

FURTHER COMMENTS ON THE EVIDENCE FOR MULTIPLE STABLE POINTS IN NATURAL COMMUNITIES

Peterson (1984) argues that we have applied unnecessarily strict criteria in evaluating evidence for the existence of multiple stable points in natural communities (Connell and Sousa 1983). In particular, he disagrees with the blanket application of our criterion that "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" (Connell and Sousa 1983, p. 792). Peterson (1984, p. 128) suggests that this criterion would eliminate from consideration cases in which "the differences in environment between sites occupied by alternative communities may be extreme, merely as a historical consequence of feedbacks between the biota and the physical environment. Furthermore, if cases of multiple stable points do exist in natural systems, this feedback between the organisms and their local environment would seem to me to be one of the most likely mechanisms involved in maintaining the alternative states."

We agree that if this suggested feedback actually operates in nature, it represents an important mechanism. Therefore, we will address two points in this paper: (1) the nature of the evidence needed to demonstrate the feedback mechanism; and (2) the adequacy of the evidence supporting any proposed examples of it.

In regard to the first point, we propose two criteria that need to be satisfied before evidence can be accepted as demonstrating the existence of the feedback mechanism. (1) If significant differences are observed between the two sites in any relevant environmental variables, they must be shown to result from the influence of the different resident populations rather than being of extrinsic abiotic origin. (By "relevant" we mean those environmental variables that exert a statistically significant effect on density or rate of population growth.) (2) The environment on each of the two sites, modified as above, should have properties that both result in self-replacement of the resident population, and reduce the likelihood of invasion of the alternative population from the other site.

Our second point concerns the adequacy of evidence for the existence of the feedback mechanism in natural populations. Peterson (1984, p. 128) gives several "potential (but not yet adequately demonstrated) examples" of it. He is correct in this assessment and we would like to discuss their inadequacies in regard to each of the above criteria. One of his examples satisfies both criteria for one of the two proposed alternative stable states. Vivrette and Muller (1977) showed that the ice plant, *Mesembryanthemum crystallinum*, increases the salt content of the soil beneath it. This apparently inhibits germination of grasses and enhances that of its

own species. This mechanism does not produce alternative stable states since the ice plant continues to invade the stands of grasses at both this and other sites in California. Peterson's other terrestrial examples all concern fire in forests (Stone and Vasey 1968; Mutch 1970; Williamson and Black 1981). They give evidence satisfying the first criterion: each resident species produces litter that specifically modifies the fire regime. No evidence satisfying the second criterion was given in any of these papers.

The remaining examples all come from populations in marine soft sediments (Ronan 1975; Woodin 1976; Highsmith 1982) and do not satisfy one or both criteria. Ronan (1975) studied the effect of burrowing by the shrimp *Callianassa* on the tube-builder *Phoronopsis*. We find no evidence in Ronan (1975) that *Callianassa* "is unable to invade areas occupied by dense aggregations of *Phoronopsis*" as stated by Peterson (1984, p. 130). Both C. H. Peterson and P. K. Dayton, however, have told us that the late T. E. Ronan presented such evidence in scientific lectures. In Ronan (1975) some contrary evidence exists demonstrating that burrowing *Callianassa* can break and disorient phoronid tubes.

As in the terrestrial examples above, Highsmith (1982) and Woodin (1976) give evidence satisfying our first criterion: resident organisms often alter the chemistry, flocculence, water content, grain size, or stratigraphy of the soft sediments they occupy. One of Highsmith's (1982) findings (see below) partially satisfies our second criterion; there is little evidence, however, that such sedimentary changes maintain alternative stable states in these communities. Highsmith (1982), on the basis of laboratory experiments, suggested that two different populations (sand dollars and tanaid crustaceans) living in the same physical environment could exist in alternative stable states. One of the mechanisms proposed did involve a modification of the local physical environment. A chemical released by the sand dollars and adsorbed on the sand grains acts as an attractant to their larvae; it does not affect the crustaceans, however. The mechanisms more likely to maintain two stable states were direct interactions between the species, not habitat modifications. Highsmith (1982) suggested that the crustacean assemblage would eat all the settling larvae of the sand dollars, while the population of adult sand dollars, by their shifting movements, would displace and eliminate all crustaceans. Woodin's (1976) examples also indicate that larval settlement in soft sediments is more often reduced by the direct activities of resident adults (burial or predation) than by modification of the physical characteristics of the sediments. None of the assemblages she describes satisfy our second criterion.

Peterson (1984) suggests that in a California coastal lagoon there may exist two alternative stable states, one dominated by the ghost shrimp *Callianassa*, one by the clam *Sanguinolaria*. To support this suggestion, he cited evidence, from both Peterson (1977) and more recent data in his table 1, indicating more recruitment of *Sanguinolaria* in sites from which *Callianassa* had been removed ($2\frac{1}{2}$, $13\frac{1}{2}$, and $36\frac{1}{2}$ mo earlier) than in control sites. Although the earlier (1977) comparisons were significantly different, those using a different sample size in his table 1 are not ($P > .05$, t -tests). No evidence was given concerning the alternative state dominated by *Sanguinolaria*. Thus neither the aforementioned results of Ronan's

(1975) study nor Peterson's evidence is sufficient to indicate that the dominant species in this soft-sediment community exist in alternative stable states using our two criteria.

We agree that organisms can and do modify the physical environment in their vicinity, and we accept the possibility that such modifications could enhance their own self-replacement and inhibit that of their competitors. If both of these latter possibilities are shown to occur in two sites occupied by different populations, then they should probably be classed as alternative stable states, provided that (1) the two sites had the same background physical regime (i.e., having no significant differences in the averages or patterns of variation of relevant physical variables), and (2) the populations on both sites persisted for more than one turnover. At present, we are unaware of any examples of alternative stable states that satisfy these criteria.

Peterson (1984, p. 131) suggests that our criteria for evaluating evidence concerning ecological stability or persistence were "arbitrarily strict." While we disagree that we were being arbitrary, we do feel it necessary to be strict in scrutinizing any evidence suggesting that theoretical concepts apply to natural populations. The new criteria proposed in this paper for judging evidence for Peterson's feedback mechanism seem to us to represent the minimum necessary. The fact that none of the examples suggested by Peterson adequately demonstrates the mechanism (as he pointed out) may signify either that it is rare or nonexistent in nature or that the studies to date have not addressed the question in sufficient depth. The aim of this paper is to stimulate the latter activity.

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