THE EFFECTS OF CLIMATE ON TERRESTRIAL AND MARINE POPULATIONS

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ABSTRACT

Climate impacts all biological systems. Human culture and health have been related to climatological variables.

Terrestrial biological populations are regulated by both intrinsic (e.g. genetics, physiology, behavior) and extrinsic (e.g. climate, predators, competitors, parasites, food, shelter) agents. Climate appears to be a major extrinsic regulatory agent for some organisms, most notably the more *r*-selected ones. Random meteorological events are reflected in environmental and population variability and instability. In some cases, it may be that regularly recurrent climatic patterns generate cyclic biological fluctuations.

The variability associated with marine populations in the California Current system is largely due to climatic fluctuation. The interplay of short (upwelling) and longer term (water mass influx) changes in the physical environment have been shown to regulate diatom blooms. In most cases, however, the mechanisms involved in climatic-biological interaction are not yet clear.

RESUMEN

El clima afecta todos los sistemas biológicos. La cultura humana y la salud han estado relacionadas con variables climatológicas.

Las poblaciones biológicas terrestres están reguladas por agentes intrínsecos (p. ej., genética, fisiología, conducta) y extrínsecos (p. ej., clima, predadores, competidores, parásitos, alimento, habitición). El clima parece ser un agente regulatorio extrínseco de mayor importancia para algunos organismos, notablemente para los más *r*-selectos. Acontecimientos meteorológicos del azar se reflejan en la variabilidad e inestabilidad del medio ambiente y las poblaciones. En algunos casos, puede ser que patrones climáticos que regularmente se repiten generen fluctuaciones biológicas cíclicas.

La variabilidad asociada con poblaciones marinas en el sistema de la Corriente de California se debe principalmente a la fluctuación climática. Se ha mostrado que el juego entre los cambios de períodos cortos (surgencias) y más largos (influencia de las masas de agua) en el ambiente físico rige los florecimientos de diatomeas. Sin embargo, en la mayoría de los casos, los mecanismos que intervienen en las interacciones climáticas y biológicas aún no están definidos.

INTRODUCTION

Environment is the setting in which an organism lives and functions. One may safely assume then that changes in the environment affect the resident biota. Considering that climatic change alters both terrestrial and marine environments, one can then state that climatic change will impact the biological community. It is difficult not to accept this point of view. Nevertheless, the effects of climatic change on biological populations have been one of the most controversial subjects in the history of science. The major part of this controversy has not been whether climatic change affects organisms, but rather how important those effects are in regulating the distribution and abundance of organisms comprising a population. In this paper, we review literature dealing with this subject. The extensive literature precludes a comprehensive review but allows for flexibility in approach.

The study of climate's impact on biological systems requires an interdisciplinary approach, integrating biological and meteorological time series of sufficient length and regularity as to yield significant results. Partly because of this constraint, most research effort has been directed toward terrestrial populations where time series are more readily available.

TERRESTRIAL STUDIES

Man

The preoccupation with climate-induced changes on human populations reaches back to early stages of human culture. Hippocrates in "Airs, Waters, Places" made an elaborate attempt to explain cultural differences between various races and nations (Greeks, Scythians, Egyptians, etc.) on the basis of different climatic regions. One of the most influential and lasting contentions of Hippocrates was that diseases were caused not by divine forces, but by atmosphere, waters, and places. As has been pointed out by Glacken (1973), by the time Huntington's "Main Springs of Civilizations" appeared in 1945, investigators of various disciplines had discussed the relation of environment—particularly climate—to health and disease, diet, creativity, labor efficiency, mental diseases, genius and intelligence, race, social and political organization, national character, and the suitability of the tropics to white settlement.

Because of direct relevance and potential beneficial application, there has been considerable effort to elucidate the functional role of climate in relation to human health. For instance, Sulman (1976) discusses the role of weather in producing hormonal change, psychic reactions, and ailments. He claims that the positive electric field, which surrounds living organisms, interacts with the strong negative field on Earth to cause headaches, eye flickering, and other disturbances. He suggests that neurohormonal changes in the blood may account for psychological depression of populations in northern countries which experience long, cold, gloomy winters.

Climatological variables, such as electromagnetic waves, barometric air pressure, temperature, and oxidative potential, have been related by Petersen (1947) to mortality, disease, and blood pH. He emphasizes Aristotle's concept of Man as a cosmic resonator, relating solar (sunspot cycle) and lunar rhythms to human health. In another article, Petersen (1940) concludes, "It is very likely that many as yet unexplainable observations in the biological literature will become understandable when once the major changes in the meteorological environment of the time are taken into consideration."

Climate and Other Terrestrial Organisms

Factors that regulate the number of organisms in a given population have been of great interest to population biologists. According to Krebs (1972), prior to 1950 three schools of thought predominated, which stressed extrinsic factors as regulatory agents: the "climate," the "biotic," and the "comprehensive" schools. Later, another theory evolved, emphasizing intrinsic regulatory factors. This "self-regulation" school (Chitty 1960) developed theories based on genetics (Pimentel 1968) and behavior (Wynne-Edwards 1965).

The concepts of density dependence and density independence were introduced by Smith (1935). These terms, interlaced among the various theories on population regulation, are discussed in detail by Solomon (1958). Smith (1935) stated that density-dependent factors are mainly biotic (e.g. competition, predation), whereas density-independent factors are mainly abiotic (e.g. climate). The biotic school views climate as operating density independently, thus claiming that climate cannot function as a regulatory mechanism per se.

In opposition to this view, Andrewartha and Birch (1954) maintain that weather can operate density dependently in some cases. They believed that density-independent factors, in a strict sense, do not exist. Klomp (1962) concluded that if weather operates density independently, it alone cannot regulate animal numbers. However, in conjunction with density-dependent factors, such as limited shelter or a density-related genetic change, weather may serve as a regulatory agent.

Environmental and biological systems exhibit a high degree of natural variability. Solomon (1949) reviews theories attempting to explain periodic fluctuation, based on overpopulation, predator-prey relationships, and meteorology. Palmgren (1949) suggested that population cycles may be regarded as random fluctuations with serial correlation between populations of successive years (autoregression). This interpretation has been both supported (e.g. Cole 1954) and refuted (e.g. Keith 1963). Overall, this theory has proved invaluable, since it has prompted critical reinspection of data series that had previously been regarded as cyclic. Furthermore, it has shown the value of a stochastic approach to understanding biological systems.

Slobodkin (1961) notes that because population numbers can be assessed only theoretically, the reality of oscillations must be interpreted in this context. The appearance of cycles may be attributed to data smoothing or unreliable census counts. Slobodkin concludes, moreover, that population fluctuations are intrinsically regulated and do not necessarily reflect a one-to-one correspondence with environmental fluctuations.

From an evolutionary standpoint, several theories have been formulated to explain biological-environmental interaction. Using the theory of r- and K-selection (MacArthur and Wilson 1967), based on population levels in relation to the carrying capacity of their environment, Pianka (1970) presents the following correlates: 1) r-selection with variable or unpredictable climate, density-independent mortality, and unstable population size; 2) K-selection with constant or predictable climate, density-dependent mortality, and stable population size. Pianka (1970) suggests that insects, for example, are more r-selected, whereas terrestrial vertebrates are more K-selected.

Prior to 1930, population studies dealt mainly with insects. The study of other invertebrate, vertebrate, and plant populations had scarcely begun. Experimentally, the impact of the physical environment on insect populations has been demonstrated (e.g. Gause 1932). In the field, it has been shown that the distributional range of some insect populations is controlled by climate (e.g. Morris 1963).

One way to examine the effect of climate on higher vertebrate species is to focus on a classic example from the literature that deals with fluctuations of northern wildlife populations. Keith (1963) reviews these fluctuations. Most of this literature concerns the 3-4-year (e.g.Pitelka 1958) and the 9-10-year (e.g. Elton and Nicholson 1942) cycles with mammal and bird populations in northern latitudes.

Elton (1924) speculated on astronomical and geophysical causes of these animal fluctuations. He suggested that sunspots, lunar tides, and volcanoes may indirectly generate periodic cycles of abundance among mammal and bird populations. Lack (1954) claims that there exists no clear evidence that these fluctuations are due to climate, since different geographic regions within the same climatic zone often cycle out of phase.

A popular example of a 10-year fluctuation is the North American snowshoe hare-lynx cycle. This 10-year cycle was first observed in the late 1700's from records provided by the fur trade industry in Canada (Keith 1963). Moran (1953) proposed that the lynx-hare cycle is a classic predator-prey type relationship. However, since the oscillations are so strongly synchronized over all of Canada, he reasoned that large-scale meteorological factors must be responsible for this synchronicity. He cites two observations that conflict with the predator-prey interpretation but support the sychnronicity by meteorological factors. These are 1) other animals not dependent on snowshoe hares were synchronously fluctuating, and 2) introduced hares on lynx-free Anticosti Island were apparently cycling together with those on the mainland.

To determine how climate affects the lynx-hare cycle, Moran (1953) studied several potentially climate-influenced targets: lynx birth and death rate, snowshoe hare food source, and trapping effeciency. The inclusion of trapping efficiency, which implies unreliable census data, is interesting in that the observed correlations between temperature and lynx numbers may result from the effect of climate on trappers (i.e. unfavorable climate for trapping) rather than on the lynx. Although the effect of climate on vegetation is likely to be the root cause of synchronizing the 10-year lynx-hare cycle, Moran (1953) concludes only that climate is the synchronizing agent and that these populations are dependent on meteorological factors.

MARINE STUDIES IN THE CALIFORNIA CURRENT SYSTEM

Compared to a large number of terrestrial studies, some of which have been briefly summarized in the preceding section, marine studies dealing with the biological effects of climatic change have been few in number (this article does not deal with paleobiological studies; for those, see Soutar and Isaacs 1969). This is not due to lack of interest but rather to a scarcity of time series that are both reliable and of sufficient length. Despite these shortcomings, however, during the last few years there has been an efflorescence of studies relating climatic fluctuations to changes in the distribution and abundance of marine organisms.

The groundwork for these types of studies was laid by the pioneering work of Hubbs and Schultz (1929) and Walford (1931). They noted that during the anomolously warm years of 1926 and 1931, a heavy influx of southern fish species into the waters of California occured. Radovich (1960) reached similar conclusions after comparing fish catch statistics of the 1957-58 period, which again was characterized by anomously high sea-surface temperatures, with the catch statistics of the preceding years. For the same 1957-58 period, Brinton (1960) reported a northerly extension of several species of euphausiids which, in previous years, were confined to more southerly latitudes. Similarly, Balech (1960) stated that during the 1957-58 period, "one is impressed with the striking change in the character of the planktonic populations from south to north and the far northward extension of typically warm water forms."

These findings are what one may expect from purely physical oceanographic considerations. According to Reid et al. (1958), four distinct water masses characterize the surface waters of the California Current system. These come from the north (California Current), west, south, and below (due to upwelling). Changes in the circulation patterns of these water masses frequently occur, and these changes are reflected in sea-surface temperature (SST), salinity, nutrient concentration, and sea level. A lessening of the flow of the California Current, for example, results in the incursion of a subtropical water mass into the region, which in turn is reflected by higher SST, salinity, and sea level, but lower nutrient concentrations. Hydrodynamically passive organisms, such as diatoms, are expected to be carried along with the water masses they inhabit. Mobile organisms, either due to temperature tolerances or feeding strategies, may also undergo a geographical shift. Since these shifts are accompanied by anomolous circulation patterns in the atmosphere (for various physical aspects of climatic changes, see Namias 1975), climatic change has been implicated as an important factor in regulating the abundance and distribution of several organisms as well as the composition of species inhabiting the California Current system. However, due to mixing, food considerations, and wide differences in species temperature tolerance, a complete community shift rarely occurs.

Obviously, long-term changes (months, years) in the circulation pattern of water masses can account for only part of the variability observed in marine populations. For example, unlike climatic change, upwelling is a short-period phenomenon (weeks) which is important in promoting diatom blooms (e.g. Moberg 1928). However, as has been shown by one of us (Tont 1976, in preparation), although upwelling is a short-period phenomenon, its efficacy depends on long-term changes that precede its occurrence. Thus, if upwelling takes place after the influx of subtropical water masses into the region, its effectiveness in bringing nutrients to the surface from a water mass already low in nutrients is clearly limited. The reverse is true if upwelling occurs when the flow of California Current, which is the chief supplier of nutrients in this region, is strong. Indeed, diatom blooms observed during periods of high SST's and sea levels were smaller by several orders of magnitude than those observed when conditions were reversed. Thus, occurrence of diatom blooms off the coast of southern California is regulated by weather (upwelling instigated by alongshore wind stress), but the magnitude of each bloom, in turn, is modulated by climatic change (large-scale atmospheric change coupled with similar change in the ocean).

Wind-induced upwelling, which results in diatom blooms, may have opposite effects on dinoflagellate concentrations, according to Lasker (1978). His examination of a major upwelling event that occurred in February of 1975 indicates that dinoflagellates, which were abundant before the upwelling, were dissipated because of it.

Recent work by the Food Chain Group at Scripps Instutution of Oceanography (SIO) further illustrates the interconnection between variables, some of which are clearly related to climatic changes. According to Eppley et al. (1978), much of the spatial and temporal variability in phytoplankton standing stocks near the coast of southern California is related to changes in the vertical concentration gradient of nutrients and is reflected in sea surface temperature anomalies. Based on these findings, Eppley and McPeak (in preparation) hindcasted Z_n—the depth were nitrate concentration becomes measurable—from SIO pier temperatures and correlated these values with the commercial kelp harvest. They found that although natural mortality appears to be a chief determinant of kelp biomass, variation in the estimated Z_n accounted for 10% of the variability in the kelp harvest overall and for 20% if only the fall averages of both variables are used.

DISCUSSION

It should be apparent from this brief review that climate is an important factor regulating both the abundance and distribution of terrestrial and marine organisms. Further research is needed, however, to differentiate between the various pathways through which climatic change impacts a biological population. These effects could be *direct*, such as when high mortality rates occur due to temperature changes, or *indirect*, as when climatic change alters the nutrient concentration available to the organisms in question. Another important point to consider is that climatic change may have different effects upon the various life stages of an organism. Perhaps more importantly, climatic change may be correlated with several interrelated trophic levels. That is, a change in the abundance of a particular prey species may be the result of the effect of climatic change on the predator species or vice versa, as in the lynx-hare system. Increased data collection over a long period of time and careful analyses will undoubtedly answer these questions.

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