

CLIMATE AND BIOGEOGRAPHY : CONTINUOUS VERSUS CATASTROPHIC EFFECTS ON ROCKY INTERTIDAL COMMUNITIES

CLIMA Y BIOGEOGRAFIA : EFECTOS CONTINUOS VERSUS EFECTOS CATASTROFICOS SOBRE COMUNIDADES INTERMAREALES ROCOSAS

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One of the goals of ecology is to understand the mechanisms that determine the patterns of distribution and abundance of organisms. The rocky intertidal zone, with its striking patterns of zonation of species on elevational gradients, has served as a model system for the experimental analysis of the mechanisms controlling local distribution and abundance. It is also amenable to the study of controls on geographic distributions on latitudinal gradients. The controls on both local and geographic distribution can be the result of processes that operate at relatively constant intensity from year to year or catastrophic events interspersed with relatively benign conditions. In this paper I will use examples of both kinds of processes to examine local and geographic distribution of species.

In the development of our understanding of rocky shore communities, we have largely abandoned the simplistic view that local upper and lower shore limits are set entirely by physical factors (upper shore limits by intolerance of heat/desiccation, and lower shore limits by intolerance of submersion) (e.g. Colman, 1933; Doty, 1946). Based on studies of a wide variety of shores it is generally true that local upper shore limits are set by physical factors like heat and desiccation (e.g. Foster, 1971), or by lack of larval settlement (e.g. Connell, 1961), and local lower shore limits are often set by biotic interactions (predation/competition/disturbance) (e.g. Connell, 1961; Paine, 1974; Menge, 1976). Studies of biogeography have followed the same intellectual path as those of local zonation.

The simplistic view that intolerance of cold or heat determines northern or southern limits of geographic distribution (e.g. Hutchins, 1947)

has been questioned because geographic ranges of species are often much narrower than would be predicted by temperature studies in the lab (e.g. Barnes, 1958). It seems reasonable to expect that some geographic distributional limits may be set by biotic interactions in much the same way as local upper and lower shore limits in the intertidal zone (Wethey, 1983).

In this paper I examine three examples of the inter-relationships of physical stress and biotic interactions which have implications for the study of rocky shores on both large and small spatial and temporal scales. I restrict myself to two kinds of processes.

1. Those that are predictable and hence have easily documented effects which repeat in most years.
2. Those which are unpredictable, but which have catastrophic effects and a good historical record of occurrence.

The reason for restricting the discussion to these kinds of processes is that they can be more effectively modelled than events for which there is no historical record (catastrophic competitive or predatory events). Modelling can be used to examine the sensitivity of population growth and interspecific interactions to different frequencies and intensities of meteorological events. The examples that I have chosen are the following :

1. Solar radiation stress and its influence on local zonation and geographic limits of species.
2. Large scale meteorological events and their catastrophic effects on intertidal habitats.
 1. Sea ice in cold winters.
 2. El Niño.

KEY WORDS : Experimental ecology, competition, catastrophic and natural events.

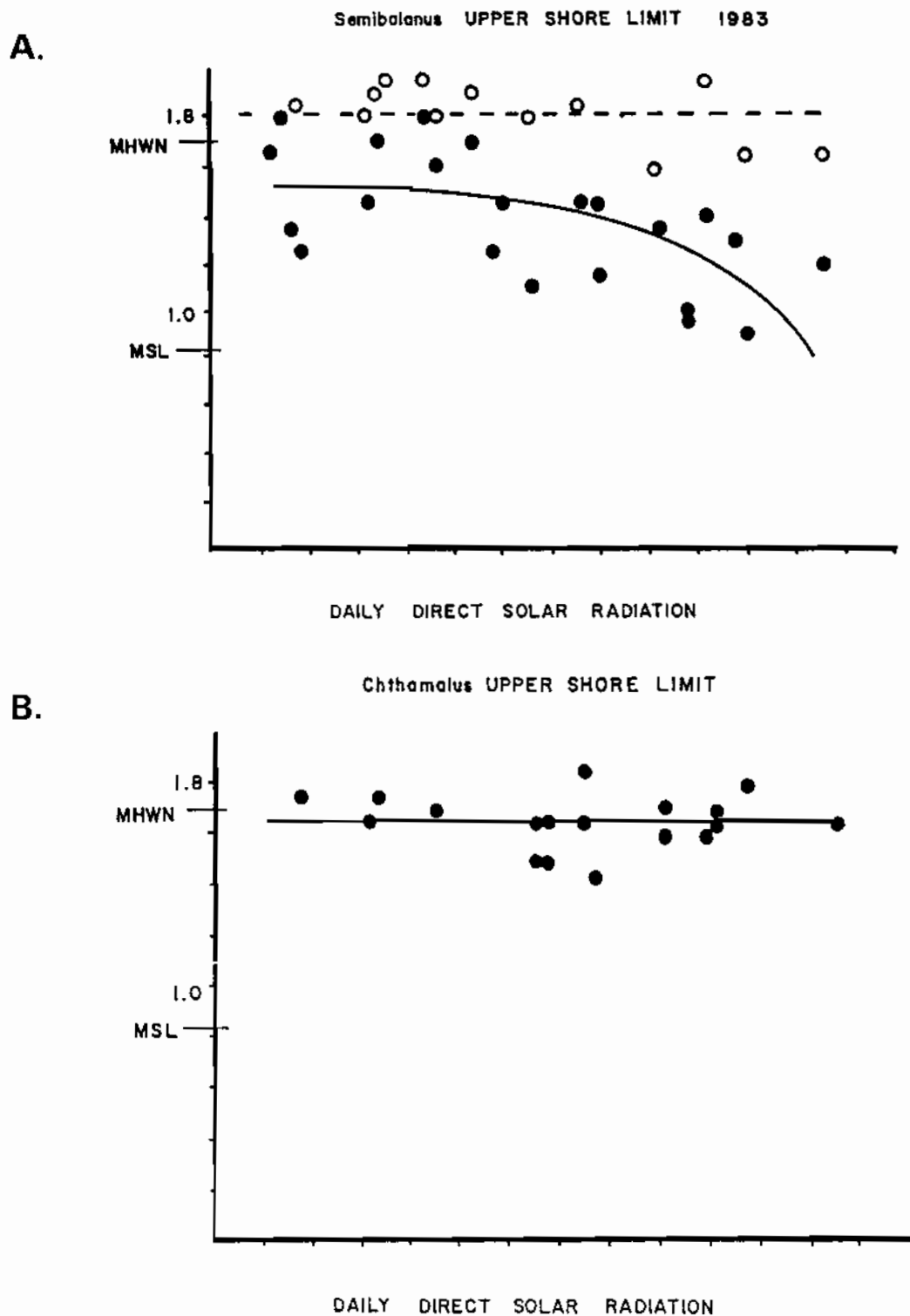


FIGURE 1. Upper shore limits of the barnacles *Semibalanus* and *Chthamalus* as a function of relative daily solar radiation impinging on their rock surface in mid summer. Open symbols represent the distribution of larval settlement, solid symbols represent the distribution of dense 1 year old populations. MHWN = mean high water of neap tides, MTL = mean tide level, MLWN = mean low water of neap tides.

SOLAR RADIATION STRESS

The barnacles *Semibalanus balanoides* and *Chthamalus fragilis* in the USA or *C. stellatus* and *C. montanui* in Europe provide a good example of the interplay between heat and desiccation stress and the intensity of biotic interactions. *Semibalanus* is the dominant competitor in the system and can kill *Chthamalus* in a variety of ways including crushing, undercutting, overgrowing and smothering (Connell, 1961; Wethey, 1984). In the absence of *Semibalanus*, *Chthamalus* can live at all intertidal shore levels (Connell, 1961), as well as subtidally (Barnes 1956), so the local lower shore limit of *Chthamalus* is not set by intolerance of submersion. The zonation of *Semibalanus* and *Chthamalus* changes latitudinally. Near the polar limit of *Chthamalus* in Scotland or New England, it generally occupies a narrow zone at high shore levels near mean high water of neap tides (Connell, 1961; Wethey, 1983). Below it there is close to 100% cover of *Semibalanus* (Connell, 1961; Wethey, 1983).

On a local scale, the zonation changes as a function of slope and aspect of the shore. On vertical surfaces, the *Chthamalus* zone is narrow; it is wider on equator-facing than pole-facing surfaces, and much wider on gentle slopes or horizontals (Wethey, 1983). This implies a relation between solar radiation intensity and zonation, because pole-facing surfaces receive less daily sunlight than equator-facing surfaces. By knowing the track of the sun through the sky on a midsummer day, one can calculate the relative daily direct solar radiation on surfaces of known slope and aspect (Gates, 1978). The larvae of both species settle up to mean high water of neap tides (Figure 1), independent of the direct solar radiation received by the surface. There is a significant depression in the upper shore limit of adult *Semibalanus* as daily direct solar radiation increases (Figure 1 A). There is no such effect on *Chthamalus* (Figure 1 B). *Semibalanus* survival is therefore strongly affected by heat and desiccation, which are correlated with daily direct solar radiation, whereas *Chthamalus* survival is not. This is consistent with the physiological tolerance measures made by Foster (1971). Thus *Chthamalus* has a refuge from competition in sunny locations where *Semibalanus* cannot survive the heat and desiccation (e.g. Connell,

1961; Wethey, 1983, 1984). The refuge can be eradicated by placing an opaque plastic roof over a section of shore, providing a small area of shade where *Semibalanus* survives and competitively reduces *Chthamalus* survival; under a clear plastic roof *Semibalanus* dies and *Chthamalus* persists (Wethey, 1984).

On a geographic scale, the relative size of the refuge from competition for *Chthamalus* changes. In more polar locations beyond the geographic limit of *Chthamalus* (northern Massachusetts), *Semibalanus* does not die back in summer on the high shore, so there is no refuge from competition for *Chthamalus*. The shift in zonation between the more tropical pattern of a high shore refuge from competition to the more arctic pattern of no high shore refuge happens over a 3 kilometer section of the Cape Cod Canal in Massachusetts. At the northern end of the Canal, the water is 5 °C colder than at the southern end. Two road bridges, both constructed at the same time of the same granite blocks, spaced 3 kilometers apart, show the two zonation patterns. On both bridges, the upper shore limit of *Chthamalus* is near mean high water of neap tides (Figure 2). On the northern bridge, *Semibalanus* occupies nearly 100% of the space below mean high water of neap tides, whereas on the

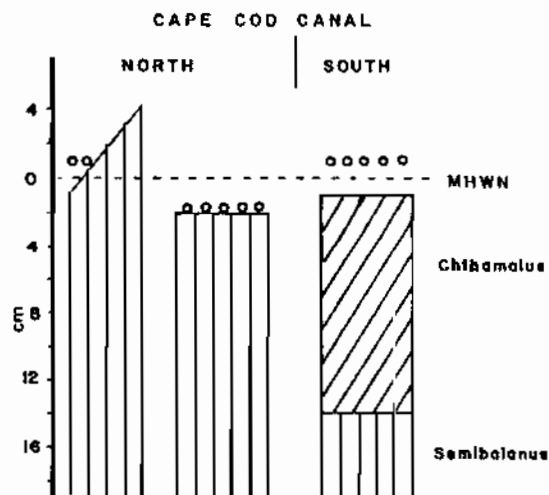


FIGURE 2. Zonation of *Semibalanus* and *Chthamalus* on similarly oriented surfaces on granite piers of bridges on the Cape Cod Canal. The two bridges are approximately 3 km apart. The open symbols represent the upper shore limit of scattered *Chthamalus*. The scale on the elevations relative to MHWN is in centimeters. Areas marked with vertical shading represent *Semibalanus*, areas shaded with diagonal lines represent *Chthamalus*.

southern bridge it is sparse down to 14 cm below mean high water of neap tides. In the zone above *Semibalanus*, *Chthamalus* is abundant on the southern (warmer) bridge, where it has a refuge from competition. On the northern (colder) bridge, the refuge has disappeared, and there are perhaps no more than 50 individuals of *Chthamalus* on the entire bridge, compared to tens of thousands on the other bridge. The reason for the abrupt shift over 3 kilometers of waterway probably lies in the pattern of flow of water through the canal. The tides are at different times of day on opposite sides of Cape Cod, so water flows back and forth through the canal. Because of the water temperature difference at the two ends of the canal, the northern bridge is exposed to cold water for more of the day than the southern bridge, so its equilibrium temperature is probably lower. After a few hours of heating in the sun, it will reach a lower temperature than the southern bridge which starts out hotter. Thus barnacles living on the piers of the two bridges are likely to be exposed to different thermal regimes. Even on surfaces that face in the same direction. One would expect, based on these observations that at lower latitudes, the refuge of *Chthamalus* from competition would enlarge as *Semibalanus* becomes more and more stressed by the heat. In localities at lower latitudes, *Chthamalus* occupies most of the intertidal zone (Southward and Crisp, 1954; Barnes, 1958, personal observation) and *Semibalanus* is sparse or rare.

In summary, the example I have discussed provides a good demonstration of the principle that biotic interactions, whose intensity is mediated by latitudinally varying environmental stress, may be responsible for setting geographic limits of species. In this particular example, on both sides of the north Atlantic, the high latitude limit of distribution of a tropical species is set not by intolerance of cold, but rather by the intolerance of heat by its arctic competitor. Beyond the high latitude limit of *Chthamalus*, it has no refuge from competition on the high shore, because its competitor *Semibalanus* settles and survives over the whole shore. At lower latitudes, *Chthamalus* has a refuge from competition in areas where *Semibalanus* cannot survive the heat. Thus the same processes that determine local zonation also are responsible for setting geographic limits in this example.

LARGE SCALE METEOROLOGICAL EVENTS : SEA ICE

The depauperate nature of the intertidal fauna on the east coasts of continents compared to west coasts of continents in the North Atlantic and North Pacific oceans provides an example of the potential effects of catastrophic events on communities. In many parts of the world there are abundant, large, long-lived sessile species that live primarily on the low shore, and which do not reproduce in their first year. Examples are the barnacle *Semibalanus cariosus*, the mussel *Mytilus californianus* and the anemone *Anthopleura xanthogrammica* on the North American Pacific coast. Species of this type are missing from the North American Atlantic coast and from the Pacific coast of Siberia (Gosner, 1971; Zenkevitch, 1963).

The barnacle *Semibalanus balanoides* is a common inhabitant of the north Atlantic and Pacific intertidal zones, where it lives at all shore levels at high latitudes. In New England on the Atlantic coast, its survival is influenced by biotic processes like predation by gastropods, competition with mussels (Menge, 1976), and physical habitat destruction as a result of scouring by sea ice in cold winters (Wethey, 1985). Sea ice reduced survival to less than 1% of the normal value on the mid shore in wave exposed locations. The shore was essentially denuded, except for a narrow band near mean high water of neap tides (Wethey, 1985). The cause was a band of floating ice 10 m wide which scraped the shore as the tide came in and out.

Because there are good records of weather and climate for New England back to the 1620's, it was possible to model the effect of sea ice on this intertidal system using 300 years of weather data. The historical records and winter temperatures indicated that between 1620 and 1780 the frequency of ice winters was 20%, between 1780 and 1880 the frequency was 45% and since 1880 it has dropped once again to 20%. The "little ice age" climatic minimum was responsible for the period of maximum ice disturbance. By knowing the mortality and fecundity patterns of populations in years with and without ice, it is possible to construct a population projection model in which populations are exposed to historical or hypothetical sequences of

years with and without ice. It is also possible to model the effects of habitat specificity, and life history characteristics like age at first reproduction on population growth or decline. The simplest sort of model uses the projection techniques of Leslie (1945), in which the age-specific fecundity and survival values are placed in a matrix, which is used to multiply a vector of numbers of individuals in each age class, in order to calculate the age distribution of the population at some future date. By choosing one of several alternative projection matrices (corresponding to years with or without ice, and to specific habitats) at each iteration of the model, one can explicitly examine the effects of environmental fluctuations on population survival or extinction (Wethey, 1985). By replacing empirically measured survival and fecundity distributions with hypothetical ones, one can examine the implications of changes in age at first reproduction on extinction probability. By varying the dispersal of larvae from one habitat or shore level to another, one can model the implications of specialization on a specific habitat (like the mid shore) on extinction.

Habitat generalists, which are reproductively mature in their first year can invade and persist in a habitat with the kind of disturbance rates experienced in New England over the past 300 years. Specialists on the mid shore are much more likely to become extinct under these kinds of conditions, especially if they exhibit delayed reproduction (Wethey, 1985). With repeated destruction of shore populations in 45 % of the winters, few recruits would ever become sexually mature before the next ice scouring event. Thus invasion or persistence of large, long lived mid intertidal specialists with delayed reproduction is unlikely. The geographic boundaries of *Semibalanus cariosus* in the North Pacific are suggestive of this mechanism. The species is known in Northern Japan and in the Commander Islands, neither of which are heavily iced, but is absent from the ice-dominated shores of the sea of Okhotsk (Zenkevitch, 1963). In Alaska, *S. cariosus* is common only in areas which are not heavily scoured (O'Clair *et al.* 1979).

In summary, climatic events like cold winters, which may happen only 20 % of the time, may have lasting effects on the species richness of some habitats, as a result of extinction events.

Thus the climatic events may control the membership in the species pool of a geographic region. It is very important to distinguish this process which can determine the upper bounds to species richness in a region, from the processes which determine local distribution and abundance. In ice-free years, similar processes control distribution and abundance of species found on both sides of the Atlantic. In cold winters, catastrophic habitat destruction occurs in New England but not in Europe. The catastrophic events may ultimately be responsible for the depauperate fauna and flora of New England and Siberia, by limiting membership in the species pool.

LARGE SCALE METEOROLOGICAL EVENTS : EL NIÑO

The large scale changes in ocean surface temperature and productivity that constitute El Niño events result in large reductions in populations of plankton, fish, seabirds and other organisms in the eastern tropical Pacific (e.g. Barber and Chavez, 1983). Depending upon the importance of particular trophic groups to the control of local distribution and abundance of shore faunas and floras, these events could have strong impacts on patterns of distribution and abundance of sessile organisms. Such effects can be documented in terms of changes in age-specific survival and fecundity distributions, so that projection models like those discussed in the sea ice example can be applied. As in the case of sea ice, it is possible to reconstruct the past history of such events. There are moderately complete historical records back to 1780 (Quinn *et al.* 1978), indicating that these events have occurred in 20 % of the years since 1880 and in 16 % of the years before that time. The strongest events are generally separated by at least 7 years, so long term data are necessary for reconstruction of community changes, or alternatively simulations can be based on data collected during "severe" versus "mild" conditions. By examining the geographic extent of the effects of severe El Niño events on survival and fecundity patterns, it should be possible to estimate their importance in limiting membership in the species pool in the eastern Pacific coastal zone.

SUMMARY

The patterns of distribution and abundance of organisms on intertidal shores can be strongly influenced by the interplay between biotic and physical factors. Not only are local zonation patterns affected, but also geographic and temporal distributions. Thus high summer temperatures for example influence the spatial distribution of refuges from competition (and perhaps also predation), on both local and geographic scales, setting local elevational limits and geographic distributional limits in the case of *Chthamalus* in New England. The effects of catastrophic events are somewhat different: they are likely to limit membership in the overall species pool of an area. Thus a whole group of sessile species with delayed reproduction, which specialize on the mid intertidal zone have perhaps been excluded from the Siberian and eastern North American coasts by the catastrophic scouring by ice in cold winters. Large scale climatic effects, represented by both the mean and the variance of the processes, may thus affect the local and geographic distribution of organisms, on the one hand by modulating biotic interactions, and on the other hand by restricting the cast of characters which interact.

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