ON THE EVIDENCE NEEDED TO JUDGE ECOLOGICAL STABILITY OR PERSISTENCE

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"The balance of nature has been a background assumption in natural history since antiquity" (Egerton 1973, p. 322). This continues to be true today; some modern field ecologists, assuming that natural ecosystems are stable, have applied ideas of mathematical stability theory to the actual communities they are studying. We believe that, before one applies such theory to a natural population or community, one should first decide whether or not it is stable. Our aim here is to describe the sorts of evidence one would need to obtain from natural populations or communities in order to decide whether they are stable or persistent, as defined below. One aspect we shall stress in particular is whether any given real community exists in multiple stable states in different places at the same time or in the same place at different times (Sutherland 1974).

When considering changes in natural populations and communities, it is important to distinguish between two viewpoints. As Holling (1973) has pointed out, one view is concerned with the degree of constancy in the numbers of organisms. With this view, stability is the property of interest. In contrast is the view that concentrates, not on constancy of numbers, but on presence or absence. He states (1973, p. 1): "If we are dealing with a system profoundly affected by changes external to it, and continually confronted by the unexpected, the constancy of its behavior becomes less important than the persistence of the relationships. Attention shifts, therefore, to the qualitative and to questions of existence or not."

Past discussions of stability have sometimes confused these two viewpoints and have also applied identical terms to both. Therefore we would like first to define and discuss the terms we will use in this paper, as well as those previously used. Some of these terms have also been applied by theoretical and mathematical workers to model ecosystems under particular specified assumptions. We want to emphasize that our usage applies not to these models but only to the real world. We are not interested in testing the assumptions of these models, nor in using them to interpret data from actual ecosystems. We do not seek to contribute here

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to the theory of stability in model ecosystems. With that caveat, let us consider the following definitions.

We will first discuss the quantitative viewpoint, that of stability. For a system to be considered stable, there must exist one or more equilibrium points or limit cycles (1) at which the system remains when faced with a disturbing force or (2) to which it returns if perturbed by the force. (Theoretically a system could have unstable equilibrium states which satisfy 1 but not 2; we will not consider this possibility further.) This concept requires two things: (*a*) the existence of stable equilibrium states which for the remainder of this paper refer either to stable points or stable limit cycles; and (*b*) the existence of forces that may be capable of perturbing the system so that it is no longer at equilibrium. (A stable equilibrium is defined as a particular state of a characteristic, e.g., population density, at which a population will remain, or if moved away from it, to which the population will return.)

In regard to the first point, i.e., remaining at equilibrium when faced with potentially disturbing forces, the terms used have been *inertia* (Murdoch 1970; Orians 1974), *persistence* (Margalef 1969), and *resistance* (Boesch 1974). Some workers have considered the situation of a simple lack of change in numbers, without reference to the existence of disturbing forces. For this the following terms have been applied: *constancy* (Orians 1974; Whittaker 1974; Golley 1974), *persistence* (Boesch 1974), *conservatism,* and *endurance* (Margalef 1969). However for any situation to be included under the concept of stability as defined here, there must also exist disturbing forces; without them, simple lack of change in numbers is of little interest. In general the term *resistance* seems most appropriate for this aspect of stability since it implies that a force has been applied and resisted.

The second aspect, return to equilibrium after being perturbed, has been called *adjustment* by Margalef (1969). It is usually considered in two parts. The first concerns the speed of return; this has been called either *elasticity* (Orians 1974) or *resiliency* (Boesch 1974). The second part is concerned with the distance from which the system is capable of returning; Hurd et al. (1971) and Orians (1974) call this *amplitude*.

The term *resilience* has also been used to refer to the amplitude concept, namely, "how much disturbance—of kind, rate and intensity—a system can absorb before it shifts into a fundamentally different behavior" (Holling 1975, p. 249). Holling (1973, p. 17) also used the term resilience to refer to "the ability of these systems to absorb changes . . . and still persist." He draws a distinction between resilience and stability in that resilience refers to the behavior of the system far from equilibrium, whereas stability refers only to its behavior very near to equilibrium points. However his use of the area and height of the boundaries of the model "basin of attraction" as a measure of resilience (Holling 1973, fig. 4) indicated that it is related to the distance from which the model system is capable of returning, and therefore should be included under the amplitude aspect of stability. Because resilience has been used in very different ways by Holling (1973) and Boesch (1974) we suggest that amplitude and elasticity be used for the two aspects of adjustment stability.

A stable model system that, if perturbed sufficiently, can return to one or more different equilibria, has *multiple stable points* (Lewontin 1969). We will apply this term to natural populations if, for example, a given population can exist either at different stable densities at different places at the same time or at different times at the same place.

In contrast to the quantitative viewpoint of stability, is the qualitative one of "questions of existence or not" (Holling 1973). Here there is no requirement for the existence of equilibrium, and attention shifts away from the idea of a return to equilibrium, and focuses instead on the boundaries of fluctuations, on whether a system persists or not, on "how the population is buffered against extinction in adverse periods" (Whittaker 1974). Jacobs (1974) also drew this distinction between stability as defined above and "persistence of a given state." Others have used the term differently, as "persistence of a community in time with little fluctuation in species populations" (Boesch 1974; also used similarly by Margalef 1969; Lie and Evans 1973). In contrast, we will use *persistence* to indicate that a population or species either did not become extinct during a given period of time and in a given area, or if it did, that it recolonized the area within the time span required for one turnover of all individuals of that species in the place.

We would like to make one further point. Local extinctions or invasions of a new species often occur as a result of shifts in the boundaries of species ranges, probably as a result of slight shifts in climates. For example Holbrook (1977) has demonstrated such changes in rodent communities in Arizona and New Mexico over the past 1,000 yr. Historical records of shifts in geographic boundaries are common. For example the armadillo has expanded north from Texas to Nebraska since the early 1900s (Humphrey 1974). Such shifts are not the concern of this paper; we will deal only with the question of whether, under the same average climatic regime, populations are stable or persistent in the face of discrete, punctuated disturbances.

SCALES OF OBSERVATION APPROPRIATE FOR JUDGING STABILITY OR PERSISTENCE OF
REAL ECOLOGICAL SYSTEMS

Several scales must be recognized in judging the stability or persistence of a natural population or community. These are the intensity and time scale of the perturbations and the time and spatial scales of the observations of the responses of the populations themselves.

If the intensity of the disturbing force does not cause a significant change in the characteristic of interest, there is no perturbation; the assemblage has resisted the force. A perturbation is a significant change in the characteristic of interest (see Sutherland [1981] for an alternate interpretation). If, for example, the characteristic were biomass or energy flow (McNaughton 1977), then a perturbation would be a significant change in these variables. Here we are interested in numerical abundance of populations and relative abundance of species in guilds and communities, so a perturbation is a significant change in either numbers of a population or relative abundance of species in a community. Clearly there are small and large perturbations and the spectrum of change is a continuum.

The time scale of the perturbation is also important. Concepts of stability or persistence refer to responses to discrete, punctuated disturbances that perturb abundances but do not cause long-term changes (i.e., longer than the turnover time of the assemblage) in the abiotic environment. They do not refer to responses to changes in the average values of the abiotic variables themselves (e.g., climate), which are known to affect abundances and species composition of communities. Thus, when alternate or multiple stable states are postulated to exist, it is essential to establish that any relevant conditions of the abiotic environment are similar (in average value and in variance) in both situations. For example, Matthews (1979) suggested that two different end points of a plant succession on a glacial moraine beginning with the same pioneer species represented alternate stable points. But the two end points were at different elevations, slopes, and aspects on the moraine, so were more likely to have been a result of different average environmental conditions than of different histories of succession within the same environment.

Appropriate scales of time and space must also be specified for the observations of the responses of the populations, before meaningful judgments concerning stability or persistence can be made. With regard to time, Frank (1968) warned of the tautology in reasoning that mature communities are stable, when in fact the reason for their constancy is that they are composed of long-lived individuals. His warning was reiterated by Pielou (1977, p. 1). There are two ways to avoid this tautology. One must either observe the replacements for all adults or else predict the transition probabilities of future replacements for all adults. In either case the minimum time period is at least one complete turnover of all individuals, including discrete colonies or clones. The usual method of calculating the transition probabilities in a community of long-lived species is to use the relative abundance of the juveniles of the different species present (Horn 1975; Culver 1981; Runkle 1981). This assumes that each juvenile has an equal chance of surviving to become a replacement; none of the studies cited tested this assumption. It also assumes constant probabilities, which is very unlikely under natural conditions.

By observing or predicting patterns of replacement over at least one complete turnover of all individuals, the stability or persistence of each population will be scaled to the particular life histories of its members, allowing comparisons between different populations. Since the ultimate fate of all species is extinction, judgments concerning the persistence or stability of a particular population or community characteristic must necessarily be relative (Maynard Smith 1974; Botkin and Sobel 1975).

The spatial scale of a study will also affect judgments of the stability or persistence of a population or community. If the population or community is defined for the purposes of the study as the assemblage on a small area, it is unlikely to be either stable or persistent, since even small perturbations could cause local extinction. In contrast, if the same assemblage is monitored over a very large area (which in effect averages out the variation in dynamics of subpopulations), it will be found to be persistent and possibly stable unless the species in question is (are) becoming extinct globally.

Usually the choice of spatial scale for a study (including those discussed here) is

arbitrary. In our view, a better but more demanding approach is to search for the minimum area in which a population or community is stable and/or persistent. We will define this as the smallest area that provides adequate conditions (i.e., enough propagules and the environmental conditions required for the development, growth, and survival of offspring) for the replacement of existing adults somewhere within that area. These conditions must occur within the area during the course of at least one turnover of the population or community. For example, if both the production of seeds and the growth and survival of juveniles within a particular hectare of forest is sufficient to provide replacements for all adults on the same hectare, then the minimum area within which the assemblage of trees is stable is indeed one hectare. In contrast, if there are adults present whose seeds and seedlings cannot survive in the hectare, requiring, for example, very large light gaps for germination and growth, then the minimum area on which the assemblage is stable and/or persistent is much larger, encompassing the area within which enough large light gaps will occur within the lifetime of those trees to allow their replacement.

One may determine the minimum area for a species either directly or indirectly. To do so directly one must follow the replacement of all adults on a number of different spatial scales for the minimum period of one turnover. The smallest of these scales on which replacement is found to occur would constitute the minimum area. One might also estimate it indirectly using the life history characteristics and age structure of the populations on an area in which suitable habitats are expected to occur within the period of adult replacement. Obviously the larger the area studied, the more likely it is that the minimum area will be encompassed. Species whose propagules do not travel far and whose offspring are able to survive and grow in the vicinity of the adults probably tend to have small minimum areas. Species with highly mobile propagules and offspring that require conditions very different from those in areas occupied by their adults, probably tend to have relatively large minimum areas, e.g., species with planktonic larvae. Thus both the minimum area and the minimum time period for which an assemblage may be judged as stable or persistent are functions of the life history characteristics of the species being considered. The minimum area may also change with the location of the study area within the species range(s) and with temporal and spatial variation in the environment, all of which influence recruitment, growth, and survival and thus the likelihood of replacement.

Most detailed ecological studies are done on small areas, so that it would not be surprising if stability were seldom found. This could simply mean that the study area was smaller than the minimum area and if one looked longer or over a wider area, stability (or persistence) would be found. This might well be true (although perhaps not, if the species was in the process of dwindling to complete extinction as in some very rare species today). However, providing that the data are adequate and our minimal criterion of time is satisfied, a judgment that the assemblage is neither stable nor persistent certainly applies within the spatial scale studied, though perhaps not on some larger scale. We believe that such judgments are useful even if they apply only to small scale studies which, after all, comprise most ecological work. The finding of nonstable conditions on a local scale and/or

over the course of a few turnovers has important ecological and evolutionary implications. Disturbances causing local nonstable or persistent conditions are frequently essential for the stability or persistence of species on larger scales (Hutchinson 1951; Andrewartha and Birch 1954; Dayton 1971; Levin and Paine 1974; Sale 1977; Hastings 1977; Caswell 1978; Connell 1978; Sousa 1979; Paine and Levin 1981). In addition, recent evolutionary theory suggests that nonequilibrium conditions in local populations (e.g., differential proliferation or extinction, founder effects, etc.) can significantly alter their genetic structure (Wright 1940; Levins 1970; Boorman and Levitt 1973; Wade 1978; Templeton 1980).

STABILITY: HOW CAN IT BE DEMONSTRATED?

We will first discuss *resistance,* the tendency of a population to withstand being perturbed from equilibrium (Boesch 1974). When comparing the resistance of two populations, one must first know the strength of the disturbing force. Long-term records showing that one population changed more than another are not sufficient, since the force of the disturbances may have been unequal. Unless one has either measured or experimentally applied the force one cannot begin to judge the degree to which an assemblage is resistant to change. Accurate measurement of such forces is difficult and controlled disturbance experiments have been conducted in only a few systems (e.g., Likens et al. 1970; Hurd et al. 1971; Hurd and Wolf 1974; Bormann et al. 1974; Hall et al. 1980; Sousa 1980). In addition, the original state from which a population or community is hypothesized to be resisting change must be demonstrated to be a stable equilibrium one using our temporal and spatial criteria. These criteria have not been met by any of the perturbation studies just cited.

The second aspect, *adjustment* stability, is equally difficult to demonstrate. For short-lived organisms, adjustment stability could be demonstrated if a single population or community is perturbed and returns to the same stable equilibrium point or limit cycle. Likewise if two populations or two communities were changed to the same degree, the one which returned more rapidly and/or with greater fidelity or from a greater amplitude of perturbation to its original equilibrium state would be judged to possess greater adjustment stability. Again as discussed earlier, in these instances both the original state and that to which the system returns must be demonstrated to be equilibria using our criteria for space and time.

Unfortunately it will seldom be feasible to evaluate the adjustment stability of any real community, because natural perturbations are often so frequent that there is not enough time between them for a community to achieve a stable equilibrium state. In such cases it is impossible to define the equilibrium state and thus to demonstrate adjustment stability (Sutherland 1981). Using the pollen history of forests in northern Minnesota, Botkin and Sobel (1975) point out that disturbances and climatic changes sometimes occur at such frequent intervals that they prevent a system from ever assuming a stable state (i.e., one that lasts for at least one turnover of the member populations). Their conclusions are supported by a more recent analysis of pollen records from the same forests by Amundson

and Wright (1979). Many recent papers have demonstrated that physical and biological disturbances are ubiquitous in natural communities and strongly influence their structure (see Heinselman and Wright 1973; Levin and Paine 1974; Connell 1978; Sousa 1979; White 1979; Paine and Levin 1981; Pearson 1981; Thistle 1981 for recent reviews). If an equilibrium state cannot be identified, how can conclusions be made about this form of stability in real ecosystems?

There is also the danger of mistakenly concluding that communities subject to frequent disturbances are less stable than those less frequently disturbed, simply because the former will not have had as much time as the latter to recover completely. The more disturbed community may in fact be more stable because the species in the frequently disturbed community may colonize and grow so rapidly that they can recover completely between disturbances. Comparative statements concerning the tendency of a system to return to equilibrium depend both on accurate measurements of the regime of disturbance and on knowledge of the biology of the species concerned, both of which are very difficult to obtain. Clearly the existence of multiple stable states, though possible in theory, would be even more difficult to demonstrate than single stable points.

THE EVIDENCE FOR MULTIPLE STABLE STATES

Several papers have recently delineated the theory of multiple stable states in ecology using mathematical models (Lewontin 1969; Holling 1973; Noy-Meir 1975; Gilpin and Case 1976; Southwood and Comins 1976; Southwood 1977; May 1977, 1979; Peterman 1977; Levin 1978; Ludwig et al. 1978; Peterman et al. 1979; Clark and Holling 1979; Anderson 1979; Botsford 1981). Here we are concerned, not with this body of theory, but with whether there is good evidence for the existence of multiple stable states in actual populations or communities. First we will review the examples given in the theoretical papers cited above. These all have various shortcomings that fall into one of three categories listed below: (1) Examples in which the evidence is inapplicable since the physical environment is different in the different alternate states. (2) Examples in which one or both of the alternative states persists only when artificial controls are maintained. (3) Examples in which the evidence is simply inadequate.

Under the first category are examples in which either the assemblages occupying a particular site before and after a change in the physical environment are interpreted as alternate stable states or the assemblages at separate sites differing in their background physical environments are interpreted as alternate stable states. As discussed earlier, one would expect such differences in the environment to cause differences in population size or community composition; they should not be considered to be examples of alternate stable states of the kind described above or as originally proposed by Lewontin (1969). For example, Holling (1973) cites several instances in which changes in average nutrient levels in lakes, as a result of road-building, pollution, agricultural runoff, etc., caused changes in the planktonic and/or benthic communities (Hasler 1947; Edmondson 1961; Beeton 1969; Hutchinson 1970). Similarly there were changes in breeding fish populations when average flow rates, water temperatures, and sediments in

streams were altered to a new level as a result of deforestation of the watersheds (Smith 1968).

Another example is the often-cited instance of the Australian herbivorous insect *Cardiaspina albitextura* that feeds on *Eucalyptus* (Clark 1964; Clark et al. 1967; Southwood and Comins 1976). In some places the numbers were usually kept low by a complex of many species of natural enemies, with occasional outbreaks in numbers which caused defoliation and death of trees and subsequent crashes in numbers of the insect back to the normal "endemic" low levels. In other places, densities on host trees remained high and yet did not result in defoliation, so the high numbers were regarded as an alternate stable "epidemic" state. However, the latter situation occurred only when the environment was greatly changed. The epidemics persisted only where the host trees had been cleared or thinned by settlers, which would change the physical structure of the habitat and according to Clark et al. (1967) probably reduced the natural enemies as well as preventing the normal dispersal of *Cardiaspina*. In addition, where the epidemic state persisted, a new species of hyperparasite, *Echthroplexis psyllae*, appeared, greatly increasing the mortality of the natural enemies and so preventing them from reducing *Cardiaspina* (Clark 1962).

Another example comes from drastic changes in fish species in the Great Lakes. Between 1920 and 1950 several species were overexploited and their populations collapsed. Holling (1973) suggests that this is a case in which populations had been moved from one domain of attraction to another because "once the populations were lowered to a certain point the decline continued even though fishing pressure was relaxed" (p. 8). However the only evidence for a relaxing of fishing was the prohibition of deep trap netting for lake whitefish in Lake Huron after 1935 (Smith 1968). In other instances, fishing continued, with new species replacing the ones that had been overfished; yet the original species continued to be caught in small numbers by the fishery. The nonrecovery of the original species probably resulted from several extreme changes in the physical and chemical environment, plus the introduction of an effective predator, the sea lamprey, as well as several probable competitors (alewife, carp, and smelt). Given all these interventions and alterations by man, it is difficult to accept the conclusion that the native fish assemblage in the Great Lakes had been moved into an alternate basin of attraction below a "breakpoint" by a reduction in population caused simply by overfishing.

The second category consists of examples in which one state is artificially maintained, e.g., where natural enemies are kept in either high or low numbers by man's intervention, e.g., overfishing, pesticide spraying, overgrazing of rangelands, etc. One example cited by Holling (1973) is the perch in Lake Windemere which, after being greatly reduced by experimental fishing, did not return to its former level even though no longer fished. The reason for its nonrecovery, however, was probably man's continual intervention. After the removal of perch was stopped, another species, the pike, continued to be fished. Since only the larger pike were caught, the population structure was changed, so that the remaining pike were smaller sized but much more numerous. These pike attacked the young perch and apparently kept the population from increasing. As stated by LeCren et al. (1972, p. 830): "preliminary calculations show that consumption of

young perch by pike is of similar order of magnitude to the production of young perch.''

Another example comes from the management of grazing systems. For pastures in Australia and New Zealand which are continually managed to improve plant production, the evidence seems adequate to support the theory of multiple stable points (Noy-Meir 1975; May 1977). For unmanaged, extensive range systems, however, the evidence is only anecdotal. For these three examples, populations were kept at a different, possibly stable state only by man's intervention.

Our third category includes examples in which the evidence is inadequate. The assemblage of invertebrate colonies studied by Sutherland (1974, 1981) and Sutherland and Karlson (1977) comprised a marine fouling community which was considered stable if it occupied and held most of the space on a panel until it died and fell off. The vacated space was then colonized and held by other species until they died. Since each of these states was defined as being a stable equilibrium point, the sequence was defined as a system with multiple stable points. The criterion for stability was that the colonies had persisted "for some period of time in a given physical locality, in spite of forces with the potential of altering their structure'' (Sutherland 1974, p. 860). The forces in this case were planktonic larvae capable of colonizing the panel but apparently prevented from doing so by the presence of the occupants. However, the time scale is too short; if this scale were accepted, almost any set of organisms that, within their lifetimes, prevented another set from invading could be regarded as a stable population or community. In none of the instances cited by the above authors, either from their own work or from studies of animals or algae in the marine intertidal zone, vegetation on coral reefs, zooplankton in lakes, protozoa and algae in phytotelmata, or perennial grasses and woody vegetation in Britain, has it been shown that assemblages maintain a persistent or stable composition beyond the lifetimes of individual members by preventing invasion of other species. The same is true of examples cited by Gray (1977). The problem is that, although Sutherland's study clearly showed that historical events did determine the structure of the communities studied, none of them was shown to be stable at appropriate scales of space and time.

Another case is that of the European spruce sawfly (*Diprion hercyniae*) introduced into Canada. Southwood (1977) has calculated that it has two stable points, a lower one determined by both introduced parasitoids and virus disease and an upper one when the disease alone controls it. However the populations rise to the epidemic level only occasionally, and there is no evidence that the population is stable there. It seems likely that the parasitoids would soon respond functionally and numerically (Solomon 1949) to the high densities and drive the prey back to the lower endemic level. Until evidence is adduced to show why this should not happen, the upper, epidemic, level cannot be regarded as stable.

The same reasoning applies to the well-known case of the spruce budworm (Morris 1963). It has been proposed (Holling 1973; Ludwig et al. 1978; Peterman et al. 1979) that the upper epidemic level is an alternate equilibrium point to the lower endemic levels. However the budworm at epidemic levels is not stable, but defoliates and kills the mature fir and spruce trees it lives on and then crashes. The

forest then regenerates and eventually the budworm irrupts to epidemic levels. As May (1977) points out, this could represent a single stable limit cycle rather than alternate stable points.

May (1977) has suggested that parasites or pathogens might exhibit alternate stable states. In all his examples one of the states was the absence of the parasite. This follows MacDonald (1965) who proposed that bisexual parasites, such as helminths, could maintain a population only if they exceeded a numerical "break-point" determined by the probability of finding mates. Since there is only one state at which the population is stable, this is hardly a relevant example. Anderson (1979) has since proposed a theoretical model in which the parasite could persist at two stable states; no supporting examples from actual populations have yet been cited.

A case has been made (Holling 1973; Peterman 1977; Peterman et al. 1979) that some species of exploited Pacific salmon exhibit alternate stable states. The pink salmon (*Oncorhynchus gorbuscha*) has a 2-yr life cycle, so that the stocks in alternate years do not meet each other. In some streams one stock was consistently very much larger than the other. For example at Sooke, B.C., the odd-year stock was 100 times larger than the even-year one for the 12 yr of record (Neave 1953). A similar record for over 24 yr from another region is given by Peterman (1977). In other areas the stocks often differed, but the difference did not persist (Neave 1953). The mechanism maintaining the consistent difference between the stocks is not known for certain but Neave (1953) suggested the following hypothesis. Predation on the young fish as they migrate out of the streams is often proportionately heavier on smaller than on larger populations. If this is so, the smaller stocks would be kept at a low "endemic" level while the larger ones would not be significantly affected by the predation. If this proves to be the correct explanation it would provide strong evidence for the existence of alternate stable states in an exploited population.

Some of the examples cited above as evidence for multiple stable points use the two states at high versus low densities of predators as the alternative states. There is much evidence that a population which has been kept low by intense predation will rise to a high level when all the predators are removed, or vice versa. Many examples from biological control of introduced pests and from ecological field experiments testify to the generality of this finding (DeBach 1974; Connell 1975). Two examples of this have been frequently cited as supporting the notion of multiple stable states. Sutherland (1974) proposed it for some marine invertebrate fouling communities when fish were experimentally excluded. Similarly, Simenstad et al. (1978) suggested that very different nearshore communities found on Aleutian islands with and without sea otters (Estes and Palmisano 1974; Estes et al. 1978) represent alternate stable states. On islands where sea otters were absent, removed either by fur traders or apparently much earlier by aboriginal hunters, their herbivorous invertebrate prey were common and had eliminated much of the fleshy macroalgae. In contrast, on islands where the numbers of otters had recovered, herbivores were scarce and a dense macroalgal canopy had developed. The lush kelp beds on islands with otters provided habitat for fishes which in turn supported populations of seals and eagles. However, in Sutherland's

study the prey species were not shown to be stable for the necessary minimal time scale, and in both studies the state without predators could only be maintained with human intervention. Fish were absent only when experimentally excluded from the fouling communities, and sea otters (now under federal protection) are gradually reoccupying the Aleutians (Palmisano and Estes 1977; Estes et al. 1978).

Therefore, we endorse Paine's (1977) suggestion that communities without consumers should seldom be regarded as being stable. If the consumers disappear (or are experimentally removed) and prey increase until they dominate the space, this situation will persist only as long as the consumers are absent. Since any situation in which prey are present is attractive to consumers, if it is possible for them to reinvade, they probably will (e.g., starfish predation on mussels, Landenberger 1968; Paine 1974, 1976; sea otter predation on grazers, Estes et al. 1978). If the consumers return, they will either reduce the prey again, or if the prey have reached an invulnerable size (as in some of the examples cited by Sutherland 1974), the consumers will eat most or all of the offspring (unless there is parental care, which does not apply to these cases). When invulnerable individuals eventually die, whatever the cause, the situation will return to the original state that existed before the consumers were eliminated. Thus, the situation without the consumer will rarely be a stable one, and only in instances in which there are extremely effective barriers to movement of the consumers, will systems without them be stable. Small isolated islands, mountain tops, or lakes seem to us to be the only good possibilities for this sort of stability. However, to regard a situation having barriers to movement of consumers as a multiple stable state adds nothing; the explanation is clear, why obfuscate it?

EVIDENCE FOR STABILITY OR PERSISTENCE BEYOND ONE COMPLETE POPULATION TURNOVER

We now examine other studies that satisfy our criterion that populations be followed for at least one complete turnover of all individuals. Our purpose is to assess whether, from census data alone, it is possible to distinguish a subset of populations or communities that exist in an equilibrium state. We have not included studies that attempt to predict the next generation from the age structure of the present one; in our opinion, none of those published have yet sufficiently evaluated either the assumption that the relative abundances of the different species of younger individuals is an adequate estimate of their probabilities of replacing the present adults or the assumption that the probabilities are constant (Hartshorn 1975; Horn 1975; Culver 1981; Runkle 1981).

Long-term records (i.e., over a number of turnovers) of the numbers of individuals of two or more species in a community, especially where the mechanisms of interaction have been demonstrated with field experiments, are rare. Most long-term studies are of changes in the densities of populations of one species rather than of assemblages of interacting species. Few of these studies have gathered data on more than one spatial scale. We have limited the following review to studies in which detailed records of density have been kept for more than a turnover of the population and in which sufficient demographic information has

been collected to estimate turnover times. The latter is not a problem for annual species. For other organisms we have used either the estimates of specialists of particular taxa, or the maximum lifespan of the species recorded during a particular study as the time required for one turnover of its population. This method undoubtedly underestimates the actual number of observed turnovers for studies of species other than annuals.

It should be noted that the studies included in this review are probably neither an exhaustive nor an unbiased sample of natural populations. Some are economically important, either as pests of agriculture or forests. These species as well as some of the others listed, e.g., small mammals, are conspicuous by virtue of large fluctuations in their numbers. Others have been studied because they are easy to count accurately. The fact that some of the available long-term records are of populations that undergo large fluctuations makes it difficult to generalize how common a particular type of persistence is in natural systems. Also such evidence can never be completely conclusive because it is always possible that further sampling might reveal a different pattern of population dynamics. The best we can do is to examine those long-term data that are available to determine whether present evidence supports the notion that a particular form of stability or persistence exists in nature. We hope this effort will stimulate the collection of data on other sorts of species.

Although there are long records for many exploited populations of fish, furbearers, game, etc., they have certain drawbacks for our purpose. First, in most instances there is no way of accurately estimating the proportion of the total mortality that has been imposed by the harvesting itself; only for certain species (e.g., some species of salmon) is this proportion known with accuracy. (See Weinstein [1977] and Winterhalder [1980] for further discussion of this problem.) Second, it is difficult to estimate the effect of this additional harvesting mortality since, to our knowledge, no study has had a control population which is not harvested, to serve as a comparison. For these reasons we have referred to only one exploited population, the muskrat (*Ondatra zibethicus*), because accurate information has been gathered on the effects of natural perturbations on local extinction and recolonization.

Appendix table A1 lists the details of all the studies we have found that had population censuses extending for at least one complete turnover of all individuals in a local population. In some instances such data were taken for several local populations of a species. To estimate the total variation observed for each local population (independent of mean population size), we calculated the standard deviation of the logarithms of the numbers in censuses separated by at least one turnover. This enables us to compare species having different lengths of life. This index is sensitive to low values (because logarithms are used); another commonly used index, the coefficient of variation, is sensitive to high values (P. Chesson, personal communication). Since we were more interested in population variation at low numbers, we used the former index. The sample sizes vary among studies: For some long-lived species only one turnover was available, in contrast to some annuals in which many turnovers were observed.

The standard deviations for all populations are listed in Appendix table A2;
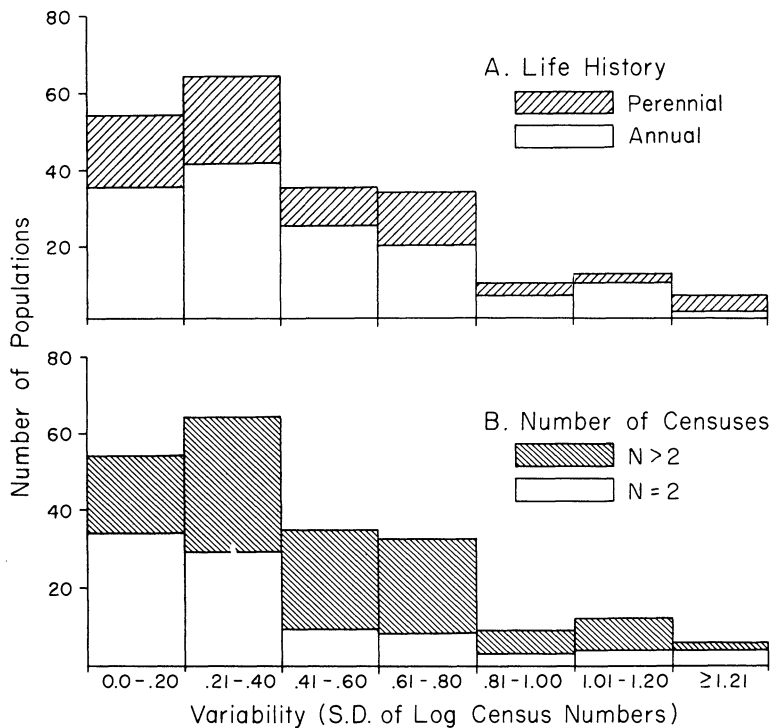
FIG. 1.—Distribution of variability among all populations studied. The shaded/unshaded portions of each column indicate the proportions of the populations in categories of *A*, life history and *B*, number of censuses.

these are presented in two frequency distributions in figure 1. Figure 2 shows the same sort of frequency distribution but includes only one variation estimate per species; when more than one population of a species was studied, the median standard deviation was used.

As can be seen in these figures, there is a continuum of variability among the populations or taxa studied. The distributions of variability in populations of annual and perennial species (fig. 1*A*) were not significantly different (Kolmogorov-Smirnov test, $P > .95$). There is no evidence that populations of perennial species in general fluctuate any less than populations of annual species when scaled to turnover time. The number of censuses taken, however, does appear to influence the degree of variation measured (fig. 1*B*). The variation calculated for populations censused only twice is less than that calculated for populations censused more than two times (Kolmogorov-Smirnov test, $P < .005$). Thus, relatively short-term studies spanning only one turnover tend to give a false impression of constancy in numbers. Terrestrial plants, terrestrial insects, and aquatic invertebrates span the full range of variation. Birds (with one exception) and mammals are not represented in either the least or most variable class, but this may be because few long-term studies of these taxa were available. Parasites
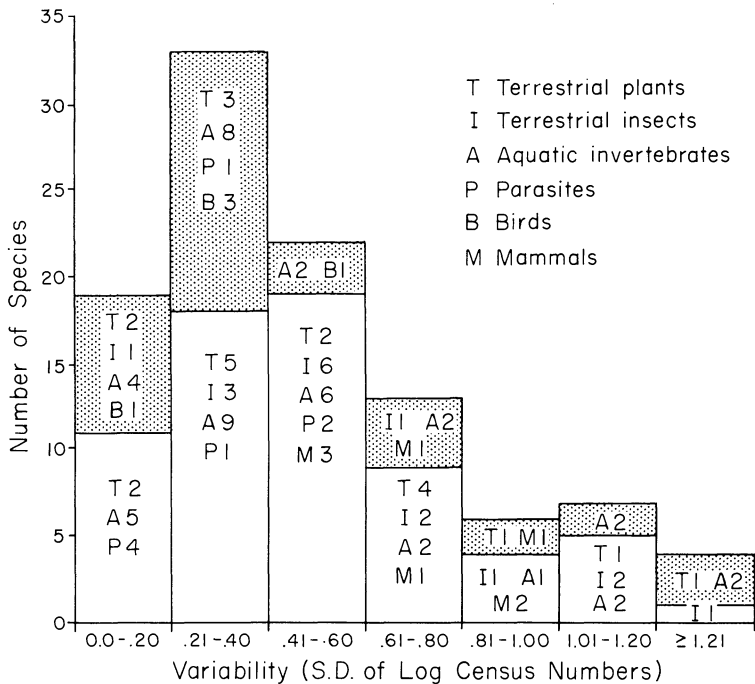
Fig. 2.—Distribution of variability among all species studied. For each species the median value of the SD of log census values was used. The number of species within a particular taxonomic category that exhibited a given level of variability is indicated. Within a taxonomic category, species are identified as possessing either a perennial (shaded) or annual (unshaded) life history.

occur only in the three least variable classes; whether this is a consequence of the few studies or an indication of genuine low variability cannot be decided until a more extensive survey is available.

Within single species, populations in different localities varied considerably. As shown in the tables, one mid-ocean copepod species spanned the entire range of variation found among all organisms surveyed, and five other species each spanned two thirds of the range (McGowan and Walker 1983). Different local populations of the same species of Polish dune plant (*Corynephorus canescens*) spanned most of the entire range (Symonides 1979a). Variation in populations of the beetle *Pterostichus coerulescens* on a small area of heath spanned half the entire range of all species (den Boer 1971).

Within local populations a few species exhibit rather regular numerical fluctuations which could be regarded as stable limit cycles; the larch tortrix moth in Switzerland is probably the best-known example (Baltensweiler 1968). Whether the fluctuations in other populations of birds and mammals represent regular cycles has long been debated (Cole 1951, 1954; Garsd and Howard 1981). Our survey has revealed a continuum of variation among complete turnovers in populations, ranging from remarkable constancy to wild fluctuations, with many in-

stances of local extinction (see footnote to table A1 for a list of these instances). Which, if any, of the populations of species listed in table A1 exist in an equilibrium state would be difficult to decide, given the distribution of variation illustrated in figures 1 and 2.

There is also a continuum of change in the structures of species guilds over time. The separate species of some guilds (e.g., insectivorous birds) vary in abundance to about the same degree while in other guilds the abundances of the individual species vary quite differently (e.g., meiobenthic copepods, oceanic copepods, dune plants, annual grasses, grassland rodents). The relative abundances of intertidal snails and forest moths vary to an intermediate degree. (See data from study nos. 41, 4, 5, 27, 28, 47, 12, 33, and 34, respectively, in table A2.) As before, when faced with this continuum of variation, it is impossible to decide which of the assemblages of species are in equilibrium and which are not.

Is there any evidence from these studies of multiple stable states or cycles of population density of relative abundance in different places under the same environmental conditions? If so it would indicate that historical events have generated true multiple stable states or cycles (sensu Lewontin 1969; Sutherland 1974). The problem, however, is to rule out the possibility that differing environments in the different places affect biological interactions in such a way as to produce alternate patterns of population or community structure and change.

Some of the studies in table A1 document differences in the dynamics of populations or relative abundances of species in different locations. The intensity and periodicity of insect outbreaks, for example, vary with the environment. Larch tortrix moth outbreaks become increasingly less periodic and intense at lower altitudes in the Alps (Baltensweiler 1968). However, at a given altitude where presumably the physical environment is more similar than at different altitudes, there is considerable synchrony in their periodicity and intensity over wide areas. Similar variation between different sites in patterns of population fluctuation have been reported for small mammals and gallinaceous birds (Keith 1963). The relative abundances of species within a guild also sometimes show differences among sites. The relative abundances of insectivorous birds differed to a fair degree at different sites, changing much less at one site than at another through time (Perrins 1965; Lack 1966). However none of these examples can be used as evidence for multiple stable states, because the differences can be more parsimoniously ascribed to differences in the physical environments of the various locations.

In contrast, other studies document similarities in the dynamics of populations or the relative abundances of species in different locations. The periodicity and range of fluctuations of some insect species (e.g., thrips, Davidson and Andrewartha 1948a, 1948b; pine looper moth, Klomp 1966; Varley et al. 1973; checkerspot butterflies, Ehrlich et al. 1975) appear to be similar in different places although the average density levels about which the fluctuations occur are sometimes different. Fluctuations in numbers of the great tit have been quite synchronous at several sites in England and Holland for over 17 yr (Perrins 1965; Lack 1966). In some cases the relative abundances of species also remain very much the same over a number of turnovers in different locations. The rank order of the relative abundances of forest moths remain approximately the same over large

areas of England, Holland, and Germany (Klomp 1968). Likewise the rank order
of mid-ocean copepods varied little between two cruises 16 yr apart (McGowan
and Walker 1983).

Our interpretation of the above evidence is that natural populations, guilds, or
communities have not yet been demonstrated to assume multiple stable levels,
cycles, or relative abundances over more than one turnover at different sites or at
different times at one site under the same environmental conditions. In most cases
the rank order of relative abundances of species at a particular site remained the
same for the duration of the study but in several instances it changed erratically
throughout the period showing little evidence of stability. Spatial differences in
the characteristics of population fluctuations or in the relative abundances of
species are either not very consistent or if they are, seem attributable to the
effects of differences in the physical environment.

EVIDENCE OF ADJUSTMENT STABILITY

Do the populations in table A1 display adjustment stability? Adjustment to an
equilibrium state can usually be rejected as irrelevant, since only a few of the
records show evidence of the existence of such a state. However some of the
populations in table A1 fluctuate in a cyclic manner; of these the response to
perturbations was studied in detail in only two. Errington (1939, 1940) carefully
documented the effects of drought and disease on muskrat populations. In a
number of marshes local muskrat populations completely disappeared and recov-
ery resulted from immigration. Cycling then resumed in these reestablished popu-
lations. In this example, readjustment to a cyclic pattern of population fluctuation
occurred and the mechanism of recovery is well understood.

An experimental study was made of the effects of an artificial perturbation on
the population dynamics of the larch tortrix moth, populations of which cycle
regularly in the European Alps (Bovery 1966 in Baltensweiler 1968). Two forest
plots were sprayed with pesticides in 1963 just before the peak density of a 7-yr
cycle; the density of larvae in these plots and in a third control plot were then
monitored. The pesticide killed approximately 95% of the larvae in the treatment
plots. Trees in these plots were not defoliated that year while those in the control
plots suffered heavily. In 1964, both treated populations returned, by a 15-fold
increase, to approximately the same density as that existing before the treatment.
The population in the control plot changed relatively little, increasing only 1.5
times in density. In 1965 all three populations declined dramatically and in 1966
this trend continued. The years 1965 and 1966 were part of the general decline
phase of the cycle in the region of Switzerland where the experiment was con-
ducted. Thus the perturbed populations returned to near control densities in one
generation, then began cycling as before. The mechanisms of adjustment to a
cycle are not as well understood in this case as in the muskrat study and no
mention is made of natural perturbations which might act in the same manner as
the treatment with pesticides.

McGowan and Walker (1979, 1983) studied the zooplankton (copepod) assem-
blage in the north Pacific Ocean central gyre, sampling nearly the same locations
on two cruises 16 yr apart. This very large area is regarded as geologically old and

relatively homogeneous and isolated from exchange of either nutrients or species with neighboring water masses (McGowan 1977). In the interval between the sampling cruises an exceptional natural disturbance occurred, apparently as a result of increased vertical turbulence in the thermocline region (Hayward and McGowan 1979). As a result, the primary productivity approximately doubled and there was a large increase in the biomass of the zooplankton. However, in spite of this large perturbation, the numerical rank order of the copepod species changed little between the two cruises. Our analysis indicated that in certain species none of the different local populations showed much variation whereas the populations of other species varied considerably. We interpret this result to indicate that, although those species showing little variation may have displayed adjustment stability, others in the same community probably did not.

Two other studies in table A1 documented changes following disturbances, but neither gives evidence of adjustment stability. Jónasson's study of *Chironomus anthracinus* showed that subsequent to a decline in numbers caused by the input of sewage, larval densities returned to near original levels, though the pattern of larval recruitment was quite different. The study continued for another 2 yr but this was insufficient to document the maintenance of these new larval densities over a number of turnovers.

Boesch et al. (1976) sampled 16 species in an estuary for 6 yr before a severe hurricane and 4 yr thereafter. Four species were "more or less equally abundant" before and after the storm, four were much reduced, and five were much more abundant afterwards, and three were classified as "irruptive," both before and after. The first four species which changed the least nevertheless were very irregular and at times became locally extinct. Fourteen of the 16 species persisted for the entire period but since no stable states or cycles were demonstrated, by definition there was no adjustment stability. In none of the other accounts of studies listed in table A1 is there any mention or analysis of the effects of disturbances.

There are at least two reasons for our conclusion that adjustment stability has been demonstrated in only three instances, one of which involved an artificial perturbation. First it may be that no significant natural perturbation occurred while the other systems were under observation; this seems unlikely, given the long periods of study. Alternatively, the investigators may have regarded them as "noise," unworthy of study. Physical perturbations are often considered to be extraneous and exceptional events, relatively unimportant to population and community structure. A prevalent view is that one should minimize the chance of such annoying events occurring so that the "real" processes affecting populations and communities can be identified. With this attitude, the effects of perturbations will not be scrutinized in nearly as much detail as have the effects of strictly biological interactions.

AN ALTERNATIVE: PERSISTENCE WITHIN BOUNDS

We conclude (as does Murdoch 1979) that ideas of population or community stability based upon the existence of equilibrium states have seldom if ever been tested adequately because of the difficulty of defining the equilibria, measuring the

strength of the disturbing forces and measuring the rate or degree of recovery in natural communities. Given the difficulties of testing these notions of stability it seems more useful to study the broader class of mechanisms which ensure population persistence regardless of whether equilibria can be identified. These mechanisms include both those which reduce the likelihood of extinction or irruption and those which result in the reestablishment of communities if populations of some of the component species become extinct locally. The idea that populations or communities persist because they seldom exceed bounds (defined stochastically) rather than (or in addition to) having one or more equilibria, is discussed theoretically by Lewontin (1969), Holling (1973), and Chesson (1978). To see whether this idea applies to real ecological systems one would need to show that there were no trends in population numbers and no upward trend in the magnitude of population fluctuations, i.e., of extinctions or irruptions of numbers in populations within communities. To do so requires either experimental manipulations of population density (Eisenberg 1966, 1970; Stimson and Black 1975; Black 1977), or long-term observations during which the numbers approach hypothesized bounds but rarely exceed them. Demonstrating the existence of density-dependent mechanisms that were effective in preventing the population from exceeding the bounds would strengthen the evidence for a particular case (Murdoch 1979). Stochastic boundedness without equilibria would be suggested if, in a number of experiments or observations under the same physical conditions, the density of a population moved away from the extreme levels to which it had been perturbed but did not consistently move to the same level between the bounds after each perturbation. Our previous comments concerning the influence of spatial scale on judgments of stability apply as well to the notion of boundedness. The bounds of population fluctuation will in most cases narrow as the spatial scale of observation becomes larger.

IMPLICATIONS FOR STUDIES OF NATURAL COMMUNITIES

We have made the criteria for assessing community stability and persistence quite strict, and few of the studies reviewed were rigorous enough to establish unambiguously the relative stability and/or persistence of the population or community being studied. To achieve this depends in part on the characteristic we choose to study. If it is broad enough there is little difficulty: i.e., will the community adjust back to a forest versus a grassland; to a mussel bed versus an algal bed; to corals versus turtle grass, etc.? For example, pollen records from bogs indicate that forests have occupied parts of western and northern North America for longer than the turnover time of the trees, despite widespread fires recorded as charcoal layers in the cores (Heinselman and Wright 1973). If, however, we are interested in more detailed changes, e.g., in the composition or relative abundances of the species, judgments about stability and/or persistence are much more difficult. Yet these are characteristics that Lewontin (1969), Holling (1973), and others refer to in their theoretical discussions of community stability. There is, to our knowledge, no evidence to show that following a disturbance any community has adjusted back to an original species configuration

which then resisted change beyond one complete turnover. Most records are too short to demonstrate this. The evidence for alternate stable communities is inadequate for the same reason. Most supposed cases are due simply to the persistence of long-lived individuals and are therefore tautological (Frank 1968).

To evaluate the likelihood of community stability and/or persistence and avoid the tautology is difficult, especially for long-lived organisms. When studying an assemblage composed of both short-lived and long-lived species, it might be possible to use our rigorous criteria for the members short lived enough that a complete turnover of individuals can be documented. To assess the likelihood of local replacement of the more long-lived species, several methods are possible. The first is the method described above, using age structures to forecast the probability of replacement. Obviously this strategy is only as good as the assumption that the present age structure of a species is a good predictor of the likelihood of its future replacement. If this assumption is evaluated and the scales of the study clearly specified, judgments of the relative stability and/or persistence of communities with long-lived members could be made. To our knowledge this assumption has not yet been sufficiently evaluated in any study. A second method is to reconstruct the past history of a community assuming that the climate has not changed significantly over the period. Long-term studies using, for example, pollen records are probably ruled out for the latter reason, but shorter-term reconstructions may be possible. As far as we are aware, there are only a few published instances of such reconstructions, e.g., Peterkin and Tubbs (1965), Henry and Swan (1974), Oliver and Stephens (1977), etc. In none of these instances was the minimum area evaluated; however, within the spatial scales studied, there was no evidence of stable states. A third method is to look for mechanisms producing density dependence in recruitment, growth, and mortality that would tend to prevent local extinctions and irruptions.

ON THE STABILITY AND PERSISTENCE OF ECOLOGICAL SYSTEMS

Elton (1930, pp. 16, 17), in discussing the then current views of the effects of disturbances on ecological communities, had this to say:

It is further suggested that if we knew enough about the ecological relations of the animals we could predict the effect of any interference, just as a clockmaker can work out the ultimate effect of the twirling of one wheel upon the rate of revolution of any of the others. At the same time it is assumed that an undisturbed animal community lives in a certain harmony, referred to as "the balance of nature," and that although rhythmical changes may take place in this balance, yet that these are regular and essentially predictable and, above all, nicely fitted into the environmental stresses . . . . The picture has the advantage of being an intelligible and apparently logical result of natural selection in producing the best possible world for each species. It has the disadvantage of being untrue. "The balance of nature" does not exist and perhaps never has existed. The numbers of wild animals are constantly varying to a greater or less extent, and the variations are usually irregular in period and always irregular in amplitude. Each variation in the numbers of one species causes direct and indirect repercussions on the numbers of others, and since many of the latter are themselves independently varying in numbers the resultant confusion is very remarkable. The simile of the clockwork mechanism is only true if we imagine that a large proportion of the cogwheels have their own mainsprings, which do not unwind at a constant speed. There is also the difficulty that each wheel retains the right to

arise and migrate and settle down in another clock, only to set up further trouble in its new home. Sometimes, a large number of wheels would arise and roll off in company, with no apparent object but to escape as quickly as possible from the uncomfortable confusion in which they had been living.

In our opinion, the evidence gathered about numbers of animals and plants over the past 50 yr upholds Elton's description. If a balance of nature exists, it has proved exceedingly difficult to demonstrate.

SUMMARY

To see whether real ecosystems (as opposed to model ones) are stable, i.e., whether they exhibit resistance to short-term perturbations or adjustment following them, stable equilibria must be identified. To do this and still avoid trivial results, certain criteria of scale must be satisfied. To judge resistance, the strength of the perturbation capable of overcoming it must be estimated, and this usually requires experimentation. On a temporal scale, the fate of all adults of the population or community must either be followed for a minimal period of at least one complete turnover, or their replacement probabilities estimated. In regard to space, if one finds instability, this may apply only to the area studied, not to larger areas. However it is useful to define the spatial scale for which instability versus stability applies.

An analysis of census data from many long-term studies revealed a continuum of temporal variability in the dynamics of natural populations and communities. There is no clear demarcation between assemblages that may exist in an equilibrium state and those that do not. Only a few examples of what might be stable limit cycles were found. There was no evidence of multiple stable states in unexploited natural populations or communities. Previously published claims for their existence either have used inappropriate scales in time or space, or have compared populations or communities living in very different physical environments, or have simply misconstrued the evidence. Rather than the physicist's classical ideas of stability, the concept of persistence within stochastically defined bounds is, in our opinion, more applicable to real ecological systems.

TABLE A1

LONG-TERM STUDIES OF POPULATIONS WHICH SPAN AT LEAST ONE TURNOVER

I. AQUATIC ORGANISMS

Study No.	Species and Code No.	Span of Yr Sampled	Turnover Time (yr)	No. of Censuses Used	Details and Locations of Data Used	Source
1	Insect larva Chironomus (sp. 1)	13	2	9	No. at 20 m depth in large lake, Denmark, first year emergence no.	Jónasson 1971
2	Zooplankton Limnocalanus (sp. 1) Keratella (sp. 2)	3+	<1	4	No. per m² of lake bottom, Canada, April samples used	Rigler et al. 1974
3	Zooplankton Epischura (sp. 1) Diaptomus (sp. 2)	5+	<1	6	No. per m³ in lake, USA, August samples used	Richards et al. 1975
4	Meiobenthic copepods Paronychocamptus (sp. 1) Canuella (sp. 2) Tachidius (sp. 3) Halicyclops (sp. 4)	8+	<1	8	No. per 10 cm² in brackish pond, Belgium, annual peak densities used	Heip 1980
5	Open ocean copepods, 11 spp. Code no. refers to order given in figs. 6 and 7 of source	16	<1	2	% relative abundance in each sample. Two cruises, 1964 and 1980, with 6 stations in order along 155° longitude, at latitudes 26°, 27/28°, 30°, 34/35°, 36/37°, 38/39° in central Pacific gyre. Only spp. that had a relative abundance of at least 10% in at least one station on either cruise were used	McGowan & Walker 1983
6	Oyster larvae Crassostrea (sp. 1)	25	8	4	Mean no. of oyster larval set per 100 shell-surfaces in sound, USA	Loosanoff 1966
7	Starfish larvae Asterias (sp. 1)	25	8	4	Mean no. of starfish set per 100 shell-surfaces in sound, USA	Loosanoff 1964
8	Starfish Asterias (sp. 1)	17	8	3	No. per 3,048 m dredging in sound, USA	Loosanoff 1964

TABLE A1 (Continued)

LONG-TERM STUDIES OF POPULATIONS WHICH SPAN AT LEAST ONE TURNOVER

Study No.	Species and Code No.	Span of Yr Sampled	Turnover Time (yr)	No. of Censuses Used	Details and Locations of Data Used	Source
9	Starfish Pisaster ochraceus (sp. 1)	19	19+	2	No. per 20 m of shoreline sampled in 1961 and 1980, USA	Connell, unpubl. data
10	Barnacles Chthamalus (sp. 1)	22–23	20+	2	No. per cm² at .1, .6 and 1.1 yr after settlement counted at or just below the high adult zone. Comparisons for the .1 yr age-class were made between the yr-classes of 1954 and 1977, of the .6 yr age-class between the yr-classes of 1957 and 1979, of the 1.1 yr age-class between the yr-classes of 1953 and 1976. Intertidal shore, Scotland	Connell 1961b, 1983
	Balanus (sp. 2)	24–29	12+	2	No. per cm² at .1, .6 and 1.1 yr after settlement counted at several intertidal levels. Comparisons for the 0.1 yr age-class were made between the yr-classes of 1953 and 1977, of the 0.6 yr age-class between the yr-classes of 1954 and 1982, of the 1.1 yr age-class between the yr-classes of 1952 and 1981. Intertidal shore, Scotland	Connell 1956, 1961a, 1983
11	Barnacles Balanus glandula (sp. 1)	21	10	3	% cover at mid-tidal level on large concrete pier. Censuses in 1959, 1969, and 1980, USA	Connell 1970, unpubl. data
	B. cariosus (sp. 2)	21	20	2	% cover at mid-tidal level on large concrete pier. Censuses in 1959 and 1980, USA	

No.	Taxon				Description	Reference
12 ········	Snails *Nucella* *emarginata* (sp. 1) *N. lamellosa* (sp. 2) *N. canaliculata* (sp. 3)	21	10	3	Total population on large concrete pier sampled in 1959, 1969, and 1980, USA	Connell, unpubl. data
13 ········	Amphipod *Gammarus* (sp. 1)	4+	1	5	No. per m² in 3 areas in brackish pond, England. Dec./Jan. censuses used	Barnes et al. 1979
14 ········	Clam *Cardium* (sp. 1)	13	10	2	Total population size in May within an inlet, England	Hancock 1971
15 ········	Benthic invertebrates *Spiophanes* (sp. 1) *Angulus* (sp. 2)	25 25	1 10	25 3	Mean no. per .1 m² in autumn samples taken at intermediate depths (13–16m) in 3 areas of the North Sea	Ziegelmeier 1978
16 ········	Benthic invertebrates *Acteocina* (sp. 1) *Nephtys* (sp. 2) *Mulinia* (sp. 3) *Pectinaria* (sp. 4) *Paraprionospio* (sp. 5)	14+ 14+ 14+ 14+ 14+	1 2 1 2 1	10 5 10 5 10	Mean no. per m² in summer in estuary, USA	Boesch et al. 1976
17 ········	Benthic invertebrates *Abra* (sp. 1) *Cyprina* (sp. 2) *Diastylis* (sp. 3) *Terebellides* (sp. 4) *Pectinaria* (sp. 5)	10 10 10 10 10	5 3 2 5 2	2 4 4 2 4	Mean no. per m² in area of the Baltic Sea	Arntz 1980

II. PARASITIC ORGANISMS

No.	Taxon				Description	Reference
18 ········	Acanthocephalan *Pomphorhynchus* In intermediate amphipod (sp. 1) In definitive fish host (sp. 2)	8 9	1 1	8 6	Mean % of hosts infected in river, England	Kennedy and Rumpus 1977

(Continued)

TABLE A1 (Continued)

LONG-TERM STUDIES OF POPULATIONS WHICH SPAN AT LEAST ONE TURNOVER

Study No.	Species and Code No.	Span of Yr Sampled	Turnover Time (yr)	No. of Censuses Used	Details and Locations of Data Used	Source
19	Cestode in fish Ligula (sp. 1)	7	1	6	% of hosts in most susceptible size-class infected in July. Small lake, England	Kennedy and Burrough 1981
20	Cestode in fish Eubothrium (sp. 1)	14,20	1	10,15	% of smolts and underyearling fish infected in 2 areas of a lake, Canada	Smith 1973
21	Protozoan in humans Entamoeba (sp. 1)	3	.1	3	Mean % of host infected in 4 villages in rainy season and in dry season, Gambia	Bray and Harris 1977
22	Protozoan in fly Trypanosoma (sp. 1)	7	.1	5	% of hosts infected in Ogbornosho, Nigeria	Riordan 1977
23	Virus in humans Rubella (sp. 1)	40	.02	17	% of hosts infected at 4-mo intervals in USA	Krugman 1973
24	Trematode in humans Schistosoma (sp. 1)	7	2	3	Mean % of hosts infected in 54 villages, Iran	Rosenfield et al. 1977

III. TERRESTRIAL ORGANISMS

Study No.	Species and Code No.	Span of Yr Sampled	Turnover Time (yr)	No. of Censuses Used	Details and Locations of Data Used	Source
25	Plants Astrebla (sp. 1)	24,25	24	2	No. of plants per 20 m² and per 40 m² in two ungrazed grasslands, Australia	Williams and Roe 1975
	Eragrostis (sp. 2)	25	22	2	No. of plants per 40 m² in an ungrazed grassland, Australia	
	Dichanthium (sp. 3)	25	10	3	No. of plants per 40 m² in an ungrazed grassland, Australia	
	Danthonia (sp. 4)	16	10	2	No. of plants per 200 m² in an ungrazed grassland, Australia	
26	Plants Anthyllis (sp. 1)	4–5	3–4	2	No. of flowering plants per m² in 5 coastal populations and 1 inland population, Netherlands	Sterk 1975
27	Plants Spergula (sp. 1)	3	1	3	No. of fruiting or flowering plants per m² in 5 populations on dunes in Poland	Symonides 1974

	Taxon				Description	Reference
	Cerastium (sp. 2)	8	1	8	No. of plants per .01 m² on dunes in Poland	Symonides 1979c
	Androsace (sp. 3)	8	1	8	No. of plants per m² on dunes in Poland	Symonides 1979b
	Plantago (sp. 4)	8	5	8	No. of plants per m² on dunes in Poland	Symonides 1979b
	Jasione (sp. 5)	2	7	8	No. of plants per 16 m² on dunes in Poland	Symonides 1979c
	Corynephorus (sp. 6)	2		8	No. of plants per 4 m² in 3 populations on dunes in Poland	Symonides 1979a
28	Plants	7	1	8	% cover in annual grassland, USA. Data from control pens	Fitch and Bentley 1949
	Erodium (sp. 1)					
	Bromis mollis (sp. 2)					
	Festuca (sp. 3)					
	Lotus (sp. 4)					
	Lupinus (sp. 5)					
	B. rubens (sp. 6)					
	Plagiobothrys (sp. 7)					
	Hemizonia (sp. 8)					
	Trifolium (sp. 9)					
	B. rigidus (sp. 10)					
29	Beetles	2–5	2	3–11	No. per trap in 9 populations on about 1 km² of heath, Netherlands	den Boer 1971
	Pterostichus (sp. 1)					
	Calathus (sp. 2)					
30	Spruce budworm	16	1	16	Mean no. of larvae per 10 ha forest plot, Canada	Morris 1963
	Choristoneura (sp. 1)					
31	Spruce sawfly	17	1	17	No. of 5th instar larvae per 150 trees in forest plot #1, 1942–1958 in Canada	Neilson and Morris 1964
	Diprion (sp. 1)					
32	Blackheaded budworm	12	1	12	Mean no. of larvae per .09 m² of foliage in forest plot, Canada	Morris 1959
	Acleris (sp. 1)					
33	Forest moths	17	1	17	No. of individuals per 1,000 shoots in pine plantation, Holland	Klomp 1966, 1968
	Bupalus (sp. 1)	16	1	16		
	Panolis (sp. 2)	16	1	16		
	Thera (sp. 3)	15	1	15		
	Hyloicus (sp. 4)					
34	Forest moths	60	1	60	No. of pupae per m² of forest floor, pine plantation, Germany	Schwerdtfeger 1935, 1941 in Varley 1949
	Panolis (sp. 1)					
	Bupalus (sp. 2)	60	1	60		
	Hyloicus (sp. 3)	50	1	50		

(Continued)

TABLE A1 (*Continued*)

LONG-TERM STUDIES OF POPULATIONS WHICH SPAN AT LEAST ONE TURNOVER

Study No.	Species and Code No.	Span of Yr Sampled	Turnover Time (yr)	No. of Censuses Used	Details and Locations of Data Used	Source
35	*Dendrolimus* (sp. 4)	60	1	60	No. of larvae per m² of forest floor	Varley and Gradwell 1968
	Winter moth *Operophtera* (sp. 1)	17	1	17	No. of larvae per m² in oak forest, England	Varley 1971
36	Winter moth parasitoids and predator				No. of individuals per m² in oak forest, England	
	Cratichneumon (sp. 1)	16	1	16		
	Cyzenis (sp. 2)	16	1	16		
	Philonthus (sp. 3)	9	1	9		
37	Larch moth *Zeiraphera* (sp. 1)	18	1	18	Mean no. of larvae per 7.5 kg of branches in forested valley, Switzerland	Baltensweiler 1968
38	Checkerspot butterfly *Euphydryas* (sp. 1)	15	1	15	Sizes of 3 populations on coastal ridge, USA	Ehrlich et al. 1975
39	Apple-blossom thrip *Thrips* (sp. 1)	7	.3	7	Mean no. of thrips per rose per day in April, August, and December. Rose garden, Australia	Davidson and Andrewartha 1948a
40	Insectivorous birds *Parus major* (sp. 1)	18	7	3	No. of breeding pairs in nest boxes in 2 forests in England	Lack 1966
	P. caeruleus (sp. 2)	18	7	3	No. of breeding pairs in nest boxes in a forest in England	

Study no.	Species				Description	Reference
41	Insectivorous birds				No. of breeding pairs in nest boxes in a 129 ha forest in Holland	Kluijver 1951; Perrins 1965
	Parus major (sp. 1)	52	7	8		
	P. caeruleus (sp. 2)	32	7	5		
	P. ater (sp. 3)	32	7	5		
	P. cristatus (sp. 4)	32	7	5		
42	Ruffed grouse	27	5	5	No. per 2.6 km² in 1,741 ha forest stand, USA	Marshall 1954
	Bonasa (sp. 1)					
43	Brown lemming	18	1	18	No. caught on 2 traplines set in 16 km² area of tundra, USA	Pitelka 1973
	Lemmus (sp. 1)					
44	Voles	29	1	25	No. caught per 100 ha of forest, USSR	Koshkina 1966
	Clethrionomys rufocanus (sp. 1)					
	C. glareolus (sp. 2)					
45	California vole	19	1	19	No. caught in pit-fall traps in 2 grasslands, USA	Garsd and Howard 1981
	Microtus (sp. 1)					
46	California vole	13	1	13	No. per acre (4,047 m²) on island, USA. Feb./March samples	Lidicker 1973
	Microtus (sp. 1)					
47	Grassland rodents					Blaustein 1981
	Microtus (sp. 1)	2	1	2	No. per ha in a coastal grassland, USA	
	Mus (sp. 2)	2,3	1	2,3	No. per ha in 2 coastal grasslands, USA	
	Reithrodontomys (sp. 3)	2,3	1	2,3		
48	Snowshoe hare	10–14	6	2–3	Estimated no. of hares in 5 study areas ranging from 16–259 ha, Canada. Values for April (mostly adults) were used	Keith and Windberg 1978
	Lepus (sp. 1)					
49	Muskrat	9–14	4	3–4	No. on 3 lakes in spring (mostly adults). Lakes were 282, 450, and 935 acres. USA	Errington 1954
	Ondatra (sp. 1)					

Note.—Local populations of 18 of the above species became locally extinct during the period of observation (study no./species code no.: 5/6, 5/12, 7/1, 12/1, 12/3, 15/1, 16/1, 16/3, 16/4, 16/5, 19/1, 33/4, 38/1, 43/1, 47/1, 47/2, 47/3, 48/1).

TABLE A2

VARIABILITY (SD of the logarithms of the censuses) FOR EACH POPULATION, ARRANGED UNDER THE SAMPLE SIZE (no. of censuses) AND THE POPULATION SIZE (mean of log census values) (Each entry gives the following information: study number from table A1; species code from table A1; SD × 100.)

POPULATION SIZE (mean of log census values)	SAMPLE SIZE (no. of censuses)								
	11+	10/9	8/7	6/5	4	3	2	2	2
−1.51−−2.00	34/1/68								
	34/3/67								
	34/4/107								
	33/4/67								
	34/2/115								
−1.01−−1.50			28/7/65				10/1/140		
−.51−−1.00			28/8/59				10/1/34		
−.01−−.50			28/9/21				10/1/189		
			28/10/61				10/2/54		
.00−.50	33/2/34		28/5/107			12/3/71	5/1/12	5/11/21	5/13/21
	36/2/24		28/6/63			47/2/71	5/4/0	5/11/43	5/13/21
			39/1/21				5/4/12	5/11/43	5/13/34
							5/4/12	5/12/0	5/17/0
							5/6/43	5/12/21	5/17/0
							5/6/64	5/12/67	5/17/21
							5/7/12	5/13/21	5/17/21
							5/11/0	5/13/21	26/1/28
							5/11/21		
.51−1.00	33/3/41		27/2/3	19/1/50	17/2/20	15/2/40	5/1/4	5/4/34	5/17/24
	36/1/45		28/3/36	41/3/18		24/1/31	5/1/7	5/6/4	5/17/74
	44/1/57		28/4/74	41/4/22		25/3/90	5/1/34	5/6/21	5/107/93
	44/2/51		39/1/17			47/3/34	5/2/14	5/6/37	5/107/114
						48/1/85	5/2/16	5/7/9	26/1/28
							5/2/21	5/7/29	26/1/47
							5/2/34	5/7/38	27/6/7
							5/2/78	5/7/40	47/1/113
							5/3/10	5/7/76	47/2/111
							5/3/45	5/11/111	47/3/129
							5/4/0	5/12/85	
							5/4/7	5/13/74	

1.01–1.50	15/1/70, 15/1/74, 15/1/83, 20/1/25, 33/1/50, 37/1/145, 38/1/65, 43/1/70	16/3/115, 20/1/31	4/4/136, 18/1/3, 28/2/33	41/2/23	17/5/25, 29/1/55	11/1/37, 12/1/105, 15/2/25, 40/1/21, 40/1/155, 40/2/35, 48/1/75, 48/1/83	5/1/0, 5/1/29, 5/2/19, 5/3/12, 5/6/24, 5/12/34, 9/1/22, 10/2/7, 11/2/45, 27/6/2
1.51–2.00	32/1/77, 35/1/45, 43/1/76, 45/1/45, 45/1/54, 46/1/33	16/1/81, 16/5/75, 36/3/27	4/2/45, 4/3/44, 28/1/21, 41/1/23	16/2/54, 16/4/105, 18/2/2, 22/1/13, 42/1/44	29/2/67	8/1/21, 15/2/17, 21/1/7, 21/1/17, 27/1/2, 27/1/3, 48/1/105	10/2/9, 17/4/14, 25/1/4, 25/1/44, 25/2/179, 26/1/8, 26/1/47, 27/6/91, 48/1/78
2.01–2.50			4/1/52, 27/3/29, 27/4/42, 39/1/21	3/2/38, 29/1/7, 29/1/35, 29/2/70, 29/2/77	29/1/20, 49/1/88	27/1/1, 27/1/1, 27/1/4, 29/1/64, 29/2/66, 49/1/25, 49/1/79	17/1/11, 17/1/11, 27/5/1, 29/1/6, 29/2/24
2.51–3.00	31/1/41, 38/1/44			3/1/41	7/1/123, 17/3/27, 29/1/14, 29/2/39, 29/2/71, 6/1/34	12/2/39, 29/1/10, 29/2/62	14/1/71, 29/1/4, 29/2/18
3.01–3.50	30/1/104, 38/1/40	1/1/51					
3.51–4.00				13/1/45, 13/1/48, 13/1/57			25/4/24
4.01–4.50	23/1/45			2/2/24, 2/1/17			
4.51 + ...							

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