The Restoration Potential of the Mesopotamian Marshes of Iraq
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The fraction of titles that have survived from Antiquity has been even more uncertain. Present results suggest that a substantial proportion of the more popular texts circulating in the early Middle Ages probably has survived. If a dozen parchment copies of any one of the four Bede texts existed in Carolingian times, and if each copy has had a one-in-seven chance of surviving to the present, the likelihood is greater than 80% that at least one of these would survive today, and thus that the text itself would survive. If a population of a potentially popular text such as those in Table 1 started with $M_0 = 1$, so that the unlimited birth-and-death process would apply as an approximation, the text would have roughly a $\mu/\lambda \leq 0.07$ chance of ultimate extinction (*3*). Thus, if all 35 of the mostly nontechnical works that Bede lists in his *Historia Ecclesiastica Gentis Anglorum* (731 A.D.) (*15*) likewise had an extinction probability of $\mu/\lambda \leq 0.07$, one might expect no more than two or three to be extinct. In fact, three are extinct (*16*), suggesting that present results apply as an approximation to Bede's nontechnical as well as technical works, and quite possibly to contemporary textbooks in general.

Taken together, present results suggest that many if not most scientific and technical works that circulated in Latin on parchment in the early Middle Ages or even in late Antiquity survive in some form. But why then have so few actually survived from Antiquity? For instance, only one of seven works by Pliny the Elder and only a small fraction of the approximately 2000 works on which he based his *Naturalis Historia* (77 A.D.) (*17*), the foremost scientific encyclopedia of the Middle Ages, have survived. The answer may lie in copyists' changeover from papyrus to parchment during the third and fourth centuries (*18*). Surviving texts may be mostly those similar to Pliny's (*19*), which happened to have been in demand during and soon after the transition to the new and more durable medium.

Only further research will tell how accurate or how representative present estimates are. The important point is the apparent feasibility of quantitatively investigating the dynamics of knowledge transmission in ancient and medieval times by demographically analyzing centuries' worth of accumulated paleographic data.

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Supporting Online Material
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The Restoration Potential of the Mesopotamian Marshes of Iraq

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Uncontrolled releases of Tigris and Euphrates River waters after the 2003 war have partially restored some former marsh areas in southern Iraq, but restoration is failing in others because of high soil and water salinities. Nearly 20% of the original 15,000-square-kilometer marsh area was reflooded by March 2004, but the extent of marsh restoration is unknown. High-quality water, nonsaline soils, and the densest native vegetation were found in the only remaining natural marsh, the Al-Hawizeh, located on the Iranian border. Although substantially reduced in area and under current threat of an Iranian dike, it has the potential to be a native repopulation center for the region. Rapid reestablishment, high productivity, and reproduction of native flora and fauna in reflooded former marsh areas indicate a high probability for successful restoration, provided the restored wetlands are hydraulically designed to allow sufficient flow of noncontaminated water and flushing of salts through the ecosystem.

The Mesopotamian marshes of southern Iraq (30° to 33°N, 45° to 48°E) are considered by many to be the "cradle of western civilization" and are often referred to as the Garden of Eden (*1*, *2*). Their ecological and cultural value derive from their large expanse of wetland habitat in southwest Asia, once covering nearly 15,000 km^2 (*3*, *4*) (Fig. 1A). Unique to the Mesopotamian marshes is the indigenous population of marsh dwellers, commonly called the Marsh Arabs, who already have a special place in the anthropological and cultural literature for their alluring way of life, living in harmony in relative isolation within the marsh environment for the past 5000 years on man-made reed islands and along the periphery of the marshes (*1*, *5*, *6*). Notably, the marshes were once the permanent habitat for millions of birds and a flyway for millions more migrating between Siberia and Africa (*7*, *8*).

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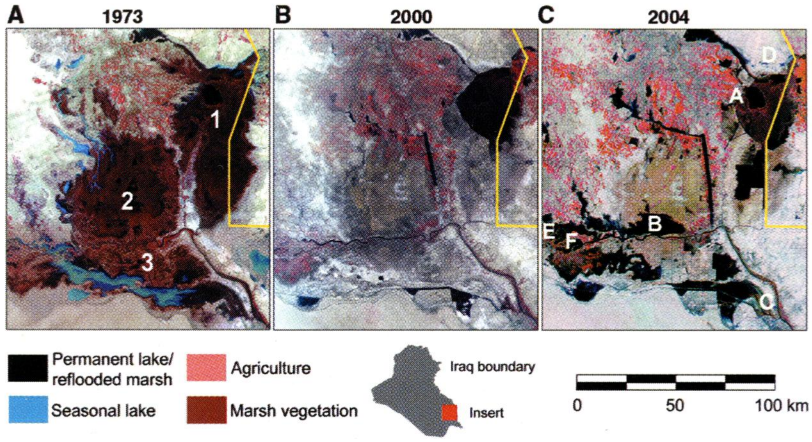

Fig. 1. (**A**) A composite satellite view of the Mesopotamian marshlands from Earth observation Landsat scenes taken in 1973 to 1976 from a mosaic of 4 Landsat 1 and 2 false-color, near-infrared images (*3*). Dense marsh vegetation [mainly *P. australis* based on field observations in 1970s (*29*)] appears in dark red, seasonal lakes in blue, agriculture in pink, and permanent lakes in black. The red elongated patches along riverbanks are date palms. The three main marsh areas are the Al-Hawizeh, Central marsh, and Al-Hammar, labeled on the map as 1, 2, and 3, respectively. (**B**) In this Landsat 7 Enhanced Thematic Mapper (*3*) mosaic taken in 2000, most of the drained marshes appear as grayish brown patches indicating dead marsh vegetation or low shrub desert plants and dry ground. The very light to gray patches are bare areas with no vegetation and in some areas indicate salt evaporites or shells covering the bottoms of former lakes as we discovered in 2003. The drained former marsh area (shown in brown, gray, and white) indicates that 85% of the 8926 km² of permanent marsh shown in 1973 marshlands (A) had been destroyed by 2000. Only 3% of the Central marsh and 14.5% of the Al-Hammar remained in 2000 (*3*). The largest expanse (≅1025 km²) of the remaining natural marsh Al-Hawizeh near the Iranian border is shown in dark red. To complete this destruction the Glory River, shown as a straight line canal across the top and down the east side of the Central marsh, was constructed by the Hussein Regime in 1993 to completely dry up the Central marsh by stopping water inflow from the Tigris River. (**C**) February 2004 false-color image of the remaining Mesopotamian marshlands show the areas newly reflooded since the war in black (courtesy of Moderate-Resolution Imaging Spectroradiometer Rapid Response Project at NASA). Reflooded areas adjacent to the Al-Hawizeh, the western area of the Al-Hammar, and waterways in the northern and southern parts of the Central marshes are also clearly visible in black. The Al-Hawizeh (called Hawr Al-Azim by Iran) is the best remaining natural marsh in the region (site A). It straddles the Iraq-Iran border (yellow line). During a field survey in February of 2004, we discovered an Iranian dike under construction that, if completed, will traverse directly through the Al-Hawizeh marsh, along the Iraq/Iranian border and, as a result, will notably reduce the water input from the Karkheh and Karun rivers to the marsh. The ecological affects of this massive water diversion are unknown, but it will substantially impact the last remaining natural marsh system in Iraq. Our sampling sites A to F are indicated on (C) with matching ground photos shown in Fig. 2, A and B, and fig. S1, A to D.

Today, less than 10% of the marshes in Iraq remain as fully functioning wetlands because of extensive drainage and upstream agricultural irrigation programs on the Tigris and Euphrates rivers implemented during Saddam Hussein's regime, particularly from 1985 to 2000 (*3*, *7*). Remnant marshes are located mainly in the northern portion of Al-Hawizeh, which straddles the Iran-Iraq border (Fig. 1A, site 1). Two other marshes, the Central and Al-Hammar located to the west and south, respectively (Fig. 1A, sites 2 and 3), were almost totally desiccated by 2000 (Fig. 1B) (*9*). This environmental disaster has been compared in scale to the drying up of the Aral Sea in Central Asia and to the deforestation of the Amazon (*3*). If substantial portions of the marshes are not restored quickly, 66 bird species may now be at risk (*3*, *8*). Coastal fisheries in the Persian Gulf, which used the marshlands for spawning migrations and nursery grounds for penaeid shrimp (*Metapenaeus affinis*), have drastically declined in numbers (*9*). The marshlands also once served as a natural filter for waste and other pollutants in the Tigris and Euphrates rivers, protecting the Persian Gulf, which is now noticeably degraded along the coast of Kuwait (*3*, *7*, *10*).

Because of limited access until 2003, little is known about the current water quality of river discharges, the ecological conditions of remaining marsh areas, or the potential for the restoration of the drained marshes. This problem was compounded by a loss of historic hydrologic flow data during the looting of local offices of the Ministry of Water Resources. It has been postulated that only 15 to 20% of the drained marshes can be restored as a result of excessive salt buildup, pollution, the dumping of toxic wastes and poisonings during the war, a severe reduction in available water, and a loss of the seed bank of native plant species (*3*, *11*, *12*). Moreover, the long-term quantity of water and sediment available to restore the marshes is uncertain because construction of 32 dams on the Tigris and Euphrates, mainly since the 1960s, substantially altered the marsh hydrology even before Hussein's massive drainage program of the 1990s (*3*). Complicating the marsh restoration are projects such as the massive Ataturk Dam built in Turkey in 1998, which has a reservoir capacity greater than the Euphrates annual flow of 30.7 billion cubic meters at the Turkish border (*3*). A massive dike project observed in the field in February of 2004 along the Iran-Iraq border will add to the problem by cutting off the main water supply to the only natural remaining marsh, the Al-Hawizeh.

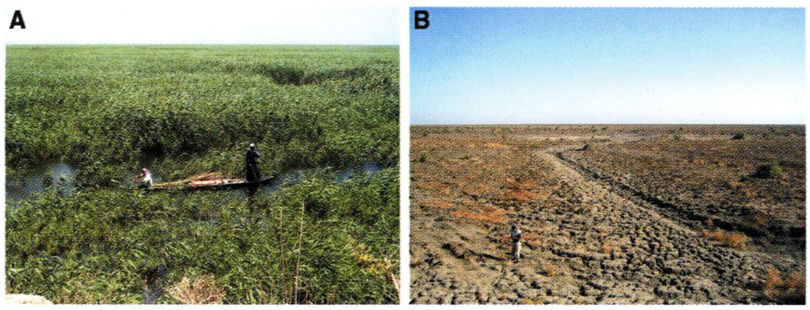

Fig. 2. (**A**) Marsh Arab fishermen collecting reeds (*P. australis*) in the natural Al-Hawizeh marsh (lat 31°38′583″N, long 47°35′203″E) near the Iranian border in June of 2003. (**B**) A view of the totally drained Central marsh near Chibayish (lat 30°58′102″N, long 47°09′033″E) in June of 2003. An Iraqi engineer from the Ministry of Water Resources is viewing the cracked and desiccated marsh soil adjacent to a dried out streambed.

Here, we present an analysis, beginning in June 2003, of soils, water, and ecological conditions for the remaining natural, reflooded, and the totally drained marshes along with an assessment of water constituents in the Tigris and Euphrates upstream and the Shatt Al-Arab downstream of the marshes. The effects of extensive drainage and uncontrolled reflooding on water quality, soil conditions, and ecological recovery are the focus of this study.

Major differences occur in the physical and chemical characteristics (*13*) of the natural (Fig. 2A), drained (Fig. 2B), and reflooded (fig. S1, A and B) marsh soils, as shown by principal component analysis (PCA) in Fig.

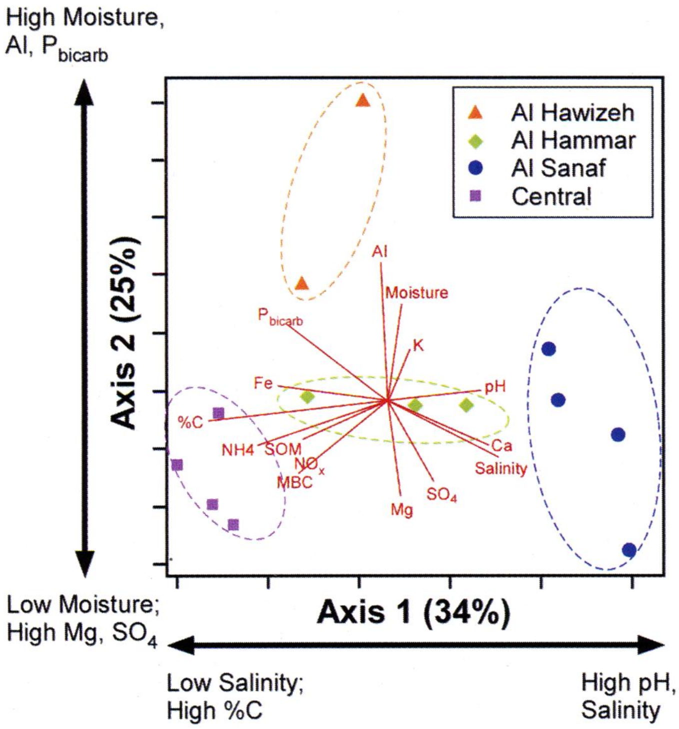

Fig. 3. A PCA of the marsh soils of southern Iraq. Axis 1 accounted for 33.9%, axis 2 accounted for 25.4%, and axis 3 accounted for 13.0% of the total variance. A number of soil properties, including salinity (0.31) and exchangeable calcium (Ca) (0.31), had strong positive loadings on axis 1 and showed distinct differences among marsh sites. Soil properties with strong negative loadings on axis 1 included percentage C (–0.40) and soil organic matter (–0.33) as well as extractable Fe (Fe) (–0.32). Soil moisture (0.33) had a strong positive loading on axis 2. Strong negative loadings on axis 2 occurred for soil organic matter (SOM) (–0.43), MBC (–0.42), NH_4-N (–0.35), and No_x-N (–0.35).

3. PCA on axis 1 separated the reflooded Al-Sanaf marsh (fig. S1B), a diked wetland with no outflow and dominated by stands of the halophyte glasswort (*Salicornia* spp.), from the totally drained Central marsh (Fig. 2B), which was barren of wetland species, primarily on higher soil salinities (26.0 ± 18.6 dS/m versus 10.6 ± 0.9 dS/m, where errors are the standard deviation), lower percentage of carbon (3.5% ± 0.2 versus 7.6% ± 0.6), and soil organic matter (SOM) (7.5 ± 2.2% versus 15.1 ± 1.1%) (Fig. 3). The higher SOM content in the Central marshes (Fig. 2B) supports earlier reports (*1*, *14*) that this area with deeper lakes historically had high plant productivity, with reeds growing up to 8 m in height. Surprisingly, the soil organic matter has not been completely oxidized after nearly a decade of drainage. The highest microbial biomass carbon (MBC) (842 ± 185 mg C/kg soil) was also found in the drained Central marsh, whereas the MBC values of the natural and reflooded marshes were 50% lower. The Central marsh had the highest total soil N and second highest P content (0.53 ± 0.04% N, 794 ± 86 μg/g P) as compared to the Al-Hawizeh (0.30 ± 0.10% N, 935 ± 388 μg/g P), the Al-Hammar (0.27 ± 0.15% N, 618 ± 104 μg/g P), and the Al-Sanaf (0.06 ± 0.03% N, 507 ± 58 μg/g P). We encountered the most vigorous and vast monocultures of native reed (*Phragmites australis*) communities in the Al-Hawizeh (Fig. 2A). This marsh had the highest levels of readily available bicarbonate extractable phosphorus (130 ± 57 μg/g) and soil moisture (41.7 ± 0.3%) and the lowest salinity (1.8 dS/m). The natural marsh was separated on PCA axis 2 from the disturbed marshes along a gradient correlated with Al, Mg, P sulfate (SO_4), and moisture (Fig. 3). These baseline soil chemistry differences support a different geological parent material for the Al-Hawizeh, as suggested by Buringh (*15*). The eastern Al-Hammar marsh (fig. S1A) has high residual soil salinities (17.5 ± 18.8 dS/m) and high sulfur content (extractable SO_4-S, 1.0 ± 0.9 mg/g), which may be responsible for the lack of reestablishment of native vegetation in reflooded areas as of March 2004.

As a second step, we analyzed for the presence of pesticides, polychlorinated biphenyls, polycyclic aromatic hydrocarbons, and potentially toxic metals and assessed salinity of the soils in all four marshes (*13*) to evaluate constraints on future marsh restoration. We found no detectable concentrations of any organic xenobiotics in the marsh soils, which was similar to a study on downstream sediments in 1997 to 1998 (*10*) but in contrast to reports of serious pesticide pollution in the 1980s (*12*). Metal concentrations (*13*) were within normal ranges reported earlier for the marsh soils of Iraq (*14*, *15*). Soil salinity, however, exceeded 16 dS/m in both the Al-Sanaf and eastern portion of Al-Hammar marshes. These levels are severe and suitable only for plants highly tolerant of saline or sodic conditions (*16*, *17*). The presence of main species like halophytic saltbush (*Atriplex* spp.), Athel tree (*Tamarix aphylla*), and glasswort in these two former marshes (fig. S1, A and B) also suggests a soil salinity problem and indicates that these areas will not be easily restored to native marsh vegetation unless saline conditions can be reduced. Only the natural Al-Hawizeh marsh displayed healthy reed vegetation (Fig. 2A) and had salinity concentrations consistently below 2 dS/m, which can be classified as nonsaline. The Central marsh has a wide range (6 to 17 dS/m) of salinities. Salinities ranging from 5 to 10 dS/m will stimulate *Phragmites* seed germination but salinities ≥25 dS/m will inhibit germination (*18*), as well as plant productivity. The yield of most crops such as rice and wheat, which are traditionally grown at the edge of the marshes by the Marsh Arabs (*19*), could also be severely reduced at salinities >8 dS/m (*20*, *21*).

We sampled surface water quality at a number of upstream locations on the Tigris and Euphrates rivers to examine whether concentrations of inorganic and organic chemicals would be detrimental to marsh restoration as well as to determine compatibility with marsh and downstream waters in the Shatt Al-Arab (table S1) (*13*, *22*) [supporting online material (SOM) text]. All upstream and marsh surface waters were highly oxygenated, but O_2 was significantly ($P < 0.05$) reduced in the Shatt Al-Arab, where untreated wastewater is being released from cities, including Basra. Salinity, conductivity, and total dissolved solids (TDS) values were low, and pH was above 7.5 at all sites except for the enclosed Al-Sanaf, where these variables were significantly higher ($P < 0.05$). These findings suggest that the restricted water outflows in the Al-Sanaf coupled with regional evapotranspiration rates in excess of 245 cm/year (*15*) have resulted in extremely high ion concentrations, pH, and TDS values (table S1), similar to those found on highly salinized portions of the Jordan River (*23*). Similar salinity trends in the soils data (Fig. 3) provide strong evidence that even the release of high-quality waters into former marshlands with existing saline soils and without adequate flow will result in failed marsh restoration because of the creation of a highly toxic saline-sodic environment.

Concentrations of most minor constituents (such as Cu, Fe, Ni, and Al) and trace metals (such as As, Cd, Pb, and Rb) (*13*) were low except in the enclosed Al-Sanaf. Of major concern was our finding of high concentrations of Se (12.3 ± 6.4 μg/liter) in Al-Sanaf and in upstream waters, which were more than twice the recommended U.S. national water quality criterion of 5 μg/liter (*24*, *25*). The source of Se is agricultural soil waters drainage, which is then concentrated by evapotranspiration in confined marshes. Water quality standards for Se in both fresh and marine water have been set at 2 μg/liter in many parts of the world to prevent reproductive failures in fish and birds caused by higher food-chain bioaccumulation (*26*). Our findings of high Se in Al-Sanaf and other marsh waters suggest that the placement of waters into fully diked areas may set in motion an insidious mode of toxicity that could have serious consequences for marsh restoration, migratory bird populations, and future agriculture unless prudent management actions are taken in the years ahead to avoid the total containment of waters into holding areas, which concentrate ions under the extremely high evaporative desert conditions.

In February 2004, we established monitoring stations (*13*) in the reflooded marshes of Abu Zarag (western Central marsh, site E in Fig. 1C, and fig. S1C) and Suq Al-Shuyukh (western part of Al-Hammar, site F in Fig. 1C, and fig. S1D) to assess the ecological recovery and restoration status of two former wetlands reflooded in 2003. With Iraqi scientists, we analyzed water quality and surveyed the dominant flora and fauna in the natural Al-Hawizeh to compare with the two reflooded marshes (*13*). Salinity and conductivity values closely followed the dominant cation concentrations (Na^{+1} > Ca^{+2} > Mg^{+2} > K^{+1}), which were significantly lower ($P < 0.05$) in Abu Zarag than in Al-Hawizeh (except for Ca^{+2} and Mg^{+2}) and Suq Al-Shuyukh (table S2). Suq Al-Shuyukh had the highest concentrations of most constituents, which indicates that this reflooded site is more saline and chemically enriched compared with the other two sites (table S2). Notably, Se concentrations were extremely low in both Abu Zarag and Al-Hawizeh and were within recommended standards (*24–26*) at Suq Al-Shuyukh. Overall water quality at Abu Zarag and Al-Hawizeh was similar because both now receive higher quality Tigris waters. However, our current water chemistry values (table S2), when compared with a historical survey completed before drainage in the Al-Hammar marsh (*14*, *27*), revealed an increase in conductivity (240%), TDS (140%), Na^{+1} (170%), Mg^{+2} (158%), Ca^{+2} (240%), Cl^{-1} (160%), and HCO_3^- (180%) in the Suq Al-Shuyukh region during the past 20 years. In contrast, measured salinities in 1981 (*14*) from seven locations in the Central marsh averaged 0.6 (±0.4) mS/cm, values very similar to our current measurements at Abu Zarag (table S2). Collectively, our studies indicate that the reflooded portions of the western Al-Hammar at Suq Al-Shuyukh (table S2) and eastern Al-Hammar (Fig. 3) have experienced substantial increases in saline conditions. The long-term effects of this level of salinity increase are unknown, but present levels are within the normal variation between wet season and dry season found with the marshes (*28*, *29*). The cause for this marked increase is unknown but probably relates to a rise in salinity in the Euphrates as well as increased flux into the water column of ions concentrated in the soil after 10 years of drainage and evaporation. In the case of eastern Al-Hammar, an increased influence of tidal seawater flowing from the Shatt Al-Arab into the marsh has also occurred from breaches in dikes in 2003 and may be preventing reestablishment of freshwater marsh species (fig. S1A).

Our summer ecological survey (*13*) (SOM text) completed one year after reflooding indicates that water flowing into the marshes from the Euphrates and especially the Tigris is of higher quality than we originally hypothesized, and as a result, early successional stages of marsh restoration are occurring in a number of drained former marshes (Fig. 1C, sites E and F, and fig. S1, C and D). The reflooding of Abu Zarag with Tigris water has resulted in better water quality, higher algal productivity, and more diversity of plant and bird species than at Suq Al-Shuyukh, which receives higher salinity Euphrates water (tables S2 and S3). Both marshes show partial reestablishment of many of the dominant plant species, but biomass and species numbers are low compared with historical records at Suq Al-Shuyukh (*29*). Chlorophyll a concentrations reveal mesotrophic conditions (table S3) at all sites, which are within historic values except for Suq Al-Shuyukh (*14*). Abu Zarag, the site with the lowest salinity, Na^{+1}, Cl^{-1}, and TDS has the highest chlorophyll a concentrations and concomitantly the highest O_2 production (tables S2 and S3). Our macrophyte analysis indicates that *P. australis*, as in the past, is the dominant macrophyte species. Many key amphibian, fish, bird, and mammal species are not yet present or, if present, are in lower numbers, especially at Suq Al-Shuyukh (table S3).

We conclude that restoration is proceeding in the two marshes but at different rates and species composition. Unknown is the fate of the many highly threatened species (*2*, *3*) of the marshlands and the future of these restored marshes as a major flyway for Asia's wintering wildfowl. Here, the quality of water and food supplies as well as the diversity of communities, including mature habitats, will be critical to the return of many of these species. For example, our main observations of otter (*Lutra lutra*) were only from the natural Al-Hawizeh. The high water quality, low salinity, and the presence of permanent lakes and dense vegetation in the remaining natural Al-Hawizeh marsh give hope that this area can function both as a refugium and native repopulation center for the region, provided it is not desiccated by Iran's dike construction activities.

Because future water supplies for marsh restoration may be limited by upstream dams, soil conditions need to be carefully monitored before reflooding new areas to prevent the establishment of saline-sodic soil conditions that will impede marsh revegetation, as seen at eastern Al-Hammar (fig. S1A) and Al-Sanaf (fig. S1B). Severe water quality degradation may be avoided in some reflooded marsh areas if they are hydraulically designed to allow enough high-quality water to flush salts from the ecosystem. Of concern from our study is the potential for the bioaccumulation of Se up the food chain, which could result in severe toxic effects in the marshes for higher trophic levels (*24*). Finally, it is unknown if sufficient water supplies can be made available, especially in drought years, to maintain long-term successful marsh restoration over large areas. However, the high quality of water, the existing soil conditions, and the presence of stocks of native species in some regions indicate that the restoration potential for a substantial portion of the Mesopotamian marshes is high. The stakes are also high: The future of the 5000-year-old Marsh Arab culture and the economic stability of large portions of southern Iraq are dependent on the success of this restoration effort.

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Supporting Online Material
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Genotypic Diversity Within a Natural Coastal Bacterioplankton Population

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The genomic diversity and relative importance of distinct genotypes within natural bacterial populations have remained largely unknown. Here, we analyze the diversity and annual dynamics of a group of coastal bacterioplankton (greater than 99% 16*S* ribosomal RNA identity to *Vibrio splendidus*). We show that this group consists of at least a thousand distinct genotypes, each occurring at extremely low environmental concentrations (on average less than one cell per milliliter). Overall, the genomes show extensive allelic diversity and size variation. Individual genotypes rarely recurred in samples, and allelic distribution did not show spatial or temporal substructure. Ecological considerations suggest that much genotypic and possibly phenotypic variation within natural populations should be considered neutral.

Molecular evidence increasingly demonstrates the remarkable genetic diversity of the microbial world (*1*, *2*), yet ecological interpretation of this diversity remains elusive. This is largely because microbiologists rely on studies of clonal isolates or environmental gene libraries to infer biogeochemical and pathogenic functions of natural bacterial populations. What is missing, however, is quantitative information regarding the environmental prevalence of individual genotypes that would allow inference of their ecological importance or competitive success. It may be expected that ecologically distinct populations display relatively high clonality, because bacterial genomes have a high potential for adaptive mutations, which may lead to purging of genotypic diversity from within the population by selective sweeps (*3*, *4*). However, this view is increasingly difficult to reconcile with recent observations of high levels of differentiation among closely related genomes [e.g., (*5*, *6*)] and the recovery of vast numbers of similar but nonidentical homologous genes from environmental samples (microdiversity) (*7*–*9*). Therefore, questions include whether competition among individual strains is strong enough to result in frequent selective sweeps or instead whether natural populations accumulate large neutral allelic and perhaps even genomic variation (*8*). However, the diversity and prevalence of individual variants within environmental bacterial populations has not been extensively explored, and so questions regarding the ecological importance of genotypic variation remain unanswered.

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To analyze genotypic diversity and overall population size quantitatively, we combined culture-dependent and -independent methods to assess the number, extent of variation, and relative frequency of genotypes within a well-defined natural bacterial population. We chose a coastal assemblage of *Vibrio splendidus*, previously identified as a phylogenetically discrete cluster denoted by nearly identical (<1% divergent) 16S rRNA sequences in an analysis of bacterioplankton community structure (*8*). We have proposed that such ribotype clusters represent ecologically differentiated units, i.e., ecotypes or populations (*8*). Thus, we defined the *V. splendidus* cluster as a population of naturally co-occurring genomes that can be tracked quantitatively in the environment and identified in strain collections by their distinct rRNA genes.

Quantification of the *V. splendidus* population over an annual cycle by quantitative polymerase chain reaction (QPCR) (*10*) revealed that it is consistently present as a member of the coastal bacterioplankton community and displays seasonal variation in abundance (Fig. 1A). Concomitant with quantification, we isolated strains from five temporal samples on *Vibrio*-selective media and identified strains by 16S rRNA sequence analysis (Fig. 1B) (*11*). Overall, 20 distinct *Vibrio* (and closely related *Photobacterium*) taxa grew on the media (Fig. 1, B and C), but the majority of isolates (232 of 333) were identified as members of the *V. splendidus* population (red sectors in Fig. 1B). This dominance in all collections, except the cold-water sample (March 2003) (Fig. 1B), roughly parallels the culture-independent quantification by QPCR (Fig. 1A).

Determination of sequence diversity of a universally distributed protein-coding gene (*Hsp60*) among all 333 *Vibrio* isolates showed high heterogeneity but confirmed the monophyly of the *V. splendidus* population detected by the rRNA sequence analysis (*12*). We observed 141 different *Hsp60* alleles among the 232 *V. splendidus* isolates (Fig. 2), and extrapolation using the Chao-1 richness estimator (*13*) suggests a minimum of 436 alleles in