

Echinoids, epizootics and ecological stability in the rocky subtidal off Nova Scotia, Canada

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ABSTRACT: Mass mortalities of *Strongylocentrotus droebachiensis*, attributed to disease, have occurred along the Atlantic coast of Nova Scotia from 1980 to 1982. An amoeboid protist has been tentatively identified as the pathogenic agent. Temperature appears to play an important role in triggering epizootics and determining the extent of mortality. Epizootics have occurred in the autumn of each year during months of record high temperatures. The virtual elimination of echinoids over a large area of coast has enabled regeneration of kelp beds. Disease may play a key role in determining the structure and stability of benthic communities off Nova Scotia and elsewhere by controlling echinoid abundance.

INTRODUCTION

A growing body of empirical observations and theoretical studies indicate that natural communities may have multiple stable states (see reviews by Sutherland, 1974; May, 1977). That is, alternative community structures, exhibiting some degree of stability or persistence, may exist in different places at the same time or in the same place at different times. In rocky subtidal habitats, alternation of fleshy macroalgal communities (kelp beds) and echinoid-dominated coralline algal communities (barren grounds) is mediated by echinoid grazing (see reviews by Lawrence, 1975; Lawrence & Sammarco, 1982). An examination of factors controlling echinoid population dynamics is of primary importance in understanding the dynamics and assessing the stability of these alternative communities.

The transformation of kelp beds to barren grounds may occur due to a reduction in echinoid predators, usually associated with human intervention (Mann, 1977; Simenstad et al., 1978; Duggins, 1980). There is evidence that overfishing of the lobster, *Homarus americanus*, may have resulted in increased densities of the echinoid, *Strongylocentrotus droebachiensis*, and destructive grazing of kelp beds off the coast of Nova Scotia (see reviews by Mann, 1977, 1982; Wharton & Mann, 1981). Recent mass mortalities of *S. droebachiensis* attributed to disease (Miller & Colodey, 1984; Scheibling & Stephenson, 1984) have reversed this process: kelp beds are regenerating in areas where echinoids have died off.

This paper reviews recent studies on the etiology and ecology of the disease of *Strongylocentrotus droebachiensis* and examines the potential regulatory role of disease in determining structure and stability in the rocky subtidal community off Nova Scotia and in other benthic communities dominated by grazing echinoids.

GEOGRAPHIC DISTRIBUTION OF EPIZOOTICS: 1980–1982

Between 1980 and 1982 outbreaks of disease devastated populations of *Strongylocentrotus droebachiensis* along the entire Atlantic coast of Nova Scotia (Fig. 1). Mass mortalities of echinoids first were observed between Halifax Harbour and St. Margaret's

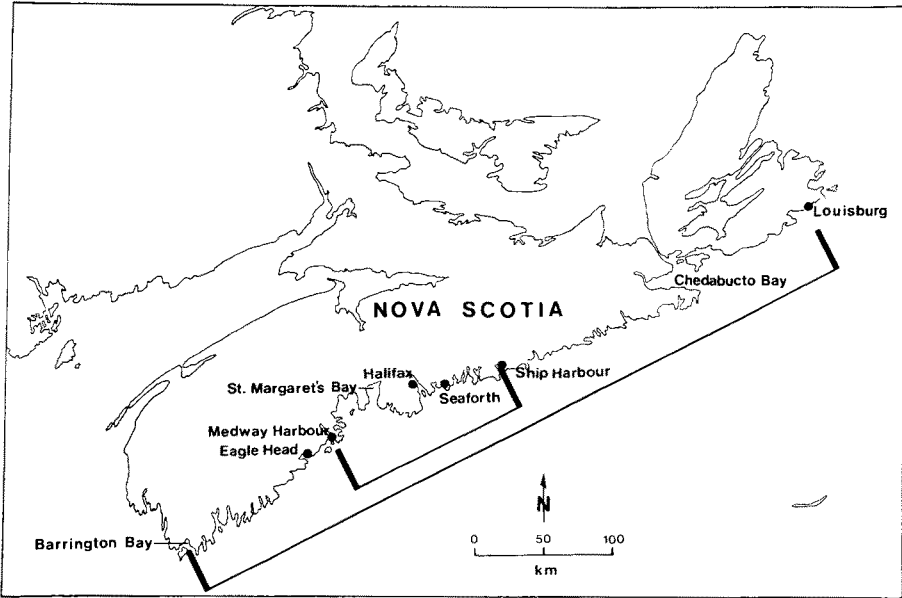


Fig. 1. Map of Nova Scotia showing locations referred to in text. Outer bracket delineates recorded range of mass mortalities of *Strongylocentrotus droebachiensis* from 1980 to 1982. Inner bracket delineates area of heaviest mortality in 1981 (after Miller & Colodey, 1983)

Bay in the autumn of 1980 (Wharton, Biomarine Consulting, Halifax, unpubl. report; Miller & Colodey, 1983). In the autumn of 1981, diving surveys recorded near complete mortality of echinoids between Medway Harbour and Ship Harbour, and aerial surveys of accumulations of echinoid tests on beaches indicated at least partial mortality as far as Louisburg along the northeastern coast (Miller & Colodey, 1983). In the autumn of 1982, diving surveys recorded mass mortalities of echinoids along the southwestern coast from Barrington Bay to Eagle Head (Moore & Miller, unpubl. data; Scheibling & Stephenson, 1984), and aerial surveys indicated further mortalities along the northeastern shore from Seaforth to Chedabucto Bay (Moore & Miller, unpubl. data).

In 1980 and 1982, echinoid mortalities generally were highest in nearshore, shallow (< 5 m) areas (Wharton, unpubl. report; Scheibling & Stephenson, 1984). This may be associated with a higher density of echinoids nearshore (Miller & Colodey, 1983; Scheibling & Stephenson, 1984). In 1981, Miller & Colodey (1983) reported near complete mortality in a variety of rocky habitats from 0–13 m depth. In 1982, diving surveys near the head of Halifax Harbour indicated that echinoids were absent above 25 m but abundant at greater depths (at least to 35 m; Scheibling, unpubl. data).

CHARACTERISTICS OF DISEASE

Overt symptoms of the disease of *Strongylocentrotus droebachiensis* indicate a general loss of peripheral muscular control, including inability to extend tube feet, spines and pedicellaria (tactile stimulation elicits little or no response), and gaping of the peristome and jaws of Aristotle's lantern. This is followed by progressive spine loss and necrosis of the epidermis. In nature, diseased echinoids usually occur aboral-side-down and unattached to the substratum.

Throughout the year, a small proportion (< 5 %) of echinoids have localized necrotic areas of test devoid of spines, pedicellaria and epidermis (Scheibling & Stephenson, 1984). These lesioned areas are darkly pigmented and test plates may be layered and friable. The lesions generally range from a few millimeters to 2 cm in diameter. The remaining area of the test appears normal and the animals can attach to the substratum, feed and right themselves when inverted. Following epizootics, recovering echinoids may have extensive lesioned areas of test. These may represent secondary infections associated with spine loss and abrasion.

Li et al. (1982) found that tissues of diseased *Strongylocentrotus droebachiensis* were heavily infected by an amoeboid protist, tentatively classified as *Labyrinthomyxa* species. They observed edematous lesions and numerous spherical cysts containing amoeboid infective units in both digestive tract and gonadal tissues. High concentrations of coelomocytes were observed in tissues heavily damaged by the infection. Recently, Jones, Hebda & Scheibling (in prep.) found extensive degeneration of muscle and connective tissue of the spine base, tube feet and ampullae of diseased echinoids. They observed amoebae more closely resembling *Paramoeba* in these tissues and within the vascular and coelomic fluids.

THE ROLE OF TEMPERATURE

Mass mortalities of *Strongylocentrotus droebachiensis* occurred each year during a 2–3 month period (between August and November) shortly after the peak (15°–18°C) in the annual cycle of seawater temperature (Miller & Colodey, 1983; Scheibling &

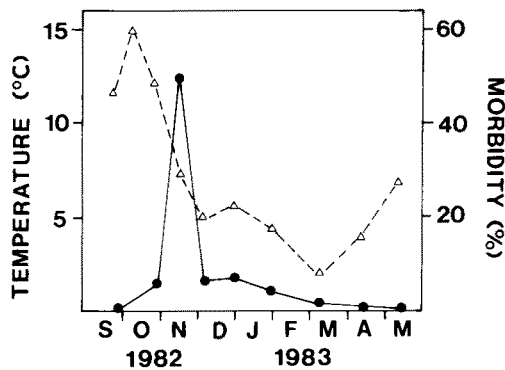


Fig. 2. Bottom temperature (open triangles, dashed lines) and percentage frequency of morbid *Strongylocentrotus droebachiensis* (solid circles, solid line) at Eagle Head Station 1 (after Scheibling & Stephenson, 1984)

Stephenson, 1984; Fig. 2). The transmission and progression of disease is rapid and mortality rate is high at this time (Scheibling & Stephenson, 1984; Fig. 3). As seawater temperature drops, the transmission and/or progression of disease slows; below 10°–12°C it is arrested and affected echinoids may recover. Echinoids in deeper, colder waters may have a temperature refuge from disease.

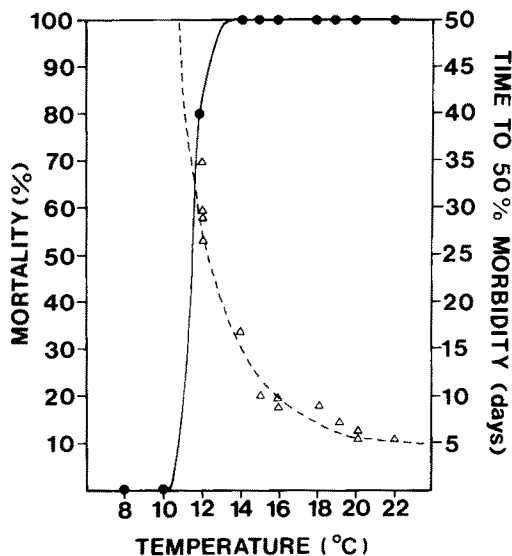


Fig. 3. Percentage mortality (solid circles, solid lines) and median time to morbidity (open triangles, dashed line) for *Strongylocentrotus droebachiensis* exposed to morbid conspecifics as described in Scheibling & Stephenson (1984). No morbidity/mortality occurred in control groups of echinoids exposed to healthy conspecifics

Thermal stress per se does not induce morbidity in *Strongylocentrotus droebachiensis* within its tolerance limits. Echinoids elevated to temperatures of up to 22°C in the laboratory did not develop disease symptoms unless exposed to diseased conspecifics (Fig. 2). Echinoids exhibiting initial symptoms of disease (after exposure to diseased conspecifics at 16°C) recovered when placed in seawater $\leq 8^\circ\text{C}$ (Scheibling & Stephenson, 1984). After 5 months at 5°–10°C, they were elevated to 18°C. Within 1 week, they redeveloped disease symptoms and died (Scheibling, unpubl. data). These results suggest that, once infected, echinoids may harbour a pathogenic agent over winter. High temperatures in summer and autumn may trigger pathogenicity by decreasing echinoid resistance and/or increasing agent virulence. This would result in recurrent epizootics during peak temperatures as long as chronically infected animals remain.

Scheibling & Stephenson (1984) showed that the extent of disease-related mortality in *Strongylocentrotus droebachiensis* between 1980 and 1982 was correlated with the magnitude and duration of temperatures above the lower temperature threshold for transmission and/or progression of the disease. Mass mortalities in these years occurred during months of record-high seawater temperatures (Fig. 4). There is anecdotal evidence that mass mortalities of echinoids occurred ~30 years ago off southwestern Nova

Scotia coincident with a period of high seawater temperatures off the Scotian Shelf (Scheibling & Stephenson, 1984). Recently mass mortalities of the intertidal asteroid *Heliaster kubiniji* in the Gulf of California have been attributed to outbreaks of disease during periods of abnormally high seawater temperatures in the western Pacific (Dungan et al., 1982).

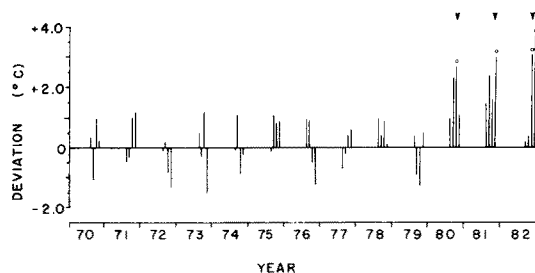


Fig. 4. Deviation of monthly mean sea surface temperatures in Halifax Harbour for August through to November, 1970–1982, from long-term (1926–1967) monthly means. Arrows indicate outbreaks of mass mortality of *Strongylocentrotus droebachiensis*; circles indicate months of record high temperatures (from Scheibling & Stephenson, 1984)

THE IMPACT OF DISEASE ON ECHINOID POPULATIONS

Miller & Colodey (1983) estimated that near complete mortality of *Strongylocentrotus droebachiensis* (> 99% of biomass) exceeded 84,000 t freshweight over 160 km of shoreline in 1981. Scheibling & Stephenson (1984) estimated that 70% mortality of echinoids in a nearshore area in 1982 resulted in a decrease in echinoid biomass of 2 kg fresh weight m^{-2} . They found that mortality was highest in adult echinoids (> 20 cm test diameter) resulting in 73% decrease in the reproductive potential of the population. Differential mortality also caused a shift in the size frequency distribution of the population from unimodal to bimodal (Scheibling & Stephenson, 1984).

Mortality of *Strongylocentrotus droebachiensis* may be directly or indirectly related to disease. Crabs (*Cancer irroratus*, *Carcinus maenas*) and asteroids (*Asterias vulgaris*, *Henricia sanguinolenta*) scavenge morbid echinoids during epizootics. Predation may become an important cause of mortality at temperatures below 10°C when affected echinoids may recover, but remain temporarily debilitated. Laboratory experiments indicate the rock crabs (*Cancer irroratus*) and asteroids (*Asterias vulgaris*), given a choice between healthy and diseased *Strongylocentrotus droebachiensis*, feed almost exclusively on morbid echinoids and at a much higher rate than crabs and asteroids offered only healthy echinoids (Scheibling, in prep.). Feeding experiments using narcotized, healthy echinoids indicate that disease may increase vulnerability to predation by inactivating natural defence mechanisms. Another cause of mortality in diseased echinoids is abrasion and displacement by wave action. Affected echinoids lose all attachment and may be swept across the rocky substratum by wave surge and deposited upon shore.

The pathogen of *Strongylocentrotus droebachiensis* appears to be relatively host specific. There is no evidence that co-occurring echinoderms, including irregular echinoids (*Echinarachnius parma*), ophiuroids (*Amphipholis squamata*) and asteroids

(*Asterias vulgaris*, *Henricia sanguinolenta*) are affected (Wharton unpubl. report; Scheibling & Stephenson, 1984). Asteroids and rock crabs that scavenged morbid urchins in the laboratory showed no ill effects (Scheibling & Stephenson, 1984; Scheibling, in prep.).

THE IMPACT OF DISEASE ON THE ROCKY SUBTIDAL COMMUNITY

Breen & Mann (1976) showed that even low densities of *Strongylocentrotus droebachinesis* could maintain barren grounds by their grazing activity. The virtual elimination of echinoids by epizootics along extensive tracts of coastline has enabled a rapid recolonization of the rocky subtidal by fleshy macroalgae. Luxuriant kelp beds have been re-established in areas around Halifax Harbour and St. Margaret's Bay within 3 years of the echinoid mass mortalities.

These events suggest that disease is a key mechanism underlying large-scale oscillations between the two alternative states of the subtidal system: kelp beds and echinoid-dominated barren grounds (Fig. 5). The periodicity of such oscillations is in the order of decades as indicated by fluctuations in kelp and echinoid biomass in St. Margaret's Bay, Nova Scotia. In the late 1960's, K. H. Mann and colleagues described what appeared to be a stable kelp bed system in the bay (Miller et al., 1971; Mann, 1972a, b). However, in the early 1970's expanding populations of *Strongylocentrotus droebachiensis* formed dense feeding aggregations which destructively grazed the kelp and transformed the rocky subtidal into echinoid-dominated barren grounds. Kelp and other fleshy macroalgae only occurred in certain refuges, such as the wave-battered infralittoral fringe, where echinoids could not graze effectively. In the autumn of 1980, an outbreak of disease markedly reduced echinoid density in parts of the bay. In the autumn of the following year, remaining echinoids were eliminated by a recurrence of the disease, allowing the regeneration of fleshy macroalgae. On the western shore of St. Margaret's Bay, the biomass of regenerating macroalgae 1 year after the elimination of echinoids (1.5 kg fresh weight m⁻²; Chapman, unpubl. data) was 42% of the biomass reported for mature kelp beds prior to destructive grazing (3.6 kg fresh weight m⁻²; Chapman, 1981). There is anecdotal evidence of past fluctuations between kelp beds and echinoid-dominated barren grounds in other areas off the coast of Nova Scotia (Breen, 1980; Pringle et al., 1982; Wharton & Mann, 1981).

A heavy recruitment of juvenile *Strongylocentrotus droebachiensis* occurred along the western shore of St. Margaret's Bay in the summer of 1982. Refuge populations in deeper, colder water may have been a source of planktonic larvae. The average growth of these juveniles was less than 1 cm in their first year (Scheibling, unpubl. data), although growth rate may accelerate with increasing macroalgal biomass and productivity. The growth and survivorship of these and subsequent echinoid cohorts may determine the ecological stability or persistence of the kelp bed configuration in the bay. Predators such as crabs, lobsters and fish may retain echinoid density below a critical level required to initiate destructive grazing (Bernstein et al., 1981). A reduction in predation pressure (e.g. by overfishing) could result in a return to echinoid-dominated barren grounds (Mann, 1977, 1982).

The persistence of echinoid-dominated barren grounds may be dependent on both endogenous and exogenous factors affecting echinoid populations. The nutritional

condition of *Strongylocentrotus droebachiensis* decreases over time on barren grounds in the absence of fleshy macroalgal food resources (Lang & Mann, 1976; Wharton & Mann, 1982; Scheibling & Stephenson, 1984). This may predispose echinoids to parasitic infection. However, Scheibling & Stephenson (1984) found that nutritional condition had little or no effect on the mortality rate of echinoids exposed to diseased conspecifics in the laboratory. A high population density, characteristic of echinoids in barren grounds (Chapman, 1981; Bernstein et al., 1981), also may be a pre-condition for an epizootic. In recent epizootics mortality was highest in areas of high echinoid density (Scheibling & Stephenson, 1984). Given such biotic preconditions, epizootics may be triggered by periods of anomalously high seawater temperature. Thus, the large scale dynamics of the rocky subtidal ecosystem off Nova Scotia result from the complex interplay of echinoids, their prey, predators and parasites (pathogens), and physical factors such as temperature (Fig. 5).

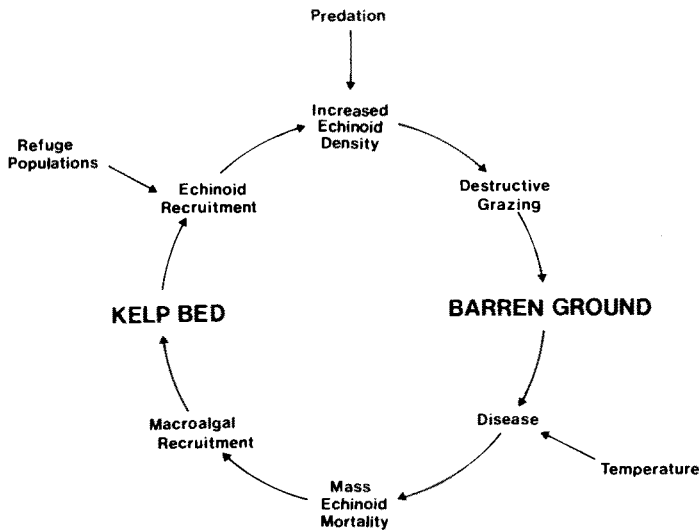


Fig. 5. Hypothetical model of ecological interactions underlying the cyclicity between alternative states (kelp bed and barren ground) of the rocky subtidal community off Nova Scotia. See text for details

Recently, Connell & Sousa (1983) have proposed stringent criteria for assessing stability or persistence of natural populations or communities. The time scale of observations should equal or exceed one complete turnover of individuals; the spatial scale should encompass the minimum area that provides adequate conditions for replacement of individuals. Kelp bed and barren ground communities off Nova Scotia have persisted well beyond the life spans of the respective dominant species: ~ 4 years for *Laminaria longicruris* (Chapman, pers. comm.) and ~ 6 years for *Strongylocentrotus droebachiensis* (Miller & Mann, 1973). At different times or places, these communities have extended along hundreds of kilometers of coastline (Wharton & Mann, 1981). Thus, kelp beds and barren grounds represent relatively persistent and stable alternative states of the subtidal community. Continued observation and experimentation are required to elucidate mechanisms, such as disease, which may destabilize a given state and lead to a transformation of the community.

OUTBREAKS OF DISEASE IN OTHER ECHINOID SPECIES

Localized mass mortalities of *Strongylocentrotus franciscanus* due to disease occurred off California in the summers of 1970 (Johnson, 1971) and 1976 (Pearse et al., 1977). Johnson (1971a, b) described lesions on the test similar to those of *S. droebachiensis*. Pearse & Hines (1979) monitored macroalgal succession and expansion of kelp beds following the 1976 die-off of *S. franciscanus*.

Outbreaks of disease and mass mortalities of *Paracentrotus lividus* were reported at various locations in the western Mediterranean in the summers of 1978 and 1979 (Bourdouresque et al., 1981; Höbaus et al., 1981). Two other echinoids, *Sphaerechninus granularis* and *Arabacia liculua*, also were affected. The symptoms of this disease were similar to those described for *Strongylocentrotus* species, including loss of spines and lesioned test areas. During autumn and winter, morbid echinoids appeared to recover and regenerate lesioned areas. Bourdouresque et al. (1981) report an explosive growth of epiphytes on seagrass due to the decline of *P. lividus*.

Mass mortalities of *Echinocardium cordatum* and *Paracentrotus lividus* off the coast of Ireland in the autumns of 1971 and 1979, respectively were attributed to dinoflagellate blooms (Helm et al., 1974; Cross & Southgate, 1980).

Mass mortalities of the tropical echinoid *Diadema antillarum* recently have occurred on coral reefs off Panama, Columbia, Costa Rica, Jamaica and Florida, (H. Lessios, Smithsonian Tropical Research Institution, Panama, pers. comm.). The die-off appears to be due to disease with symptoms similar to those described for other echinoid species. Co-occurring echinoid species, *Tripneustes ventricosus*, *Echinometra viridis*, *Eucidaris tribuloides*, *Lytechinus williamsi*) are not affected. A rapid growth of benthic algae has occurred on reefs where *Diadema antillarum* has been eliminated.

Although similar overt symptoms of disease have been described for mass mortalities of echinoids in widely separated geographic localities, in no case has a causative agent been conclusively identified. Diseases affecting echinoids have no doubt occurred in the past. The advent of scientific diving in the last few decades has increased the likelihood of detecting and documenting these phenomena. The importance of echinoid grazing in structuring marine benthic communities has been well documented (see reviews by Lawrence 1975; Lawrence & Sammarco, 1982). Mass mortalities of echinoids have a dramatic impact on these communities, as indicated by studies off Nova Scotia and elsewhere. Therefore, disease may play a key role in regulating the structure and stability of echinoid-dominated communities.

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LITERATURE CITED

- Bernstein, B. B., Williams, B. E. & Mann, K. H., 1981. The role of behavioural responses to predators in modifying urchin's (*Strongylocentrotus droebachiensis*) destructive grazing and seasonal foraging patterns. – Mar. Biol. 63, 39–49.
- Bourdouresque, C. F., Nedelec, N. & Shephard, S. A., 1981. The decline of population of the sea urchin *Paracentrotus lividus* in the Bay of Port-Cros (Var, France). – Rapp. P.-v. Réun. Comm. int. Explor. scient. Mer Méditerr. 27, 233–244.

- Breen, P. A., 1980. Relations among lobsters, sea urchins, and kelp in Nova Scotia. – Can. tech. Rep. Fish. aquat. Sci. 954, 24–32.
- Breen, P. A. & Mann, K. H., 1976. Destructive grazing of kelp by sea urchins in eastern Canada. – J. Fish. Res. Bd Can. 33, 1278–1283.
- Chapman, A. R. O., 1981. Stability of sea urchin dominated barren grounds following destructive grazing of kelp in St. Margaret's Bay, Eastern Canada. – Mar. Biol. 62, 307–311.
- Connell, J. H. & Sousa, W. P., 1983. On the evidence needed to judge ecological stability or persistence. – Am. Nat. 121, 789–824.
- Cross, R. F. & Southgate, T., 1980. Mortality of fauna of rocky substrates in southwest Ireland associated with the occurrence of *Gyrodinium aureolum* blooms during autumn 1979. – J. mar. biol. Ass. U. K. 60, 1071–1073.
- Duggins, D. O., 1980. Kelp beds and sea otters: an experimental approach. – Ecology 61, 447–453.
- Dungan, M. L., Miller, R. E. & Thompson, D. A., 1982. Catastrophic decline of a top carnivore in the Gulf of California rocky intertidal zone. – Science, N. Y., 989–991.
- Helm, M. M., Hepper, B. T., Spencer, B. E. & Walne, P. R., 1974. Lugworm mortalities and a bloom of *Gyrodinium aureolum* Hulbert in the eastern Irish Sea, autumn 1971. – J. mar. biol. Ass. U. K. 54, 857–869.
- Höbaus, E., Fenaux, L. & Hignette, M., 1981. Premières observations sur les lésions provoquées par une maladie affectant le test des oursins en Méditerranée occidentale. – Rapp. P.-v. Comm. int. Explor. scient. Mer Méditerran. 27, 221–222.
- Johnson, P. T., 1971a. Studies on unhealthy-appearing urchins from Whites Point. – A. Rep. Calif. Inst. Tech. Pasadena 1970–1971, 55–69.
- Johnson, P. T., 1971b. Studies on diseased urchins from Point Loma. – A. Rep. Calif. Inst. Tech., Pasadena 1970–1971, 82–90.
- Lang, C. & Mann, K. H., 1976. Changes in sea urchin populations after the destruction of kelp beds. – Mar. Biol. 36, 321–326.
- Lawrence, J. M., 1975. On the relationship between marine plants and sea urchins. – Oceanogr. mar. Biol. 13, 213–286.
- Lawrence, J. M. & Sammarco, P. W., 1982. Effects of feeding on the environment: Echinoidea. In: Echinoderm nutrition. Ed. by M. Jangoux & J. M. Lawrence. Balkema, Rotterdam, 499–519.
- Li, M. F., Cornick, J. W. & Miller, R. J., 1982. Studies of recent mortalities of the sea urchin *Strongylocentrotus droebachiensis* in Nova Scotia. – C.M./ICES, L 46.
- Mann, K. H., 1972a. Ecological energetics at the seaweed zone in a marine bay on the Atlantic Coast of Canada. I. Zonation and biomass of seaweeds. – Mar. Biol. 12, 1–10.
- Mann, K. H., 1972b. Ecological energetics of the seaweed zone in a marine bay on the Atlantic Coast of Canada. II. Productivity of the seaweeds. – Mar. Biol. 14, 199–209.
- Mann, K. H., 1977. Destruction of kelp-beds by sea urchins: a cyclical phenomenon or irreversible degradation. – Helgoländer wiss. Meeresunters. 30, 455–467.
- Mann, K. H., 1982. Kelp, sea urchins and predators: a review of strong interactions in rocky ecosystems of eastern Canada, 1970–1980. – Neth. J. Sea Res. 16, 414–423.
- May, R. M., 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. – Nature, Lond. 269, 471–477.
- Miller, R. J. & Colodey, A. G., 1983. Widespread mass mortalities of the green sea urchin in Nova Scotia, Canada. – Mar. Biol. 73, 263–267.
- Miller, R. J. & Mann, K. H., 1973. Ecological energetics of the seaweed zone in a marine bay on the Atlantic coast of Canada. III. Energy transformations by sea urchins. – Mar. Biol. 18, 99–114.
- Miller, R. J., Mann, K. H. & Scarratt, D. J., 1971. Production potential of a seaweed-loster community in eastern Canada. – J. Fish. Res. Bd Can. 28, 1733–1738.
- Pearse, J. S., Costa, D. P., Yellin, M. B. & Agegian, C. R., 1977. Localized mass mortality of red sea urchin, *Strongylocentrotus franciscanus*, near Santa Cruz, California. – Fish. Bull. U. S. 75, 645–648.
- Pearse, J. S. & Hines, A. H., 1979. Expansion of a central California kelp forest following the mass mortality of sea urchins. – Mar. Biol. 51, 83–91.
- Pringle, J. D., Sharp, G. J. & Caddy, J. F., 1982. Interactions in kelp bed ecosystems in the northwest Atlantic: review of a workshop. – Can. spec. Publ. Fish. aquat. Sci. 59, 108–115.

- Scheibling, R. E. & Stephenson, R. L., 1984. Mass mortality of *Strongylocentrotus droebachiensis* (Echinodermata: Echinoidea) off Nova Scotia, Canada. – *Mar. Biol.* **78**, 153–164.
- Simenstad, C. A., Estes, J. A. & Kenyon, K. W., 1978. Aleuts, sea otters and alternate stable state communities. – *Science*, N. Y. **200**, 403–411.
- Sutherland, J. P., 1974. Multiple state points in natural communities. – *Am. Nat.* **108**, 859–873.
- Wharton, W. G. & Mann, K. H., 1981. Relationship between destructive grazing by the sea urchin, *Strongylocentrotus droebachiensis*, and the abundance of American lobster, *Homarus americanus*, on the Atlantic Coast of Nova Scotia. – *Can. J. Fish. aquat. Sci.* **38**, 1339–1349.