THE EFFECTS OF CLIMATE ON TERRESTRIAL AND MARINE POPULATIONS

SARGUN A. TONT
Scripps Institution of Oceanography
University of California San Diego
La Jolla, CA 92032

DAMON A. DELISTRATY
Virginia Institute of Marine Science
College of William and Mary
Gloucester Point, VA 23062

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.

INTRODUCTION
Environment is the setting in which an organism lives and functions. One may safely assume 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 eluci-
date the functional role of climate in relation to human health. For instance, Saltman (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 neuro-hormonal 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 independently 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 meteorologi-
cal factors must be responsible for this synchronicity. He
cites two observations that conflict with the predator-prey
interpretation but support the synchrony by meteorolo-
gical 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-influ-
cenced targets: lynx birth and death rate, snowshoe hare
food source, and trapping efficiency. 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 trap-
ning) rather than on the lynx. Although the effect of cli-
mate on vegetation is likely to be the root cause of syn-
chronizing the 10-year lynx-hare cycle, Moran (1953)
concludes only that climate is the synchronizing agent
and that these populations are dependent on meteorolo-
gical 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 pre-
ceding 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 short-
comings, however, during the last few years there has
been an efflorescence of studies relating climatic fluctua-
tions 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 anomalously
warm years of 1926 and 1931, a heavy influx of southern
fish species into the waters of California occurred. Radov-
ich (1960) reached similar conclusions after comparing
fish catch statistics of the 1957-58 period, which again
was characterized by anomalously high sea-surface tem-
peratures, 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 ex-
ample, 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 geo-
ographical shift. Since these shifts are accompanied by
anomalous circulation patterns in the atmosphere (for
various physical aspects of climatic changes, see Namias
1975), climatic change has been implicated as an impor-
tant 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 pro-
moting 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 effi-
cacy depends on long-term changes that precede its oc-
currence. Thus, if upwelling takes place after the influx
of subtropical water masses into the region, its effective-
ness in bringing nutrients to the surface from a water
mass already low in nutrients is clearly limited. The re-
verse is true if upwelling occurs when the flow of Cali-
ifornia 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 Institution of Oceanography (SIO) further illustrates the interconnection between variables, some of which are clearly related to climatic changes. According to Epplley 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, Epplley and McPeak (in preparation) hindcasted $Z_n$—the depth where 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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