Oecologia (Berl.) 46, 290–294 (1980)

Oecologia

Stability in an Annually Defaunated Estuarine Soft-Bottom Community*

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Summary. The concept of biological stability is so complex that at least six different meanings have been ascribed to it. We propose that one definition, "the ability of a system once perturbed to return to its previous state" be utilized as a working definition. Using quantitative data collected monthly from a soft-bottom community that undergoes an annual natural catastrophic defaunation coupled with a recently developed analytical technique, we demonstrate the feasability of a working definition and show the existence of stability in the soft-bottom community. The utility of a working definition of stability in the evaluation of disturbance is discussed.

The concept of biological stability is one of the most nebulous in ecology. For instance, Orians (1974) lists six different ways stability is commonly defined: (1) lack of change; (2) resistance to change; (3) speed of return to an initial state following a perturbation; (4) zone from which the system will return to a stable state; (5) stable limit cycles; (6) trajectory stability. Various investigators (May, 1971, 1972a, b, 1974a, b; Rosenzweig, 1971, 1972a, b; Rosenzweig and MacArthur, 1963) defined stability based on theoretical predator/prey or competition interactions; May (1973), in his monograph, defined a stable system as one in which all of the eigenvalues of the equilibrium community matrix have negative real parts. McQueen (1975) used demographic parameters of populations to define stability, whereas Peterson (1975) used statistical methods to analyse stability in mollusc populations. Sutherland (1974) explained stability as multiple stable points varying spatially and temporally in response to historic events. The above-mentioned works are a small number chosen from a vast literature to illustrate a major problem concerning the concept of biological stability: no one definition of stability has surfaced as an acceptable working definition.

The definition which we feel most closely approximates a working definition and the one we have chosen for this study has been referred to by several terms: *adjustment stability* (Margalef 1969), *stability* (Holling 1973), *elasticity* (Orians 1974), and *resiliency* (Boesch 1974; Westman 1978). These terms refer to the definition that we feel can be tested most easily: the ability of a system once perturbed to return to its previous state.

Regardless of the definition, most investigators are in agreement that two types of stability are distinguishable, neighborhood or local stability and global stability (Lewontin 1969; May 1973; Boesch 1974; Gray 1976, 1977). Local stability refers to the ability of a system to return to the same initial point following a small-scale disturbance, whereas global stability concerns the ability to return to the same initial point following a disturbance of any magnitude (Boesch 1974).

We feel that the ephemeral nature of the stability concept and the lack of objective methodologies have been contributing factors leading to the proliferation of stability concepts without the establishment of an acceptable working definition. To remedy this situation, we chose a definition that has the potential to be evaluated objectively (some definitions are quite abstract and would not lend themselves to any experimental application) and then applied that definition. The main problem in the past has been the lack of methods to determine objectively from actual data whether stability, however it might have been defined, existed in the system.

Quantitative community data normally consist of species identifications and number of individuals per species. It is thus possible to test changes in number of species, changes in total number of individuals, changes in number of individuals for any given species and changes in various diversity indices (combining the number of species and the distribution of individuals over these species) between quantitative samples taken before and after some perturbation. These tests usually take the form of a t-test or its non-parametric analog. However, these tests do not allow a simultaneous consideration of the total numbers of species and the distribution of individuals over each species while preserving the identity of that species. Recently, Bloom (1980) devised an objective measure of stability compatible with the proposed working definition and based partially on a multivariate analytical technique which simultaneously utilizes all information in quantitative community samples. With this measure we establish the utility of a working definition of stability and demonstrate from a field study, the existence of local stability in an estuarine soft-bottom community that undergoes an annual catastrophic natural defaunation.

Methods and Materials

Study Area

The study area (Fig. 1) is located ca. 50 m ESE from the Ballast Point pier on the western shore of Hillsborough Bay, Tampa, Florida, USA at approximately 27°53′ N and 82°28′ W. Depth varies from 4–5 m; sediments are mostly fine particles (mean percent of silt/clay = 10.3).

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0029-8549/80/0046/0290/$01.00

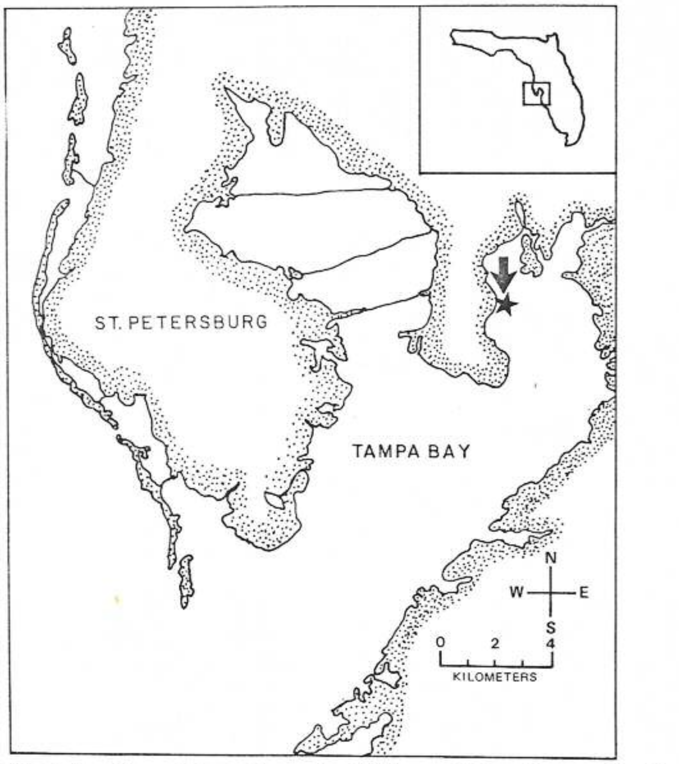

Fig. 1. Location of the study area in Hillsborough Bay, Tampa, Florida, USA. Star denotes sampling site

Tidal flow is slight, ≈0.5 knots. This location is a portion of a site that experiences a large areal (>3 km^2) total defaunation, most likely due to hypoxia, occurring annually during the summer and producing a cyclical pattern of defaunation/recolonization (Santos and Simon, in manuscript).

Sample Collection

During the period February 1975–July 1978, monthly samples (with a single exception) were collected with SCUBA-diver-operated, hand-held PVC cores (inside diameter = 7.62 cm, surface area = 45.60 m^2) to a depth of 15 cm. Ten cores were deemed sufficient to characterize the fauna adequately (Santos and Simon, in manuscript). All samples were sieved through a 500 μm mesh screen. The portion remaining was narcotized in a 0.15% solution of propylene phenoxetol (McKay and Hartzband 1970) and fixed in 10% formalin to which rose bengal stain had been added (200 mg/l Mason and Yevich 1967). All benthic fauna were sorted from the sediment, identified to the lowest possible taxon and enumerated.

Stability Analysis

A standard matrix (species as rows and sites [times in this instance] as columns) was constructed. The entities in the matrix were density values on a per square meter basis. These values were transformed in two ways: log-transformed, $X = \ln(x+1)$ (quantitative) or presence/absence (1, 0) values (qualitative).

As complete details of the method may be found in Bloom (1980), only a summary will be presented here. The analysis was performed in several steps. Both transformed data matrices were subjected to principal coordinates ordination analysis (Gower 1966; Sneath and Sokal 1973) which extracts the eigenvalues of the matrix. The eigenvalues account for the variance in the matrix and as the matrix must be symmetrical, it is possible to extract as many eigenvalues as there are rows or columns. However, because of the iterative nature and time consumption of the technique subsequent to the principal coordinates analysis, only the first three axes loadings (first three eigenvalues) were utilized. The eigenvalues are used as cartesian coordinates in an n-dimensional coordinate system. The eigenvalues of all samples collected prior to the initial perturbation are plotted in the coordinate system and thus define a space. Confidence limits (95%) are then constructed, using an iterative procedure and a Mann-Whitney U-test (Siegel 1956), around that space in each dimension, so that the end product of the pre-perturbation values is a 95% confidence polygon in s dimensions ($s = 3$ in this study). Using their eigenvalues as coordinates, post-perturbation samples are then sequentially plotted. When the post-perturbation sample coordinates fall within the 95% confidence limits for all dimensions, the system is statistically indistinguishable from the pre-perturbation state. The relative distance of the sample point to the nearest surface of the 95% confidence polygon can be calculated and for visual presentation, can be plotted against time.

All computer programs were written in Fortran IV and run on an IBM 370 computer at the University of South Florida Computer Research Center. Computer plotting was performed by a Cal-Comp model 563 plotter. A listing of the stability analysis program is available from the second author.

Results

A total of 80 taxa were present during the study period. The number of species present at any sampling period ranged from 0–29 and the density (#/m^2) ranged from 0–216,5000 (for more detailed biological and hydrographic data, see Santos and Simon, in manuscript). Over the 42 months of study, total defaunation as indicated by the total absence of macrofaunal individuals (and therefore of species and biomass) occurred three times at approximately yearly intervals (September 1975, July 1976 and August 1977) (Fig. 2). We, therefore, recognize three complete defaunation/recolonization cycles: (1) cycle 1 = 1975–1976; (2) cycle 2 = 1976–1977; (3) cycle 3 = 1977–1978. The latter portion of a presumed cycle was also observed during February 1975–September 1975.

The results of the stability analysis on quantitiative and qualitative data sets are presented in Fig. 3 and 4 respectively. The zero point of the figures, represented by a broken line parallel to the abscissa, corresponds to the edge of the 95% confidence limit envelope. Once the point has dropped below this line, the point is indistinguishable from the preperturbation points. Months 0, 10 and 24 represent months of the die-offs and month 19 is the period of no sampling. At these times the points are at their maximum distance from the edge of the envelope and represent samples devoid of species or individuals. A return to the pre-defaunation state occurred in 2 or the 3 cycles studied and the elapsed time for both recoveries was 7 months (Figs. 3 and 4). Subsequent to the third die-off (month 24, Figs. 3 and 4), the points never entered the 95% confidence limits and therefore, were considered different from the pre-defaunation points.

Discussion

It was not our contention to show one definition of stability as superior to any other nor to urge the adoption of a single definition. What we have attempted is to demonstrate, with an objective stability measure, the utility of a working definition of stability. If we consider the six definitions listed by Orians (1974) in relation to our working definition, the following scheme emerges: (a) definitions (1) and (2), lack of change and resistance

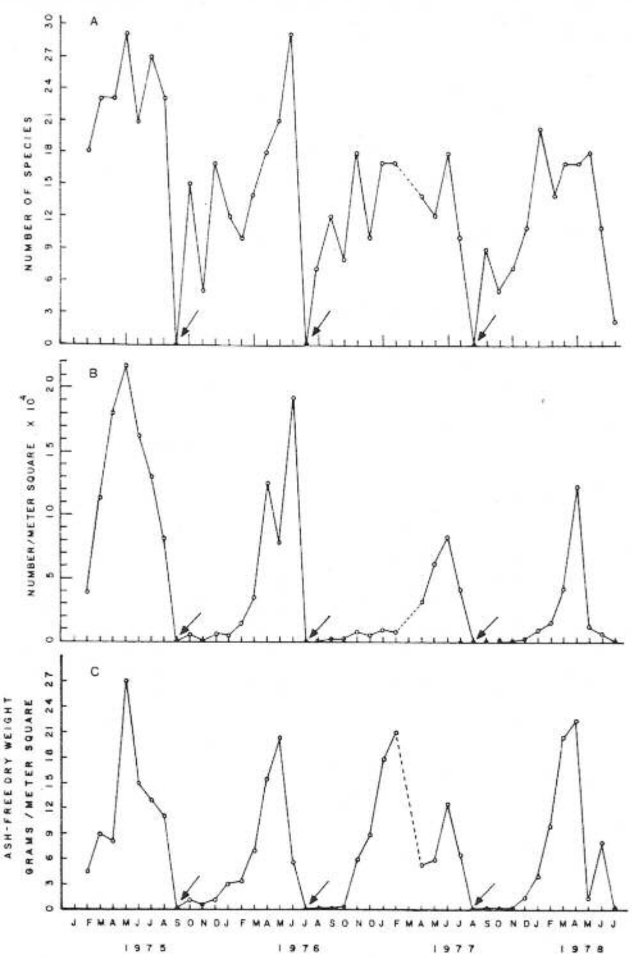

Fig. 2. Trends of number of species, number of individuals and ash-free dry wet over 42 months of study. Arrows denote defaunation events and the broken line represents a period of no sampling

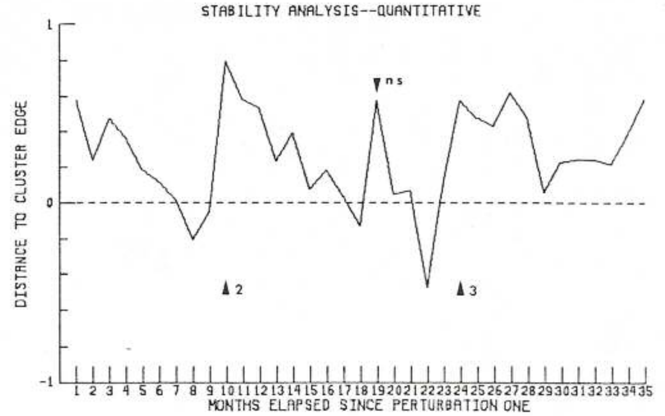

Fig. 3. Visualization of the quantitative stability analayis. The edge of the 95% confidence limit envelope is represented by the broken line. Once the point has dropped below this line, it is statistically indistinguishable from the pre-perturbation samples. Months of the die-offs are 0, 10, 24 and 36 with 10 and 24 being denoted by a caret. The caret labelled ns refers to month 19, the month of no sampling. Month 0 corresponds to September 1975 in Fig. 2

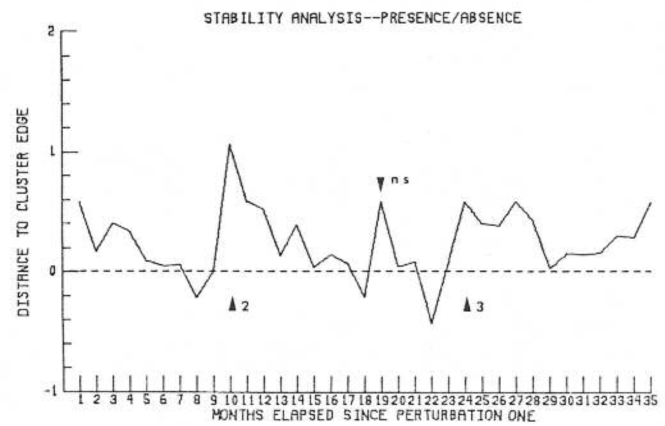

Fig. 4. Visualization of the qualitative stability analysis. See legend of Fig. 3 for explanation

to change, although mutually exclusive of the working definition, may be evaluated directly with the stability measure; (b) definitions (3) and (4), speed of return to an initial state and zone from which the system will return to a stable state, are in accord with the working definition and can also be evaluated directly with the Bloom (1980) measure; (c) definitions (5) and (6), stable limit cycles and trajectory stability, cannot at this time be evaluated in relation to the working definition and stability measure. Using the proper experimental design, one can test the four compatible concepts with data sets generated by current ecological research methods. No need exists to generate esoteric data sets specifically for use with the definition or measure.

The working definition and the Bloom measure (Bloom 1980) can be extended to use in experimental systems. If an experimental control is taken as the pre-perturbation baseline, experimental treatments can be evaluated in terms of whether or not the treatments caused a statistically distinct change in the community being perturbed.

However, a caveat concerning the use of the technique is in order. We wish to emphasize the importance of suitable data sets. It is necessary that comparable data be available before and after the perturbation. It is also conceivable that if the data set used to define the pre-perturbation cluster has a large variance, which is common with small sample size, any post-perturbation sample may fall within the prescribed confidence limits. Therefore, it is essential that a reasonable experimental design be used when employing this technique.

The stability measure is quite selective and discriminating. For example, six species numerically dominated during each cycle (Santos and Simon, in manuscript). During cycles 1 and 2, the same species dominated, but during cycle 3, two of the six were replaced by different species but of comparable densities. This was detected by the measure. Again we must emphasize that our data displayed relatively little sampling variance. The analysis of both quantitative and qualitative data sets demonstrated essentially the same results. Ordinarily the analysis of quantitative data sets displays more rigor than the analysis of presence/absence data, and until additional data sets are made available for testing, we must reserve discussion on this aspect of the measure.

According to the proposed working definition of stability, i.e., a community's return to its previous point following a perturbation, the soft-bottom community in Hillsborough Bay, Florida, can be regarded as stable for the first two cycles (Figs. 2 and 3). During the third cycle, however, the community did not return and therefore, by definition, was declared unstable. Because the technique measures local stability which is of a relative nature, that is, the community can only be declared stable or unstable relative to some predetermined point, the nonreturn of the community can be interpreted in two ways: (1) the community has become truly unstable or (2) the community has shifted to a new stable point. The definition and measure, therefore, are not incompatible with Sutherland's (1974) multiple stable point hypothesis, but may in fact lend empirical support to it.

Points, representing samples, plotted through time may walk back into the 95% polygon and thus the recovery trajectory will fall below the broken line in plots like Figs. 3 and 4; alternatively, the samples may form a new, cohesive cluster removed from the original pre-perturbation cluster. This would be represented by the recovery trajectory settling down with relatively little variance about some value paralleling the broken line. This pattern would be indicative of a new stable point.

When dealing with ecological events (in this case whether a shift to a new stable point has occurred), the determination of a proper time scale is a monumental problem (Levandowsky and White 1977). Ordinarily the time scale chosen by most investigators is determined solely by convenience or by the amount of resources available. What may appear a surely reasonable time to the investigator may be only a segment of the actual processes under investigation. This is especially relevant for cyclic events. In the present study, although a three year data set is sufficient to observe a shift from one point to another, whether the shift is to another stable point cannot be determined without additional data (preliminary analysis of the data from the following two years indicates that this new point appears stable).

Another major problem associated with stability is the relationship of stability to diversity (e.g. Goodman 1975) and the implications of that relationship to managing disturbances. Elton (1958) and others supported the view that stability was proportional to diversity, i.e. the number of species. May (1973) has emphasized that mathematically the opposite is true, and Boesch (1974) and Horn (1974) have supported May's contention.

If "low diversity systems are more stable (in terms of speed of recovery) than high diversity systems" is recognized as a viable *albeit* "applied" concept, a far-reaching impact on man's activities would result. Such disturbances as dredge and fill, spoil disposal, industrial and domestic sewage effluent discharges, slash and burn, etc. would be regarded in a different light. Odum (1969) and Rhoads et al. (1978) have pointed out that properly managed disturbances can be beneficial because of increased productivity during the ensuing recolonization. In order to achieve the ideal balance between productivity and managed disturbance, the areas chosen should not be those that are slow to recover. One current view, that those areas considered the most complex are the most stable is erroneous, as some of the most complex systems (i.e. coral reefs and tropical forests) (Connell 1978) have proven to be very unstable. Any large-scale disruption of the status quo of these complex systems causes damages, which, at least on a time scale related to our ability of observation, will be irreparable.

Conclusions

The concept of biological stability remains multifaceted, but we have demonstrated the pragmatic nature of a working definition of stability. On the basis of this definition we have shown that a soft-bottom infaunal community in Hillsborough Bay, Florida, USA subjected to severe annual stress displays high stability. In fact it appears that the community actually shifted from one stable point to another. These data are interpreted to mean that operationally low diversity systems can be highly stable when resiliency is viewed as the most critical aspect of stability.

Acknowledgements. We would like to thank Dr. J.L. Simon for allowing us the use of some unpublished data. An earlier draft of this manuscript benefited greatly from the suggestions of Drs. R.W. Virnstein and E. McCoy. Support for writing was provided by a postdoctoral fellowship (SLS) from Harbor Branch Institution. This research was partially funded by Florida Sea Grant R/EM-7 awarded to Dr. J.L. Simon.

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Received May 1, 1980