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INFERENCE IN ECOLOGY: THE SEA URCHIN PHENOMENON IN THE NORTHWESTERN ATLANTIC

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A fundamental concern in ecology is the absence of a consensus on how to "do" this science. Over the past few years, diametrically opposed treatises have been offered on establishing ground rules both for how to conduct ecological research and for what constitutes evidence to support the most basic ecological premises (see Salt 1983). The appeals of Platt (1964), Strong (1980, 1983), and Simberloff (1983) for replicate testing, the exclusion of null hypotheses, and the use of "strong inference" to advance ecological understanding are compelling because they have proved effective in other sciences. Nonetheless, Quinn and Dunham (1983) presented convincing arguments against the use of rigid hypothetico-deductive reasoning in ecological research. Similarly, Roughgarden (1983) attempted to discredit the "strong-inference" methodology, arguing for a "commonsense" approach using simple system models to build understanding. Salt (1983) seemingly added to the dilemma by attempting to rationalize the various ecological research procedures. More recently, Slobodkin (1986) advocated working on the simplest manifestations of problems because of the extreme nature and complexity of the "big questions" in ecology.

Although such debate has failed to resolve the fundamental concern, it has served to highlight the lack of consensus on problem solving among grass-roots ecologists, who are not philosophers. Although some of the dissention exists because even the basic definition and goals of ecology remain vague and some of the questions are "too big" to adequately focus upon (Slobodkin 1986), there appears a need for more rigor in conducting and interpreting ecological research. We contend that, because of the lack of rigor and guidelines, the tendency to rely on "weak" inference and "common sense" is pervasive, resulting in a propensity to cling uncritically to "pet" concepts rather than to test multiple hypotheses (Chamberlin 1897). Such a soft approach has promoted circular reasoning, aided in the development of paradigms, and retarded ecological discovery.

In this paper, we critically analyze the ecological approach and the interpretation of the resulting data used in a series of related publications to explain the alternation between macroalgal beds and coralline barrens in the sublittoral off

Nova Scotia, Canada. In the process, we show that many of the studies relied on weak inference, which contributed to the development of a keystone paradigm for the American lobster. We also contend that this paradigm has been retained by a series of ad hoc revisions rather than experimentation. We express these views with trepidation, realizing full well that a posteriori criticism is easier than designing and carrying out crucial experiments. However, as expressed by Underwood and Denley (1984) in their examination of rocky-intertidal studies, our criticism is intended to foster ecological progress and not to denigrate those who worked on this marine system.

We do not suggest that our example is more extreme than other problem areas in ecology; indeed, this research provoked much discussion and introduced several innovative techniques. However, despite considerable research efforts, some fundamental answers to the sea urchin phenomenon remain as elusive today as they were 15 years ago. Recent comments by Keats (1986), Breen (1987), and Miller (1986, 1987) highlight the questionable progress in the research. In response to a perspective by Miller (1985a) that questioned the impact of predators in controlling sea urchin populations, Keats argued that we are back to "square one" concerning the actual and potential role of predation; Breen argued the opposite. We believe that a more-rigorous experimental approach (Connell 1974; Paine 1977), based on stronger natural-history observations, would have yielded greater advances in understanding the ecology of this nearshore system.

NATURE AND SOURCE OF THE EVIDENCE

In the early 1970s, explanations were sought for a population explosion of sea urchins and the resulting intensive grazing that converted macroalgal beds into coralline barrens along the Atlantic coast of Nova Scotia (Mann and Breen 1972). Concomitantly, commercial landings of the American lobster had declined dramatically, suggesting, with the hypothesis that lobsters were keystone predators (in the sense of Paine 1969), a causal relationship between these events. An analogous explanation, with sea otters acting as the keystone predator, was advanced to explain differences in the community structure off Alaska (Estes and Palmisano 1974; Estes et al. 1978).

Our review examines core papers and one abstract (through 1985) directly relating to the lobster–sea urchin problem. To ascertain the flow of research—specifically, the questions posed, the ecological approaches used, and the interpretations made—we analyzed these publications chronologically (table 1) according to the following criteria. What was the purpose or objective(s) of each study? Did the study rely on weak or strong inferences (in the sense of Platt 1964)? For the strong-inference category, we considered whether null or implicit hypotheses were advanced, whether experiments were conducted, and, if so, whether controls were employed. Classified under weak inference were affirmative approaches (i.e., those designed to prove hypotheses), literature surveys, and anecdotal and speculative reasoning. In addition, we surveyed the sources of data or information used in each publication. The information sources have been categorized as laboratory experiments, physiological indexing (i.e., extending

TABLE I
 RESEARCH APPROACHES AND METHODS OF DATA COLLECTION USED IN STUDIES ON THE LOBSTER-
 SEA URCHIN-KELP INTERACTION OFF NOVA SCOTIA, CANADA

STUDY	STATED PURPOSE	INFERENCE ^a													
		STRONG							WEAK						
		CE	NH	IH	AA	LS	AS	LE	PI	FS	FE	SM			
1. Miller et al. 1971	Factors limiting lobster yield				+	+							+		
2. Mann & Breen 1972	Advisory on overfishing lobsters					+					+				
3. Mann 1972	Environmental management					+									
4. Miller & Mann 1973	Urchin energetics and trophic relations											+			
5. Mann 1973	Role of algae in coastal productivity												+	?	
6. Breen & Mann 1976a	Effect of urchin on kelp	+		+	?						+			+	
7. Breen & Mann 1976b	Urchin, lobster, kelp interactions	+		+	+						+			+	+
8. Lang & Mann 1976	Persistence of barren grounds	+		+									+		
9. Evans & Mann 1977	Lobster prey preferences		+	+	+										
10. Mann 1977	Persistence of barren grounds			+	+										
11. Mann & Clark 1978	Comparative environmental impact			?	?										
12. Hirtle & Mann 1978	Lobster senses for predation	+		+	?										+

13. Bernstein et al. 1981	Behavior of urchins toward predators	+	+	+	?	+	+	+	+
14. Wharton & Mann 1981	Advisory on lobster production		+	+	+	+	+	+	+
15. Mann 1981	Behavior of managed ecosystem under stress		+	+	+	+	+	+	+
16. Bernstein & Mann 1981	Review of destructive grazing and fisheries management				+	+	+	+	+
17. Johnson & Mann 1982	Survival of urchins on barrens				+	+	+	+	+
18. Bernstein & Mann 1982	Review of destructive grazing and fisheries management				+	+	+	+	+
19. Drummond-Davis et al. 1982	Evaluation of crab predation on urchins				+	+	+	+	+
20. Mann 1982a	Trophic relationships				+	+	+	+	+
21. Bernstein et al. 1983	Behavioral basis of destructive grazing				+	+	+	+	+
22. Mann et al. 1984	Sensory behavior of urchins				+	+	+	+	+
23. Mann 1985a	Explanation of the urchin phenomenon				?	+	+	?	?
24. Mann 1985b (abstract)	Explanation of urchin outbreaks				?	+	+	+	+

^a Based on Platt's (1964) ideas. CE, Control experiments; NH, null hypotheses; IH, implicit hypotheses; AA, affirmative approach; LS, literature survey; AS, anecdotes and speculation.

^b LE, Laboratory experiments; PI, physiological indexing; FS, field surveys; FE, field experiments; SM, simulation model.

^c The results negated the hypothesis but were themselves discounted or rejected in the discussion.

physiological data to field situations), field surveys, field experiments, and simulation models (see table 1).

Of the 23 papers, at least 7 addressed the advisory or management implications of overfishing lobsters and the resulting changes in the nearshore ecosystem due to the sea urchin population explosion. Another 4 focused on trophic relations, including those limiting lobster production. Four others discussed the creation and persistence of barren grounds caused by sea urchins. Behavioral aspects of predator-prey interactions were examined in 5 papers. Sea urchin energetics and system control by environmental or disease factors were covered in the remaining 3 papers.

Eight papers used an experimental (laboratory or field) approach (7 reported controls), whereas 11 were based primarily on the literature and speculative comments (table 1). Four others were also based on literature and speculation, as well as either physiological indexing or field surveys. Therefore, almost two-thirds of the publications in this series represent a nonexperimental approach. Although it was difficult to evaluate the nature of the hypotheses presented, implicit tests seemed apparent in 10 papers, but only 1 paper had a clearly stated null hypothesis. The remaining publications usually had a stated purpose and reasonably clear objectives, but these were often of a socio-environmental or general nature. "The purpose of this paper is to draw attention to the deteriorating condition of the lobster-producing system of Atlantic Nova Scotia and to attempt to change the consensus of management personnel from 'not proven' to something like 'seems plausible, worth investigating further'" (Wharton and Mann 1981, p. 1340). "This paper reviews our knowledge of the strong interactions in the kelp ecosystem of the Atlantic coast of Nova Scotia" (Mann 1982a, p. 415). "This paper deals with a problem related to the management of a valuable resource, the American lobster. . . . The questions that arise . . . are at the interface between population dynamics and ecosystem theory. . . . I hope that this paper will help draw attention to the need to build bridges between the two lines of advance" (Mann 1977, p. 455). Many of the stated purposes were confirmatory and not scientifically testable.

In addition, affirmative or supporting language was used in 11 papers and may have been used in 6 others. In most papers (through the 1970s and early 1980s), confirmation was sought for the keystone role of lobsters. "The hypothesis is thus supported by the evidence: lobsters appear likely as a key predator on sea urchins" (Breen and Mann 1976b, p. 140). "These . . . factors were explored in a computer model which *verified* that it was reasonable to suppose that urchin populations were controlled by lobsters" (Mann 1981, p. 6). The bias of this approach, and the circularity that it leads to, is also apparent in other papers: "The intention was to *look for* evidence of kelp bed destruction, changes in sea urchin populations and changes in predator populations, *particularly* in stocks of lobsters" (Mann 1982a, pp. 418–419); "We have thus witnessed a change in the whole community, at all trophic levels, *triggered* by removal of a key predator" (p. 421; italics added).

One further remark is needed to show the ambiguous use of hypotheses and experimental results. In 3 of 10 papers in which working hypotheses were appar-

ent, results that did not support the hypothesis were explained away. "The finding that lobsters prefer crabs over urchins raises difficulties in acceptance of the theory . . . that lobsters are the key predators controlling sea urchins in nature. . . . The experiments indicated that the preference of lobsters for crabs is a real one, even if in nature the lobsters do not always have the opportunity to indulge it" (Evans and Mann 1977, p. 2206). "Sea urchin remains were found in only 2% of crab stomachs, and the crabs showed a clear preference of mussels over urchins. . . . We should, however, be cautious about jumping to the conclusion that rock crabs do not play a significant role in controlling urchin populations. . . . The conclusion, then, is that . . . they [lobsters] could be expected to exact a significant predatory control over other invertebrate species, including . . . urchins" (Drummond-Davis et al. 1982, pp. 638–639). Although the contradictory results do not absolutely refute the keystone-predator hypothesis (i.e., lobsters do not have to prefer urchins to all other prey in order to act as a keystone, and, similarly, crabs might still control urchins where mussel prey are rare), they do highlight the need for careful formulation of hypotheses and appropriate experimentation.

The 31 proposed system components, defined as the ecological mechanisms involved in explaining a scenario (in the 23 papers and 1 abstract), are analyzed chronologically in table 2. As system components are introduced with each publication, the cumulative number of components identified grows. However, depending on the frequency with which retractions or omissions occurred, the total number of system components actually invoked in explaining the scenario shows an irregular pattern of peaks and declines. Although the pattern itself is not necessarily unproductive, the changes, as discussed below, are not due to experimentation. Seemingly, the pattern reflects a series of ad hoc reformulations of an early hypothesis that urchin abundance controls production in the nearshore ecosystem.

The following statements are the major components presented in these publications, given chronologically and in the phraseology of the authors: (1) lobster yield depends on seaweed production for food, (2) lobster yield depends on seaweed production for shelter, (3) seaweeds are of trophic value to the nearshore ecosystem, (4) man is important in degrading the system by overfishing lobsters, (5) lobsters are keystone predators, (6) system changes are cyclic phenomena, (7) fish are important urchin predators, (8) lobstering is best in kelp habitats, (9) the system will recover if lobstering is stopped, (10) a management approach is advocated for the total nearshore ecosystem, (11) crabs are important urchin predators, (12) sea urchins are the preferred prey of lobsters, (13) sea stars are important urchin predators, (14) a critical sea urchin density is required for the onset of destructive grazing, (15) sea urchin aggregation leads to destructive grazing, (16) sea urchin-created barrens are irreversible states, (17) predation in general is important to the maintenance of the system, (18) lobsters are important only as complementary predators, (19) kelp removal leads to faunal impoverishment, (20) lobster abundance is under environmental control, (21) drift seaweeds are important in the system, (22) urchins aggregate in given conditions, (23) sea urchins deaggregate in given conditions, (24) a critical sea urchin density is

TABLE 2
CHANGES IN THE PROPOSED SYSTEM COMPONENTS OCCURRING IN THE SUBLITTORAL
OFF NOVA SCOTIA, CANADA

Study and Year ^a	No. of New System Components	No. of Previous System Components Maintained	No. of System Components Omitted or Retracted from Previous Paper	Cumulative No. of Components Identified in System	No. of Active System Components
1. 1971	2	—	—	2	2
2. 1972	5	1	1	7	6
3. 1972	2	4	3	9	6
4. 1973 ^b	0	2	NA	NA	NA
5. 1973	1	4	2	10	5
6. 1976	7	3	4	17	10
7. 1976	3	5	7	20	8
8. 1976	1	5	4	21	6
9. 1977 ^c	0	3	NA	NA	NA
10. 1977	0	9	3	21	8 ^d
11. 1978	1	6	5	22	7
12. 1978 ^e	0	1	NA	NA	NA
13. 1981	3	11	3	25	14
14. 1981	3	15	7	28	18
15. 1981	1	11	12	29	12
16. 1981	0	18	5	29	18
17. 1982	0	10	9	29	10
18. 1982	1	16	4	30	17
19. 1982 ^f	0	2	NA	NA	NA
20. 1982	1	14	7	31	15
21. 1983	0	9	9	31	9
22. 1984	0	7	3	31	7
23. 1985	0	11	2	31	11
24. 1985 ^g	0	5	7	31	5

NOTE.—NA, These papers are not applicable to this analysis.

^a Published studies as in table 1.

^b Energetic study of limited scope and thus not amenable to these analyses.

^c Laboratory feeding study of limited scope and thus not amenable to these analyses.

^d Increases in the number of active system components without the addition of new components reflect the reintroduction of previously dismissed components.

^e Laboratory study of limited scope and thus not amenable to these analyses.

^f Laboratory predation study of limited scope and thus not amenable to these analyses.

^g Abstract and thus not fully amenable to these analyses.

required for the initiation of defensive aggregations against predators, (25) sea urchin behavior varies seasonally, (26) spiral degradation of the ecosystem involves a feedback mechanism, (27) lobster production along eastern Nova Scotia was influenced by the restriction created by the Canso causeway, (28) ecological conditions in Nova Scotia are unique or different from other systems, (29) disease controls sea urchin populations, (30) temperature patterns and changes control the abundance of sea urchins, and (31) an improved theoretical framework is required to understand ecosystem function.

Essentially, this series of publications and the ideas contained therein, to explain the shift from macroalgae to barrens, can be broken into four chronological scenarios (figs. 1–4): (1) a 3–4-yr cycle, catalyzed by lobsters; (2) an irrevers-

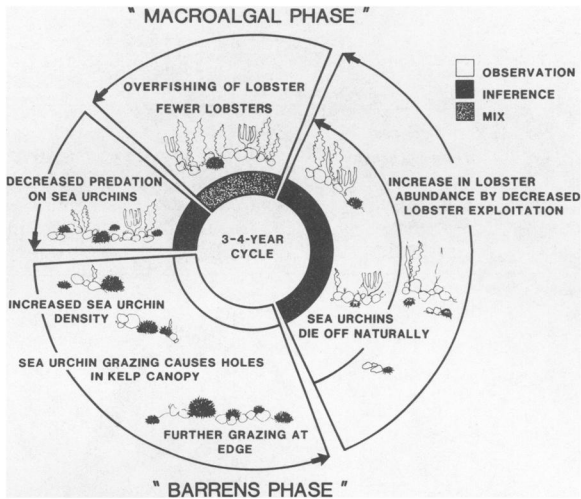


FIG. 1.—Proposed system components during scenario 1 (about 1970–1975) occurring in the sublittoral off Nova Scotia, Canada; 3–4-yr cycle (see the tables) between sea urchin-denuded barrens and macroalgal phases.

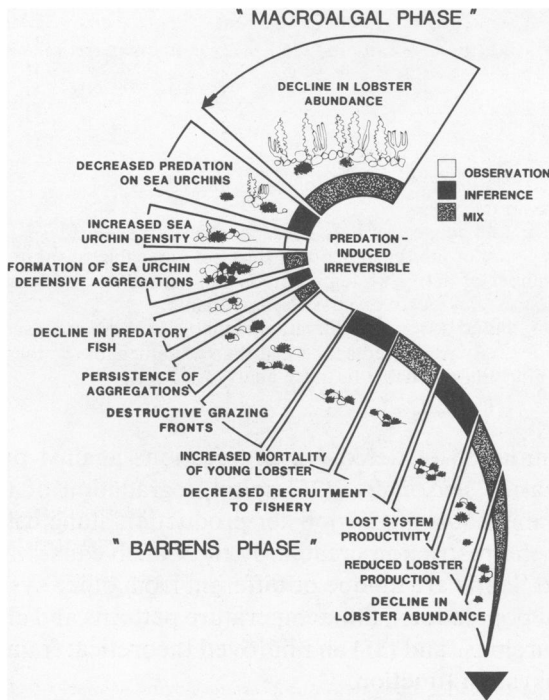


FIG. 2.—Proposed sequence of system components during scenario 2 (about 1975–1978); from macroalgal phase to predation-induced, irreversible-barrens phase (see the tables).

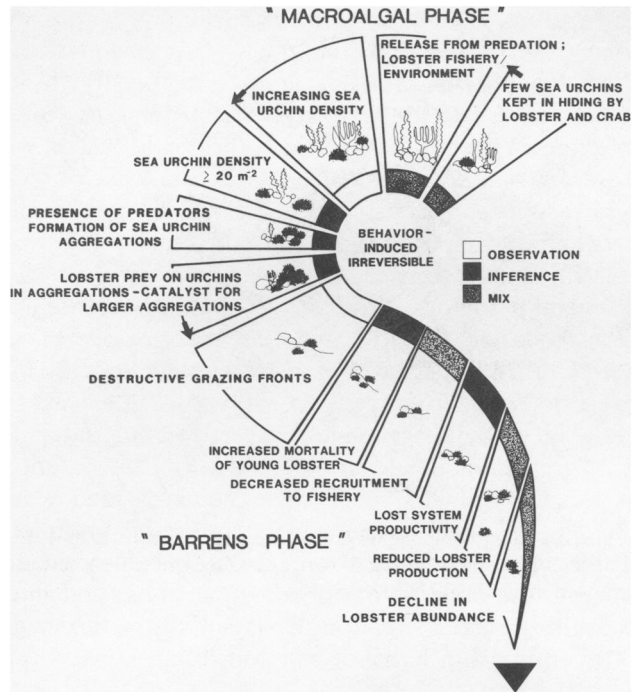


FIG. 3.—Proposed sequence of system components during scenario 3 (about 1978–1983); from macroalgal phase to behaviorally induced, irreversible-barrens phase (see the tables).

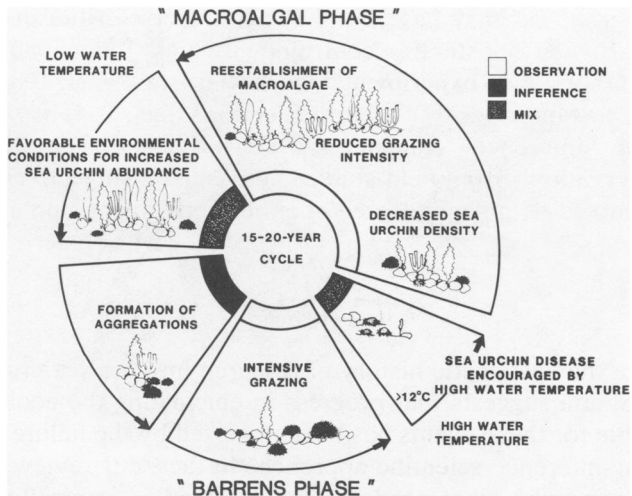


FIG. 4.—Proposed sequence of system components during scenario 4 (1984–?); temperature- and disease-induced 15–20-yr cycle between sea urchin-denuded barrens and macroalgal phases (see the tables).

ible change in the system, catalyzed by the removal of predators; (3) an irreversible change in the system, catalyzed by complex behavioral interactions; and (4) a 10–15-yr cycle, catalyzed by extraneous events. For scenario 1, a simple 3–4-yr cycle was proposed and related to the removal of lobsters, the keystone predator, which kept sea urchins in check. In scenario 2, the whole system was stated to be in a degradative spiral, catalyzed by decreased predation on sea urchins and simple behavioral responses (persistence of defensive aggregations) by sea urchins. The same downward spiral was proposed in scenario 3, but this time the catalyst was determined to be a series of complex behavioral interactions between sea urchins and several predators. Here, the sea urchins increase as a result of the decline in lobster predation, but the subsequent formation of aggregations is reportedly induced by the “presence of predators.” Additionally, the formation of even-larger aggregations is represented as a result of lobsters’ feeding on the smaller defensive aggregations. Clearly, the presence of predators is important to the formation of aggregations in scenarios 2 and 3, but the paradox is that these same predators are supposed to be in lower numbers than when the sea urchin outbreak began. In scenario 4, a sea urchin die-off brought about yet another cycle, but this time of 10–15 yr. Here, sea urchins increase during advantageous (low-temperature?) conditions, form aggregations, and intensively graze kelp beds. The resulting barren situation persists until the next high-temperature (>12°C) period favorable to a lethal sea urchin disease. The cycle then begins anew.

We emphasize that the abandonment of scenarios 1 and 3 by the authors was not caused by testing the system components through experimentation but, rather, by the force of extraneous events. Specifically, the barrens in scenario 1 persisted longer than the postulated 3–4-yr cycle, whereas the shift to scenario 4 was due to the sea urchin die-off. The reason for the change from scenario 2 to 3 is not readily apparent but may have been due to adverse criticism of the role of predators (in particular, lobsters) in controlling urchins (Elnor 1980; Pringle et al. 1982) and the authors’ own experimental work (Bernstein et al. 1983). In general, we note that important aspects of all four scenarios (figs. 1–4) have continued to be based on the “inference” category and are not tested. The other categories comprise “observation” from field studies and “mix,” subjectively assessed as “inference” coupled with some degree of either experimentation and/or “observation.”

DISCUSSION

Our review of the systematic history of research into the sea urchin phenomenon off Nova Scotia suggests that progress in elucidating the ecological mechanisms responsible for these events has been thwarted by the failure to use a more effective, strong-inference scientific approach. In fact, our review, although not excluding the possibility that predation is involved in controlling sea urchin populations, concludes that the evidence to date is not cause to dismiss what should have been the original null hypothesis, “predators have no effect.”

Initially, a single hypothesis that lobsters are a keystone predator was advanced

(Mann and Breen 1972; Breen and Mann 1976*b*) to account for the increased abundance of sea urchins. The original notion, plus various system components, was seductive and remained a virtually unchallenged paradigm until a workshop in 1980 (Pringle et al. 1982) provided a forum in which studies of the lobster–sea urchin interaction were debated. The need for such a workshop was fueled by the purported economic consequences of the barren grounds on valuable lobster-fishery resources.

The establishment of the keystone explanation as a paradigm (a point of view so dominant that it makes other approaches to a discipline appear irrelevant; Strong 1980) without adequate evidence served to divide the scientific community. After the 1980 workshop, researchers formed two camps: proponents of a keystone system versus critics. Proponents continually urged fisheries managers to adopt strategies commensurate with the keystone paradigm (Mann 1981, 1982*a*; Whar-ton and Mann 1981; Bernstein and Mann 1982). Indeed, at one point, when the ecosystem was judged to be in irreversible decline, a proposal was made to destroy urchins over large areas by using quicklime (Bernstein and Welsford 1982). In hindsight, fisheries scientists were critical enough not to accept the nature of the evidence (Pringle et al. 1982) and, by virtue of either their conserva-tive nature or their inertia, were still considering the situation (Pringle 1986) by the time natural events forced a reappraisal of factors controlling the system. Mean-while, the lobster was identified in textbooks (Barnes and Hughes 1982; Mann 1982*b*; Clark 1983; Andrewartha and Birch 1984; Valiela 1984; Warner 1984; Sze 1986), reviews (Hughes 1980; Paine 1980; but see Harrold and Pearse 1988), scientific papers (Duggins 1983*a*; Briscoe and Sebens 1988), and popular articles (Duggins 1983*b*; but see Elner 1983) as a practical example of a keystone predator. Unfortunately, popular thinking is particularly difficult to change because the mechanisms of, and evidence for, scientific interpretations are usually not consid-ered by those outside the debate (Durant et al. 1989).

In review, this literature study highlights four key areas of concern. First, as tables 1 and 2 suggest, testing procedures that gave results contradictory to theory were explained away. The results were argued to have no direct bearing on the “real-world” situation and thereafter ignored. Thus, the original hypothesis was retained (see Evans and Mann 1977 and Drummond-Davis et al. 1982 regarding the impact of lobsters and rock crabs on sea urchins).

Second, system components of the scenarios tended to become ingrained as “truths” by repetition over several publications, obscuring weaknesses in the original evidence. The role of fish as sea urchin predators is a case in point. Corollary evidence between fish abundance, number of urchin aggregations, bro-ken test material, and exposed urchins, together with limited observations from fish guts, was argued by Bernstein et al. (1981) as suggesting that intensive predation from fish, particularly wolffish, might have destroyed sea urchin feeding fronts. Using the same evidence, Mann (1981) stated that wolffish are capable of breaking up aggregations of urchins and, further, that aggregations can persist only if there are insufficient numbers of predatory fish. The importance of fish as sea urchin predators was repeated in subsequent papers. Moreover, the hypothet-ical role of fish predation as a system component was further entrenched;

overfishing of wolffish was invoked as complementary to overfishing of lobsters in being instrumental in the sea urchin population explosion (Wharton and Mann 1981). Clearly, the predatory abilities of fish on sea urchins were never tested; moreover, Miller (1985*a*), in a review of predator–sea urchin interactions, failed to demonstrate the importance of fish, either as predators per se (but see Keats et al. 1986, 1987) or as behavioral “catalysts” for the destruction of aggregations.

Our third concern is that fidelity to the constituent system components appears to have been independent of testing (table 2). Certain components, such as the interactions among lobsters, crabs, and sea urchins, have been maintained throughout the unfolding of the various scenarios. However, others have been modified, perhaps as a result of adverse criticism (Elner 1980; Pringle et al. 1982; Miller 1985*a*). The role of lobsters has ranged from that of a keystone predator, to a complementary predator, to an aggregation catalyst. Similarly, the purported relationship between crabs and sea urchins has been maintained through several forms, whereas markedly contrasting explanations have been provided for the predatory abilities of sea stars. Although actual testing has had various effects on hypotheses, the consequences of extraneous events have been more conclusive. In particular, the hypothesized temporal basis of the macroalgal-barrens phenomenon has varied from a 3–4-yr cycle, soon after intensive grazing was first observed (early 1970s), to an irreversible, barren state a few years later, to a longer, 15–20-yr cycle when macroalgae reestablished (early 1980s, after widespread sea urchin mortality; see the figures). Clearly, there is a dichotomy in logic; modifications as a consequence of experimentation were arbitrary, but extraneous events forced a posteriori changes of the scenarios. Although such nonexperimental evidence can be at least as powerful as experimental data in refuting a hypothesis, the reliance on natural events to compel scenario changes highlights the comparative impotence of the ecological research employed to elucidate the scenarios.

Our fourth concern, as illustrated by tables 1 and 2, is that the evolution of the system components into a burgeoning complex creates problems with plausibility. Rather than being accepted or replaced, the original single hypothesis was doggedly adhered to, manicured, and supplemented (see papers using scenarios 2 and 3). Additionally, problems of logic and inconsistency are apparent in some papers. For example, Breen and Mann (1976*b*) presented evidence for sea urchins’ being the major item in lobster diets, whereas Wharton and Mann (1981) argued that lobsters suffer a reduced food supply on barrens dominated by urchins. Hence, we seriously question the ecological utility of both approaches that lack appropriate tests and the system “models” they create (see also Dayton and Oliver 1980). Hypothesis testing appears to have been abandoned, and any evidence that could not be ignored was incorporated into the system components. The latest scenario of sea urchin control by disease, for example, was induced by increased sea temperature and/or large-scale movements of warm water masses (Scheibling and Stephenson 1984; Jones and Scheibling 1985) but has yet to be tested. In a recent qualitative model of Nova Scotian kelp-bed dynamics, Johnson and Mann (1988) maintained the urchin-disease mechanism for the succession from barren ground to kelp. However, for the switch back to the barrens, they postulated that the

increase in urchin abundance is due to recruiting success and/or decreases in urchin mortality as a result of predator removal.

On a positive note, it appears worthwhile to highlight what is known about the lobster–sea urchin–kelp system in the northwestern Atlantic. The urchin population explosion and resulting events prompted much research, and various ecological techniques were either improved or developed to study the phenomenon (Bernstein and Welsford 1982, 1983; Vadas et al. 1986; Margosian et al. 1987). Documentation of the perturbations of the system over time (Arnold 1976; Chapman 1981; Miller and Colody 1983; Miller 1985*b*; Michaud 1986; Scheibling 1986; Raymond and Scheibling 1987) has resulted in a comprehensive a posteriori appreciation of the ecological events surrounding intensive grazing episodes and the subsequent reestablishment of kelp beds, if not the mechanical “trigger(s)” for the sequences. Furthermore, the core literature has provoked a large body of experimental studies (Himmelman et al. 1983; Jones and Scheibling 1985; Miller 1985*c*; Vadas et al. 1986; Elner and Campbell 1987; Johns and Mann 1987; Mohn and Miller 1987; Johnson and Mann 1988). These workers, while probing specific points from the core, have augmented our knowledge of the system and invoked their own hypotheses (reviews in Miller 1985*a*; Pringle 1986).

Alternative hypotheses proposed with regard to triggers for changes from the macroalgal phase to barrens have advocated factors such as fish (Keats 1986) and, in Pacific waters, sea otters (Estes and Palmisano 1974; Estes et al. 1978) and large-scale episodic recruitment of sea urchins (Foreman 1977; Ebert 1983). The possibility that massive pulses in sea urchin recruitment contribute to the barrens phenomenon has been postulated (Scheibling 1986) but not tested for the northwestern Atlantic. It is noteworthy that the latter scenario does not involve predators at all but, rather, draws on the current ecological paradigm of “supply-side ecology” (Gaines and Roughgarden 1985; Underwood and Fairweather 1989).

CONCLUDING REMARKS

While our review does not resolve the superiority of one philosophical approach to ecology over another, we warn against affirmative studies and the creation or extension of paradigms, both of which appear to have contributed to the confusion in our understanding of the sea urchin phenomenon off Nova Scotia. We strongly subscribe to the approaches advocated by Platt (1964) of testing critical fulcra and Strong (1980) of using multifaceted experiments coupled with strict controls. We believe that sound natural-history observations and possibly long-term data sets (Coull 1985) are prerequisites to an effective generation of hypotheses in community ecology. So-called “natural experiments” (e.g., Schoener and Spiller 1987) can, in our opinion, yield only tentative conclusions and patterns for further testing (see McGuinness 1988). We also prefer long-term experiments to short-term manipulations, the latter of which may provide misleading conclusions (e.g., Jackson and Kaufmann 1987). Our advocacy for a hierarchical framework of approaches in community ecology parallels the earlier calls for procedural rules for studies of competition and coevolution (Connor and Simberloff 1979; Strong et al. 1979; Connell 1980).

In the final analysis, the shrewdness of the scientific community is essential in

directing the progress of science. A high ratio of review to research papers on a particular topic should be regarded as indicative of data starvation and, perhaps, an unconscious need to perpetuate a set of paradigms by repetition (Chamberlin 1897). We think that emphasis on where and how changes are occurring in the unfolding of an ecological scenario is important. Specifically, have the constituent statements or proposed system components been explained through testing, natural events, or appeals to common sense? From an overall picture (such as presented by tables 1 and 2), it becomes apparent (1) whether hypotheses have been advanced and experimentally rejected, (2) what system components have been tested, and (3) whether the fidelity of components has been maintained.

Our review indicates a need for a more critical attitude in ecology and supports Wiens (1981) in his argument for a renewed skepticism in science. We should all learn to be more cautious about accepting asserted statements as facts. We also advocate repeating key manipulative experiments performed by others, as suggested by Connell (1974). Lastly, we advocate that studies be challenged both as entities in themselves and as constituent fragments of the bigger picture. In this way, ecologists should be able to establish the train of truths necessary to unravel the complexities of ecological systems.

SUMMARY

We have reviewed the considerable body of research into the sea urchin phenomenon responsible for the alternation between macroalgal beds and coral-line barrens in the northwestern Atlantic. In doing so, we have identified problems with both the scientific approach and the interpretation of results. Over a period of approximately 20 years, explanations for the phenomenon invoked four separate scenarios, which changed mainly as a consequence of extraneous events rather than experimental testing. Our specific concerns are that results contrary to the keystone-predator paradigm for the American lobster were circumvented, system components of the various scenarios became accepted without testing, and modifications of some components appeared arbitrary. Our review illustrates dilemmas that, we suggest, have hindered ecological progress in general. We argue for a more rigorous experimental approach, based on sound natural-history observations and strong inference. Moreover, we believe that the scientific community needs to be cautious about allowing paradigms to become established without adequate scrutiny.

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