



50 YEARS AGO

An almost unexplored record of the Earth's history is preserved in the sediment under the great oceans. Profiles of the uppermost layers have been obtained by many different types of corer, and to this list Prof. B. Kullenberg has now added a modified version of his elegant piston corer which should reach deeper than ever before... The new corer carries the same weight as the old model, 1,500 kgm., but has greater penetrating power, because with a length of only 2.3 metres there is a relatively small area of wall in frictional contact with the sediment... The corer sinks down through the sediment to a depth determined by the length of cable wrapped around its upper end. When all this cable has been unwound, the piston, which up to now has been locked at the lower end of the corer, is released and a core is taken. Although this ingenious corer has reached down to 29 m., and is expected to reach 50 m. in soft sediment... there still remains the ultimate problem of how to reach and take a continuous profile of sediment which can be a full kilometre thick. From *Nature* 12 January 1957.

100 YEARS AGO

The issue of *Science* for November 23 contains an article by Prof. McKeen Cattell on the selection, and arrangement in order of merit, of a thousand American men of science... Prof. Cattell also investigates the geographical distribution of American men of science according to place of birth... The production or "birth rate" of men of science per million of the population ranges from about 109 in Massachusetts—which stands far above the other States—and eighty-seven in Connecticut down to rates of only one or two in several of the southern States. It is argued that differences in stock can scarcely be great enough to account for this, and that accordingly the production of scientific men must be largely a matter of circumstance. From *Nature* 10 January 1907.

EVOLUTIONARY BIOLOGY

Genetics and bisexuality

Vincent Savolainen and Laurent Lehmann

A population-genetic model indicates that if there is a gene responsible for homosexual behaviour it can readily spread in populations. The model also predicts widespread bisexuality in humans.

For human societies at large, homosexuality is a sensitive issue. For biologists it is an intriguing one^{1,2}. How can genes influencing homosexual — and so non-reproductive — behaviour be favoured by natural selection? An answer is offered by Gavrillets and Rice in a paper that has just appeared in *Proceedings of the Royal Society*³. They provide a population-genetic analysis that explains why, in theory, a gene predisposing an individual to homosexual behaviour would spread in a population, and that predicts its widespread occurrence in humans and other sexually reproducing species.

No predisposing gene for homosexual behaviour has been identified, but there is evidence that genetic controls are involved: for example, human twins are more likely both to be gay compared with non-identical brothers; and male homosexuality is more often inherited maternally, indicating that heritable maternal effects and/or genes linked to the X chromosome are in operation^{2,3}. However, unlike heterosexuals, who devote a significant amount of time to reproductive sex, homosexuals are involved in non-reproductive sex, hampering the direct transmission of any gene underlying this behaviour. Homosexuality has a cost to fitness — that is, the ability of an individual to produce offspring that survive and reproduce — and it can only evolve if it otherwise provides indirect benefits to reproduction.

Three main mechanisms have been proposed in which variety in genes controlling homosexuality could be maintained in a population: overdominance, sexually antagonistic selection, and kin altruism²⁻⁴. For simplification, we will consider here male homosexuality, but these mechanisms also apply to female homosexuality. They also apply no matter how many genes contribute, but Gavrillets and Rice's analysis deals with a single theoretical gene and its two variants (alleles).

First, in the case of overdominance, a 'gay allele' would result in homosexual behaviour in an individual who has received this allele from both parents (homozygous), but would provide an advantage to the heterozygote (where only one parent has transmitted the gay allele). This situation would be similar to the renowned example of sickle-cell anaemia in Africa, a genetically inherited disease controlled by a deficient allele. Homozygotes for this allele suffer severe disorders. But because this allele confers resistance to malaria when heterozygous, it is maintained in human populations exposed to malaria. Under this scenario, heterozygotes

for the gay allele may have higher success in attracting females and/or their sperm may have some competitive advantage⁵.

In the second case, sexually antagonistic selection, a gay allele would result in a cost when expressed in males ('feminization' and loss of fitness), which would be counter-balanced by a fitness advantage when it is expressed in females.

In the third hypothesis, kin altruism, homosexuals would help their own family members, increasing the fitness of their relatives and therefore the probability that a gay allele is passed on to the next generation^{2,4}.

These hypotheses have previously been speculative, but they have now been modelled and formalized by Gavrillets and Rice³. The authors adapted the classical population-genetic equations established by J. B. S. Haldane^{6,7} and describe the evolution of the frequency of two alleles at one locus, in large populations for which each allele may result in sex-specific effects on fitness. Considering hypothetical straight and gay alleles, Gavrillets and Rice document the conditions of relative costs and benefits to fitness under which the gay allele can enter a population of straight alleles and be maintained subsequently. They establish the conditions under both the overdominance and sexually antagonistic-selection hypotheses for a homosexual gene that would be located on autosomes (non-sexual chromosomes) or on the X chromosome. These conditions still remain to be evaluated in the kin-altruism hypothesis.

Crucially, in these population-genetic models, a gay allele will produce variable degrees of homosexual behaviour, which is equivalent to the fitness cost of that behaviour (which, for example, could be interpreted as the proportion of time devoted to homosexual rather than reproductive sex). If one homozygous individual is not at all involved in reproductive sex, then the cost of homosexuality is maximal and this individual's phenotype is obviously strictly gay; however, in all other combinations, homozygous individuals exhibit a degree of bisexual behaviour depending on the costs.

Gavrillets and Rice show that, for a large set of costs and benefits, the gay allele can invade a population. Under overdominance, once a gay allele has entered a population it will be maintained in a polymorphic equilibrium, and this is easier if the homosexual gene is autosomal rather than X-linked. Further, under sexually antagonistic selection, the gay allele may even

go to fixation — that is, each individual will become homozygous for this allele — thus implying widespread bisexuality.

This theoretical framework³ is an advance in evolutionary biology and studies of human behaviour because it generates several testable predictions: for example, if a gene influencing homosexuality is linked to the X chromosome, then it would support the sexual-antagonism hypothesis rather than overdominance. The framework will be used to guide research on the genetic basis of male and female homosexuality, and will help in resolving the 'Darwinian

paradox of male homosexuality'². But it is of course theory only. Tasks for the future are to establish more precisely the costs and benefits of such behaviour in natural populations¹. Such knowledge will help fine-tune these models of sexual orientation and show whether overdominance or antagonistic selection has been operating in mammals and throughout human history. ■

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OCEANOGRAPHY

A marine nitrogen cycle fix?

Douglas G. Capone and Angela N. Knapp

Some of our suppositions about the marine nitrogen cycle may be wrong. An innovative analysis of nutrients at the ocean's surface reveals a feedback mechanism that might hold the whole cycle in balance.

The flow of nitrogen compounds between the oceans and the atmosphere is central to life, as nitrogen is a fundamental component of biomass and is essential for many biological processes. Although we have learned much about the nitrogen cycle of the oceans, two burning questions remain unanswered: is the marine nitrogen budget currently in balance, and are the processes that add and remove nitrogen to and from the seas closely linked? On page 163 of this issue, Deutsch *et al.*¹ provide evidence that the primary process responsible for putting nitrogen compounds into the sea — biological nitrogen fixation — is intimately associated, both geographically and temporally, with marine nitrogen removal. Furthermore, their work implies that the ratio of nitrogen to phosphorus in sea water may be the central factor that regulates nitrogen fixation.

Biological nitrogen fixation — the enzyme-catalysed reduction of nitrogen gas (N_2) — continually adds nitrogen to the sea in the form of compounds that can be used as nutrients. Nitrogen fixation is commonly associated with certain cyanobacteria that inhabit the warm, sunlit surface waters of low-latitude oceans². These photosynthetic bacteria can tap the immense reservoir of dissolved N_2 gas in sea water, but their growth is often limited by the scarcity of other nutrients such as phosphorus and iron².

Fixed nitrogen is eventually converted to nitrate by nitrifying bacteria. Ultimately, the loss of nitrogen from the ocean occurs by denitrification, a process that converts nitrogen compounds such as nitrate back to N_2 . Denitrification occurs mostly at depths of 200–700 metres in the 'oxygen minimum zones' (OMZs) of the ocean — that is, in the eastern tropical north Pacific, the eastern

tropical south Pacific and the Arabian Sea — and in marine sediments^{3–5}.

Nitrogen fixation and denitrification are generally assumed to dominate the flows of nitrogen into and out of the ocean^{3,4,6}. Some estimates suggest that the rate of marine denitrification substantially exceeds that of nitrogen fixation^{3,4}. However, if this is the case, the ocean

would be progressively depleted of biologically available nitrogen, which is not supported by geochemical evidence⁵. If we accept that, in the oceanic nitrogen cycle, sources need to balance sinks^{5,6}, then either the inputs are underestimated or the outputs are overestimated.

For the inorganic compounds dissolved in deep ocean water, the ratio of nitrogen to phosphorus is expected to be about 16:1, as noted by the oceanographer Alfred Redfield⁷ in the early 1930s. Several of Deutsch's co-authors have previously analysed inorganic nutrients in oceanic subsurface waters, using a parameter N^* to discern areas with nitrogen-to-phosphorus ratios higher or lower than the 'Redfield' ratio⁸. They discovered large regions that have elevated nitrogen-to-phosphorus ratios, particularly in the north Atlantic, and speculated that these nutrient patterns resulted from the subsurface

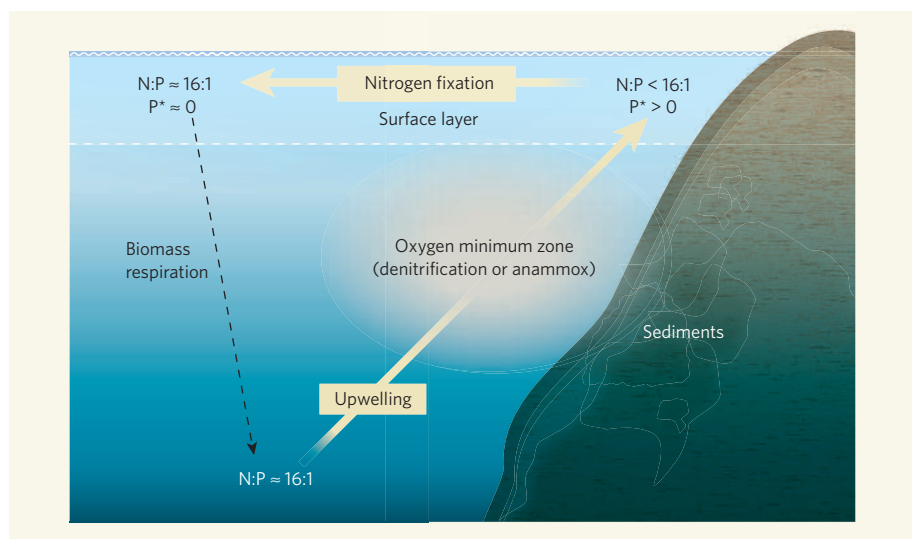


Figure 1 | Coupling between marine nitrogen fixation and denitrification zones. Nitrogen enters the marine nitrogen cycle by 'fixation' when microbes at the ocean's surface convert nitrogen gas (N_2) into biomass. This biomass may then release nitrogen compounds into the ocean. Denitrification and 'anammox' processes remove nitrogen from the sea by converting inorganic nitrogen compounds into N_2 ; this occurs in the 'oxygen minimum zones' (OMZs) of deeper waters and in marine sediments. The expected ratio of nitrogen to phosphorus in the deep ocean is about 16:1. Deutsch *et al.*¹ define a parameter P^* that identifies deviations of relative phosphorus levels from this ratio. In upwelling waters in contact with OMZs, the nitrogen-to-phosphorus ratio is less than 16:1, and surface waters over the OMZs have an excess P^* ($P^* > 0$). As these surface waters flow offshore, the 'excess' of phosphorus decreases back to the expected ratio ($P^* \approx 0$), presumably as nitrogen fixers extract phosphorus without absorbing any nitrogen compounds. Residual nitrogen and phosphorus compounds are used by phytoplankton, which redeliver some of these compounds, with a nitrogen-to-phosphorus ratio of about 16:1, to the deep sea.