ANTHROPOGENIC IMPACTS

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Definition
Anthropogenic impacts in this volume refer to the adverse effects of human activities on estuarine environments.

Introduction
Estuaries rank among the most heavily impacted aquatic ecosystems on earth, being affected by a wide array of anthropogenic activities both in adjoining coastal watersheds and in the water bodies themselves (Kennish, 2002). Most of these activities can be linked to ongoing rapid human population growth and development of the coastal zone. For example, about four billion people live within 60 km of the world’s coastlines (Kennish, 2002; Kennish et al., 2008). In the USA, more than 125 million people now reside in coastal counties nationwide. People inhabiting low-lying coastal areas are more vulnerable to sea-level rise, coastal storms and storm surges, inundation and flooding, and other coastal hazards.

While many people simply prefer to live near the ocean, others inhabit the coastal zone for economic opportunity involving tourism, recreational and commercial fisheries, mariculture, transportation and shipping, domestic and industrial construction, electric power generation, oil and gas recovery, and other human activities. Escalating human settlement has altered land use/land cover in coastal watersheds, creating impervious surfaces that facilitate nonpoint-source pollution input to estuaries. Much of this is coupled to developing infrastructure such as construction of roadways and bridges, electric utilities, as well as water, sewer, and gas lines. Other major pollutant delivery systems are point-source inputs. Some human activities have physically altered estuarine shorelines and habitats, impacting biotic communities. Included here are the construction of bayshore housing, lagoons, bulkheads and other shore protection features, harbor and marina development, dredging and dredged material disposal, wetland reclamation, and channel and inlet stabilization. Upland modifications (e.g., dams and reservoirs, deforestation and habitat fragmentation, and channelization) can significantly exacerbate other anthropogenic stresses leading to greater pressures in estuarine systems. Increasing freshwater diversions for agriculture and other human needs, such as in California (USA), can significantly alter salinity, circulation, and biotic communities in estuaries.

Estuarine impacts
Kennish et al. (2014a) identified 12 major anthropogenic stressors on estuarine ecosystems. These include (1) eutrophication; (2) sewage and organic wastes; (3) habitat loss and alteration, shoreline hardening, and erosion; (4) chemical contaminants; (5) human-induced sediment/particulate inputs; (6) overfishing; (7) intensive aquaculture; (8) introduced/invasive species; (9) human-altered hydrological regimes; (10) climate change; (11) coastal subsidence; and (12) floatables/debris. An additional stressor of importance is a group of pathogens that can impact human use of estuaries. According to Kennish and Paerl (2010), anthropogenic stressors can be categorized into those that degrade water quality and are primarily chemical and biological in nature (e.g., nutrient enrichment, chemical contaminants, and pathogens), impact habitat and are mainly physical factors (e.g., shoreline hardening, lagoon construction, dredging and dredged-material disposal), and alter biotic communities and are effectively driven by multiple stressors (e.g., overfishing, introduced/invasive species, human-altered hydrological regimes, and climate change).

Eutrophication
Nutrient enrichment, notably nitrogen and phosphorus, has led the eutrophication of many estuaries, particularly shallow systems with long water residence times (Kennish and de Jonge, 2011). Reactive nitrogen inputs...
to estuaries have been increasing through time, resulting in escalating eutrophication of estuarine water bodies (Howarth et al., 2002a; Rabalais, 2002; Bricker et al., 2007; Burkholler et al., 2007; Howarth, 2008; Anderson et al., 2010). Of the 138 estuaries in the USA examined by Bricker et al. (2007), 84 were determined to be highly eutrophic. Greater nitrogen and phosphorus loads to estuaries and coastal marine waters are attributed to accelerating coastal development and intensification of agriculture (Howarth et al., 2002b; Galloway et al., 2008; Howarth, 2008; Anderson et al., 2010). Aside from agriculture sources, these nutrients derive from lawn fertilization, stormwater runoff, municipal and industrial wastewaters, malfunctioning septic systems, groundwater seepage, and atmospheric deposition. The eutrophication of estuaries is manifested by an array of damaging cascading changes in ecosystem structure and function such as decreased dissolved oxygen levels, increased microalgal and macroalgal abundance, occurrence of harmful algal blooms (HABs), loss of seagrass habitat, reduced biodiversity, declining fisheries, imbalanced food webs, altered biogeochemical cycling, and diminished ecosystem services (Kennish and de Jonge, 2011).

Sewage and organic wastes
Sewage and organic wastes also increase nutrient and organic carbon loading that can exacerbate estuarine eutrophic conditions (Kennish, 2001a). Organic carbon enrichment is coupled to elevated biochemical oxygen demand and depleted dissolved oxygen levels in some water bodies. These wastes derive from domestic and industrial sources, livestock and fish processing facilities, wildlife inputs, aquaculture operations, and other sources. Hypoxia of estuarine and coastal marine environments has increased worldwide over the past several decades due to eutrophication driven by nutrient enrichment and organic carbon loading (Diaz and Rosenberg, 1995, 2008).

The calefaction of estuarine waters by the release of heated effluent from electric generating stations and other industrial facilities can also deplete dissolved oxygen levels. Thermal discharges from electric generating stations have commonly increased mortality of susceptible estuarine organisms in near-field regions of outfall sites. Aside from increased mortality due to reduced dissolved oxygen, heat-shock and cold-shock mortality at electric generating stations has occasionally caused mass mortality of finfish populations which cannot adapt to the rapid changes in water temperature associated with abrupt changes in station operation (Kennish, 1992).

Habitat loss and alteration
Coastal population growth and development have led to substantial estuarine habitat loss and alteration, impacting biotic communities. Physical alteration is associated with the dredging of channels and other subtidal areas, the construction of hardened shorelines, and the removal of vegetation and soils during construction of buildings, roadways, and other infrastructure elements in watersheds that convert natural habitats to impervious cover and increase erosion, runoff, and nonpoint pollution to estuarine water bodies. Water quality is often degraded as a result. Other adverse effects include habitat fragmentation, ecosystem isolation, and functional degradation of upland and wetland complexes (Kennish, 2001a). Some of these changes can be intractable.

Historically, salt marshes and other wetland habitat bordering estuarine basins have been altered extensively by grid ditching, marsh diking, draining and filling (for agriculture), impoundments for wildlife, and reclamation for domestic and industrial development. The hydrology of wetland systems has been invariably changed by construction of impoundment dikes, water-control embankments, levees, dams for flood control, as well as canals and spoil banks. Tidal flooding, water flow, and drainage are often modified, reducing sediment loading to the marsh surface and even arresting vertical accretion and hastening marsh submergence (Kennish, 2001b). Concomitantly, the loss of marsh in many regions is accelerating due to climate change-driven sea-level rise. Human activities have eliminated more than 50% of the original tidal marsh habitat in the USA and more than 70% of the mangroves fringing the coast of Puerto Rico (Kennish, 1997; Alongi, 1998). The destruction of wetland habitat decreased substantially in the USA after enactment of the 1972 Clean Water Act.

Localized areas along estuarine shorelines have been affected by construction and use of docks, piers, boat ramps, and marinas. Other shorelines have been modified by marine engineering structures such as bulkheads and revetments for bank stabilization, jetties at inlets, stormwalls, and other protective features. Constructing physically static structures in dynamic estuarine environments has impacted the function of sensitive habitats often diminishing their ecological value.

Chemical contaminants
Many estuaries receive a wide range of chemical contaminants because they are located in close proximity to heavily populated metropolitan centers and other developed coastal areas. Urbanized estuaries are often the most heavily impacted. Major sources and delivery systems include agricultural and urban runoff, municipal and industrial discharges, groundwater inputs, riverine inflow, and atmospheric deposition. Chemical contaminants entering estuaries may concentrate in the water column, accumulate in bottom sediments and organisms, or exit to coastal waters. Bottom sediments of estuaries are typically repositories of chemical contaminants because many of these substances are particle reactive, sorbing to grain surfaces, and ultimately settling to the estuarine floor.

Among the most important groups of chemical contaminants found in estuarine environments are halogenated hydrocarbons, polycyclic aromatic hydrocarbons (PAHs), and metals. These contaminants are potentially damaging to estuarine habitats and hazardous to estuarine
and marine organisms. Substances such as aromatic and aliphatic hydrocarbons derived from oil spills and seepages, as well as volatile organic compounds, can be acutely toxic to biotic communities (Kennish, 1997).

The halogenated hydrocarbons are a ubiquitous group of environmental contaminants consisting of low- to high-molecular-weight compounds. Examples are organochlorine biocides (insecticides, herbicides, and fungicides), low-molecular-weight compounds (chlorofluorocarbons), and high-molecular-weight chemicals (chlorinated aromatics and chlorinated paraffins). PCBs and DDT are two of the most notable halogenated hydrocarbons that have historically impacted estuarine environments (Kennish, 2001a).

PAHs consist of a group of chemical carcinogens, mutagens, and teratogens that originate from both natural (e.g., volcanic activity and oil seeps) and anthropogenic sources, although the inputs from anthropogenic sources (e.g., fossil fuel combustion, waste incineration, municipal and industrial wastewaters, and land runoff) typically predominate in estuaries (Kennish, 1992). The low-molecular-weight PAHs are more toxic than the high-molecular-weight forms. Hepatic neoplasia and other diseases in aquatic organisms have been attributed to PAH exposure (Kennish, 1997). A range of biochemical, physiological, behavioral, and other sublethal responses has also been documented in estuarine organisms that can adversely affect biotic community structure.

Oil spills and leakages from marine vessels and fixed installations, as well as from nonpoint-source inputs from coastal watersheds, are hazardous to estuarine organisms and habitats. The lethal and sublethal effects of polluting oil on estuarine and marine organisms are well established (Kennish, 1992, 1997, 2001a). Both aromatic and aliphatic components are problematic as noted above. Benthic organisms are particularly susceptible to oil accumulation, and contaminated habitats such as salt marsh systems can be adversely impacted by the oil for decades due to oil-contaminated sediments which are hazardous to settlement and recruitment of the organisms.

Metals
The literature is replete with pathological responses of estuarine and marine organisms to toxic levels of metals, including neurological, digestive, reproductive, and respiratory disorders, tissue inflammation and degeneration, and developmental abnormalities. Feeding behavior and growth inhibition are commonly observed. Transition metals (e.g., copper, cobalt, iron, and manganese), metalloids (e.g., arsenic, cadmium, lead, mercury, selenium, and tin), and organometals (e.g., methylmercury, tributyltin, and alkylated lead) can be toxic, particularly the organometals (Kennish, 1997; Kennish, 1998; Kennish et al., 2008). Metals are persistent in estuarine environments. They tend to bioaccumulate in organisms, and some metals such as methylmercury undergo biomagnification, with highest levels found in upper-trophic-level organisms that often serve as a food source for humans. Hence, the health of humans consuming metal-contaminated seafood can be impaired. There are many potential sources of metals in estuaries, including industrial activity (e.g., mining, smelting, refining, and electroplating operations), fossil fuel combustion, landfill leachates, shipping, marinas, and ash disposal. Delivery pathways are river discharges, groundwater inputs, and atmospheric deposition.

Human-induced sediment/particulate inputs
Human activities in coastal watersheds have facilitated inputs of sediments and other particulates to estuaries. The removal of natural vegetation and increase in impervious cover with watershed development hasten the delivery of sediments to estuarine basins. Silviculture operations, particularly in developing countries, have dramatically increased sediment loads to coastal areas (Kennish et al., 2008). One of the adverse effects is altered water and sediment quality. An increase in water column turbidity leads to the attenuation of light and shading of the estuarine floor that can reduce primary production and cause a decline of seagrasses and other essential benthic habitat. For example, Moore et al. (2012, 2014) correlated dieback of seagrasses in the Chesapeake Bay system in part to elevated turbidity levels.

Overfishing
Overfishing or overharvesting of finfish and shellfish populations not only results in depleted stocks but also the alteration of the food web structure of estuaries. While estuaries historically have had exceptional recreational and commercial fisheries, overexploitation of the biotic resources has been a concern through time. In mid-Atlantic coastal bays, overharvesting of shellfish, together with disease and predation, has been implicated in the dramatic decline of oyster and hard clam populations. Overfishing may have played an important role in the decline of Chinook salmon (Oncorhynchus tshawytscha), delta smelt (Hypomesus transpacificus), and striped bass (Morone saxatilis) fisheries in San Francisco Bay (USA) after the 1970s. Similarly, overfishing may have been a factor in the reduction of commercial finfisheries in Albemarle-Pamlico Sounds, North Carolina, and Sarasota Bay, Florida (Kennish, 2000).

Intensive aquaculture
A significant amount of the seafood consumed by humans (>25 %) now derives from aquaculture, which may partially compensate for overfishing (Engelman et al., 2008). Shellfish aquaculture predominates in countries of the Far East (e.g., China, Vietnam, and the Philippines). Much finfish aquaculture also occurs in countries of the Far East, but in many other countries as well. Intensive aquaculture has caused considerable coastal pollution, water and sediment quality degradation, and diseases resulting from the feces and uneaten food of the feedlot operations (New, 2002).
Aside from degraded water and sediment quality, aquaculture operations also cause habitat conversion and changes in hydrological regimes.

Introduced/invasive species
Organisms that are not endemic to an estuary, but are introduced or invade the water body, can have significant ecological impacts. Many species are introduced for commercial or recreational interests, an example being the introduction of the striped bass (*Morone saxatilis*) to San Francisco Bay (USA). In fact, the dominant species of organisms in San Francisco Bay are mainly introduced forms, with more than 200 nonindigenous species now inhabiting bay waters and wetland habitat (Kennish, 2000). Some exotic species inhabiting estuaries have been accidentally introduced via ballast water or some other means. Nearly all estuaries are affected by introduced or invasive species (Carlton and Geller, 1993; Kennish, 2002; Kennish et al., 2008).

Introduced and invasive species can be a danger to the stability and biodiversity of an estuarine ecosystem. In those cases where native controls are lacking, these species can have a significant competitive advantage, often rapidly dominating plant or animal communities. The food web structure is commonly disrupted, and native species may be displaced or greatly reduced in abundance. Changes in species composition and distribution commonly occur (Cohen and Carlton, 1998). Species diversity in these systems may drastically decline as well via intense competition and predation. For instance, the Asian clam (*Potamocorbula amurensis*), introduced into Suisun Bay (USA), has decimated the phytoplankton community and outcompeted the native shellfish species (*Macoma balthica* and *Mya arenaria*).

The introduction or invasion of exotic species is expected to increase in the future due to an expanding world population, the effects of climate change, and greater shipping and other human activities at sea and in estuaries. These changes will likely promote additional ecological disruption. More mariculture ventures, particularly in developing countries, will also add to these effects (Kennish, 2002).

Human-altered hydrological regimes
As population growth increases in coastal regions, so does the demand for freshwater to meet domestic, industrial, and agricultural needs. The urbanization of coastal watersheds also results in greater impervious land cover leading to accelerated freshwater runoff and higher river discharges. The increase in freshwater flow decreases the water residence time in estuaries, while increasing their capacity to dilute, transform, or flush contaminants (Kennish, 2000). In contrast, dams and reservoirs constructed upland reduce downstream freshwater flow. Other changes that can significantly alter water-flow regimes along coasts include channelization, marsh impoundment, and wetland habitat destruction which affect natural water storage capacity (Kennish et al., 2008). Shifts in water quality and quantity are important drivers of change in the abundance, distribution, reproductive success, and productivity of estuarine organisms (Kennish, 2000). Estuarine circulation can also significantly change. The impact of freshwater diversions is perhaps best exemplified by San Francisco Bay (USA), where 50% of the freshwater flow has been diverted for human use, resulting in a modified salinity regime as well as altered biotic communities in the bay.

Freshwater diversions are used for ecological applications as well, such as coastal wetland restoration. Teal et al. (2012), for example, discuss diversions of river water into coastal wetlands as part of plans to mollify the areal loss of coastal wetlands in Louisiana by reversing or slowing the rates of degradation. However, freshwater diversions such as those noted by Teal et al. (2012) can cause major changes in estuarine water quality, notably large reductions in salinity and increased nutrient availability that affect plant communities, herbivory, and overall marsh stability.

The use of flood control structures has been shown to completely modify some estuarine ecosystems. For example, acute changes in water inflow to the Haringvliet, Grevelingenmeer, and Oosterschelde estuaries in southwest Netherlands occurred subsequent to the construction of dikes to avert flooding problems, such as those incurred in 1953, resulting in major changes in the physical-chemical conditions and biotic communities of the water bodies. While the Oosterschelde remained a productive estuary after these structural changes, the Haringvliet basin was altered to a highly polluted freshwater body, and the Grevelingenmeer became a saltwater system. Tidal marshes and tidal flat habitats also changed considerably (Kennish et al., 2008). Changes such as those observed in the Haringvliet, Grevelingenmeer, and Oosterschelde estuaries demonstrate the magnitude of human influence on coastal environments, particularly in regard to human-altered hydrologic regimes.

Climate change
An accumulating database indicates that human factors are important drivers of change of world climate (Skinner, 2012). Increasing global temperatures, ascribed in large part to carbon dioxide emissions, have been linked to greater frequency and severity of damaging storms, coastal flooding, droughts and fires, and other hazards projected by climate forecasting models for the twenty-first century (IPCC, 2007). Extreme climate events and ongoing sea-level rise will be hazardous to coastal communities worldwide.

During the twentieth century, global sea-level rise amounted to 0.5–30 cm, being largely attributed to the increase in global surface temperatures (mean = +0.6 ± 0.2 °C), melting of glaciers and ice sheets, and thermal expansion of the oceans (IPCC, 2007). Global sea-level rise during the twenty-first century is projected to increase by 52–98 cm (IPCC, 2013). Relative sea-level rise will be even
greater in some regions due to coastal subsidence, as in the case of New Jersey and other mid-Atlantic states in the USA.

Rising sea level and coastal inundation will lead to significant loss of some coastal wetlands, eliminating buffer and rendering coastal communities more vulnerable to extreme events. Human-induced climate change will also alter temperature and salinity regimes and the structure and function of biotic communities in estuaries (Kennish, 2002). Configurations of estuarine basins will be modified as they widen and deepen. Shifts will occur in nutrient and sediment supply as well as freshwater inputs. Tidal prisms and tidal ranges will change in many systems. More frequent flooding and inundation of bayshore areas will pose hazards to vulnerable coastal communities worldwide (Kennish et al., 2008).

Coastal subsidence

Subsiding coasts result in similar impacts as rising sea level on estuarine and wetland systems. For example, as coastal subsidence increases, estuarine shoreline retreats and land submergence accelerates causing the loss of fringing wetland habitat. The wet surface area of the estuary expands, together with the basin volume, thereby altering the system bathymetry and configuration. The salinity regime, circulation, and other physical-chemical characteristics of the estuary can change considerably as well, which will also affect biotic communities.

The effects of coastal subsidence are becoming more evident around the world with accelerating population growth and development in coastal watersheds. Human activities have contributed greatly to the subsidence problems in some areas via excessive groundwater withdrawal for domestic and agricultural use and oil and gas extraction. Natural factors, such as subsurface sediment compaction, crustal (tectonic) movements, and sinkhole formation by karst processes, are more significant in some regions. In the USA, subsidence has been well chronicled at Galveston Bay, Texas, due to oil and gas extraction (Shipley and Kiesling, 1994), along the Louisiana coast due to sediment compaction (DeLaune and Pezeshki, 1994), and at Chesapeake Bay due to groundwater withdrawal and other factors (Boon et al., 2010).

Significant coastal subsidence has also been documented in other countries (e.g., Po Delta, Italy, and Tokyo, Japan) (Kennish et al., 2008). Coastal subsidence problems will take on added significance during the twenty-first century, exacerbating those due to eustatic sea-level rise (Kennish, 2002). Subsidence rates, such as those noted by Boon et al. (2010) at Chesapeake Bay (−1.3 to −4.0 mm year), will likely continue unabated into the future. It will be necessary for coastal decision makers to carefully consider the management options necessary to reduce their impacts.

Floatables/debris

Marine debris, notably plastics, has become an international problem in estuarine and marine environments. The use of plastic products has reached an all-time high in many developed countries; plastic debris has been an ongoing problem in coastal waters of the USA (Ribic, 1998; Kennish, 2001a). Plastics are particularly damaging to aquatic environments because they essentially do not degrade, thereby polluting habitats for many years. They pose a threat to many organisms, particularly fish, turtles, birds, and mammals that ingest some of the materials or become entangled in fishing line, nets, and packing bands. Some organisms mistake floatables for prey (Shaw and Day, 1994). The ingestion of plastics and other marine debris can suffocate the animals or obstruct their digestive systems, causing death.

Pathogens

Estuaries worldwide are susceptible to the entry of pathogenic microorganisms (i.e., bacteria and viruses) from land runoff and sewage wastes that pose a risk to human health. Fecal pollution (i.e., fecal coliform bacteria, enterococci, and coliphage) and human enteric pathogens and enteroviruses can greatly impair human use of impacted estuarine and coastal marine waters (Lipp et al., 2001). Faulty septic systems, sewage treatment plant effluent, and wildlife wastes often degrade estuarine water quality, which must be continually monitored. Treated municipal wastewater and urban stormwater runoff may contain more than 100 enteric pathogens (National Research Council, 1993). These organisms, which are widely distributed by coastal storms (Fries et al., 2007), pose a hazard to humans who swim in contaminated estuarine waters or consume contaminated seafood products.

Parasites, notably helminths and protozoa, are commonly associated with waterborne diseases as well. Helminths linked to untreated sewage in estuarine and other aquatic systems include hookworms, roundworms, tapeworms, and whipworms. Pathogenic enteric protozoa derived from sewage contamination can be equally devastating to human health.

Summary

A wide array of anthropogenic factors contributes to estuarine degradation. Chief among these are (1) nutrient loading and eutrophication; (2) sewage and organic wastes; (3) habitat loss and alteration, shoreline hardening, and erosion; (4) chemical contaminants; (5) human-induced sediment/particulate inputs; (6) overfishing; (7) intensive aquaculture; (8) introduced/invasive species; (9) human-altered hydrological regimes; (10) climate change; (11) coastal subsidence; and (12) floatables/debris. Pathogens coupled to human waste discharges and wildlife are also significant since they adversely affect water quality. Anthropogenic stressors can be categorized into those that degrade water quality and are primarily chemical and biological in nature (e.g., nutrient enrichment, chemical contaminants, and pathogens), impact habitat and are mainly physical factors (e.g., shoreline hardening, lagoon construction, dredging and dredged-material
disposal), and alter biotic communities and are effectively driven by multiple stressors (e.g., overfishing, introduced/invasive species, human-altered hydrological regimes, and climate change). Human activities can significantly impact the structure, function, and ecological health of estuaries.

Bibliography


Cross-references
- Anoxia, Hypoxia, and Dead Zones
- Biochemical Oxygen Demand
- Bulkheads
- Clean Water Act
- Climate Change
- Dredging
- Eutrophication
- Extreme Events (Hurricanes)
- Invasive Species
- Marsh Sediment Toxicity
- Nonpoint Source Pollution
- Oil Pollution
- Pathogens
- Polycyclic Aromatic Hydrocarbons
- Revetments
- Storm Surges
- Toxic Blooms
- Trace Metals in Estuaries
- Water Quality
- Wetlands Reclamation

ARCHAEAE

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**Synonym**
Archaeabacteria

**Definition**
Archaea constitute one of the three domains of life, as phylogenetically distinct from the domains Bacteria and Eukarya (Woese and Fox, 1977; Woese et al., 1990).

**Etymology**
Archaea (singular: archaeon) are derived from Greek ἀρχαῖος – ancient, primitive.

The term was coined to reflect the apparent antiquity of traits in archaeal species and their aptness to inhabit environments like those presumed for early Earth.

**Phylogeny**
On the phylogenetic tree of organisms, Archaea form one of the three fundamental branches called domains (Woese et al., 1990). Further branching within the archaeal domain is largely based on ribosomal RNA sequences, but also relies on evidence from comparative analysis of protein sequences. Typical markers in archaeal phylogeny are ribosomal proteins, histones, and components of the transcription system and the cell division apparatus (Brochier-Armanet et al., 2011). In addition to the initially recognized phyla Crenarchaeota and Euryarchaeota (Woese et al., 1990), four candidate phyla have been proposed: Kor-, Nano-, Thaum-, and Aigarchaeota (Brochier-Armanet et al., 2011). Given the small number of 187 sequenced archaeal genomes (Genomes OnLine Database; May 2013), archaeal phylogeny continues to be uncertain.

**Physiology and metabolism**
Archaea are single-celled organisms showing prokaryotic structure, but differ from bacterial cells by the absence of peptidoglycan from their cell wall and by the presence of histones associated with their DNA. In contrast to the phospholipid bilayer confining bacterial and eukaryotic cells, archaeal cell membranes consist of a single layer of isoprenoid diethers and tetraethers. Most archaeal genomes contain clustered, regularly interspaced palindromic repeats (CRISPR) that confer adaptive immunity against virus infections (Sorek et al., 2008; Marraffini and Sontheimer, 2010).

No chlorophyll-like pigments or photosynthetic electron transport chains are known in Archaea. However, some archaea possess bacteriorhodopsin, which functions as light-driven proton pump across the cell membrane. The reflux of protons can be exploited for ATP synthesis, completing the conversion of light energy into chemical energy for cellular metabolism.

Archaea show diverse forms of chemotrophic metabolism, including both the formation and the anaerobic oxidation of methane, both oxidation and reduction of CO, the aerobic oxidation of H₂ (knallgas reaction), most of the oxidative and reductive processes in the N and S cycle, and redox reactions of various metals and metalloids (Amend and Shock, 2001; Stolz et al., 2006; Oelgeschläger and Rother, 2008; Conrad, 2009; Knittel and Boetius, 2009; Bini, 2010).

In sulfur-based energy metabolism, oxidized and intermediate S compounds (sulfate, sulfite, thiosulfate, and elemental sulfur) are reduced by H₂ or organic compounds, while reduced and intermediate S compounds (sulfide, elemental sulfur, and thiocysteine) can be oxidized...
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