

# Celestial Mechanics, Sea-Level Changes, and Intertidal Ecology

MARK W. DENNY<sup>1,\*</sup> AND ROBERT T. PAINE<sup>2</sup>

<sup>1</sup>*Biological Sciences Department, Stanford University, Hopkins Marine Station, Pacific Grove, California, 93950; and* <sup>2</sup>*Department of Zoology, Box 351800, University of Washington, Seattle, Washington, 98195-1800*

*Celestial mechanics has long been known to affect life on Earth, but exploration of these influences has been hampered by long temporal scales and complex biological relations. Here we report on a periodic fluctuation in tidal exposure driven by the 18.6-y oscillation of the moon's orbital inclination, which can change by almost 50% the average time that intertidal organisms are exposed to air. The temperature of nearshore water and the upper limits to mussels are shown to vary with the lunar oscillation. Such variation challenges the value of ecological and physiological generalizations based on snapshot measures, and highlights the value of long-term studies.*

Mechanistic interpretations of cyclical variations in paleoclimates have been based, since the late 1800s, on celestial mechanics, especially the Earth's orbital eccentricity, orbital inclination, and axial tilt. Cycles of 41,000 and 100,000 years have characterized the periodicity of glaciation and its biological consequences for the past 2.5 million years (1, 2), and the role of such astronomical factors is a point of debate in the current concern about the reality and magnitude of anthropogenic forcing of climate, especially accelerated global warming. Although consensus has recently been reached that global warming is a reality (3), its magnitude and short-term consequences have yet to be fully determined. Warming, however, is certain to induce a rise in eustatic sea level.

Anthropologists have long recognized the importance of sea-level changes: *e.g.*, beginning in the late Pleistocene, the Bering land bridge and other human migration

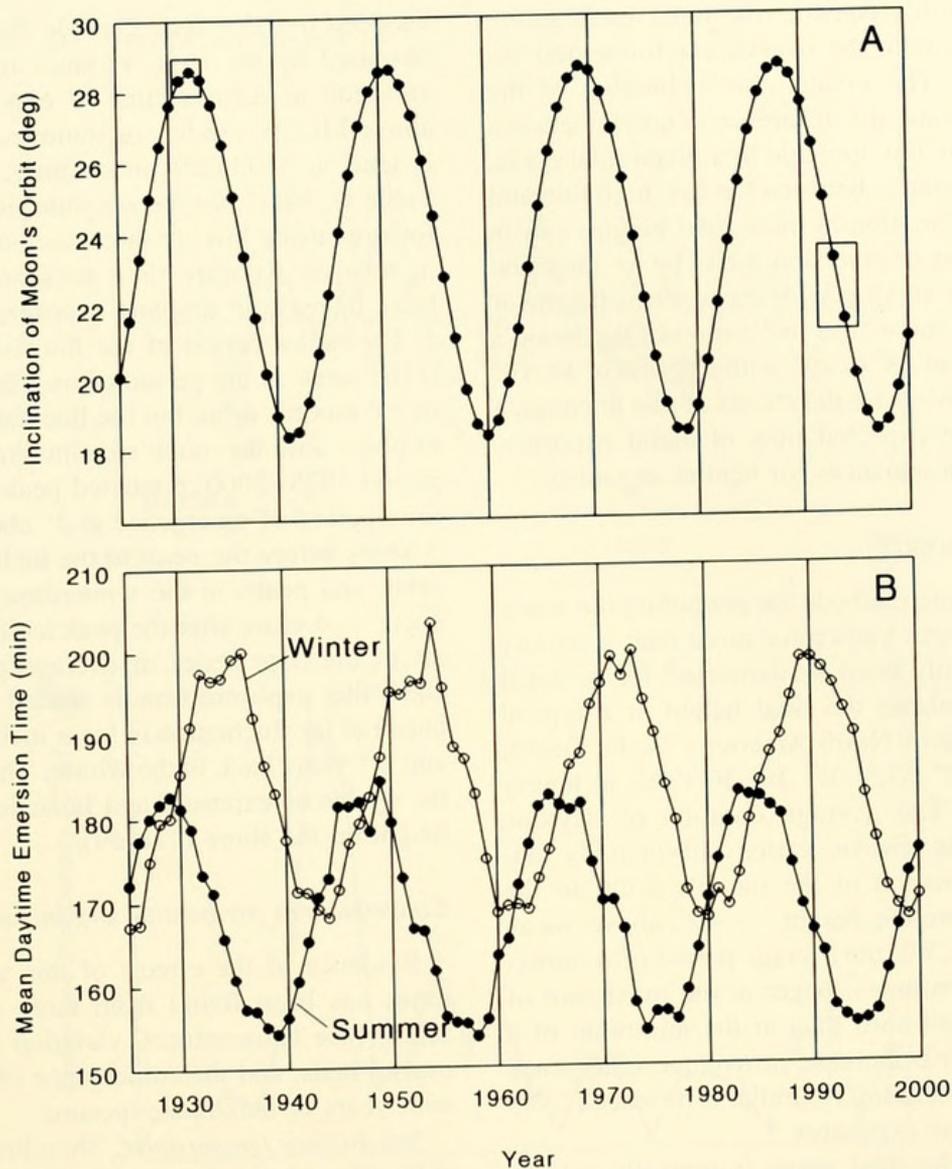
routes to and along coastal North America have disappeared as sea level has risen 120–150 m in the last 14,000 years (4). In contrast, ecologists studying the distribution and abundance of temperate marine organisms, and especially the dynamics underlying these patterns, have tended to ignore such shifts, either because the temporal scale is daunting, or because the complex of interactions influencing distribution patterns is too incompletely understood to be specified. In this paper we examine the interaction between a short-term (18.6 y) astronomical cycle and an ecological assemblage (the intertidal community of wave-swept rocky shores) that is capable of rapid response, and offer examples showing that the effects of celestial mechanics (beyond the obvious ties to tidal cycles and the moon's orbital period) must be identified if the magnitude of changes in community composition is to be understood.

The intertidal zone of wave-swept rocky shores has become a model system for experimentation in community ecology. Current ideas about the roles of competition, predation, succession, and disturbance are based in part on experiments on assemblages of intertidal organisms and serve as benchmarks in ecologists' understanding of how process underlies pattern (5–15).

The ecology of the intertidal zone is closely tied to its physical environment (16, 17). As the tides rise and fall, areas on the shore are alternately immersed and exposed. The concomitant change from marine to terrestrial conditions can place extreme demands on the physiology of intertidal organisms (which with few exceptions are of marine descent), and vertical zonation is often distinct (18). Any shift in the level of the tides is likely to have substantial consequences for the distribution, abundance, and interaction of intertidal plants and animals, many of

Received 3 October 1997; accepted 5 December 1997.

\* To whom correspondence should be addressed. E-mail: mwdenny@leland.stanford.edu



**Figure 1.** Variation in lunar orbital inclination (A) and seasonal variation in the average time for which intertidal organisms are exposed to air (B) calculated for a site 2' above MLLW at Pacific Grove, California. The boxes in (A) enclose the data corresponding to the periods during which the transect was censused, first by Hewatt (1931–1933 [23, 24] and again by Barry *et al.* (1993–1994 [22]). We used Tides 4.01 (Walner, E. P., Nautical Shareware, 32 Barney Hill Rd., Wayland, Massachusetts 01778-3602) to calculate the tides at Pacific Grove for the period 1 Oct. 1924 through 30 Sept. 2000. From these data we measured (to the nearest minute) each period that an organism would be exposed to air during daytime hours (0600–1800 Pacific Standard Time), assuming that the organism was at a known height on the shore (–1' to 6' relative to MLLW). The average period of exposure was then calculated for the winter (1 Oct. to 31 Mar.) and summer months (1 Apr. to 30 Sept.) of each year. Winter of a particular year was assumed to extend from 1 Oct. of the previous year to 31 Mar. of the given year.

which are sessile as adults and thus incapable of adjusting their spatial position to counter the whims of nature. Of particular importance is the average time of emergence—the time during which intertidal organisms are exposed to a desiccating atmosphere, extremes in temperature, hypo-osmotic stress during heavy rains, or other terrestrial insults. Time of aerial exposure is controlled primarily by two factors: the vertical level of the organism on the shore

(a factor under biological control) and the fluctuation of the tides (a matter of physics).

The level of the tides is governed by the action of gravitational attractions and centripetal accelerations acting on the water in the ocean, and may be modified by the topography of the local ocean basin, barometric pressure, and winds. Of particular interest here is a fluctuation in the angle between the plane of the moon's orbit and

the plane of the earth's equator (the lunar inclination), a factor that affects both the overall amplitude and the inequality of tides. The greater the inclination of the moon's orbit, the greater the difference in height between the high high and the low low tide in a given tidal cycle, and the less the difference between the low high tide and the high low tide. Variation in these tidal heights can in turn affect the period of emersion faced by an intertidal organism, the effect varying with the vertical height of the organism on the shore. The inclination of the moon's orbit varies from about 18° to 29°, with a period of 18.613 years (19, Fig. 1A). What are the effects of this fluctuation in inclination on the expected time of aerial exposure, and what are the consequences for benthic organisms?

#### *Effects on aerial exposure*

Fortunately, accurate methods for predicting the astronomical tides have been known for more than a century (20), and have recently been implemented for personal computers. We calculated the tidal height at a typical site on the west coast of North America (Pacific Grove, California, USA, 121° 53.3' W, 36° 36.3' N) at hourly intervals (Fig. 1B). The average duration of daytime emergence at Pacific Grove varies substantially depending on the inclination of the moon's orbit. In the example shown (shoreline height = +2' above mean lower low water, MLLW), the average period of summertime emersion is 30 minutes longer at the maximum of an exposure cycle (184 min) than at the minimum of a cycle (154 min), a 20% increase in average emergence time relative to the minimum. A similar difference (22%) is found for wintertime exposures.

At Pacific Grove the tidal range is typically -1' to +6' relative to MLLW, and the periodic fluctuation in exposure time is apparent for all heights on the shore

between 0 and 4 feet. Outside this range, the pattern is obscured by the large variance in exposure times. The variation in relative time of exposure is greatest at 0' above MLLW (48.6% in summer, 31.1% in winter) and is least at 3' (17.6% in summer, 10.5% in winter, see Table I). Note that the absolute time of exposure is low for organisms low on the shore, so that a large increase in relative exposure time does not necessarily imply a large increase in absolute exposure time (Table I).

The major period of the fluctuation in exposure time is the same as the period of oscillation in the inclination of the moon's orbit, but the fluctuation in exposure is out of phase with the moon's inclination. For example, in the period 1925–2000, predicted peaks in average summertime period of emergence at 2' above MLLW occur 1–5 years before the peak in the inclination of the moon's orbit, and peaks in the wintertime period of emergence occur 1–4 years after the peak inclination. Fourier analysis of the time series of average periods of emergence show that exposure time is shifted on average 2.5 years ahead of the fluctuation in lunar inclination in the summer and 2.1 years back in the winter. The phase shift between the cycles of exposure and lunar inclination varies with height on the shore (Table I).

#### *Consequences for benthic organisms*

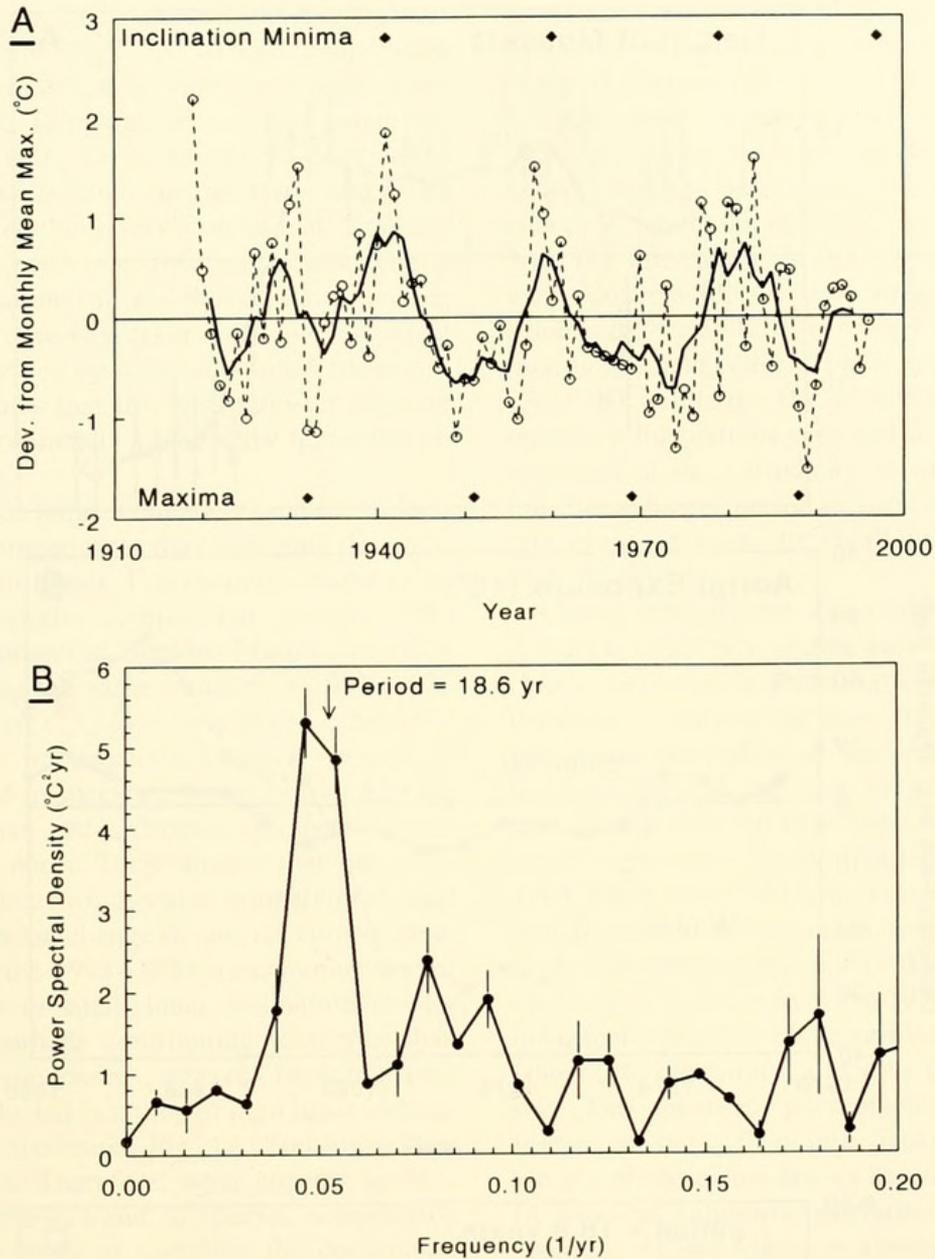
Evidence of the effects of this variation in exposure times has been found from three sources: variation in sea-surface temperatures, variation in the upper limit to mussel beds, and the coincidence of catastrophic freezes with years of maximal exposure.

*Sea-surface temperature.* Shoreline water temperatures at Hopkins Marine Station (Pacific Grove, CA) have been measured daily since 1919. A linear increase through time in both the minimum and maximum temperatures has

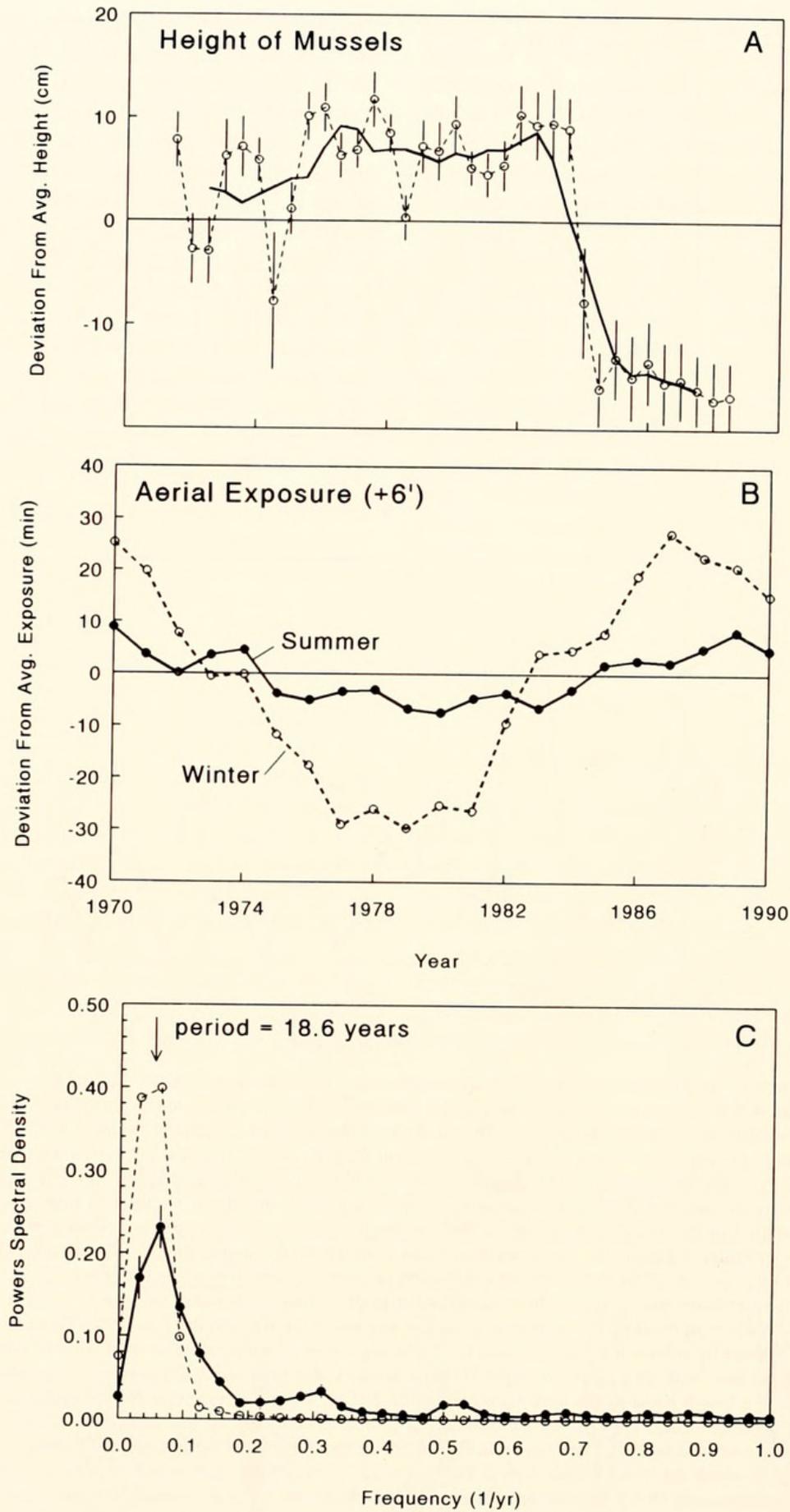
**Table I**

*Summary data for average period of daytime emergence at Pacific Grove, California*

| Season | Height on shore (feet) | Period of emergence (min) |         |         |           |         | Phase (year) |
|--------|------------------------|---------------------------|---------|---------|-----------|---------|--------------|
|        |                        | Mean                      | Maximum | Minimum | Max - Min | Max/Min |              |
| Summer | 0                      | 79.80                     | 98.38   | 66.20   | 33.18     | 1.486   | +2.67        |
|        | 1                      | 121.65                    | 138.72  | 104.13  | 34.59     | 1.332   | +3.28        |
|        | 2                      | 168.75                    | 184.32  | 153.61  | 30.71     | 1.200   | +3.33        |
|        | 3                      | 225.62                    | 238.00  | 215.43  | 22.57     | 1.105   | +2.68        |
|        | 4                      | 461.67                    | 508.76  | 417.25  | 91.51     | 1.219   | +0.44        |
| Winter | 0                      | 111.79                    | 124.38  | 94.91   | 29.47     | 1.311   | -2.43        |
|        | 1                      | 148.26                    | 165.20  | 130.95  | 34.25     | 1.262   | -2.47        |
|        | 2                      | 183.35                    | 203.30  | 167.21  | 36.09     | 1.216   | -2.05        |
|        | 3                      | 208.72                    | 226.93  | 192.92  | 34.01     | 1.176   | -1.85        |
|        | 4                      | 376.11                    | 410.90  | 342.09  | 68.81     | 1.201   | -1.75        |



**Figure 2.** (A) Fluctuations in monthly maximum water temperature at Hopkins Marine Station (open circles). A 5-y running average of the data (solid line, not used in the calculation of periodicity) is shown to accentuate the long-term periodicity. The strong El Niño/Southern Oscillation event of 1982–1983 is evident in the unusual duration of high temperatures in the early 1980s. (B) Power spectrum (vertical bars = SEM) of the data shown in (A). Similar results are obtained for a time series of monthly minimum temperatures (data not shown). The power spectrum of a process that fluctuates through time apportions the variance of that fluctuation among the frequencies that contribute to the process. Thus a peak in the power spectrum at a particular frequency shows that a substantial fraction of the overall variation occurred at that frequency. See (25) for a thorough explanation of spectral analysis. Monthly maximum and minimum water temperatures were extracted from the record at Hopkins Marine Station. Two gaps in the data (1940, 1965–1968) were filled by linear interpolation, and any long-term trend in the time series for each month was removed by subtracting from the data the linear regression of temperature as a function of time. The detrended data were then tapered using a Hanning window, the time series (78 points) was padded with zeroes to a length equal to the next higher power of 2 (128, a process necessary for the application of a fast Fourier transform [FFT]), and the normalized power spectral density was calculated using the FFT procedure outlined by (28). Data shown in Figure 2A are those averaged for January and February, a time of year in which the ocean temperature at Pacific Grove is not typically influenced by oceanic upwelling. The approximately 18.6-y periodicity evident in these data is not present in all months between October and March (the entire season when upwelling is absent), but is much reduced or absent during upwelling.



been noted (21, 22), but there are considerable fluctuations around this trend (Fig. 2A). These temperature anomalies have a period that is indistinguishable from 18.6 years (Fig. 2B). Temperatures are high when the lunar inclination is small (that is, when tidal fluctuations are small) and low when lunar inclination is large (see Fig. 1A). The cause of this effect is unknown, although we speculate that reduced tidal flushing (corresponding to small lunar inclinations) in the shallows surrounding the site of temperature measurement could allow resident surface water to be heated by solar radiation. Crosscorrelation analysis indicates that the maximum temperature anomaly occurs approximately 1 y after the minimum lunar inclination.

The 18.6-y cycle of lunar inclination (and the associated cycle in water temperature) may confound the interpretation of long-term trends. For example, Barry *et al.* (22) compared the species composition in 1993–1994 along an intertidal transect at Hopkins Marine Station to the composition along the same transect in 1931–1933 as recorded by Hewatt (23, 24). They noted substantial shifts in the relative frequencies of several species, in particular an increase in species commonly found to the south of Pacific Grove and a decrease in species commonly found to the north. They suggest that the long-term trend toward increasing water temperatures may have played a role in the change in species composition. Note, however, that the 1993–1994 measurements were conducted at a time of small lunar inclination (3–4 y before minimum), perhaps contributing to higher than average nearshore temperatures, whereas Hewatt's measurements were conducted in a time of high lunar inclination (bracketing the maximum, Fig. 1A) and lower than average temperatures. Therefore, what appears to be a long-term (at least 62-y) trend in species composition may be in part the result of sampling the community

at different phases of the 18.6-y tidal fluctuation. This phenomenon (known as *aliasing*) is a common problem in signal analysis (25).

*Upper limits To mussel beds.* Beginning in September 1971, the upper limit to the mussel (*Mytilus californianus*) bed has been measured twice yearly at Tatoosh Island, Washington state (48° 24' N, 124° 40' W; Fig. 3A). The fluctuations in this boundary vary in synchrony with the predicted variation in aerial exposure: the bed extends higher on the shore when the predicted exposure time is less and retreats when the exposure is increased (Fig. 3B). Although the relatively short time series of boundary fluctuations does not allow for a precise measurement of the periodicity of the boundary's rise and fall, the apparent period of oscillation is consistent with that expected from the oscillation in lunar inclination (Fig. 3C).

*Catastrophic freezes.* The longer a sessile intertidal organism is exposed to air, the more likely it is to encounter chance extremes in terrestrial conditions. For example, intertidal organisms are more likely to freeze (a chance occurrence depending on the weather) in years of maximal exposure. In the past 47 years, four examples of catastrophic freezing have been noted in the mussel-bed community in the Pacific Northwest of the USA (1950, 1964, 1969, 1989). With the exception of the 1964 freeze, each of these events occurred near a peak of lunar inclination, and therefore near a peak of intertidal exposure. Conversely, a severe freeze in 1978 (during a minimum in lunar inclination) exterminated Winter Wrens on Tatoosh Island (26) but did not affect the upper boundary of mussels. The apparent synchronicity between catastrophic freezes and the cycle of lunar inclination may be an example of a phenomenon known as *stochastic resonance* (27). In a system exhibiting stochastic resonance, a large response is elicited whenever a periodic input signal crosses

---

**Figure 3.** (A) Fluctuations in the upper boundary of the mussel bed (open circles); vertical bars are the SEM among the 11 locations. The solid line is a 5-y running average, plotted to accentuate the long-term fluctuation in the boundary. (This running average is not used in calculations of periodicity.) (B) Predicted variation in the aerial exposure of a site 6' above MLLW. (C) The power spectrum (solid line with SEM) of the boundary fluctuations shown in (A); the dashed line is the corresponding spectrum of a pure sine wave with a period of 18.6 y. The upper boundary of the mussel bed on Tatoosh Island was measured to the nearest centimeter twice yearly (Apr. and Sept.) at 11 locations at the site of previous studies on intertidal zonation (29). Data from Sept. 1971 to Sept. 1988 (17 years, 35 measurements) were averaged for each location, and the mean was subtracted from each individual value. The normalized power spectrum of each of these 11 time series was then calculated (by a method similar to that explained in the caption to Figure 2) and averaged across locations. Boundary data subsequent to Sept. 1988 were not included because a severe freeze in Feb. 1989 devastated the high intertidal mussels, lowering the upper boundary by as much as 2.6 m (8½'). Since the freeze, the bed has been steadily extending up the shore. The ability of our spectral analysis to detect an 18.6-y periodicity from 17 years of data was tested by calculating the normalized power spectral density for a pure sine wave with a period of 18.6 y (sampled twice yearly), but using only the first 17 years of the wave. Precise location of the low-frequency spectral peak would require a time series more than double the length available.

a threshold. In the absence of random noise, small input signals may never cross the threshold, and no response will result. In the presence of sufficient noise, however, the combination of a small signal and noise may cross the threshold, causing a response, and the periodicity of these responses will, on average, be the same as that of the underlying signal. It appears possible that the drastic response of mussels to low temperature (death by freezing) results in a stochastic resonance between the mussel bed community and the 18.6-y oscillation in exposure time, the coupling being enhanced by the random "noise" of the weather.

### Conclusions and caveats

Our ability to detect apparent environmental and ecological signatures of the 18.6-y oscillation in lunar inclination suggests that intertidal communities may indeed be sensitive indicators of long-term environmental fluctuations. The data discussed here indicate that this lunar cycle can affect nearshore water temperature, which may, in turn, have significant implications for the growth of spores and larvae, their duration in the plankton, and possibly even post-larval performance. We have shown that the lunar cycle can influence upper distributional limits, and lower limits could be influenced as well if exposure time determined the foraging limits and effectiveness of mobile consumers. Shifts in aerial exposure due to the lunar cycle will affect how stringently the physiology of intertidal organisms (*e.g.*, their thermal and osmotic tolerance) is stressed by the environment. In these respects, the effects of the 18.6-y cycle in lunar inclination mimic the effects expected to accompany global warming and its associated change in sea level. The intertidal zone may thus serve as a convenient, fast-response system in which to test our ability to predict the ecological consequences of global change. In particular, the ability to account for the influences of predictable environmental phenomena (in this case, the tides, including the effects of the oscillation in lunar inclination) should enhance interyear comparisons within this biologically noisy system, and therefore simplify the identification of anthropogenic changes.

The tidal phenomena reported here are calculated for sites with typical, mixed semidiurnal tides. The complexity of tidal physics is such that it may be dangerous to extrapolate from these results to estimate the effects in other tidal regimes, and the time series of sea-level fluctuations should be calculated directly for each site of interest. Note too that only indirect evidence is cited here for the effect of the cycle of lunar inclination on intertidal biology. We hope, however, that this evidence will stimulate others both to search past records for direct evidence of tidal effects and to carry out long-term experiments in the future.

### Acknowledgments

Support for this research was provided by the U.S. National Science Foundation (M. W. D. & R. T. P.) and the Mellon Foundation (R. T. P.). We gratefully acknowledge the Makah Tribal Council for granting access to Tatoosh Island.

### Literature Cited

1. Muller, R. A., and C. J. MacDonald. 1997. Glacial cycles and astronomical forcing. *Science* 277: 215–218.
2. Muller, R. A., and C. J. MacDonald. 1997. Spectrum of 100-kyr glacial cycle: orbital inclination not eccentricity. *Proc. Natl. Acad. Sci. U.S.A.* 94: 8329–8334.
3. Houghton, J. T., et al., eds. 1996. *Climate Change 1995: The Science of Climate Change*. Cambridge University Press, Cambridge, UK.
4. Josenhans, H., D. Fedje, R. Pienitz, and J. Southon. 1997. Early humans and rapidly changing holocene sea levels in the Queen Charlotte Islands—Hecate Strait, British Columbia, Canada. *Science* 277: 71–74.
5. Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42: 710–723.
6. Connell, J. H. 1972. Community interactions on marine rocky intertidal shores. *Annu. Rev. Ecol. Syst.* 3: 169–192.
7. Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302–1310.
8. Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* 41: 351–389.
9. Paine, R. T. 1966. Food web complexity and species diversity. *Am. Nat.* 100: 65–75.
10. Paine, R. T. 1974. Intertidal community structure: experimental studies of the relationship between a dominant competitor and its principal predator. *Oecologia* 15: 93–120.
11. Menge, B. 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. *Ecol. Monogr.* 46: 355–393.
12. Lubchenco, J. 1978. Plant diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. *Am. Nat.* 112: 23–39.
13. Sousa, W. P. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* 60: 1225–1239.
14. Paine, R. T., and R. L. Vadas. 1969. The effects of grazing by sea urchins, *Strongylocentrotus* spp., on benthic algal populations. *Limnol. Oceanogr.* 14: 710–719.
15. Paine, R. T., and S. A. Levin. 1981. Intertidal landscapes and the dynamics of pattern. *Ecol. Monogr.* 51: 145–178.
16. Lewis, J. R. 1964. *The Ecology of Rocky Shores*. The English Universities Press, London.
17. Newell, R. C. 1979. *Biology of Intertidal Organisms*. Marine Ecological Surveys, Faversham, UK.
18. Stephenson, T. A., and A. Stephenson. 1972. *Life Between Tide Marks on Rocky Shores*. Freeman, San Francisco.
19. Schureman, P. 1941. *A Manual of the Harmonic Analysis and Prediction of Tides*. Special Publ. 98, U.S. Dept. of Commerce, Washington, DC.
20. Darwin, G. H. 1898. *The Tides*. Reprinted 1962. Freeman, San Francisco.

21. **Gaines, S. D., and M. W. Denny. 1993.** The largest, smallest, highest, lowest, longest, and shortest: extremes in ecology. *Ecology* **74**: 1677–1692.
22. **Barry, J. P., C. H. Baxter, R. D. Sagarin, and S. E. Gilman. 1995.** Climate-related long-term faunal changes in a California intertidal community. *Science* **267**: 672–675.
23. **Hewatt, W. G. 1934.** Ecological studies on selected marine intertidal communities of Monterey Bay. PhD thesis, Stanford University, 150 pp.
24. **Hewatt, W. G. 1937.** Ecological studies on selected marine intertidal communities of Monterey Bay. *Am. Midl. Natl.* **18**: 161–206.
25. **Bendat, J. S., and A. G. Piersol. 1986.** *Random Data: Analysis and Measurement Procedures*. 2nd ed. Wiley and Sons, New York.
26. **Paine, R. T. 1985.** Reestablishment of an insular Winter Wren population following a severe freeze. *Condor* **87**: 558–559.
27. **Wiesenfeld, K., and F. Moss. 1995.** Stochastic resonance and the benefits of noise: from ice ages to crayfish and SQUIDS. *Nature* **373**: 33–36.
28. **Press, W. H., S. A. Teukolsky, W. T. Vetterling, and B. P. Flannery. 1992.** *Numerical Recipes in FORTRAN*. 2nd ed. Cambridge University Press, Cambridge, UK.
29. **Paine, R. T. 1974.** Intertidal community structure: experimental studies of the relationship between a dominant competitor and its principal predator. *Oecologia* **15**: 93–120.



Denny, Mark W. and Paine, R T. 1998. "Celestial Mechanics, Sea-Level Changes, and Intertidal Ecology." *The Biological bulletin* 194, 108–115.  
<https://doi.org/10.2307/1543040>.

**View This Item Online:** <https://www.biodiversitylibrary.org/item/27945>

**DOI:** <https://doi.org/10.2307/1543040>

**Permalink:** <https://www.biodiversitylibrary.org/partpdf/31295>

**Holding Institution**

MBLWHOI Library

**Sponsored by**

MBLWHOI Library

**Copyright & Reuse**

Copyright Status: In copyright. Digitized with the permission of the rights holder.

Rights Holder: University of Chicago

License: <http://creativecommons.org/licenses/by-nc-sa/3.0/>

Rights: <https://biodiversitylibrary.org/permissions>

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.