

HISTORICAL RECONSTRUCTION OF HUMAN-INDUCED CHANGES IN U.S. ESTUARIES

HEIKE K. LOTZE

Biology Department, Dalhousie University, 1355 Oxford Street, Halifax, NS B3H 4J1, Canada

Email: hlotze@dal.ca

Abstract Estuaries are vital ecosystems that have sustained human and marine life since earliest times. Yet, no other part of the ocean has been so fundamentally shaped by human activities. Understanding the magnitude, drivers and consequences of past changes is essential to determine current trends and realistic management goals. This review provides a detailed account of human-induced changes in Massachusetts, Delaware, Chesapeake, Galveston and San Francisco Bays and Pamlico Sound. Native Americans have lived off these estuaries for millennia, yet left few signs of local resource depletion. European colonisation, commercialisation and industrialisation dramatically depleted and degraded valuable species, habitats and water quality. Exploitation and habitat loss were the main factors depleting 95% of valued species, with 35% being rare and 3% extirpated. Twentieth century conservation efforts enabled 10% of species to recover. Such profound changes in species diversity have altered the structure and functions of estuarine ecosystems as well as their services for human well-being. Thus, undesirable health risks and societal costs have increased over past decades. Protecting and restoring the diversity and vitality of estuaries will enhance their resilience towards current and future disturbances, yet require better governance of these often-neglected ecosystems. Their documented historical richness and essential role for marine life and people may increase the necessary awareness and appreciation.

Introduction

Marine ecosystems have been exploited and influenced by human activities for millennia, especially along the coasts (Jackson et al. 2001, Lotze et al. 2006, Rick & Erlandson 2008). This has resulted in large changes in populations, habitats and water quality over several decades or centuries, yet current management efforts typically rely on the last two to five decades of scientific monitoring data to estimate current states and trends (Lotze & Worm 2009). The total magnitude of change is therefore often obscured by “shifting baselines” (Pauly 1995). For example, from 1970 to 2003 the biomass of Atlantic cod on the Scotian shelf totalled 342,000 t at its peak but was estimated at 1,260,000 t in 1852 (Rosenberg et al. 2005).

Akin to climate change research, knowing past long-term changes in marine populations and ecosystems is essential to understanding present states (Carlton 1998, Roberts 2003, Lotze & Worm 2009). Historical reference points from times prior to strong human influence are needed to derive sound management goals and targets for restoration and recovery. How much has a population or habitat declined from its historical abundance, and to what level could it recover or be restored? If we know historical changes in individual populations, we can further estimate changes in biodiversity, food-web structure and ecosystem functioning (Jackson et al. 2001, Lotze et al. 2005). Finally, understanding the underlying drivers and consequences of change is necessary to derive future projections and set management priorities (Carlton 1998, Clark et al. 2001a).

Recent progress and interdisciplinary collaboration among marine scientists has made it possible to reconstruct historical changes in marine ecosystems over past centuries and millennia (Rick & Erlandson 2008, Starkey et al. 2008, Lotze & Worm 2009). Several studies have aimed at reconstructing historical changes in particular regions, such as the Benguela upwelling system in Africa (Griffiths et al. 2004), the Wadden Sea in Europe (Lotze 2005, 2007, Lotze et al. 2005), the Outer Bay of Fundy in Canada (Lotze & Milewski 2004) and the Gulf of California in Mexico (Sáenz-Arroyo et al. 2005, 2006). Other studies have focused on historical changes in individual species (Rosenberg et al. 2005, McClenachan et al. 2006) or habitats (Orth et al. 2006, Airoidi & Beck 2007). All of these studies provide important insights into the magnitude and range of human-induced changes in marine ecosystems. However, so far few studies have compared historical changes across different systems, such as coral reefs (Pandolfi et al. 2003) or coastal waters (Lotze et al. 2006), highlighting similarities as well as differences in the response to human-induced changes.

In the United States, a detailed, comparative ecological history for marine ecosystems is missing, although such knowledge is needed for current ocean management and conservation (Pew Oceans Commission 2003, U.S. Commission on Ocean Policy 2004). Yet, a wealth of historical information is available for individual species, habitats or other ecosystem components (e.g., Nichols et al. 1986, Kennish 2000, Kemp et al. 2005). Such records have been compiled as part of a synthetic analysis on historical changes in 12 estuaries and coastal seas around the world, but only the summary results have been published (Lotze et al. 2006).

U.S. estuaries have each experienced a similar human history, shaped first by Native American influences and later by European colonisation and expansion. Thus, a quasi-replicated comparison of past ecological changes within a similar historical context can be made. However, each estuary has a unique physical and biological setting and experienced its own sequence of historical events that created estuary-specific histories of change. For example, the gold rush and fur trade were of huge importance in San Francisco Bay (Agriculture and Natural Resources Communication Services [ANR] 2001), the cod fishery and whaling thrived in Massachusetts Bay (Murawski et al. 1999, Claesson 2008), and the oyster fishery and eutrophication are commonly associated with Chesapeake Bay (Kemp et al. 2005). Separating estuary-specific from universal patterns can be of great value in understanding the history, drivers and consequences of human-induced changes in marine ecosystems.

The aim of this review is to provide a comprehensive and detailed history of human-induced ecological changes in selected U.S. estuaries, to compare observed changes across estuaries and to place these changes into a global context. First, the general ecological and societal importance of estuaries is highlighted, including their history of human settlement. It follows a detailed review of historical changes in six large U.S. estuaries on three coasts: Massachusetts Bay, Delaware Bay, Chesapeake Bay, Pamlico Sound, Galveston Bay and San Francisco Bay (Figure 1). Within each estuary, past changes in populations, fisheries and ecosystem characteristics, such as habitat availability and water quality, are described for before and since European colonisation mostly through human activities. Past changes are then compared and summarised across the six case studies to derive a more general picture of change in U.S. estuaries over time. This will include a comparison of the importance of different human drivers and the consequences of historical changes for ecosystem structure, functions and services. Finally, the emerging ecological history of U.S. estuaries is compared with historical changes in other marine ecosystems around the world. Overall, this review compiles essential information on historical changes, drivers and consequences in U.S. estuaries that provides an important basis for current and future ocean management and conservation.

Ecological and social importance of estuaries

Estuaries are among the most important environments in the coastal zone, both biologically (Kennish 2002) and socioeconomically (Limburg 1999), and have been essential in sustaining human and



Figure 1 Map of the United States showing all major and the selected six estuaries chosen as case studies: Massachusetts Bay (Ma), Delaware Bay (De), Chesapeake Bay (Ch), Pamlico Sound (Pa), Galveston Bay (Ga) and San Francisco Bay (SF).

marine life since earliest times. They form protective harbours for human settlement and for spawning, nursing and foraging animals; they support high diversity and primary productivity attracting animal and human consumers; and they link human trading and animal migration routes between rivers and the sea (Limburg 1999). At the land–sea interface, the interactions between humans and marine life have always been interlinked, and a long history of human-induced changes underlies the current and future states of estuarine ecosystems.

Along the U.S. coastline, nearly 900 estuaries cover about 10.9 million ha, which together with coastal lagoons occupy 80–90% of the Atlantic and Gulf of Mexico and 10–20% of the Pacific coasts (Table 1, Kennish 2002). As transition zones between terrestrial, freshwater and marine systems, estuaries create some of the most productive and fertile ecosystems on Earth caused by (1) abundant nutrient supply from land-based sources; (2) efficient nutrient retention and cycling among benthic, wetland and pelagic habitats; (3) maximised autotrophic production by pelagic and benthic algae and plants; and (4) high tidal energy, water circulation and mixing (Kennish 2002). The diverse primary producers provide a rich food supply on which all higher trophic levels depend

Table 1 Characteristics of the selected six U.S. estuaries: surface area, average depth, and estuarine drainage area for each estuary (data from Bricker et al. 1999) and primary productivity (PP) and species richness for fish and marine mammals for large marine ecosystems (LME, with Ma, De, Ch = NE U.S. Shelf, Pa = SE U.S. Shelf, Ga = Gulf of Mexico, SF = California Current, <http://www.searoundus.org/lme/lme.aspx>)

System	Surface (km ²)	Depth (m)	Drainage (km ²)	PP (mgCm ⁻² d ⁻¹)	Species richness	
					Fish	Mammals
Massachusetts Bay (Ma)	478	27.3	3,100	1451	644	42
Delaware Bay (De)	1236	6.3	17,485	1451	644	42
Chesapeake Bay (Ch)	6898	9.4	64,050	1451	644	42
Pamlico Sound (Pa)	4455	4.1	33,102	740	1168	31
Galveston Bay (Ga)	890	6.2	11,502	537	958	31
San Francisco Bay (SF)	829	6.4	17,146	578	804	46

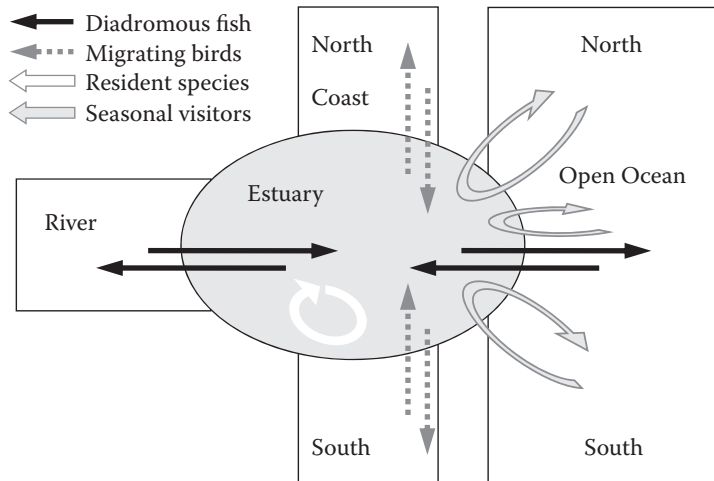


Figure 2 Estuaries are essential habitats for multiple resident species that remain in the estuary year-round (white arrow); seasonal visitors from northern, southern, or other parts of the ocean that come to feed, breed or nurse their young for part of the year (grey arrows); and migratory species that feed and stage in estuaries on their way from rivers to the ocean and vice versa (e.g., diadromous fish, black arrows) and from northern breeding to southern overwintering grounds (e.g., migrating birds, dashed arrows).

(Table 1). Extensive habitats are provided by seagrass and rockweed beds, mangrove forests and salt marshes, as well as oyster reefs, mussel beds, hydrozoan meadows, and other reef- or bank-forming organisms. Together with a mix of soft and hard bottoms, shallow and deep, calm and high-current waters and the surrounding islands, beaches, forests and grasslands, this extraordinary variety of biogeographic habitats provides essential breeding, nursery and foraging grounds and protection from predators (Kennish 2002, Lotze & Milewski 2004).

The rich food supply together with the great habitat diversity provide the special living conditions for a great variety of plants, invertebrates, fish, reptiles, birds and mammals that depend on estuarine food or habitats for their entire or parts of their life cycle (Figure 2). Many resident species live within the estuary's boundaries all their life. Others come to visit seasonally from colder or warmer ocean regions to feed, breed, nurse their young or overwinter. Still others stop over during their migrations from river to sea or northern to southern regions. Together, these species form an estuarine food web that changes dynamically with seasonal variation in environmental parameters and species presence.

Because of their special conditions, estuaries were among the first places settled and have experienced a long history of changing human activities (Limburg 1999, Lotze et al. 2006, Lotze & Glaser 2009). Many of the largest cities around the world have been built around estuaries. Today, it is generally understood that the natural structure and functions of most estuaries have been seriously degraded by human impacts, including pollution with nutrients, chemicals and pathogens; loss and alteration of habitat; overexploitation; freshwater diversion; and introduction of exotic species (Limburg 1999, Kennish 2002). Estuaries are also the regions where future threats from human-induced climate change, especially sea-level rise, will likely have the most severe consequences (Kennish 2002).

History of human settlement and activities in North America

After the melting of the ice sheet that covered large parts of North America during the last ice age, native people settled along the coasts 10–12 thousand yr ago (Tables 2 and 3). Most tribes

Table 2 Cultural periods based on human presence, technology and market conditions

Cultural period	Human presence, technology, market conditions
Prehuman	No human presence; only natural disturbance of ecosystems
Hunter-gatherer	Premarket; low population numbers; seasonal settlements; subsistence exploitation
Agricultural	Premarket; low population numbers; permanent settlements; individual or village-based resource use; subsistence and artisan exploitation
Establishment	European colonisation; establishment of local economy and market; low population numbers; trade between colonies and Europe; mostly subsistence exploitation
Development	Strong growth and expansion of economy, market and trade; rapid rise in population; commercialisation of resource use; development of luxury and fashion markets; industrialisation and technological progress; guns allow mass exploitation of mammals and birds; fishing mostly inshore and seasonal with light gear
Early global (1900–1950)	Global economy and market develop; rise in population; industrialisation and technological progress increase; increasing effort, efficiency and destructiveness of gear; accelerating exploitation, by-catch and habitat destruction, fishing possible in any season but still mostly inshore and coastal
Late global (1950–2000)	Global economy and market; industrial fishing increases after WWII and spreads offshore; multiple unselective and destructive gears enable mass fishing; pollution, eutrophication and other impacts increase; conservation efforts increase

Table 3 Estimates of real time (BC = negative, AD = positive numbers) for the beginning of each cultural period in the six estuaries

Cultural Period	Ma	De	Ch	Pa	Ga	SF
Prehuman	>–8000	>–8000	>–8000	>–8000	>–10000	>–10000
Hunter-gatherer	–8000	–8000	–8000	–8000	–10000	–10000
Agriculture	1400	1200	1200	1200	N/A*	N/A
Colonial establishment	1620	1600	1600	1600	1680	1775
Colonial development	1680	1760	1760	1700	1820	1820
Global market 1	1900	1900	1900	1900	1900	1900
Global market 2	1950	1950	1950	1950	1950	1950

* N/A = not available, meaning this period did not occur.

moved with the seasons between traditional camping, hunting and fishing grounds in pursuit of fish, game, berries and other resources, such as building materials, medicines and ornaments (Bourque 1995, Broughton 2002). Between 1200 and 1400 AD, natives around Massachusetts, Delaware and Chesapeake Bays and Pamlico Sound started to cultivate land, while people around Galveston and San Francisco Bays largely relied on a hunter-gatherer lifestyle until European contact (Table 3). With the arrival of Europeans, native populations in most parts of the continent started to dwindle from direct aggression or disease, while others were forced to give up traditional settlement places and hunting territories (Snow 1980, Sultzman 2000).

European explorers first established settlements between 1600 and 1620 AD in the four estuaries on the Atlantic coast, in 1680 in Galveston and in 1775 in San Francisco Bay (Table 3). Within a matter of years, these settlers transformed the regions culturally, economically and environmentally (Figure 3). In the period of colonial establishment, their subsistence economy mostly served to sustain the colony. People cleared land for settlements and agricultural fields and gained food through fishing, hunting and harvesting of regional resources. This establishment period lasted a few decades to more than a century, depending on the region.

Between the late seventeenth and early nineteenth century, market economies were developed with the commercialisation of fishing, hunting, forestry and shipbuilding (Tables 2 and 3), which

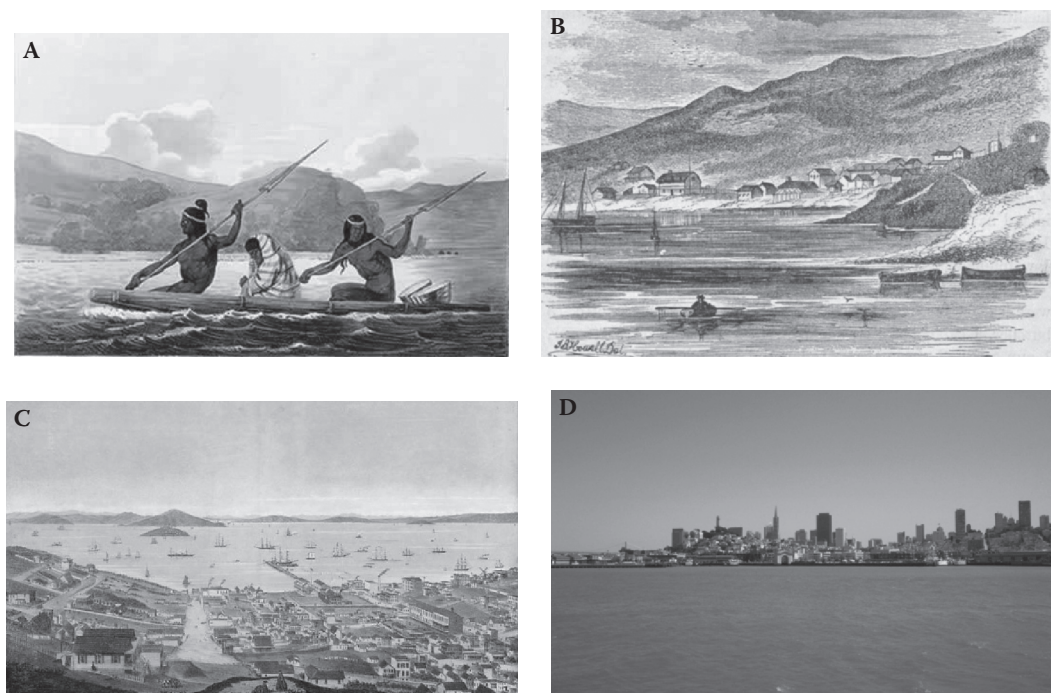


Figure 3 Human settlements through time with an example from San Francisco Bay. (A) Indians in tule boat (by L. Choris, Library of Congress Rare Book and Special Collections Division, Washington, D.C.). (B) San Francisco from the bay, 1847 (by Capt. A.E. Theberge, National Oceanic and Atmospheric Administration/Department of Commerce). (C) San Francisco, 1862, from Russian Hill (by C.B. Gifford & L. Nagel, <http://www.davidrumsey.com>). (D) San Francisco skyline, 2004 (by Capt. A.E. Theberge, National Oceanic and Atmospheric Administration/Department of Commerce).

became the cornerstones of the colonial economies. Over time, other industries were introduced, such as textile and canning industries and saw and pulp mills. Rivers were dammed to gain electricity and wetlands converted to farmland and municipal and industrial construction. The colonial economy, market and trade expanded rapidly, and the human population grew exponentially. Newly developed luxury and fashion markets spurred exploitation of natural resources for non-food purposes, such as furs, feathers and ivory. Industrialisation and technological progress enhanced the capacity for mass exploitation; however, most fishing and hunting still remained inshore and seasonal with light boats and selective gear (Smith 1994).

With the onset of the twentieth century, the globalisation of economy and markets began, and the human population continued to grow exponentially (Tables 2 and 3). Rapid technological progress led to more efficient but also more destructive fishing gears, which accelerated exploitation, by-catch and habitat destruction. With the advent of steam- and motorboats, fishing became possible in any season yet still remained mainly inshore and in coastal regions (Houde & Rutherford 1993, Smith 1994). After WWII, the global economy and market entered a second phase with new dimensions and fewer limits. Industrial fishing strongly increased its effort, efficiency and capacity, thereby spreading from inshore to offshore and towards the deep sea (Pauly et al. 2003, Lotze & Worm 2009). Fishing gear became decreasingly selective and increasingly harmful. Nutrient loading and chemical pollution increased, and aquaculture was developed. Global shipping enhanced the introduction of exotic species, and climate change became a recognised phenomenon. On the other hand, conservation efforts were strongly

increased, with the goal of protecting and recovering species that had been driven to low levels (Lotze et al. 2006).

Overall, the general sequence of human settlement, economy and market development was repeated in the different U.S. estuaries. However, the timing of the cultural periods differed, as did the estuary-specific activities, which are reviewed in the next section.

History of ecological changes in selected U.S. estuaries

Human activities have influenced the distribution and abundance of marine species throughout history (Rick & Erlandson 2008, Starkey et al. 2008, Lotze & Worm 2009). This section reviews the detailed historical changes in important species, habitats and water quality in six U.S. estuaries and their adjacent coastal waters (Table 1). Drawing on and updating data collected by Lotze et al. (2006), this covers most economically or ecologically important species for which archaeological, historical, fisheries and ecological records were available. Based on the documented records, a relative abundance index (Table 4) was derived for 22 consistent species groups over time and averaged across six taxonomic groups: mammals, birds, reptiles, fish, invertebrates and vegetation (see Lotze et al. 2006 for details). The summary data are shown for each study system and illustrated by a detailed description of historical changes. Data by species group are compared across U.S. estuaries. Together, the six case studies provide a comprehensive ecological history of U.S. estuaries.

Massachusetts Bay, Gulf of Maine

Massachusetts Bay is the northernmost of the six evaluated estuaries and one of the largest bays on the Atlantic coast. Together with Cape Cod Bay, it is separated from the larger Gulf of Maine by Stellwagen Bank (Figure 4), a very productive area for a variety of groundfish, pelagic fish and whales (Ward 1995). The native population was quite extensive in the region and engaged in hunter-gatherer activities, fishing and shellfish harvesting, with agriculture introduced around 1400 (Table 3). After European contact, the native population was much reduced by conflict and disease, from an estimated 36,700 to 5300 (Snow 1980). European colonisation began in 1620 and expanded after 1680. The backbones of the colonial economy were whaling and fishing, especially for groundfish on the many rich fishing banks in the Gulf of Maine. Stellwagen Bank was well known to fishermen, merchants, explorers and settlers by the seventeenth century (Claesson 2008). For over 400 yr, New England has been identified economically and culturally with the harvest of groundfishes (Murawski et al. 1999), but many other marine and coastal resources were exploited as well, some to extinction. Conservation efforts in the twentieth century enabled some species to recover, and in 1992 Stellwagen Bank was declared a national marine sanctuary (Claesson 2008). The general

Table 4 Judging criteria for relative abundance estimates that integrate quantitative and qualitative records of abundance

Estimate	Quantitative	Qualitative records
Pristine = 100	91–100%	High abundance, no signs of regular human exploitation
Abundant = 90	51–90%	Medium-to-high abundance, regular human exploitation without signs of depletion, species common
Depleted = 50	11–50%	Low-to-medium abundance, strong exploitation with signs of depletion (i.e., at least 50% decline in abundance, catch, CPUE, size or distribution), species depleted
Rare = 10	1–10%	Low-to-very-low abundance, at least 90% decline in abundance, catch, CPUE, size or distribution, collapse of stocks or exploitation, listed on endangered species list, species rare
Extirpated = 0	0%	Locally, regionally or globally extinct, species absent



Figure 4 Earliest known nautical chart of Massachusetts Bay and Stellwagen Bank fishing grounds including 'Inner', 'Middle' and 'Outer' Banks (Capt. T. Durrell, *A Large Draught of New England: New Hampshire, York County and Part of Nova Scotia and Accadia*, map, Taunton: U.K. Hydrographic Office, 1734).

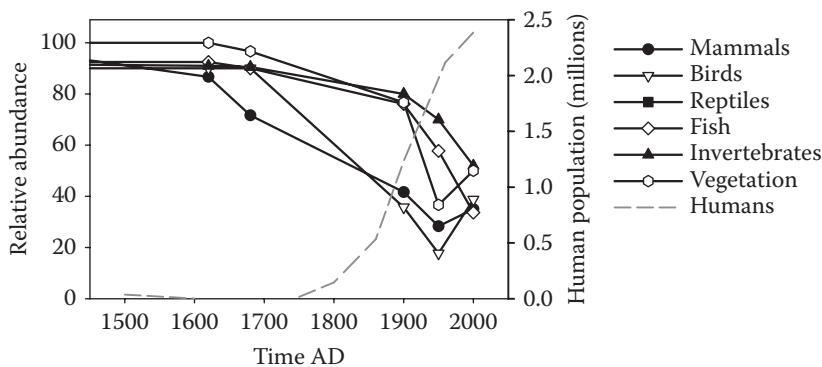


Figure 5 Timeline of changes in relative abundance of six taxonomic groups (left axis) and the human population (right axis) in Massachusetts Bay.

timeline of change in economically and ecologically important species and the human population around Massachusetts Bay is shown in Figure 5.

Marine mammals

Before 1500, an estimated 10,000 northern right whales (*Eubalaena glacialis*) were present in the north-west Atlantic. Between 1530 and 1610, whalers caught about 21,000 right whales in the north-west Atlantic, probably substantially reducing right whale numbers before the time whaling was begun by colonists in the Plymouth area in the early 1600s (Reeves 2001). Stellwagen Bank was famous for its many visiting right whales, but there were also fin (*Balaenoptera physalus*), minke (*B. acutorostrata*) and humpback (*Megaptera novaeangliae*) whales (Ward 1995, Claesson

2008). By the late 1600s, right whale populations were severely depleted, but whaling continued from the eastern United States until the early 1900s (Perry et al. 1999). In the 1700s, 29 right whales were killed in Cape Cod Bay, but catches in New England declined, and shore whaling ceased in the 1720s due to the lack of whales (Waring et al. 2001). However, U.S. whalers seeking other whales caught approximately another 250–300 right whales in 1820–1899 (Reeves & Mitchell 1983). The remaining approximately 58–60 right whales that survived were protected by the League of Nations in 1935 (Reeves 2001). By the 1990s, the population had reached about 300 individuals, slowly increasing by about 2.5% per yr (Knowlton et al. 1994).

Another coastal whale that was easy to catch, the Atlantic grey whale (*Eschrichtius robustus*), had become extinct by the late 1800s (Mead & Mitchell 1984). In the nineteenth century, whaling focused on humpback and fin whales along the north-east coast of the United States (Katona et al. 1993), and heavy whaling pressure continued into the early twentieth century. By the 1960s, all great whales were considered rare (Gambell 1999), and commercial whaling ceased with the 1972 Marine Mammal Protection Act (MMPA) and the 1986 moratorium by the International Whaling Commission (IWC) (Perry et al. 1999). Today, all great whales are listed as endangered (U.S. Fish and Wildlife Service [USFWS] 2009). Despite protection, however, recovery of large whales in the North Atlantic is slow, and whales continue to be threatened by collision with ships, entanglement in fishing gear, pollution, habitat degradation and inbreeding depression (Brown & Kraus 1996, Laist et al. 2001).

In the Gulf of Maine, natives hunted harbour seals (*Phoca vitulina*), grey seals (*Halichoerus grypus*) and harbour porpoises (*Phocoena phocoena*) for their meat, skins and oil (Snow 1978, Prescott & Fiorelli 1980). Seals were abundant before European colonisation (Snow 1978) but hunted to low numbers as direct targets and for a bounty paid by the government until the 1960s (Bigelow & Schroeder 1953, Lotze & Milewski 2004). The MMPA ended seal exploitation in 1972, and populations started to rebound (Waring et al. 2001). The harbour porpoise hunt for oil ended in the early twentieth century because of cheaper mineral oil (Prescott & Fiorelli 1980). Still, the harbour porpoise was in decline in the 1960s (Katona et al. 1993, Read 1994) and was considered a candidate species for the endangered species list in the 1990s. The main current threat is by-catch in fisheries (Waring et al. 2001).

A species that became extinct in the course of extensive hunting for its fur was the sea mink (*Mustela macrodon*). This species used to occur in New England and based on archaeological remains had a range from at least Connecticut to the Bay of Fundy (Campbell 1986). It is unclear how abundant the sea mink used to be as it became globally extinct in 1894 (Committee on the Status of Endangered Wildlife in Canada [COSEWIC] 2002).

Birds

Native people throughout North America hunted birds for their meat, eggs and feathers. In archaeological middens near Boston, bone remains of geese, cormorants, ducks and loons were plentiful (Luedtke 1980). During colonial times, geese, swans and many other birds were very abundant: “Some have killed a hundred geese in a week, fifty ducks at a shot, forty teals at another” (Wood 1634). Intense hunting, egg and feather collection and habitat loss reduced many species during the nineteenth century. Swans were considered rare in 1854 (Cronon 1983), and populations of herons, egrets and other birds with beautiful feathers were strongly decimated because of the millinery trade in the late 1800s (Palmer 1962). The now-extinct great auk (*Pinguinus impennis*) used to be common in the north-west Atlantic, including Massachusetts Bay, in the sixteenth and seventeenth centuries (Greenway 1967). Although it occurred in large populations, the great auk was intensely hunted for its meat, oil and feathers to global extinction in 1844 (Kirk 1985). Similarly, the Labrador duck (*Camptorhynchus labradorius*) inhabited the Gulf of Maine but became extinct in 1875, probably as a result of hunting (Chilton 1997).

In the early twentieth century, efforts to increase bird protection started with the introduction of the Migratory Bird Treaty Act in 1918, but many species continued to be affected by ongoing habitat loss and hunting. In the second half of the twentieth century, however, many bird populations started to recover (Palmer 1962). Yet in the 1960s–1970s, pollution from DDT (dichlorodiphenyl-trichloroethane) and other chemicals had strong negative effects on many species by impairing reproduction (Fitzner et al. 1988). For example, only 11 breeding pairs of osprey (*Pandion haliaetus*) were left in Massachusetts in 1963, but the ban of DDT in the 1970s enabled ospreys to recover to about 350 breeding pairs in 2000 (Massachusetts Division of Fisheries and Wildlife [MDFW] 2009). By the late twentieth century, numbers of many waterfowl and shorebird populations were considered reduced but fairly stable (Veit & Petersen 1993).

Fishes

Archaeological remains show that native people around the Gulf of Maine have harvested a variety of groundfish, pelagic and diadromous fishes over the past millennia (Claesson 2008). For example, remains of large Atlantic cod (*Gadus morhua*) have been very abundant in many prehistoric sites (Steneck 1997, Bourque et al. 2008). With arrival of the Europeans, groundfisheries became the cornerstone of the New England economy, targeting a mixture of bottom-dwelling species (Murawski et al. 1999). Stellwagen Bank supported an abundant and diverse community of Atlantic cod and halibut (*Hippoglossus hippoglossus*) (Figure 6), haddock (*Melanogrammus aeglefinus*), pollock (*Pollachius virens*), skates (Rajidae), yellowtail flounder (*Limanda ferruginea*) and winter flounder (*Pseudopleuronectes americanus*), goosefish (*Lophius americanus*), longhorn sculpin (*Myoxocephalus octodecemspinosus*) and spiny dogfish (*Squalus acanthias*). Common migratory species included herring (*Clupea harengus*), alewife (*Alosa pseudoharengus*), bluefish (*Pomatomus saltatrix*), bluefin tuna (*Thunnus thynnus*), swordfish (*Xiphias gladius*) and mackerel (*Scomber scombrus*) (Ward 1995). Arriving in Massachusetts Bay in 1630, Francis Higginson reported “the abundance of sea fish are almost beyond believing,” and “Codfish in these seas are larger than in NewFound Land, six or seven here making a quintal, whereas there they have fifteen to the same weight” (Baird 1873).

Nearshore fish populations significantly deteriorated between 1800 and 1900 (Claesson & Rosenberg 2009). Halibut used to congregate in winter in the gully between Cape Cod and Stell-



Figure 6 Pictures of (A) Atlantic cod in the 1880s (courtesy of R. Steneck) and (B) Atlantic halibut in 1910 caught in the Gulf of Maine (Census of Marine Life, History of Marine Animal Populations Program).

wagen Bank. Around 1820–1825, a demand for halibut developed in the Boston market, and large amounts were caught in Massachusetts Bay. By 1850, halibut had been nearly fished out, and the fishery moved to other parts of the Gulf of Maine and farther (Bigelow & Schroeder 1953). By the 1890s, almost all halibut sold in Gloucester came from Iceland (Murawski et al. 1999). Other large predators, such as swordfish, had been overfished to near extirpation on Stellwagen Bank by the late nineteenth and early twentieth centuries (Claesson & Rosenberg 2009).

In 1906, the first trawler was introduced to American waters in Boston, and by 1930 the trawler fleet had grown to over 300 vessels. Between 1915 and 1940, cod landings remained relatively stable as haddock, redfish (*Sebastes* spp.) and other species were the main targets. Haddock landings in the Gulf of Maine had been relatively low prior to 1900 but increased to over 100,000 t by the 1920s and declined in the early 1930s (Murawski et al. 1999). Still, until the mid-1960s, haddock remained the mainstay of the New England groundfishery. In 1965, landings reached a record high of 154,000 t but rapidly declined afterwards.

In 1960–1965, total groundfish landings increased from 200,000 to 760,000 t, primarily composed of silver hake (*Merluccius bilinearis*), haddock, red hake (*Urophycis chuss*), flounders and cod (Murawski et al. 1999). Yet by 1970, groundfish abundance and landings had severely declined. In 1977, the Magnuson Fishery Conservation and Management Act (Wang & Rosenberg 1997) was implemented and excluded foreign fishing. However, subsequently the U.S. otter-trawl fishing effort essentially doubled. By the mid-1980s, catch rates and abundance had dropped by half, and Georges Bank haddock had collapsed. Because southern New England yellowtail flounder also declined to low levels, the fishery then almost completely relied on cod. Exploitation rates of groundfish reached their highest levels in the early 1990s, and stock biomasses fell in many cases to record lows (Murawski et al. 1999). An emergency closure on Georges Bank has since helped haddock but not cod to increase again (Rosenberg et al. 2006).

In colonial times, diadromous fish such as alewives also occurred “in such multitudes as is almost incredible, pressing up such shallow waters as will scarce permit them to swim” (Wood 1634). Alewives supported a fishery well into the twentieth century, with a peak in 1956 and a decline thereafter (National Marine Fisheries Service [NMFS] 2009). Atlantic salmon (*Salmo salar*) and sturgeons (*Acipenser* spp.) were important subsistence and commercial resources throughout history. Overexploitation, however, together with pollution and habitat loss in rivers resulted in the extirpation of all native salmon runs south of Kennebec River, Maine, in the 1920s (Anderson et al. 1999c) and large declines of Atlantic (*Acipenser oxyrinchus*) and shortnose (*A. brevirostrum*) sturgeon in the 1800s. Today, only remnant sturgeon populations remain, and the lack of fish passage facilities at dams and poor habitat conditions continue to impair their reestablishment (Friedland 1998).

Invertebrates

Many invertebrates have been used for subsistence by both natives and Europeans (Claesson 2008). Commercial fisheries for clams and oysters in Massachusetts Bay began with European colonisation (Skinner et al. 1995). Banks of the eastern oyster (*Crassostrea virginica*) were “a mile long, and oysters a foot long” (Wood 1634), and “people [were] running over clam banks, huge individual clams as big as a white penny loaf” (Cronon 1983). After more than 200 yr of oyster fishing, mechanical harvesting with tongs started in 1880. The commercial fishery peaked in 1900, strongly declined in the 1920s, and started a series of fishing down the U.S. Atlantic coast (Kirby 2004). Clams were continuously fished over the centuries, but landings increased in the twentieth century, peaking in the 1970s, followed by a decline (Anderson et al. 1999a,b). Landings of lobster (*Homarus americanus*) in the Gulf of Maine have steadily increased since 1940. Although lobster abundance has increased, current fishing mortality is nearly double the overfishing level, and the fishery totally depends on new recruitment (Anderson et al. 1999a).

The decline in traditionally important groundfish and invertebrate fisheries has resulted in the search for new target species, such as sea urchin (*Strongyocentrotus droebachiensis*),

for which a fishery was developed in the 1980s. Landings rapidly increased in Massachusetts, reaching the second highest in north-east U.S. nearshore landings with an average yield of 11,400 t. However, catch per unit of effort (CPUE) and landings have steadily declined since 1993 (Anderson et al. 1999b).

Vegetation

Since European colonisation, salt marshes have been important to feed livestock and harvest hay (Chapman 1977), but many have been transformed for agriculture and urban development (Bromberg et al. 2009). Saltmarsh eradication for industrial development and mosquito control began in the midnineteenth century (Russell 1976). By 1940, about 80% of the original salt marshes had been removed or filled in (Chapman 1977). In the 1960s, legislation was developed to protect salt marshes, and restoration began in the 1980s (Chapman 1977, Massachusetts Bays Program [MBP] 2004). Based on historical maps, Massachusetts has lost about 41% of its salt marshes since 1777, with losses in the Boston area as high as 81% (Bromberg & Bertness 2005).

Seagrass beds have also suffered substantial losses, especially in the twentieth century (Wilbur 2009). In the 1930s, an outbreak of wasting disease decimated eelgrass populations by more than 90% throughout the North Atlantic. Eelgrass beds generally recovered in the 1940s, but since the 1950s eelgrass habitat has been drastically reduced by water quality degradation (MBP 2004). Current beds in Massachusetts Bay appear to be stable (Wilbur 2009), but abundance is low (Bricker et al. 1999). Although not located in Massachusetts Bay, quantitative estimates of historical seagrass loss exist for southern Massachusetts. In Buzzards Bay, seagrass covered about 9700 ha in the 1600s. By the 1930s, this was reduced to 81 ha due to the wasting disease, from which it recovered to about 5700 ha in the 1970s (Costa 1988, 2003). In the 1990s, seagrass beds decreased again to about 3200 ha due to eutrophication and disturbance. Thus, overall seagrass loss has been about 67% since the 1600s (Costa 2003). In nearby Waquoit Bay, increased development resulted in an almost complete loss of eelgrass beds by the mid-1990s (Costa 2003).

Water quality

Over time, increased development around Massachusetts Bay has resulted in increasing sewage loads, land run-off and other point and non-point sources of pollution (MBP 2004). A 1990s survey indicated moderate eutrophication levels for Massachusetts Bay and high levels in Boston Harbour (Bricker et al. 1999). High nitrogen inputs have led to increased chlorophyll concentrations, algal blooms and low oxygen concentrations. Over the past 10 yr, some improvements have been made to wastewater treatment, reducing the discharge of sewage solids, organic matter, toxic chemicals and nutrients to Boston Harbour (MBP 2004).

Delaware Bay, Atlantic Coast

In 1609, Henry Hudson entered the Delaware Bay (Figure 7) in search of a trade route to the Far East for a Dutch company (Delaware State History 2009). The Dutch tried to establish a settlement in 1631, which was destroyed by natives. A few years later, Sweden established the first permanent settlement, which was later taken over by England. The native population may have numbered about 20,000 before European contact, but several wars and at least 14 epidemics reduced their numbers to about 4000 by 1700 (Sultzman 2000). The colonial economy flourished under English rule, supported by whaling, sealing, fishing, farming and the lumber industry. By 1760, about 35,000 people lived in the Delaware region, and the population continued to grow rapidly over time (Delaware State History 2009). The general timeline of change is shown in Figure 8.

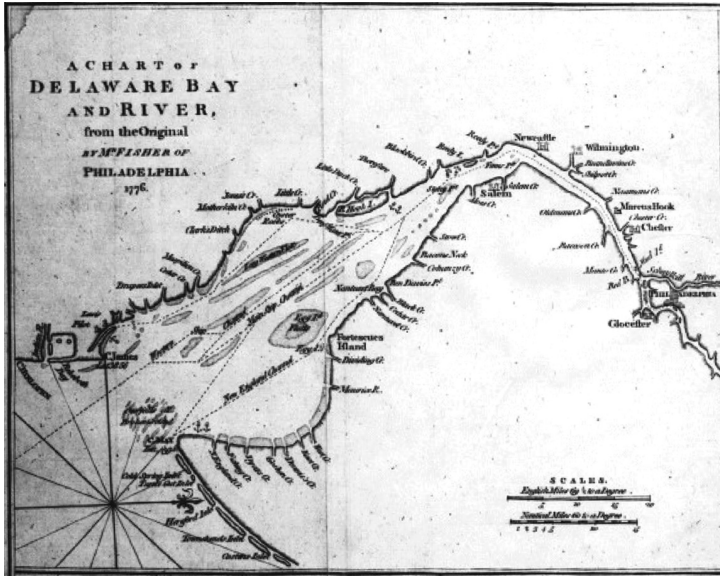


Figure 7 Delaware Bay and River, 1776 (Delaware Public Archives).

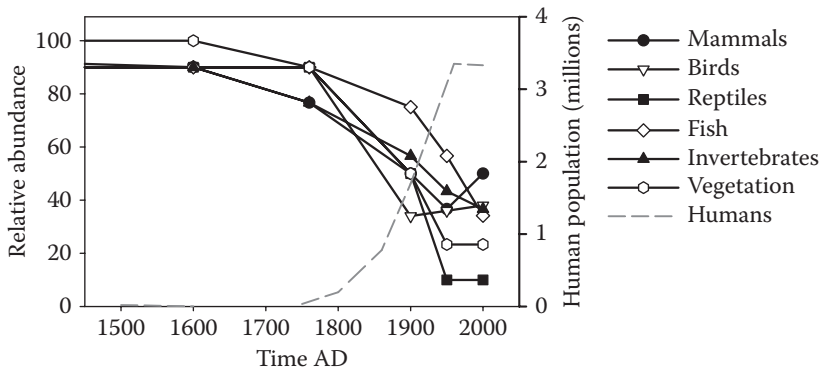


Figure 8 Timeline of changes in relative abundance of six taxonomic groups (left axis) and the human population (right axis) in Delaware Bay.

Marine mammals

In December 1630, the Dutch ship *De Walvis* sailed from Holland to Delaware Bay with immigrants, food, cattle and whaling implements. The Dutch planned to open a whale and seal fishery as well as a settlement and plantation for the cultivation of tobacco and grains (Delaware Living History 2009). A persistent shore whaling enterprise was developed in Delaware Bay and along the New Jersey shore (Reeves et al. 1999). The peak of right whaling at the mouth of Delaware Bay was reached in 1680: “Mighty whales roll upon the coast, near the mouth of the bay of the Delaware; eleven caught and worked into oil in one season. We justly hope a considerable profit by whalery, they being so numerous” (William Penn 1683, cited in Watson 1868). Although right

whaling was most profitable in the early 1700s, it continued until at least the 1820s. However, a virtual crash of right whaling occurred in 1760, and organised whaling ceased by 1840 (Reeves et al. 1999). Today, fin, humpback and right whales are all listed as endangered in Delaware (USFWS 2009).

Birds

Historical information on birds in Delaware Bay is sparse and largely descriptive. Many species were used by natives and Europeans for their meat, eggs and feathers (Goddard 1978). In the nineteenth century, some uses were commercialised, such as the use of feathers for the millinery industry (Animal Welfare Institute [AWI] 2005). As a consequence, thousands of herons, egrets and other birds with flamboyant plumage were shot for their feathers, while many other species were hunted solely for sport without any regulations in place. Habitat loss, especially the loss and ditching of wetlands, had severe effects on many waterfowl populations (Cole et al. 2001). By the twentieth century, many species of waterfowls, wading birds, sea- and shorebirds were at very low numbers.

Hérons were saved from extinction by the federal Lacey Act of 1900, which forbid foreign and interstate trade of wildlife parts, and the Migratory Bird Treaty Act of 1918, which also helped to protect many other species of birds (AWI 2005). However, in the 1940s DDT poisoning resulted in severe declines in ospreys, bald eagles (*Haliaeetus leucocephalus*) and peregrine falcons (*Falco peregrinus*) (Sullivan 1994). After the ban of DDT, ospreys showed improved nesting success in the late 1980s (Clark et al. 2001b). The bald eagle had been listed as endangered in the 1970s but has recently been de-listed (USFWS 2009).

Other birds experienced recent population declines, for example, nine species of wading birds declined from about 12,000 to about 7000 breeding pairs in 1989–2000 (Rattner et al. 2000). Numbers of Canada geese (*Branta canadensis*) have declined since the 1980s, resulting in the closure of the regular hunting season in 1995 along most ‘Atlantic flyway’ states (Malecki et al. 2001). Some declines have been attributed to the degradation of estuarine habitats (Erwin 1996). Another threat has been the increasing harvest of horseshoe crabs (*Limulus polyphemus*), which provide essential food for up to 1 million migrating birds travelling from South American wintering to Arctic breeding grounds. The timing of their arrival coincides with hundreds of thousands of horseshoe crabs laying their eggs in the sandy beaches, which fuel the long-distance migration of the birds (Walls et al. 2002).

Reptiles

Sea turtles have been harvested for their meat, eggs and shells by natives and Europeans in Delaware Bay (Pearson 1972, Goddard 1978). Delaware Bay provides critical sea turtle habitat, but turtle abundance has declined through hunting, habitat loss and fisheries by-catch. Today, all sea turtles are listed as endangered or threatened in Delaware (USFWS 2009).

Fishes

In a letter in 1683, William Penn described the fishes of Delaware Bay: “Sturgeons play continually in our river. Alloes ... and shades are excellent fish. They are so plentiful that six hundred are drawn at a draught. Fish are brought to the door, both fresh and salt” (Watson 1868). The exact time when the fishery for sturgeon reached a considerable extent is unknown, but after 1870 the business expanded rapidly (Cobb 1900). During 1880–1900, Delaware Bay supported the most abundant and commercially important sturgeon population in the United States (Secor & Waldman 1999); “The average catch ... is about 1000 fish to a vessel for the month of April” (Collins 1887). In 1890, the abundance of female Atlantic sturgeon, the principal target, was estimated at 180,000, yet “there has been an almost continuous decrease in the number of sturgeon taken” (Cobb 1900). Landings along the U.S. Atlantic coast were about 7 million pounds yr⁻¹ (1 pound = 0.4536 kg) just prior to the turn of the century, 90% of which came from Delaware (Figure 9). By 1920, sturgeons

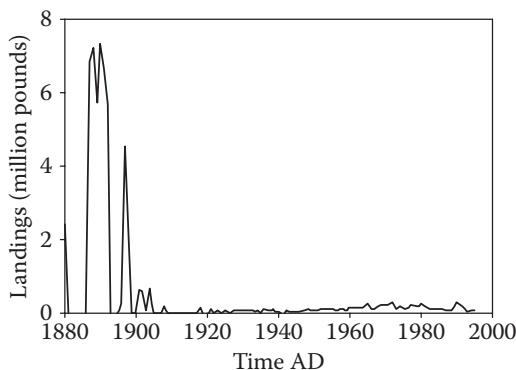


Figure 9 Commercial landings of Atlantic sturgeon for the United States (data from NMFS 2009).

were very rare (Brundage & Meadows 1982). Still, from 1950 to the mid-1990s, landings reached 100,000–250,000 pounds annually along the coast. Overharvesting of sturgeon for flesh and eggs (caviar) continued until the Atlantic States Marine Fisheries Commission (ASMFC) and federal government implemented a coastwide moratorium in the late 1990s (ASMFC 2009). It has been estimated that Atlantic sturgeon stocks are reduced more than 20-fold from their nineteenth century abundances and are now either biologically extinct or extremely depleted throughout their range (Secor & Waldman 1999). There are still about 6000–14,000 shortnose sturgeon in the upper Delaware River (Hastings et al. 1987), which are endangered (USFWS 2009).

American shad (*Alosa sapidissima*) were also very abundant in the Delaware River: “The numbers of shad taken ... vary in different seasons. Perhaps it would not be far from the truth to estimate them at 30,000 at each shore fishery. Formerly, when fisheries were fewer, the number far exceeded this amount” (McDonald 1887). Annual landings in 1890–1901 were 11–17 million pounds, several times greater than in any other river system in the United States (Chittenden 1974). Abundance declined rapidly in the early 1900s, and fewer than 0.5 million pounds were landed in 1920. Since then, abundance has remained low (Chittenden 1974). A historically important commercial and recreational fishery also existed for striped bass (*Morone saxatilis*) (Anderson et al. 1999c). Like other diadromous fishes, striped bass has been severely affected by habitat loss and pollution in rivers. Since 1950, commercial catches declined, but recreational fishing increased. In the 1990s, stocks were severely depleted, and protection measures were taken to enhance recruitment (Anderson et al. 1999c).

An important fishery for weakfish (*Cynoscion regalis*) began in the 1800s (Lowerre-Barbieri et al. 1995). “In 1880, while only 10,000 pounds were caught south of Cape Henlopen, 2,608,000 pounds were taken by the fishermen along the shores bordering Delaware Bay” (Collins 1887). In the 1960s, the fishery strongly declined, yet landings and maximum size and age increased during the 1970s (Lowerre-Barbieri et al. 1995). Catches peaked at 1.8 million pounds in 1980, followed by a decline to 24,604 pounds in 2007 (NMFS 2009).

Invertebrates

“Of shell-fish, we have oysters, crabs, coccles, conchs, and mussels; some oysters six inches long, and one sort of coccles as big as the stewing oysters” (William Penn 1683, cited in Ingersoll 1881). European colonists in the 1600s described huge shoals and banks of oysters between Cape Henlopen and Cape May (Miller 1971), and a chart by Peter Lindestrom showed the entire Delaware shore lined with oyster beds (Ford 1997). A commercial oyster fishery began right after European arrival, yet in 1719, a first law was introduced to protect the resource: “That no person ... shall rake or gather up any oysters or shells from and off any of the beds ... from the tenth day of May to the first

day of September” (McCay 1998). Numerous acts followed but were largely ineffective in protecting oysters, which were badly depleted by the late 1700s. In 1820, the use of dredges was banned (McCay 1998), and the first planting of oysters in Maurice River Cove was authorised in 1856 (Hall 1894). The oyster industry declined alarmingly in the mid-1890s but increased again in 1902 (Miller 1971). The first recorded landings in the late 1890s were at 21 million pounds of oyster meats (Ford 1997). Average landings from 1880 to 1931 were 13.9 million pounds but dropped to 6.5 million pounds in 1932–1956. In the late 1950s, the MSX oyster parasite strongly decreased oyster production, and landings were 550,000 pounds in 1963. Resurgence of MSX forced the closure of seed beds in the mid-1980s. A limited oyster fishery opened in 1990, but the Dermo parasite *Haplosporidium nelsoni* caused strong mortality to entire oyster beds (Ford 1997).

A significant hard-shell clam (*Mercenaria mercenaria*) fishery has existed in Delaware Bay since early times (Ford 1997). Large-scale utilisation began in the late 1940s, and landings peaked at 770,000 pounds of meat in 1951, followed by a sharp decline. The dredge fishery ceased to operate in 1966–67 because of clam depletion. The bay’s hydrography, tidal exchange and predation by horseshoe crabs were identified as causes for low clam densities. Several surveys in the 1970s confirmed the presence of hard-shell clams in or near oyster beds but at numbers insufficient to support commercial harvesting (Ford 1997).

Horseshoe crabs were commercially harvested for fertiliser and livestock feed from 1870 to the 1960s (Walls et al. 2002). During this period, catch records in Delaware Bay exhibited a progressive decline from more than 4 million to fewer than 100,000 crabs per yr. In the 1950–1960s, the horseshoe crab fishery was minimal, and populations increased at least 13-fold. Since then, a commercial fishery developed to provide bait for catching American eel (*Anguilla rostrata*) and whelk (*Busycon* spp.). The fishery employed trawls, dredges, gill nets and hand gathering and increased dramatically in the 1990s. Horseshoe crabs are also fished for biomedical purposes. Total landings in 2000 were reduced to 40% of 1995–1997 levels, and a marine reserve was implemented at the mouth of Delaware Bay. The commercial harvest is controversial as horseshoe crabs are essential food for migrating birds (Walls et al. 2002).

Vegetation

Today, Delaware Bay has about 160,000 ha of wetland area, which is at least 21–24% less than the original extent (Kennish 2000). In Delaware State, more than half of the wetlands have been converted since the 1780s (U.S. Geological Survey [USGS] 2009a). In the 1930s, ditching of wetlands as a mosquito control programme began. In the 1940s, the common reed (*Phragmites*) invaded coastal marshes comprising one-third of wetland vegetation today (Cole et al. 2001). A 1970s survey estimated that tidal wetlands were reduced from 80,418 to 74,688 acres (1 acre = 0.4047 ha) from 1938 to 1973 (Cole et al. 2001). Compared with other regions, the relatively low loss has been attributed to the lower human population (Sullivan 1994). The Wetland Protection Act of 1970 and the Clean Water Act of 1972 slowed the rate of further wetland loss.

Submerged aquatic vegetation (SAV) is nearly absent from the Delaware Estuary and its coastal bays (Sullivan 1994, Bricker et al. 1999). It is generally assumed that relatively high natural turbidity prevents the establishment of SAV, although some reports from the early twentieth century indicated eelgrass in the backwaters of Cape May County and possibly in Delaware Bay: “It is present to some extent in Cape May Harbor and in back waters of Cape May County, but is very scarce in the upper part of Delaware Bay” (Richards 1929, cited in Sullivan 1994).

Water quality

Delaware Bay water quality began to decline in the early 1800s, with marked increases in pollution and disease since the 1880s (Kennish 2000). In the 1940s–1950s, dissolved oxygen concentrations reached minimum values of 0.1 mg L⁻¹ every year. Wastewater treatment plants were built in the 1960s, and water quality began to improve. Minimum oxygen concentrations increased to 3 mg

L^{-1} by the late 1960s and 8 mg L^{-1} by the late 1980s. Nitrogen and phosphorus concentrations decreased 1.33- and 4-fold, respectively, from 1960 to 2000, but loading was still $7500 \text{ mmol nitrogen m}^{-2} \text{ yr}^{-1}$ and $600 \text{ mmol phosphorus m}^{-2} \text{ yr}^{-1}$. Nitrogen and phosphorus loads in Delaware Bay are about 10 times higher than in Chesapeake and two to four times higher than in San Francisco Bay (Kennish 2000), yet overall eutrophication conditions are low (Bricker et al. 1999).

Chesapeake Bay, Atlantic Coast

Chesapeake Bay is one of the U.S. largest estuaries and probably one of the best studied around the globe (Figure 10). Native Americans have lived in the bay region since the last ice age, beginning agricultural practices around 1200. In 1600, about 25,000–45,000 natives lived in the region (Feest 1978a,b, Ubelaker & Curtin 2001). In 1900, the native population numbered about 2000, compared with 1,120,135 European descendants. European settlement began with the establishment of Jamestown, Virginia, in 1607 (Chesapeake Bay Program [CBP] 2009a), and the colony grew rapidly (Figure 11). Next to agriculture and forestry, the colonial economy was built on an incredible abundance of marine life. Strachey (1612) noted: “Grampus, porpois, seales, stingraies, brets, mulletts, white salmons, troute, soles, playse, comfish, rockfish, eeles, lampreys, cat-fish, perch of three sorts, shrimps, crefishes, cockles, mishells, and much more like, like needles to name, all good fish”, and Burnaby in 1759 indicated: “These waters are stored with incredible quantities of fish, such as sheeps-head, rock-fish, drums, white perch, herrings, oysters, crabs, and several other sorts” (Pearson 1942). The general timeline of historical change is shown in Figure 11.

Marine mammals

Humpback, fin and right whales occur in coastal waters off Virginia and Maryland and occasionally enter Chesapeake Bay (Swingle et al. 1993). Today, these large whales are at low population levels along the U.S. Atlantic coast (Waring et al. 2001) and are listed as endangered (USFWS 2009). Yet, large whales were much more abundant in earlier times. Historical records describe the hunting of large whales in Chesapeake Bay in the 1600s–1700s (Wharton 1957, Pearson 1972). These were probably right or Atlantic grey whales, which were the first whales to be pursued by whalers because

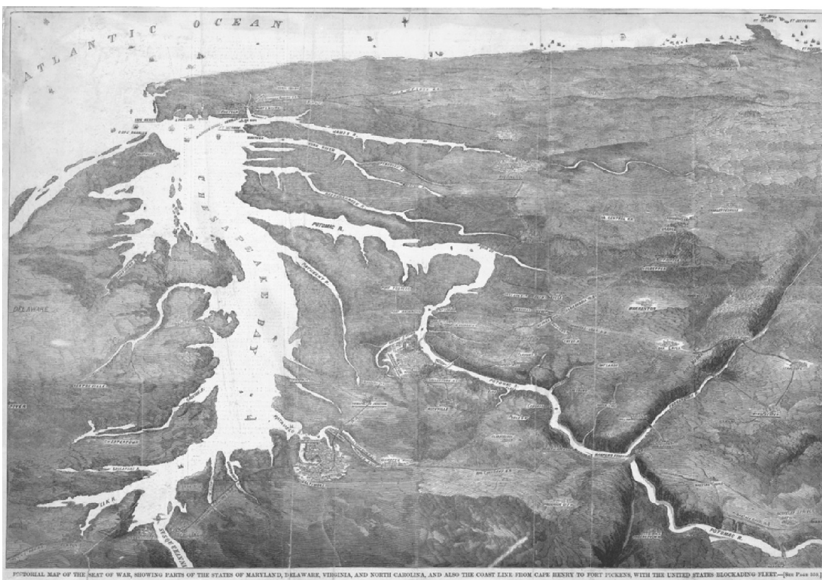


Figure 10 Chesapeake Bay, 1861 (Library of Congress, Geography and Map Division).

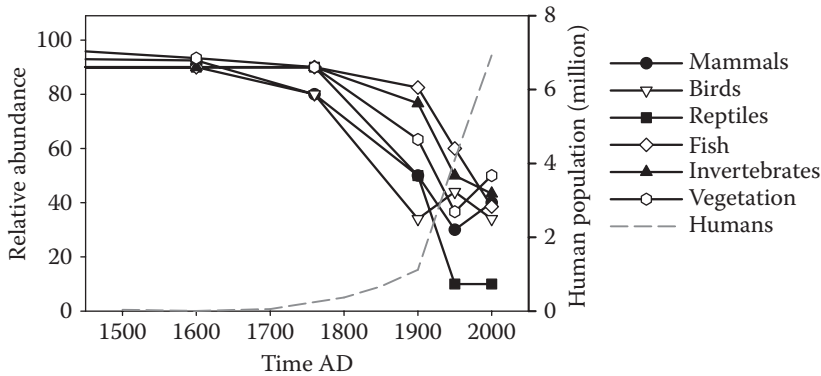


Figure 11 Timeline of changes in relative abundance of six taxonomic groups (left axis) and the human population (right axis) in Chesapeake Bay.

they were coastal, slow swimming, easy to catch and would not sink when dead. In the 1600s and early 1700s, right whales were reduced to very low numbers on the U.S. eastern coast (Reeves et al. 1978), and the Atlantic grey whale was extirpated in the 1800s (Mead & Mitchell 1984).

Historical accounts of Europeans arriving in Chesapeake Bay in the 1500s included reports of dolphins, porpoises, seals and manatees (*Trichechus manatus*) (Carleill 1585, Smith 1910, Bruce 1935, Wharton 1957, Pearson 1972). Coastal bottlenose dolphins (*Tursiops truncatus*) were exploited by a shore-based net fishery from 1797 to 1925, mostly in North Carolina. The historical population numbered 13,748–17,000 animals for the entire coast, while today’s stock is listed as depleted under the MMPA (Blaylock 1988, Waring et al. 2001). “A good fish, which is common and found in large numbers is the porpoise,” wrote Michel in 1701, and seals were also described as common at that time (Pearson 1942). The repeated sightings of a “sea monster”, nicknamed “Chessie”, in Chesapeake Bay date to the early twentieth century and possibly include manatee sightings that were not properly identified. The annual migration of manatees from Florida to Chesapeake Bay may have been common in previous centuries (USGS 1996).

Sea turtles

“The waters and especially the tributaries are filled with turtles,” wrote Michel in 1701 (Wharton 1957). Sea turtles were found in great numbers (Billings et al. 1986) and have been commercially harvested for their meat, eggs and shells since the early 1600s (Pearson 1972). Years of exploitation have greatly reduced all sea turtle populations, with the leatherback (*Dermochelys coriacea*), Kemp’s ridley (*Lepidochelys kempii*) and hawksbill (*Eretmochelys imbricata*) turtles listed as endangered today and the loggerhead (*Caretta caretta*) and green (*Chelonia mydas*) turtles as threatened in Virginia and Maryland (USFWS 2009). Incidental by-catch in commercial shrimp trawling is a continuing source of mortality adversely affecting recovery of some species (Office of Protected Resource [OPR] 2009). Today, 5000–10,000 sea turtles enter Chesapeake Bay each spring and summer, mostly young loggerhead or Kemp’s ridley using the Bay as a feeding ground. Leatherback and green turtles also occur, but only one hawksbill turtle has been seen in recent times (Virginia Institute for Marine Science [VIMS] 2009).

Birds

Historically, millions of geese, swans, ducks and other waterfowl overwintered in Chesapeake Bay, supported by profuse seagrass beds, SAV and a rich supply of invertebrates. In the seventeenth century, Alsop reported that waterfowl so blanketed the Bay that “there was such an incessant clattering made with their wings on the water where they rose, and such a noise of those flying higher up,

Table 5 Average number of birds wintering on Susquehanna Flat

Period	Canada geese	Tundra swans	Diving ducks	Dabbling ducks
1959				2500
1959–1962	625	750	2225	1275
1966–1972	2030	770	1660	390
1973–1976	3175	50	275	175

Note: The decline in tundra swans and diving and dabbling ducks was attributed to the decline in submerged aquatic vegetation, while Canada geese switched to feeding on adjacent agricultural fields (data from Bayley et al. 1978).

that it was as if we were all the time surrounded by a whirlwind” (Blankenship 2004). In the 1600s, flock size of ducks was estimated at 7 mi² (Bruce 1935). Over time, the deterioration of shallow-water habitats; the loss of wetlands, seagrass beds and SAV; the degradation of water quality; human disturbance and overhunting have greatly reduced waterfowl numbers (Blankenship 2004). By the late nineteenth and early twentieth century, the dwindling number of waterbirds raised concerns. First conservation measures were introduced with the Lacey Act in 1900 and the Migratory Bird Treaty Act in 1918 (Blankenship 2004, AWI 2005). This effectively ended commercial hunting and increased habitat protection, but sport hunting continued. Waterfowl populations never returned to historic levels, and today about 1 million waterfowl spend their winter in Chesapeake Bay, a third of the entire Atlantic flyway waterfowl population (Blankenship 2004).

Since the 1960s, bird numbers have remained relatively constant, but species composition has changed (Table 5; Bayley et al. 1978). Duck populations rely more heavily on aquatic habitats and have decreased nearly 80% since the 1950s, whereas geese populations can feed away from the bay in agricultural fields and have increased (Blankenship 2004). American black ducks (*Anas rubripes*) are particularly intolerant of human disturbance and rely heavily on underwater grasses, which have declined (Krementz et al. 1991, Blankenship 2004). Similarly, the redhead (*Aythya americana*) exclusively feeds on underwater grasses and did not switch to other foods. A few decades ago, about 80,000 wintered here, but only a few thousand remain today (Blankenship 2004). Canvasback (*Aythya valisineria*) was the most abundant diving duck in Chesapeake Bay, but the “large rafts of canvasbacks and other diving ducks that made the flats famous are no longer observed” (Bayley et al. 1978). In the 1930s, about half a million canvasbacks congregated each autumn off Poole’s Island in Maryland. They used to feed on wild celery almost exclusively, but the sharp decline in wild celery caused canvasbacks to shift their diet to small clams. Today, only about 50,000 come to the Chesapeake each fall (Blankenship 2004).

Raptors were also abundant around Chesapeake Bay. Historical records indicate that more than 1000 pairs of bald eagles nested around the bay every year in the early 1990s (Reshetiloff 1997). The population declined because of direct killing, habitat loss and decline of prey. In the 1940s, the Bald Eagle Protection Act (AWI 2005) made it illegal to kill, harm, harass or possess bald eagles, alive or dead, including eggs and feathers. However, the increasing use of DDT to control mosquitoes posed a new threat by causing reproductive failure (Reshetiloff 1997). By the 1970s, the number of breeding pairs had dropped to 90, and the bald eagle was listed as endangered. In 1972, DDT was banned in the United States, and nesting success steadily increased. In 1996, there were 179 nesting pairs producing 508 young (Reshetiloff 1997). The bald eagle was reclassified as threatened in 1995 and was removed from the endangered species list in 2007.

Fishes

More than 295 species of fishes are known to occur in the Chesapeake Bay region; 32 of these species are year-round residents (CBP 2009b). Native Americans used a wide variety of fish and shellfish species (Dent 1995). European colonisers first developed subsistence fisheries to supply the

new colony and later commercial fisheries to trade with Europe and other regions (Pearson 1942). Important fisheries in Chesapeake Bay included those for sturgeon, shad, menhaden, mackerel and many ground- and flatfish (CBP 2009b).

Atlantic sturgeon was extremely abundant, and hundreds could be seen migrating up the tributaries to spawn every year (Billings et al. 1986). Their average size was more than 3 m in late summer (Bruce 1935), and they were eaten widely by colonists (Smith 1910). “Sturgeon and shad are in such prodigious numbers, that ... some gentlemen in canoes, caught above 600 of the former with hooks, and of the latter above 5000 have been caught at one single haul of the seine,” wrote Burnaby in 1759 (Pearson 1942). Sturgeon and caviar were exported to England beginning in the early 1600s (Pearson 1942). Sturgeon was the first primary cash crop of Jamestown, Virginia, and was second only to lobster among important fisheries in the late 1800s (ASMFC 2009). Commercial sturgeon landings in Chesapeake Bay peaked in 1890 at about 250,000 kg (Secor et al. 2000). Afterwards, the mid-Atlantic fishery rapidly declined (ASMFC 2009), and Atlantic sturgeon was thought to be extirpated by the 1920s (Secor et al. 2000). Today, Atlantic sturgeon stocks are extremely depleted and nearly extirpated throughout their range in the United States (Secor & Waldman 1999), and shortnose sturgeon is listed as endangered (USFWS 2009).

American shad have been valued for both their delicious meat and roe. From the mid-1800s to the early 1900s, the American shad fishery was the largest fishery in Chesapeake Bay, with annual catches reaching 17.5 million pounds (Figure 12). By the mid-1930s, annual catches had dropped to less than 4 million pounds and to less than 1 million pounds in the 1980s. Stocks were in such poor condition that a moratorium on taking shad was implemented in Maryland in 1980, while fishing continued in Virginia (Chesapeake Bay Field Office [CBFO] 2009). After catches dropped below 500,000 pounds in 1992, Virginia implemented a moratorium as well. The long decline seems primarily the result of overfishing and habitat degradation in spawning areas (CBFO 2009).

The abundance of menhaden (*Brevoortia tyrannus*) was noted by early European explorers of the mid-Atlantic region (Menhaden Research Council [MRC] 2009). Native Americans showed colonists how to use menhaden as fertiliser, and the colonists soon developed a fishery. Menhaden

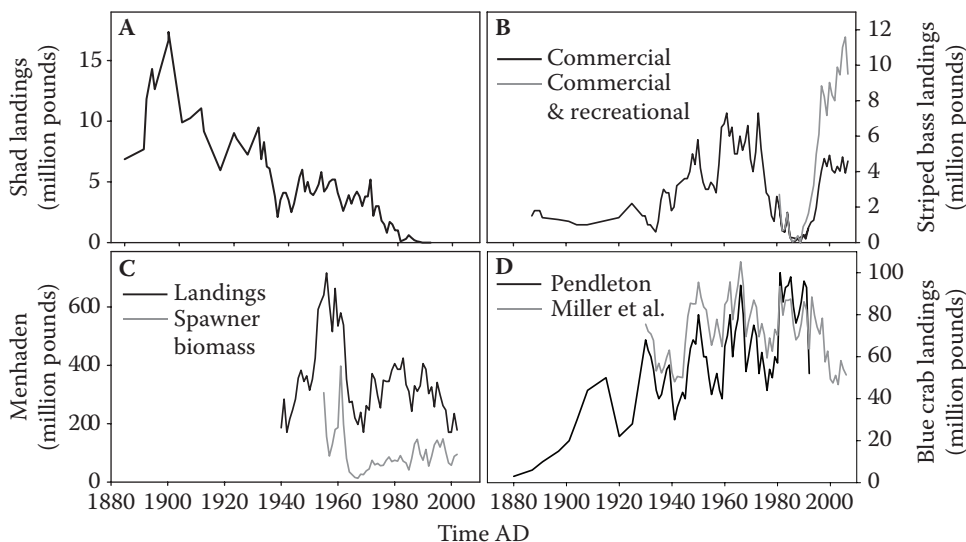


Figure 12 Time series of historical fisheries in Chesapeake Bay for (A) American shad (data from Pendleton 1995), (B) striped bass (data from Pendleton 1995, ASMFC 2008), (C) Atlantic menhaden for the Atlantic coast (data from ASMFC 2004), and (D) blue crabs (data from Pendleton 1995, Miller et al. 2005).

were taken with large seines set from shore, and farmers applied 6000–8000 fish per acre (MRC 2009). The menhaden fishery for reduction had its origins in New England in the early 1800s and spread south after the Civil War. Coal-fired steamers gradually replaced sailing ships in the late 1800s, and diesel and gasoline engines replaced steam engines following WWI (Chesapeake Bay Ecological Foundation [CBEF] 2009). The primary use of menhaden changed from fertiliser to animal feed after WWII, and the industry grew rapidly to peak production of more than 700,000 t in the 1950s (Figure 12). In the 1960s, landings declined to less than 200,000 t, resulting in factory closings and fleet reductions. During the 1970s–1980s, landings improved but declined again during the 1990s (ASMFC 2004). During the same time, the spawning stock biomass of the Atlantic stock declined from 176,000 t in the 1950s–1960s to 32,800 t in 1999 (Figure 12). The population has suffered from poor recruitment in Chesapeake Bay since the 1990s because of not only habitat loss and predation but also disease, toxic algal blooms, parasites and occasional mass mortalities due to low dissolved oxygen levels (CBEF 2009).

Other fish species that have experienced strong declines during the twentieth century include the weakfish, Atlantic croaker (*Micropogonias undulatus*), red drum (*Sciaenops ocellatus*), bluefish, summer flounder (*Paralichthys dentatus*) and Spanish mackerel (*Scomberomorus maculatus*), among others (Chittenden et al. 1993, CBP 2009b). Yet, not all fish stocks have declined. Striped bass, which has supported an important fishery since colonial times, steeply declined in the 1980s, but strict regulations enabled the species to increase to high abundance levels. Both the commercial and the recreational fishery followed with increasing landings over the past decade (Figure 12; ASMFC 2008).

Invertebrates

When Europeans first visited Chesapeake Bay, they found extensive oyster bars exposed at low tide and in shallow waters (Rothschild et al. 1994). In the Maryland portion of Chesapeake Bay, natural oyster bars covered 116,000 ha in 1907–1912 (Figure 13). Today, these bars are virtually nonexistent (Rothschild et al. 1994). The fishery peaked in 1840–1890 at 600,000 t (Figure 13), accompanied by strong overfishing and destruction of oyster habitat by fishing gears (Héral et al. 1990, Rothschild

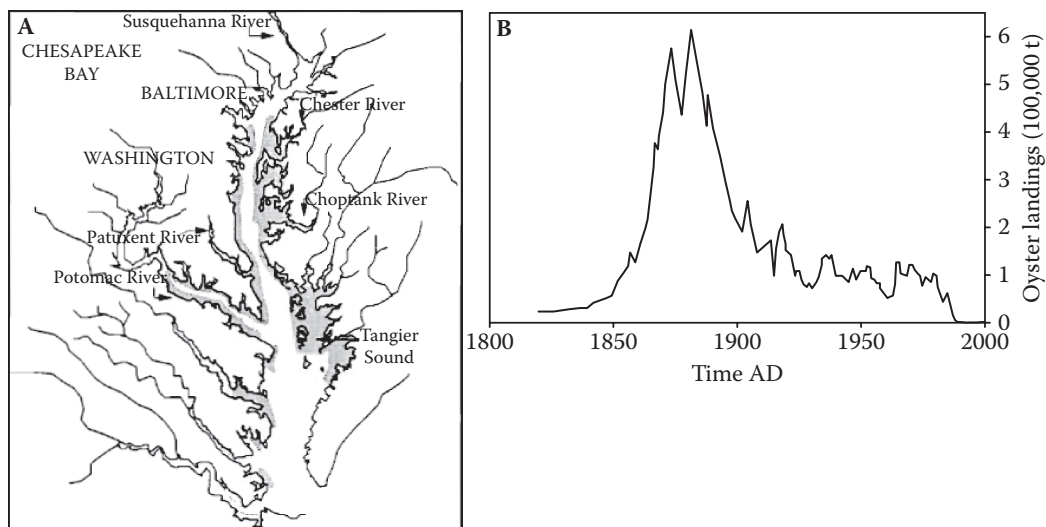


Figure 13 Historical distribution (A) of oyster bars in Chesapeake Bay around 1900 according to Yates 1913 (from Rothschild et al. 1994; reprinted with permission from Inter Research) and oyster landings (B) in Maryland's portion of Chesapeake Bay (data from Rothschild et al. 1994, Wieland 2007).

et al. 1994). Landings strongly decreased in the early 1900s and stabilised at 80,000 t due to failing reseedling plans connected to heavy sedimentation and anoxic summer conditions. In 1981–1988, oyster production further declined due to high mortalities related to disease, predation and management practices. Since 1986, landings have remained under 15,000 t (Figure 13; Rothschild et al. 1994).

In the Maryland portion of Chesapeake Bay, the yield per habitable area, which is proportional to biomass, declined from 550 to 22 g m⁻² in 1884–1991 (Rothschild et al. 1994). Newell (1988) estimated that the pre-1870 oyster biomass could have potentially filtered the entire water column during the summer in less than 3–6 days, while current oyster stocks need 244–325 days. Thus, the loss in oyster biomass has resulted in a dramatic reduction in filter activity and phytoplankton removal from the water column (Newell 1988).

Another invertebrate that has been harvested since colonial times is the blue crab (*Callinectes sapidus*). A commercial fishery was started in the late nineteenth century, and Maryland and Virginia historically harvested and marketed more blue crabs than any other North American region (Rugolo et al. 1998a). Commercial harvests rapidly increased from 1880 to 1940 and varied between 60 and 100 million pounds annually until the 1990s (Figure 12). However, in recent years baywide harvests fell to around 50 million pounds (Miller et al. 2005). Since 1945, directed effort has increased 5-fold, and CPUE has declined exponentially (Rugolo et al. 1998b). The constant harvest pressure and the loss of SAV habitat, which young crabs require for shelter and food during their development, have contributed to the decline.

Vegetation

At the time of European arrival, forests covered about 95% of the land surrounding Chesapeake Bay, yet forest cover rapidly declined throughout the 1700s and 1800s (Figure 14). By the mid-nineteenth century, deforestation had stabilised, and eventually forest cover slightly increased to 58% of the watershed today (Pendleton 1995, Kemp et al. 2005, CBP 2009c). Chesapeake Bay had also extensive wetlands, which have been partly converted to agricultural, urban, industrial and recreational uses. Since 1780, Maryland has lost about 64% and Virginia 42% of their wetland areas, leaving currently 591,000 acres in Maryland and 1 million acres in Virginia (USGS 2009a). Dominant wetland types include non-tidal forested (60%) and shrub-scrub wetlands (10%) and salt and freshwater marshes (10% each) (Pendleton 1995). Today, wetland conservation has high priority, and any conversion, alteration or development needs to be permitted.

During 1700–1930, SAV consisting of eelgrass (*Zostera marina*) and other macrophytes was a persistent feature of shallow-water habitats in Chesapeake Bay (Orth & Moore 1984). These meadows provided important breeding, nursery and feeding habitats for a variety of invertebrates, fish, birds, sea turtles and manatees. In 1760, land clearing increased sediment loads and water turbidity with possible adverse effects on SAV. Sediment records have revealed declines of *Najas* spp. in the late eighteenth century and eelgrass in the late nineteenth century (Orth & Moore 1984). In the 1930s, extensive losses of eelgrass were caused by the wasting disease, but many eelgrass beds recovered. At six stations in Chesapeake Bay, SAV (mainly *Zostera* and *Ruppia*) increased from 1500 to 2310 ha in 1937–1960 but declined to 570 ha in 1980 (Figure 14; Orth & Moore 1983). Large-scale SAV declines occurred throughout the bay in the 1960s–1970s due to nutrient and sediment loads, turbidity, eutrophication and tropical storms (Bayley et al. 1978, Orth & Moore 1984). Since 1978, aerial surveys have shown an SAV increase from 16,500 to 36,222 ha (Orth et al. 2003), compared with an estimated 83,514 ha that existed in the 1930s–1970s based on historical aerial photographs (Figure 14; Moore et al. 2004).

A long-term estimate of seagrass decline comes from sediment core data (Cooper & Brush 1993), in which the relative abundance of *Cocconeis* (an epiphytic diatom on seagrass leaves) can be used as a proxy for seagrass occurrence. *Cocconeis* abundance was 10% in sediment layers in 550 AD but dropped to 5–7% until 1800 (Figure 14). In the 1800s and early 1900s, values were

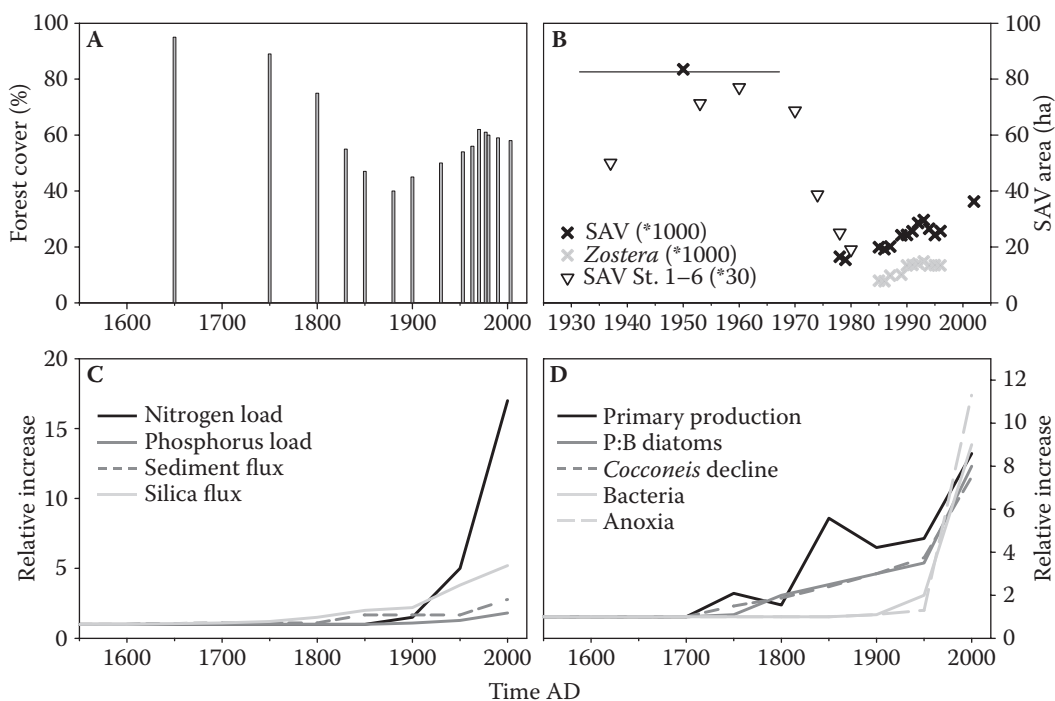


Figure 14 Historical changes in vegetation and water quality in Chesapeake Bay: (A) Forest cover (data from CBP 2009b); (B) submerged aquatic vegetation (SAV) and eelgrass (*Zostera*) in the entire bay (horizontal line = average estimate 1930–1970) and at selected stations (St.1–6) (data from Orth & Moore 1983, Orth et al. 2003, Moore et al. 2004); (C) nutrient and sediment loads and (D) primary production, pelagic:benthic (P:B) diatom ratio, epiphytic diatom *Cocconeis* (relative decline), bacterial matter, and anoxic conditions (data from Cooper & Brush 1993, Zimmerman 2000, Colman & Bratton 2003, and Fisher et al. 2006). See text for details.

1–3%, declining to 0–2% in the 1980s (Cooper & Brush 1993). This represents an 80–100% loss of seagrass at the particular location of the sediment core but may not reflect baywide trends.

Water quality

Since European settlement, Chesapeake Bay's water quality has undergone substantial changes which have been studied in detail using sediment core data (Figure 14). Average sedimentation rate in the estuary increased from 0.06 to 0.19 cm yr⁻¹ from before to after European colonisation (Brush 2001), and biogenic silica flow, a measure of nutrient loading, increased more than 5-fold (Colman & Bratton 2003). There are no direct long-term measures of nitrogen and phosphorus loads, but hydrochemical modeling and land-use yield coefficients suggest that current input rates are 4–20 times higher than under forested conditions 350 yr ago (Fisher et al. 2006). Since the 1960s, fertiliser use increased from 15 to 40 million kg nitrogen yr⁻¹ (Kemp et al. 2005). As a consequence, primary production has increased 4- to 12-fold since European contact based on total organic carbon (TOC) and organic matter fluxes (Cooper & Brush 1993, Zimmerman 2000). This was accompanied by an increase in the ratio of planktonic:benthic diatoms, indicating a shift from benthic to pelagic production (Figure 14). Bacteria decompose this increased amount of organic matter and have thus strongly increased, especially since 1950 (Figure 14). Finally, anoxic conditions have increased, as indicated by reactive sulphur, sediment colour and anaerobic bacteria (Zimmerman 2000).



Figure 15 Pamlico Sound, 1893 (Library of Congress, Geography and Map Division).

Pamlico Sound, Atlantic Coast

Similar to the other estuaries, Pamlico Sound (Figure 15) has experienced a long history of human-induced changes. Native people started agriculture about 800 yr ago and Europeans colonised and transformed the land about 400 yr ago. Larson (1970) estimated that there were about 1000 natives in the coastal plains in 1600, who were reduced to fewer than 500 after European contact. Since European colonisation, the human population around the watershed increased to more than 215,000 in 1990 (Forstall 1996). Over the last two to three centuries, overexploitation, habitat loss and pollution have resulted in the depletion of many marine species that have been of economic or ecological importance (Figure 16). Of the 44 marine mammals, birds, reptiles, fishes, invertebrates and plants

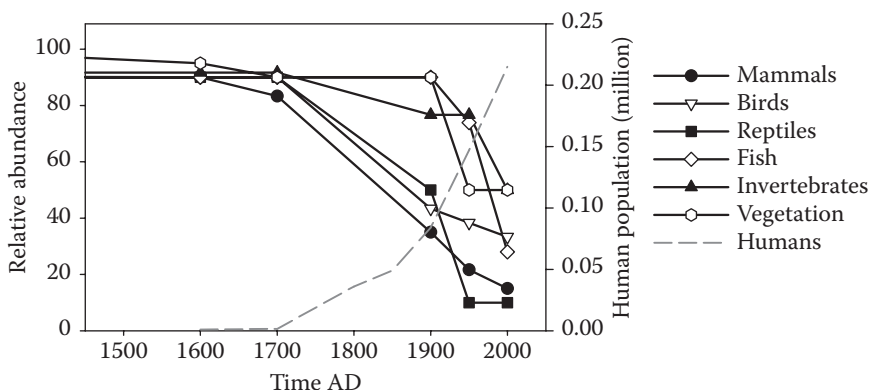


Figure 16 Timeline of changes in relative abundance of six taxonomic groups (left axis) and the human population (right axis) in Pamlico Sound.

reviewed, 24 have become depleted (>50% decline from former abundance), 19 rare (>90% decline), and 1 extirpated (100% decline) by the year 2000 (Lotze et al. 2006).

Marine mammals

Native Americans hunted whales all along the coast southward of Canada; catch records only occur for the Tequesta Indians in Florida, who hunted whales from the Keys to Cape Canaveral in the 1500s (Larson 1970). In the 1660s, Europeans began hunting whales along the coast off Pamlico Sound, especially the Atlantic grey whale, which was probably the only whale that entered the sound (Larson 1970, Mead & Mitchell 1984). With the youngest grey whale skeleton carbon dated to 1675, extinction must have occurred later, probably in the 1800s (Mead & Mitchell 1984). Whales were described as numerous along the Carolina coast by early explorers (Lawson 1712, Brickell 1737), but shore-based whaling reduced their numbers rapidly. In the early 1800s, coastal whaling strongly declined, and whalers moved offshore to target sperm whales (*Physeter macrocephalus*) (Reeves & Mitchell 1988). Today, fin, right, humpback and sperm whales are all listed as endangered in North Carolina (USFWS 2009).

In the early 1700s, “the bottle-nose are found everywhere in Pamlico Sound” (Brickell 1737), and the colonists developed a shore-based net fishery. Mitchell (1975) estimated that the coastal population had at least 13,748 bottlenose dolphins in the 1800s, but the fishery strongly depleted the population and ended in 1925 (Mead 1975). The population was at high levels again prior to an anomalous mortality event in 1987–88, which reduced the numbers by as much as 53% (Northeast Fisheries Science Center [NEFSC] 1997). In the 1990s, the western North Atlantic coastal stock was listed as depleted under the MMPA, with a minimum population estimate of 2482 dolphins (NEFSC 1997). Surveys counted 2114–2544 dolphins in 2002 along the coast (NEFSC 2005) and 950–1050 in the estuaries of North Carolina (Read et al. 2003). Annual by-catch or other fishery-related mortality and serious injury exceed 10%, which is considered to be significant (NEFSC 2005).

Another marine mammal hunted by natives and Europeans was the West Indian manatee (Larson 1970, Hartman 1979, Catesby 1996). In 1720, they were common in North Carolina sounds (Hartman 1979). Over time, however, numbers were reduced historically by exploitation and more recently by decline of seagrass (its main food and habitat), boat accidents and other threats. In 1967, the manatee was added to the endangered species list, and only few have been spotted in North Carolina in the last 20 yr (USFWS 2008).

Birds

Archaeological records suggest that there were many thousands of brown pelicans (*Pelecanus occidentalis*) in Pamlico Sound that were used by natives (Larson 1970). European colonisers in the early 1700s also described thousands and thousands of pelicans (Catesby 1996). Over time, hunting and more recent DDT poisoning in the 1960s lead to their listing as endangered in the 1970s (Larson 1970). Since then, the population has increased and is now considered stable with approximately 4000 nesting pairs. Major current threats include human disturbances at nesting sites, loss of nesting habitat, fish kills and fishing lines (National Audubon Society [NAS] 1997a).

Pamlico Sound was and still is a haven for waterbirds. Geese, swans, ducks, herons, egrets and many more waterfowl and wading birds occurred in great abundance in the past, although they were hunted throughout history. Brickell (1737) noted about wild geese: “They are plenty here all the Winter, come and go with the Swans ...; vast numbers are shot every year”. He also described great numbers of many kinds of ducks and mallard, and that the eggs of the black ducks were taken (Brickell 1737). In the late nineteenth century, geese, swans and other waterfowl were heavily hunted by European settlers, strongly reducing their numbers by the early twentieth century (Serie et al. 2002). In the 1930s, the loss of seagrass contributed to further declines in waterfowl directly feeding on seagrass or associated invertebrates (Mallin et al. 2000). With the recovery of seagrass,

some species have increased in population size since the 1950s (Serie et al. 2002), yet habitat degradation and loss continue to be a major threat (Golder 2004).

Birds with beautiful feathers were heavily hunted in the late nineteenth century for the millinery industry. Terns and gulls were highly prized for their wings and skins; great egrets (*Ardea alba*) and snowy egrets (*Egretta thula*) were sought for their aigrettes, and these species were shot by the tens of thousands (NAS 1997b). Those nesting in colonies were easy targets for market hunters: “They don’t much like to leave their young. I have often shot at these ‘strikers’ [terns] so fast that I had to put my gun overboard to cool the barrels” (NAS 1997b). This relentless shooting took a tremendous toll on populations, and several species of herons, egrets and terns were pushed nearly to extinction (NAS 1997b, Golder 2004). The least tern (*Sterna antillarum*) once numbered in the thousands but became a rare sight in the early 1900s (NAS 1997b). The extinction of many species was prevented by the Lacey Act in 1900 (AWI 2005) and the Migratory Bird Act of 1918 (AWI 2005). Since then, the main threats to these species are habitat degradation and loss in breeding, migratory stopover and wintering areas (Golder 2004). Surveys in the 1970s–1980s revealed alarming declines in nesting sites of colonial waterbirds due to chronic human disturbances, lack of suitable nesting habitats and erosion. This led to the establishment of the North Carolina Coastal Islands sanctuary system in 1989 and to intensified efforts to protect coastal birds and their habitat (NAS 1997b). Today, waterfowl number about 10,000 and shorebirds about 70,000 on Cape Hatteras (Golder 2004). Many gulls show stable or increasing population trends, while several terns, herons and egrets are declining and listed or proposed for listing on the endangered species list (NAS 1997a).

Reptiles

American alligators (*Alligator mississippiensis*) and sea turtles were hunted by natives throughout history (Larson 1970, Catesby 1996). Because Pamlico Sound is the northern extent of the range of the alligators, they may have never been very plentiful in this area. However, in the early 1700s, European explorers described them as frequent along the sides of the rivers (Lawson 1712). “Alligators are common and reach 18 feet,” reported Brickell (1737). In the early 1900s, populations were severely affected by commercial hunting for their belly skin (Brandt 1991, Britton 2009). Commercial hunting pressure was particularly strong in Louisiana and Florida, and by the 1920s, alligator numbers were severely depleted throughout their range. In the 1940s, alligators were only occasionally spotted in North Carolina. Hunting was prohibited in the 1960s, but illegal poaching continued into the 1970s. Because of the risk of extinction, additional changes were introduced in the law to control the movement of hides, which helped the species survive. Since the 1980s, populations have improved considerably throughout their range and are now only considered to be threatened in a few areas by habitat degradation (Brandt 1991, Britton 2009). Today, the entire population is estimated at 1 million, and the species is listed under the Convention on International Trade in Endangered Species (CITES) (Appendix II) and as low risk and least concern by the International Union for Conservation of Nature (IUCN; Britton 2009).

European explorers encountered lots of sea turtles in the North Carolina Sounds, which were hunted first by natives and later by Europeans (Catesby 1996). In the nineteenth century, commercial harvesting increased, and by 1880, a reduction in sea turtle numbers was noticed (Epperly et al. 1995). However, the inshore waters of North Carolina harboured enough green turtles to support a commercial fishery before exploitation ceased in the early 1900s (Epperly et al. 1995). In the 1970s, high mortality occurred through by-catch in the shrimp fishery, and sea turtles were listed as endangered (USFWS 2009). In the 1990s, the waters of Pamlico Sound continued to provide important developmental habitats for loggerhead, green, and Kemp’s ridley, while leatherback and hawksbill turtles were infrequently found (Epperly et al. 1995). Today, all sea turtles are listed as endangered or threatened in North Carolina (USFWS 2009).

Fishes

Native Americans caught a large variety of fishes in Pamlico Sound, including large hammerhead (*Sphyrna* spp.) and small sharks (Larson 1970). European explorers described “Shovel-nose sharks [hammerheads] four to six thousand pounds,” and “dogfish weigh normally 20 lbs or more, and are commonly caught when fishing for mackerel” (Brickell 1737). There is not much historical information on sharks in Pamlico Sound. In recent decades, the two most abundant species in North Carolina were sandbar (*Carcharhinus plumbeus*) and Atlantic sharpnose (*Rhizoprionodon terraenovae*) sharks, and sandbar and blacktip (*Carcharhinus limbatus*) sharks are the main targets of the North Carolina shark fishery (North Carolina Division of Marine Fisheries [NCDMF] 2008). The status of large sharks in general is of concern, and the sandbar shark is considered overfished. Although harvest restrictions have been in place since 1993 and a closure to commercial harvest occurred in 1997–2006, there is no conclusive evidence to suggest that stocks as a whole are recovering for these slow-growing, late-maturing animals (NCDMF 2008). Since the 1980s, there was also an increase in fishery yields for small sharks, especially spiny dogfish. The population declined during the 1990s and was considered overfished in 2003. Although the stock was considered recovering in 2008, the continued decrease in female abundance, imbalance in sex ratio and low recruitment are concerns for the current stock status (NCDMF 2008).

“The Drum-fish, whereof there are two sorts, ... the Red and the Black. ... There are greater numbers of them to be met with in Carolina, than any other sort of Fish” (Brickell 1737). But by the twentieth century, a decline in the fishery for drums occurred due to high fishing pressure and loss of reef habitat (Lenihan et al. 2001). The red drum was listed as overfished but is now recovering, with the adult stock protected from exploitation (NCDMF 2008). Similarly, there have been declines in other reef- or bottom-dwelling fish, including the gag grouper (*Mycteroperca microlepis*), weakfish, southern flounder (*Paralichthys lethostigma*) and summer flounder, mainly caused by overfishing and loss of reef habitat (Lenihan et al. 2001). Today, these species are considered as depleted or of concern. Among all 73 species of reef fish in the region, 17 are considered overfished (NCDMF 2008).

Other fish species that have been valued and fished at least since colonial times are striped mullets (*Mugil cephalus*), sturgeon and shad, all of which were described as plentiful in the 1700s (Brickell 1737, Larson 1970). Today, their abundance is much reduced. Since the 1950s, striped mullets produced consistently large annual landings of more than 2 million pounds, which ranked the species among the top seven finfish fisheries in North Carolina (NCDMF 2004). However, rapid surges in roe value in the late 1980s, followed by rising commercial fishing effort and landings through the mid-1990s, caused concern for the stock. Because commercial exploitation targets pre-spawned, roe-carrying adults, this directly reduces the yearly reproductive output. Recreational exploitation of juveniles for bait is also of concern (NCDMF 2004). In 2008, striped mullet was considered viable (NCDMF 2008).

In the 1700s, Lawson (1712) described the abundance of sturgeon: “In May, they run upwards the heads of rivers, where you see hundreds of them in one day”, and Brickell (1737) noted “The Sturgeon is the first of these whereof we have great plenty. ... The Indians kill great Numbers of them with their Fish-gigs and Nets”. The Europeans also fished Atlantic sturgeon over the centuries, and a heavy fishery for roe operated in the twentieth century, leading to strong declines in the population. In North Carolina, landings have been low since the 1960s, and in 1991 the NC Marine Fisheries Commission made it illegal to possess sturgeon in North Carolina (NCDMF 2004). Currently, the stock is considered depleted along the entire Atlantic coast (NCDMF 2008). American shad was another highly abundant and highly valued species. At one time, North Carolina produced more American shad than any other state, mostly in the Neuse River (Smith 1907). Shad catches have plummeted from more than 8 million pounds in 1896 to an average of 252,469 pounds in 1998–2007, and the stock is considered of concern (Smith 1907, NCDMF 2008).

Invertebrates

Many invertebrate species, including oysters, clams, scallops and crabs, were used by natives and Europeans around Pamlico Sound. Among the crustaceans, blue crabs were abundant in Pamlico Sound and easily trapped (Catesby 1996). Thus, a small-scale fishery was developed in the early 1700s (Lawson 1712). In the twentieth century, commercial and recreational harvesting became very popular, and in 1996 over 65.5 million pounds of blue crabs were harvested commercially. After these record landings, catches were strongly reduced in 2000–2002, which has caused increased concern for the health of the resource (NCDMF 2004). In 2007, the fishery yielded the lowest landings since 1998, and the stock is currently considered of concern (NCDMF 2008).

Among molluscs, the bay scallop (*Argopecten irradians*), hard clam, and oysters were much used by natives, and fisheries were developed by European colonists, first on a small scale but expanding over the centuries (Larson 1970, Catesby 1996). Declines in bay scallops were noticed in the 1980s due to reduced water quality, toxic red tides, loss of seagrass habitat and heavy fishing pressure (Peterson et al. 1996). Another recent factor negatively affecting the bay scallop population is increased predation by cownose rays (*Rhinoptera bonasus*), which have increased due to declines in their predators, large sharks (Myers et al. 2007). Thus, in the early 2000s, landings decreased essentially to nothing; the harvest was closed in 2007 due to limited availability of scallops, and the stock is now considered depleted (Myers et al. 2007, NCDMF 2008). Hard clam declines in the 1980s were also related to disturbance of seagrass beds, the impact of mechanical harvesting and high fishing pressure (Peterson et al. 1987). Currently, data are insufficient to evaluate the status of this stock (NCDMF 2008).

In the early 1900s, Kellogg (1910) noted, “The history of the oyster industry in Pamlico Sound is a record of the usual series of events. Natural beds were discovered, dredging became excessive, the beds were soon impoverished, many of them being completely destroyed”. He continued, “The ruin of a large natural source of wealth was begun. All this occurred much more rapidly than in Chesapeake Bay”. In the 1700s, oysters were found in every creek and gut of saltwater (Lawson 1712). In several places, there were such quantities of large oyster banks that they were very troublesome to vessels (Brickell 1737). However, as the fishery took its course, North Carolina passed “An Act to Prevent the Destruction of Oysters” in the 1820s (Campbell 1998). Mechanical harvesting began in the 1880s, and Pamlico Sound gained commercial importance as an oyster-producing region in 1889, when the scarcity of oysters in Chesapeake Bay let the industry move to North Carolina (Grave 1905). The fishery peaked in 1900, followed by strong declines caused by overfishing, habitat destruction and disease (Kellogg 1910, Lenihan & Peterson 1998). Although the stock may have improved slightly in recent years, it is considered of concern (NCDMF 2008).

Vegetation

Historical accounts from the late 1800s indicate that the bays and waterways near the mainland once had extensive beds of seagrass, while today seagrass is limited to the landward side of the barrier islands (Mallin et al. 2000). A progressive decline of seagrass beds started in the early 1900s (Stanley 1992a). In the 1930s, wasting disease caused extensive seagrass losses. In most regions, seagrass recovered, yet in the 1970s, strong die-offs occurred in Pamlico Sound that were even more severe than those in the 1930s (Stanley 1992a). Long-term estimates of seagrass decline come from the relative abundance of *Cocconeis* in sediment cores. In Pamlico Sound, *Cocconeis* abundance was 13% in 1540, varied between 7 and 9% during 1700–1900, then declined to less than 7% in the early 1900s, less than 2% in the 1980s, and 0.4% in 2000, an overall 97% decline in seagrass at the location where the sediment core has been taken (Figure 17; Cooper 2000).

Before European colonisation, North Carolina had about 11 million acres of wetlands, of which only 5.7 million still exist today. About one-third of the wetland conversion, mostly to managed forests and agriculture, has occurred since the 1950s (USGS 2009a). Today, the coastal plains contain

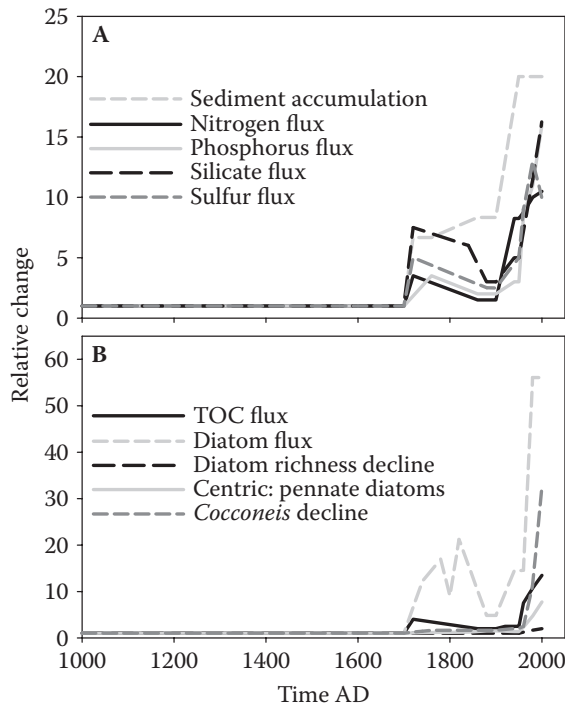


Figure 17 Historical changes in water quality in Pamlico Sound as measured in sediment cores: (A) relative increase in sediment accumulation and nutrient fluxes and (B) fluxes of total organic carbon (TOC) and diatoms, increase in the centric:pennate diatom ratio and declines in diatom species richness and the abundance of *Cocconeis*, an epiphytic diatom on seagrass. (Data from core M4, Cooper 2000, Cooper et al. 2004.)

about 95% of North Carolina's wetlands. Since 1850, the amount of cropland has increased 3.5-fold, and today 20% of the basin area consists of agricultural land, 60% is forested and 2% urbanised (Stanley 1992a). Over the last three decades, the production of swine has tripled and the area of fertilised cropland almost doubled (Cooper et al. 2004).

Water quality

Changes in land use patterns and increased point and non-point nutrient loading have induced multiple changes in water quality, with greatest changes occurring during the last 50–60 yr (Cooper et al. 2004). Sediment core data from the Pamlico Estuary (core M4, Cooper 2000, Cooper et al. 2004) indicated an overall increase in sediment accumulation (20-fold) and the fluxes of nitrogen (10-fold), phosphorus (16-fold), TOC (13.5-fold), silicate (6.25-fold), sulphur (10-fold) and diatoms (56-fold) from baseline levels in 1000–1700 (Figure 17). Moreover, the ratio of planktonic:benthic diatoms increased 7.75-fold, indicating a shift from benthic to planktonic primary production (Cooper et al. 2004).

Phosphorus loading was greatly enhanced by phosphate mining, which began in 1964 and accounts for half of the total phosphorus loading (Copeland & Hobbie 1972, Stanley 1992a). Nitrogen loading from point sources in summer months accounts for up to 60–70% and atmospheric nitrogen deposition for 15–32% of total nitrogen load (Steel 1991, Paerl et al. 2002). High surface sediment concentrations of arsenic, chromium, copper, nickel and lead are found in the Neuse Estuary, possibly associated with industrial and military operations, while high cadmium and silver levels most likely result from phosphate mining discharges (Cooper et al. 2004). In 1960, hypoxia was first reported in the Pamlico Estuary (Hobbie et al. 1975). Since then, records of hypoxic and

anoxic waters were mostly of short duration but have resulted in many fish kills (Cooper et al. 2004). Nuisance and toxic algal blooms are reported periodically (Bricker et al. 1999).

Galveston Bay, Gulf of Mexico

Galveston Bay (Figure 18) has been the focus of many human activities throughout history. About 14,000 yr ago, Paleo-Indians hunted mammoth, mastodon and bison around the bay, leaving traces of their activities in shell middens from about 8000 BC (Galveston Bay National Estuary Program [GBNEP] 1994, Lester & Gonzalez 2002). Native Americans continued to live around and use the bay for food, and Spanish and French explorers began visiting in the sixteenth to eighteenth centuries. European colonists encountered a rich abundance of wildlife to serve subsistence needs. The seemingly endless flocks of ducks, geese and swans and a bounty of fish and shellfish established a viewpoint that the New World's wildlife resources were inexhaustible (LaRoe et al. 1995). The native population probably never exceeded 10,000 (Markowitz 1995), yet the European colony grew rapidly, especially after the establishment of the first towns in 1820. The first settlers were mainly farmers, cotton planters and merchants, but marine resources were also exploited (Figure 19, GBNEP 1994). Over time, the watershed has been transformed for urban development, agriculture, and petroleum and petrochemical production, while the estuary itself has been used for fisheries, transportation, oil and gas production and recreation (GBNEP 1994). Today, Galveston Bay is surrounded by the eighth largest metropolitan area in the United States and has experienced heavy industrial pollution. Half of the wastewater of Texas gets discharged into the estuary; more than 50% of all chemical products manufactured in the United States are produced here, and 17% of the oil produced in the Gulf of Mexico is refined here.

Marine mammals

Natives of Galveston Bay used to hunt harbour porpoise, of which they offered pieces to the Europeans (Cox 1906). Stevenson (1893) reported: "Porpoises are numerous on the Texas coast, and large schools of them are often seen in the bays as well as outside along the coasts." He also noted: "It is reported, however, that they have never yet been taken for commercial purposes." Today, the most common marine mammal in Galveston Bay is the bottlenose dolphin, yet it is listed

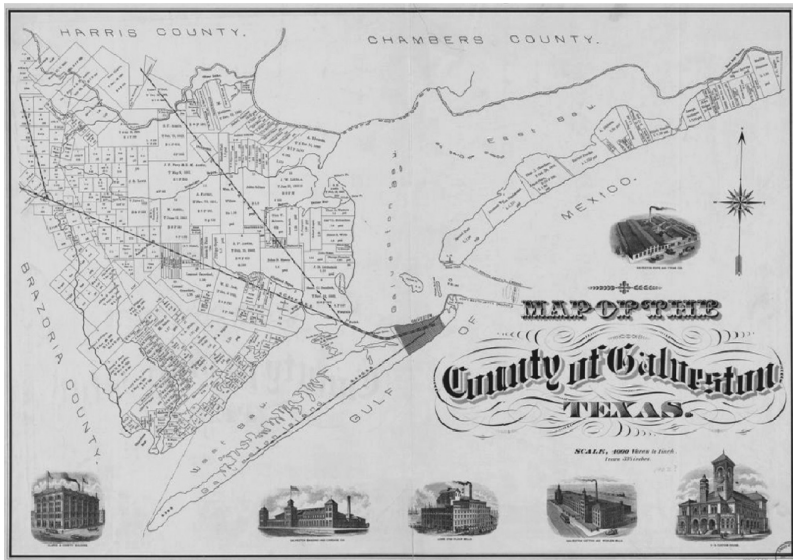


Figure 18 Map of the county of Galveston, Texas, 1902 (Library of Congress, Geography and Map Division).

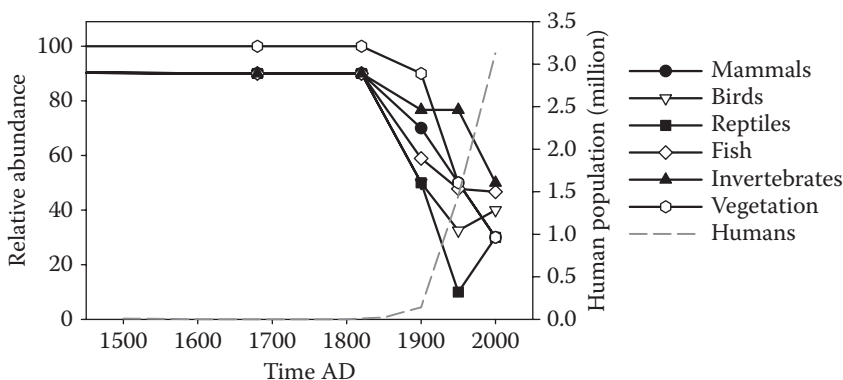


Figure 19 Timeline of changes in relative abundance of six taxonomic groups (left axis) and the human population (right axis) in Galveston Bay.

as depleted under MMPA (Swartz et al. 1999, Lester & Gonzalez 2002). Dolphins in Galveston, East, and Trinity Bays, considered the Gulf of Mexico estuarine and sound stock, number 107–152 (Waring et al. 2001). Many factors have led to the decline in bottlenose dolphin. During 1972–1989, 490 bottlenose dolphins from the estuarine and sound stock were removed to oceanaria for research and public display (Waring et al. 2001). In the 1990s, mortality events caused high numbers of dolphin deaths, suggesting these stocks are stressed. Some dolphins had pesticide concentrations at levels of possible toxicological concern. Finally, about 3% of stranded bottlenose dolphins showed evidence of human interactions as the cause of death, including gear entanglement, mutilation and gunshot wounds (Waring et al. 2001).

Of the large whales, several species occur in the Gulf of Mexico, and some may occasionally enter Galveston Bay. Right whales are rare along the Texas coast, but minke and Bryde's (*Balaenoptera edeni*) whales are found (Waring et al. 2001). The latter may represent a resident stock, but consisting only of about 35 animals. Sperm whales occur during all seasons in the northern Gulf of Mexico, but generally in deeper waters, with an estimated abundance of about 530 animals. A commercial fishery for sperm whales operated in the Gulf of Mexico during the late 1700s to the early 1900s, but the exact number of whales taken is not known (Waring et al. 2001). The only pinniped that might have occurred in the Galveston Bay area is the Caribbean monk seal (*Monachus tropicalis*), which did live in the Gulf of Mexico, Florida and the West Indies but became extinct in 1950 (Vermeij 1993, McClenachan & Cooper 2008). Some sightings, although unconfirmed, have been found along the coast of the western Gulf of Mexico from before the 1800s and around 1900 (McClenachan & Cooper 2008).

Birds

Pelican Island was a noted nesting site for brown pelicans in 1820 (Lester & Gonzalez 2002). In 1918, about 5000 pelicans nested on the Texas coast, but relentless killing by fishermen and pesticide pollution in the 1960s strongly reduced their numbers and nesting success. In 1967–1974, fewer than 10 pairs bred each year along the Texas coast, and the species was listed as endangered. The elimination of certain pesticides together with legal protection has enabled brown pelicans to re-establish their nesting colonies in Galveston Bay since 1993. The population grew to more than 800 breeding pairs in 2000 (Figure 20; Lester & Gonzalez 2002).

Early European colonists found huge flocks of ducks, geese and swans in Galveston Bay. Waterfowl hunting has a rich tradition in Texas and along the Gulf of Mexico coast. In 1998–1999, there were 58,177 hunting licenses sold in the five counties surrounding Galveston Bay. Duck breeding population estimates compiled by the USFWS for the years 1955–2001 indicate declines in

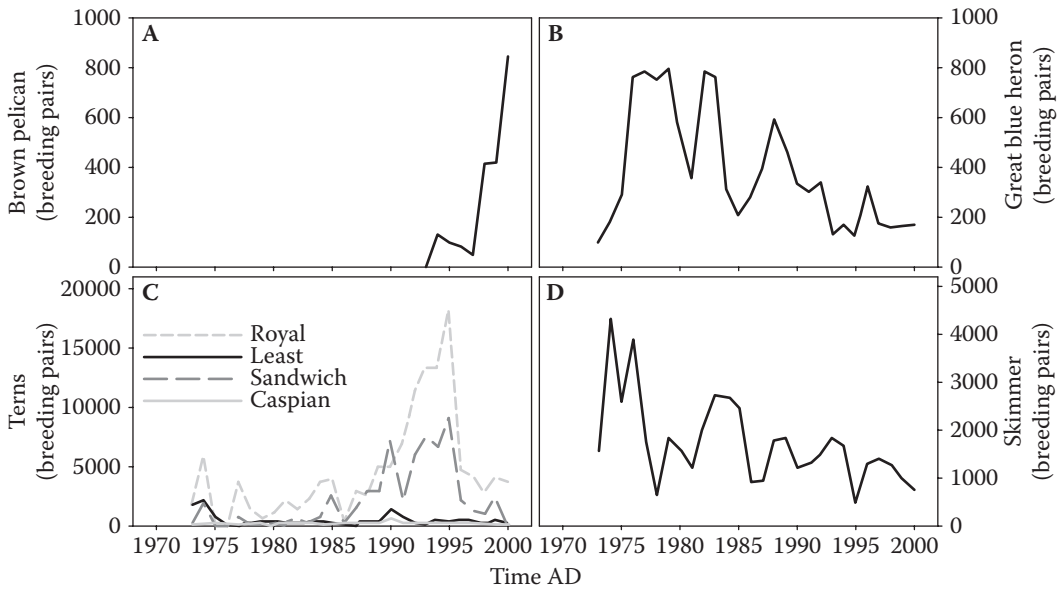


Figure 20 Changes in the number of breeding pairs of (A) brown pelican, (B) great blue heron, (C) terns, and (D) skimmer in Galveston Bay. (Data from Lester & Gonzalez 2002.)

breeding populations of mallard (*Anas platyrhynchos*), American wigeon (*A. americana*), northern pintail (*A. acuta*) and scaup (*Aythya affinis*) over the 46-yr period. However, increasing trends are seen for gadwall (*Anas strepera*), blue-winged teal (*A. discors*), green-winged teal (*A. carolinensis*), northern shoveler (*A. clypeata*), redhead (*Aythya americana*) and canvasback (*A. valisineria*). Some geese populations have also increased since 1955 (Lester & Gonzalez 2002).

Most wading birds, seabirds, shorebirds and raptors have historically been reduced by hunting, habitat loss, pollution and disturbance. Protective laws in the early twentieth century enabled many populations to increase again, yet others continue to be impacted, especially by habitat loss and disturbance of nesting sites. During 1973–1998, six colonial waterbird species exhibited increasing trends: the white ibis (*Eudocimus albus*), brown pelican, neotropic cormorant (*Phalacrocorax brasilianus*), and the sandwich tern (*Thalasseus sandvicensis*), gull-billed tern (*Gelochelidon nilotica*) and royal tern (*Thalasseus maximus*) (Figure 20). Ten species experienced stable trends, and four species declined: the great blue heron (*Ardea herodias*), roseate spoonbill (*Platalea ajaja*), black skimmer (*Rynchops niger*) and least tern (*Sternula antillarum*) (Figure 20; McFarlane 2001). In 2000, the three most commonly sighted colonial waterbirds that utilised Galveston Bay to feed and nest were the laughing gull (*Leucophaeus atricilla*), cattle egret (*Bubulcus ibis*) and royal tern (Lester & Gonzalez 2002).

Reptiles

The French explorer René Robert Cavelier, Sieur de La Salle, explored the Gulf of Mexico in the seventeenth century, noting: “There are also many alligators in the rivers, some of them of a frightful magnitude and bulk. ... I have shot many of them dead” (Cox 1906). Alligators living in the fresh and brackish waters and wetlands around the bay have been hunted throughout history, but especially in the early 1900s when their belly skin was highly prized for its leather. By the mid-twentieth century, alligators were very rare and became listed as an endangered species. Since then, regulated hunting and trade of alligator products have enabled the species to increase in number. Currently, the greatest threat to alligator populations around Galveston Bay is that posed by encroaching development (Lester & Gonzalez 2002).

René Robert Cavalier also commented on turtles: “We had plenty of land and sea tortoises, whose eggs served to season our sauces” (Cox 1906). Turtles were among other seafood species that were being sold at the Galveston dock during colonial times (Lester & Gonzalez 2002). In the late nineteenth century, Stevenson (1893) reported: “Large green turtle (*Chelonia mydas*) occur more or less abundantly all along the Texas coast”, but he also described the increasing pressure on the population: “Green turtle are gradually becoming less abundant on the coast of Texas, yet on account of the increasing demand for them, the annual catch is probably increasing.” A brackish water turtle, the diamondback terrapin (*Malaclemys terrapin*), was also highly valued as a delicacy and exploited heavily in the 1800s (LaRoe et al. 1995). After strong declines over the last 150 yr, terrapin populations have recovered somewhat in recent decades but are now threatened by habitat loss and degradation (Lester & Gonzalez 2002). Today, the most common turtle in nearshore waters is Kemp’s ridley. In 1940–1990, the Galveston Bay region was among the three most important areas for this species (Manzella & Williams 1992). A population decline in recent years has been linked to declines in blue crabs, their primary prey (Lester & Gonzalez 2002). All sea turtles are listed as endangered or threatened in Texas today (USFWS 2009).

Fishes

Early European colonisers made use of a wide variety of seafood, including redfish, flounder, mullet, skate and many other fishes (Lester & Gonzalez 2002). The fishing industry for the whole state of Texas was small, with only 291 fishermen listed as full time in 1880. Most fishing was done inside Galveston Bay, and the most popular market fish were redfish, sea trout (*Cynoscion* spp.), mullets, croakers and sheepshead (*Archosargus probatocephalus*) (Table 6; Stevenson 1893, GBNEP 1994). A marked decline in fish populations was noted before 1900, and in 1907, the total fish catch from Galveston Bay was 185,119 pounds. This was not enough to supply local markets, and breeding season closures were instituted in most of the bay to protect nursery grounds. Fish hatcheries were also

Table 6 Commercial finfish and shellfish landings (1000 pounds) from Galveston Bay in the years 1890 and 1989)

Species common name	1890	1989
Fish		
Red drum	404.2	0.0
Black drum	4.0	21.8
Flounder	46.0	14.6
Mullet	39.3	108.0
Sheepshead	17.0	16.2
Striped bass	5.0	0.0
Trout	427.4	0.0
Other fish	542.9	60.5
Total fish	1485.8	221.1
Shellfish		
Oyster	1647.1	705.5
Crabs	162.5	2149.5
Shrimp	138.0	4056.1
Terrapins (turtles)	2.4	0.0
Other shellfish	0.0	13.4
Total shellfish	1950.0	6924.5
Total fish and shellfish	3435.8	7145.6

Source: Data from Green et al. 1992.

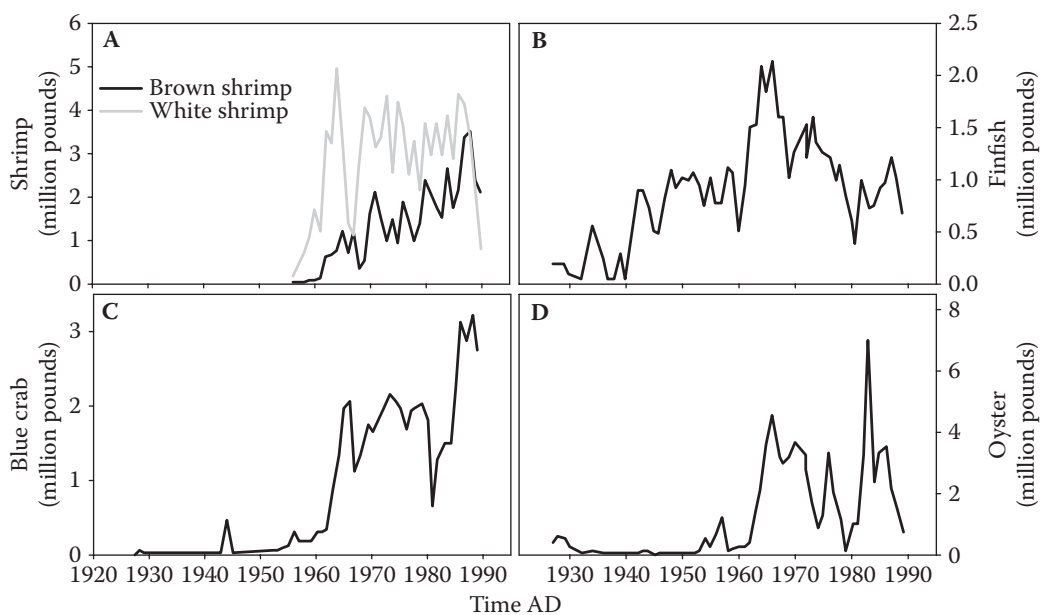


Figure 21 Commercial landings for (A) shrimp, (B) finfish, (C) blue crab, and (D) oyster in Galveston Bay. (Data from Green et al. 1992.)

proposed to overcome the shortage. However, controversy between fishermen and the commissioner over the closures prevented restrictive laws from being passed until 1929, when all littoral waters were closed permanently to drag seines, which were replaced by gill nets (Tucker 1929).

Significant increases in commercial landings occurred in the 1950s (Figure 21) when the pet food industry began harvesting fish in the northern Gulf of Mexico (Massley & Slater 1999). Commercial landings of drums (red drum and black drum, *Pogonias cromis*) and croaker peaked at more than 32,000 t in 1956, more than 20,000 t above that of 1953 (Massley & Slater 1999). The strong increase in fishing pressure resulted in an overall decline in finfish landings from Galveston Bay in the 1960s and 1970s (Figure 21). Yet, commercial landings of red drum from offshore stocks increased rapidly in the 1980s, when public demand suddenly grew for a new seafood preparation called blackened redfish (Massley & Slater 1999). In the 1970s, however, red drum abundance strongly declined and stayed low throughout the 1980s. Thus, in 1981 the Texas State Legislature banned the sale of red drum and spotted seatrout (*Cynoscion nebulosus*) to stem the decline of these two species (Stanley 1992b).

Another species that has dramatically declined over the last 150 yr is the striped bass. In addition to fishing, this species has been severely affected by habitat alteration in the form of dams, bay closures and shell dredging (Lester & Gonzalez 2002). From the late nineteenth to the late twentieth century, commercial landings of finfish have declined 7-fold, while landings of shellfish, especially shrimp and crab, increased almost 4-fold (Table 6). Commercial finfish catches account for only 14% of overall catches from Galveston Bay; most of these catches are recreational (Lester & Gonzalez 2002).

Invertebrates

Around 1840, a young Irishman described the shrimp fishery in Galveston Bay. Fishermen would use seines and catch the shrimp as they migrated out of the bay at the inlets at each end of Galveston Island. The quantity of one seine haul was 70 pails of shrimp plus many pails of fish, with shrimp

6 to 7 in. in size (Lester & Gonzalez 2002). The shrimp harvest was done by hand until after 1900. In addition to large migrating shrimp, small shrimp were harvested with cast nets and haul seines in the marshes. These were sun-dried or pickled in salt for export (Iversen et al. 1993). After 1920, shrimp fishing became a vital commercial fishing industry in Galveston Bay and the Gulf of Mexico. Catches of brown (*Penaeus aztecus*) and white (*P. setiferus*) shrimp increased significantly from the late 1950s to 1990, with recent years showing a slight decrease from these maximum values (Figure 21; Nance & Harper 1999). The shrimp grow up in estuaries like Galveston Bay and migrate out into the gulf as they mature.

Blue crabs have been a major source of seafood throughout history in Galveston Bay. Only in the mid-twentieth century, however, did commercial landings strongly increase (Figure 21). After a strong decline in the early 1980s, landings have sharply risen again to an all-time high of more than 3 million pounds in 1986 (Stanley 1992b). In 1998, more than 2.6 million pounds of blue crab were harvested in Galveston Bay. However, scientific surveys indicated that blue crab populations have declined in abundance over the past three decades. Recent declines in adult size classes also indicate overharvesting from high fishing pressure (Lester & Gonzalez 2002).

Oysters and clams have been important for people living around Galveston Bay for thousands of years. Shell middens containing *Rangia cuneata* clams and oysters occur along the Texas coast from Corpus Christi Bay to the Louisiana border (Aten 1983). The oyster industry in Galveston Bay was limited to local trade until after the 1870s, when cold shipping and processing industries were developed. In 1885, the oyster industry employed 50 boats and 500 men working in the bay. Galveston shipped about 25,000 oysters daily to markets within the state, but the city itself was said to consume 25,000–30,000 oysters daily during the season (Lester & Gonzalez 2002). Stevenson (1893) reported that, “Galveston Bay has a greater area of natural oyster beds than any other bay in Texas, but the reefs are not so plentifully supplied with oysters as some others in the State. This is to some extent due to overfishing”. In 1895, the state tried to control the heavy fishing pressure on natural oyster reefs and established the Oyster and Fish Commission.

In the twentieth century, commercial shell dredging started and operated until the 1960s. This destructive practice greatly diminished oyster reefs. Ward (1993) estimated that 135,000 acre-feet (1 acre-foot = 1233.5 m³) of shell were removed by shell dredgers, not oyster fishermen, between 1910 and 1969. Prior to the 1950s, tongers harvested 20–60% of the oysters, but tongers were replaced almost entirely by dredgers by the 1960s (Hofstetter 1982, 1983). In 1970, Carter (1970) wrote: “Fifty years ago perhaps nearly a fifth of the bay bottom was covered by exposed oyster shell, much of it lying in extensive semifossilized shell reefs”. Old maps of the Texas coast indicate that there were much more extensive oyster reefs along the shoreline than seen today in Galveston Bay. One study reported a significant increase in the extent of oyster reefs over the last 20 yr, but this has not yet replaced the large amounts of shell that were removed (Lester & Gonzalez 2002). Despite the decline in reef area, harvesting of oysters for food strongly increased after the 1960s (Figure 21). As oyster production in many other estuaries such as Chesapeake plummeted, Galveston Bay became an important supplier for cities throughout the United States. Yet, landings strongly declined in the late 1970s and in the 1980s. Between 1994 and 1998, the annual oyster harvest from Galveston Bay averaged close to 4 million pounds (Lester & Gonzalez 2002).

Vegetation

Texas has lost about 50% of its original wetlands and 35% of its coastal marshes as a result of agricultural conversion, overgrazing, urbanisation, construction of navigation canals, water table declines and other causes (Texas Environmental Profiles [TEP] 2009, USGS 2009a). In Galveston Bay, coastal marshes declined from 165,500 to 130,400 acres between 1950 and 1989. In the 1990s, Pulich & Hinson (1996) estimated 120,132 acres of coastal marshes based on aerial photographs. In recent years, about 4500 acres of marsh habitat have been restored, protected or created (Lester & Gonzalez 2002).

Most SAV once present in Galveston Bay has been lost since the late 1950s (Pulich & White 1991). By 1989, the distribution of shoal grass (*Halodule wrightii*) and widgeon grass (*Ruppia maritima*) decreased from 2500 to 800 acres (White et al. 1993). In 1995, there were 280 acres in Christmas Bay plus some amount of widgeon grass in Trinity Bay. The overall decline in SAV was about 80% of the 1950s extent (White et al. 1993, Lester & Gonzalez 2002). The most significant losses occurred along the margins of western Galveston Bay, caused by subsidence and Hurricane Carla in 1970. In West Bay, nearly 2200 acres of seagrasses have been completely lost due to industrial, residential and commercial development; wastewater discharges; chemical spills and increased turbidity from boat traffic and dredging (Pulich & White 1991).

Water quality

Historically, Galveston Bay had good water quality because of its shallow, well-mixed, and well-aerated conditions (Lester & Gonzalez 2002). Galveston Bay undergoes a total water exchange more than four times a year due to freshwater inflow and tidal action. However, land-based industrial and municipal activities, especially in the western, most urbanised part of Galveston Bay, strongly reduced water quality in the twentieth century. Prior to the mid-1970s, portions of the Houston Ship Channel were among the 10 most polluted water bodies in the United States (Lester & Gonzalez 2002). Nitrogen loading increased almost 4-fold from the early 1900s to the 1970s (Figure 22), causing eutrophication and oxygen depletion in the tributaries and bays. Oxygen levels were really low in the 1960s, with regular hypoxia ($<2 \text{ mg O}_2 \text{ L}^{-1}$) and frequent anoxia ($0 \text{ mg O}_2 \text{ L}^{-1}$) in bottom waters (Kennish 2000). The biological oxygen demand (BOD) loading increased 20-fold from 1920 to the late 1960s (Figure 22). In 1971, stringent discharge goals were established for industrial and municipal point sources, and wastewater treatment facilities were upgraded and expanded (Lester & Gonzalez 2002). Nitrogen and BOD loading dropped by half, and oxygen concentrations started to improve in the 1970s (Figure 22, Kennish 2000). Over the last three decades, concentrations of ammonia and phosphorus have decreased baywide, and chlorophyll-a has declined to less than 25% of its 1975 value (Lester & Gonzalez 2002). Chemical and heavy metal concentrations have declined as well. Some of the most polluted parts of Galveston Bay, such as the Houston Ship Channel, have experienced considerable improvements in water quality and the return of some species of fish (GBNEP 1994).

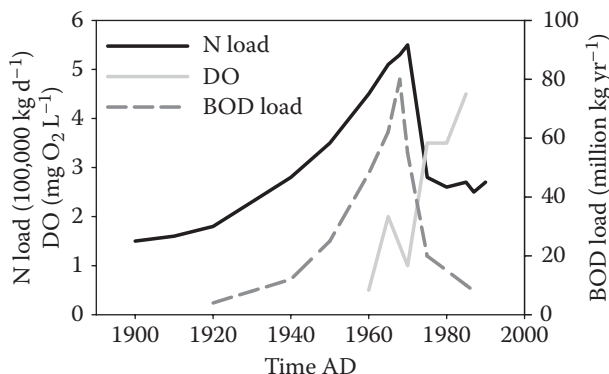


Figure 22 Trends in water quality in Galveston Bay: nitrogen (N) loads, dissolved oxygen concentrations (DOs) and biological oxygen demand (BOD) loading. (Data from Kennish 2000.)

San Francisco Bay, Pacific Coast

San Francisco Bay (Figure 23) has been inhabited by Native Californians for at least 10,000 yr (Ainsworth 2002). With declining sea levels about 6000 yr ago, the San Francisco, San Pablo and Suisun Bays emerged, and thousands of acres of intertidal mudflats and salt and brackish marshes developed. Living conditions were good; the large number and size of shell middens suggest that the native population was fairly large. They utilised a wide variety of terrestrial and marine resources, including shellfish, fish, birds and marine mammals, and constructed a cultivated landscape through controlled burning, pruning, weeding, seeding and tillage over many centuries. From about 2600 to 700 yr ago, the native population grew significantly. At the same time, indications of resource depression appeared in the archaeological record, suggesting that some valuable resources were overexploited (Ainsworth 2002, Broughton 2002). Spanish explorers arriving in 1769–1775 described a very dense native population with many villages around the bay (Ainsworth 2002). They also described many whales, dolphins, sea otters, grizzly bears and thousands of pelicans in the bay (Galvin 1971). Over the following decades and centuries, San Francisco Bay was rapidly and substantially transformed (see Figure 3). Europeans brought the fur trade, whaling and the gold rush, among other enterprises. The general timeline of human population growth and changes in marine fauna and flora is depicted in Figure 24.



Figure 23 Font's map of the entrance to San Francisco Bay, 1776 (The John Carter Brown Library at Brown University).

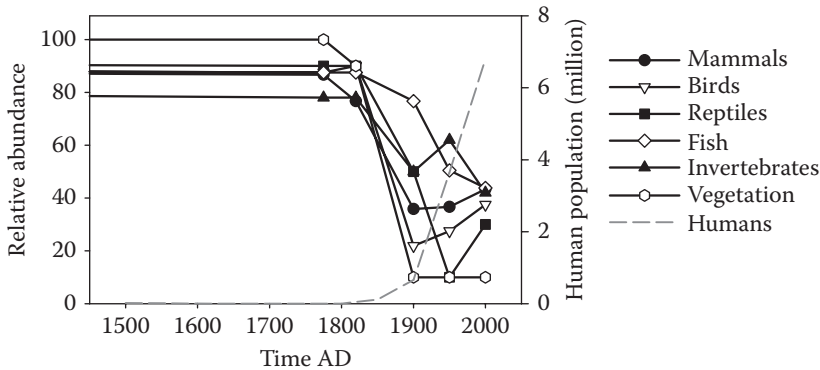


Figure 24 Timeline of changes in relative abundance of six taxonomic groups (left axis) and the human population (right axis) in San Francisco Bay.

Marine mammals

Native Californians hunted a large variety of marine mammals whose remains have been found abundantly in shell middens around San Francisco Bay (Ainsworth 2002, Broughton 2002). From 2600 to 700 yr ago, remains of large-bodied pinnipeds such as Steller's sea lion (*Eumetopias jubatus*), California sea lion (*Zalophus californianus*) and northern fur seal (*Callorhinus ursinus*) decreased relative to smaller harbour seal (*Phoca vitulina*) and sea otter (*Enhydra lutris*), likely caused by intense hunting and overexploitation (Broughton 1997). Relative abundance of sea otter first increased but later decreased, indicating intensified use followed by resource depletion. This was accompanied by an increase in the ratio of adult to juvenile otter remains, suggesting that breeding colonies or microhabitats favoured by females with young were abandoned as hunting pressure increased (Broughton 2002). There is little evidence that native people systematically hunted whales prior to European influence, but stranded whales were scavenged. Frequent remains of killer whales (*Orcinus orca*) in shell middens suggest that they were common in the bay (Margolin 1978).

With the arrival of Europeans, resource use changed. The Spanish trade in sea otter pelts began in 1786 and was the most important industry in coastal California for several decades (ANR 2001). San Francisco Bay was filled with sea otters (Galvin 1971, Margolin 1978), and they were killed by the thousands (Skinner 1962). The Russians hunted them from canoes under the guns of the Spanish fort (Eldredge 1912). In 1812, per week 700–800 sea otters were taken (Huff 1957), and in the 1820s, about 2000 otters were removed every year in the bay and up the coast (von Chamisso 1822, Ogden 1941). As William Heath Davis described in the 1820s: “Otters were then numerous in the bay and their skins plentiful. Murphy hunted them and sold their pelts to the Boston traders for from \$40 to \$60 each” (San Francisco News Letter [SFNL] 1925). Until 1830, the Russians took 5000–10,000 sea otters per year along the California coast (Eldredge 1912), and the sea otters grew scarce and eventually became extinct in San Francisco Bay (Olofson 2000). By 1900, sea otters were widely regarded as extinct in California, but fortunately a small group of less than 50 to 100 survivors were discovered in 1914 near Point Sur in Monterey County (ANR 2001). It took many decades for the population to increase again in numbers and spread north and south from Point Sur. Until the 1990s, there were no documented sightings of otters in San Francisco Bay, but several sightings were confirmed since then (Olofson 2000). In the early 1980s, population growth ceased, and concerns were raised regarding incidental entanglement and drowning in fishing gear, with annual mortality rates of 80–100 animals (ANR 2001).

Fur seals were also highly sought by fur traders. They were abundant along the coast and on the islands but were rapidly and drastically reduced. In 1810–1811 alone, the Russian ship ALBATROSS

took 73,402 fur seals, and fur seals became scarce by 1840 (Eldredge 1912). It took until 1911, however, for fur seals and sea otters to be protected by the International Fur Seal Treaty (ANR 2001). The Guadalupe fur seal (*Arctocephalus townsendi*) was believed to be extinct until 1926 but is making a very gradual recovery. Today, the eastern North Pacific fur seal stock is listed as depleted under the MMPA, but numbers are increasing (ANR 2001).

In the 1860s–1870s, many pinnipeds, including harbour seal, northern elephant seal (*Mirounga angustirostris*) and sea lions, were killed for their oil or body parts, and many females were captured for display. Pinnipeds were hunted commercially until 1938, when California law implemented complete protection. Nevertheless, sport and commercial fishermen were allowed to kill sea lions and harbour seals that were interfering with fishing operations (ANR 2001). Since the passage of the MMPA in 1972, the number of California sea lions has increased and seasonally occur in Central Bay (Schoenherr 1992, Olofson 2000). However, harbour seals have not increased in San Francisco Bay since the early 1970s, despite steadily growing numbers along the California coast (International Marine Mammal Project [IMMP] 2009). It has been suggested that shoreline development has reduced many haul-out areas and breeding beaches used in the past and thus the number of animals that could survive in the region. In 1991, harbour seal numbers severely dropped at the primary pupping site in southern San Francisco Bay (IMMP 2009).

In 1822, the first whalers anchored in San Francisco Bay (Huff 1957). The early shore-based whaling industry in California primarily caught Pacific grey and humpback whales within 10 mi of the coastline. Occasionally, right, blue and fin whales were also caught, which were highly prized due to the greater oil content of their blubber (ANR 2001). In 1860, about 1000 barrels of whale oil were processed per day in Sausalito (Huff 1957). The completion of the transcontinental railroad in 1869 made it possible to ship whale products over land and facilitate trade. Yet, whale numbers started to decline. In 1895, only 40 barrels were processed per day in Sausalito, and whaling for profit came to an end (Huff 1957). Nevertheless, modern whaling vessels continued to catch some grey and many humpback whales in California waters (ANR 2001).

Around 1900, there were about 15,000 humpback whales in the North Pacific Ocean, which were reduced to dangerously low levels. In 1966, the IWC established a harvest moratorium, and the humpback was listed as endangered. Since then, the population has recovered to about 8000 individuals, with the California feeding population counting about 1000 animals and growing at about 8% per yr (ANR 2001). With protection, the Pacific grey whale also increased from about 1000 animals in the early 1900s to 18,000–29,000 animals in recent census counts (Rugh et al. 2005, Christensen 2006). Estimates of prewhaling population size for grey whales based on catch data range between 19,480 and 35,430 and suggest that the current population may have recovered. However, alternative preexploitation estimates are higher, including 70,000 from population models (Wade 2002) and 96,000 based on genetic diversity (Alter et al. 2007).

Birds

Archaeological evidence suggests that native people around San Francisco Bay abundantly used and depleted some highly valued large geese and cormorants (Broughton 2002). Double-crested (*Phalacrocorax auritus*) and Brandt's (*P. penicillatus*) cormorants were among the most abundant bird taxa in shell middens. While remains of geese consistently declined from 2600 to 700 yr ago, remains of cormorants increased over the first 800 yr and strongly declined thereafter. An increasing ratio of adult to young cormorants indicates the loss or abandonment of local breeding colonies (Broughton 2002). There also used to occur a flightless duck, *Chenodytes lawi*, in California and Oregon, which became extinct in prehistoric times (Vermeij 1993).

The first European observers reported that migrating birds blackened the sky over the estuary (Skinner 1962): “Thousands of pelicans took to the air from a rocky island as we passed by entering the bay” (Galvin 1971). Canvasbacks were historically very abundant, and in 1776 Jose Canizares mapped areas in the northern estuary as “forests of the red duck” (Olofson 2000). Yet, marine

birds suffered relentless exploitation from European settlers, especially at the Farallon and other islands during and after the gold rush from 1850 to 1900 (ANR 2001). Hunters delivered millions of waterbirds, shorebirds and their eggs to the tables of a growing population and egret plumes to hat makers (Skinner 1962). Prior to 1880, the snowy egret was considered locally common (Grinnell & Miller 1944), but hunting for its feathers was devastating and nearly wiped this species out. By the early 1900s, the snowy egret was thought to be extinct in California, yet some rare stragglers were noted at two locations in the bay in the 1920s (Grinnell & Wythe 1927, Olofson 2000).

Common murres (*Uria aalge*) were heavily exploited for their eggs. There were no regulations, and the murre population declined by an order of magnitude by the 1900s; only a few thousand individuals were left in the 1930s. The murre population did not recover for several decades and even now is far below numbers of the 1800s. Today, the breeding population numbers 363,200 with stable or increasing trends (ANR 2001). Shorebird populations such as plovers (Charadriinae), dowitchers (*Limnodromus* spp.) and godwits (*Limosa* spp.) were markedly reduced in the late twentieth century due to market hunting and destruction of breeding habitat (Olofson 2000).

With the Migratory Bird Treaty Act in 1918, many bird populations started to recover (Olofson 2000), but habitat loss and DDT pollution continued to threaten many species (Skinner 1962). The San Francisco Bay region is 1 of 34 waterfowl habitats of major concern in the North American Waterfowl Management Plan. Also, half the migratory birds along the Pacific flyway, about 500,000 birds, use the bay's wetlands for wintering each year (The Bay Institute [TBI] 1998, Olofson 2000). Since the 1950s, however, waterfowl surveys indicated a 25% decrease in abundance, with some species suffering much larger declines. For example, wintering northern pintails declined from 200,000 to fewer than 20,000 since the 1950s, and canvasbacks declined by 50% since the 1970s. Other species experienced more favourable population trends, including snow geese, egrets, cormorants, pelicans and bald eagles (Olofson 2000).

Fishes

Requiem sharks (Carcharhinidae), bat ray (*Myliobatis californica*), sturgeon and salmon were very abundant among fish remains in shell middens around San Francisco Bay (Broughton 1997). From 2600 to 700 BP, relative abundance and size of white sturgeon (*Acipenser transmontanus*) declined significantly, indicating that native people had a substantial impact on this species (Broughton 1997, 2002). White sturgeon represented the highest-value fish available, reaching up to 6.1 m long, weighing 816 kg, and with a high-fat content (Broughton 1997). Between 1860 and 1901, Europeans developed a commercial fishery for white sturgeon, stimulated by growing demand for smoked sturgeon and caviar on the eastern coast of America. The fishery concentrated in San Francisco Bay. Green sturgeon (*A. medirostris*) was also taken but was of minor importance (ANR 2001). The commercial catch peaked at 1.65 million pounds in 1887 but declined to 0.3 and 0.2 million pounds in 1895 and 1901, respectively, when the commercial fishery was closed. However, sport fishing for sturgeon increased dramatically in 1964, and 2258 sturgeon were landed in 1967 (ANR 2001). In 1990, angling regulations reduced harvest to less than 50% of 1980s levels. Adult abundance of white sturgeon fluctuated in 1967–1998, with a high of 142,000 individuals in 1997 (ANR 2001).

Chinook (*Oncorhynchus tshawytscha*) and Coho (*O. kisutch*) salmon were also highly valued and abundant. A few hundred years ago, one visitor reported salmon runs so dense that the rivers looked like silver “pavements” (Skinner 1962). Salmon fisheries existed long before European arrival, with estimated harvests exceeding 8.5 million pounds annually (ANR 2001). A small commercial river fishery began in the early 1800s (Smith & Kato 1979) and a large-scale fishery with the gold rush (ANR 2001, Francis et al. 2001). After 1849, the gold rush caused high siltation, destroying important river and bay habitat (Skinner 1962). In 1860, about 3220 t of salmon were caught, but populations were in decline (Smith & Kato 1979). In 1880, there were 20 canneries operating in the Sacramento-San Joaquin river system. Fishing was intense, with peak landings of 12 million

pounds in 1882 (ANR 2001). Shortly after, the fishery collapsed, and dramatic population declines were linked to pollution and habitat degradation combined with high fishing pressure. The last cannery closed in 1919, and one by one all rivers were closed to commercial fishing (ANR 2001). Both species are on the endangered species list today (USFWS 2009).

California halibut (*Paralichthys californicus*) was the first groundfish targeted by commercial fisheries in the late nineteenth century (Francis et al. 2001). The highest recorded catch was 4.7 million pounds in 1919, followed by a decline to 950,000 pounds in 1932. Average catch has remained at about 910,000 pounds since then (ANR 2001). Other groundfish were lightly exploited until the 1960s (Rogers & Builder 1999), but catches rapidly increased thereafter (Francis et al. 2001). In the 1980s, rockfish (*Sebastes* spp.) stocks declined, and overall groundfish landings decreased by 60% in the 1990s. The current status of many rockfish and lingcod (*Ophiodon elongatus*) off the western coast is poor, and the fishery was closed in 2000 (ANR 2001).

In 1936–1944, a shark fishery for vitamin oil boomed, with more than 24 million pounds landed, mainly soupfin sharks (*Galeorhinus galeus*). The fishery collapsed in the mid-1940s from overexploitation and development of synthetic vitamins. Yet, because of the strong decimation of soupfin sharks, particularly in nursery areas in San Francisco and Tomales Bays, the population never fully recovered (Olofson 2000). In the mid-1970s, interest in shark fishing renewed, this time for their meat for human consumption (Olofson 2000). The commercial fishery peaked off California in the mid-1980s, with local resource depletion and large catches of immature sharks. Since then, regulations have reduced total fishing effort and catches, and at least one species, the common thresher (*Alopias vulpinus*), may be recovering (Anderson et al. 1999b). In contrast to large sharks, skate and ray landings increased about 10-fold in the 1990s, but CPUE decreased, and concerns of overfishing have been raised (Olofson 2000).

A pelagic fishery for Pacific herring (*Clupea pallasii*) began in the early 1800s and fluctuated with markets over time (Skinner 1962). The fishery off California peaked at 3600 t in 1916–1919, 4500 t in 1947–53, and more than 10,000 t in 1982 (Jacobson et al. 1999). Since 1965, there was also a lucrative herring roe-on-kelp fishery in San Francisco and Tomales Bays. San Francisco Bay has the largest spawning population of herring and supplies over 90% of the U.S. herring catch (Jacobson et al. 1999). Other coastal pelagics were much more abundant 100 yr ago. The biomass of pelagic predators such as hake and mackerel declined by 75% from 1900 to 1950 and another 50% from 1950 to 2000 (Francis et al. 2001). Sardine (*Sardinops sagax*) abundance fluctuated with climate conditions throughout the last 2000 yr (Francis et al. 2001). In the nineteenth century, abundance was low, but a legendary California sardine fishery began in the early 1900s and supported the largest fishery in the Western Hemisphere in the 1930s–1940s (Jacobson et al. 1999). However, the fishery began to decline from north to south in the 1920s, strongly declined after WWII, and finally collapsed in the late 1950s. Sardine biomass remained negligibly low for about 40 yr but has increased since 1986 (Jacobson et al. 1999).

Invertebrates

Shellfish were a staple food for native people around San Francisco Bay and are abundant in shell middens (Ainsworth 2002). Archaeological evidence suggests that large molluscs such as California oyster (*Ostrea conchaphila*) and bay mussel (*Mytilus edulis*) decreased significantly over time relative to smaller species (Broughton 2002). In the 1840s, a small fishery for native oyster served the San Francisco market (Nichols et al. 1986). In 1867, native oysters died after an earthquake and heated bottom waters (Ingersoll 1881). The American oyster (*Crassostrea virginica*) was introduced in 1869 and displaced the remaining native population (Shaw 1997). Maps from the early 1900s depict extensive deposits of native oyster shells across the bottom of the bay, indicating the former abundance of this species (Packard 1918). These shells were dredged for various purposes in the early twentieth century (Galtsoff 1930). Today, only remnant populations of native oysters exist in the bay.

California Indians fished abalones extensively in coastal areas and on the Channel Islands (ANR 2001). During the 1850s, Chinese Americans started a fishery targeting intertidal green (*Haliotis fulgens*) and black (*H. cracherodii*) abalones, with peak landings of 4.1 million pounds of meat and shell in 1879 (ANR 2001). Landings crashed in the 1890s (Anderson et al. 1999a), and shallow waters were closed to commercial harvest in 1900 (ANR 2001). An increase in landings of red abalone (*H. rufescens*) began in 1916, with a peak of 3.9 million pounds in 1935, followed by a decline to 164,000 pounds in 1942 (ANR 2001). Catches averaged 2.1 million pounds in 1931–1967 but have strongly declined since the mid-1960s. The harvest of black abalone was closed in 1993, and white abalone (*H. sorenseni*) has been proposed as an endangered species (Anderson et al. 1999a). By 1990, landings of red abalones declined to 17% of the 1931–1967 average, and all abalone species are considered depleted (ANR 2001).

Dungeness crabs (*Cancer magister*) were harvested by natives and taken commercially from San Francisco Bay in 1848 (ANR 2001). Before 1944, the fishery centred in the San Francisco area with average annual landings of 2.6 million pounds. While the bay fishery declined in the early 1900s (Wright & Phillips 1988), commercial catches increased to 10 million pounds (Galvin 1971). The fishery was relatively stable until 1956 but declined to 710,000 pounds in the early 1960s and remained seriously depressed up to 1985. Recently, catches increased again to about 2 million pounds; however, fishing intensity is extreme, and in most years 80–90% of all available legal-sized male crabs are captured (ANR 2001).

A commercial bay shrimp (*Crangon franciscorum*) fishery began in San Francisco Bay in the early 1860s. By 1871, Chinese immigrants established fishing camps along the shores and exported large quantities of dried shrimp meal to China. At the height of the fishery in the 1890s, more than 5 million pounds were landed each year (ANR 2001). Concerns were raised regarding damage of bottom habitat and by-catch of other species, and seasonal closure and prohibition of Chinese shrimp nets were implemented in 1911 but modified in 1915 (ANR 2001). Shortly after, commercial shrimp harvesters introduced beam trawl nets, and landings increased, peaking at 3.4 million pounds in 1935. Afterwards, landings steadily declined to 1500 pounds in the early 1960s, and no shrimp were landed in 1964 (ANR 2001). Since 1965, the bay shrimp fishery mostly supplies live bait for sport fishing, with landings of 75,000–150,000 pounds (ANR 2001).

Archaeological evidence shows that sea urchins have been fished by coastal American Indians for centuries, whereas a commercial fishery only developed in the last 30 yr for red sea urchin (*Strongylocentrotus franciscanus*) (ANR 2001). The fishery began in southern California in 1971 and expanded to northern California in the late 1970s–1980s (Anderson et al. 1999a). The northern California fishery rapidly grew to 30 million pounds in 1988 but declined to less than 5 million pounds in the late 1990s. Still, the sea urchin fishery has been one of California's most valuable fisheries for more than a decade (ANR 2001).

Vegetation

Data on the historic areal extent of eelgrass within San Francisco Bay are limited, although it is believed that extensive eelgrass meadows occurred in the past. The gold rush and hydraulic mining beginning in the 1850s caused large amounts of siltation and sediment loading that covered the central portion of the bay, creating mudflats that were once seagrass beds (Nichols et al. 1986). In the 1950s, there were about 480 acres of seagrass beds, and some recovery was noticed, but increasing turbidity caused new seagrass declines in the 1980s (Olofson 2000). By 1989, eelgrass beds were limited to relatively small patches of 316 acres. Overall, at least one-third of historical eelgrass beds have been lost to fill and development (ANR 2001).

Before 1850, San Francisco Bay sustained about 1400 km² of freshwater wetlands and 800 km² of salt marshes (Figure 25). From 1850 to 1970, intense sedimentation due to the gold rush, wetland conversion and filling reduced the amount of undiked marshes to only 125 km², a 95% loss of crucial habitat (Atwater et al. 1979, Nichols et al. 1986).

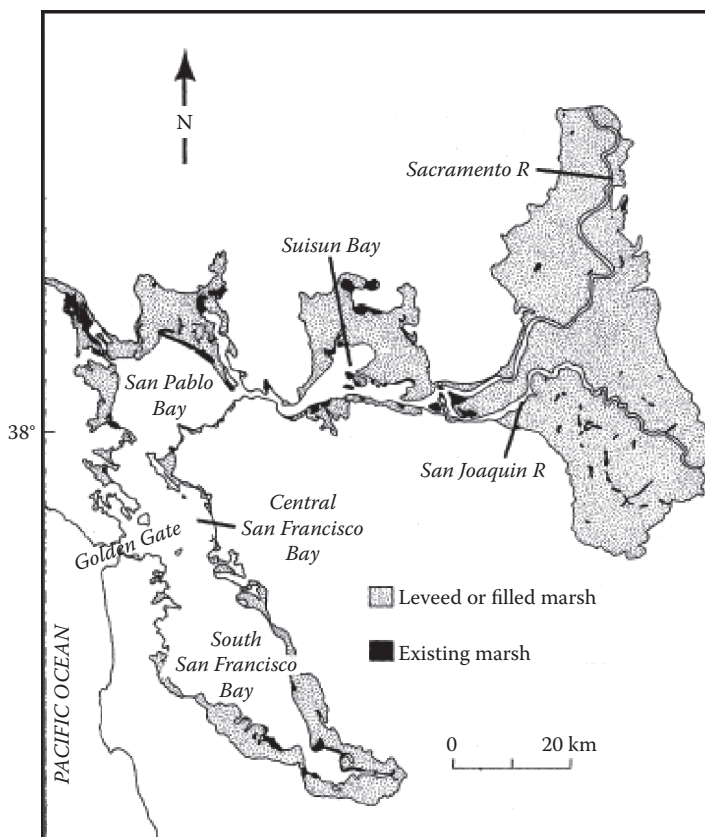


Figure 25 Distribution of undiked tidal marshes around San Francisco Bay before 1850 (grey) and in the 1980s (black). (From Nichols et al. 1986. *Science* 231. Reprinted with permission from AAAS and F.H. Nichols.)

Water quality

San Francisco Bay is located at the mouth of the Sacramento-San Joaquin river system, which drains about 40% of California's surface areas (Nichols et al. 1986). In the course of European settlement and the gold rush, sediment and nutrient loads rapidly increased, while natural filters such as marshes, wetlands and oysters were diminished. From 1852 to 1914, sediment transport to San Francisco Bay increased from 1.5 to 14 million $\text{m}^3 \text{yr}^{-1}$, and large deposits of these sediments still reside in San Francisco Bay today (van Geen & Luoma 1999). As the city of San Francisco grew, so did municipal and industrial discharges. From 1950 to 1980, nitrate concentrations in the San Joaquin River mouth increased about 7.5-fold (Nichols et al. 1986, Cloern 2001). By the 1990s, about 3.2 billion L of wastewater entered the bay every day plus 4500 to 36,000 t of toxic pollutants (Monroe and Kelly, 1992).

Although discharges have continually increased, inputs of at least some contaminants have declined, especially after 1970, when advanced waste treatment was introduced and some chemicals such as DDT and PCBs were banned. Also, several heavy industries have closed since 1970, and mining activities ceased, reducing pollutant and heavy metal loads. Thus, ammonia concentrations declined 10-fold in the 1970s (Figure 26; San Francisco Bay Institute [SFBI] 2003), and phytoplankton concentrations declined from an annual average of $10.27 \mu\text{g chlorophyll L}^{-1}$ in 1976–1980 to $2.38 \mu\text{g L}^{-1}$ in 1997–2001 (Figure 26; SFBI 2004). In 1986, the invasive clam *Potamocorbula amurensis* was introduced to San Francisco Bay and rapidly increased in abundance (Figure 26).

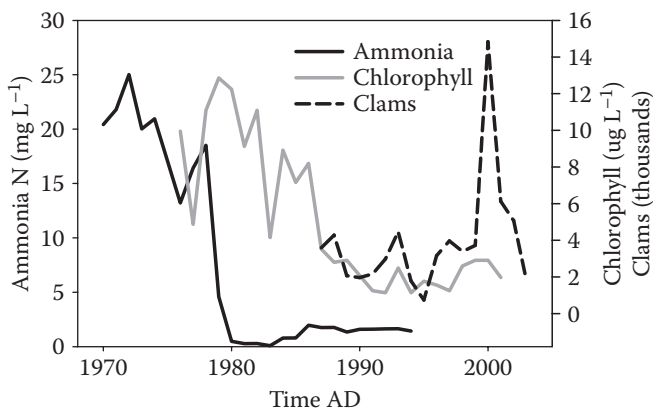


Figure 26 Recent trends in water quality in San Francisco Bay: ammonia concentrations in wastewater effluents, chlorophyll-a concentrations in Suisun Bay and abundance of the invasive clam *Potamocorbula* in Suisun and San Pablo Bays. (Data from SFBI 2003, 2004.)

This filter-feeder probably contributes to keeping phytoplankton at low levels compared with other estuaries (SFBI 2004). Oxygen concentrations have been relatively stable from 1972 to 1978 and 1993 to 2001 and remained mostly at or above the water quality standard of 5 mg L^{-1} , and harmful algal blooms occur infrequently (SFBI 2003).

Comparison of historical changes across U.S. estuaries

Magnitude of ecosystem degradation and species declines

Despite their wide geographic distribution and unique regional histories, the six estuaries showed remarkably similar trajectories of species decline, habitat loss and water quality degradation over time. Averaged across taxonomic groups, overall ecosystem degradation was relatively small during the hunter-gatherer, agriculture and colonial establishment periods (Table 2) but accelerated in the colonial development and global market I periods before slowing and stabilising in the global market II period (Figure 27). The low levels of ecosystem deterioration documented during native and early European occupation suggests that humans had limited impact on marine resources when exploitation was primarily for subsistence purposes and the human population was small. Yet, significant local resource depletion by hunter-gatherers has been documented in San Francisco Bay, where the native population was quite dense (Broughton 2002). Although no such signs were found in the other five estuaries, increasing archaeological research may uncover more rather than less ancient human impacts (Rick & Erlandson 2008).

During the periods of colonial development and global market I, ecosystem changes accelerated (Figure 27). This was a period of rapid human population growth accompanied by increasing demand for natural resources. Exploitation for food, oil, furs, feathers and luxury items was intensified and commercialised, and technological progress allowed more efficient but also less-selective and more destructive harvesting. Many marine mammal, bird and reptile populations were already depleted by 1900 and driven to even lower levels by 1950, while many fish, plant and oyster populations declined continually during this time (Figure 28). At the end of the development period in 1900, San Francisco Bay was by far the most degraded estuary, probably due to the strong impact of the gold rush and associated human activities (Figure 27).

In the global market II period, essentially 1950–2000, overall degradation trends slowed in most regions with enhanced management and conservation efforts (Figure 27). Several species groups

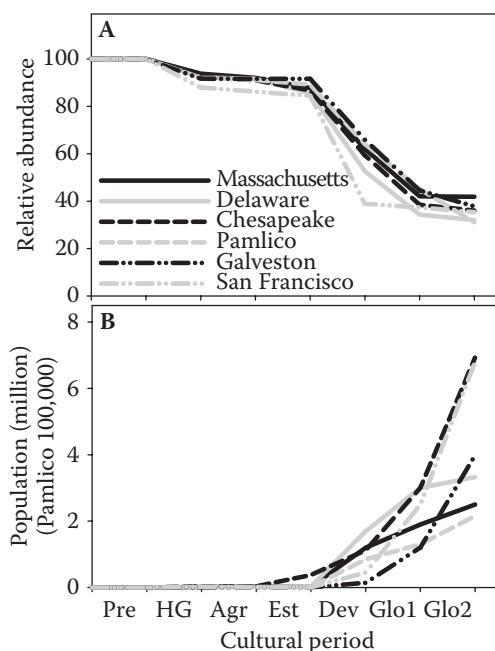


Figure 27 Ecosystem change across cultural periods in the six study systems: (A) average relative decline across six taxonomic groups and (B) human population growth. (Data adapted from Lotze et al. 2006.)

showed signs of stabilisation or recovery, including large whales, all bird groups, reptiles and plants (Figure 28). Yet, all fish groups continued to decline, and all invertebrates except oysters showed accelerated losses. This mirrors the enhanced focus on invertebrate fisheries after the decline of traditional finfish fisheries, a phenomenon known as ‘fishing down the food web’ (Pauly et al. 1998). At the end of the twentieth century, the average relative abundance of taxonomic groups in the six estuaries was 31–43% of the prehuman state (Figure 27), with Massachusetts Bay the least degraded. Declines of species groups ranged from 91% of pre-exploitation levels for large whales to 36% for pinnipeds and otters (Figure 28) and were similar in all estuaries, as indicated by the relatively small error bars. These general trajectories suggest that degradation of estuarine resources and ecosystems was driven by human history rather than natural change.

Species depletions, extinctions and recoveries

Native Americans and early European visitors encountered a rich abundance of marine animals in the estuaries they populated across the United States. By the end of the twentieth century, however, an average of 95% of all recorded species in the estuaries were depleted (reduced to <50% of former abundance; Table 4), with 35% rare (<10%), 3% extirpated or extinct (0%), and only 10% of species recovering (from extirpated or rare to >10%) (Lotze et al. 2006). Patterns were relatively similar across the six study systems (Figure 29). Depleted and rare species belonged to all taxonomic groups, while extirpated species were dominated by fish and recovering species by birds. Pamlico Sound had the most depleted or rare species, while Massachusetts Bay had the most extirpated species (7%). This masks trends in some systems, though, where species had been extirpated by the late 1800s or early 1900s but re-established themselves or were reintroduced later. The list of currently endangered or threatened marine animals in each estuary (by state) ranges from 11 in Delaware Bay to 27 in San Francisco Bay and includes species from all taxonomic groups (Table 7). Despite

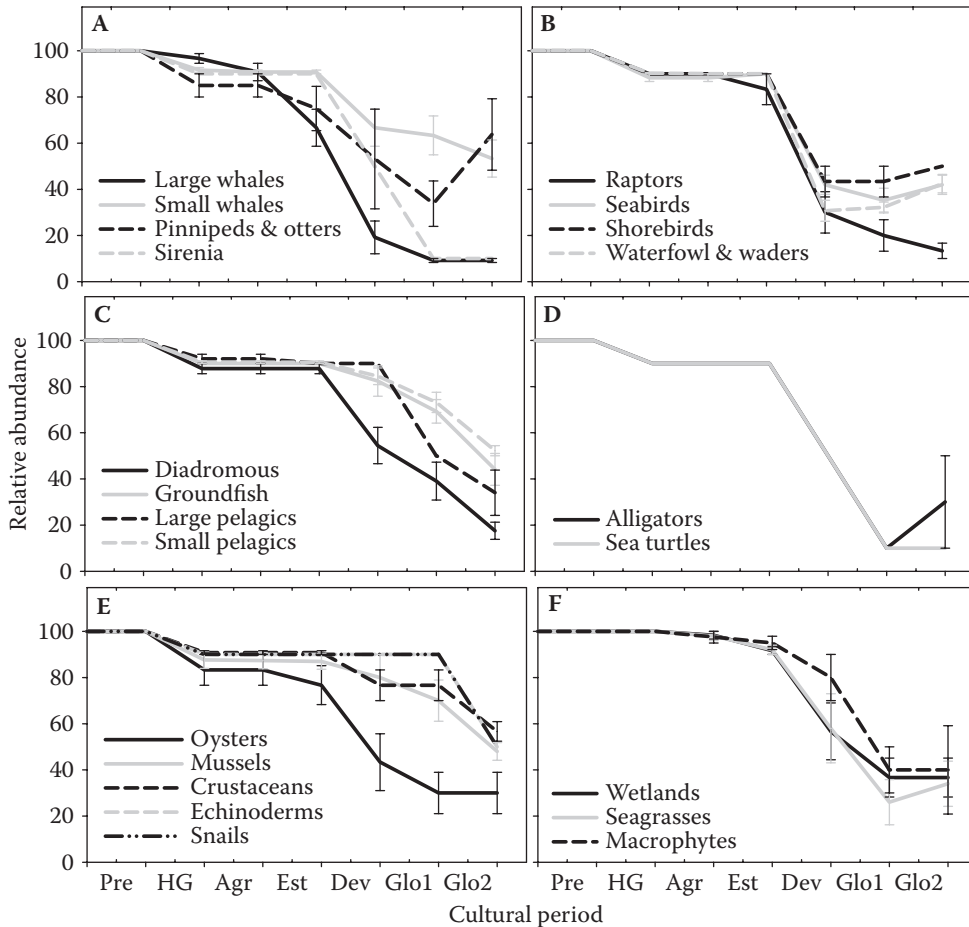


Figure 28 Change in relative abundance of different species groups (average \pm SE of six estuaries) within (A) mammals, (B) birds, (C) fish, (D) reptiles, (E) invertebrates, and (F) vegetation. (Data adapted from Lotze et al. 2006.)

the high number of endangered species, San Francisco Bay has experienced the highest percentage (20%) of recovering species (Figure 29). Although affected by an intense history, including the gold rush, the fur trade and general human impacts from a huge population, today's California has a good record with conservation successes.

Habitat alteration and loss

Coastal wetlands, seagrass meadows and oyster reefs are important breeding, nursery, foraging and staging habitats for numerous marine and coastal animals (Beck et al. 2001). Moreover, they are important natural filters and buffer zones between land and sea because they retain and cycle nutrients, sediments and organic matter (Costanza et al. 1997). Today, habitat conservation and restoration are high priorities in many estuaries and coastal states of the United States (USGS 2009a). However, large extents of original habitat have been lost since European colonisation. In the six estuaries, an average of 55% of historical wetland area has been lost or transformed, with the highest loss of 94% occurring in San Francisco Bay and the lowest in Galveston and Delaware Bays (Figure 30). Pamlico Sound had by far the highest extent of past and present wetland area.

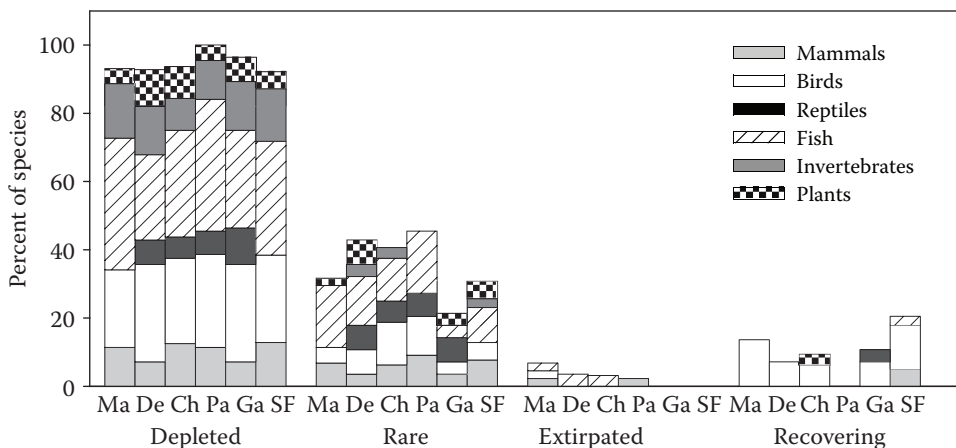


Figure 29 Percent of recorded species by taxonomic group that were depleted (<50%), rare (<10%), extinct or extirpated (0%), and recovering (from <10% to >10%) at the end of the twentieth century in the six study systems.

According to the USGS, wetland loss by state since 1780 ranged from 28% in Massachusetts to 91% in California (USGS 2009a).

Historically, most U.S. estuaries had extensive seagrass beds and other SAV that provided habitat for many species and food for waterfowl, invertebrates, green turtles and manatees. A 1990s survey (Bricker et al. 1999) estimated current SAV status as low (10–25% cover) to very low (0–10% cover) for most systems and non-existent for Delaware Bay (Figure 31). Estimates of past SAV area are limited and mostly confined to the twentieth century. In Chesapeake Bay, SAV extent was reduced by 56% in 1930–1970 (Moore et al. 2004). In Galveston Bay, seagrass area has decreased by 86% and in San Francisco Bay by 34% since the 1950s (White et al. 1993, ANR 2001). Yet, seagrass beds were affected much earlier in many estuaries. Sediment core data from Pamlico Sound indicate a decline in the seagrass epiphyte *Cocconeis* from 13% in 1540 to 0.4% in 2000, an overall decline of 97% (Cooper 2000). Similarly, in Chesapeake Bay *Cocconeis* declined by 80–100% since 550 AD (Cooper & Brush 1993). Combining these different estimates (Figure 31) gives an average seagrass or SAV loss of 68–75% in the estuaries studied.

Oyster banks or reefs also provided important habitat in most estuaries, yet the pressure and destructive practices of the oyster fishery strongly decimated the abundance and health of most oyster reefs (Kirby 2004). Although the long-term trend of the oyster fishery can be well reconstructed from catch data (Figure 28), there is little quantitative information on the former extent of oyster reef area. Historical reports and maps, however, indicate that oyster reefs were extensive in the bays and along the shorelines in most of the studied estuaries. In Chesapeake Bay, one of the more well-studied estuaries in the country, it is known that about 111,600 ha of natural oyster bar habitat originally existed on the Maryland side. This declined by more than 50% from 1907 to 1982, with localised losses of up to 95% (Rothschild et al. 1994).

Water quality

Comparable data on the history of changes in water quality for U.S. estuaries are very limited. However, a survey in the 1990s (Bricker et al. 1999) indicated that all six estuaries were experiencing low-to-moderate signs of eutrophication, which were most pronounced in Chesapeake Bay and lowest in Delaware Bay (Figure 32). A comparison of primary and secondary symptoms as well as the main drivers and trends of eutrophication in the main bays and subsystems are shown in

Table 7 Endangered (E) and threatened (T) marine species listed for each state related to the six study systems

Common name	Scientific name	MA	DE	VI	MD	NC	TX	CA
Mammals								
West Indian manatee	<i>Trichechus manatus</i>						E	
Southern sea otter	<i>Enhydra lutris nereis</i>							T
Guadalupe fur seal	<i>Arctocephalus townsendi</i>							T
Steller sea lion	<i>Eumetopias jubatus</i>							T/E
Killer whale	<i>Orcinus orca</i>							E
Blue whale	<i>Balaenoptera musculus</i>	E						E
Finback whale	<i>Balaenoptera physalus</i>	E	E	E	E	E	E	E
Humpback whale	<i>Megaptera novaeangliae</i>	E	E	E	E	E	E	E
Right whale	<i>Balaena glacialis</i>	E	E	E	E	E		
Sei whale	<i>Balaenoptera borealis</i>	E						E
Sperm whale	<i>Physeter catodon</i>					E		E
Birds								
Short-tailed albatross	<i>Phoebastria albatrus</i>							E
Whooping crane	<i>Grus Americana</i>						E	
Eskimo curlew	<i>Numenius borealis</i>	E	E	E	E	E	E	E
Marbled murrelet	<i>Brachyramphus marmoratus</i>							T
Brown pelican	<i>Pelecanus occidentalis</i>					E	E	E
Piping plover	<i>Charadrius melodus</i>	T	T	T	T	T	T	
Western snowy plover	<i>Charadrius alexandrinus nivosus</i>							T
California least tern	<i>Sterna antillarum browni</i>							E
Least tern	<i>Sterna antillarum</i>						E	
Roseate tern	<i>Sterna dougallii dougallii</i>	E		E		E		
Reptiles								
Green sea turtle	<i>Chelonia mydas</i>		T	T	T	T	T	T
Hawksbill turtle	<i>Eretmochelys imbricata</i>	E	E	E	E	E	E	
Kemp's ridley turtle	<i>Lepidochelys kempii</i>	E	E	E	E	E	E	
Leatherback turtle	<i>Dermochelys coriacea</i>	E	E	E	E	E	E	E
Loggerhead turtle	<i>Caretta caretta</i>	T	T	T	T	T	T	T
Olive ridley turtle	<i>Lepidochelys olivacea</i>							T
Fishes								
Tidewater goby	<i>Eucyclogobius newberryi</i>							E
Chinook salmon	<i>Oncorhynchus tshawytscha</i>							T/E
Coho salmon	<i>Oncorhynchus kisutch</i>							T/E
Smalltooth sawfish	<i>Pristis pectinata</i>					E	E	
Smelt, delta	<i>Hypomesus transpacificus</i>							T
Steelhead	<i>Oncorhynchus mykiss</i>							T/E
Unarmoured threespine stickleback	<i>Gasterosteus aculeatus williamsoni</i>							E
Shortnose sturgeon	<i>Acipenser brevirostrum</i>	E	E	E	E	E		
Invertebrates								
White abalone	<i>Haliotis sorenseni</i>							E
Shasta crayfish	<i>Pacifastacus fortis</i>							E
Total		13	11	12	11	15	14	27

Source: Data from USFWS 2009.

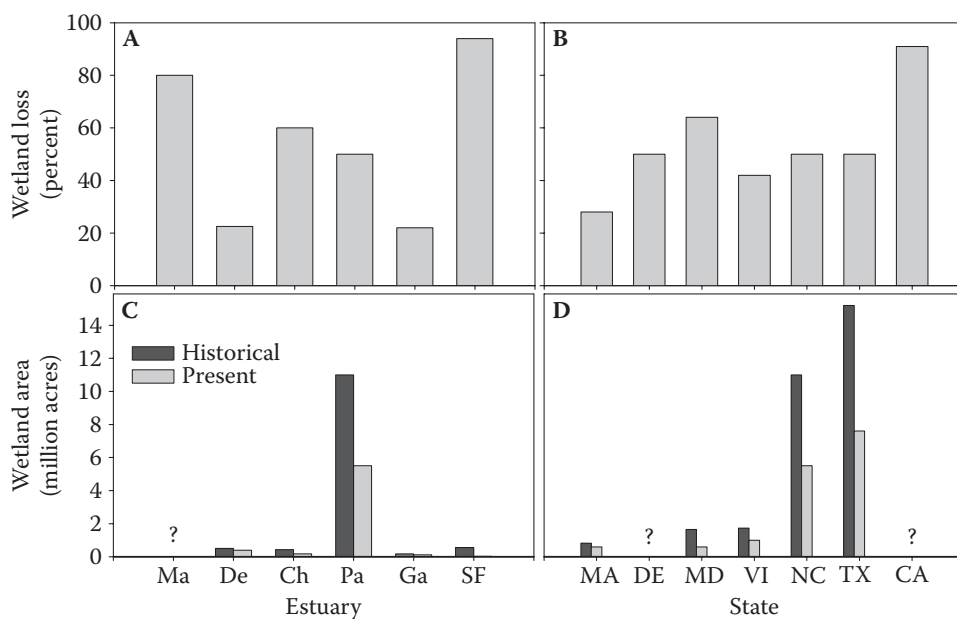


Figure 30 Estimated percent loss of wetland area by (A) estuary and (B) state and historical and present extent of wetland area by (C) estuary and (D) state. (Estuary data from Chapman 1977, Nichols et al. 1986, White et al. 1993, Kennish 2000, USGS 2009a.)

Table 8. All systems showed increased chlorophyll concentrations, indicating enhanced pelagic production, while macroalgae and epiphytes seem only problematic in Chesapeake and Massachusetts Bays. Secondary symptoms, including low oxygen levels, SAV loss or harmful algal blooms, are also found in all systems to varying degrees. Human impacts, especially nitrogen inputs, have been consistently identified as the main driver of eutrophication, but the susceptibility of each system is also an important factor. At the time of the survey, projected trends toward 2020 indicated improvement only in Boston Harbour in Massachusetts Bay, while suggested trends for other systems were stable or worsening (Bricker et al. 1999). Where long-term sediment core or hydrographical data were available, trajectories indicated that degradation of water quality started with European colonisation (Figure 32; Lotze et al. 2006). Initially, land clearing mobilised sediments and nutrients, which enhanced primary production in the estuary. These trends stabilised until the late 1800s, when discharges began to increase with growing municipal and industrial activities. After WWII, artificial fertilisers further enhanced nutrient loads, and eutrophication became a well-known phenomenon with increasing occurrence of algal blooms, SAV loss and oxygen depletion (Cloern 2001).

Species invasions

Another change humans brought to estuarine systems was the introduction of exotic species. This was sometimes intentionally done (e.g., by importing exotic aquaculture species), but often invaders arrived via ship hulls, ballast water or associated with aquaculture species. This includes a variety of species, from viruses to fish and mammals, but the bulk of known estuarine and marine invaders consists of invertebrates, plants and algae (Cohen & Carlton 1998, Carlton 2003, Fofonoff et al. 2003). Time series of recorded species invasions indicated an increase in numbers after European colonisation and further acceleration in the late nineteenth century (Figure 33), likely driven by increasing global navigation and commercial exchange, but also increased awareness and recording (Ruiz et al. 1997). The overall rate of invasions increased about 5-fold from an average of 2.6 per

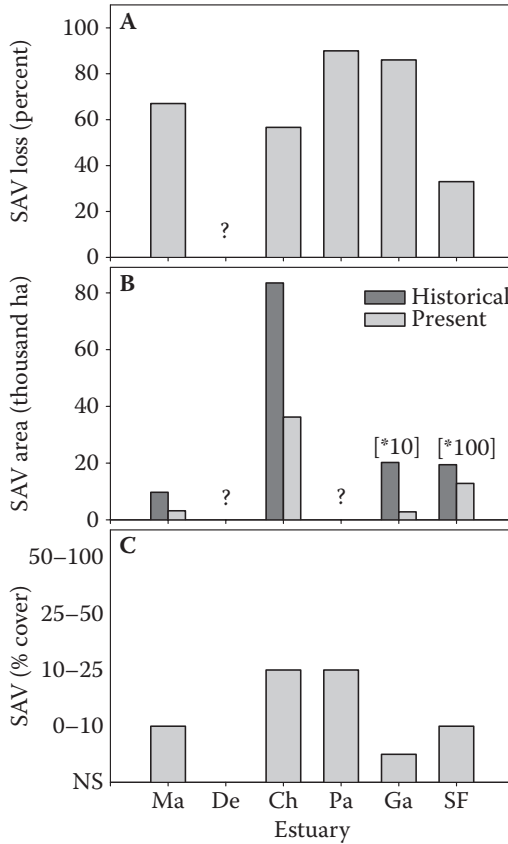


Figure 31 Changes in submerged aquatic vegetation (SAV) in each estuary: (A) percent loss of SAV area (with data from Buzzards Bay for Ma and estimates based on *Cocconeis* decline for Pamlico Sound); (B) historical and present SAV area (data for Galveston multiplied by 10 and San Francisco Bay by 100) (see case studies for the various data sources); and (C) today's SAV status estimated by Bricker et al. 1999.

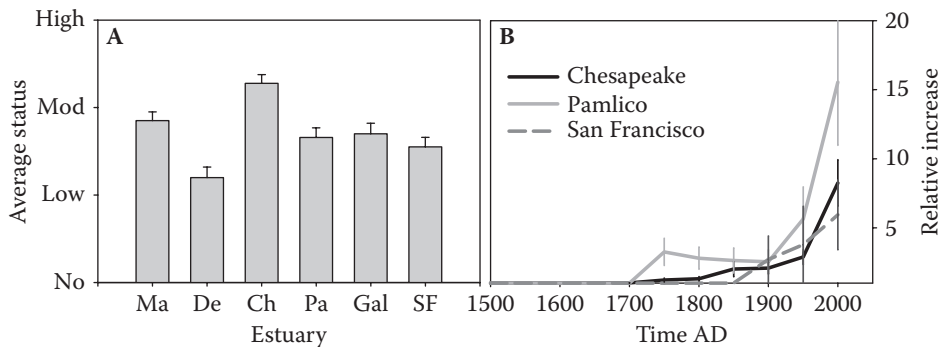


Figure 32 Average current eutrophication signs (A) in the six estuaries (based on data by Bricker et al. 1999) and timeline (B) for water quality degradation based on sediment core and hydrographic data (mean \pm SE across parameters; see case studies for various data sources).

Table 8 Eutrophication signs in the six estuaries and subsystems ranking from no (—), low, moderate (mod) to high

	Primary symptoms			Secondary symptoms			Influencing factors				Trend 2020
	Overall	Chl.a	Macroalgae	Epiphytes	DO	SAV loss	HAB	Human	Susc.	N input	
Massachusetts Bay	Mod	Mod	—	High	—	Low	Mod	Mod	Low	High	▼
Boston Harbor	High	Mod	High	Mod	Mod	Low	—	High	Mod	High	▲
Delaware Bay	Low	Mod	—	—	Low	—	—	High	Mod	High	—
Chesapeake Bay	High	High	High	—	High	High	—	High	High	Mod	▼
Patuxent River	High	High	?	—	Mod	High	High	High	High	Mod	▼
Potomac River	High	High	?	Low	High	Mod	Mod	High	High	Mod	▼
Rappahannock River	High	High	—	—	Mod	—	—	High	High	Mod	▼
Choptank River	Mod	Mod	High	Mod	Low	High	Mod	High	High	Mod	▼
Tangier/Pocomoke Sound	High	High	High	High	Low	High	Low	High	High	High	▼
Pamlico Sound	?	Mod	—	—	Low	Low	Mod	Mod	?	Mod	—
Pamlico/Pungo Rivers	High	High	—	—	Mod	Mod	Mod	High	High	Mod	—
Neuse River	High	High	—	—	High	Low	High	High	High	High	—
Albermale Sound	Low	Low	—	—	Low	Low	Low	Mod	Mod	Mod	▼
Galveston Bay	High	Mod	—	—	Low	High	Low	High	Mod	Mod	▼
San Francisco Bay	High	High	—	—	Low	High	—	High	Mod	Mod	▼
Central/Suisun/San Pablo	Mod	Mod	—	—	Low	Mod	High	Low	Low	Mod	—

Source: Data from Bricker et al. 1999.

Note: Primary symptoms include chlorophyll levels (Chl.), macroalgae and epiphyte abundance; secondary symptoms include low dissolved oxygen (DO) levels, submerged aquatic vegetation (SAV) loss, and harmful algal blooms (HAB); influencing factors include human impacts, the system's susceptibility (Susc.) and nitrogen (N) inputs; projected trends toward 2020 are worsening ▼, improving ▲, or stable —.

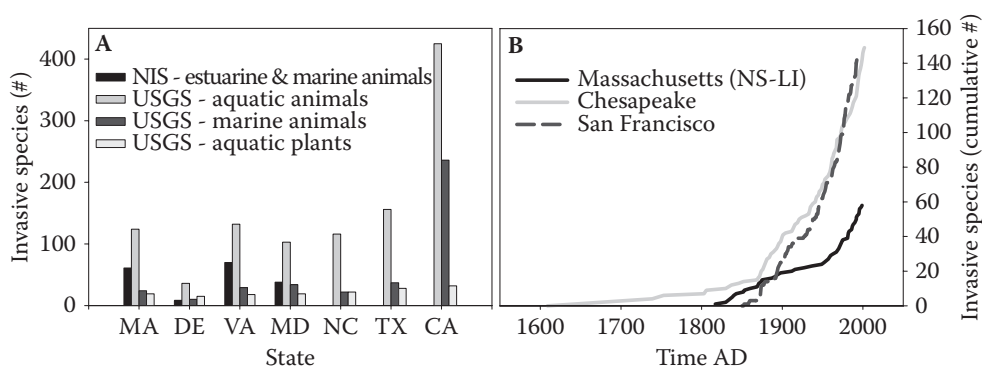


Figure 33 Recorded non-indigenous species (NIS) (A) by state, with VA and MD for Chesapeake Bay (NIS data from Ray 2005 for four NE U.S. states, USGS data from USGS 2009b), and (B) over time, with data for Massachusetts referring to Nova Scotia–Long Island Sound (data from Cohen & Carlton 1998, Carlton 2003, and Fofonoff et al. 2003).

decade in the first 50 yr of available time series to 13.2 in the last 50 yr, with higher increases in Chesapeake and San Francisco Bays compared with the area from Nova Scotia to Long Island Sound, which includes Massachusetts Bay (Cohen & Carlton 1998, Carlton 2003, Fofonoff et al. 2003). Today, different agencies and organisations are recording invasive species in the United States by state. In the northeastern United States, Ray (2005) reported between 8 (Delaware) and 70 (Virginia, Chesapeake Bay) invasive estuarine and marine animals. Data by the USGS (2009b) indicated between 36 (Delaware) and 425 (California) aquatic (freshwater and marine) invasive species (Figure 33). Delaware Bay had consistently the lowest and San Francisco Bay the highest number of recorded invasive species.

Causes and consequences of historical changes

Importance of human impacts

The six case studies and the summary reveal that humans have had a variety of impacts on estuarine and coastal species and ecosystems. However, exploitation clearly stood out as the major driver of species declines and extirpations, followed by habitat loss (Figure 34). Pollution, general human disturbance, disease and eutrophication were less-prominent drivers of decline. This is consistent with studies summarising marine species extinctions, depletions and their threats (Dulvy et al. 2003, Kappel 2005). Importantly, cumulative human impacts, mostly the combined effects of exploitation and habitat loss and in some cases pollution, were important in 58% of the recorded extinctions and 41% of depletions (Lotze et al. 2006). The records also suggest that reversing these human impacts enabled 10% of recorded species to recover (Figure 34). Reducing or banning exploitation and protecting habitat were the main drivers for recovery, but controlling pollution and disease also helped in some cases. Notably, in 77% of recoveries it was the reversal of multiple human impacts that worked, in most cases the combination of reduced exploitation and habitat protection. This indicates that cumulative human impacts can pose severe threats to species survival, and that basic needs, including shelter, food, habitat and health, need to be met to promote species recovery. Therefore, management of multiple human impacts needs to be integrated to maintain biodiversity and ecosystem function.

Yet, current management also needs to take new human impacts into account. Among past drivers of depletion and extinction, invasive species and climate change did not play a major role. However, these factors become more prevalent in coastal waters worldwide (Ruiz et al. 1997, Scavia

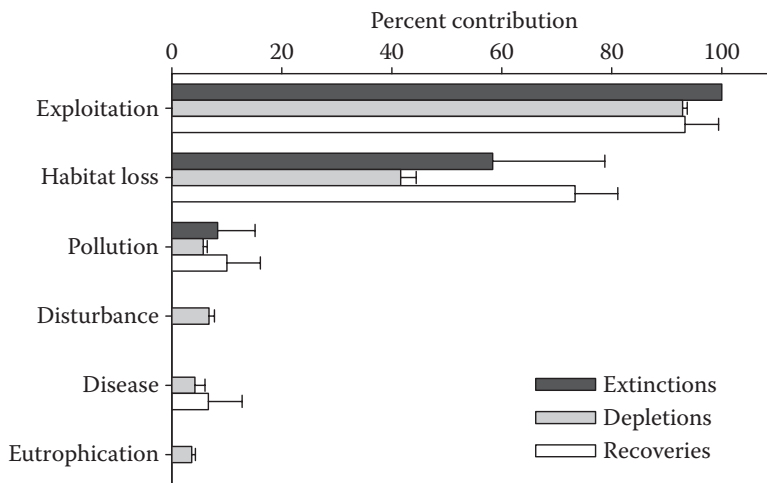


Figure 34 Importance of different human impacts (average \pm SE) in causing or contributing to species extinctions and depletions, and the reduction or ban of those has an impact on enabling recoveries. (Data adapted from Lotze et al. 2006.)

et al. 2002, Harley et al. 2006), causing additional threats and possible interactions with existing human impacts. Climate warming may enhance the effects of eutrophication (Lotze & Worm 2002), disease risk (Harvell et al. 2002) and invasions (Stachowicz et al. 2002). On the other hand, management aimed at reducing overexploitation, protecting habitat and controlling pollution may decrease the importance of these threats to estuarine species in the future.

Species richness and diversity

The number of species extinctions and invasions changes local species richness and diversity. In many estuaries and coastal waters, invaders by far outnumber extirpated species (Lotze et al. 2005, 2006, Byrnes et al. 2007), thereby enhancing actual species richness. However, many species have been depleted by more than 90% compared with historical abundance and may be considered rare or ecologically extinct, which would strongly reduce the functioning species diversity in those ecosystems (Byrnes et al. 2007, Jackson 2008). Also, the species groups most strongly affected by depletions and extinctions do not correspond to those affected by invasions. While declines have occurred predominantly among large mammals, birds, reptiles and fishes, invasions mostly consist of smaller invertebrates, plants and microscopic algae, protozoans, viruses and bacteria (Lotze et al. 2006). This mismatch creates a strong shift in species composition and diversity of estuarine and coastal systems where large, long-lived, slow-growing and late-maturing species have been replaced by small, fast-growing and high-turnover species (Byrnes et al. 2007). Given past and current trends, this shift in diversity is likely increasing in the future although partly dampened by recoveries.

Ecosystem structure, functions and services

The recorded changes in diversity have likely profoundly altered the structure and function of estuarine ecosystems (Hooper et al. 2005), but the question is how? Not only have all taxonomic groups experienced depletions in the estuaries examined, but also all important functional groups, including large and small carnivores, herbivores, suspension-feeders and submerged vegetation and wetlands (Figure 35). This means that estuarine ecosystems have lost a large amount of top-down control, while increasing nutrient loads have enhanced bottom-up control. Changing the strength of these

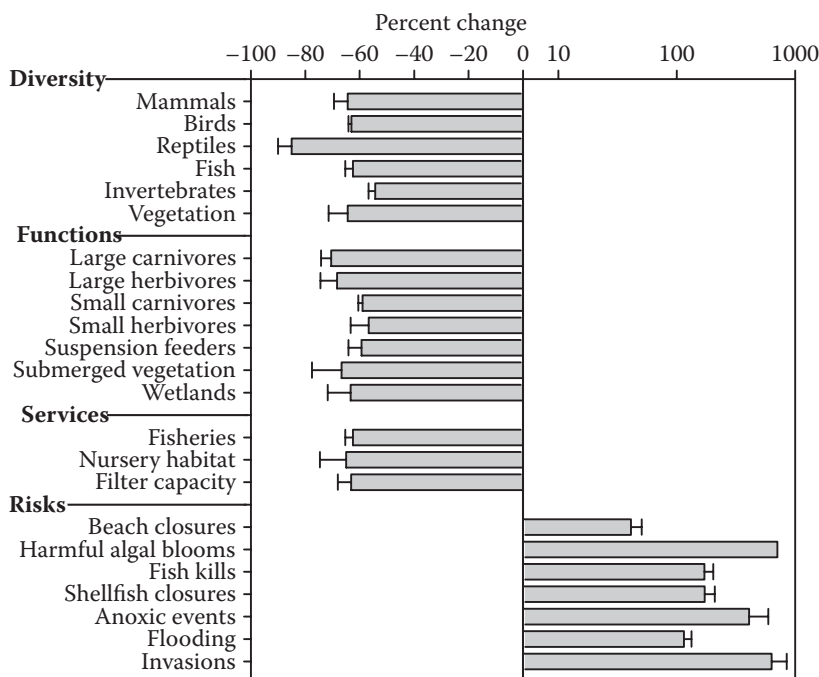


Figure 35 Summary of historical ecosystem changes in U.S. estuaries (average \pm SE). Diversity has been changed by declines in relative abundance in all taxonomic groups. This has also affected relative abundance of different functional groups and the services the estuarine ecosystems perform. The loss of diversity, functions and services has contributed to the increase in a range of risks to environmental and human health. (Data for diversity and functions adapted from Lotze et al. 2006, for services and risks from Worm et al. 2006.)

basic forces likely has severe consequences on species abundance, food web interactions, ecosystem productivity and functioning (Worm et al. 2002, Worm & Duffy 2003). The loss of predation may have released prey or competitors, while recovering top predators may suffer from depletion of their prey (Dayton et al. 2002). The loss of essential habitat and water quality degradation may have altered the carrying capacity for many species. An important open question is how—if ‘everything’ was more abundant in the past—could former ecosystems have sustained that abundance? Relative to current ecosystem structure, alternative past scenarios may involve very slow growth rates and turnover of large animals or more efficient transfer of primary production to higher trophic levels (Steele & Schumacher 2000). In both cases, the composition and dynamics of estuarine ecosystems have profoundly changed, with potentially severe consequences for the maintenance of their diversity, productivity and stability.

Changes in ecosystem structure and functioning translate into changes in ecosystem services that benefit people, including food, clean water, fibres, shelter and aesthetic and cultural services (Daily 1997, Millennium Ecosystem Assessment [MEA] 2005). Over the past 50 yr, human activities have changed ecosystem structure and function more rapidly and extensively than in any other period in history (Vitousek et al. 1997, MEA 2005). This has degraded approximately 60% of global ecosystem services, with consequences on all components of human well-being (MEA 2005). In estuaries and coastal waters, the decline in taxonomic and functional groups has affected the provision of fisheries and seafood, spawning and nursery habitats to sustain marine resources and filter capacity to maintain good water quality (Figure 35). The losses of these functions and services have brought rising health risks and costs to society, such as increasing beach closures, harmful algal blooms, fish kills, shellfish closures, oxygen depletion, flooding and invasions (Worm et al. 2006).

To reverse these undesirable effects and ensure the continued provision of important ecosystem services, it is essential to strengthen the resilience of both the ecosystem and the social or governance system. While the first can be achieved by promoting biodiversity and limiting human impacts, the latter rises with societal abilities to learn and adapt (Lotze & Glaser 2009).

National and global comparisons

Other U.S. estuaries

The six reviewed estuaries are among the largest and possibly most impacted estuaries of the United States, some of them surrounded by major cities and industries. However, other U.S. estuaries have experienced similar histories of human-induced changes with potentially similar consequences on the status of species, habitats and water quality. Historically, more than 50% of all U.S. fishery yields came from estuaries or estuarine-dependent species (Houde & Rutherford 1993). Yet today, in 22 of the 28 estuaries designated as National Estuary Program sites in the United States, declines of fish and wildlife populations are considered to be high- or medium-priority problems (Kennish 2002). This is not just driven by past and present exploitation pressure. A survey of the status and impacts of eutrophication across 138 U.S. estuaries (Bricker et al. 1999) indicated that 50% of systems experience impaired resource use in commercial and recreational fisheries, shellfish harvesting, fish consumption, swimming, boating and tourism. Overall, 44 estuaries were identified as highly and 40 as moderately eutrophic, with projected trends to worsen in 86 estuaries (Bricker et al. 1999). The main management targets of concern to curb eutrophication in the 138 estuaries included agriculture, wastewater treatment and urban run-off. Past and present habitat loss is also of concern in many U.S. estuaries. At the time of European settlement, there were about 221 million acres of wetlands within the area currently covered by the political boundaries of the United States (Dahl & Allord 1999). By the mid-1980s, only 103 million acres remained. Six of the 50 U.S. states have lost 85% or more of their original wetlands, and 22 lost more than 50%. The estuaries selected for this review lost 22–94% of their wetlands.

Global context

This review indicated very similar histories of change in the selected estuaries, likely because they experienced the same historical context of first Native American and later European occupation and finally becoming part of the United States. In a comparative analysis of 12 estuaries and coastal seas around the world, these six U.S. systems showed a higher magnitude of degradation compared with Canadian but less degradation than European systems (Lotze et al. 2006). Although the Canadian Bay of Fundy and Gulf of St. Lawrence experienced the same North American historical context, human population density and impact is generally less intense in these regions, with smaller cities and fewer industrial activities along the coast. However, the European systems experienced a much longer and more severe history of human activities compared with the United States. Resource depletion, wetland loss and water quality changes in the northern Adriatic Sea can be traced to Roman times 2000 yr ago (Lotze et al. 2006). In the Wadden and Baltic Seas, strong human influence started in medieval times 1000 yr ago. Although past changes in resources, habitats and water quality followed similar trajectories in all systems, they played out more rapidly in North America and Australia in the course of European colonisation in the past 150–300 yr (Lotze et al. 2006). Detailed historical reconstructions of ecological changes in the Bay of Fundy (Lotze & Milewski 2004) and the Wadden Sea (Lotze 2005, 2007, Lotze et al. 2005) mirror the changes described for the U.S. estuaries in this review.

Human impacts have not only affected estuarine environments in the past. Evidence is increasing that many coastal ecosystems, including the Benguela upwelling system (Griffiths et al. 2004),

coral reefs (Pandolfi et al. 2003) and offshore islands (Craig et al. 2008), have experienced similar histories of ecological change. For example, across 14 coral reefs in the Atlantic, Red Sea and Australia, very similar trajectories of change emerged, with the rapid depletion of large carnivores and herbivores in the course of European colonisation, followed by declines in smaller animals and architectural species (Pandolfi et al. 2003). The reefs of today were 30–80% degraded from pristine levels. Together, these studies revealed a much longer history of human-induced changes in estuarine and coastal ecosystems than previously assumed. On the continental shelves, human-induced changes generally occurred only in the past 100–200 yr and moved from there into the open ocean about 50 yr ago and into the deep sea 10–20 yr ago. This spatial expansion of resource use was accompanied by a temporal acceleration of induced changes in population depletion (Lotze 2007, Lotze & Worm 2009).

An increasing body of literature in marine historical ecology is also revealing stronger declines in valuable species groups than previously assumed. A review across 256 estimates of past population changes from 95 studies indicated an average decline of 89% from historical abundance levels. Recent recovery in about 15% of the species reduced this estimate to an 84% average decline today (Lotze & Worm 2009). These rates of decline are comparable to those of the species considered rare (>90% decline) in the U.S estuaries of this study. A review of more recent changes in 232 fish stocks indicated an average 83% decline from maximum breeding population size over 10–73 yr (Hutchings & Reynolds 2004). Similarly, an analysis of exploited marine mammal populations suggested declines of 76% across all species and 81% for the great whales since the beginning of exploitation (Christensen 2006). Finally, a meta-analysis of cod stocks in the North Atlantic indicated an average decline of 96% from carrying capacity (Myers & Worm 2005). All these figures indicate that many populations have been reduced to very low levels that correspond to threatened or endangered status following criteria by the IUCN, and many species have been listed as threatened or endangered (e.g., Table 7).

In addition to species depletion, habitat loss is a global phenomenon. A review of historical habitat losses around Europe suggests that more than 50% of coastal wetlands and seagrass beds have been lost or transformed, with losses of more than 80% in many regions (Airoldi & Beck 2007). Native oyster reefs were ecologically extinct by the 1950s along most European coastlines and in many estuaries and bays well before that. Today, less than 15% of the European coastline is considered in ‘good’ condition (Airoldi & Beck 2007). In tropical systems, about 20% of coral reefs have been lost and 20% degraded over the past 50 yr, and 35% of mangrove area has been lost over the past two decades (MEA 2005).

Outlook

Scientific progress in marine historical ecology

Over the past decade, scientists from a variety of disciplines, including palaeontology, archaeology, history, fisheries science and ecology have made tremendous progress in marine historical ecology, tracing human impacts on marine animal populations back hundreds and sometimes thousands of years (Rick & Erlandson 2008, Starkey et al. 2008, Lotze & Worm 2009). Palaeontological records have identified natural long-term, often climate-driven changes in population abundance that place recent anthropogenic changes into context. Archaeological studies suggest significant human impacts on local marine resource abundance, distribution and size long before commercial and industrial exploitation started. Furthermore, historical records imply that many highly valued species were severely depleted before the midtwentieth century, often reaching their low point decades to more than a century ago. Thus, marine historical ecology expands our usual ecological data horizon of a few years or decades way into the past, thereby revealing dramatic changes before general scientific inquiry began. It also shows that wherever we study marine ecosystems today, we

should be aware of their ‘unnatural’ state because of the long history of change they have undergone prior to our assessment (Carlton 1998, Jackson et al. 2001, Roberts 2003).

Knowledge gaps and future research

Many studies in marine historical research have focused on single species, and few studies have aimed at combining results for various species or functional groups (such as Pandolfi et al. 2003, Lotze et al. 2006). Even past trajectories of multiple ecosystem components do not answer the question of how past food webs and ecosystems have functioned. There are many unanswered questions regarding how trophic flows, system biomass and productivity have changed ecosystem performance over time. The best way to explore this may involve ecosystem modeling tools (Pitcher et al. 2002, Coll et al. 2006). Also, historical research has revealed the importance of exploitation and habitat loss in driving population declines over the past centuries, while climate variability played a major role in population fluctuations over much longer periods. However, climate change may become critical for predicting future trends in populations and ocean ecosystems (Brander 2007), and a renewed focus on the consequences of past climate fluctuations might help project future ecosystem changes (Rose 2004, Enghoff et al. 2007).

Using historical reference points for management and conservation

Around the world, many fisheries and coastal ecosystems are in trouble, and although many management agencies are aiming at halting or reversing past trends of depletion and degradation, there are some major factors that perpetuate the current crisis. First, the historical context is generally overlooked, thereby failing to acknowledge the total magnitude of population declines and ecosystem change. If management relies on the past 20–50 yr of scientific monitoring data, the necessary reference points are obscured by shifting baselines (Pauly 1995, Sáenz-Arroyo et al. 2005, Pinnegar & Engelhard 2007). Second, the ecosystem context is often ignored, yet it is not single species or stocks that have changed, but their predators, prey and habitat as well, thereby changing the overall ecosystem structure and functioning (Steele & Schumacher 2000). This may prevent recovery, as, for example, witnessed in the non-recovery of North Atlantic cod. Finally, management continues to focus on single species and single human impacts, which are easier to assess and manage. Although recognition of an ecosystem approach to management is increasing, there is little understanding of how to actually do this. The Pew Oceans Commission (2003) and U.S. Commission on Ocean Policy (2004) outlined goals for an ecosystem-based management approach that include the restoration of historical levels of native biodiversity and a vision for healthy, productive, resilient marine ecosystems that provide stable fisheries, abundant wildlife, clean beaches, vibrant coastal communities and healthy seafood. But, what are historical levels of native biodiversity? And, to which levels should ecosystems be restored? The largest gap in this approach is the lack of historical baselines as basic reference points to determine sound management and conservation goals (Carlton 1998, Roberts 2003). The present review may fill some of these gaps for U.S. estuaries.

Recovery, restoration and resilience

The environmental or ecological history of an ecosystem can provide perspective on the possible diversity, abundance and health of an ecosystem that is otherwise missing. Although we may never be able to restore an ecosystem to ‘pristine’ levels, the past provides a vision for conservation and recovery (Carlton 1998, Clark et al. 2001a). Many populations and ecosystems are quite robust and can recover from perturbations, although they may not necessarily bounce back to their original abundance or state (Palumbi et al. 2008). In general, it is most important to keep all the parts, which means maintaining the biodiversity of the system. Higher diversity has been linked to greater stability, productivity and recovery potential both in small-scale experiments and large-scale ecosystem comparisons (Worm et al. 2006).

Fortunately, despite several extinctions, most species and functional groups still persist in U.S. estuaries today, albeit in greatly reduced numbers. Thus, the potential for recovery remains, and where human efforts have been focused on protection and conservation, recovery has been possible, albeit often with significant lag times. Long-lived species may need several decades to rebound to previous levels of abundance (Caddy & Agnew 2004, Lotze & Milewski 2004), and life-history characteristics and the magnitude of depletion are important determinants for recovery. Across 232 fish populations, only 12% recovered 15 yr after a collapse, mostly clupeids, while 40% showed no recovery (Hutchings & Reynolds 2004). A review of historical population changes found that 15% of 256 examples, mostly marine mammals, have experienced some recovery in past decades, increasing on average from 13% to 39% of former abundance levels (Lotze & Worm 2009).

Although several species, habitats and water quality parameters have shown recovery or improvement in the presented U.S. estuaries, it is unclear whether this contributed to an overall recovery of the ecosystem. But, what would that look like? An example from the Thames estuary in the United Kingdom shows that improving oxygen levels led to the return of about 110 fish species that were absent during times of heavy pollution (Cloern 2001). A 10-fold reduction in nitrogen loads in Tampa Bay in Florida led to reduced phytoplankton levels, increased water clarity, decreased blue-green algae and, finally, after 10 yr, the return of seagrass (Cloern 2001). Studies of marine protected areas show that species richness and productivity increased within compared with outside protected zones (Worm et al. 2006). These examples indicate that at least partial ecosystem recovery can be possible, even in heavily degraded systems. Today, pollution controls, habitat protection and restoration and no-exploitation or no-go zones are increasingly part of coastal management plans. Thus, the major drivers of past changes are increasingly addressed and may eventually lead to enhanced recovery in the future.

Governance and a sustainable future

A major challenge is to reverse ecosystem degradation while meeting increasing societal demands for the services these systems provide. Yet, protecting and restoring marine biodiversity are key to maintaining essential ecosystem services (Worm et al. 2006). This concept is fairly new, however, and lacking broad public awareness and acknowledgement. Balancing exploitation and protection, degradation and restoration needs good and strong governance, but economic, social and political incentives often favour over- rather than underutilisation.

In the United States, the Magnuson-Stevens Act requires recovery plans for overexploited fish stocks. By 2004, half of the 74 fish stocks requiring recovery showed some signs of increase, but only 3 reached their recovery target (Rosenberg et al. 2006). The latter were stocks for which fishing pressure had been significantly reduced toward or below the target fishing mortality. Of the other stocks, 54 were considered overfished, and 34 continued to experience overfishing despite having a recovery plan. Thus, a recovery plan does not help in itself; it also needs to be implemented, which falls into the realm of governance and political will rather than scientific analysis and advice. Unfortunately, a survey of fisheries management effectiveness around the world indicates that only 7% of coastal states have rigorous scientific assessments, 1.4% also have a participatory and transparent conversion of scientific advice into policy, and 0.95% also have mechanisms that ensure compliance with regulations, while none was also free of excess fishing capacity or subsidies (Mora et al. 2009). Yet, in systems where management measures have been taken seriously and implemented, even heavily exploited large-scale ecosystems such as the California Current or small-scale regions such as Kenya's coastal waters can achieve recovery of important fish and fisheries (Worm et al. 2009).

One coastal ecosystem that was heavily degraded but has undergone remarkable recovery over the past decades is Monterey Bay in California (Palumbi 2009). Comparable to the ecological histories experienced in the U.S. estuaries of this review, Monterey Bay went through periods of whaling, fur and feather trade, heavy exploitation of fish, birds and abalone, and intense pollution at the height of the canning industry in early to mid-1900s. After the collapse of sardine stocks, the last

major fishery, it was the vision, perseverance and governance led by one person, Julia Platt, that turned the tide for Monterey Bay. Over the past decades, extensive marine and coastal reserves, a commitment to conservation education and nature tourism and a balance between resource use and protection has enabled the bay's ecosystem to recover and once again teem with life (Palumbi 2009). This hopeful example is proof of the ability of marine ecosystems to recover and of human communities to make it possible.

Many estuaries and coastal bays around the world have undergone similar histories of depletion and degradation as Monterey Bay, yet recovery signs and prospects seem so far more limited. This review provides a detailed account of such ecological histories in selected U.S. estuaries. On the one hand, the reconstruction of former species and habitat abundance and ecosystem health may serve as historical reference points for setting sound future management and conservation targets. On the other hand, the rediscovery of the past offers a vision of the former richness and importance of estuaries that may inspire better governance for estuarine diversity and productivity supporting animal and human life.

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