transition state mimics are developed, observations of time-dependent, yet reversible, inhibition kinetics are becoming more common (*8*). Both esters and ketones are similar in terms of many physicochemical properties, including reactivity toward nucleophiles. Substitution of some of the hydrogen atoms α to the carbonyl with fluorine enhances the electrophile reactivity of carbonyls with a putative serine at the catalytic site of esterases. This substitution should not jeopardize the affinity for the enzyme through steric hindrance, since both the hydrogen and fluorine atoms have very similar steric properties (molar refractivities of 1.03 and 0.92, respectively) (*9*). Thus, it is likely that these trifluoroketones act as "transition state analogs" with juvenile hormone esterase.

Figure 1A shows the inhibition of crude juvenile hormone esterase by one such transition state analog, OTFP (3-octylthio-1,1,1-trifluoropropan-2-one). This compound, which has a molar refractivity very similar to that of juvenile hormone, is the most potent inhibitor yet reported for the enzyme from the cabbage looper, *Trichoplusia ni*, with a dissociation constant of $1.2 \times 10^{-10} M$ (*2*). The less selective phosphorylating agent paraoxon also is a powerful inhibitor of juvenile hormone esterase. The irreversible inhibition caused by paraoxon (Fig. 1B) supports the hypothesis that juvenile hormone esterase is a serine esterase and that the trifluoropropanones bind to the enzyme by a structure similar to the hydrated state of the trifluoropropanone in aqueous solution.





The smooth inhibition curves in most species support the hypothesis that similar catalytic sites are responsible for most of the juvenile hormone hydrolysis in the hemolymph; however, the broken line in the case of *Manduca sexta* indicates that at least two distinct catalytic sites are involved (Fig. 1).

Departments of Entomology and Environmental Toxicology, University of California, Davis, CA 95616.

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*Permanent address: Plant Protection Department, College of Agriculture, Assiut University, Assiut, A.R. Egypt.