Ecological Effects of Climate Fluctuations

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Climate influences a variety of ecological processes. These effects operate through local weather parameters such as temperature, wind, rain, snow, and ocean currents, as well as interactions among these. In the temperate zone, local variations in weather are often coupled over large geographic areas through the transient behavior of atmospheric planetary-scale waves. These variations drive temporally and spatially averaged exchanges of heat, momentum, and water vapor that ultimately determine growth, recruitment, and migration patterns. Recently, there have been several studies of the impact of large-scale climatic forcing on ecological systems. We review how two of the best-known climate phenomena—the North Atlantic Oscillation and the El Niño–Southern Oscillation—affect ecological patterns and processes in both marine and terrestrial systems.

Ecological processes are influenced by prevailing climatic conditions (*1*). Early studies typically focused on local weather parameters such as temperature, precipitation, and snow depth. By so doing, an important dimension is overlooked: the holistic nature of the climate system (*2*). Recently, therefore, increasing attention has been given to large-scale patterns of climate variability with marked ecological impacts on interannual and longer time scales. Of particular interest are the North Atlantic Oscillation (NAO) (*3*) and the El Niño–Southern Oscillation (ENSO) (*4*, *5*). These patterns account for major variations in weather and climate around the world and have been shown to affect terrestrial vegetation (*6*, *7*), herbivores and carnivores (*8*, *9*), and marine biology and fish stocks (*4*, *10*, *11*) through both direct and indirect pathways.

Increasing awareness among and interactions between biologists and climate scientists are rapidly advancing our insights into the critical issue of the response of ecosystems to climate variability and climate change. Moreover, mutual interest in climate processes is serving as an impetus for new interdisciplinary research.

Effects of Climate: Spatial Synchronization and the Moran Effect

Climate as a synchronizing agent for population fluctuations in space, the so-called Moran effect, has received much attention (*12*, *13*). Rainfall changes associated with ENSO, for instance, produce a highly synchronic pattern of massive germination of annuals (*14*), rodent outbreaks (*15*), and vertebrate predators responses (*16*) over arid and semi-arid regions of South America. Similarly, across the boreal forest of Canada, lynx and snowshoe hare population cycles have a closely related dynamic structure within climatologically based regions defined by the spatial influences of the NAO (*17*). This indicates that climate affects the hunting behavior (and success) of the lynx, presumably through snow condition (*17*). Also, muskrat (*Ondatra zibethicus*) and mink (*Mustela vison*) populations are more synchronous over eastern Canada, where the influence of the NAO is strongest (*18*).

Some of the best-documented effects of the NAO on terrestrial ecosystems involve the breeding phenology of plants (*19*), amphibians (*20*), and birds (*20*, *21*). Despite some noteworthy inconsistencies (*22*), these organisms have generally started breeding earlier in much of Europe because of increasingly warm and wet winters associated with long-term changes in the NAO (Fig. 1B). Also, year-to-year changes in the NAO are correlated with breeding and first-flowering dates. Other species (e.g., deer), however, have a fairly fixed breeding time, whereas their food supply may vary owing to environmental conditions.

Synchrony between predator and prey may be particularly important. The match-mismatch hypothesis states that the growth and survival of cod larvae depend on synchronous production with their main food items, early stages of zooplankton. Although

this has long been recognized as a fundamental concept within fisheries biology (*23*), in a terrestrial setting the match-mismatch hypothesis sheds new light on the tight multitrophic interactions involved in the timing of reproduction and growth (Fig. 3A). The same match-mismatch may also occur in a spatial setting: Phenology in summer and wintering areas may be disrupted for long-distance migrators such as many bird species (*24*, *25*) or more locally between high- and low-altitude migrating species (*26*).

Effects of Climate: The Temporal Patterns

Climate affects marine ecosystems particularly through sea surface temperature and wind conditions. The temporal and spatial population dynamics of *Calanus finmarchicus* and *C. helgolandicus* zooplankton were among the first to be linked to the NAO (*27*, *28*). Four types of mechanism have been proposed to explain the observed correlation: reduction in the volume of Norwegian Sea Deep Water where the overwintering population resides, variations in the transport of individuals from the Faeroe- Shetland channel into the North Sea, changes in food availability (phytoplankton production), and alteration of the competition balance between the two species (*29*). Early stages of the *Calanus* zooplankton species are the main food resources for larvae and early juveniles of many fish species throughout the North Atlantic and thus regulate fish recruitment.

Cod (*Gadus morhua*) is one of the major North Atlantic fish resources, for which there are fisheries records dating back 500 years or more. Sea temperatures strongly affect many stocks of cod. Variations in sea temperatures driven by NAO variations have been linked to fluctuations in cod recruitment both off Labrador and Newfoundland (*30*) and in the Barents Sea (*29*, *31*).

The biological characteristics of small pelagic fish, such as sardine (*Sardina pilchardus*, *Sardinops sagax*, *Sardinella* spp.), anchovy (*Engraulis* spp.), and herring (*Clupea harengus*), make them highly sensitive to environmental fluctuations (*32*). In northern Europe, catch records date back as far as to the 10th century. These records show that the fisheries were intense during some periods and nonexistent during others with marked asynchronous spatial dynamics. The fluctuations occur on decadal time scales as a response to different regimes of prevailing wind directions related to NAO anomalies

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(33). The teleconnection patterns between the dynamics of the herring and sardine populations are further evidence of climate dependency. Despite distances of several thousand kilometers between the populations, they seem to react to the same basin-wide forcing (33).

The effects of adverse environmental conditions on heavily fished populations are dramatic. Off equatorial South America, a strong

Fig. 1. The North Atlantic Oscillation (NAO), and examples of its ecological effects. The NAO (3, 61) is a north-south alternation in atmospheric mass between the subtropical atmospheric high-pressure center over the Azores and the atmospheric subpolar low-pressure center over Iceland. It measures the strength of the westerly winds blowing across the North Atlantic Ocean between 40°N and 60°N. Variability in the direction and magnitude of the westerlies is responsible for fluctuations in wintertime temperatures and the balance of precipitation and evaporation across the Atlantic and the adjoining landmasses (3, 62). (**A**) During positive phases of the NAO, the westerly winds are strengthened and moved northward, causing increased precipitation and temperatures over northern Europe and the southeastern United States and dry anomalies in the Mediterranean region. Roughly opposite conditions occur during the negative-index phase. [Graph courtesy of M. Visbeck; www.ldeo.columbia.edu/NAO] (**B**) Temporal evolution of the NAO over the past 140 winters (index at www.cgd.ucar.edu/~jhurrell/nao.html). High- (low-) index winters are shown in red (blue) (63). (**C**) Simplified food web for the Barents Sea including phytoplankton, zooplankton, capelin (*Mallotus villosus*), herring (*Clupea harengus*), and cod (*Gadus morhua*). Positive phases of the NAO affect the Barents Sea through increasing volume flux of warm water from the southwest, cloud cover, and air temperature, all leading to increased water temperature, which influences fish growth and survival both directly and 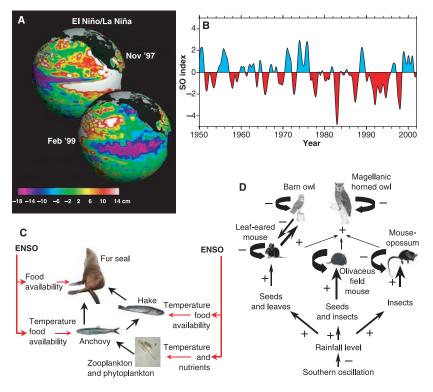indirectly (31). (**D**)The breeding ranges of the pied flycatcher (*F. hypoleuca*) and collared flycatcher (*F. albicollis*) overlap in central Europe. The two species compete for resources such as nest sites (64). Isoclines (i.e., density-combinations for which each of the species does not change in density) as deducedfrom Sætre

et al. (56). During periods with high positive values of the NAO index, the collared may outcompete the pied flycatcher, whereas during periods with lower values of the NAO index there may be a balanced competitive interaction between the two species leading to stable coexistence.

Fig. 2. The El Niño Southern Oscillation (ENSO), and examples of its ecological effects. Fluctuations in tropical Pacific SST are related to the occurrence of El Niño, during which the equatorial surface waters warm considerably from the international date line to the west coast of South America. (**A**) Ocean-surface elevation measured by TOPEX/Poseidon. El Niño conditions are shown at the upper left, with high elevation (white/red) indicating warm-water anomalies westward from equatorial South America; La Niña conditions are at the lower right. [Images from Jet Propulsion Laboratory at http://topex-www.jpl.nasa.gov/science/el-nino.html] (**B**) The Southern Oscillation (SO) is a global-scale "see-saw'" in atmospheric mass, involving exchanges of air between eastern and western hemispheres centered in tropical and subtropical latitudes. It is characterized by the inverse variations in sea level air pressure (SLP) at Darwin in northern Australia and Tahiti in the south Pacific. A simple index of the SO (indexed at www.cgd.ucar.edu/cas/catalog/climind/soi.html) is, therefore, often defined by the normalized Tahiti minus Darwin SLP anomalies. Although changes in tropical Pacific sea surface temperatures (SSTs) may occur without a swing in the SO, El Niño (EN) and the SO are linked so closely that the term ENSO is used to describe the atmosphere-ocean interactions over the tropical Pacific. Warm ENSO events, therefore, are those in which both a negative SO extreme and an El Niño occur together (4, 5). Different phases of ENSO shift the location of the heaviest tropical rainfall, and these changes in the diabatic heating of the atmosphere distort the flow of air over thousands of kilometers, producing anomalous cold and warm regions at the Earth's surface. (**C**) Massive die-offs of plankton, fishes (anchovy and hake), and their main predators (marine mammals and seabirds) have been widely reported as a result of El Niño (65, 66). (**D**)

Food web involving three small mammals and two owl species. The relative importance and strength of the intraspecific, interspecific, and trophic interactions are represented by the thickness of the arrows (16).

coastal upwelling of water enriched in nutrients normally sustains an exceptional high biological productivity (*34*). In the early 1970s, the Peruvian anchovy fishery was the most productive fishery in the world. For instance, during a single day in 1972, over 180,000 metric tons were hauled. A few weeks later, the warm waters of a full-scale El Niño event had spread along the South American coast, the upwelling stopped, and the Peruvian anchovy population crashed (*35*). However, an earlier recruitment failure during 1971 suggests that El Niño alone may not deserve all the blame. The sudden crash in anchovy abundances may be a result of an interaction between overfishing and unfavorable environmental conditions (*36*).

Nearly 70% of the world's annual tuna harvest derives from the Pacific Ocean. Skipjack tuna (*Katsuwonus pelamis*) dominates the catch. Skipjack catches are highest in the western equatorial Pacific warm pool. Spatial shifts in the skipjack population were linked to the large zonal displacements of the warm water pool that occur during El Niño events (Fig. 2A). Thus, predictions of ENSO may act as forecasts of the location of the highest abundances of skipjack tuna with resulting important implications for the commercial tuna fishing and management (*37*). Warm events related to El Niño episodes are increasingly reported to disrupt marine ecosystems, also along the coast of North America (*38*).

Variations in climate also lead to contrasting ecological effects over relatively small geographical regions. For instance, winter precipitation over the west coasts of Scotland and Norway is positively correlated with the NAO index (*3*, *39*). Across Scotland, most of this precipitation falls as rain, and wetting of an animal's coat is energetically expensive owing to reduced resistance to heat flux (*40*). Mortality of Soay sheep (*Ovis aries*) and red deer (*Cervus elaphus*) therefore increases with positive values of the NAO index (*39*, *41*). In Norway, warmer temperatures with positive NAO-index winters decrease snow depth and increase rainfall at low elevations (*42*). Because snow depth is the main difficulty to overwintering ungulates in this region (Fig. 3C), body weight (*43*) and survival (*44*) of red deer calves increase during positive-index winters—in contrast to the fate of Scottish ungulate populations.

Effects of Climate: The Processes

These above examples highlight both the strengths (regarding the existence of clear patterns) and the limitations (regarding the uncertainty of underlying mechanisms) of trying to explain ecological effects through climate variations. Indeed, climate impact on individuals and populations may operate either directly through physiology (metabolic and reproductive processes) or indirectly through the ecosystem, including prey, predators, and competitors. There are at least five effects to consider.

First, delayed effects of climate are important in both marine and terrestrial ecosystems (*45*) (Fig. 3D). Individuals born in a specific year may be larger or smaller than the average, depending on the climatic conditions in the year of birth. Such cohort effects have been reported in both ungulate and cod populations (Fig. 1C) as the result of NAO-related climate variability (*46*, *47*). Furthermore, cohorts with large individuals when young tend to be abundant when older (*29*).

Second, climate has differential influences on sexes and age-classes. Survival of young and old Soay sheep individuals is affected by NAO variations more than is survival of prime-aged individuals,
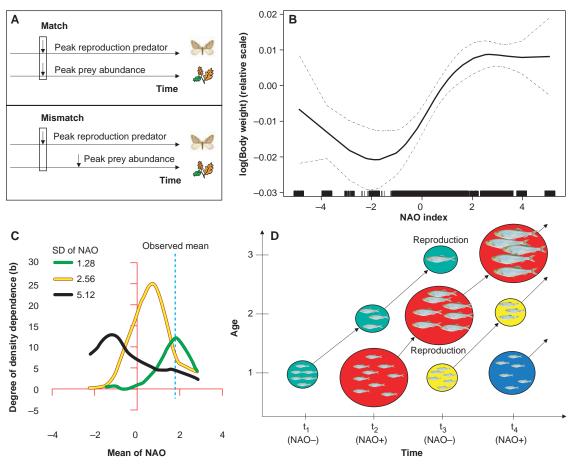

Fig. 3. Climate may affect ecological processes in a variety of ways. (**A**) Climatic fluctuations may affect the relative timing of food requirement and food availability (*67*); in the marine literature this is generally referred to as the "match-mismatch hypothesis" (*68*). (**B**) Climate fluctuations may affect biological processes linearly or nonlinearly (*43*). (**C**) Between-individual interaction and density dependence may vary nonlinearly with the value of the NAO index depending on the distribution of the climatic fluctuations; Coulson *et al.* (*48*) showed that density-dependent overcompensation was influenced by both the NAO level and its variation (as the value of the parameter *b* increases, the degree of density-dependent overcompensation increases). (**D**) Climatic fluctuations may give rise to delayed effects by affecting the critical early development of entire cohorts. Good climate conditions during reproduction and early life may produce larger cohorts with larger individuals, which in turn may survive at a higher rate, reach maturity earlier, and reproduce at a higher rate during their entire life-span. Hjort recognized a century ago the importance of environmental conditions during early life for determining recruitment to the large Barents Sea cod stock (*69*, *70*). Similarly, cohorts of Soay sheep on St. Kilda, Scotland, born after warm, wet, and windy winters (positive NAO index) were lighter at birth, born earlier, less likely to have a twin, and matured later than cohorts born following cold and dry winters [negative NAO index (*47*)].

and male survival is affected more than female survival (48). The effect of the NAO on population development is hence dependent on the sex- and age-structure of the population (48). Whenever younger age classes are more affected, the ecological effects of climate are more difficult to detect because of cohort effects (49).

Third, climate change may lead to a higher frequency of extreme events, which often are ecologically more relevant than are fluctuations in the mean climate (50–53). An example is the effect of frost formation (54), including plant death, or damage of sensitive parts of plants (e.g., flower buds, ovaries, and leaves) (54). In addition, nonlinear effects may arise from climate variability (43) (Fig. 3B).

Fourth, climate variability might directly affect a particular organism (55), or the effect could derive from primary to secondary producers (19). However, the mechanistic links and their consequences may be complex (43). In subalpine mixed deciduous forest near Dlouhá Louka in the Czech Republic (56), adverse effects of positive NAO on breeding density of the collared flycatcher allowed a weaker interspecific competitor (the pied flycatcher, *Ficedula hypoleuca*), unaffected by the NAO, to live in sympatry with the stronger competitor (the collared flycatcher, *F. albicollis*) (56) (Fig. 1D).
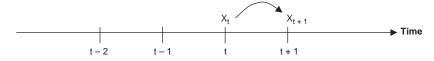
Effects of the ENSO may be as intricate. A recent study (16) of climate influences on population dynamics of three small mammal species in Chile showed that the differences observed in the magnitude of population fluctuations between species were caused by different feedback structures (i.e., density dependence) and their interaction with ENSO-driven rainfall anomalies (Fig. 2D).

Fifth, the effects of climate may ultimately depend on other ecological factors (i.e., interactions). Although warm winters positively affected the abundance of golden plovers (*Pluvialis apricari*) in the United Kingdom, direct density dependence strongly depressed their numbers over time despite increasing warmth associated with the recent upward trend in the NAO index (20). A variety of other factors may similarly interact with climate effects. Indeed, failure to include other important factors may lead to spurious relations between indices of climate and the trait studied (46, 57).
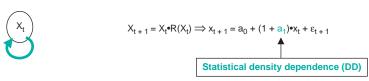
Future Challenges

Intrinsic density dependence and extrinsic processes due to a stochastic environment typically interact in rather complex ways within populations and ecosystems (58). The study of large-scale climatic fluctuations has revealed strong nonlinearities and interactions of intrinsic and extrinsic processes in the shaping of populations dynamics [see, for example, (17)]. Such complex interactions

Reading the fingerprint of density dependence and density independence (such as climate) from biological time series

(i) Density dependence only

$$X_{t+1} = X_t \cdot R(X_t) \Rightarrow x_{t+1} = a_0 + (1 + a_1) \cdot x_t + \varepsilon_{t+1}$$

Statistical density dependence (DD)

(ii) Density dependence and climate, noninteractive (additive) effects

$$X_{t+1} = X_t \cdot R(X_t, \text{Clim}_t) \Rightarrow x_{t+1} = a_0 + (1 + a_1) \cdot x_t + g(\text{Clim}_t) + \varepsilon_{t+1}$$

Additive effect of climate

(iii) Density dependence and climate, interactive effects

$$X_{t+1} = X_t \cdot R(X_t, \text{Clim}_t) \Rightarrow x_{t+1} = a_0 + [1 + a_1(\text{Clim}_t)] \cdot x_t + \varepsilon_{t+1}$$
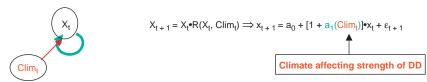
Climate affecting strength of DD

Fig. 4. Ecological time-series models have typically been developed, either for single populations or for trophic interactions (59), with data on some focal species only, and without explicitly modeling the climatic component; $x_t = \ln X_t$, where X_t is the number of individuals in the population at time t. In some cases, the effect of climate has been incorporated additively; however, climate may also affect the populations nonadditively—where climate affects either the direct or delayed density dependence (17, 48).

present major challenges—the solution of which requires the involvement of ecologists, climatologists, and statistical modelers.

The need for proper experiments exploring the underlying causal mechanisms is clear. The joint analysis of ecological and climatological time series will certainly continue to teach us much about how climate variability affects ecological patterns and processes (59, 60) (Fig. 4). Disentangling the ecological consequences of climatic variation is not a simple task. Most of all, we need to understand the density-dependent and density-independent structure that may interact with the climatic signal (59). To study such interactions further, we need detailed knowledge about the interface of climate and ecological systems. The challenge of incorporating different mechanistic links between the dynamics of populations and climate variability will, we believe, provide a new step forward in time-series modeling (60)—the results of which may have profound implications beyond ecology.

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