UC San Diego
Oceanography Program Publications

Title
Quantifying Scale in Ecology: Lessons from a Wave-Swept Shore

Permalink
https://escholarship.org/uc/item/5dt499wb

Journal
Ecological Monographs, 74(3)

Authors
Denny, M W
Helmuth, B
Leonard, G H
et al.

Publication Date
2004-08-01

Peer reviewed

QUANTIFYING SCALE IN ECOLOGY: LESSONS FROM A WAVE-SWEPT SHORE

Mark W. Denny,[1,4] Brian Helmuth,[1,2] George H. Leonard,[1,3] Christopher D. G. Harley,[1] Luke J. H. Hunt,[1] and Elizabeth K. Nelson[1]

[1]*Stanford University, Hopkins Marine Station, Oceanview Boulevard, Pacific Grove, California 93950 USA*
[2]*University of South Carolina, Department of Biological Sciences, Columbia, South Carolina 29208 USA*
[3]*Monterey Bay Aquarium, Division of Conservation Research, 886 Cannery Row, Monterey, California 93950 USA*

Abstract. Understanding the role of scale is critical to ecologists' ability to make appropriate measurements, to ''scale up'' from local, short-term experiments to larger areas and longer times, to formulate models of community structure, and to address important conservation problems. Although these issues have received increased attention in recent years, empirical measurements of the scales of ecologically important variables are still rare. Here, we measure the spatial and temporal scales of variability of 15 ecologically relevant physical and biological processes in the wave-swept intertidal zone at Mussel Point, near Hopkins Marine Station in California. We analyze temporal variability in wave height, ocean temperature, upwelling intensity, solar irradiance, and body temperature for periods ranging from ten minutes to fifty years. In addition, we measure spatial variation in shoreline topography, wave force, wave-induced disturbance, body temperature, species diversity, recruitment, primary productivity, and the abundances of grazers, predators, and the competitive dominant occupier of space. Each of these spatial variables is measured along three horizontal transects in the upper intertidal zone: a short transect (44 m long with sampling locations spaced at ~0.5-m intervals), a medium transect (175 m long with sampling locations spaced at ~1.7-m intervals), and a long transect (334 m long with sampling locations spaced at ~3.4-m intervals). Six different methods are used to quantify the scale of each variable.

Distinct scales are evident in all but one of our temporal variables, demonstrating that our methods for quantifying scale can work effectively with relatively simple, periodic phenomena. However, our spatial results reveal basic problems that arise when attempting to measure the scale of variability for more complex phenomena. For a given variable and length of transect, different methods of calculating scale seldom agree, and in some cases estimates differ by more than an order of magnitude. For a given variable and method of calculating spatial scale, measurements are sensitive to the length of a transect; the longer the transect, the larger the estimate of scale. We propose that the ''1/f noise'' nature of the data can explain both the variability among methods for calculating scale and the length dependence of spatial scales of variation, and that the 1/f noise character of the data may be driven by the fractal geometry of shoreline topography. We conclude that it may not be possible to define a meaningful spatial scale of variation in this system. As an alternative to the boiled-down concept of ''scale,'' we suggest that it is more appropriate to examine explicitly the pattern in which variability changes with the extent of measurement (e.g., the spectrum). Knowledge of this pattern can provide useful ecological scaling ''rules'' even when a well-defined scale (or hierarchy of scales) cannot be discerned.

Key words: 1/f noise; California; rocky intertidal ecology; scale; scaling; spatial pattern; spatial statistics; spectral analysis; temporal pattern; wave exposure.

INTRODUCTION

In ecology (as in the rest of science), we strive to measure the variability present in the natural world and to understand the causes of that variability. However, the spatial and temporal pattern in which nature varies can affect both our ability to measure a particular phe-

nomenon and our perception of its causes, and it is for this reason that the concept of ''scale'' is important.

Consider, first, the issue of measurement. A trivial example illustrates the problem. If one desires to measure a representative air temperature for a site, one must be aware that there are both daily and seasonal fluctuations. Measurements made solely at night in January or at noon in July would not be accurate predictors of the temperature for a time chosen at random. Knowledge of the major temporal scales of variation in temperature (in this case, scales of one day and one year)

is, thus, necessary for appropriate measurement. Similar concerns apply to the measurement of virtually any ecological variable; one must measure over a long enough time (or a large enough space) to ensure that one's measurements include all relevant variation.

Similarly, issues of scale affect our ability to predict how the world works. In this case, there are several entwined effects, each having to do with the transfer of information across scales (e.g., Wiens 1989, Peters 1991, Levin 1992, Rossi et al. 1992, Schneider 1994, Williams and Rastetter 1999).

First, processes that function effectively at one scale of time or space may not work at another scale. For example, it is very difficult for algae to recruit into small patches cleared in an intertidal mussel bed because molluscan grazers that shelter among the mussels are capable of removing any recruits that appear. Foraging distance is small, however, and as a result there is a distinct limit to the size of patch that grazers can clear. In a patch with a radius greater than the foraging distance, grazers cannot reach the center, and algae are free to recruit there. Because of the scale of grazing, measurements made in the center of large patches would likely miss the phenomenon of ''grazer clear cutting'' seen in small patches. Conversely, measurements made in small patches could lead one to seriously underestimate the potential for algal recruitment in large patches.

Second, interaction among scales varies among phenomena. For example, a wind storm lasting a single day can decimate a population of trees, thereby affecting the community structure of the local forest for decades. In this case, information at a small temporal scale is carried over to larger scales. In contrast, an isolated wind storm today will likely have no measurable effect on the wind conditions two weeks from now. It is evident that if we desire to use measurements of events at one scale to make predictions about events at another scale, we need to know how information is transferred among scales.

Third, this knowledge is central to our ability to construct models of the real world. Given limited computing power, no practical model can include all the detail present at all spatial and temporal scales. However, an understanding of the hierarchical roles of scale (if present) may allow the modeler to ignore detail for the scales at which it is not important, while retaining detail when necessary.

Finally, a comparison of scales among processes can, by correlation, provide a hint of causality. For example, the spatial scales of ''patchiness'' in phytoplankton are often similar to the scales of turbulent eddies, suggesting that (at least for a range of scales) phytoplankton are passively distributed by water motion (Levin 1992).

So, scale is important. It is, however, a large and exceedingly complex issue. In this report, we explore one focused (but central) aspect of the overall problem:

can an ecological pattern be decomposed into scales of variation that can be defined and measured? This question is addressed using data from a wave-swept rocky intertidal shore.

Scales in the intertidal zone

The intertidal zone of wave-swept rocky shores has served as a model system for the experimental investigation of community ecology for many years. Much of current theory relating to predation, competition, recruitment, disturbance, and patch dynamics originated in the intertidal zone (e.g., Connell 1961, Paine 1966, Dayton 1971, Menge and Sutherland 1976, 1987, Connell and Slatyer 1977, Sousa 1979, Paine and Levin 1981, Menge and Olson 1990), and this work has served as a benchmark for ecologists' ability to predict community structure and function. While the intertidal zone has been the stage for a wealth of ecological studies, our ability to generalize from these results has been difficult (Dayton 1984, Underwood and Denley 1984, Foster 1990), in large part because it requires an in-depth understanding of the underlying scales of the relevant interactions.

In some cases, our knowledge of spatial and temporal patterns in the intertidal zone is relatively complete. For example, ocean tides are predictable, allowing for the calculation of approximate times of emersion for organisms at any height on the shore (e.g., Denny and Paine 1998). The ability of plants and animals to cope with the resulting temporal pattern of heat and desiccation has been well studied, and the combination of tidal prediction and physiological response goes far toward explaining the upper distributional boundary of many intertidal organisms (Lewis 1964, Newell 1979, Somero 2002). In this case, the vertical extent of ecological processes is governed by the local range of the tides.

The spatial extent of other processes is equally well understood. For instance, competition on rocky substrata is primarily for space in which to settle and grow (Connell 1961, Jackson 1977, Buss 1985), ensuring that the distance at which competitive interactions act is small (1–10 cm, the size of individual organisms). In contrast, many intertidal plants and animals exhibit a dispersal phase during their life cycle. Although there is considerable variation in (and debate about) the exact extent of dispersal (e.g., Roughgarden et al. 1987, Reed et al. 1988, Bertness and Gaines 1993, Ebert et al. 1994, Palumbi 1995, Gaylord and Gaines 2000), there is little doubt that the dominant competitors for space on wave-swept intertidal shores (such as mussels and barnacles) are capable of dispersing tens to hundreds of kilometers.

Building on this type of information, Menge and Olson (1990) proposed that important ecological processes on wave-swept shores (predation, competition, recruitment, wave-induced disturbance, and temperature) operate in a hierarchy of spatial scales. They as-

sume that competition and predation act at small scales, operating within larger-scale domains of constant recruitment, temperature, and disturbance. In turn, recruitment is assumed to vary with a larger scale than does disturbance, and the important effects of temperature operate at a larger scale than that of recruitment. Given this assumed hierarchy of scales, Menge and Olson proposed simple, conceptual models that predict how intertidal communities should change with a change in any of these processes. Note, however, that if this hierarchy does not in fact exist (that is, if each process varies in important ways at all relevant scales), our ability to make simple models is jeopardized, and with it the ability to make predictions.

Unfortunately, our current understanding of the pattern of variation in the intertidal zone is inadequate to evaluate the ecological roles of scale on wave-swept shores. In this paper, we consider two examples. The first concerns the pattern of spatial variation horizontally along the shore. Although studies have examined some aspects of horizontal variation in population and community structure (e.g., Underwood and Chapman 1996, 1998, Leonard et al. 1998, Azovsky et al. 2000, Helmuth and Hoffmann 2001, Wethey 2002, Harley 2003), information is scant regarding the alongshore spatial scale of variation in wave-induced hydrodynamic force (''wave exposure''), maximum temperatures, disturbance, larval recruitment, juvenile mortality, and adult growth rates.

Our second example concerns the temporal pattern of variation in the physical environment at a given location on the shore. While the temporal pattern of the tides is well understood, variation in other important processes is not. What is the dominant scale of variation in the timing of extreme wave-induced forces? At what temporal scales do water temperature, body temperature, and nutrient concentration vary? At present, we do not know.

These examples are used to explore both the potential advantages and the practical pitfalls involved with measuring the scale of ecological variation.

Past measurements of intertidal scale

Much of current ecological experimentation regarding issues of spatial scale, especially in marine systems, utilizes the approach of analysis of variance (ANOVA) and its modifications (nested ANOVA, ANCOVA, MANOVA, etc; Underwood 1981). In practice, measurements can be made at only a few scales, and these must be chosen before the experiment begins. As a result, the use of general linear models and the nested (or hierarchical) approach to understanding scale assumes that ecologists, using intuition and some understanding of their study system, can predict scales a priori. This approach has been (and continues to be) a powerful approach in ecology. It allows the examination of a broad range of scales (e.g., Underwood and Chapman 1996, Murdoch and Aronson 1999, Azovsky

et al. 2000). It also lends itself to sampling and experimental methodology, and its results can provide clues about the causative factors that may be acting.

However, there are several limitations to this approach. First, as mentioned above, it requires the investigator to choose the relevant spatial scales a priori (Wiens 1989). Although this may be based on ecological experience and sound judgment, it opens the door to the misinterpretation of the variation that might, in fact, be occurring at unstudied scales. Unless samples are taken across all relevant scales (e.g., Underwood and Chapman 1996), the hierarchical approach cannot unambiguously determine the scale(s) at which variation occurs.

The nested ANOVA approach can also be selective in the parameters that it samples. For example, along intertidal shores, the spatial scale of variation in population abundance has commonly been explored by sampling in small quadrats within mid-scale transects at a given site (e.g., Benedetti-Cecchi 2001). These transects are then replicated at different sites to provide information about larger-scale variation. However, sites are often matched as to their wave exposure and topography (e.g., midintertidal benches fully exposed to the prevailing waves). By matching sites at the large scale, these studies explicitly remove from the comparisons any large-scale variation in the wave exposure and the topography of the shore. This can be advantageous if one desires to separate (for instance) the scale-dependent effects of exposure from those of recruitment, but this approach can also obscure patterns due to interactions between these parameters at scales not included in the experiment.

In this report, we analyze the patterns of variation in an intertidal community utilizing six different methods, none of which requires a priori decisions regarding scale. Our results suggest that it may be difficult to measure well-defined scales of variability on wave-swept rocky shores, necessitating alternative approaches to studying the ecological effects of pattern.

DEFINING SCALE

In much of the ecological literature, the term ''scale'' is used without careful definition. This is a dangerous precedent. As with any concept in science, if a parameter cannot be precisely defined, it cannot be quantified. And if it cannot be quantified, it has little practical value. Because the primary objective of this paper is to empirically measure the scale of ecological phenomena, a careful definition of ''scale'' is necessary.

The term ''scale'' is used in at least two different contexts in ecology. Indeed, we have already used both in this paper. First, ''scale'' is used as shorthand for ''convenient scale of measurement.'' For example, by noting that, in the intertidal zone, competition occurs at the scale of individual organisms, we have used the size of individuals as a unit for measuring environmental or biological phenomena. Similarly, one could

use the width of bird's territory, the visual radius of a predator, or the diameter of a tree gap as a unit for measuring space; the handling time for a prey item or the reproductive lifetime of an animal could serve as a unit for measuring time. As long as one accurately defines the unit, the application of this definition of scale is straightforward, and will not be explored here.

In contrast, ''scale'' is often used as shorthand for ''scale of variability'' (e.g., Powell 1995). In this context, the term ''scale'' involves more than the definition of an appropriate ruler. For example, one could easily extend a transect through a forest that was 50 average tree gaps in length. However, to understand the spatial variation in seed fall along this transect, one would need to know, in addition to the transect's length, how many tree gaps were present and how they were arranged. The scale of variability intrinsically involves aspects of pattern as well as measures of space (or time). As a consequence, use of the term ''scale'' in this context is problematic. These problems are the central subject of this report.

The scale of variability can be quantified in a variety of ways, of which we have chosen six. In the first three of our definitions, we define the scale of variability, L, as the distance or time over which a phenomenon is more or less constant, as illustrated in Fig. 1A. It would be unusual for the real world to exhibit such a simple pattern of variation. Instead, the pattern of fluctuation in a phenomenon (the ''signal'') is likely to be much more complex (Fig. 1B), and we are left to devise an appropriate statistic that maintains this initial concept of the ''scale of variability'' while incorporating the complexity of the signal.

This can be accomplished through standard techniques in spectral analysis (see Appendix A), which allow one to decompose the overall variance of a signal into its frequency-specific components. For example, the complex, fluctuating signal of Fig. 1B can be expressed as the sum of the 10 sinusoids shown in Fig. 1C–L. Note that these sinusoids are harmonic. That is, the frequency (cycles per time) in Fig. 1D is twice that in Fig. 1C, the frequency in Fig. 1E is three times that in Fig. 1C, etc. The lowest-frequency harmonic has a wavelength equal to the overall length (or extent, sensu Wiens 1989) of the data record (x_{max}). From the amplitude of these harmonics we can calculate the variance associated with each, and a graph of variance as a function of the frequency of the harmonics (Fig. 2A) is one expression of the power spectrum of this signal, $S(f)$. The sum of these frequency-specific variances is equal to the overall variance of the signal. The spectrum is used in the first three definitions of the scale of variability.

The peak scale.—If the variation in a process is dominated by fluctuations at specific temporal or spatial frequencies, these peak frequencies, f_p, can be used as a measure of the characteristic scales of variation (e.g., the peak at the seventh harmonic in Fig. 2A). To be
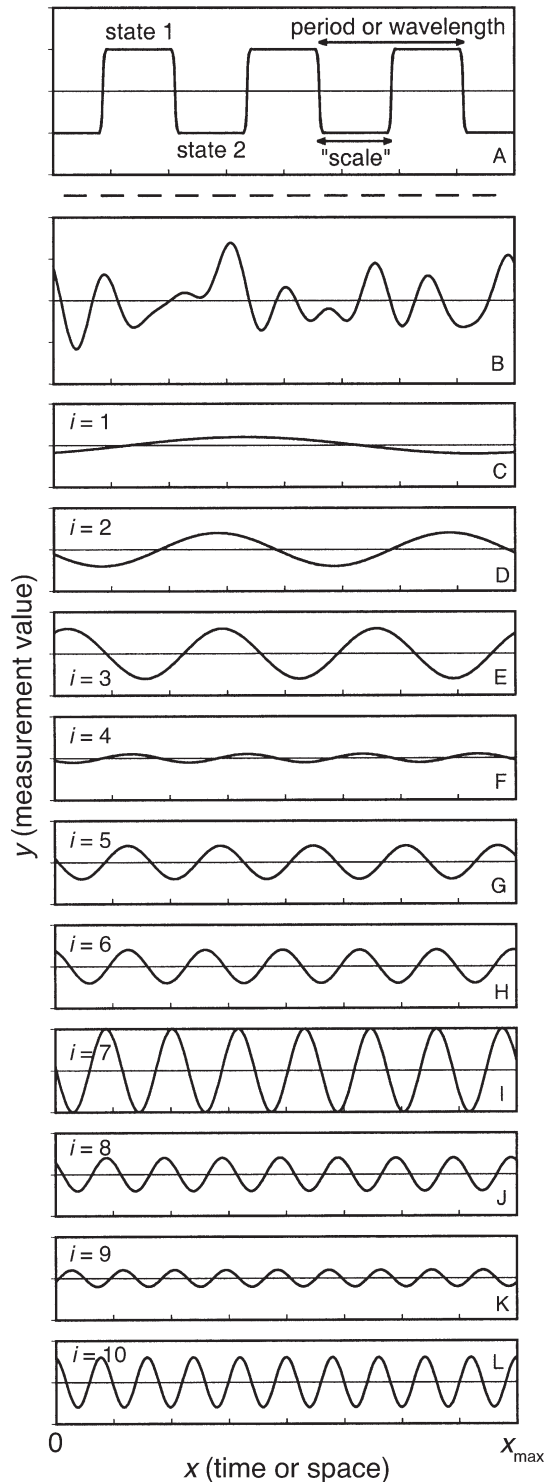

FIG. 1. (A) A definition of ''scale.'' The process varies in time or space, and the interval or distance over which the process remains constant is its scale. Note that the scale as defined here is equal to half the period or wavelength. (B) A more typical, complicated pattern of variation is the summation of the 10 individual sinusoidal variations shown in panels C–L. Note that these sinusoids are harmonics of the fundamental frequency shown in panel (C). The number of the harmonic, i, is shown in each panel (see Eq. A.4 in Appendix A).
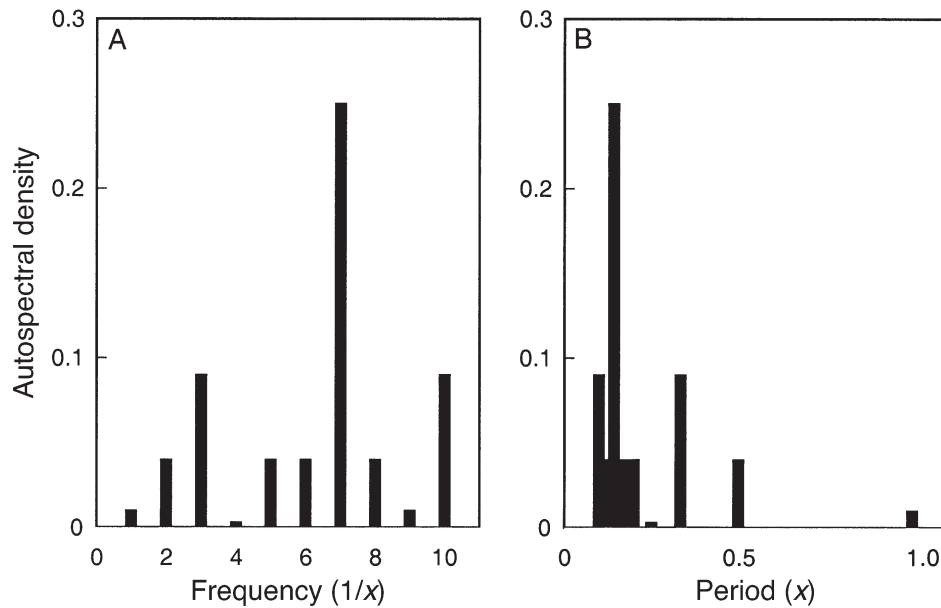
FIG. 2. The spectrum of the signal shown in Fig. 1B. (A) The overall variance is divided among frequencies. (B) The same spectral data graphed as a function of period rather than frequency.

precise, if a phenomenon repeats itself with a period T, the frequency, f, with which it occurs is $1/T$. If a signal varies in space rather than time, the spatial equivalent of frequency is technically known as the wave number, but we refer to it here as a spatial frequency, the inverse of the wavelength, λ; $f = 1/\lambda$. Because frequency is the inverse of period (or wave length), the peak period (or peak wavelength) is $1/f_p$. By our current definition, scale is equal to half the period (or wavelength) at which a signal varies (Fig. 1A). Thus, the peak scale (or p-scale for short) is

$$L_p = \frac{1}{2f_p}. \tag{1}$$

For operational details of this (and subsequent) definitions of scale, consult Appendix B.

The frequency scale.—The peak scale is most useful if there is one or, at most, a few, clear-cut peaks in the spectrum. In such cases, each peak corresponds to a defined scale. However, the peak scale ignores all variation other than that at spectral peaks. How can scale be specified if (as is common) there are no dominant peaks? In such a case, it may be appropriate to calculate an average scale that incorporates all measured variances. For example, we can calculate the weighted average frequency at which a signal varies as

$$\bar{f} = \frac{\displaystyle\int_0^\infty fS(f)\,df}{\displaystyle\int_0^\infty S(f)\,df}. \tag{2}$$

To give this equation some intuitive meaning, imagine

the spectrum shown in Fig. 2A as stacks of coins resting on a yardstick (the abscissa). The height of each stack is proportional to the variance at that frequency, and the point at which the yardstick could be balanced on your finger is the weighted average frequency.

By analogy to Eq. 1, the scale associated with this average frequency is

$$L_f = \frac{1}{2\bar{f}}. \tag{3}$$

This is the definition of scale proposed by Roughgarden (1977). Because it is based on the weighted average frequency, we refer to it as the frequency scale, or the f-scale for short.

The wavelength scale.—By calculating the average frequency from the spectrum (Eqs. 2 and 3), we are in effect giving equal weight to signals that have equal amplitudes, regardless of their frequency. For instance, according to Eq. 2, we would weight a fluctuation that raises body temperature to 40°C for 1 s the same as a fluctuation that raises body temperature to 40°C for 1 h. This equality of weighting might, or might not, be physiologically valid. As an alternative weighting, we propose the following. Fig. 2A can be redrawn, spacing the components of variance on an axis of period (or wavelength) rather than frequency (Fig. 2B). If we now search for the point at which our abscissa balances, we find that those variations associated with long periods or wavelengths are given larger weighting. This presentation of the data allows us to calculate an alternative measure of scale based on the wavelength, λ, as follows:

$$L_w = \frac{\int_0^\infty \lambda G(\lambda)\, d\lambda}{2 \int_0^\infty G(\lambda)\, d\lambda}. \qquad (4)$$

Here $G(\lambda) = S(f)$ for $f = 1/\lambda$. We will refer to this definition as the wavelength scale, or w-scale.

We do not mean to suggest that the w-scale is better than the f-scale; it is simply a different method for calculating scale. Note that for a monochromatic fluctuation (a sinusoidal wave with only one frequency), the f-scale is equal to the w- and p-scales. For more complex patterns of variation, the w-scale is larger than the f-scale.

We now explore three alternative approaches to the definition of scale, each of which is only secondarily related to the spectrum.

The integral scale.—The autocorrelation function of a signal, $\rho(x)$, measures how correlated the value of a phenomenon at one time or location is with another value some time or distance (the lag) away (Appendix C), and the area under the autocorrelation function provides an alternative measure of the scale at which a phenomenon remains more or less constant. Expressed mathematically, this integral scale (or i-scale) is

$$L_i = \pi \int_0^{(a)} \rho(x)\, dx \qquad (5)$$

where a is the distance along the axis of time or space (the magnitude of the calculated lag, x) at which the autocorrelation first crosses 0. The factor of π is included so that L_i has the same value as the previous scales when applied to a monochromatic signal.

The derivative scale.—Powell (1995) proposes a definition of scale, drawn from his work on the structure of phytoplankton communities in lakes. This derivative scale (d-scale) is

$$L_d = \frac{\pi \sqrt{\overline{(q(x) - \bar{q})^2}}}{\sqrt{\overline{\left(\frac{dq}{dx}\right)^2}}} = \frac{\pi \sqrt{\overline{\sigma^2}}}{\sqrt{\overline{\left(\frac{dq}{dx}\right)^2}}}. \qquad (6)$$

Here $q(x)$ is the function defining the variation in a phenomenon with respect to time or space, $\bar{q}$ is the mean value of the phenomenon, and σ^2 is its variance. If most of the variation in the signal occurs at small scales, the derivative of the signal, dq/dx, is (on average) large and the L_d is consequently small. If variation typically occurs at large scales, dq/dx is (on average) small, and the calculated scale is large. As with the i-scale, the factor of π is included so that the derivative scale gives the same value as the previous scales when applied to a monochromatic signal.

The variance scale.—The last of our scales takes yet another approach. As noted previously, one need for a knowledge of scale is to ensure that measurements in-
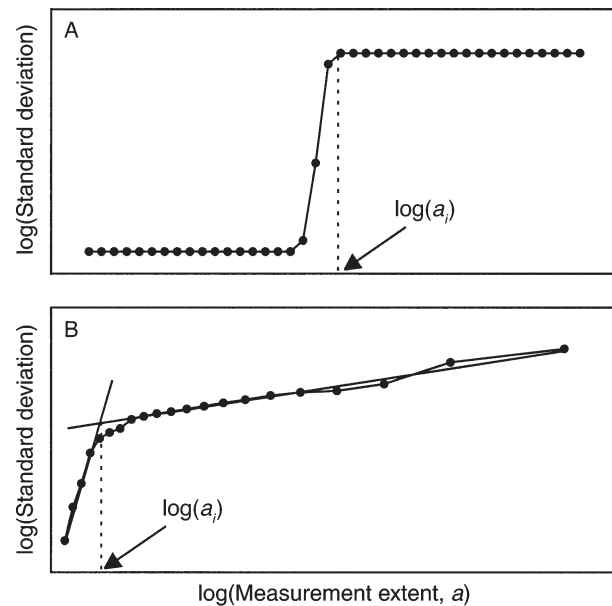

FIG. 3. Definition of the variance scale. (A) An idealized process in which all variation occurs over a small range of measurement extents. (B) A real-world example. Variance continues to increase with any increase in the extent of measurement, but a clear inflection point is nonetheless evident.

corporate all of the relevant variation. If we can quantify how the variance (or standard deviation, σ) of a signal increases as we measure the signal at larger and larger extents, a, we can potentially identify the scale at which "enough" variance has been included. Ideally, the curve of standard deviation vs. the extent of measurement (σ vs. a) would look like Fig. 3A. Above the indicated extent of measurement, there is no increase in measured standard deviation, and the scale of variability is unambiguous. Real-world signals are seldom this clear-cut. Typically, the standard deviation continues to increase with an increase in the scale of measurement. In cases such as this, we resort to searching for an inflection point in the curve of standard deviation vs. measurement scale. This corresponds roughly to the common interpretation of a "sill" in a variogram (Isaaks and Srivastava 1989). For our data, it is typically the case that a plot of the log σ vs. log a shows a clear inflection (e.g., Fig. 3B). A regression line can be fit to the linear increase in log σ at small log a and a second line to the linear increase in log σ at large log a. The measurement extent at which these lines intersect quantifies the log of the scale of inflection, a_i (see Fig. 3B). Because our concept of scale is based on half the period or wavelength (represented here by a), the final estimate of what we call the variance scale (the v-scale) is

$$L_v = \frac{a_i}{2}. \qquad (7)$$

Effects of grain, extent, and spectral shape

Each of these six scales can be affected by the extent of the data series, as well as by the interval between
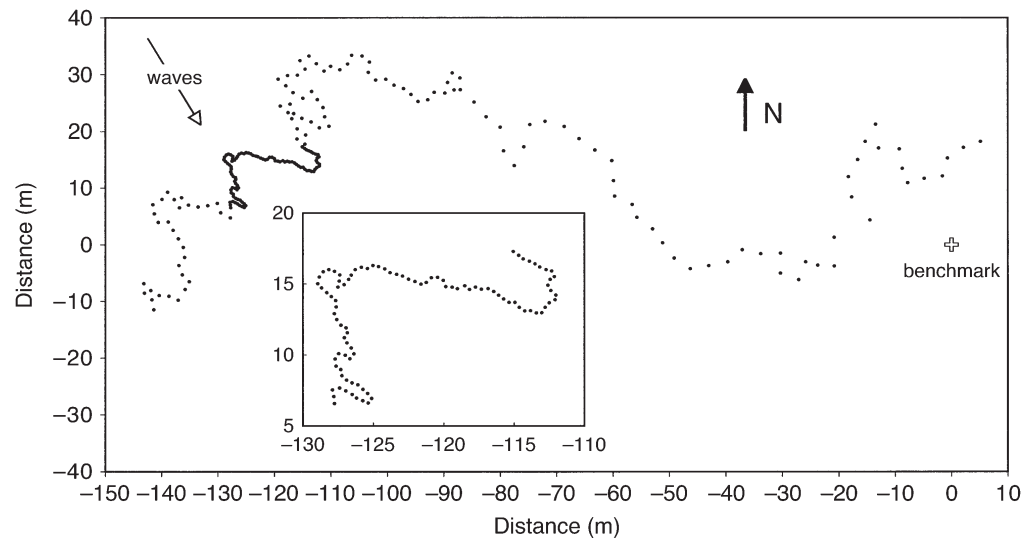
Fig. 4. A map of the three intertidal transects at Hopkins Marine Station. The inset at an expanded map scale shows the details of the short transect. All measurements were taken with reference to a USGS benchmark at the position shown.

individual data points (the grain of the measurement, sensu Wiens 1989). These effects are discussed in Appendix B.

As noted above, our six scales have been calibrated using a sine wave as the archetypical pattern of variation, and we test this calibration using a simulated monochromatic signal that varies with a 10-m wavelength, sampled as it would be for our real-world data. However, many natural data series are not so precisely periodic. In particular, it is common that frequency-specific variance is highest at low frequencies, and decreases rapidly as frequency increases. To be precise, in cases of this sort,

$$S(f) = \frac{\kappa}{f^{\beta}}. \qquad (8)$$

β is, thus, the slope of the spectrum when plotted on log-log axes. This type of signal is known as $1/f$ noise, and the shape of its spectrum affects the calculated scale. We explore this effect by calculating our six scales of variability for random, synthesized $1/f$ noise data sets with a range of β (see Appendix B).

The six definitions outlined above are used to examine spatial and temporal scales of variation in 15 physical and biological variables in the intertidal zone on a moderately exposed shore (Mussel Point) at Hopkins Marine Station, Pacific Grove, California. As we will see, there can be complications in the practical implementation of these definitions of the scale of variability. In several cases, these complications are sufficiently severe and basic that we may need to re-evaluate "scale of variability" as a useful concept for describing pattern in ecology.

Materials and Methods

Spatial variation of physical processes

Three horizontal transects were laid out in 1998–2000. One transect consisted of 97 experimental lo-cations at an average height of 1.80 m (1 SD = 0.06 m) above mean lower low water (MLLW), in the middle of the "mussel zone" (Fig. 4). Experimental locations on this transect (the "short" transect; inset, Fig. 4; also see Plate 1) were installed at an interval of 0.46 m. This interval was measured with a large caliper, and thus represents a straight-line distance between locations rather than the distance a flexible tape measure would yield if it conformed to the complexity of the shore. The second transect consisted of 103 experimental locations at an average height of 1.69 m above MLLW (1 SD = 0.16 m). The straight-line spacing of locations along this "medium" transect was 1.72 m. The medium transect incorporated the short transect by using every fourth location on the short transect. Although the interval on the medium transect is not exactly four times that on the short transect, the difference in spacing (0.11 m) is only 3% of the shortest spatial period that can be discerned (the Nyquist interval, see Appendix A) for the medium transect, and is therefore negligible for present purposes. A third, "long" transect consisted of 98 experimental locations at an average height of 1.70 m above MLLW (1 SD = 0.12 m). The straight-line spacing along this transect was 3.44 m. The long transect incorporated points from the short and medium transects. This overlapping arrangement of transects has the advantage of maximizing the range of measurement scales at which the shore can be examined, while maintaining a practical number of measured locations. This design has the disadvantage, however, that each length of transect (with its specific grain and extent) is not replicated.

Each experimental location on the transects was fitted with a mounting for either a recording dynamometer (for measurements of maximum wave-induced hydrodynamic force) or a recording thermometer (for measurements of maximum temperature). The record-

PLATE 1. A wave breaking on a portion of the ''short'' transect at Hopkins Marine Station. The drag spheres (wiffle golf balls) of several recording dynamometers are visible, marking site locations, and the complex topography of the shoreline is evident. Photo credit: B. Helmuth.

ing dynamometers were similar in construction to those described by Bell and Denny (1994) and Denny and Wethey (2000) (Appendix D).

Maximum force was recorded for each location on 28–74 occasions. For each measurement interval, the maximum offshore significant wave height (the average height of the highest one-third of waves, an index of the ''waviness'' of the ocean) was determined. A bottom-mounted wave gauge (SeaBird SBE26; Sea-Bird Electronics, Bellevue, Washington, USA) was installed at a depth of ~10 m, 50 m offshore of the transects, and measurements of significant wave height were recorded four times daily during the deployment of dynamometers. These measurements allowed for the construction of a nonlinear regression of maximum force as a function of significant wave height (Helmuth and Denny 2003). The value of this regression for an offshore significant wave height of 2 m (representative of moderate wave conditions) was used as our index of wave exposure.

The recording mercury thermometers (Forestry Suppliers, Jackson, Mississippi, USA) operate in a fashion similar to that of a fever thermometer, but over a temperature range (0–100°C) sufficient to include the range of temperatures encountered in the intertidal zone. Only 50 thermometers were available. As a result, none of the transects could be measured in its entirety on any single occasion. Instead, the measurements were normalized by dividing the temperature from each intertidal thermometer (in °C) by the maximum temperature recorded during the same interval by a standard thermometer at an unshaded terrestrial location directly above the transects. Maximum temperature was recorded at each of the experimental locations on 2–20 occasions (mean = 7) between November 1998 and May 1999. The maximum temperatures reported here are the average of the normalized values for these measurements. The dynamometers and thermometers shared locations on the transect. As a result, simultaneous measurements of maximum force and maximum temperature were not available. Maximum tempera-

tures were measured only on the short and medium transects.

The topography of the substratum was quantified along all transects using an index of the potential effect of topography on wave exposure proposed by Helmuth and Denny (2003) (see Appendix D).

Spatial variation of biological processes

Species diversity was measured on all three transects in June 2002 and again in September 2002. At each location, a rectangular quadrat (21 cm wide by 30 cm high) was centered on a point 21 cm to the right of the force/temperature emplacement. The quadrat was divided into 70 squares to facilitate visual estimation of percent cover. The amount of primary space occupied by each species was determined by counting the number of squares and portions of squares (down to one-eighth square) occupied by a species. Organisms present but occupying a total of less than one-eighth of a square were designated as ''trace'' species and considered to occupy 0.1% of the quadrat. Highly mobile creatures (e.g., crabs and nemertean worms) were excluded from these counts, but gastropods were included. These estimates of percent cover allowed computation of the Simpson diversity index, D, for each location: $D = 1 - \sum_{i=1}^{k} A_i^2$, where A_i is the fraction of space covered by species i in a particular quadrat. The proportion of substratum not occupied by organisms was also included as a ''species'' so that D equals zero when no macroscopic life is present. A total of $k = 63$ taxa were counted. Simpson's index was used because it depends most strongly on the abundance of the most common organisms and is relatively insensitive to any inaccuracies in the measurement of rare species (Margurran 1988).

The measurements made as a part of this diversity survey allowed us to quantify several other variables of ecological relevance. Along the west coast of North America, the mussel *Mytilus californianus* is the competitive dominant for space in the mid to upper intertidal zone (Seed and Suchanek 1992). Our survey al-

lowed us to measure the spatial variation in *M. californianus* cover along each of our three transects, and thereby to measure the scale of the variation in this proxy for competitive dominance. As noted above, our survey did not include counts of highly mobile predators such as crabs and birds, but it did allow us to measure the spatial variation in abundance of the molluscan predator, *Nucella emarginata*. We use this abundance as a proxy for the intensity of predation. Similarly, data from our survey allowed us to quantify the abundance (measured as percent cover) of grazing molluscs. These included two species of littorine snails and several species of limpets and chitons.

In November and December 2002, the shore at Hopkins Marine Station was subjected to unusually severe wave action, and patches of mussels were removed at several locations along the transects. The spatial scale of this disturbance was measured by noting for each site the change in percent cover of mussels before and immediately after the autumn storms.

Three additional processes were measured for each location on the medium transect. Recruitment of mussels (*Mytilus* sp.) was measured with a Tuffy brand plastic kitchen scrubber (The Clorox Company, Oakland, California, USA) bolted to the rock at each location. Each scrubber was left in place for one month, retrieved, and returned to the laboratory. Organisms were rinsed from the scrubbers and examined under a dissecting microscope. The values reported here are the average numbers of mussels collected per month per scrubber for the period 1 May 1999 through 30 June 2000.

Microalgal primary productivity was estimated as the rate of algal film accumulation in the absence of herbivores. A small settlement plate was installed at each location to measure the monthly accumulation of algal film, and a sheet of copper foil was sandwiched between the settlement plate and the substratum. The resulting border of copper served as an effective barrier to molluscan grazers. The settlement plates were installed downslope of the recruitment scrubbers to ensure that any toxic runoff from the copper sheets did not adversely affect mussel recruitment. Plates were retrieved monthly between July 1999 and September 2000 and returned to the laboratory for analysis (see Appendix D). Productivity estimates are presented as micrograms of chlorophyll *a* per 100 square centimeters per month.

Temporal variation in physical processes

In addition to these measurements of spatial variability, we obtained and analyzed a variety of data regarding temporal variation in the physical environment. Ocean surface temperature has been measured daily at Hopkins Marine Station since 1919. One notable gap in the data (all of 1940) was filled by inserting the corresponding data from 1939. Smaller gaps were filled by linear interpolation. Temperatures representative of the body temperature of intertidal organisms were measured in February 2002. A brass ball (2.5 cm diameter), painted black, served as a surrogate organism, and its "body" temperature was recorded to the nearest 0.5°C every 10 min for 2 wk in February 2002 (see Appendix D for details). Two additional time series were gleaned from the literature. The Coastal Data Information Program maintains a wave-rider buoy at the Farallon Islands, California. Significant offshore wave height is measured four times per day. We averaged these measurements daily from 1982 to 1995. Along the coast of California, the inshore ocean surface temperature and the concentration of nutrients are both affected by the intensity of wind-driven upwelling. The National Marine Fisheries Service calculates a monthly index of upwelling ($m^3 \cdot s^{-1}$ per 100 m of coastline) for various locations along the California coast. Records of the monthly upwelling indices from 1946–1995 were gleaned from Schwing et al. (1996) for an area centered on 36°N, 122°W, a site off the central California coast.

Spectral analysis

Spectral analyses of the spatial and temporal data (a step in the calculation of the p-, f-, w-, and v-scales) were carried out using standard methods as detailed in Bendat and Piersol (1986) (see Appendix A).

RESULTS

The time (or spatial) series for measured variables and their associated spectra are shown in Appendix E.

Temporal scales

The temporal scales of variation are shown in Table 1. The scale of variation in solar irradiance provides a useful starting point for examining our results. It is light for roughly half the day, and dark for the other half, so we would intuitively expect a temporal scale of ~0.5 d. This expectation is born out in our data. There is a clear peak in the spectrum at a frequency of $1.0 \ d^{-1}$ (Fig. 5), so the peak scale is indeed 0.5 d. This dominant peak accounts for 72% of the overall variance. (The peaks at harmonics of $1.0 \ d^{-1}$ are due to the nonsinusoidal shape of the daily light fluctuations, and do not imply the existence of further p-scales [see Appendix A].) Calculated average scales range from 0.17 d for the derivative scale to 0.5 d for the variance scale. As expected, the frequency scale (0.32 d) is less than the wavelength scale (0.48 d), indicative of the presence of some long-term variation in the light signal. The relatively low value for the derivative scale is likely due to the presence of a substantial amount of high-frequency fluctuation in light, a result of passing clouds and fog. In summary, when provided with a relatively simple signal, our techniques for calculating the scale of temporal variability produce results that more or less match our expectations.

The scale of variability in "body" temperature yields similar results (Table 1), probably because body tem-

TABLE 1. Temporal scales of variability: peak, frequency, wavelength, variance, derivative, and integral scales.

Variable	Units	Temporal scale					
		p	f	w	v	d	i
Solar irradiance	days	0.50	0.32	0.48†	0.50	0.17	0.44
Intertidal body temperature	days	0.50	0.32†	0.62	0.50	0.16	0.65
Sea-surface temperature	years	0.50	0.053†	1.00†	0.50	0.059	1.61
Significant wave height	years	0.50	0.016	0.17†	0.0028	0.0122	0.13
Upwelling index	years	nm	0.20†	1.22†	0.092	0.252	1.12

Note: An entry of ''nm'' indicates that the variable was not measureable.

† These scales are strongly dependent on the grain or extent of the measurements (see Appendix B).

perature is strongly coupled to solar irradiance. The peak scale is 0.5 d, and the dominant peak accounts for 67% of the overall variance. The slightly wider range in scale estimates (from 0.16 d for the derivative scale to 0.65 d for the integral scale) is a reflection of the added complexity of this variable. For example, while it is basically dark all night, setting a near-constant baseline for the signal of solar irradiance, the temperature of an intertidal organism can continue to decrease after dark as it loses heat by radiative transfer. Furthermore, body temperature is strongly affected by local water temperature when the organism is immersed, so the pattern of variation is affected by the tides. As expected, these complexities lead to a disparity between the frequency and wavelength scales. The tidal influence, in conjunction with the wavelength scale's tendency to accentuate the importance of long-period fluctuations, leads to the relatively large scale estimated by this method (0.62 d). Despite these details, the scales calculated here for body temperature are all within a factor of 2.5 of our expected scale of ~0.5 d. As we will see, this is a relatively small amount of variation among methods.

The calculated scales for the sea-surface temperature at Hopkins Marine Station and wave height at the Farallon Islands present a different picture. Each is highly

variable across the methods of calculation. The scale of variation in sea-surface temperature varies from 0.053 yr (~19 d) for the frequency scale to 1.61 yr for the integral scale. There is a clear peak in the spectrum corresponding to a period of 1 yr (L_p = 0.5 yr, Fig. 8A), but this peak includes only 31% of the overall variance. The complexity of this signal is amplified in different ways by the different techniques to yield estimates of scale that differ by a factor of more than 30.

The scales of variation in wave height at the Farallon Islands are similarly variable, ranging from a low of 0.0028 yr (1 d, the minimum measurable scale) for the variance scale to 0.17 yr (62 d) for the wavelength scale. In this case, none of the calculated average scales comes close to what we might expect—a seasonal scale of 0.5 yr. The peak scale is indeed 0.5 yr, but the dominant peak accounts for only 22% of the overall variance (Fig. 9A).

The spectrum for the upwelling index presents another contrast (Fig. 6). In this case, there is no well-defined dominant peak, so the p-scale cannot be defined. (A minor peak at a frequency of 0.90/yr (a period of 1.11 yr) contains only 6% of the overall variance.) In general, the higher the frequency, the lower the associated variance, approximating $1/f$ noise. As we will see, this pattern is common in our spatial data. Temporal scales for the upwelling index range from 0.092
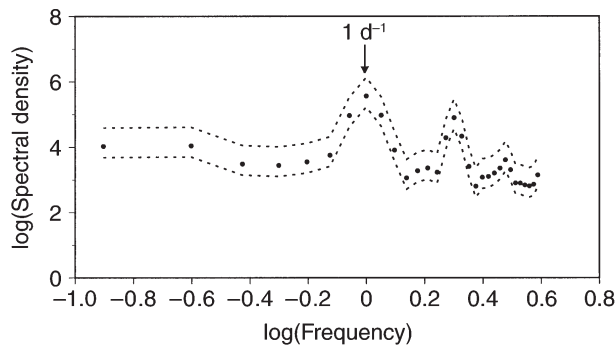

FIG. 5. The spectrum for the signal of solar irradiance. Note the presence of a dominant peak at a frequency of 1 d^{-1}. The secondary peaks at harmonics of 1 d^{-1} are due to the nonsinusoidal shape of the irradiance signal. Dashed lines show the 95% confidence intervals for spectral estimates. Irradiance was measured in W/m^2, and the units for frequency were d^{-1}.
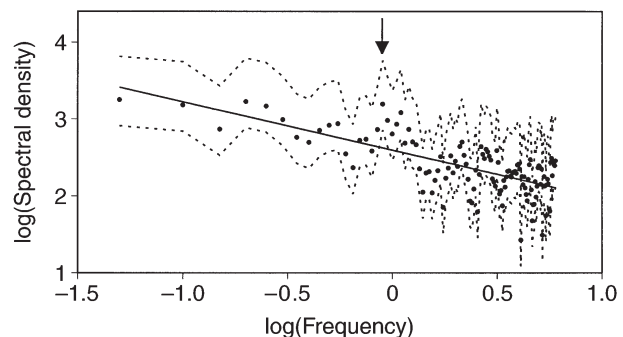

FIG. 6. The spectrum of the upwelling index, measured as $(m^3 \cdot s^{-1}$ per 100 m$)^2 \cdot$yr. The sole defined peak (arrow) accounts for only 6.3% of the overall variance. Dashed lines show the 95% confidence intervals for spectral estimates.

yr for the variance scale to 1.22 yr for the wavelength scale.

Various caveats for, and complications with, the temporal estimates of scale are explored in *Discussion*.

Spatial scale

Five results are evident from our spatial variables.

1) With the exception of the spectra for mobile predators, all of the spectra for our spatial variables more closely match the spectrum of upwelling than for those of the other temporal variables; that is, variance is inversely related to the frequency, indicative of $1/f$ noise. For these spectra, the exponent β in Eq. 8 has been estimated using an ordinary linear regression on log-log transformed spectral data, and the values and regression coefficients are given in Table 2. Because there are no clear peaks in these spectra, the peak scale cannot be determined.

2) For any variable measured on a given transect, there is little agreement among the six different methods for quantifying scale (read across any line in Table 3). Among the methods, there is commonly a difference of greater than an order of magnitude in the calculated scale. Typically, the v-scale gives the smallest estimate, and the w- or i-scale the largest estimate.

3) The $1/f$ noise character of the data can help to explain the variation among method for quantifying scale. As expected, application of the six methods of calculating scale to a monochromatic data series with a wavelength of 10 m yields a reliable 5-m scale for each of the transect lengths for each of the p-, f-, w-, v-, and i-scale calculations. However, calculations from synthesized $1/f$ noise data series of varying β are quite variable (Fig. 7). In the range of β encountered in this study (0.034–1.356), the v-scale generally gives the smallest estimate, and the w- or i-scale the largest estimate, the same pattern noted in our empirical data. Note that the large standard deviations inherent in this random $1/f$ noise data preclude making precise predictions of the rank order of scale estimates.

4) For any given method of calculating spatial scale, the measured value increases with an increase in the grain and extent of the measurement, that is, with an increase in the interval between measurements and an increase in the overall length of the transect (Table 3). As a consequence, "scale" as defined here may be an ill-posed statistic for characterizing the spatial variability of ecological phenomena in the intertidal zone, and this possibility is discussed in depth below.

5) For the limited stretch of shoreline for which we have data (334 m), there is no evidence for a hierarchy of spatial scales in the phenomena measured here. For example, for any given method of calculating scale, the spatial scales of variation in mussel cover (an index of competitive dominance for space), mussel recruitment, mussel disturbance, wave force, maximum temperature, and primary productivity are all roughly equivalent. In particular, note that the spatial scale of vari-

TABLE 2. Values of the spectral exponent, β, for all $1/f^β$ noise variables.

Variable	β	r^2	Probability	n
Force				
Short	1.267	0.810	0.000	18
Medium	0.709	0.603	0.000	20
Long	0.965	0.714	0.000	19
Topographic index				
Short	0.848	0.654	0.000	18
Medium	0.605	0.532	0.000	20
Long	0.295	0.194	0.059	19
Temperature				
Short	1.283	0.734	0.000	18
Medium	0.730	0.443	0.001	20
Chlorophyll				
Medium	1.356	0.729	0.000	20
Diversity				
Short	0.148	0.109	0.182	18
Medium	0.359	0.336	0.007	20
Long	0.608	0.476	0.001	19
Mussel density				
Short	0.442	0.488	0.001	18
Medium	0.728	0.562	0.000	20
Long	0.917	0.679	0.000	19
Mussel disturbance				
Short	0.463	0.363	0.008	18
Medium	0.187	0.032	0.448	20
Long	0.445	0.265	0.024	19
Mussel recruitment				
Medium	0.611	0.452	0.001	20
Predators				
Short	defined scale			18
Medium	0.106	0.096	0.184	20
Long	0.034	0.002	0.858	19
Grazers				
Short	0.041	0.004	0.795	18
Medium	0.795	0.489	0.001	20
Long	0.930	0.603	0.000	19
Upwelling				
50-yr record	0.636	0.520	0.000	119

Notes: "Short," "medium," and "long" refer to the overall extent of the transect in question (see *Materials and methods*). There is a defined scale for the variation in predator abundance on the short transect, and as a consequence, no spectral exponent is calculated.

ation in the topographic index is similar to all the other scales.

The role of topography

This similarity among scales for different variables may have a mechanistic basis. For example, the pattern of variation in microalgal productivity can be mechanistically tied to shoreline topography. The algae on our plates apparently grew best when they stayed moist throughout a low tide, a condition that is assured if, due to topography, the plants are either shaded or exposed to wave-induced spray (or both). Thus, along our medium transect, primary productivity is positively

TABLE 3. Spatial scales of variability.

Variable	Extent (m)	Spatial scale					
		p	f	w	v	d	i
Force							
Short	44	nm	2.10†	4.82†	0.29	1.95	7.86
Medium	175	nm	5.04†	13.29†	1.09	5.04	12.06
Long	334	nm	11.41†	25.41†	2.19	16.18	15.14
Topographic index							
Short	44	nm	1.42†	3.34†	0.37	1.68	7.01
Medium	175	nm	4.63†	11.25†	1.18	4.66	7.67
Long	334	nm	7.56†	15.39†	2.09	8.47	16.30
Temperature							
Short	44	nm	2.21†	5.49†	0.26	2.13	9.64
Medium	175	nm	5.62†	16.06†	1.06	5.28	25.95
Chlorophyll							
Medium	175	nm	8.95†	21.01†	1.05	8.21	27.46
Diversity							
Short	44	nm	0.98†	1.79†	0.60	1.07	0.82
Medium	175	nm	3.65†	8.68†	2.12	4.25	7.78
Long	334	nm	9.25†	17.28†	4.30	9.13	18.04
Mussel density							
Short	44	nm	1.10†	2.65†	0.32	1.21	3.95
Medium	175	nm	5.51†	17.15†	1.04	5.20	20.14
Long	334	nm	12.18†	30.36†	4.14	10.68	34.87
Mussel disturbance							
Short	44	nm	1.09†	2.08†	0.42	1.17	1.34
Medium	175	nm	3.28†	7.21†	1.07	3.85	4.76
Long	334	nm	8.23†	19.86†	4.43	8.37	13.12
Mussel recruitment							
Medium	175	nm	4.33†	9.64†	2.58	4.54	11.06
Predators							
Short	44	1.1	1.06†	2.21†	0.71	1.13	1.46
Medium	175	nm	3.15†	5.98†	2.20	3.75	4.14
Long	334	nm	6.97	11.91	5.44	8.17	9.48
Grazers							
Short	44	nm	0.90†	1.77†	0.65	1.10	5.57
Medium	175	nm	5.46†	13.46†	1.94	4.94	8.66
Long	334	nm	10.00†	21.25†	4.75	10.90	16.77

Note: An entry of ''nm'' indicates that the variable was not measureable. ''Short,'' ''medium,'' and ''long'' refer to the overall extent of the transect in question (see *Materials and methods*).

† These scales are strongly dependent on the grain or extent of the measurements (see Appendix B).

correlated with wave exposure and negatively correlated with maximum temperature (Fig. 8A and B). In turn, there is a correlation between wave exposure and temperature (Fig. 8C). At Hopkins Marine Station, waves arrive from the northwest, whereas rocks are most effectively heated by sunlight if they face south. Thus, a location that is exposed to waves is unlikely to get very hot. Because of the tight correlation between temperature and force, the combination of wave force and maximum temperature predicts only slightly more of the overall variation in microalgal primary productivity (64%) than does either effect alone (44% and 62%).

DISCUSSION

The results obtained here suggest that the broad concept of ''scale of variability'' as used in ecology is likely to encounter nagging problems when applied to specific cases. If (as demonstrated by our spatial data) measurements of scale are themselves scale dependent, or if different measures of scale yield estimates that differ by orders of magnitude, it is difficult to see how current concepts that rely on defined scales of variation can be used productively.

Our inability to measure clear spatial scales at our intertidal site leads us to draw three conclusions. (1) Except in those rare cases where a single, well defined peak scale exists, ''scale of variability'' may not be the appropriate statistic by which to characterize ecological pattern. We propose that ecologists should focus their attention on the entire spectrum, which encompasses variation at all scales, rather than attempt to boil the spectrum down into a single statistic. (2) There are

FIG. 7. The calculated scale varies among methods when applied to $1/f$ noise data. Vertical bars indicate ± 1 SD, and for clarity, data points have been staggered slightly along the abscissa. In general, the larger the spectral exponent, β, the larger the calculated scale. For any given exponent, the rank order of scales approximates that found in our spatial data.
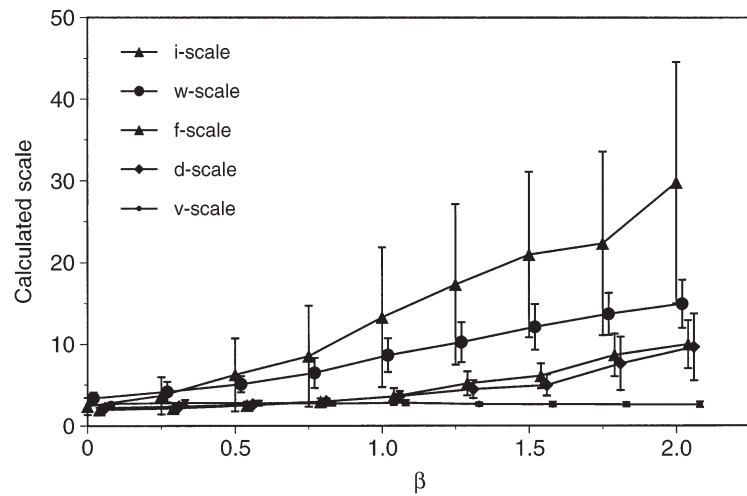
intrinsic problems associated with measuring scale in $1/f$ noise processes, but the existence of $1/f$ noise in intertidal ecological variables can nonetheless be used (albeit with caution) as a mechanism for extrapolating from small-scale measurements to make large-scale predictions. (3) The spatial variation in intertidal ecological processes may be driven by the spatial variation in topography.

Scale is not the appropriate statistic

The concept of ''scale of variability'' as defined here suffers from two basic problems. The first is inherent to statistics: it is quite possible that the index being calculated is not functionally representative of the phenomenon being considered. We are reminded of the joke regarding two naïve statisticians who go duck hunting. A duck flies over, and both statisticians shoot at it. One shot passes 1 m in front of the duck, the other 1 m behind. The statisticians then proceed to congratulate each other because, on average, they nailed the duck dead center.

This issue is central to measurement of the f-, w-, i-, and d-scales for the wave-swept shores at Hopkins Marine Station. Each scale involves taking an average across all measured variation. However, because these different methods average in different ways, the estimated scales vary. For example, our data from the long transect suggest that within our 334 m of shoreline, wave exposure (maximum wave force) varies at scales that range from 11 to 25 m, depending upon whether one chooses the f-, w-, i-, or d-scale (Table 3). Which of these scales captures the essence that we seek? It is difficult to say, because the components of each spectrum disappear in the averaging process and its interaction with the $1/f$ noise character of the data. For example, the f-, w-, and i-scales are each designed to be an index of the scale over which a process remains more or less constant, and, although it is predictable that such widely varying answers are obtained (see Fig. 7), this variation is nonetheless disturbing. In fact, it

would be dangerous to interpret any of these scales as implying that in reality there are stretches of shore 11–25 m long in which exposure is high, alternating with 11–25-m stretches where exposure is low. A quick glance at the data (Appendix E, Fig. A11) shows that the distribution of wave forces isn't that simple. In summary, although we can arrive at a calculated scale for a given set of data, the loss of important information as we attempt to express the pattern of variation in a single index makes it difficult to see how these measures of the scale of variability can be realistically interpreted and productively utilized.

We propose that, in cases such as this, it may be counterproductive to calculate ''the'' scale of variability. Instead, attention should be focused on the spectrum (or an equivalent statistic, such as a variogram), which contains all available information regarding the pattern of variability.

The second problem is a result of the practical limitations on measurement. In an ideal world, we would be able to measure ecological phenomena at frequencies ranging from 0 to ∞, encompassing all possible scales of variation. In practice, however, both the grain and the extent of measurement are limited, and these limits can affect the calculated scale. For example, the typical, $1/f$ noise shape of the spectra (the lower the frequency, the larger the variance) ensures that the spatial scales calculated here are sensitive to both the grain and extent of the measurements (see Appendix B): when the same shore is measured with increasing grain and extent, the measured scales increase (Table 3). If the calculated scale is itself dependent on the grain and extent of measurement, it is difficult to see how this scale can be productively utilized.

As discussed in Appendix B, the dependence on grain and extent is not an inevitable result of the techniques of calculation. Rather, the dependence of our estimates on the grain and extent of measurement (Table 3) is a function of the type of variation we encounter on the shore. It is because our spatial data resemble $1/f$ noise
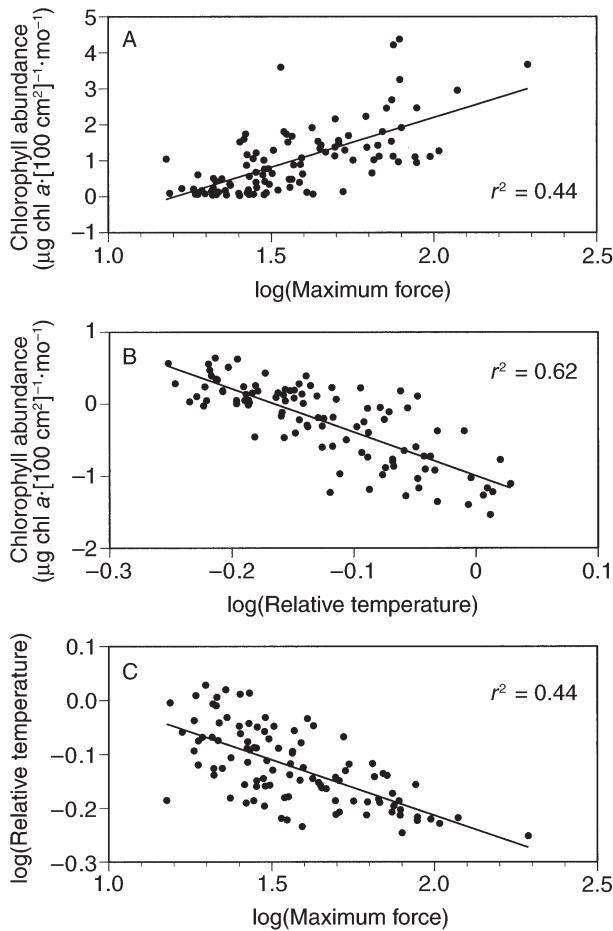
FIG. 8. Chlorophyll abundance (a measure of microalgal productivity) is (A) positively correlated with maximum wave force and (B) negatively correlated with relative maximum temperature. In both cases, the correlations are significant (t = 2.680, P = 0.009 for force; t = −8.108, P < 0.0001 for temperature). (C) Temperature and force are themselves negatively correlated (t = −8.937, P < 0.0001).

(or at least that they have no well-defined peaks in their spectra) that our methods of calculating scale are sensitive to the grain and extent of measurement.

An alternative to ''scale''

The difficulties inherent in measuring the scale of variation of an ecological variable need not be a problem, however, because, even in the absence of a well-defined scale, the spectrum allows us to quantify environmental variation appropriately. If, from other sources, we can determine the measurement scale (as opposed to the scale of variability) at which biological processes take place, we can use this ''biological ruler'' in conjunction with the measured spectrum of the physical environment to quantify the variability with which an organism must contend.

There are many biological processes that have defined (or at least definable) measurement scales. For example, the distance that a predatory snail can crawl at high tide sets a spatial measurement scale for its

potential daily interaction with wave forces. Measurements on the substratum at Hopkins Marine Station show that a *N. emarginata* crawls at an average speed of 1.73 cm/min (1 SE = 0.07 cm/min; P. Martone, *personal communication*). Over the course of a single high tide (~6 h), a snail crawling at this pace travels a maximum distance of 6.2 m. If it stops to feed at some random point within that distance, what is the potential variation in wave force that it might encounter? A distance of 6.2 m corresponds to a spatial frequency of 0.161/m. This value, in association with the measured spectrum of maximum wave force (Fig. 9A), allows us to estimate the variability in ''exposure'' the snail would encounter, variability that can affect not only the survivorship and behavior of this predatory species, but also the spatial variability of its prey (Benedetti-Cecchi 2000, 2003).

In this case, the variability is relatively small. Given that the size of the snail is of the same order as the size of the balls attached to our dynamometers (and therefore that the variability in our measurements is approximately equal to that encountered by the snail), the variance in maximum force for an excursion of 6.2 m is ~400 N². The standard deviation of force at this scale is thus $\sqrt{400}$ = 20 N, a small variation when compared to either the overall maximal force (158 N) or the mean maximum force (44 N) observed on the transect for which this spectrum was calculated. In other words, if the snail has survived where it is, it is likely to be able to survive the conditions it encounters within a tide's crawl. If (as seems likely) the
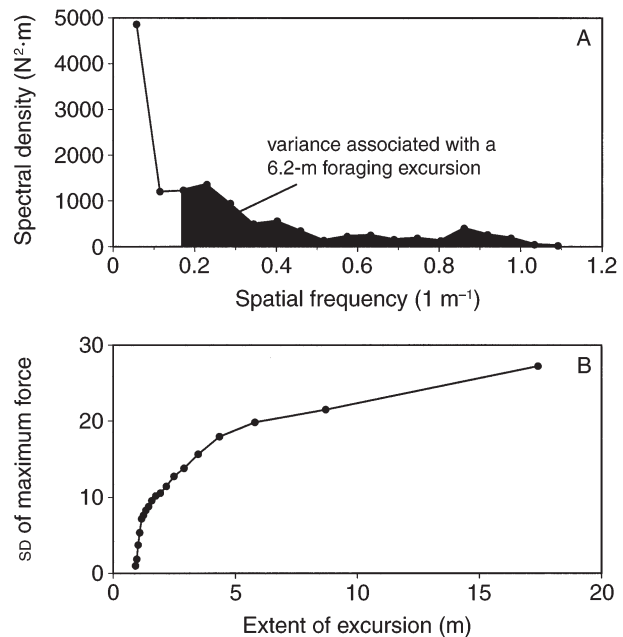

FIG. 9. (A) The area under the spectrum of maximum wave force is a measure of the variance in force associated with a foraging excursion of a given extent. (B) By calculating this area as a function of foraging distance, a curve of standard deviation of force can be drawn.

snail does not crawl continuously during high tide, a smaller variation can be expected. For example, if the snail crawls only 2 m, the standard deviation of force is ~11 N. On the other hand, if the snail could crawl farther, more variability would be encountered (as shown in Fig. 9B), and our conclusion might need to be altered. Note, however, that for distances beyond about 5 m, the increase in σ with an increase in excursion distance is reduced.

Knowledge of the temporal spectrum can be of similar potential use. For example, intense upwelling can lead to high nutrient levels in coastal waters, with concomitant high concentrations of phytoplankton. This standing crop can have substantial ''bottom up'' effects on intertidal communities (Menge et al. 1997). Knowledge of the fluctuation in upwelling can thus potentially be important in our understanding of year-to-year variability in intertidal community processes. Although the overall variability in upwelling has no dominant spectral peak (Fig. 6), we can make productive use of this temporal spectrum if we approach it with a biologically defined measurement scale. For example, we might know a priori that the effective reproductive lifetime of an intertidal mussel is 5 yr. With this biological scale and the spectrum in hand, we can estimate that the standard deviation of upwelling encountered by a typical mussel in its reproductive lifetime is ~43 $m^3 \cdot s^{-1}$ per 100 m of coastline. This value can be compared to the overall average upwelling index of 109 $m^3 \cdot s^{-1}$ per 100 m of coastline. Whether this magnitude of variation (39% of the mean) has substantial ecological impact is a viable question for further research. Again, the standard deviation is most sensitive to changes in extent at small extents.

Scaling up

As noted above, spectra of the sort seen in our spatial data are characteristic of a broad set of processes collectively known as $1/f$ noise (see Appendix F). They are very common in both nature and technology, having been found in electronic devices, geophysical time series, traffic flow, music, protein dynamics, DNA base sequences, and ecological and evolutionary time series, to name just a sample (Lawton 1988, Halley 1996). (An alternative explanation for the shape of our spectra—autoregression—is explored, and then eliminated, in Appendix G.)

As noted in the Introduction, one of the most important tasks before ecologists is to elucidate methods for ''scaling up'' information from small-scale experiments to large-scale patterns and processes. The apparent $1/f$ noise behavior of our spatial spectra suggests a simple method for extrapolating from small-scale measurements. Having measured the spectrum over a range of relatively small extents, we have estimates of both κ and β in Eq. 8, and standard regression techniques provide us with estimates of our confidence in each of these values (e.g., Zar 1972). If we assume that these coefficients are constant (a brash assumption), we can estimate the spectrum for lower frequencies than we have actually explored, allowing us to estimate the variability associated with a given process at larger spatial or temporal scales than those we have directly measured. In essence, the $1/f$ noise pattern of variation in small-scale measurements provides a ''scaling law'' by which variation can be estimated at larger scales of measurement. This use of $1/f$ noise as a scaling law is similar to the use of scaling laws in physiology and biomechanics (Schmidt-Nielsen 1984).

For example, the spectrum of mussel recruitment at Hopkins Marine Station can be modeled as $1/f$ noise: $S(f) = 50.6f^{-0.61}$. By integrating this empirical scaling relationship between a lower frequency set by the extent of our interest and an upper frequency set by the interval between measured locations on our transect ($f = 0.291$ m^{-1}), we can predict the variance of mussel recruitment among sites at any scale we please.

For instance, we might want to estimate the variability in recruitment that occurs between Point Conception and Monterey Bay. These two prominent biogeographic boundaries on the California coast are separated by 2.5° of latitude (2.78×10^5 m), which corresponds to a spatial frequency of 3.60×10^{-6} m^{-1}. Using this lower bound for our integration, we predict the standard deviation of recruitment from Point Conception to Monterey to be 8.96 individuals per collector per month, with a 95% confidence range from 6.79 to 13.77 individuals per collector per month. The Partnership for Interdisciplinary Study of Coastal Oceans (PISCO) center at the University of California, Santa Cruz, has measured mussel recruitment at five intertidal sites along this stretch of coastline using techniques identical to those employed here. The measured standard deviation among these sites is 11.77 individuals per collector per month, well within the bounds of our estimate. This result suggests that measurements of recruitment made at a single site (334 m of shoreline) can be used to provide an accurate estimate of the variability in recruitment along 278 km of shore, a spatial extrapolation of greater than 800-fold.

This conclusion should be taken with a large grain of salt, however. The PISCO data extends to 12 other sites in California (from San Diego to north of Santa Cruz, a distance of 358 km), and the standard deviation at this larger scale of measurement is 25.81 individuals per collector per month, well outside the 6.8 to 13.9 individuals per collector per month predicted by the data from Hopkins Marine Station. The disparity gets even worse if sites in Oregon and Washington are included. At this very large scale (1330 km) the measured standard deviation among sites is 1455 individuals per collector per month, far above the 6.8–14.5 individuals per collector per month predicted from the Hopkins data. Evidently, there is a source of variability operating at these larger scales that is not evident in our small-scale measurements. Large-scale variation in the
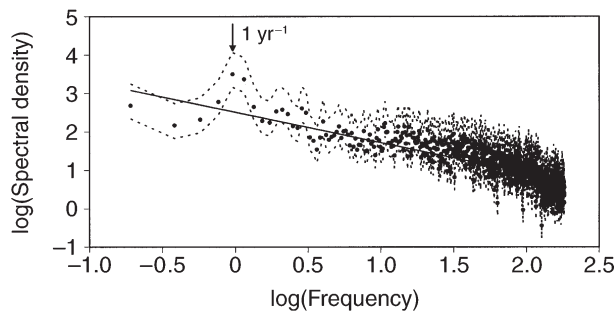
FIG. 10. The spectrum for significant wave heights measured (in cm²·yr) at the Farallon Islands. A dominant peak is evident at a frequency of 1 yr⁻¹, but the spectral density decreases approximately as $1/f$ noise for higher frequencies. The regression line shown was calculated for all frequencies between 1 mo⁻¹ and 0.14 mo⁻¹ (1 per 7 mo). Dashed lines show the 95% confidence intervals for spectral estimates.

supply of larvae to the shore is an obvious possibility. Clearly there are limits to the viability of this method of extrapolation.

A second sort of limitation is evident if $\beta > 1$ for the variable in question. In this case, the $1/f$ noise character of a process implies that the variance increases without limit as we increase the scale of our extrapolation (Appendix F), an implication fraught with difficulties. One suspects that for any process the variance cannot increase above some critical extent. The main question, then, is whether this critical scale is ecologically relevant.

Our temporal data provides a pertinent example. For times less than ~7 mo ($f > 1.7$ yr⁻¹), the temporal spectrum of significant wave heights at the Farallon Islands approximates a $1/f$ noise process with $\beta = 1.13$ (Fig. 10). Measurements of the ocean's ''waviness'' over a few weeks could therefore provide an accurate estimate of the spectrum of this process, and these data could be extrapolated to the scale of months. This information could then be used to accurately estimate the variance in wave heights that are relevant to a species of seaweed (such as *Postelsia palmaeformis*, Paine 1979) that recruits, reproduces, and dies all within a year. As seen in Fig. 10, however, the shape of the spectrum changes drastically at frequencies below 1 yr⁻¹ (times >1 yr). Extrapolation from a short series (with its large β) to times in excess of a year would lead to a gross overestimation of variance at long temporal scales, and could therefore lead to errors when extrapolating short-term measurements to predict (for instance) the ecology of perennial seaweeds.

In this case, we have measurements from a long enough period to warn us of the critical change in behavior of the wave-height spectrum at the annual frequency. In other cases, we have not made measurements at extents large enough to expose a critical value. There are hints, however, that a critical value may exist. For example, in our measurements of the topographic index, β is significantly lower on the long transect than

it is on the short transect (Table 3; $F_{1,33} = 6.794$, $P = 0.014$), hinting that the $1/f$ noise behavior of shoreline topography may be confined to a limited band of spatial frequencies. This behavior is not general among our data, however. The β for wave force on the long transect is not significantly lower than that on the short transect (Table 3; $F_{1,33} = 1.994$, $P = 0.167$), while the β for grazers is significantly higher on the long transect than on the short (Table 3; $F_{1,33} = 16.272$, $P < 0.001$). In all other cases, there is no significant difference in β among the transect lengths. Thus, at present, we cannot confidently predict how the spectrum will behave at scales larger than those we have measured. In cases such as these, gross extrapolation from small-scale data would be ill advised, and we again suggest that extrapolations that assume a constant β be used with caution.

Problems inherent in making measurements in a $1/f$ noise environment (including the accurate measurement of the mean) are explored in Appendix H.

An exception: the scale of predators

The spatial distribution of the predatory snail, *N. emarginata*, is the sole exception to the rule among our data that variation in space increases with an increase in the extent of the measurement. In this case, the spectrum for the short transect revealed a clear peak at spatial frequencies centered on 0.46 m⁻¹, corresponding to a wavelength of 2.2 m (Fig. 11). This peak accounts for 57% of the overall variance. Spectra for the medium and long transects are indistinguishable from white noise ($\beta = 0$, Table 3; $F_{1,33} = 1.913$, $P = 0.184$; $F_{1,33} = 0.033$, $P = 0.858$, respectively). Note that 0.46 m⁻¹ (the peak frequency) is above the Nyquist frequency for both the medium and long transects, and that the size of the quadrats used in measuring these data is likely to be sufficient to negate any problem with aliasing (see Appendix A). Thus, the lack of clear peaks on the medium and long transects is consistent
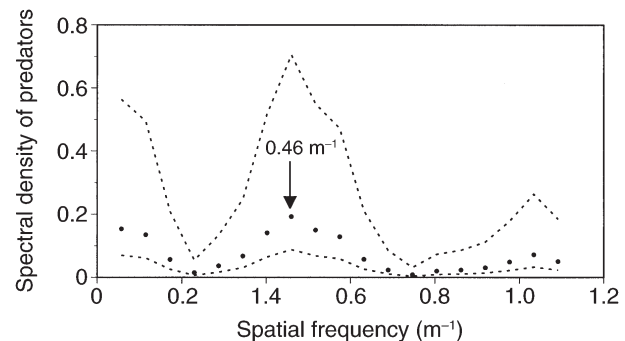

FIG. 11. The spectrum for the abundance of predators on the short transect. The abundance of predators was measured as no./0.063 m², and frequency is 1 m⁻¹, making units for spectral density (no./0.063 m²)²·m. A dominant peak is evident at a spatial frequency of 0.46 m⁻¹. Dashed lines show the 95% confidence intervals for spectral estimates.

with variation at a wavelength of 2.2 m (a scale of 1.1 m), but does not confirm it.

This apparent small-scale variation in the predator abundance is similar to that reported by Underwood and Chapman (1996). They propose that this scale is set by the behavior of snails.

The role of topography

With the exception of the upwelling index, all of our temporal data show well-defined scales of variation, and, in most cases, we can easily point at the mechanism that accounts for that scale (e.g., the rotation of the Earth for the one-per-day frequency of variation in solar irradiance). In contrast, there is a well-defined spatial scale in only one of our 10 spatial measurements, and the scaleless variables seem to act approximately as $1/f$ noise. Why do we repeatedly find $1/f$ noise behavior in our spatial data? At present, we can offer only a guess. Shorelines are well known to have fractal topography (Mandelbrot 1982), and the shoreline at Hopkins Marine Station is no exception (Fig. 4). If the spatial variability of a fractal shoreline is measured using an appropriate index (e.g., the spatial pattern of the azimuth of the local shoreline or the topographically based wave exposure index used here), the resulting spectrum has the shape characteristic of $1/f$ noise (Hastings and Sugihara 1993). For processes directly related to the fractal topography of the shoreline, $1/f$ noise behavior can therefore be expected.

As noted in *Results*, simple, mechanistic relationships appear to exist among chlorophyll abundance, wave exposure, and maximum temperature, and these relationships combine with the fractal geometry of the shore to form a complex spatial pattern of primary productivity (Fig. E9).

It is difficult to judge how close we should expect the relationship between to be between ecology and topography. The β values calculated for the short and medium transects are indistinguishable among the topographic index, wave force, and maximum temperature ($F_{2,54} = 2.159$, $P = 0.127$ [short]; $F_{2,54} = 0.184$, $P = 0.832$ [medium]), and it is tempting to view this similarity as potential evidence of a causal relationship. However, the β value for wave force (0.965) is greater than that for topographic index (0.295) on the long transect (Table 3; $F_{1,34} = 10.365$, $P = 0.003$), and the β value for primary productivity (1.356) is significantly greater than that for the topographic index (0.605; $F_{1,36} = 10.124$, $P = 0.003$). Until further measurements have been conducted, and mechanisms have been explored, it would be rash to draw firm conclusions regarding the mechanistic ties between shoreline topography and the scales of wave force and maximum temperature. The possible existence of causal relationships among variables could be tested by repeating our measurements on shores with topography that is not fractal.

We note that our results are consistent with those of other studies that have examined variation in the phys-ical environment (e.g., Bell et al. 1993): the larger the scale, the more variation is observed. In contrast, our results in general differ from those of Underwood and Chapman (1996), who found that most of the variation in spatial density of intertidal snails occurred at small scales. They attributed this pattern of variability in snails to the locomotory behavior of these mobile organisms. Note, however, that in their study Underwood and Chapman measured variation at large scales by replicating their sites on matched topography. Thus, much of the potential for large-scale variation related to topography may have been filtered from their measurements. It remains to be seen whether this apparent difference (a spectrum weighted at the low-frequency end for environmental factors, a spectrum weighted at the high-frequency end for behavioral factors) is general, or whether it is due to differences in topography (and the way it was incorporated into the measuring scheme) that are specific to these two cases.

The hierarchy of scales

Our measurements provide no evidence of a hierarchy of spatial scales of variability in intertidal ecology. As we noted in *Introduction*, the presence of a hierarchy has been used as a simplifying assumption in the construction of predictive models (Menge and Olson 1990), and the lack of a hierarchy may complicate the process of understanding how wave-swept communities function. However, our results are limited by the extent of our largest transect (334 m), and, as a result, cannot act as a critical test of the type of hierarchy proposed by Menge and Olson (1990). A different story may emerge as measurements are made at larger scales. Nonetheless, the extent of our measurements is greater than that of many (if not most) intertidal study sites. Thus, the patterns we have documented here may well accurately describe the local variation that underlies many of the studies to date. As noted previously, larger scales have been studied in the intertidal zone, but only through the use of matched sites, which filter the potential effects of topography.

CAVEATS

Several caveats should be noted with regard to the results presented here. First, our ability to discern peaks in our spectra (and thereby our ability to accurately define the peak scale) is constrained by the broad confidence limits around our estimates. There may be additional definable scales in the variables we have examined, but current data are insufficient to reveal them. It would therefore be advantageous to increase the statistical confidence in these spectra. In this regard, two factors should be noted: (1) Narrowing the confidence limits without unduly jeopardizing the range of scales at which the environment is sampled will require a tremendous amount of work. For example, a 100% increase in the number of experimental locations in our measurements (to ~200) would reduce the width of the

upper 95% confidence limit by a factor of only 37% (Bendat and Piersol 1986:286). (2) By greatly narrowing our confidence limits we would undoubtedly be able to discern subtle peaks, but the ecological importance of these small peaks would then be open to question. If there were truly well-defined scales of variation along our transects at Hopkins Marine Station, we feel that their existence would be evident in our data even with the current broad limits to our confidence.

Second, the dichotomy between the $1/f$ noise spectra of our spatial data on the one hand and the peaked spectra of our temporal data on the other is more apparent than real. The variables used in our temporal analyses were chosen at least in part to demonstrate that not all environmental processes are $1/f$ noise. As a consequence, they are a biased sample.

Finally, we note that the results presented here may apply only to the shore at Hopkins Marine Station. Clearly, measurements must be made across a range of scales at other locations to determine if our conclusions are robust. However, there is reason to believe that our ideas have application in other systems. One recent study in vascular plant communities in Great Britain has shown that plant diversity is extremely scale dependent. Using a sampling and statistical approach very different from ours, Crawley and Harral (2001) found that the rate of increase in plant diversity is greatest at intermediate scales and least at both small and large scales. These authors, like ourselves, found that these processes do not vary consistently with scale. In addition, Losos and Schluter (2000) reached similar conclusions about the influence of island size on speciation rates in *Anolis* lizards. In contrast, B. J. Enquist and K. J. Niklas (*unpublished data*) found that, in trees, the scaling relationship between the number of individuals and stem biomass is invariant to changes in species diversity, latitude or geographic sampling area. In this case, allometric models developed from first principals were found to be remarkably robust to changes in scale. Our results, although limited in scope, provide additional insight into this growing debate on the scale-dependency of ecological and evolutionary processes in natural systems.

Literature Cited

Azovsky, A. I., M. V. Chertoprood, N. V. Kucheruk, P. V. Rybnikov, and F. V. Sapozhnikov. 2000. Fractal properties of spatial distribution of intertidal benthic communities. Marine Biology **136**:581–590.

Bell, E. C., and M. W. Denny. 1994. Quantifying "wave exposure": a simple device for recording maximum velocity and results of its use at several field sites. Journal of Experimental Marine Biology and Ecology **181**:9–29.

Bell, G., M. J. Lechowicz, M. Chandler, E. DeBlois, L. Jackson, B. Mackenzie, R. Preziosi, M. Schallenberg, and N. Tinker. 1993. The spatial structure of the physical environment. Oecologia **96**:114–121.

Bendat, J. S., and A. G. Piersol. 1986. Random data: analysis and measurement procedures. Second edition. John Wiley and Sons, New York, New York, USA.

Benedetti-Cecchi, L. 2000. Variance in ecological consumer–resource interactions. Nature **407**:370–374.

Benedetti-Cecchi, L. 2001. Variability in abundance of algae and invertebrates at different spatial scales on rocky sea shores. Marine Ecology Progress Series **215**:79–92.

Benedetti-Cecchi, L. 2003. The importance of the variance around the mean effect size of ecological processes. Ecology **84**:2335–2346.

Bertness, M. D., and S. D. Gaines. 1993. Larval dispersal and local adaptation in acorn barnacles. Evolution **47**:316–320.

Buss, L. W. 1985. Competition and community organization on hard surfaces in the sea. Pages 517–536 *in* C. Diamond, editor. Community ecology. Harper and Row, New York, New York, USA.

Connell, J. H. 1961. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. Ecological Monographs **31**:61–104.

Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist **111**:1119–1144.

Crawley, M. J., and J. E. Harral. 2001. Scale dependence in plant biodiversity. Science **291**:864–868.

Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs **41**:351–389.

Dayton, P. K. 1984. Processes structuring some marine communities: are they general? Pages 181–197 *in* D. R. Strong, Jr., D. Simberloff, L. G. Abele, and A. B. Thistle, editors. Ecological communities: conceptual approaches and the evidence. Princeton University Press, Princeton, New Jersey, USA.

Denny, M. W., and R. T. Paine. 1998. Celestial mechanics, sea-level changes, and intertidal ecology. Biological Bulletin **194**:108–115.

Denny, M., and D. Wethey. 2000. Physical processes that generate patterns in marine communities. Pages 3–37 *in* M. Bertness, S. Gaines, and M. Hay, editors. Marine community ecology. Sinauer Associates, Sunderland, Massachusetts, USA.

Ebert, T. A., S. C. Schroeter, J. D. Dixon, and P. Kalvass. 1994. Settlement patterns of red and purple sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*) in California, USA. Marine Ecology Progress Series **111**:41–52.

Foster, M. S. 1990. Organization of macroalgal assemblages in the Northeast Pacific: the assumption of homogeneity and the illusion of generality. Hydrobiologia **192**:21–33.

Gaylord, B., and S. D. Gaines. 2000. Temperature or transport? Range limits in marine species mediated solely by flow. American Naturalist **155**:769–789.

Halley, J. M. 1996. Ecology, evolution and $1/f$ noise. Trends in Ecology and Evolution **11**:33–37.

Harley, C. D. G. 2003. Abiotic stress and herbivory interact to set range limits across a two-dimensional stress gradient. Ecology **84**:1477–1488.

Hastings, H. M., and G. Sugihara. 1993. Fractals: a user's guide for the natural sciences. Oxford University Press, Oxford, UK.

Helmuth, B., and M. W. Denny. 2003. Predicting wave exposure in the rocky intertidal zone: do bigger waves always lead to larger forces? Limnology and Oceanography **48**: 1338–1345.

Helmuth, B., and G. E. Hoffman. 2001. Thermal heterogeneity and physical gradients of stress in the rocky intertidal zone. Biological Bulletin **201**:374–384.

Isaaks, E. H., and R. M. Srivastava. 1989. An introduction to applied geostatistics. Oxford University Press, Oxford, UK.

Jackson, J. B. C. 1977. Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. American Naturalist **111**:743–767.

Lawton, J. H. 1988. More time means more variation. Nature **334**:563.

Leonard, G. H., J. Levine, P. Schmidt, and M. D. Bertness. 1998. Flow-driven variation in community structure in a Maine estuary. Ecology **79**:1395–1411.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology **73**:1943–1967.

Lewis, J. R. 1964. The ecology of rocky shores. English University Press, London, UK.

Losos, J. B., and D. Schluter. 2000. Analysis of an evolutionary species–area relationship. Nature **408**:847–850.

Mandelbrot, B. B. 1982. The fractal geometry of nature. W. H. Freeman, San Francisco, California, USA.

Margurran, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, New Jersey, USA.

Menge, B. A., B. A. Daley, P. A. Wheeler, and P. T. Strub. 1997. Rocky intertidal oceanography: an association between community structure and nearshore phytoplankton concentration. Limnology and Oceanography **42**:57–66.

Menge, B. A., and A. M. Olson. 1990. Role of scale and environmental factors in regulation of community structure. Trends in Ecology and Evolution **5**:52–57.

Menge, B. A., and J. P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. American Naturalist **110**:351–369.

Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. American Naturalist **130**:730–757.

Murdoch, T. J. T., and R. B. Aronson. 1999. Scale-dependent spatial variability of coral assemblages along the Florida Reef Tract. Coral Reefs **18**:341–351.

Newell, R. C. 1979. Biology of intertidal animals. Third edition. Marine Ecological Surveys, Faversham, UK.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist **100**:65–75.

Paine, R. T. 1979. Disaster, catastrophe, and local persistence of the sea palm *Postelsia palmaeformis*. Science **205**:685–687.

Paine, R. T., and S. A. Levin. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. Ecological Monographs **51**:145–178.

Palumbi, S. R. 1995. Using genetics as an indirect estimator of larval dispersal. Pages 369–387 *in* L. McEdward, editor. Ecology of marine invertebrate larvae. CRC Press, Gainesville, Florida, USA.

Peters, R. H. 1991. A critique for ecology. Cambridge University Press, Cambridge, UK.

Powell, T. M. 1995. Physical and biological scales of variability in lakes, estuaries, and the coastal ocean. Pages 119–138 *in* T. M. Powell and J. H. Steele, editors. Ecological time series. Chapman and Hall, New York, New York, USA.

Reed, D. C., D. R. Laur, and A. W. Ebeling. 1988. Variation in algal dispersal and recruitment: the importance of episodic events. Ecological Monographs **58**:321–335.

Rossi, R. E., D. J. Mulla, A. G. Journel, and E. H. Franz. 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. Ecological Monographs **62**: 277–314.

Roughgarden, J. D. 1977. Patchiness in the spatial distribution of a population caused by stochastic fluctuations in resources. Oikos **29**:52–59.

Roughgarden, J., S. D. Gaines, and S. W. Pacala. 1987. Supply side ecology: the role of physical transport processes. Pages 491–518 *in* Organization of communities past and present. The 27th symposium of the British Ecological Society. Blackwell Scientific Publications, Oxford, UK.

Schmidt-Nielsen, K. 1984. Scaling. Cambridge University Press, Cambridge, UK.

Schneider, D. C. 1994. Quantitative ecology. Academic Press, London, UK.

Schwing, F. B., M. O'Farrell, J. Steger, and K. Baltz. 1996. Ocean upwelling indices, west coast of North America 1946–1995. NOAA Technical Memorandum NOAA-TM-NMFS-SWFSC-231. U.S. Government Printing Office, Washington, D.C., USA.

Seed, R., and T. H. Suchanek. 1992. Population and community ecology of *Mytilus*. Developments in Aquaculture and Fisheries Sciences **25**:87–169.

Somero, G. N. 2002. Thermal physiology and vertical zonation of intertidal animals: optima, limits, and costs of living. Integrative and Comparative Biology **42**:780–789.

Sousa, W. P. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. Ecology **60**:1225–1239.

Underwood, A. J. 1981. Techniques of analysis of variance in experimental marine biology and ecology. Oceanography and Marine Biology Annual Review **19**:513–605.

Underwood, A. J., and M. G. Chapman. 1996. Scales of spatial patterns of distribution of intertidal snails. Oecologia **107**:212–224.

Underwood, A. J., and M. G. Chapman. 1998. Spatial analyses of intertidal assemblages on sheltered rocky shores. Australian Journal of Ecology **23**:138–157.

Underwood, A. J., and E. J. Denley. 1984. Paradigms, explanations, and generalizations in models for the structure of intertidal communities on rocky shores. Pages 151–180 *in* D. R. Strong, Jr., D. Simberloff, L. G. Abele, and A. B. Thistle, editors. Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton, New Jersey, USA.

Wethey, D. S. 2002. Biogeography, competition, and microclimate: the barnacle *Chthamalus fragilis* in New England. Integrative and Comparative Biology **42**:872–880.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology **3**:385–397.

Williams, M., and E. B. Rastetter. 1999. Vegetation characteristics and primary productivity along an arctic transect: implications for scaling-up. Journal of Ecology **87**: 885–898.

Zar, J. H. 1974. Biostatistical analysis. Prentice-Hall, Inc. Englewood Cliffs, New Jersey, USA.

APPENDIX A

A brief primer on spectral analysis is presented in ESA's Electronic Data Archive: *Ecological Archives* M074-011-A1.

APPENDIX B

Details of the definitions of scale are presented in ESA's Electronic Data Archive: *Ecological Archives* M074-011-A2.

APPENDIX C

A brief discussion of autocorrelation is presented in ESA's Electronic Data Archive: *Ecological Archives* M074-011-A3.

APPENDIX D

A more detailed presentation of the materials and methods used in this work is available in ESA's Electronic Data Archive: *Ecological Archives* M074-011-A4.

APPENDIX E

A series of figures showing the data series and associated spectra for the variables is available in ESA's Electronic Data Archive: *Ecological Archives* M074-011-A5.

APPENDIX F

A review of $1/f$ noise is presented in ESA's Electronic Data Archive: *Ecological Archives* M074-011-A6.

APPENDIX G

A discussion of alternatives to $1/f$ noise is presented in ESA's Electronic Data Archive: *Ecological Archives* M074-011-A7.

APPENDIX H

An examination of the process of making measurements in a $1/f$ noise environment is presented in ESA's Electronic Data Archive: *Ecological Archives* M074-011-A8.