stimulation of the premotor cortex produced large limb movements, yet the patients never reported any sense of urge, nor awareness of such movement. Therefore, conscious intention—or at least the parietally generated aspect of it—seems to be a specific class of experience generated within the brain, rather than a sensation of slight tension in the muscles. Thus, Desmurget *et al*. confirm that the parietal cortex contributes to conscious experience of volition. Just how the frontal, motor aspect of this experience differs from the parietal, sensory aspect is the next question.

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ECOLOGY

Some Like It Cold

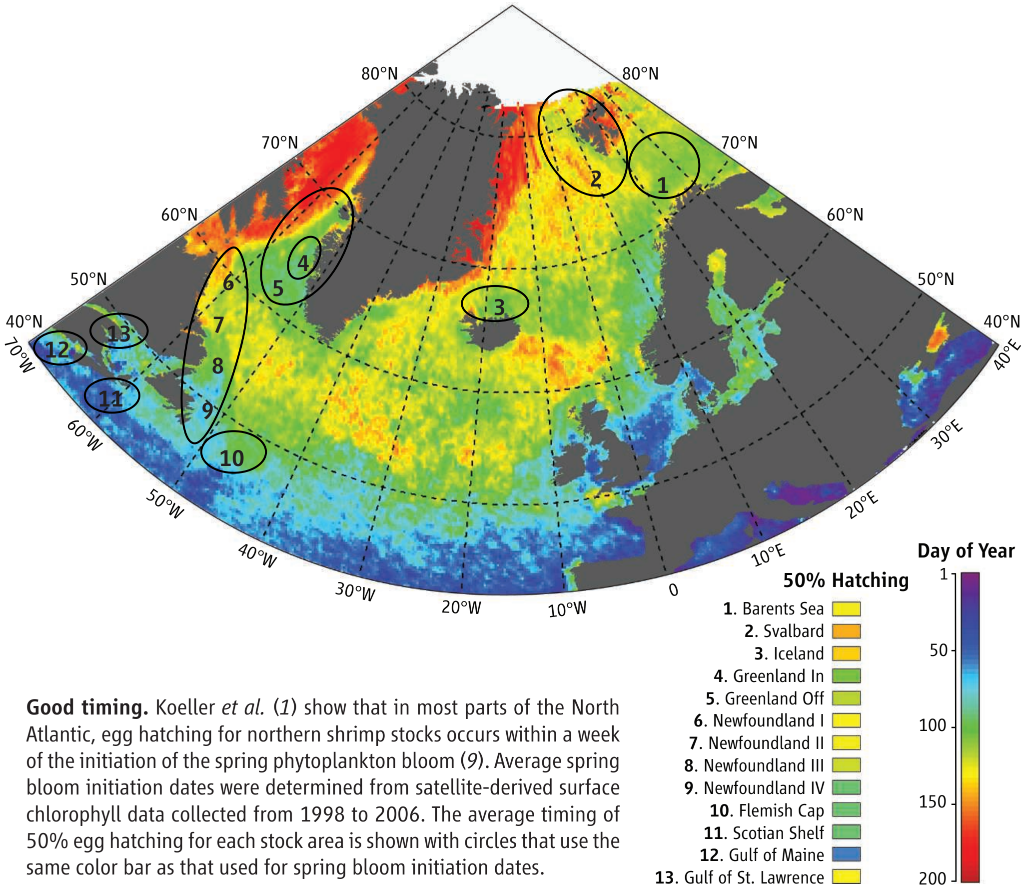
Northern shrimp stocks thrive when climatic conditions lead to cold bottom waters.

Charles H. Greene,* Bruce C. Monger, Louise P. McGarry

The northern shrimp, *Pandalus borealis*, makes up ~70% of the 500,000 tons of cold-water shrimp harvested annually from the world's oceans. Commonly captured in shelf waters deeper than 100 meters, it supports major fisheries throughout the North Atlantic. On page 791 of this issue, Koeller *et al*. (*1*) report that the reproductive cycles of most northern shrimp stocks are finely tuned to match the timing of egg hatching with that of the local spring phytoplankton bloom (see the figure). This remarkable degree of local adaptation on a basin scale is achieved by females regulating the initiation date of their temperature-dependent egg incubation period so that eggs hatch on average within a week of the expected spring bloom. Thus, in typical years, eggs hatch at the time of maximum food availability. The potential downside of this reproductive strategy is its sensitivity to climate-associated changes in the ocean environment.

A species' sensitivity to the vagaries of climate is often most evident at the limits of its distributional range. In the Gulf of Maine, the northern shrimp's southern limit in the northwest Atlantic, the temporal match between egg hatching and the spring bloom is relatively poor (*1*). Here, the deeper offshore waters are warmer than in other parts of the species' range because they are partially derived from the relatively warm and salty slope waters entering the gulf from the North Atlantic (*2*). Because northern shrimp are bottom dwelling and eggs develop faster at higher temperatures, eggs hatch earlier in the gulf stock than in any other stock investigated, and well before the spring bloom. Egg hatching would occur even earlier if gulf females did not exhibit a behavior seen nowhere else in the species' range. During winter, egg-bearing females migrate from offshore into the colder, shallower nearshore waters, a behavior that Koeller *et al*. suggest is an adaptation to delay egg development and improve the match between egg hatching and the spring bloom.

Bottom temperatures in the northwest Atlantic's shelf waters often respond to climate-associated changes in ocean circulation, and such responses can impact the population biology of northern shrimp. The North Atlantic



Good timing. Koeller *et al.* (*1*) show that in most parts of the North Atlantic, egg hatching for northern shrimp stocks occurs within a week of the initiation of the spring phytoplankton bloom (*9*). Average spring bloom initiation dates were determined from satellite-derived surface chlorophyll data collected from 1998 to 2006. The average timing of 50% egg hatching for each stock area is shown with circles that use the same color bar as that used for spring bloom initiation dates.

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Oscillation (NAO) is the main mode of interannual to interdecadal climate variability in the North Atlantic. By altering circulation patterns in the northwest Atlantic, the NAO can affect the bottom temperatures throughout the region. During positive NAO conditions, volume transport in the Labrador Current increases, resulting in colder bottom temperatures and lower salinities in the shelf waters north of the tail of Newfoundland's Grand Banks (*3*). The reverse occurs during negative NAO conditions. Paradoxically, because of a bifurcation in the Labrador Current near the tail of the Grand Banks, responses to the NAO downstream of this point are reversed, with bottom waters tending to be warmer and saltier during positive NAO conditions and colder and fresher during negative NAO conditions.

During the 1960s, negative NAO conditions predominated, and the Gulf of Maine stock of northern shrimp thrived in the colder bottom temperatures. During the 1970s, the NAO shifted into a predominantly positive phase and the stock collapsed. Although overfishing cannot be excluded as a contributing factor to this collapse (*1*), environmental conditions in the gulf were certainly more favorable physiologically for northern shrimp in the 1960s than the 1970s.

The NAO has remained in a predominantly positive phase since the 1970s, yet northern shrimp stocks throughout the northwest Atlantic increased to relatively high abundances during the early 1990s (*1*). This increase has been attributed to two factors. First, the abundance of groundfish predators (especially cod) that feed on northern shrimp declined, mostly as a result of overfishing (*4*). This release of predation pressure must have boosted shrimp survivorship dramatically. Second, atmospheric changes in the Arctic resulted in two large salinity anomalies—pulses of anomalously cold, low-salinity water—entering the northwest Atlantic's shelf circulation (*5*). Throughout the region, surface waters freshened and became more stratified, enhancing phytoplankton production during autumn and winter. Favorable feeding conditions during these seasons may have contributed to the reproductive success and larval survival of northern shrimp.

The future distributional range of northern shrimp will reflect the interplay between climate-associated changes in the ocean and the demographic responses of a stock-structured population. It is commonly assumed that more northerly species will contract their ranges in response to climate warming, but just the opposite has been seen during recent decades in at least one part of the northwest Atlantic (*5*). In shelf ecosystems upstream of the tail of the Grand Banks, the predominantly positive NAO conditions since the 1970s have led to colder bottom waters that are physiologically favorable for boreal species like the northern shrimp. Episodic large salinity anomalies have reinforced this bottom-water cooling for several years in each decade since the 1970s (*6*).

Colder bottom temperatures not only offer physiological advantages for northern shrimp; they also provide an ecological advantage by slowing the growth and reproductive rates of cod, its principal predator (*7*). The recovery of cod stocks from overfishing has been suppressed by the same cold temperatures that have enabled stocks of northern shrimp and snow crab to flourish. The expanded shrimp and snow crab fisheries have been more lucrative than the cod fishery ever was. The sustainability of marine fisheries will depend on scientific advances that enable managers to better anticipate the responses of stock-structured populations to an ever-changing climate (*8*).

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PLANT SCIENCE

An Invasive Plant Paradox

One reason that invasive plants may thrive in new environments is their interactions with soil microbes that increase nitrogen cycling.

Marnie E. Rout and Ragan M. Callaway

Why some plants attain extremely high densities in communities where they are exotic, yet remain at low densities in their native ranges is a mystery. The pattern has been called a "paradox" because it conflicts with long-held ideas about the importance of local adaptation for the ecological performance of organisms (*1*). This biogeographical shift may be connected to other apparent ecological paradoxes that occur with plant invasions involving processes mediated by soil microbes. Invasions can decrease plant species diversity but also increase plant productivity. Rather than depleting soil resources as productivity increases, invasions often increase soil stocks, pools, and fluxes of nitrogen through processes regulated by microbial communities.

Plant species richness and functional diversity can increase local net primary productivity (see the figure), predominantly through more complete use of resources, or "niche complementarity" (*2*). Exotic plant invasions locally reduce native plant diversity, often to the point of becoming the only plant species present (*3*). However, contrary to what diversity-productivity experiments would predict, net primary productivity typically increases with exotic invasions (*4*–*6*). In a recent meta-analysis of 94 studies, the average increase in annual net primary productivity was over 80% in invaded ecosystems (*6*). This "invasion-diversity-productivity" paradox cannot be explained by niche complementarity, but differences in plant-soil-microbe interactions in the invaded and native ranges could perhaps provide part of the answer. Soil microbes can have strong density-dependent effects on plants, often called plant-soil-microbe feedbacks (*7*). These feedbacks are usually neutral or negative for plants in soils from their native ranges, but can be positive for invasive plants in soils from invaded ranges (*8*, *9*). This directional shift is likely due to the absence of evolved species-specific plant-pathogen relations for the invasive plants (*9*). This absence likely enhances the competitive dominance of plant species in new ranges and increases their productivity.

Nitrogen is the primary factor limiting net primary productivity in most ecosystems (*10*),

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