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.

Rammed by the Exxon Valdez: a reply to Paine

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Paine's critique of my paper (Foster 1990) covers a number of objective and subjective issues. Because the reader of his critique and this reply may not have read my paper, the following preamble may help clarify the objective issues.

Recent papers have noted the current debate over the state of ecological science, particularly community ecology. This debate is occurring at a variety of levels from philosophic to methodologic (Loehle 1987, McIntosh 1987, Peters 1988, Underwood 1990). As McIntosh (1987) states, it has arisen from a dissatisfaction over ecology's lack of predictive ability and other characteristics more typical of 'hard' science. Elner and Vadas (1990) provide an excellent case study, clearly illustrating some of the problems and solutions. I think this debate is healthy, and hope that Loehle (1987) is correct that it is "a sign of ecology's incipient emergence as a hard science". A number of ways to improve ecological science have been advanced, and many are discussed in the papers cited above or the references therein. My work on the ecology of hard benthic communities at a number of sites in California identified what I consider to be another important problem in ecological science and ways that it might be solved. This was the genesis of the paper in question.

One way ecologists ascribe scientific importance to processes found at their study sites and, in part, how others also assess the importance of these processes, is to suggest the findings at their sites are generally true over a large geographic area. This is often done by providing evidence that the structure of the sites investigated is similar to that of sites in the larger area. While similarity in structure does not necessarily reflect similarity in process (Dethier and Duggins 1988), it is a reasonable assumption based on experience, and is usually considered to be confirmatory evidence. Conversely, other processes or interactions are suggested by structural differences. The evidence for similarity may be statements based on personal experience or, more frequently, implied by reference to other publications that describe the larger region or other sites within it.

In my view, the problem for the science of ecology is that good evidence for similarity, based on a properly designed sampling program in the larger area, is often lacking. As stated by Andrew and Mapstone (1987), "Observed patterns are the building blocks of the models from which we generate hypotheses, both about the patterns themselves and about processes that may govern them." Given the considerable variation in most communities and the processes and interactions that can cause this variation, it is almost inevitable that some future study at a different site will find that different processes are important. This leads to controversy over primacy of process, with a resulting lack of scientific progress, and 'soft science'.

My experience from a debate over kelp community organization (Foster and Schiel 1988) and from research in rocky intertidal communities (Foster 1982, Foster et al. 1988) indicated that the science of ecology would be improved if higher standards of evidence were required for claims of geographic generality of ecological processes. I also had quantitative, descriptive information from a number of wave-exposed, rocky intertidal sites over a relatively large geographic area in central and northern California that could be used to examine how similar community structure might be. This could provide a more rigorous context for determining if prior generalities about the organization of rocky intertidal communities in this region of the northeast Pacific were valid. In particular, this information allowed a determination of the commoness of rocky shores with distinct zones (assemblages) of high cover in the region sampled. This was of interest because most studies of rocky shore processes have been done on this type of shore (Foster et al. 1988).

I used numerous papers, including Paine's early work

(1966, 1974), as examples of generalization. In his studies, Paine found particular processes to structure the mussel assemblage at two wave-exposed sites in Washington, one site at Mukkaw Bay and the other at Tatoosh Island. He generalized these processes to a larger geographic area by stating that the structure of his sites was similar to that in the larger area: "Along exposed rocky intertidal shorelines of western North America the mussel *Mytilus californianus* exists in a characteristic, well defined band" (Paine 1974: Summary) and "On rocky shores of the Pacific Coast of North America the community is dominated by a remarkably constant association of mussels, barnacles, and one starfish" (Paine 1966:66). In a later paper that I (Foster 1990) did not cite, Paine (1984:1340) again states when discussing work at local sites, "With little effort, the "local" could be extended to include similar exposed sites from ~ 29–58°N latitude." I examined whether these statements were reasonable, based on my quantitative descriptions of wave-exposed shores in part of this region. My paper was not concerned with the processes that structure a particular site, and I did not question Paine's (1966, 1974) findings, only the evidence for generalizing them.

Objective issues

Paine questions how an understanding of process can come from a description of pattern alone. It cannot. As discussed above, however, part of the understanding of process does come from the study of pattern by providing the context for the process. Paine's antagonism over lack of treatment sites is surprising because at the end of the paragraph from which he quotes I stated, "Ultimately, the most complete generalities will be obtained when *experimental* sites span the range of site variability identified in the region."

Paine states that I should have distinguished between barnacle genera. While barnacles certainly can interact, my point was that their overall low and variable total abundance at my sites, combined with a high percentage of unoccupied space, indicated that they were probably not competing for space. This is contrary to the common suggestion that competition for space is important in the intertidal zone. In this context, lumping is justified, and the observations are capable of suggesting process (e.g. low recruitment, removal by predators, etc.) although I did not suggest any.

Paine questions the significance of the variation reported in my Fig. 2. I did briefly discuss absolute vertical position and, as reiterated by Paine, that it was probably related to differences in wave exposure and slope. I did not say the pattern of these positions was haphazard, and would expect a statistically significant pattern. The major point was the amount of variation in the *limits* of vertical distribution of various algal species *relative to each other*, especially *Iridaea flaccida*. This is contrary to much of the literature concerning intertidal zonation (including my 1982 paper that was also critiqued in Foster 1990), and suggests that processes other than oft-evoked competition may be operating. I agree with Paine that grazing could cause these differences. I did not sample all sites "relatively instantaneously," but doing this would not affect the pattern of relative vertical limits. Paine chooses to judge my distributional analyses as incomplete or premature. Perhaps they are for his purposes; they were not for mine.

Paine argues that natural variation in mussel abundance is to be expected, that I avoided data from his studies showing this variation, and that such variation is not a barrier to understanding process or developing generalizations. Perhaps I was not clear in my paper, but the first two criticisms are not relevant to my analyses. I wanted a quantitative measure of how similar the structure at Paine's (1966, 1974) two sites was to that found at my sites. My data were percent cover of mussels so I needed the same measure from his sites for comparison. Paine did not report cover in these papers, but he describes mussels and associated barnacles as forming a "conspicuous band" at Mukkaw Bay. Other descriptions and photographs in these papers and Paine and Levin (1981) all suggest his study sites were dominated by extensive bands of mussels with stable upper and lower boundaries and very high mussel cover. In another paper, Paine (1984:1340) states that these sites were mussel "monocultures" of >80% cover, and refers the reader to Dayton (1971) for a general description. Thus, Dayton's (1971) cover data from an exposed portion of Tatoosh Island seemed representative.

Contrary to the statement in Paine's response, I could not use cover estimates from the other papers he cites. The data in Table 2 of Leigh et al. (1987) are not cover but estimates of vertical distances above MLLW of the upper and lower limits of species. The method used to obtain them ("transit and surveyor's rod," Leigh et al. 1987) was not comparable to mine (point contacts at evenly-spaced distances along five replicate transects at each site for broad-scale surveys at 20 sites, and point quadrats for surveys within mussel beds at six of these sites; Foster 1990). I do not know how Paine derived his cover values from Leigh et al.'s (1987) table. I did not use data based on disturbance rates in Paine and Levin (1981) because cover is a function of disturbance and recovery. The disturbance rate alone cannot be used to estimate the magnitude of the variation in cover. Even if I could have somehow obtained cover estimates from the data in Leigh et al. (1987) and Paine and Levin (1981), they would have been pertinent to my analyses only if they were from Paine's (1966, 1974) study sites because these are the ones from which he generalized.

I agree that a snapshot is a poor indicator of variation. Twenty snapshots at 20 widely separated sites is highly suggestive. Because it is relevant to my paper, I point out that Paine's only evidence for stating that mussel abundances at my sites are "both characteristic and to be expected" come from the exposed shore of Tatoosh Island, Washington. We have continued to sample mussel cover in the fall and spring at the six sites for over four years. Only one site has shown significant year-to-year variation (in prep., results available upon request). Finally, I agree that variation is not a barrier to understanding process or developing generalizations. However, knowing the variation is essential to both.

I did not argue that claims of generality from a few unreplicated experiments (I assume by unreplicated Paine means not repeating a properly replicated experiment at other sites) should be dismissed. I (Foster 1990) did argue that such claims should be "evaluated with higher standards of evidence." Paine cites other studies published after his 1974 paper, presumably to provide additional evidence that his results are general. These papers are not relevant to the issues addressed in my paper. I do not deny the possibility that predation *may* structure mussel assemblages at every site in the northeast Pacific where mussels are found. It is relevant that the papers he cites also show the importance of organisms other than sea stars, and processes such as physical effects and recruitment, to mussel bed structure.

Paine argues that the present experimental base provides a sounder basis for interpreting regional variation in mussel dynamics than an intensified sampling effort. I do not think that either provide a sound base for such an interpretation. The former clearly show that one process, predation, can control distributional limits and, as a consequence, what is attached to the rock in a particular structural context. My sampling data showed that the structural context varies. Paine may believe that one process, predation, explains this variation. For the reasons discussed in Foster (1990) and summarized above, I do not think the evidence warrants this leap of faith. Our observations and surveys have suggested a number of processes, including predation, that might produce the variation described, and this information is being used to develop testable hypotheses. However, elaboration of this was neither germane nor necessary to my paper.

Paine points out that the relationship described in his 1974 paper between mussel abundance and diversity applies only to the primary substratum, defined in that paper as rock or encrusting coralline algae. My understanding was based on the 1966 paper where, in my opinion, the inference is far from clear. I failed to recognize the explicit statement in the 1974 paper. However, the variable cover of mussels within the mussel assemblage at six of my sites (27–93%, Foster 1990: Table 2) suggests that competitive displacement of other sessile organisms on the primary substratum does not always occur.

It is true that mussels can displace other sessile species from, and reduce diversity on, the primary substratum. However, and perhaps more importantly, not considering that these species can exist quite well on top of mussels seems unnaturally restrictive. Species attached to surrounding mussels can affect the structure in patches within a mussel bed (Sousa 1984), and epibionts can have negative (decreased growth, reproduction and survivorship; Dittman and Robles 1991) and positive (protection from freezing; D. Brosnan, Oregon State University, pers. comm.) effects on the mussels themselves. Recent studies by Lohse (1990) indicate that when all available substrata are included, the diversity of sessile species would be unaffected if mussels were to occupy all available rock surfaces at his sites. Lohse also found that the population dynamics of some of these species were enhanced by living on mussels rather than rock. What is the ecological reason for excluding these organisms? Perhaps Paine excluded them because, as suggested by his 1966 paper, they were rare at his two sites.

Subjective issues

Paine begins his critique by questioning the quality of publications in symposia proceedings, and then implies that I am guilty by association. I trust that the reader can see through this device, and evaluate my paper on its own merits as they would any other. It did go through the normal review and editing process, and the number of reprint requests suggests the journal is widely-read.

Paine ends his critique by setting three criteria that, in his opinion, represent minimal standards for scientific criticism. I agree with the first, and invite readers to read my paper and those cited in it and, in light of Paine's response and this reply, decide for themselves about quality of criticism.

I also agree that purposeful sarcasm is inappropriate, as are assaults on professionalism and character. I again invite readers to decide for themselves, while keeping in mind that, like beauty, the interpretation of language can be subjective. I will respond to Paine's two specific problems with my language. I did not "ridicule" Leigh et al. (1987), I simply used a statement from their paper as an example of a generalization about the northeastern Pacific based on a citation to work done in a much more limited geographic range. In my acknowledgements I thanked A. J. Underwood for pointing out "areas of doubt." It was a specific reference to areas of doubt he had about parts of a draft of Foster (1990) which he brought to my attention using this phrase. I do not understand what innuendo is suggested or implied.

I strongly disagree with Paine's second criterion. Not only does it negate the legitimate questioning of existing knowledge, it represents what I perceive as a major problem in ecological science: an emphasis on process and generalization at the expense of understanding natural variation and its causes. Nihilism is an alternative, but there are numerous others. As discussed in the last two pages of Foster (1990), the better alternative is rigorous sampling programs to identify variation in the region of interest, and well-designed experiments to test hypotheses about processes causing variation.

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