OPINION

Opinion is intended to facilitate communication between reader and author and reader and reader. Comments, viewpoints or suggestions arising from published papers are welcome. Discussion and debate about important issues in ecology, e.g. theory or terminology, may also be included. Contributions should be as precise as possible and references should be kept to a minimum. A summary is not required.

Between Scylla and Charybdis: do some kinds of criticism merit a response?

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Community ecology has suffered from past excesses of interpreting pattern when supporting evidence was weak or absent (Simberloff 1982). Indeed, arguably because of constructive aspects of the resulting debates, ecology has become much more rigorous through increased appreciation of null models and improved statistics. However, just as misleading as reporting pattern where none may exist is the rejection of pattern and generalizations based on it when it is present. A common medium for expressing ecological criticism and thus initiating debate, whether profitable or not, are minimally edited contributions published as book chapters or symposia (see also McIntosh 1987). Such procedures encourage judgements based on unsupported allegations, misrepresentations and out-of-context quotations. A not uncommon procedure is to ridicule a single word or term, ignoring the context in which it was embedded. Rebuttal is difficult because major or widely-read journals are hesitant to publish responses to opinions presented elsewhere, many have editorial policy inhibiting exchanges, and also because such responses are distasteful to write due to the perceived triviality or inaccuracy of the initial critique.

Foster (1990) provides a nearly perfect example of this style of criticism although others exist. I have chosen his paper because it deals explicitly although hardly entirely with my research, is centered on an assemblage I am familiar with, and provides some data of his own to illustrate the proper way questions should be framed and research conducted.

Foster's primary concern is with the generality of more synthetic overviews. His basic premise is that descriptive surveys taken at numerous geographically separated sites reveal so much variation (in this case, in the pattern of intertidal zonation on rocky shores) that generalizations based on a limited number of spatially restricted studies may not apply. Fair enough, if correct. He disapproves of the current attempts at synthesis and generalization, believing the effort premature at the least. His solution (p. 30) is to sample further: "A more rigorous way out is to be able to compare the structure of research sites (samples) with that of unbiased estimates of the general structure of sites in the region of interest (population)." Where does an understanding of the role of those numerous processes generating the patterns (structure) come from? My view would be less antagonistic if one or more of the sites had been termed "treatment" sites and subjected to some systematic manipulation. Departure of the variables of choice beyond the expected range of variation would then suggest possible sources of that variation. Examples can be found in Schindler et al. (1985), Schindler (1988) and Paine (1986) among others. His claim of extensive variability in abundance, measured as mean percent cover for "characteristic" sessile organisms, is based on samples from 20 sites scattered along the coast of central and northern California. Barnacle cover, for instance, varies from 0–10%. However, to attain this measure the genera *Chthamalus* and *Balanus* were not distinguished. Such lumping is particularly unwarranted for these taxa, whose ecological interactions have been explored experimentally in classic (e.g., Connell 1961, Dayton 1971) studies. Foster's barnacle sampling scheme should fail to detect patterns relating to these taxa and, furthermore, is incapable of producing insights on why an essential resource, space, appears generally unoccupied at his research sites.

Foster also provides preliminary data (his Fig. 2) on the distribution and abundance of common marine algae at these same sites, emphasizing (p. 27) the "...considerable site to site variation in absolute vertical position...". However, it is not difficult to discover statistically significant pattern when it is sought for. Rank ordering of the algae *Endocladia, Mastocarpus* and *Iridaea* by the tidal height of their maximum abundances reveals a consistent pattern, not haphazard positioning (Friedman Test, $p<0.005$) when all 18 (of 20) sites at which they co-occur are examined. Further, no indication is given on the relative exposure or slope of the 20 sites ("...but these factors have not yet been evaluated", p. 27). Since MLLW (mean lower low water) varies with barometric pressure and prevailing wind direction, and it is unlikely that his sites could have been sampled relatively instantaneously, between station variation, perhaps as much as 0.5 m, is to be expected. It is impossible to know whether such efforts towards standardization would reduce the observed between-site variation in upper and lower limits. I suspect it would and in the process reduce the extent of apparent geographic variation emphasized in that figure. Finally, grazers are widely recognized as factors influencing benthic algal distribution and abundance (Lubchenco and Gaines 1981). What they might contribute to the variation apparent in Foster's studies is unknown.

Just as Foster's algal distribution analysis is incomplete (or premature), his evaluation of mussel (*Mytilus californianus*) bed biology is misleading. At these same 20 stations Foster found percent cover of mussels to vary from 0–44%. Six stations were picked for further sampling within the mussel assemblage; in this more restrictive view percent cover varied from 27–93%. Comparisons are then drawn between his findings and those from a latitudinally restricted region of Washington State. Gratuitously appended to these data are comments on competition between mussels and the associated benthic algae. What's improper about his analysis? Just about everything. Leigh et al. (1987), a paper mildly ridiculed (p. 24) by Foster, provides in its Table 2 estimates of percent cover by mussels obtained in a fashion entirely comparable to Foster's. Cover, when the entire intertidal zone is included, varies from 28–50% at 5 sites specifically picked to bracket the wave exposure gradient on Tatoosh Island. Is there an excuse for avoiding these data while employing Dayton's (1971) tidal-height estimates which included only the mussel and barnacle bands? Similarly, in a lengthy paper, Paine and Levin (1981) provide estimates of annual disturbance to the mussel beds at Tatoosh. For 20 sites examined for up to 12 yr, interannual variation in disturbance, defined as winter removal of the mussels, ranged from 0–65%. Of these 20 sites, 15 experienced removals of more than 30% in any one year; further, substantial evidence for regional and interannual variation in disturbance rate are given. What relevance do such data have for interpreting Foster's "snapshot" view of the intertidal zone? Plenty. Variation in percent cover by mussels is to be expected. It is a natural attribute of the assemblage, and is driven by a very general process – wave action on exposed shores. The long-term, multi-site data from Tatoosh are intrinsically as variable as those from Foster's latitudinal surveys. Variations in mussel abundance as revealed in his sampling are both characteristic and to be expected. The fact that (p. 26) "consistent abundance patterns were not apparent" at most reflects reality. In no way does it stand as an insuperable barrier to understanding natural processes or developing generalizations from them.

Foster argues that many of the claims for generality are based on a few unreplicated experiments undertaken in an area of limited geographic extent. Should they be dismissed because of this? I have shown that predation by the seastar *Pisaster ochraceus* determines the lower limit to intertidal mussel beds at two sites on the Washington State outer coast: Mukkaw Bay (Paine 1966, 1974) and Tatoosh Island (Paine 1974, 1984). B. A. Menge has repeated this result in coastal Oregon 500 km to the south. Robles (1987) found via lobster exclusion experiments in Southern California that mussels potentially dominated intertidal sites. Finally, Wolfson et al. (1979) have shown that bands of stinging anemones, by limiting *Pisaster* access, can account for the dense aggregations of mussels on the legs of oil platforms near Santa Barbara, California. There are two instances known to me in which *Pisaster* removals failed to generate a local increase in mussel density or space coverage (Dayton 1971, Van Blaricom 1988). In both, mussels failed to recruit during the removal interval.

I continue to believe that the few *Pisaster* and lobster manipulations identified above provide a sounder basis for interpreting regional variation in mussel dynamics both in terms of percent cover and local distributional limits than could even an intensified sampling effort, employing further airplane surveys and subsequent ground truthing. What has the latter yielded in terms of understanding natural intersite variation, in the identification of causal processes, or in the formation of testable hypotheses?

An expected biproduct of discussing my research on mussels and *Pisaster* is a consideration of the generality of the "keystone" or critical species concept. It is a temptation Foster should have resisted. In developing and modestly expanding this idea, I considered by extensive inference (Paine 1966) and explicitly (Paine 1974) only the relations between mussels and potential competitors inhabiting primary space, i.e. rock. Organisms living epizooitically on mussel shells or the rich associated community were acknowledged and excluded from further consideration. Foster's commentary (p. 29) on the above body of work is incomplete and founded on misrepresentation. The bottom line is that papers should be read and understood before being criticized.

In determining the nature of this response I set three criteria. First, is there internal evidence that the author has examined the papers cited? Or, equally, could other published papers pertaining to the same body of work have been cited which might have clarified the uncertainty. At issue are selective reading, self-serving bias and lack of evidence for consistent scholarship. Second, are alternative hypotheses offered to explain the natural phenomena in question, or is the paper of the nihilist school stating that nothing is correct, that little hope exists? Last, does the language employed seem purposely sarcastic (a temptation difficult to resist), designed to offend rather than amuse or instruct? Foster has not met minimal standards of scientific criticism as identified in the first two points. Further, a not so subtle sarcasm imbues many of the paragraphs, continuing even into the "Acknowledgements" where unsupported innuendo is employed.

Community ecology should continue to develop and thrive as a result of critical reanalysis of published studies. However, to be useful such analyses themselves must be rigorous and constructive. I have identified three essential criteria above; unfortunately, Foster's critique satisfies none of them. Papers like his are awkward to respond to because of their general lack of substance. Failure to respond, however, implies acceptance. Generalization and associated speculation should continue to stimulate ecological understanding by promoting reasoned and reasonable debate.

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