ACCELERATED DEVELOPMENT IN PLANKTONIC FORAMINIFERA: ADAPTIVE RESPONSE TO REDUCED OCEAN MIXING

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Planktonic foraminifera grow by adding chambers to their shells, increasing shell size and changing shell shape. Shell development can be distinguished from shell size either by counting the chambers or by measuring the allometry associated with developmental shape changes. It is necessary to make this distinction when trying to understand the life history adaptations of planktonic foraminifera to their environment because there is wide variation in shell size among individuals at the same stage of development.

While the life cycle of many species of planktonic foraminifera is adapted to the monthly lunar cycle, certain deep-living species such as *Globorotalia truncatulinoides* and *G. hirsuta* are adapted to the annual cycle of late winter nutrient upwelling and spring bloom, the mechanism that drives primary productivity in subtropical latitudes. These deep-living species grow while sinking from the surface ocean through the upper 500 to 1000m of the water column and then reproduce at depth. Juveniles must somehow return to surface waters.

For such a life cycle, size may affect reproductive success in two opposing ways: while the number of gametes produced is directly proportional to size, the bouyancy of the offspring and so the likelihood that they will reach surface waters are inversely proportional to size. The balance between the reproductive benefits of large size and the difficulty of returning large juveniles to surface waters can be altered by vertically mixing the water column. The deep mixing that brings nutrients to surface waters can also help juvenile foraminifera reach the surface.

Today the largest shells of *G. truncatulinoides* are found in populations growing on the poleward margins of the subtropical gyres, areas where the scale of mixing is greatest. As the vertical scale of this mixing decreases toward the tropics, shells at each stage of development shift toward smaller average sizes. This apparent acceleration in development reflects a loss of large shells, which decreases both the average size and the overall abundance of the species.

The relationship of apparent developmental rate to the scale of vertical mixing produces the previously reported "ecophenotypic cline" in which *G. truncatulinoides* changes from a compressed biconvex form in high latitudes to a highly conical form in the tropics. By design, the study reporting this observation was based on shells from a narrow range of size in an attempt to minimize any developmental sources of morphologic variation. Paradoxically, this strategy focussed observations on the systematic shift in the relationship between shell size and development caused by differences in upper ocean mixing. The apparent cline consists of shells of the same size but at different stages of development. A similar explanation may account for the apparent gradual "evolution" observed in *G. truncatulinoides* during the Late Pleistocene.