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Fall and Rise of the Black Sea Ecosystem

Ahmet E. Kideys

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Coupled with model simulation results, multiproxy reconstructions can elucidate the roles of natural and anthropogenic forcing in past climate change and inform our assessment of likely future changes. Simulations using a moderate sensitivity to radiative forcing (1.5° to 2.5°C for CO_2 doubling) (*9*, *17*–*19*) show a close overall agreement with multiproxy temperature reconstructions (see the figure). One of these simulations, which incorporates an interactive carbon cycle model, has been shown to reproduce observed preanthropogenic natural variations in CO_2 concentration (*17*), providing an independent verification of the model's sensitivity and temperature history. Simulations incorporating the effects of human land-use changes (*18*, *19*) provide the best agreement with reconstructions and instrumental data during the 19th and 20th centuries.

A NH extratropical, continental summer temperature tree-ring reconstruction (*5*) exhibits significantly greater cooling at various times than is evident in any multiproxy or model estimates (see the line in the figure). This discrepancy probably arises, at least in part, from enhanced extratropical continental responses to forcing, including the enhanced summer continental cooling signature of volcanic forcing.

The spatial and temporal details of climate changes during the past millennium should become increasingly better resolved through expanded and improved networks of multiproxy data. It should therefore soon be possible to use high-resolution reconstructions of the past 500 to 1000 years or so as a template for calibrating networks of longer-term, lower-resolution proxy data. This possibility holds prospects for reconstructing the spatial details of climate changes over several millennia, potentially resolving key details regarding the climate changes of the entire postglacial period of the past 10,000 years.

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PERSPECTIVES: ECOLOGY

Fall and Rise of the Black Sea Ecosystem

Ahmet E. Kideys

During the 1980s and early 1990s, the Black Sea ecosystem was in a catastrophic condition [for reviews see (*1*–*4*)]. The deterioration of this ecosystem was the result of two principal factors: eutrophication (that is, nutrient enrichment due to domestic or agricultural waste) and invasion by the comb jelly *Mnemiopsis* (see the figure, bottom). These factors were exacerbated by pollution and overfishing. Remarkably, since the mid-1990s, the impact of both eutrophication and *Mnemiopsis* has declined and virtually all ecosystem indicators now show signs of recovery (*5*), suggesting that the Black Sea has returned to a healthier state. The rapid recovery of this large inland sea is encouraging for other marine ecosystems, most notably that of the Caspian Sea, which is itself currently under threat.

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Despite its relatively large surface area (423,500 km^2) and water volume (537,000 km^3), only a thin surface layer (about 10% of the average total depth) of the Black Sea supports eukaryotic life. The water mass below 150 to 200 m is devoid of dissolved oxygen, making the Black Sea the largest anoxic body of water in the world. Such anoxic conditions, exacerbated by limited water exchange with the Mediterranean, render the Black Sea extremely vulnerable to anthropogenic effects. The Black Sea is bounded by a narrow coastal strip along the southern and eastern coasts, and its northwestern region (covering about 25% of the entire basin) has a wide continental shelf with a depth of less than 200 m. Three rivers—the Danube, the Dnieper, and the Dniester—fed by a drainage basin of >2 million km^2 in the northwestern/northern region are responsible for about 85% of total riverine input to the Black Sea (about 340 km^3/year) (*1*).

In the 1970s and 1980s, increased nutrient input via the major rivers during the agricultural revolution in Iron Curtain countries resulted in strong eutrophication of the shallow northwestern/northern Black Sea. The concentration of inorganic phosphorus and nitrogen measured at the mouth of the Danube increased from 0.3 µM and 1.6 µM, respectively, during 1960–1970 to 6.4 µM and 13.6 µM, respectively, during 1976–1980 (*6*). Although phosphorus and nitrogen increased, the amount of silicon decreased (from 36.7 µM to 30.6 µM). Given that silicon has a strong affinity for particulate matter in sea water, this decrease seemed to reflect a diminution of solid flow due to the numerous dams built on the Danube and its tributaries (*7*).

Differential changes in the quantities of these essential nutrients were accompanied initially by alterations in the composition and quantity of pelagic primary producers (phytoplankton) and later of other food chain components. There were several adverse events in the northwestern/northern Black Sea, but not eastern coastal and deep regions—there was an increase in number and peak abundance of phytoplankton blooms including several red-tide events (*7*), modification of the phytoplankton composition in favor of flagellates (*6*), decreased oxygen concentration and expansion of hypoxia (*3*), reduced transparency of the water column (*8*), a decrease in nongelatinous zooplankton (*9*), mass mortality among the entire benthos (*4*), demersal and pelagic fish populations (*10*), and a decrease in overall biodiversity (*3*).

During the summer of 1978–1986, the mean surface chlorophyll concentration in the northwestern/northern Black Sea exceeded that in deeper regions by a factor of about 18, a difference clearly visible from satellite data (*11*). Despite increases in the northwestern/northern regions of chlorophyll a (evaluated by Secchi disk depth, a measure of the water's transparency), inorganic phosphate, primary production and phytoplankton biomass (*12*), there were no reports of dele-

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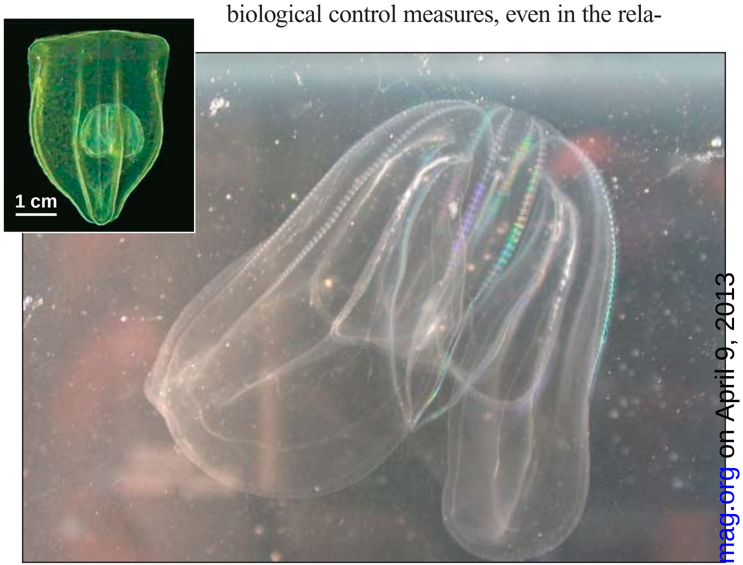
terious eutrophication in the eastern coastal and deeper Black Sea regions. However, data do suggest that in the 1940s the oligotrophic state of these regions (*13*) gave way to a eutrophic state in the northwestern shelf and a mesotrophic state in the east, resulting in increased primary production. This increase in fertility (trophic level) boosted catches of the anchovy *Engraulis encrasicolus* (a major plantivorous fish) particularly in the southern/eastern Black Sea during the 1970s and 1980s (*4*, *5*, *14*, *15*).

In the early 1980s, the comb jelly *Mnemiopsis* (*M. leidyi* or *M. mcradyi*), a ctenophore that normally resides off the eastern United States, was accidentally introduced into the Black Sea via ballast waters from cargo ships. This voracious zooplanktonic predator reached enormous biomass levels (>1 kg m^{-2}) in the summer of 1989 (*16*), devastating the food chain of the entire Black Sea basin. After the ctenophore bloom, there were sharp decreases in the anchovy catch (*4*) and in the biomass of nongelatinous zooplankton in all Black Sea regions (*5*, *9*). Nongelatinous zooplankton remained low for several years and then in 1994 showed a modest increase that was quickly followed by a secondary *Mnemiopsis* bloom a year later (*5*). Before the untimely arrival of *Mnemiopsis*, the anchovy was the major consumer of nongelatinous zooplankton. By feeding on the food supply of the anchovy as well as on its eggs and larvae (*17*), *Mnemiopsis* induced the collapse of the pelagic fish population leading to untold economic damage to the Turkish fishing industry. By devouring herbivorous zooplankton, *Mnemiopsis* indirectly caused a further increase in phytoplankton biomass and primary productivity within the entire Black Sea basin (*5*). The eutrophication indices for all regions of the Black Sea peaked in 1992, 3 years after the primary *Mnemiopsis* bloom.

The total nutrient input from rivers finally stabilized or even decreased after the mid-1980s when concentrations of inorganic nitrogen and phosphorus were measured as 6.9 μM and 6.5 μM, respectively (*6*), decreasing again to 6.0 μM and 2.3 μM, respectively, during the 1991–1997 period. These decreases may have been due to the weak economies of ex-Iron Curtain countries, and the introduction of several national and international programs aimed at decreasing eutrophication in countries that border the Black Sea and River Danube. Decreases in nutrient input were immediately reflected in measurements of nutrients from coastal waters (*7*). Phytoplankton biomass declined markedly and became weighted in favor of diatoms, both indications of a healthier ecosystem (*18*, *19*). Cases of fish mortality due to algal blooms decreased from more than eight species in the 1980s to only two in the 1990s. Many zooplankton (for example, the copepods *Pontella mediterranea* and *Centropages ponticus*) and fish species (such as the bluefish *Pomatomus saltatrix* and the turbot *Psetta maxima maeotica*) reappeared (*20*). A decrease in nutrient input was the main reason for improved conditions in the northwestern shelf of the Black Sea in the late 1990s. After 1992, several eutrophication indices (surface chlorophyll, inorganic phosphate levels, water transparency, nongelatinous zooplankton biomass, fish landings) also improved in the eastern and deep Black Sea, indicating recovery within the entire ecosystem despite the continued abundance of *Mnemiopsis* (*5*).

The appearance in 1997 of a predator of *Mnemiopsis*, the ctenophore *Beroe* (*B. ovata* or *B. cucumis*), helped the ecosystem to recover further. Perhaps also arriving in ballast waters of cargo ships from the northwestern Atlantic, *Beroe* feeds almost exclusively on *Mnemiopsis* (see the figure, top) (*21*). With the arrival of *Beroe*, the year-round abundance (apart from a brief peak in late summer) of *Mnemiopsis* dropped precipitously (*22*). After the decline in *Mnemiopsis*, *Beroe* itself almost disappeared from the water column, indicating its dependence on *Mnemiopsis* for its food supply. The *Mnemiopsis* population crash led to increases in nongelatinous zooplankton, anchovy landings (*23*), egg densities of anchovy (*15*), as well as increases in the biomass of two native gelatinous cnidarians (*Rhizostoma pulmo* and *Aurelia aurita*) (*24*).

Both eutrophication and the arrival of invasive species are common problems for many of the world's seas and oceans. *Mnemiopsis* and to a certain extent eutrophication are also a problem for the neighboring Caspian Sea. The Caspian Sea is similar to the Black Sea in terms of surface area (about 400,000 km^2), low salinity, and large catchment area (about 3.5 million km^2). It is fed by the River Volga (which provides 82% of total riverine inflow) and supports a large-scale fishery that catches small pelagic fish such as the kilka (*Clupeonella* spp.) (*25*). However, unlike the Black Sea, the Caspian Sea has no water exchange with other oceans rendering it even more susceptible to anthropogenic impacts, especially the effects of invasive species (*26*). *Mnemiopsis*—transported in the ballast waters of cargo ships traversing the Volga-Don canal during the second half of the 1990s (*27*)—has already caused appreciable damage to the Caspian Sea's zooplankton population (*28*) and its valuable kilka stocks (*29*). Endemic species, such as the white sturgeon (*Huso huso*) and Caspian seal (*Phoca caspica*) that feed mainly on kilka, are now under serious threat because of the *Mnemiopsis* invasion. However, the effectiveness of de-eutrophication and biological control measures, even in the relatively large ecosystem of the Black Sea and over a comparatively short period, provide encouraging news for the Caspian Sea and for other aquatic environments that are suffering from catastrophic threats.



Invading the invader. (Bottom) The arrival of the Northwestern Atlantic ctenophore (comb jelly) *Mnemiopsis* in the Black Sea via the ballast waters of cargo ships in the early 1980s devastated the natural ecosystem of this marine environment. **(Top)** *Beroe* species of ctenophore are the natural predators of *Mnemiopsis*. The arrival of *Beroe* in the Black Sea in 1997 resulted in control of the *Mnemiopsis* population and contributed to recovery of the Black Sea ecosystem. In this photograph, a *Beroe* ctenophore has ingested the smaller *Mnemiopsis*, which is visible inside its gut cavity.

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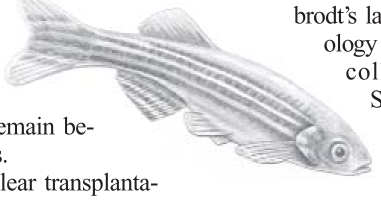
PERSPECTIVES: GENETICS AND DEVELOPMENT

Zebrafish in the Spotlight

Suresh Jesuthasan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The policewoman at the entrance to the University of Wisconsin, Madison, could hardly believe the logo on the meeting T-shirt: "You mean all these people came here to talk about a little fish?" Pioneers of the zebrafish as a model organism would probably share her surprise. At the first zebrafish meeting 10 years ago, there were fewer than 190 abstracts and the big discussion points were two developmental mutants, *spadetail* and *cyclops*. In contrast, this year's zebrafish conference featured more than 500 abstracts that discussed a wide variety of mutants and topics as diverse as learning and memory, infectious diseases, wound healing, growth control, circardian clocks, and lipid biochemistry (*1*).

With this diversity of material, it is no surprise that the talks grabbing the most attention were those reporting technical advances, particularly improved methods for manipulating gene expression and inducing targeted mutations in zebrafish. Karen Urtishak (Steve Farber's lab, Thomas Jefferson University) described a new reverse genetics tool using modified peptide nucleic acids (MPNAs) to selectively shut down the production of individual proteins. The effectiveness of MPNAs for targeted gene disruption compares well with that of morpholino antisense oligonucleotides, which were introduced at the previous zebrafish meeting two years ago. By preventing translation (knockdown) of targeted proteins, morpholinos have revolutionized our ability to test the function of genes. MPNAs (18 base pairs in length) that are complementary to specific genes such as *chordin* or *uroD* effectively prevent translation of the mRNAs encoded by these genes, resulting in abnormal development of embryos that resemble mutants. MPNAs are highly specific—mismatches of just two bases produced no phenotype (visible alteration). Although potent, these reagents are costly, and large-scale knockdown screens, in which the function of all known and predicted genes is tested by MPNA or morpholino injection, remain beyond the reach of most labs.

Cloning of fish by nuclear transplantation using donor nuclei from blastomeres has been carried out successfully in China for 50 years (*2*). Ki-Young Lee (Shuo Lin's lab, University of California, Los Angeles) reported the cloning of viable, fertile zebrafish using a zebrafish fibroblast cell line as the source of donor nuclei. The advantage of using this cultured cell line is that the zebrafish genome can be manipulated prior to cloning. In fact, Shuo Lin's group has obtained transgenic fish by transplanting nuclei from a retrovirally transformed zebrafish cell line into wild-type fish eggs. The obvious next step—transplantation of nuclei containing homologously recombined DNA—is probably one of the most eagerly awaited technical developments in the zebrafish field because it will allow the production of fish in which the expression of one or a few genes can be switched on and off at will.

Despite the unavailability of zebrafish embryonic stem cells, it is already possible to induce mutations in any given gene, as revealed in talks by representatives from the labs of Ron Plasterk (Hubrecht Laboratory) and Cecilia Moens (Fred Hutchinson Cancer Center). Plasterk's group, in collaboration with Artemis Pharmaceuticals/Exelixis Deutschland, has sequenced the *Rag-1* gene of more than 4000 F_1 progeny of fish treated with the mutagen ethylnitrosourea (ENU). Of the 15 different point mutations found in the *Rag-1* gene, one caused a premature stop codon rendering the Rag-1 protein inactive. As Erno Weinholds reported, mutant fish homozygous for this mutation were deficient in V(D)J recombination of immunoglobulin genes and presumably, like mammals carrying *Rag-1* mutations, were unable to produce antibodies. Bruce Draper from Moens's group reported on their efforts to develop a high-throughput method for identifying point mutations, borrowing the TILLING method (targeted induced local lesions in genomes) from the *Arabadopsis* world (*3*). In this approach, the CEL I endonuclease is used to identify ENU-induced point mutations in DNA from frozen F_1 fish. Clemens Grabher (Jochen Wittbrodt's lab, European Molecular Biology Laboratory) described their collaboration with Jean-Stephan Joly's lab (CNRS) to develop another method for manipulating the zebrafish genome using a meganuclease to increase transgenesis rates and improve reporter gene expression. By coinjecting the meganuclease with DNA plasmids containing a reporter gene flanked by restriction sites, germline transmission rates of up to 50% (and even nonmosaic expression) were obtained.

Many groups are using the zebrafish to answer interesting biological questions. Joseph Yost (University of Utah) described how forerunner cells—a mysterious cell population that appears in the dorsal side of the embryo during gastrulation—are essential for establishing left-right asymmetry in the developing zebrafish. These cells express mRNA encoding left-right dynein and eventually form a spherical structure called the Kupfer's vesicle. Cilia in this vesicle all beat in the same direction in wild-type zebrafish embryos, possibly establishing a gradient of growth factors within the embryo that may be responsible for establishing left-right asymmetry. Loss of forerunner cells or the Kupfer vesicle cilia abolishes left-right asymmetry in the developing zebrafish.

Christoph Seiler and Samuel Sidi (Teresa Nicolson's lab, Max Planck Institute for Developmental Biology) discussed zebrafish circler mutants that are unable to keep their balance. These investigators have applied positional cloning to the circler mutants and have identified mutations in an adhesion protein and ion channel. The Nicolson lab has strikingly combined physiological analysis (specifically microphonics, which measures the extracellular potential of sensory hair cells), genetics, and microscopy, to unravel the function of these two proteins. They show that the adhesion protein and ion channel are both required for the mechanotransduction activity of sensory hair cells in the zebrafish inner ear, where they help maintain balance, and in the skin, where they detect motion in the water. Indeed, the ability to combine in

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