that a fixed amino acid difference in *Mc1r* in another species, the great skua, accounts for its generally dark plumage. The repeated implication of this same gene suggests that there may be a more limited number of genetic mechanisms to produce dark plumage in natural populations than is suggested by genetic studies of lab mice.

The melanocortin-1 receptor (MC1R) resides in the membrane of specialized cells known as melanocytes, which are the site of melanin synthesis in birds and mammals. Circulating melanocyte-stimulating hormone (MSH) binds to MC1R, turning on the cell's melanin-making machinery. In lab mice, mutations in *Mc1r* that result in melanism are due to either hyperactivation or constitutive activation of *Mc1r*, without the need for MSH. About 15 *Mc1r* mutations, most of which are single amino acid changes, are associated with darkened or melanic coloration in a variety of vertebrates. These mutations are dominant or partially dominant—as is the case in snow geese and skuas—and thus are readily available to selection. Therefore, a single mutation in *Mc1r* leads to a visible phenotype on which selection acts with no known antagonistic effects, making *Mc1r* a particularly good target for evolutionary change.

In both the snow goose and the Arctic skua, the plumage differences are subject to sexual selection. In both, dark plumage is the derived trait. With the gene in hand, it is now possible to estimate roughly when the dark form appeared by comparing the genetic variation in the derived versus ancestral alleles with sequence differences in the same gene between species whose divergence is dated in the fossil record. For both the snow goose and the Arctic skua, Mundy *et al.* arrive at a late Pleistocene date. In other words, the polymorphism in both species may be several hundred thousand years old. The maintenance of the polymorphism over such a long time span has many implications for ecological geneticists studying patterns of sexual and natural selection in contemporary populations. Armed with genes, we can begin to look at not only the age of the phenotype but also the distribution of *Mc1r* allele frequencies across populations, and we can even estimate the strength of sexual selection acting on the dark phenotype in ways that would not be possible without understanding the genetic basis of the color polymorphism.

The independent evolution of melanism in the Arctic skua and the snow goose, while attributable to the appearance of mutations at the same gene, has not been perfectly parallel. Heterozygous snow geese show a restricted pattern of melanization, whereas heterozygous arctic skuas are generally intermediate in color. Perhaps the selection of a modifying mutation has altered the distribution of melanins in the two species. Alternatively, the genetic backgrounds in which the *Mc1r* mutations appeared may be different. Field studies of selection, coupled with characterization of the melanin pathways in each species, will eventually enable a closer tracing of the roles of selection and mutation in generating the similarities and differences between the species. Further down the road, we should be able to dissect the genetic basis of more complicated color patterns like those of the orioles.

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CLIMATE

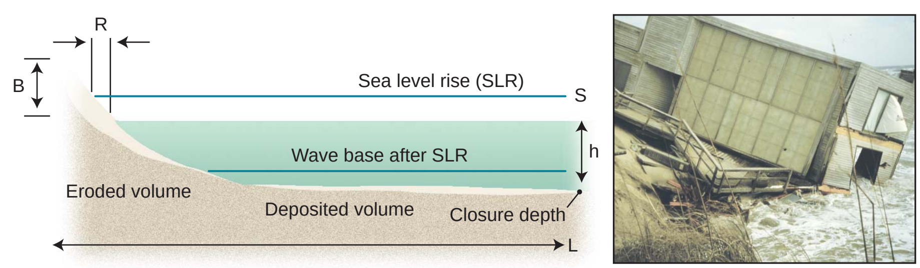
Society and Sea Level Rise

Orrin H. Pilkey and J. Andrew G. Cooper

Most of the world's shorelines are in a state of erosion. The only major exceptions are areas of high sediment supply, such as along the rims of active delta lobes and regions of glacial outwash. Many developed nations have experienced a four-decade rush to the shore, with concomitant beachfront development and exponentially increasing total values for beachfront real estate, infrastructure, and buildings. That this unprecedented accelerating coastal development has unfortunately coincided with a century of accelerating global sea level rise (SLR) means that the prediction of the future rate of shoreline retreat has become a major societal priority.

SLR is caused by a number of eustatic and tectonic factors. Eustatic rise from oceanic heating expansion and glacial melting is assumed to be one of the major fallouts from global warming that will have important impacts on our society. Sea level is rising along mid-latitude coastal plain coastlines at typical rates of 30 to 40 cm per century. Large variations in this SLR rate are found in regions dominated by deltas, areas that are currently or were formerly glaciated, and areas exhibiting tectonic activity. Two important unknowns stand in the way of useful predictions of future shoreline positions: (i) What is the future of SLR? (ii) What is the relationship between SLR and shoreline retreat? Here, we are primarily concerned with the latter.

Shoreline retreat (also called shoreline erosion) on unconsolidated shorelines is directly caused by physical shoreline processes, usually storms, over short time scales. Long-term rates of shoreline retreat are related to variations in the supply of sand to a beach, its geologic setting, and SLR. In general, the world's shorelines would not be in a ubiquitous state of erosion without SLR. Typical retreat rates along coastal plain coasts range from 30 cm to 1 m per year. It is generally not possible to isolate the impact of SLR on shoreline retreat, but it is assumed to be impor-



Swept away. (**Left**) The Bruun rule of shoreline erosion is a simple mathematical relationship with few variables (defined in the equation). The rule states that as the sea level rises, the shoreface profile moves up and back while maintaining its original shape. Sand is removed from the upper part of the profile and deposited on the lower profile. (**Right**) A house on the beach after a winter storm at South Nags Head, North Carolina. This building is on a stretch of beach that is retreating at nearly 2 m per year.

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tant, especially on very gently sloping lower coastal plains. In North Carolina, outer coastal plain slopes average 1/2000 and are as gentle as 1/10,000 (*1*), which means that in the absence of other factors, a SLR of 1 cm could result in a retreat of 20 to 100 m over the next century through inundation alone (see the figure). Shoreline response, however, involves complex physical reorganization of sedimentary materials rather than simple inundation.

It is widespread practice to predict the retreat of local shorelines either by extrapolation of the present shoreline retreat rates or by use of the mathematical model known as the Bruun rule (see the figure) (*2*). Extrapolation has problems because large temporal variations in shoreline retreat rates may occur along single shoreline reaches and because historical shoreline data to determine actual past rates are incomplete.

The Bruun rule is therefore viewed as an alternative to observations in cases where no data exist. It is a simple mathematical relationship with few variables. The rule basically states that as the sea level rises, the shoreface profile moves up and back, all the while maintaining its original shape. Sand is removed from the upper part of the profile and deposited on the lower profile. This simple model purports to relate SLR to shoreline retreat, and as a result it has found exceedingly wide application. We have identified examples of Bruun rule use as a coastal management tool (post-1995) in at least 26 countries on six continents.

The Bruun rule can be written as

$$R = (L/B + h)S = SL/B + h = (S)\ 1/\tan Ø$$

and states that for a SLR of amount S the profile will shift landward by amount R, where L is the length of the profile, Ø is the profile slope angle, B is the height of the beach berm, and h is the depth at the base of the profile beyond which significant sediment exchange is not considered to occur (the closure depth).

The rule is to be deployed only under a limited range of environmental circumstances (such as uniform sandy shorefaces with no rock or mud outcrops) (*3*). Unfortunately, these constraints on its use are widely ignored and it has been applied to such diverse coastal types as mud flats, rocky coasts, and coral atolls. Even under ideal conditions, however, the rule has never been credibly shown to provide accurate predictions. On the contrary, it has been shown to be inaccurate (*4*, *5*). Modern understanding of the complexity of shoreface processes and widely observed geologic control (rock outcrops) supports the rejection of this simple predictive model (*6*, *7*). Shoreline changes may involve barrier island migration, barrier overstepping, shoreface aggradation, and variable rates of both shoreline retreat and SLR, and the constraints on these different response modes remain qualitatively understood at best.

The Bruun rule is a "one model fits all" (*8*) approach unsuitable in a highly complex natural environment with large spatial variations in shoreline retreat. In addition, the rule, as actually applied in coastal management, reduces down to a single noninvolved variable: the slope of the shoreface (see the equation).

Models can be a hazard to society, and this is certainly an example of such. There have been recent calls for increased public use of the Bruun rule (*9*). However, plans for development, such as setback lines and response strategies, will be ill-founded if they depend on this rule. Why has the rule found such widespread use despite its shortcomings? The answer probably lies in some combination of the following factors: the appeal of a simple, easy-to-use analytical model; the lack of need for detailed field study (only a good navigation chart is needed); the lack of an alternative model; the production of a deterministic value for shoreline retreat; positive advocacy by some scientists (*10*); application by other scientists without critical appraisal; and application by coastal managers who have no understanding of Bruun rule weaknesses. Its widespread use despite its invalidity is an example of applied mathematical modeling gone awry.

We advocate recognition, and acceptance as fact, that we cannot accurately predict shoreline retreat related to SLR. We suggest instead that predictions be based on extrapolation of past rates combined with an "expert eye." The shoreline retreat expert eye should be an assessment in the context of local sand supply and expected future changes (dams on rivers, coastal engineering structure emplacement, beach replenishment plans) and a thorough understanding of various geologic constraints.

Periodic updating or revisiting of the qualitative predictions must be a requirement as knowledge of SLR rates improves and as more is learned about geologic and human constraints on the shoreline. One of the greatest difficulties in turning society back to a sound predictive path will be convincing planners and other officials to accommodate this qualitative state of affairs and accept the uncertainty of predictions. This will require major changes in coastal management public policy thinking.

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BIOCHEMISTRY

Water Photolysis in Biology

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One of nature's most fascinating and influential enzymes, the water-plastoquinone photo-oxidoreductase (also known as photosystem II, water-oxidizing complex, and O_2-evolving enzyme), is yielding to x-ray crystallography at last (*1*). This enzyme uses solar energy to drive the reduction of plastoquinone at the start of the photosynthetic electron-transfer chain using electrons stripped from water. This reaction is not only one of the main energy inputs into the biosphere, but also is the source of the oxygen in the atmosphere.

The first x-ray crystallographic structure of this enzyme appeared in 2001 (*2*). This and subsequent structures (*2*–*4*) confirmed the well-established model of the photochemical part of the enzyme, but for the cofactors, at least, the information from spectroscopy, molecular biology, comparative approaches, and modeling remained more precise. For the catalytic site, where water is oxidized, the first generation of crystal structures confirmed the location of the manganese cluster but did not extinguish dissent on the number of manganese ions, their arrangement, and their coordination. Nor was there any sign of the calcium ion that is essential for activity and considered to be integral to the cluster. In short, the first crystal structures provided relatively few new mechanistic insights into the chemistry of water oxidation (*5*–*7*).

The work by Ferreira *et al.* on page 1831 of this issue (*1*) changes all that. It assigns most of the amino acids in the protein, resolves all, or nearly all, cofactors in the re-

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