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TWO CENTURIES OF MULTIPLE HUMAN IMPACTS AND SUCCESSIVE CHANGES IN A NORTH ATLANTIC FOOD WEB

Heike K. Lotze[1,3] and Inka Milewski[2]

[1]*Department of Biology, Dalhousie University, 1355 Oxford Street, Halifax, Nova Scotia, Canada B3H 4J1*
[2]*Conservation Council of New Brunswick, 180 St. John Street, Fredericton, New Brunswick, Canada E3B 4A9*

Abstract. European colonization of North America severely altered terrestrial and aquatic ecosystems alike. Here, we integrate archaeological, historical, and recent data to derive the ecological history of the Quoddy Region, Bay of Fundy, Canada, an upwelling region rich in marine diversity and productivity. We document successive changes on all trophic levels from primary producers to top predators over the last centuries. Our objectives were to (1) construct a baseline of ''what was natural in the coastal ocean,'' and (2) analyze the sequence and potential interaction of multiple human impacts.

Archaeological records highlight the abundance and diversity of marine species used by indigenous people over the last 2000–3000 years. Europeans colonized the area in the late 1700s and rapidly transformed the environment by multiple ''top-down'' (exploitation), ''bottom-up'' (nutrient loading), and ''side-in'' (habitat destruction, pollution) impacts. Most large vertebrates were severely overexploited by 1900, leading to the extinction of three mammal and six bird species. Diadromous fish dramatically declined after river damming in the early 1800s, and recovery was prevented by subsequent river pollution. Overfishing of groundfish stocks started in the late 1800s, gradually leading to a final collapse in the 1970s. In the 20th century, decline of traditional fisheries induced a shift to low trophic level harvesting and aquaculture, which increased exponentially over the past 20 years. Eutrophication caused shifts in seaweed and phytoplankton communities: Some long-lived rockweeds were replaced by annual bloom-forming algae, and diatoms were replaced by dinoflagellates.

Today, the once unique Quoddy Region shows the most common signs of degradation found in highly impacted coastal areas worldwide. Multiple human influences have altered abundance and composition of every trophic level in the food web and reduced upper trophic levels by at least one order of magnitude. We highlight cumulative and indirect effects that impair the ability to predict and manage highly impacted coastal ecosystems. On the other hand, simple protection and restoration measures in the 20th century led to the recovery of some species. It is these successes that provide guidance for a more sustainable interaction of humans with their marine environment.

Key words: coastal ecosystem; conservation; cumulative effects; eutrophication; extinction; food web structure; habitat destruction; historical ecology; overfishing; pollution; recovery; shifting baseline.

Introduction

Although change in community configuration has been the norm throughout the history of the planet's ecosystems, anthropogenic influences have enormously increased the rates and scales of change (Vitousek et al. 1997). In the marine realm, coastal ecosystems and estuaries have been most visibly affected by anthropogenic forces (Limburg 1999). Similar patterns of degradation caused by overfishing, habitat destruction, eutrophication, and pollution are recognized in highly populated coastal regions around the globe (Steneck 1997, Vitousek et al. 1997, Pauly et al. 1998, Cloern 2001, Jackson et al. 2001, Worm et al. 2002).

Most changes in today's ecosystems, however, are not only the result of current human activities, but are based on a long history of human influences (Hutchings and Myers 1995, Steneck 1997, Jackson et al. 2001). Unfortunately, we are usually unaware of when and how humans started to alter their marine environment, and what coastal ecosystems looked like before large-scale human interference. The baseline of ''what was natural'' has shifted throughout generations (Pauly 1995). Without a baseline to measure change against, however, we might end up managing noise in relic populations (Myers and Worm 2003). Furthermore, untangling past causes and consequences of change will provide us with a long-term perspective, which is essential to understand current and predict future changes in species, communities, and ecosystems.

As a case study, we compiled the ecological history of the Quoddy Region in the outer Bay of Fundy, Canada. This coastal region was once famous for its ex-

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[3] E-mail: hlotze@dal.ca

traordinary productivity and diversity (Lotze and Milewski 2002). Passamaquoddy Bay was named by aboriginal people meaning ‘‘Bay of Pollock,’’ and A. G. Huntsman (1953*a*) noted: ‘‘Nowhere else in the world (this may be questioned) are there waters to compare with those of Passamaquoddy Bay and vicinity, where such vast quantities of locally grown fish are taken yearly from a small area.’’ We chose this region because of its rich marine life, but also because of its relatively short history of European colonization (~200 years), which is well documented because of the long-term focus on commercial fishing and marine research in the area. This allowed us to use scientific and historical data to track changes from the beginning of European influence to date. We compiled all available archaeological, historical, and recent data on abundance and distribution of marine species from all trophic levels of the food web. Our main objectives were to determine what the food web looked like before large-scale European influence, and to demonstrate when and how human impacts induced changes. Thereby, we analyzed the potential for cumulative and indirect effects of multiple human impacts, and checked for positive trends and causes for recovery and re-establishment of species that had declined.

METHODS

Study region

The Quoddy Region is located in the outer Bay of Fundy, southwestern New Brunswick, Canada (Fig. 1A), and belongs to Charlotte County. It includes the estuarine regions from St. Croix River and Passamaquoddy Bay to Maces Bay and Point Lepreau, as well as numerous islands in the archipelagos around Grand Manan, The Wolves, and West Isles (Deer Island, Campobello Island; Fig. 1B). Because of its importance for seabirds, we also included Machias Seal Island in our analysis.

The Quoddy Region is characterized by high marine productivity due to water currents and circulation patterns, high tides, upwelling, and a short, energy-efficient food chain (Lotze and Milewski 2002). The area is also characterized by high habitat diversity on a small local scale, e.g., high-current channels and calm bays, deep rocky bottoms and shallow soft sediments, inshore beaches and offshore exposed cliffs, fresh, brackish, and marine water (Lotze and Milewski 2002). Together, high productivity and habitat availability attract and sustain a high diversity of resident and migrating species, especially on higher trophic levels, such as fish (Shackell and Frank 2003), birds (Christie 1983, Huettmann and Diamond 2000), and mammals (Gaskin 1983).

Data collection and analysis

We compiled archaeological, historical, and recent data on abundance and distribution of species from all trophic levels. We also used fisheries statistics on catch and effort, and historical descriptions of early explorers, naturalists, and fisheries observers. A complete list of references used to determine occurrence, abundance, and change of species over time can be found in the Appendix. Databases and further sources of information are cited in the following paragraphs. For most species groups we were able to find (1) quantitative time series or (2) comparable data from past and present periods. Because different data sets were of variable quality, we mostly discuss order-of-magnitude changes, and try to cross-validate our conclusions with independent data or comparable trends in adjacent regions. We linked causes and consequences of changes using mechanistic studies from our and similar study systems.

Data on occurrence, abundance, distribution, and exploitation of marine mammals were extracted from the literature (summarized in Lotze and Milewski 2002, Appendix), international whaling statistics for Atlantic Canada since 1910 (1910–1983, Committee for Whaling Statistics 1951–1984, International Whaling Commission 1984–2000), and the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2002).

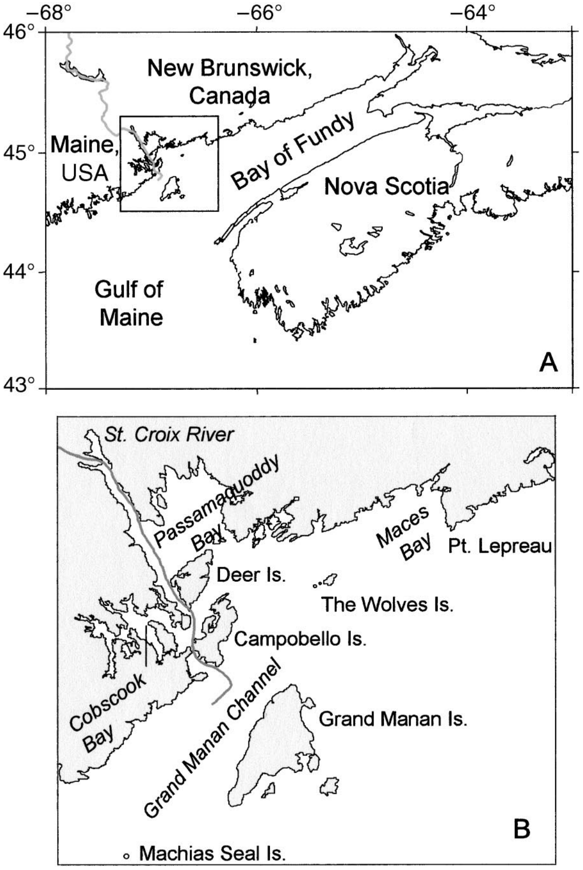

FIG. 1. (A) Location of the Quoddy Region in the outer Bay of Fundy, Northwest Atlantic Ocean; (B) detailed map of bays and islands (‘‘Is.’’) of the study area.

Data for the Quoddy Region were confirmed with population trends for the Bay of Fundy/Gulf of Maine and entire Northwest Atlantic (NEFSC 1999). From these sources, we estimated the number of marine mammal species in the Quoddy Region that have been severely reduced, or driven to extinction due to human impacts. We summarized the history of exploitation, and compared past and present abundance of species for which historical abundance estimates were available.

Marine bird data were compiled from the literature (summarized in Lotze and Milewski 2002, Appendix), and observer-based distribution and abundance surveys in the Quoddy Region: Seabird Colony Surveys since the 1920s and Coastal Surveys for 1967–1996 (Canadian Wildlife Service, Sackville, New Brunswick, Canada) in survey blocks 1–18 (Quoddy Region), and 25 (Machias Seal Island). Information on the status of endangered species came from COSEWIC (2002). From these sources, we estimated the number of bird species in the Quoddy Region that have been severely reduced, or driven to extinction due to human impacts. Only species clearly named in the literature were considered, but many more unspecified ''ducks,'' ''shorebirds,'' and ''seabirds'' might have been affected. Thus, numbers presented are minimum estimates only.

Data for marine fish were extracted from the literature (summarized in Lotze and Milewski 2002, Appendix), and annual fisheries statistics since 1869 (Fisheries Branch 1869–1919, Dominion Bureau of Statistics 1917–1968, DFO 1968–2000). We analyzed data for Charlotte County including Fisheries Statistical Districts (FSD) 50 (Grand Manan), 51 (Deer and Campobello Isles), 52 (Passamaquoddy Bay), and 53 (Maine coast from Passamaquoddy Bay to Point Lepreau), which are part of today's Northwest Atlantic Fisheries Organization (NAFO) management unit 4Xs (Clark and Paul 1999). Herring catch data by size were compiled from Huntsman (1953*b*). For herring, we calculated catch per weir (traditional, shore-based traps) for small and medium herring, since large herring were fished with gill nets (Huntsman 1953*b*). The groundfishery could be separated into two major periods: pre-1950, the groundfishery was primarily an inshore hook and line fishery with small boats, while post-1950, large trawlers became active and moved offshore (Clark and Paul 1999). No abundance data for groundfish were available pre-1950, thus we calculated catch-per-unit-effort (CPUE) as the only possible measure of relative abundance: (1) catch per boat, assuming all small boats were involved in the groundfishery, and (2) catch per handline, the traditional gear used to catch groundfish. Because the fishery was consistent in gear and area pre-1950 and not restricted by quotas, CPUE should be a conservative estimate for relative abundance, as it tends to stay high while biomass declines (Harley et al. 2001). For the post-1950 period, relative abundance data for groundfish were available from 1970 to 2000, compiled from annual stratified random surveys for strata 492 and 493 in southwestern Bay of Fundy by the DFO (Department of Fisheries and Oceans, Dartmouth, Nova Scotia, Canada) (Simon and Comeau 1994; P. Fanning, and J. Simon, *personal communication*). However, major gear changes, changes in fishing area, extension of the 200-mile limit in 1977, and the introduction of quotas (total allowable catch), make an interpretation of CPUE or catch vs. biomass difficult. To discuss trends in catch and abundance, we therefore refer to stock assessments by DFO for NAFO districts 4X and 4Xs. For past–present comparisons, we analyzed average catch in 1890–1900 and 1990–2000. Data on groundfish spawning areas were derived from Graham et al. (2002), who estimated the abundance of spawning areas over time based on GIS mapping of fishermen's knowledge. Conclusions derived from our study area are corroborated by fisheries trends throughout Atlantic Canada.

Data for diadromous fish and salmon aquaculture were compiled from the literature (summarized in Lotze and Milewski 2002, Appendix), and completed with data from St. Croix International Waterway Commission (St. Stephen, New Brunswick, Canada, L. Sochasky, *personal communication*), DFO (L. Marshall, B. Jessop, *personal communication*), and New Brunswick Department of Agriculture, Fisheries and Aquaculture (Fredericton, New Brunswick, Canada). Early abundance estimates from 1800 to 1850 were analyzed from fisheries observer data on abundance, catch and effort (Perley 1852). Potential abundance estimates based on available spawning and nursery habitat were calculated by several authors to estimate potential production and carrying capacity (Wilson 1956, Kerswill 1960, Fletcher and Meister 1982, Anonymous 1988, 1993). We discuss trends in abundance over time and compare recent, past, and potential abundance estimates.

Data for benthic invertebrates and seaweeds were compiled from the literature (summarized in Lotze and Milewski 2002, Appendix) and annual fisheries statistics (refer to sources for marine fish). Recent data were obtained from DFO (P. Lawton, E. Myers, S. Robinson, *personal communication*). We discuss these data in terms of changes in harvesting practices, fishing effort, and abundance over time. For lobster, we calculated CPUE as catch per trap. To address effects of coastal eutrophication on benthic communities, we present data from a recent field survey (Worm 2000) on community composition at eutrophied vs. non-eutrophied sites in the Quoddy Region (eight sites), southeastern Bay of Fundy (four sites), and the Atlantic coast near Halifax, Nova Scotia (four sites). For details on survey methods refer to Worm (2000).

Plankton data were compiled from the literature (summarized in Lotze and Milewski 2002, Appendix). Comparable zooplankton surveys were available for inshore Passamaquoddy Bay only. Fish and Johnson (1937) analyzed relative species abundance using rou-

TABLE 1. Faunal remains from archaeological sites (3000–1000 yr BP) of native settlements in the Quoddy Region, Bay of Fundy, Canada.

Mammals	Fish	Invertebrates	Birds
Common			
White-tailed deer	cod	soft-shelled clam	Common Loon
Beaver	pollock	barnacle	Brant
Moose	herring	blue mussel	Wood Duck
Dog (domesticated)	longhorn sculpin	northern whelk	Goldeneye
Porcupine	haddock	sea urchin	Eider Duck
			Great Auk
Less common			
Gray seal		Atlantic dogwinkle	Common Murre
Harbor seal		eastern mud whelk	Thick-billed Murre
Muskrat		Atlantic plate limpet	Greater Shearwater
Sea mink		horse mussel	**Passenger Pigeon**
Terrestrial mink		hairy colus	Eagle
Snowshoe hare		periwinkle	Osprey
Marten		northern cardita	
Red fox			
Black bear			

Notes: Species that are extinct today are marked in boldface. Data are from Black and Turnbull (1986), Bishop and Black (1988), Spiess et al. (1990), Murphy and Black (1996), and Black (2000).

tine 20-minute plankton tows with a 1-m silk mesh net #0 at the bottom, 50, and 0 m depth at several stations from March to December 1917, and July 1931 to September 1932. Legare and Maclellan (1960) determined relative species abundance using 15-minute plankton tows taken at 20, 10, and 0 m depth with a 1-meter nylon mesh net #0 (12–15 meshes per cm, i.e., 660–830 μm) at five stations from January 1957 to December 1958. Smith et al. (1984) analyzed true plankton abundance (number per cubic meter) from plankton tows with a 0.5-m, 400-μm mesh net at water depths from 20–0 m at several station from July to September 1980. Smith et al. (1984) were potentially able to sample a higher fraction of smaller zooplankton because of the smaller mesh size used. However, all studies consistently showed predominance of species >1 mm, thus different mesh sizes may not impair comparison of results. Still, because sampling gear, depth, and time differed among studies, results are not truly comparable and are used to show general patterns only. For this purpose, we determined relative composition of major species groups (that contribute >5% to community biomass) for spring (March–May), summer (June–August), and fall (September–November).

For phytoplankton, we found comparable data sets on species abundance from the 1930s (Gran and Braarud 1935) and 1990s (Martin et al. 1999). In the 1930s, water samples were taken at several depths, and subsamples were centrifuged and preserved with formalin before analysis. In the 1990s, surface water samples were taken with a bucket, subsamples were preserved with formalin and analyzed in counting chambers. Although different, these two methods have no systematic bias for the micro- and mesophytoplankton that made up the bulk of the biomass (diatoms, dinoflagellates). Most importantly, toxic species and dinoflagellates that were abundant in the 1990s would have been detected by the centrifuge method, if they had been present. Thus, we would not expect that the shift in methods have resulted in an order of magnitude shift in survey results. For consistency, we only extracted data for species occurring at >1000 cells/L, and we only analyzed data from surface water samples at similarly located study sites: Gran and Braarud's station 1C and 5, and Martin et al. station 17 and 16. Station 1C and 17 are located inside Passamaquoddy Bay near St. Andrews, and station 5 and 16 outside Passamaquoddy Bay between Campobello and The Wolves islands. Data were separated by season as spring (April–May), summer (June–July), and fall (August–September). We calculated relative species composition in percent and total phytoplankton abundance in cells per liter. Although data from the 1930s only represent one to two years of study, species composition was consistent with further early studies (Fritz 1921, Davidson 1934).

RESULTS

Archeological evidence of prehistoric settlements and exploitation

Faunal remains from prehistoric settlements in the Quoddy Region indicate an unusual abundance and diversity of marine species used by indigenous people throughout all seasons (Table 1). This unique life style has been called ''Quoddy Tradition,'' dating 2200–350 yr BP (Sanger 1986, Spiess et al. 1990, Black 2000). At most sites, 60–90% of bone remains belonged to fish, 10–30% to mammals, and 2–10% to marine birds (Bishop and Black 1988, Black 1988, Spiess et al. 1990). For mammals, 3–17% of bone remains belonged to marine species, mainly gray seals (*Halichoerus grypus*) and harbor seals (*Phoca vitulina*). Overall, vertebrates contributed 2% of all animal remains, 84% were soft-shelled clams (*Mya arenaria*), and 14% other

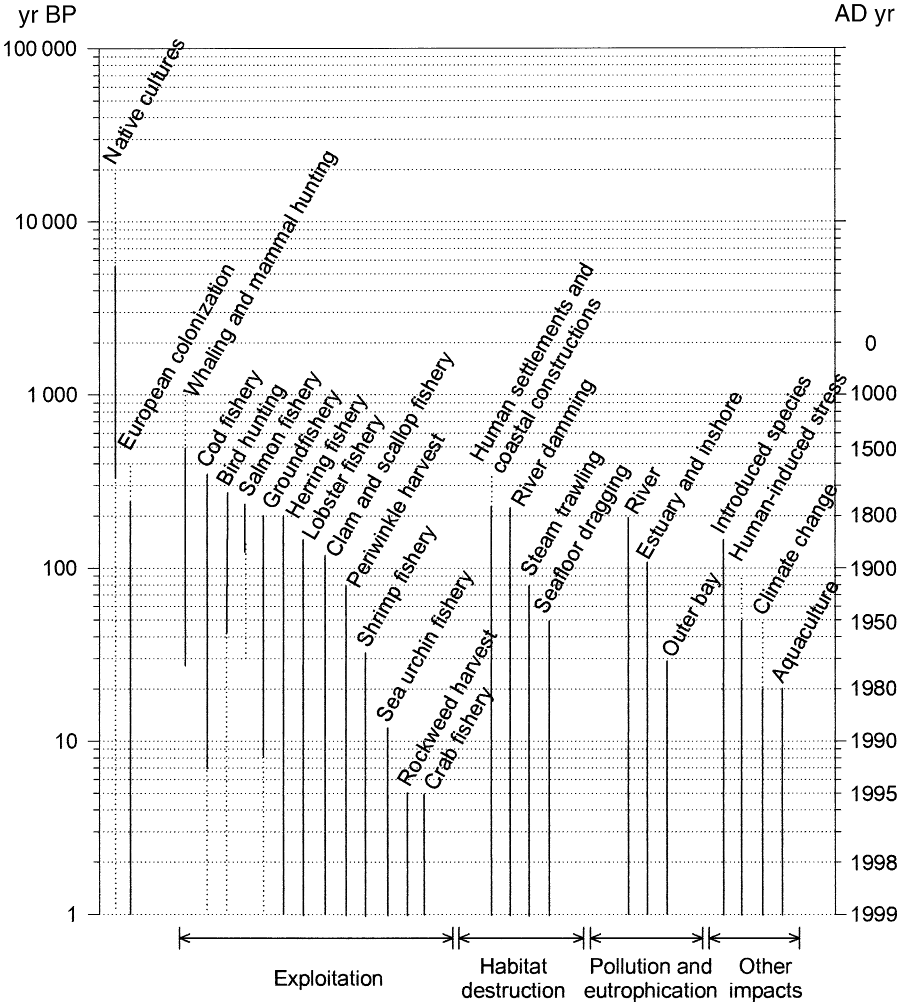

FIG. 2. Timeline of human settlement and impacts in the Quoddy Region on a log scale in years before present (yr BP, left *y*-axis) and Anno Domini (AD, right *y*-axis). For details, refer to *Results: European colonization and impacts over time.*

marine invertebrates (see Table 1; Spiess et al. 1990). Archaeological remains from this and adjacent regions indicated no signs of species extinctions, no dramatic changes in food composition or average size of common food items, and a continuous rich diversity of food items from all trophic levels over the last 2000–3000 years (Bourque 1995, Steneck 1997, Spiess and Lewis 2001). It is unknown how many Passamaquoddy Indians lived in the region, and estimates range from 1000 to 10 000 (SCEP 1997). By the end of the 17th century, however, ~70–90% of native people in Atlantic Canada had died, mainly as a result of introduced diseases (Whitehead 1991).

European colonization and impacts over time

European explorers first visited the Quoddy Region in the early 1600s, established summer settlements for fishing Atlantic cod (*Gadus morhua*) ~1650, and permanently settled in the late 1700s. During the following 100 years, the ''white'' population of Charlotte County increased to 26 000 in 1881, and then stabilized ~24 000 ± 463 (mean ± 1 SE; Statistics Canada 1984).

Since European settlement, human activities affecting the coastal environment multiplied (Fig. 2). Commercial exploitation of marine resources started in the 16th–17th century with whaling operations and a seasonal cod fishery (Fig. 2). Between the late 18th and the early 20th centuries, hunting of birds and harbor porpoise (*Phocoena phocoena*), and fishing for salmon (*Salmo salar*), groundfish, and herring (*Clupea harengus*) became important. The fishery was a cornerstone of the colonial economy, and the Quoddy Region was regarded as one of the prime fishing centers in eastern Canada. With the introduction of the canning industry in the 1860s, a lucrative fishery for American lobster (*Homarus americanus*) was developed. Other invertebrates and seaweeds were harvested at low intensity for food, fertilizer, or other uses. However, over time, commercially valuable fisheries for soft-shelled clams, sea scallops (*Placopecten magellanicus*), and later periwinkles (*Littorina littorea*) were developed. In the 1960s and 1970s, the decline of groundfish resulted in a search for new target species, which led to an experimental fishery for northern shrimp (*Pandalus borealis*), followed by fisheries for sea urchins (*Strongylocentrotus droebachiensis*), rock and Jonah crabs (*Cancer irroratus*, *Cancer borealis*), and rockweeds (*Ascophyllum nodosum*) in the 1980s and 1990s (Fig. 2).

Habitat loss and degradation occurred rapidly after European settlement and impacts started (Fig. 2). All larger islands were settled and coastlines transformed through dykes, causeways, harbors, and other constructions. As a general trend for Atlantic Canada, 60–90% of former wetlands have been lost since European arrival (Environment Canada 1986). Damming of rivers started in the late 18th century, and 30 dams occurred on St. Croix River in the 1980s (Marshall 1976, Anonymous 1988). Seafloor dredging and trawling started in the late 1900s in estuaries and inshore areas with light gear towed by sailboats over soft bottoms. Over time, development of heavier gear towed by high-powered vessels allowed fishing on all types of bottoms, and the fishery moved offshore, a trend quantitatively documented in the Gulf of Maine (Steneck 1997).

Water pollution started in rivers with run-off from land clearings for settlements and lumber harvest in the late 1700s. Numerous sawmills and pulp mills were built along St. Croix River in the 1800s, which dumped organic and chemical wastes directly into the river (Lotze and Milewski 2002). Municipal sewage and effluents from various industrial activities entered the rivers mostly untreated. Fish processing plants, industries, and more recently, aquaculture operations contributed to organic, nutrient, and chemical pollution of estuaries, inshore, and recently also offshore areas (Lotze and Milewski 2002). Although river pollution was reduced since the 1960s due to implementation of waste-water treatments, the St. Croix Estuary belongs to the 44 most eutrophied estuaries in North America (Bricker et al. 1999).

Other human impacts with environmental consequences were the introduction of mainland predators such as red foxes (*Vulpes vulpes rubricosa*) and raccoons (*Procyon lotor lotor*) to islands in the 19th century, which eliminated many bird colonies (Pettingill 1939, Ingersoll and Gorham 1978). Several nonindigenous marine species were introduced from Europe and became abundant along the coast such as periwinkle and green crab (*Carcinus maenas*) (Steneck and Carlton 2000). Increasing human activities near or on the water enhanced boat traffic, noise, light, smell, and other stresses (Lotze and Milewski 2002). Climate change resulted in an overall rise in sea surface temperature of 1°C over the last 100 years (DFO, St. Andrews, New Brunswick, Canada), and enhanced sea level rise (Forbes et al. 1997). Aquaculture operations introduced cultured and genetically modified fish, some of which escape, interbreed, and compete with wild fish, and transmit diseases and parasites to dwindling wild populations (Whoriskey et al. 1998, Anderson et al. 2000).

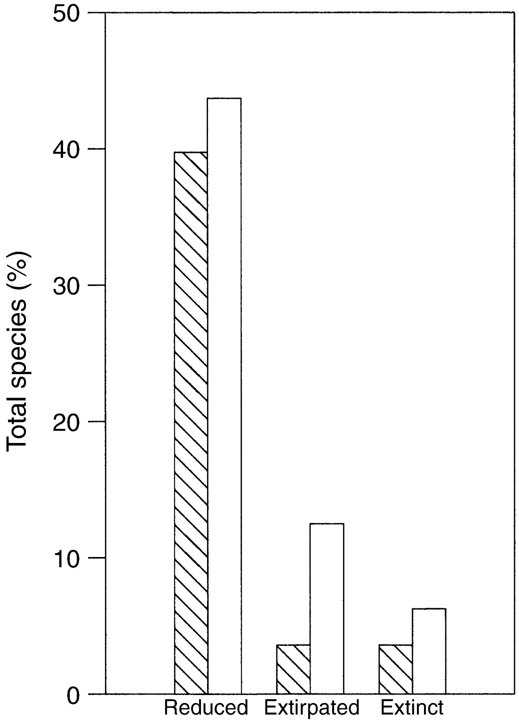

FIG. 3. Percentage of marine mammal (open bars) and bird (hatched bars) species that became severely reduced, locally extirpated, or globally extinct in the Quoddy Region in the past through human impacts. Numbers are minimum estimates of species clearly named in the literature (summarized in Lotze and Milewski [2002], and the Appendix).

Changes in marine mammals and birds

Most marine mammals and birds had been hunted to very low levels by 1900. Of the 16 marine mammal species recorded in the region (Ingersoll and Gorham 1978, Gaskin 1983, Lotze and Milewski 2002), three were hunted to extinction before 1900 (COSEWIC 2002), seven were severely reduced in the 19th and early 20th century (Fig. 3), and another four were targeted in the 20th century. The three extinct species include the globally extinct sea mink (*Mustela macrodon*; Table 1), the extirpated Atlantic walrus (*Odobenus rosmarus rosmarus*; Ingersoll and Gorham 1978), and possibly the Atlantic gray whale (*Eschrichtius robustus*), a coastal species that occurred in the northwest Atlantic (Mead and Mitchell 1984). Whaling in the northwest Atlantic started in the 1500s first targeting northern right whales (*Eubalaena glacialis*). After their depletion, humpback whales (*Megaptera novaeangliae*) became the most important targets in the 18th and 19th century. Whaling was extended to fin (*Balaenoptera physalus*) and blue (*Balaenoptera muscu-*

lus) whales in the late 19th century and shifted to sei (*Balaenoptera borealis*), minke (*Balaenoptera acutorostrata*), pilot (*Globicephala melas*), and killer (*Orcinus orca*) whales in the 20th century. Harbor porpoises were extensively hunted in the 1800s by indigenous people to trade oil with Europeans. Gray and harbor seals were hunted throughout the region's history, but hunting intensified after introduction of a bounty in the 20th century. The first protection laws were established in 1935 for the right whale, and in 1972–1986 for all mammal species (U.S. Marine Mammals Protection Act, ban on commercial whaling by IWC). Some species, especially seals, have recovered, while most whales remain at low population levels throughout their distribution range (e.g., right whale at 2–3%, Table 2; NEFSC 1999). Today, six species are listed in the endangered species list in Canada (COSEWIC 2002).

About 83 marine and coastal birds were recorded in the study area, of which at least 39 species were severely affected by human impacts (Fig. 3; Pettingill 1939, Christie 1979, Lotze and Milewski 2002). Of these 39 species, three were hunted to global extinction by the early 1900s: the Passenger Pigeon (*Ectopistes migratorius*), Great Auk (*Pinguinus impennis*), and Labrador Duck (*Camptorhynchus labradorius*). Another three species were hunted to local extirpation: the Peregrine Falcon (*Falco peregrinus anatum*), Eskimo Curlew (*Numenius borealis*), and native breeding populations of the Canada Goose (*Branta canadensis*). Ten named and many unnamed waterfowl species (ducks, geese, eiders, mergansers) were severely reduced by hunting, and egg and down collection. At least six shorebird species (sandpipers, plovers) were hunted to extremely low levels and suffered from habitat destruction, and three temporarily abandoned the region. At least 15 seabird species (gulls, terns, cormorants, alcids, and others) were severely reduced by hunting, egg and down collection, and destruction of breeding colonies by humans and introduced predators to islands. As a consequence, eight seabird species temporarily abandoned the region. Finally, two marine-oriented raptors, the Bald Eagle (*Haliaeetus leucocephalus*) and Osprey (*Pandion haliaetus*), suffered from hunting, pesticides, and habitat destruction (Pettingill 1939, Christie 1979, Lotze and Milewski 2002). The first protection laws were established in 1928 (Migratory Birds Convention Act), and the first Migratory Bird Sanctuary was designated in 1944 (Machias Seal Island). Several species recovered from dramatic declines (Lotze and Milewski 2002). However, in the seven documented cases, re-colonization of abandoned breeding colonies occurred only after a long time lag of 70 ± 12 years, e.g., 45 years for the Common Murre (*Uria aalge*) and 133 years for the Northern Gannet (*Morus bassanus*). Other species remained at low population levels, such as the Harlequin Duck (*Histrionicus histrionicus*; Table 2). Today, six species are listed under the Canadian endangered species act (COSEWIC 2002).

Changes in marine fish

Europeans have fished Atlantic cod in Atlantic Canada since the early 1600s, and a commercial fishery started in the Bay of Fundy in the 1700s (Clark and Paul 1999). After permanent settlement, the groundfishery expanded to pollock (*Pollachius virens*) and haddock (*Melanogrammus aeglefinus*), and a fishery for herring was developed. In 1826–1850, the first signs of declines in stocks were reported with decreases in average size of pollock and herring, and severe declines in cod and haddock catches (Perley 1852). From the late 18th to mid-20th century, the total catch of cod, pollock, and haddock gradually declined in the primarily inshore hook and line fishery (Fig. 4A). During the same time, fishing effort measured as the number of fishing boats and number of handlines increased 3-fold to 4.5-fold, while catch per boat and catch per handline dropped 6.6- to 8-fold, respectively (Fig. 4B, C). After World War II, a major gear change occurred and the traditional inshore hook and line fishery was replaced by modern otter trawls fishing in- and offshore. Groundfish landings strongly increased in the 1950s and 1960s (Fig. 4A), mainly because of high offshore otter trawl landings (Clark and Paul 1999). After its peak in 1965, the fishery collapsed to historically low levels in the 1970s (Fig. 4A). The declaration of the 200-mile exclusive economic zone in 1977 banned foreign fleets and led to a short period of recovery in the early 1980s (Fig. 4A). Domestic fishing pressure increased, however, and reduced stocks to very low levels in the 1990s (Fig. 4A). Today's catches are on average 3–37% of catches 100 years ago (Table 2). Similar patterns of decline in landings and stocks occurred throughout the larger NAFO 4X management unit for cod (Clark and Paul 1999), haddock (Hurley et al. 1999), and pollock (Neilson et al. 1999): landings, total allowable catches, spawning stock biomass, and recruitment declined or were low during the 1980s and 1990s, and exploitation rate was at most times well above the target level. Only for haddock do assessments indicate that the stock got stronger during the late 1990s as a result of some strong year classes and low exploitation rate (Hurley et al. 1999).

A scientific monitoring program for groundfish was implemented in 1970 (Simon and Comeau 1994). The data from stratified random surveys indicate that relative abundance of traditional groundfish (cod, pollock, and haddock) remained low throughout the last 30 years (Fig. 4A). In contrast, several noncommercial species increased in abundance per tow (spiny dogfish *Squalus acanthias*, longhorn sculpin *Myoxocephalus octodecemspinosus*; Fig. 4A) or weight per tow (spiny dogfish, thorny skate *Amblyraja radiate*; data not shown). Thus, dominance in the groundfish community shifted from gadoids to noncommercial species. In ad-

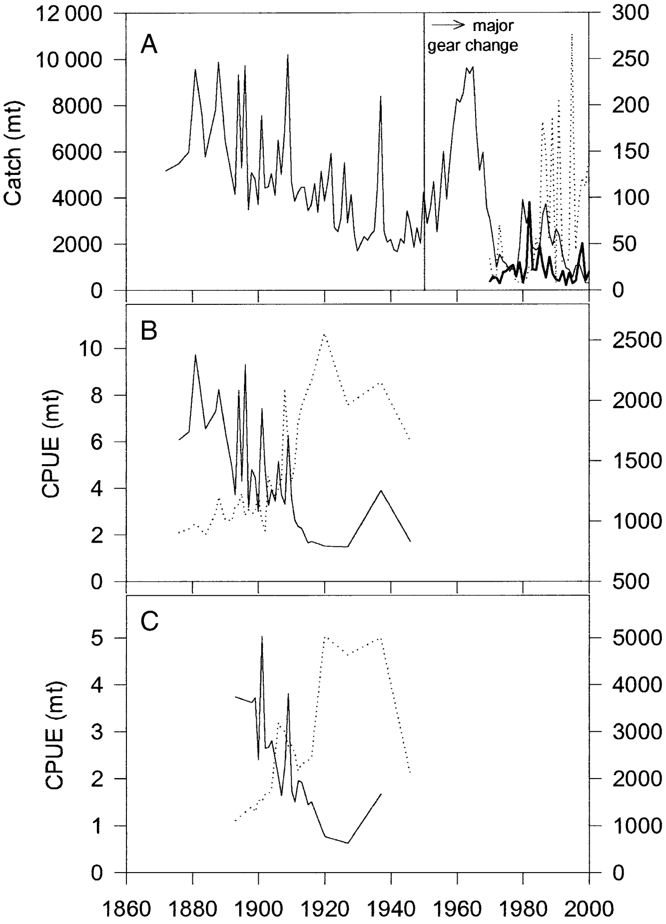

FIG. 4. (A) Total catch (mt; 1 metric ton = 1000 kg) of the traditional groundfish (cod, pollock, haddock) in Charlotte County, 1870–2000 (solid line), and relative abundance of traditional groundfish (bold solid line) and noncommercial groundfish (dogfish and sculpins; dotted line) from stratified random sampling surveys. Data on effort (dotted lines) and catch per unit effort (CPUE; solid lines) with (B) fishing boats (<10 mt) and (C) handlines (traditional gear to catch groundfish in the region) in the traditional groundfishery in Charlotte County (data from Annual Fisheries Statistics [Fisheries Branch 1869–1916, Dominion Bureau of Statistics 1917–1968; DFO 1968–2000] and DFO trawl surveys [Simon and Comeau 1994; P. Fanning and J. Simon, *personal communication*]). A major gear change took place in the 1950–1960s when the traditional inshore hook and line fishery was replaced by modern otter trawls for fishing in- and offshore.

dition to dwindling abundance, groundfish spawning areas have declined sharply over the last 30 years (Fig. 5). Data from the Gulf of Maine further indicate that the average historical size of cod of 100 cm (500–4000 years ago) declined to 80 cm in 1950, and to 20–30 cm in 1980 (Steneck 1997). In 1998, Bay of Fundy cod had an average length of 49–76 cm in 4Xrs, and 43–61 cm in 4Xq (Clark and Paul 1999).

The herring fishery first targeted large individuals (>3 years old) caught by gill nets on spawning grounds (Perley 1852, Huntsman 1953*b*). This fishery peaked in 1880, but declined to almost zero in 1920 (Fig. 6A). There was a short-term increase in catches of medium-sized herring (2–3 years old) peaking in the 1890s (Fig. 6A). In the same time, an intense fishery for small herring (1–2 years old, marketed as sardines) developed after the introduction of the canning industry (Fig. 6A). Fishing effort measured as number of active herring weirs increased from 78 in 1876 to 519 in 1927, but catch per weir showed no trend. Huntsman's (1953*b*) investigations showed that the collapse of the large-herring fishery was likely caused by overfishing of the local spawning stock, which went extinct after World War II (Coon 1999). The continued fishery for small herring was maintained by spawning stocks outside the region (Huntsman 1953*b*). Total herring catches were stable in the first half of the 20th century. With introduction and expansion of purse seine fishing in the 1950–1960s, herring catches dramatically increased to a peak of 142 000 mt (1 metric ton = 1000 kg), followed by a steady decline over the last three decades (Fig. 6B).

Changes in diadromous fish

The St. Croix River once provided habitat for several anadromous and catadromous fish, most importantly, Atlantic salmon and gaspereau (alewife, *Alosa pseudoharengus*, and blueback herring, *A. aestivalis*) (Lotze and Milewski 2002). Perley (1852) estimated that before 1825, 200 salmon were caught daily for a three-month period in summer. This would add up to 18 000 salmon caught per summer as a conservative estimate of adult abundance. Newer estimates of potential salmon production based on available spawning and nursery habitat range from 7 000 to 18 000 (Wilson 1956, Kerswill 1960, Fletcher and Meister 1982, Anonymous 1988). Potential production of gaspereau was estimated at 31.7 million fish (Anonymous 1993). Today, <1% of these return to St. Croix River annually (Fig. 7A, B, and Table 2).

TABLE 2. Comparison of today's abundance with historical abundance or catch estimates for high trophic level species in the Quoddy Region.

Species and location	Historical	Today	Percentage left
Whale abundance†			
Northern right whale, NW Atlantic	~10 000–15 000	~300	2.0–3.0
Bird abundance‡			
Harlequin duck, NE America	~5000–10 000	~1000	10.0–20.0
Diadromous fish abundance§			
Atlantic salmon, St. Croix River	~7000–18 000	33 ± 10	0.2–0.5
Gaspereau, St. Croix River	$\sim 31.7 \times 10^6$	$0.28 \pm 0.06 \times 10^6$	0.9
Groundfish catch‖			
Cod, Charlotte County	1508 ± 336	555 ± 141	36.8
Pollock, Charlotte County	2745 ± 372	515 ± 111	18.8
Haddock, Charlotte County	1654 ± 187	44 ± 15	2.7

Notes: Historical abundance refers to the period before large-scale human interference (before AD 1500 for whales; before AD 1700 for birds and fish), historical catch refers to the last decade in the 19th century (1890–1900), and today's abundance and catch refer to the last decade in the 20th century (1990–2000). For birds and whales, estimates of entire populations range over larger areas. Where possible, we present means ± 1 SE for a 10-year period.

† *Source:* Reeves (2001), and references cited therein.

‡ *Source:* Goudie (1989).

§ *Sources:* Perley (1852), Anonymous (1971, 1988, 1993), Chaput and Prevost (1998), Marshall et al. (1999).

‖ *Sources:* Annual Fisheries Statistics (Fisheries Branch 1869–1916, DFO 1968–2000).

Damming of the river led to strong declines of returning fish (Fig. 7). Over time, 30 dams were built on St. Croix River. Moreover, the river bed was polluted with sawdust and wood wastes causing oxygen depletion. Effluents from tanneries, pulp and textile mills, and other industrial activities added multiple contaminants, and domestic sewage contributed to bacterial and nutrient pollution (Lotze and Milewski 2002). By 1909, the cumulative effects of degraded water quality, deteriorated river habitat, and increased blocking of fish passage resulted in the near-extirpation of salmon in the watershed (Marshall 1976). Pollution surveys in the 1960s indicated lethal water conditions for salmon due to low dissolved oxygen levels and acid conditions.

Reduction of municipal and industrial water pollution and construction of effective fishways enabled both salmon and gaspereau to return in the 1980s (Fig. 7A, B). New stocking efforts increased the number of hatched salmons in the river (Fig. 7A). However, new threats halted this promising recovery. The successful return of gaspereau raised concerns in the sports fishing industry assuming negative effects of gaspereau on commercially valued smallmouth bass (*Micropterus dolomieui*), a species that was introduced to the system in the 1870s. Although unproven and doubted by many fishermen, two major dams on the lower river were blocked in 1991 and 1995, respectively. Subsequently, numbers of all diadromous fish greatly declined (Fig. 7). In the case of salmon, returns to rivers throughout the Northwest Atlantic underwent steep declines in the last three decades, possibly caused by high mortality at sea (Anderson et al. 2000). While wild populations dwindled, aquaculture of Atlantic salmon increased exponentially: from 1979 to 2001, number of fish farms increased to 94, and salmon production increased from 6 mt to 40 000 mt (DFO 1999*a*, Lotze and Milewski 2002).

Changes in benthic invertebrates and seaweeds

The decline of traditional fisheries induced a shift to low trophic level harvesting over the past two decades. The cumulative catch of all marine invertebrates and plants exceeded 10 000 mt in 1998, almost twice its historical maximum in 1950 (Fig. 8A). Some traditional invertebrate fisheries have enormously increased in the last 20 years, e.g., for lobster (see next paragraph), sea scallop (Fig. 8A), and periwinkle (catch increased from 50 mt in 1970s to >200 mt in 1990s; data not shown). Other traditional fisheries continued at high (soft-shelled clam; Fig. 8A) or moderate exploitation levels (e.g., dulse, *Palmaria palmata*; data not shown). New invertebrate fisheries were rapidly developed for northern shrimp in the 1960s, rock and Jonah crab in the 1970s, sea urchin in 1980s, and rockweed in the 1990s. In the last 5–10 years, landings of scallops and sea urchins dropped (Fig. 8A), as did average size of sea urchins, and concerns are raised about overexploitation and the effects of destructive fishing practices on the seafloor (DFO 2000).

The lobster fishery became important after introduction of the canning industry in the 1860s, and catches exponentially increased to a peak of 1202 mt in 1894 (Fig. 8B). In 1873, decreasing average size of lobster was already interpreted as the first sign of overexploitation, which led to first regulations in this fishery (Found 1912). Peak catches were followed by a long-term decline in lobster landings and CPUE until the mid-20th century (Fig. 8B). Increasing lobster abundance in recent decades in combination with increasing fishing effort led to increasing landings, which peaked

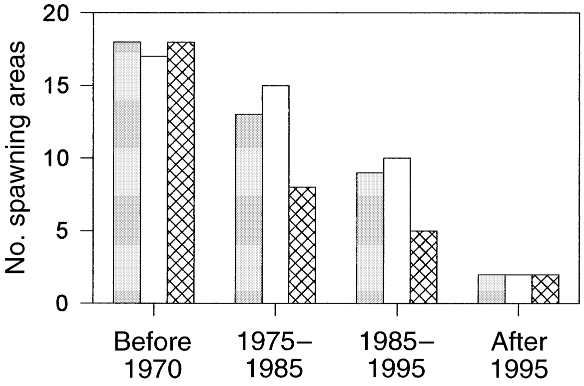

FIG. 5. Loss of spawning grounds in the study region for cod (gray bars), pollock (open bars), and haddock (cross-hatched bars) since the 1950s (data from Graham et al. [2002]).

at 1166 mt in 1999, close to the historic maximum (Fig. 8B). However, while average size of lobster caught 100 years ago was >1.81 kg (4 pounds), average size today is 0.45 kg (1 pound), which is below size at first reproduction (Rees 1995; P. Lawton, *personal communication*). Despite high catches, concern was raised about recent high exploitation levels, harvest of primarily immature lobster, and risk of recruitment failure (Lawton et al. 2001).

No long-term data were available on distribution or abundance of benthic macrophytes. However, a recent field survey indicated that species composition changed at sites subject to eutrophication (Worm 2000). Compared to un-impacted sites, high nutrient loads from municipal sewage and aquaculture operations induce eutrophication problems at point sources in the region (Bricker et al. 1999, Worm 2000). At eutrophied sites, percent cover of perennial rockweeds (*Ascophyllum nodosum*, *Fucus vesiculosus*) was, on average, reduced by 40% and replaced by annual algae (5% increase) or filter feeder (*Mytilus edulis*, *Balanus* spp., 10% increase; Fig. 9A). Annual green algae (mainly *Enteromorpha intestinalis*, *Ulva lactuca*) dominated eutrophied sites that had reduced herbivore densities, mainly periwinkles, which are harvested commercially (Fig. 9B). Filter feeders likely profited from high food concentrations at eutrophied sites (Worm 2000). Although a spatial comparison, these survey results indicate temporal shifts in species composition at eutrophied sites over the past years to decades.

Changes in the plankton

In the zooplankton community, there was no clear change in the composition of major species groups over time (Fig. 10). Although only data from 1917 and 1932 are truly comparable (see *Methods: Data collection and analysis*), all studies show the same pattern of strong predominance of calanoid copepods (mainly *Calanus finmarchicus*, *Pseudocalanus minutus*, *Centropages typicus*, *Acartia clausi*, *Tortanus discaudatus*, *Eurytemora herdmani*) in inshore Passamaquoddy Bay (Fig. 10). Other zooplankton such as barnacle and crab larvae, cladocerans, and euphausiid krill were seasonally abundant (Fig. 10), and high abundance of barnacle larvae in 1917 was interpreted as a strong recruitment pulse (Fish and Johnson 1937). Outside Passamaquoddy Bay, euphausiid krill (*Meganyctiphanus norvegica*, *Thysanoessa inermis*) are important components of the zooplankton forming concentrated surface swarms in upwelling areas and high-current passages (Smith et al. 1984). Euphausiid eggs can make up 40–60% of the zooplankton in spring and summer (Legare and Maclellan 1960).

A comparison of phytoplankton studies from the 1930s and 1990s indicated strong shifts in species composition and seasonal extent of blooms (Fig. 11). In 1931–1932, strong spring blooms occurred inside and outside Passamaquoddy Bay, while summer and fall blooms were lower (Fig. 11A, B). In 1993–1996, the opposite was observed. This probably was the consequence of high dinoflagellate abundance during summer and fall in recent years (Fig. 11C, D). Several early studies reported a strong predominance of large diatoms (Fig. 11C, D) such as *Thalassiosira nordenskioeldii* and *Biddulphia aurita* in spring, and *Chaetoceros debile* in summer and fall (Fritz 1921, Davidson 1934, Gran and Braarud 1935), while dinoflagellates

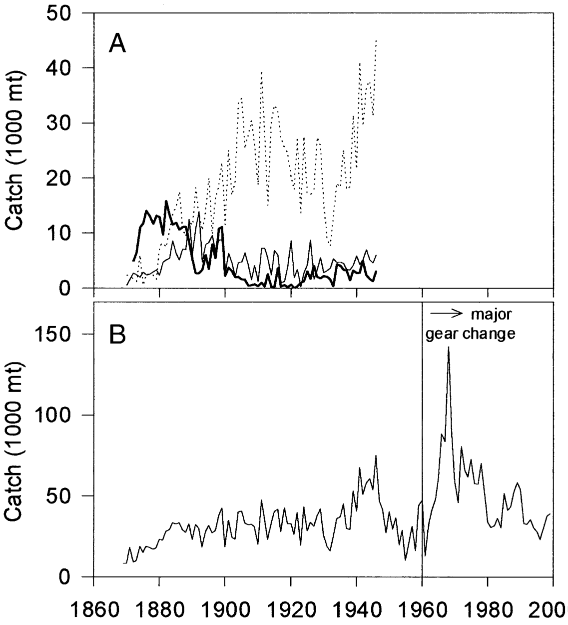

FIG. 6. (A) Shift in the herring fishery from large (bold solid line), to medium (thin solid line), to small herring (dotted line) from 1870 to 1946 in Charlotte County (data from Huntsman 1953*b*); (B) total herring catches from 1870 to 2000 (data from Annual Fisheries Statistics [Fisheries Branch 1869–1916, Dominion Bureau of Statistics 1917–1968, DFO 1968–2000]) (1 mt [metric ton] = 1000 kg). A major gear change took place in the 1950–1960s with the introduction and expansion of purse seine fishing.

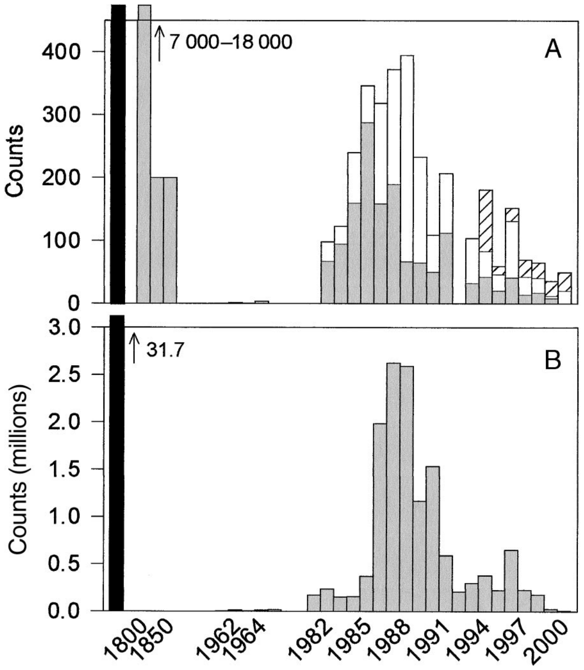

FIG. 7. Abundance of (A) Atlantic salmon and (B) gaspereau in the St. Croix River: Potential abundance estimates are based on habitat availability (black bars), wild fish (gray bars), hatched fish (open bars), and cultured fish escaped from aquaculture operations (hatched bars). Data are from Perley (1852), Anonymous (1971), Chaput and Prevost (1998), Marshall et al. (1999). Arrows and numbers in the top left corners indicate population estimates for 1800–1850.

and other phytoplankton were not abundant (Davidson 1934). Only Gran and Braarud (1935) mentioned two dinoflagellates and one silicoflagellate as being sometimes abundant in the Bay of Fundy in fall. In the 1990s, diatoms were still dominant in the phytoplankton, especially in spring (Fig. 11C, D). However, species composition had changed, as potentially harmful diatoms from the *Pseudo-nitzschia delicatissima* group have become abundant, *P. delicatissima* in late spring and early summer and *P. pseudodelicatissima* in late summer and fall (Fig. 11C, D; Martin et al. 1999). *P. pseudodelicatissima* produces domoic acid, a potent toxin causing amnesic shellfish poisoning (ASP) when blooms of >1 million cells/L develop. Toxic concentrations were reached in 1988 and 1995 outside Passamaquoddy Bay (Martin et al. 1999). In addition to this increase in harmful diatom species, dinoflagellates increased in abundance, especially in summer and fall (Fig. 11C, D), a common sign of eutrophication. Although methodology and knowledge have changed over time, it seems unlikely that the earlier studies entirely missed a dominant phytoplankton group. The dinoflagellates *Heterocapsa triquetra*, *Scrippsiella trochoidea*, and *Alexandrium fundyense* occurred in large quantities in recent years. Of these, *A. fundyense* produces saxitoxin, which causes paralytic shellfish poisoning (PSP) at concentrations of only 20 cells/L (Martin et al. 1999). Because abundance of *A. fundyense* exceeded 10 000 cells/L in recent years, shellfish closures now occur on a regular basis along the coast (Martin et al. 1999). A toxicity monitoring survey from 1944–1983 further showed increasing intensity of blooms of the toxic dinoflagellate *Alexandrium tamarensis* (formerly *Gonyaulax excavata*) in the 1970s (White 1982). PSP was linked to herring kills in 1976 and 1979, and was detected in mackerel in 1988 (White 1981, Martin et al. 1999). Other potentially toxic dinoflagellates are present, but have not caused extensive problems so far (Bates 1997, Martin et al. 1999).

DISCUSSION

The ecological history of the Quoddy Region illustrates a complex pattern of human-induced changes in a coastal food web over the last two centuries. Exploitation by European colonizers rapidly reduced abundance of many consumers, especially large predators, and caused several extinctions. Consequently, marked shifts in species abundance and composition on various trophic levels occurred (see *Discussion: Top-down impacts: hunting and fishing*) altering food web structure. Protection of marine mammals and birds led to partial recovery, whereas other predators such as cod remained depleted. The decline and collapse of traditional fishery for groundfish induced a shift towards harvesting lower trophic level species such as sea urchins and rockweeds, as well as a shift toward aquaculture. These changes are largely in accord with a top-down view of coastal ecosystems with humans as top predators. From a bottom-up perspective, eutrophication changed species composition of benthic and pelagic primary producers and induced harmful blooms of micro- and macroalgae. Habitat destruction and pollution affected several species, resulting in poor survival and abandonment of traditional habitat. Through these multiple, interacting impacts humans increasingly dominated the coastal ecosystem inducing shifts in food web composition and species interactions on every trophic level.

With regards to the history of European settlement, human impacts and their consequences on the marine environment the Quoddy Region is comparable to adjacent inshore regions along the coasts of Atlantic Canada and the northeastern U.S. The Quoddy Region, however, was and still is particularly rich in marine diversity and productivity (see *Methods: Study region*, Lotze and Milewski 2002). Compared to other regions, consequences of human actions on this marine oasis may be more severe because more species and habitats that are rare elsewhere are affected. On the other hand, conservation opportunities may be enhanced in high-diversity areas as shown recently for the open ocean (Worm et al. 2003).

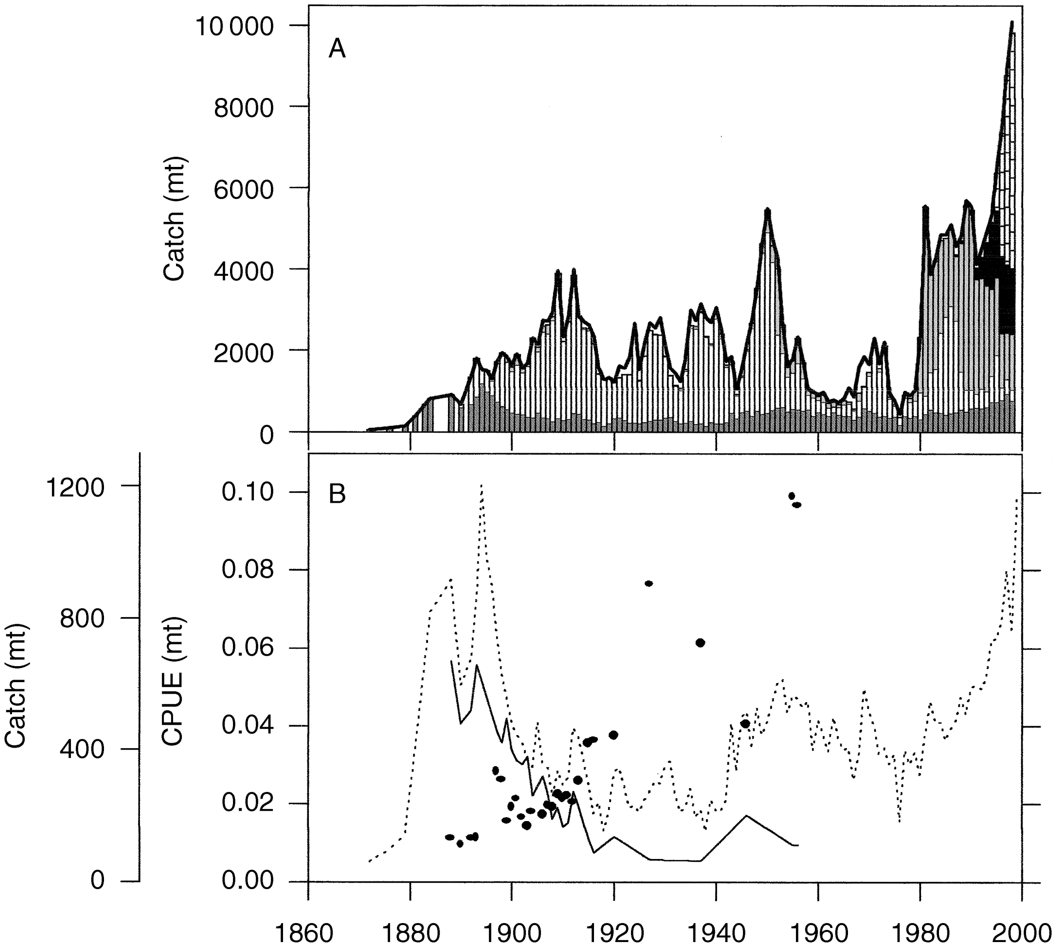

FIG. 8. (A) Total landings of low trophic level species (thick solid line), and landings of lobsters (dark gray bars), soft-shelled clams (open bars), scallops (light gray bars), sea urchins (black bars), and rockweeds (horizontal hatched bars). (B) Catch (dotted line), number of traps (solid dots), and catch per trap (CPUE; solid line) for the lobster fishery (data from Annual Fisheries Statistics). Catch data are reported in units of metric tons (mt; 1 mt = 1000 kg).

Top-down impacts: hunting and fishing

Severe food web changes occurred after European settlement. In contrast, indigenous hunters and gatherers in prehistoric times did likely not alter coastal food web structure, and may be regarded as ''low-impact omnivores'' (Fig. 12A). With European settlement, large predators such as whales, birds, and large fish became prime targets of exploitation, and birds and diadromous fish further suffered from habitat destruction and degradation. By the end of the 19th century, >40% of marine bird and mammal species were reduced to low levels, and nine species were hunted to extinction (Fig. 3). In the 18th and 19th century, European settlers mostly acted as ''top predators'' in the food web (Fig. 12B).

Throughout its history, the marine fishery underwent continuous increases in effort, efficiency, and spatial extent (Steneck 1997). In the fishery for groundfish, decrease in average size, sharply decreasing CPUE, and declining total catches suggest that groundfish stocks were already declining 100–150 years ago, similar to the groundfishery in Newfoundland and the North Sea (Hutchings and Myers 1995). Only introduction of new gear with strongly enhanced efficiency as well as extension from inshore to offshore fishing areas may have enabled the fishery to increase catches in the 1960–1970s shortly before stocks collapsed. Since then, stocks and catches have remained at low levels. The herring fishery underwent similar, although less dramatic, shifts. In both cases, high exploitation pressure and destruction of seafloor habitat and spawning grounds likely contributed to the collapse or decline of the fishery (Huntsman 1953*b*, Graham et al. 2002). The lobster fishery was also affected by strong declines in landings, CPUE, and size in the early 1900s (Found 1912). Thus, in the 20th century until the 1970s, humans acted as ''highly efficient top predators'' in the food web (Fig. 12C). Moreover, habitat destruction, pollution, and eutrophication compounded the changes due to fishing (see *Discussion: Cumulative impacts*).

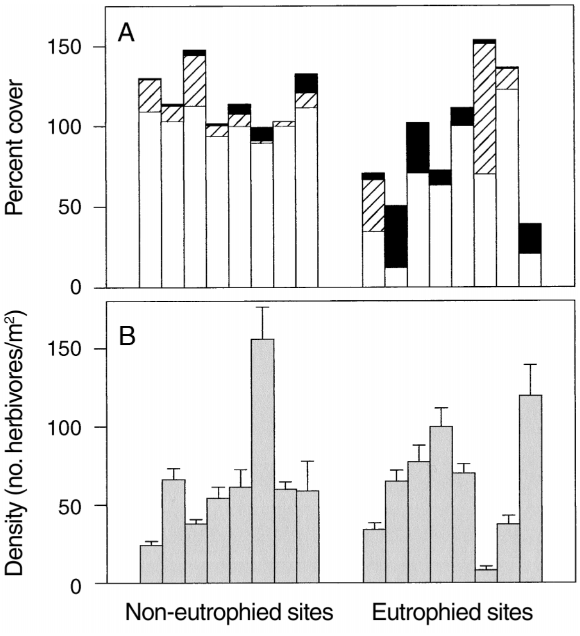

FIG. 9. (A) Relative abundance (mean percent cover, n = 10) of benthic species on intertidal rocky shores at eutrophied and non-eutrophied sites in spring 1999: perennial rockweeds (open bars), annual algae (hatched bars), and filter feeders (black bars). Cumulative estimates of canopy, understory, and epiphytic species led to estimates >100%. (B) Density of herbivores (mean + 1 SE, n = 10) at the same sites (data from Worm [2000]).

The reduction and loss of large and top predators induced shifts in food web structure. After the collapse of groundfish stocks, former prey species such as shrimp, crabs, lobster, and sea urchins increased in abundance (Steneck 1997, Worm and Myers 2003). In some cases, several lower levels of the food web may have been affected by cascading effects, as reported for marine mammals (Estes and Duggins 1995, Estes et al. 1998), birds (Wootton 1995), and large fish (Steneck 1997, Pace et al. 1999, Friedlander and DeMartini 2002). But not only lower trophic level species composition changed. After groundfish stocks collapsed, commercially less valuable species increased in abundance. Similar shifts in dominance patterns occurred in the Gulf of Maine, where skates and dogfish became the dominant groundfish on Georges Bank (Fogarty and Murawski 1998), and small sculpins, rock gunnel, shanny, and cunner became dominant on inshore grounds (Steneck 1997). This new dominance of possible competitors and larval predators could potentially inhibit recovery of previously dominant groundfish (Walters and Kitchell 2001).

With the decline and collapse of large predatory fish stocks, commercial fisheries shifted to lower trophic levels of the food web such as herbivores and plants, a worldwide phenomenon called ''fishing down the food web'' (Pauly et al. 1998). The number of commercial target species increased six-fold from 1869 to 1997, and total invertebrate and plant catch increased two-fold beyond its historical maximum. As mentioned in the previous paragraph, release from predation may explain increased low trophic level abundance and thriving invertebrate fisheries (Steneck 1997, Worm and Myers 2003). However, many species that are now subject to intense exploitation have never been targeted in the past, and often little is known about their vulnerability to overfishing, or effects of the fishery on the ecosystem (DFO 1999*b*, 2000, Robichaud et al. 2000). In some cases, first signs of overexploitation are observed and concern is raised about destructive harvesting practices (DFO 2000). In contrast to the exploitation of top predators, which may benefit prey species, exploitation of low trophic level species will negatively affect all species that depend upon them for food and habitat (Rangeley 1994, 2000). In addition to intensified low trophic level harvesting, large predatory fish such as sharks, tuna, and swordfish have received renewed interest in the region since the 1970s (Lotze and Milewski 2002). Thus, by the end of the 20th century, humans have targeted every trophic level of the food web with high intensity and can be regarded as ''top omnivores'' (Fig. 12D).

Bottom-up impacts: nutrient enrichment

Nutrient loading began to increase early in the 19th century with land clearing in the drainage basin and wood waste dumping into rivers and estuaries. Although no quantitative data are available for the Bay of Fundy, sediment cores from estuaries with a similar history such as Chesapeake Bay indicate that sedimentation rates, nutrient loads, and eutrophication symptoms increased after European settlement, accelerated in the late 19th and early 20th century, and ac-

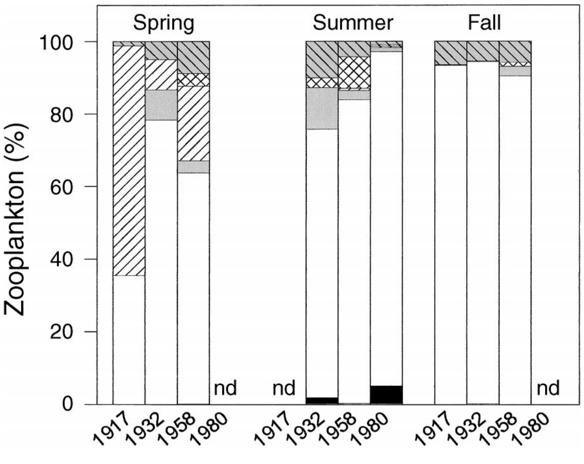

FIG. 10. Zooplankton composition in Passamaquoddy Bay, by year, season, and species group: cladocerans (black bars), copepods (open bars), euphausiids (gray bars), barnacle larvae (hatched bars), crab larvae (cross-hatched bars), and others (gray hatched bars); nd, no data. Data are from Fish and Johnson (1937), Legare and Maclellan (1960), and Smith et al. (1984).

celerated again after World War II (Cooper and Brush 1993). Increasing human population, fish processing plants, aquaculture operations, as well as loss of wetlands, introduction of artificial fertilizers, and atmospheric deposition all contributed to high amounts of nutrient loading to the marine environment (Fig. 12B–D). Although sewage treatments were implemented at some point sources over the past decades, the St. Croix Estuary still belongs to the 44 most eutrophied estuaries in North America (Bricker et al. 1999). Many inshore areas in the Quoddy Region show eutrophication symptoms, especially in the vicinity of point sources such as aquaculture operations that are not subject to regulations (Lotze and Milewski 2002). As a consequence, a decline in long-lived rockweeds was observed at eutrophied sites, where rockweeds were partly replaced by annual algae and filter feeders, resulting in the loss of three-dimensional habitat for a variety of closely associated invertebrates, fish, and birds. In the phytoplankton, increasing abundance of toxic species resulted in fish kills and shellfish closures. These changes in primary producers are commonly observed in eutrophied coastal seas around the world (Bricker et al. 1999, Paerl and Whitall 1999, Worm et al. 1999, 2002, Cloern 2001).

Side-in impacts: habitat destruction and pollution

Beginning in the rivers in the early 1800s, but extending to estuarine, inshore, and later offshore areas in the 20th century, habitat destruction, pollution, and disturbance reduced the abundance and quality of spawning, breeding, nursing, staging, foraging, and other essential habitats (Lotze and Milewski 2002). Habitat destruction may have contributed to the loss of spawning grounds (Fig. 5), the extinction of local bird, herring, and salmon populations, and the failure of groundfish to recover. Furthermore, pollution affected health and survival, increased levels of physiological stress, and reduced the amount of undisturbed time and space for many species (Lotze and Milewski 2002). Today, these side-in impacts affect most trophic levels (Fig. 12C, D).

Cumulative impacts

Throughout history, most species were affected by multiple top-down, bottom-up, and side-in impacts that may not act independently of one another. Cumulative human impacts may cause indirect effects, feedback mechanisms, and surprises, which impair our ability to predict and manage coastal ecosystems (Breitburg et al. 1999, Cloern 2001, Lotze and Worm 2002). For example, recovery of traditional groundfish species may be prevented by changes in food web structure and human impacts (Fig. 13A). Released from competition and predation, increasing dogfish may now outcompete the formerly dominant cod, pollock, and haddock or reduce survival of their juveniles (Fogarty and Murawski 1998, Walters and Kitchell 2001). Increased low trophic level harvesting now targets essential prey species, and directly (e.g., rockweed harvesting) or indirectly (e.g., seafloor dragging) destroys essential habitat for both, prey and predators (Rangeley 1994, 2000, Collie et al. 2000). The assumption that reduced fishing pressure will automatically lead to recovery of groundfish stocks may be too simplistic (Hutchings 2000). Protection of habitat and prey species would provide a valuable additional management tool (Dayton et al. 1995, Fogarty 1999, Palumbi 2001).

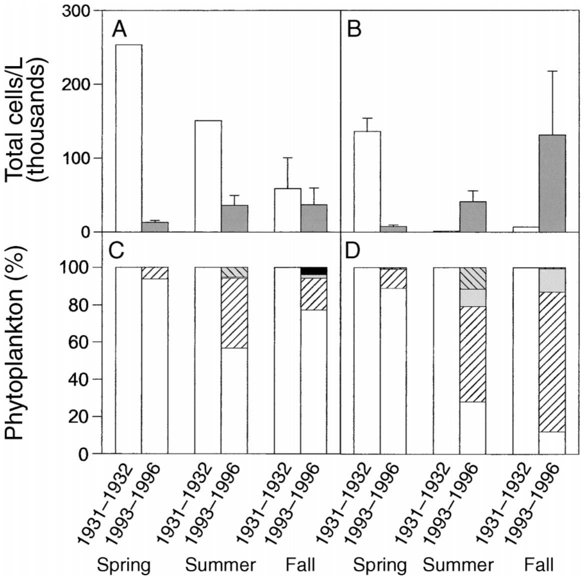

FIG. 11. Phytoplankton abundance and composition in the 1930s (data from Gran and Braarud [1935]) and 1990s (Martin et al. 1999) separated by year, season, and sampling location. Upper panels: abundance of phytoplankton as number of cells/L (mean + 1 SE) (A) inside (station 1C vs. 17) and (B) outside (station 5 vs. 16) of Passamaquoddy Bay in 1931–1932 (white bars, *n* = 2) and 1993–1996 (dark gray bars, *n* = 4). Lower panels: percentage contribution of nonharmful diatoms (open plain bars), harmful diatoms (white hatched bars), nonharmful dinoflagellates (gray bars), harmful dinoflagellates (gray hatched bars), and silicoflagellates (black bars) (C) inside and (D) outside Passamaquoddy Bay in 1931–1932 (left bars) and 1993–1996 (right bars).

The decline in long-lived rockweeds is a second example of cumulative effects (Fig. 13B). Annual algae are naturally controlled by limiting nutrients (nitrogen, phosphorus), herbivory, and space competition by perennial rockweeds (Worm et al. 1999, 2001, Lotze et al. 2000, 2001). Enhanced nutrient loads favor fast-growing annual algae, which can overgrow rockweeds and block their recruitment (Lotze et al. 2000, 2001, Worm et al. 2001). Reduced herbivore pressure also favors annual algae, especially green algae, which are the preferred food (Lotze and Worm 2000). Periwinkle harvesting, as well as chemical pollutants that affect survival of crustaceans (e.g., pesticides; Thain et al. 1990) or reproduction of gastropods (e.g., antifouling agent tributyltin; Schulte-Oehlmann et al. 1996), all

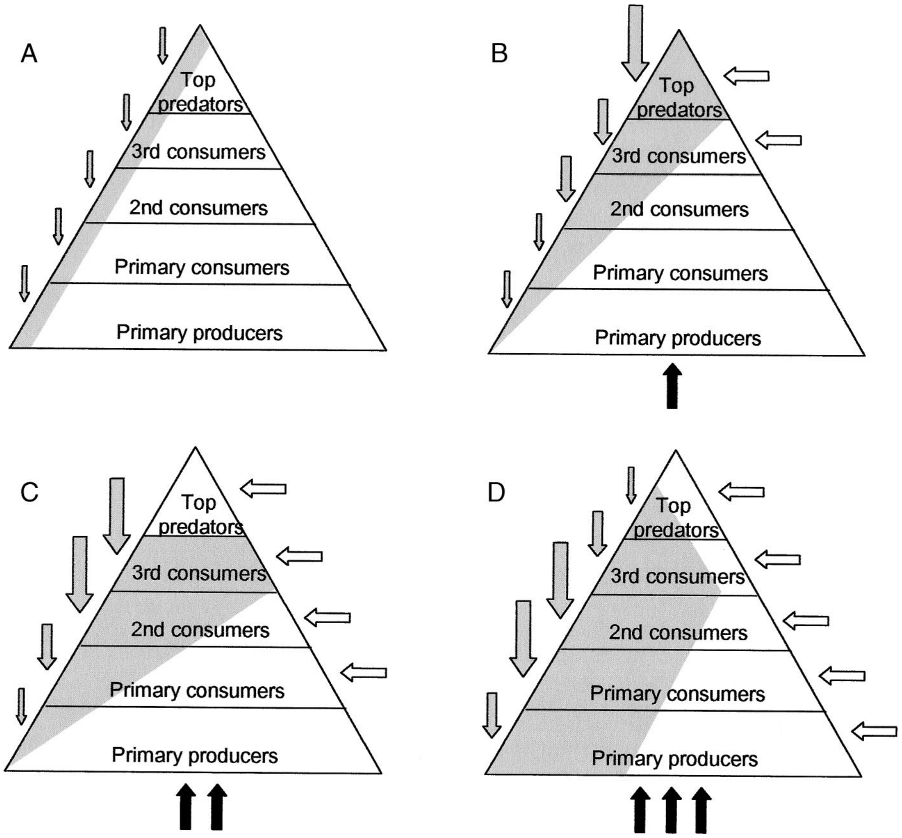

FIG. 12. Schematic illustration of relative harvesting pressures (gray areas, gray arrows) on various trophic levels in the Quoddy Region over the past centuries: (A) indigenous hunters and gatherers as ''low-impact omnivores'' before AD 1700, (B) European colonizers as ''top predators'' around 1900, (C) humans as ''highly-efficient top predators'' around 1970, (D) humans as ''high-impact omnivores'' around 2000. Other human impacts are indicated as side-in (white arrows) and bottom-up (black arrows) impacts.

contribute to reduced herbivore abundance. In addition, harvesting of rockweeds provides more open space for annual algal settlement (Worm and Lotze 2000). All these factors favor blooms of annual algae over rockweed canopies and can result in severe degradation of important invertebrate and fish habitat (Rangeley 2000, Worm and Lotze 2000). Furthermore, filter feeders thrive in nutrient-enriched areas through enhanced food supply and can outcompete rockweeds on the limited space available on rocky shores (Fig. 13B). Reduction of nutrient loads is an essential management tool to reduce algal blooms, but reductions in harvesting pressures may be required as well, depending on what other human impacts are involved on local scales (Worm and Lotze 2000, Cloern 2001).

The missing baseline

After reviewing successive changes on all trophic levels in our study region, we tried to look back and answer the question: What was in the coastal ocean before large-scale human interference? Estimates of today's vs. past abundance suggest that upper trophic level species, which have experienced strong declines over past centuries, were one to three orders of magnitude more abundant in the past (i.e., 10–0.1% is left; Table 2). For comparison, recent estimates for other marine mammals include 2–3% for bowhead whales in Davis Strait (Shelden and Rugh 1995), 4% for humpback and 15% for fin whales in the North Atlantic (Roman and Palumbi 2003), 0.5–1.4% for dugongs in Moreton Bay and Eastern Australia, 30% for sea otters in the Pacific (Jackson et al. 2001), and 30% for sperm whales worldwide (Whitehead 2002). For large predatory fish such as large groundfish, tuna, swordfish, and billfish, Myers and Worm (2003) estimated that ~10% of pre-exploitation levels have remained worldwide. Similarly, Christensen et al. (2003) estimated that large predatory fish biomass in the North Atlantic has declined by a factor of nine since 1900. Taking into account the extinct species, plus the 40% of bird and mammal species that were severely reduced, we suggest that upper trophic levels were at least 10 times more abundant before European colonization.

Determining a baseline for lower trophic levels is more complicated. Long-term reduction of higher trophic levels likely induced changes on lower levels (see

Discussion: Top-down impacts: hunting and fishing). Some species may actually be more abundant than ever because of released predation pressure, while others suffer from new harvesting pressure or other human impacts. In the case of lobster and herring, catch levels in 1990–2000 were similar to those 100 years ago (1890–1900), but average size was strongly reduced over time. However, 100 years ago, their population levels were already possibly affected by long-term exploitation of their predators, groundfish, whales, and birds. More research and modeling efforts are needed to determine past abundance of low trophic level species.

Learning from success

Dramatic declines of various species led to enforcement of conservation measures in the late 19th and throughout the 20th century. Reduction in hunting pressure and protection of breeding colonies enabled many bird species to re-establish or partly recover. The ban on commercial whaling and the end of the bounty hunt for seals has enabled some whales and seals to partly or fully recover. Clean-up of the river bed and reduced water pollution, together with functioning fishways, enabled the return of diadromous fish. Low exploitation levels during World War II and after the extension of the 200-mile limit enabled groundfish stocks to increase in abundance until exploitation was intensified again. These examples show that reduction of exploitation rate, reduction of habitat destruction, and reduction of pollution, as well as the establishment of protected areas, are successful management tools. They also show that many severely depleted species have the potential to recover or re-establish, although recovery of long-lived species may be time-lagged and can take decades to centuries (Dayton et al. 1995, Hutchings 2000). On the other hand, some species that are now protected from exploitation or habitat destruction experience new threats that may prevent recovery. We suggest that marine protected areas, which can benefit prey, predator, and habitat species simultaneously, are essential and necessary for present and future management of coastal ecosystems if the uncertainties from multiple human impacts are taken into account. This approach may be especially valuable in areas rich in marine diversity, such as the outer Bay of Fundy. A recent analysis of biodiversity hotspots in the ocean showed that protection of hotspots was by far the best option for protecting many endangered and threatened species at once (Worm et al. 2003). In addition to protection efforts, reduced levels of exploitation, habitat disruption, nutrient and chemical pollution would greatly benefit species in remaining areas (Jennings and Kaiser 1998, Cloern 2001, Palumbi 2001).

CONCLUSIONS

The results from our study show that humans have severely altered the coastal food web and ecosystem in the Quoddy Region over the last two centuries. We have strongly reduced the abundance of large predators, altered species composition, affected species interactions, and species-specific needs for food and habitat on all trophic levels. Over time, multiple top-down, bottom-up, and side-in impacts have interacted in ways that impair predictability and management. However, protection and restoration efforts have led to partial recovery of some species from dramatic declines, and these success stories provide guidance for future management directions.

Although based on a local study, these results may be broadly applicable to coastal ecosystems around the world. Global patterns of loss and decline of large predators (Jackson et al. 2001, Myers and Worm 2003, Roman and Palumbi 2003), fishing down marine food webs (Pauly et al. 1998, Friedlander and DeMartini 2002), and eutrophication-induced shifts in primary producers (Paerl and Whitall 1999, Cloern 2001, Worm et al. 2002) indicate common signs of degradation. We

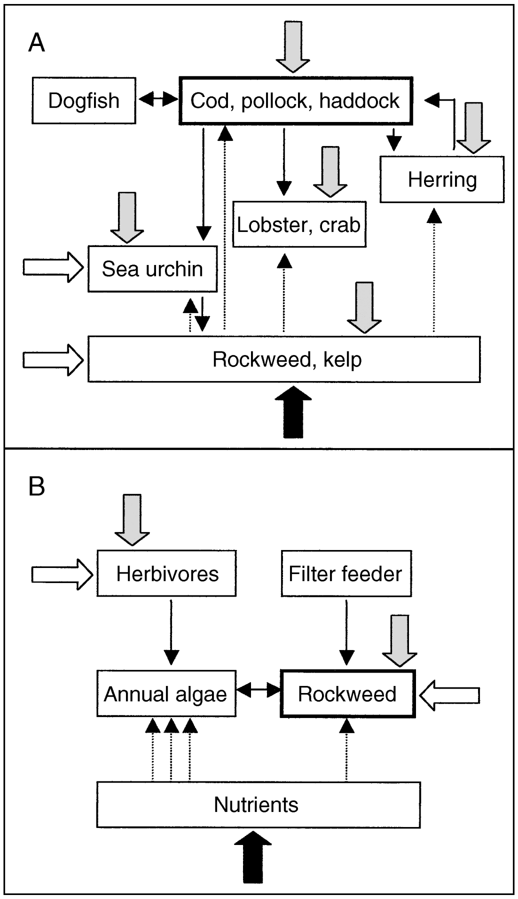

FIG. 13. Illustration of multiple top-down impacts (gray block arrows), bottom-up impacts (black block arrows), and side-in impacts (white block arrows) affecting (A) the recovery of traditional groundfish and (B) the increase in annual algal blooms. Line arrows reflect negative (solid) and positive (dotted) species interactions.

tried to combine and link causes and consequences of multiple human impacts on multiple trophic levels within one coastal food web. This historical perspective offers an understanding of long-term changes that underlie current, and may affect future, changes. Moreover, it provides us with a baseline against which we can measure the magnitude of our impacts (Jackson et al. 2001, Roman and Palumbi 2003). This baseline may hopefully enable us to set clear restoration and protection targets for the future.

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LITERATURE CITED

Anderson, J. M., F. G. Whoriskey, and A. Goode. 2000. Atlantic salmon on the brink. Endangered Species Update **17**: 15–21.

Anonymous. 1971. St. Croix River, summary report to the International Joint Commission. Advisory Board on Pollution Control, St. Croix River. St. Stephen, New Brunswick, Canada.

Anonymous. 1988. Long-term management plan for the diadromous fisheries of the St. Croix River. Canadian Manuscript Report of Fisheries and Aquatic Sciences 1969:1–73.

Anonymous. 1993. Five-year (1993–1997) operational plan for the development and management of the diadromous fishes of the St. Croix River. St. Croix Fisheries Steering Committee, St. Croix International Waterway Commission, St. Stephen, New Brunswick, Canada.

Bates, S. S. 1997. Toxic phytoplankton on the Canadian east coast: implications for aquaculture. Pages 9–18 *in* S. L. Waddy and M. Frechette, editors. Bulletin of the Aquaculture Association of Canada. St. Andrews, New Brunswick, Canada.

Bishop, J. C., and D. W. Black. 1988. The lands edge also: culture history and seasonality at the Partridge Island shell middens. Canadian Journal of Archaeology **12**:17–37.

Black, D. W. 1988. An overview of the Bliss Islands archaeology project. Maine Archaeological Society Newsletter **1**:5–9.

Black, D. W. 2000. That thing of shreds and patches: an archaeological narrative of the Bliss Islands Thoroughfare, Quoddy Region, New Brunswick, Canada. Pages 146–155 *in* M. Boyd, J. C. Erwin, and M. Hendrickson, editors. The entangled past: integrating history and archaeology. Proceedings of the 30th Annual Chacmool Archaeological Conference. Archaeological Association of the University of Calgary, Calgary, Alberta, Canada.

Black, D. W., and C. J. Turnbull. 1986. Recent archaeological research in the insular Quoddy region, New Brunswick, Canada. Current Anthropology **27**:400–402.

Bourque, B. J. 1995. Diversity and complexity in prehistoric Maritime societies: a Gulf of Maine perspective. Plenum Press, New York, New York, USA.

Breitburg, D., S. Seitzinger, and J. Sanders. 1999. The effects of multiple stressors on freshwater and marine ecosystems. Limnology and Oceanography 44, Special issue 3: Part 2.

Bricker, S. B., C. G. Clement, D. E. Pirhalla, S. P. Orlando, and D. R. G. Farrow. 1999. National estuarine eutrophication assessment: effects of nutrient enrichment in the nation's estuaries. National Oceanic and Atmospheric Administration, National Ocean Service, Special Projects Office and the National Centers for Coastal Ocean Science, Silver Spring, Maryland, USA.

Chaput, G., and E. Prevost. 1998. Annual and decadal change in Atlantic salmon (*Salmo salar*) abundance in eastern Canada. Canadian Stock Assessment Secretariat research document 99/30.

Christensen, V., S. Guenette, J. J. Heymans, C. J. Walters, R. Watson, D. Zeller, and D. Pauly. 2003. Hundred-year decline of North Atlantic predatory fishes. Fish and Fisheries **4**:1–24.

Christie, D. S. 1979. Changes in maritime bird populations, 1878–1978. Journal of the New Brunswick Museum, St. John, New Brunswick, Canada 1979:132–146.

Christie, D. S. 1983. Birds. Pages 215–229 *in* M. L. H. Thomas, editor. Marine and coastal systems of the Quoddy region, New Brunswick. Canadian special publication of Fisheries and Aquatic Sciences 64, Science stock status report. Department of Fisheries and Oceans, Ottawa, Ontario, Canada.

Clark, D. S., and S. D. Paul. 1999. Assessment of cod in division 4X in 1999. Department of Fisheries and Oceans, Canadian Stock Assessment Research Secretariat research document 99/159. Department of Fisheries and Oceans, Ottawa, Ontario, Canada.

Cloern, J. E. 2001. Our evolving conceptual model of the coastal eutrophication problem. Marine Ecology Progress Series **210**:223–253.

Collie, J. S., S. J. Hall, M. J. Kaiser, and I. R. Poiner. 2000. A quantitative analysis of fishing impacts on shelf-sea benthos. Journal of Animal Ecology **69**:785–798.

Committee for Whaling Statistics. 1951–1984. International Whaling Statistics XXVII–XCIII. Committee for Whaling Statistics, Oslo, Norway.

Coon, D. 1999. An ecological sketch of some Fundy fisheries. Conservation Council of New Brunswick, Fredericton, New Brunswick, Canada.

Cooper, S. R., and G. S. Brush. 1993. A 2,500-year history of anoxia and eutrophication in Chesapeake Bay. Estuaries **16**:617–626.

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2002. Canadian species at risk, May 2002. COSEWIC Secretariat, Canadian Wildlife Service, Environment Canada, Ottawa, Ontario, Canada.

Davidson, V. M. 1934. Fluctuations in the abundance of planktonic diatoms in the Passamaquoddy region, New Brunswick, from 1924 to 1931. Contributions to Canadian Biology and Fisheries **8**:357–407.

Dayton, P. K., S. F. Thrush, M. T. Agardy, and R. J. Hofman. 1995. Environmental effects of marine fishing. Aquatic Conservation: Marine and Freshwater Ecosystems **5**:205–232.

DFO (Department of Fisheries and Oceans). 1969–2000. Fisheries statistics. Dartmouth, Nova Scotia, and St. Andrews, New Brunswick, Canada.

DFO. 1999*a*. Interaction between wild and farmed Atlantic salmon in the Maritime provinces. Department of Fisheries and Oceans, Canada, Maritimes regional habitat status report 99/1E. Department of Fisheries and Oceans, Dartmouth, Nova Scotia, Canada.

DFO. 1999*b*. The impact of the rockweed harvest on the habitat of southwest New Brunswick. Department of Fisheries and Oceans, Canada, Maritimes regional habitat status report 99/2E. Department of Fisheries and Oceans, Dartmouth, Nova Scotia, Canada.

DFO. 2000. Southwestern New Brunswick (LFA 36-38) green sea urchin. Department of Fisheries and Oceans science stock status report C3-49 (2000). Department of Fisheries and Oceans, Dartmouth, Nova Scotia, Canada.

Dominion Bureau of Statistics. 1917–1968. Fisheries statistics. Ottawa, Ontario, Canada.

Environment Canada. 1986. Land use change in Canada. Lands Directorate, fact sheet 86-4. Environment Canada, Ottawa, Ontario, Canada.

Estes, J. A., and D. O. Duggins. 1995. Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. Ecological Monographs **65**:75–100.

Estes, J. A., M. T. Tinker, T. M. Williams, and D. F. Doak. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science **282**:473–476.

Fish, C. J., and M. W. Johnson. 1937. The biology of the zooplankton population in the Bay of Fundy and Gulf of Maine with special reference to production and distribution. Journal of the Biological Board of Canada **3**:189–322.

Fisheries Branch. 1869–1916. Annual Report of the Department of Marine and Fisheries. Ottawa, Ontario, Canada.

Fletcher, J. S., and A. L. Meister. 1982. The St. Croix River: an Atlantic salmon river management report. Atlantic Sea Run Salmon Commission, Bangor, Maine, USA.

Fogarty, M. J. 1999. Essential habitat, marine reserves and fishery management. Trends in Ecology and Evolution **14**: 133–134.

Fogarty, M. J., and S. A. Murawski. 1998. Large-scale disturbance and the structure of marine systems: fishery impacts on Georges Bank. Ecological Applications **8**(Supplement):6–22.

Forbes, D. L., J. Shaw, and R. B. Taylor. 1997. Climate change impacts in the coastal zone of Atlantic Canada. Pages 37–55 *in* R. W. Shaw, editor. Climate change and climate variability in Atlantic Canada. Environment Canada Atlantic Region occasional report 9. Department of Fisheries and Oceans, Dartmouth, Nova Scotia, Canada.

Found, W. A. 1912. The lobster fishery of Canada. Pages 50–77 *in* Commission of Conservation Canada, editor. Seafisheries of Eastern Canada. Mortimer Company, Ottawa, Ontario, Canada.

Friedlander, A. M., and E. E. DeMartini. 2002. Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: the effects of fishing down apex predators. Marine Ecology Progress Series **230**:253–264.

Fritz, C. W. 1921. Plankton diatoms, their distribution and bathymetric range in St. Andrews waters. Contributions to Canadian Biology 1918–1920:49–62.

Gaskin, D. E. 1983. The marine mammal community. Pages 245–268 *in* M. L. H. Thomas, editor. Marine and coastal systems of the Quoddy region, New Brunswick. Canadian Special Publications of Fisheries and Aquatic Sciences 64. Department of Fisheries and Oceans, Ottawa, Ontario, Canada.

Goudie, R. I. 1989. Historical status of Harlequin Ducks wintering in eastern North America: a reappraisal. Wilson Bulletin **101**:112–114.

Graham, J., S. Engle, and M. Recchia. 2002. Local knowledge and local stocks: an atlas of groundfish spawning in the Bay of Fundy. Centre for Community-Based Management, St. Francis Xavier University, Antigonish, Nova Scotia, Canada.

Gran, H. H., and T. Braarud. 1935. A quantitative study of the phytoplankton in the Bay of Fundy and the Gulf of Maine (including observations on hydrography, chemistry and turbidity). Journal of the Biological Board of Canada **1**:279–467.

Harley, S. J., R. A. Myers, and A. Dunn. 2001. Is catch-per-unit-effort proportional to abundance? Canadian Journal of Fisheries and Aquatic Sciences **58**:1760–1772.

Huettmann, F., and A. W. Diamond. 2000. Seabird migration in the Canadian northwest Atlantic Ocean: moulting locations and movement patterns of immature birds. Canadian Journal of Zoology **78**:624–647.

Huntsman, A. G. 1953*a*. How Passamaquoddy produces sardines. Studies from the Stations of the Fisheries Research Board of Canada **346**:1–8.

Huntsman, A. G. 1953*b*. Movements and decline of large Quoddy herring. Journal of the Fisheries Research Board Canada **10**:1–50.

Hurley, P. C. F., G. A. P. Black, P. A. Comeau, and R. K. Mohn. 1999. Assessment of 4X haddock in 1998 and the first half of 1999. Department of Fisheries and Oceans, Canadian Stock Assessment Secretariat research document 99/147. Department of Fisheries and Oceans, Ottawa, Ontario, Canada.

Hutchings, J. A. 2000. Collapse and recovery of marine fishes. Nature **406**:882–885.

Hutchings, J. A., and R. A. Myers. 1995. The biological collapse of Atlantic cod off Newfoundland and Labrador: an exploration of historical changes in exploitation, harvesting technology, and management. Pages 37–93 *in* R. Arnason and L. Felt, editors. The North Atlantic fisheries: successes, failures, and challenges. Institute of Island Studies, Charlottetown, Prince Edward Island, Canada.

Ingersoll, L. K., and S. W. Gorham. 1978. A history of the mammals of Grand Manan. Grand Manan Historian **20**:31–54.

International Whaling Commission. 1984–2000. Report of the International Whaling Commission 1984/85–1999/2000. International Whaling Commission, Cambridge, UK. [Online: ⟨http://luna.pos.to/whale/sta.html⟩.]

Jackson, J. B. C., et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science **293**:629–638.

Jennings, S., and M. J. Kaiser. 1998. The effects of fishing on marine ecosystems. Advances in Marine Biology **34**: 201–352.

Kerswill, C. S. 1960. Effects of proposed Passamaquoddy power project on anadromous fishes in Canadian waters. Journal of the Fisheries Research Board Canada **17**:713–720.

Lawton, P., D. A. Robichaud, M. B. Strong, D. S. Pezzack, and C. F. Frail. 2001. Spatial and temporal trends in the American lobster, *Homarus americanus*, fishery in the Bay of Fundy (lobster fishing areas 35, 36 and 38). Canadian Science Advisory Secretariat Research Document 2001/094:1–71.

Legare, J. E. H., and D. C. Maclellan. 1960. A qualitative and quantitative study of the plankton of the Quoddy Region in 1957 and 1958 with special reference to the food of the herring. Journal of the Fisheries Research Board Canada **17**:409–448.

Limburg, K. E. 1999. Estuaries, ecology, and economic decisions: an example of perceptual barriers and challenges to understanding. Ecological Economics **30**:185–188.

Lotze, H. K., and I. Milewski. 2002. Two hundred years of ecosystem and food web changes in the Quoddy region, outer Bay of Fundy. Conservation Council of New Brunswick, Fredericton, New Brunswick, Canada.

Lotze, H. K., and B. Worm. 2000. Variable and complementary effects of herbivores on different life stages of bloom-forming macroalgae. Marine Ecology Progress Series **200**: 167–175.

Lotze, H. K., and B. Worm. 2002. Complex interactions of climatic and ecological controls on macroalgal recruitment. Limnology and Oceanography **47**:1734–1741.

Lotze, H. K., B. Worm, and U. Sommer. 2000. Propagule banks, herbivory and nutrient supply control population development and dominance patterns in macroalgal blooms. Oikos **89**:46–58.

Lotze, H. K., B. Worm, and U. Sommer. 2001. Strong bottom-up and top-down control of early life stages of macroalgae. Limnology and Oceanography **46**:749–757.

Marshall, T. L. 1976. Historical perspectives of Resource Development Branch activities in restoring anadromous fishes to the St. Croix River, New Brunswick: Maine. Internal report series MAR/I-76-2, Department of Fisheries and the Environment, Halifax, Nova Scotia, Canada.

Marshall, T. L., G. J. Chaput, P. G. Amiro, D. K. Cairns, R. A. Jones, S. F. O'Neill, and J. A. Ritter. 1999. Assessments of Atlantic salmon stocks of the Maritimes Region, 1998. Canadian Stock Assessment Secretariat research document 99/25. Department of Fisheries and Oceans, Ottawa, Ontario, Canada.

Martin, J. L., M. M. LeGresley, P. M. Strain, and P. Clement. 1999. Phytoplankton monitoring in the southwestern Bay of Fundy during 1993–96. Canadian Technical Report of Fisheries and Aquatic Sciences **2265**:1–132.

Mead, J. G., and E. D. Mitchell. 1984. Atlantic gray whales. Pages 33–53 *in* M. L. Jones, S. L. Swartz, and S. Leatherwood, editors. The gray whale *Eschrichtius robustus*. Academic Press, Orlando, Florida, USA.

Murphy, B. M., and D. W. Black. 1996. Zooarchaeology in the Canadian Maritimes. Canadian Zooarchaeology **9**:2–20.

Myers, R. A., and B. Worm. 2003. Rapid worldwide depletion of predatory fish communities. Nature **423**:280–283.

NEFSC (Northeast Fisheries Science Center). 1999. U.S. marine mammal stock assessments: 1998. NOAA technical memorandum NMFS-NE-116. Northeast Fisheries Science Center, Woods Hole, Massachusetts, USA.

Neilson, J., P. Perley, and C. Nelson. 1999. The 1999 assessment of pollock (*Pollachius virens*) in NAFO Divisions 4VWX and Subdivision 5Zc. Department of Fisheries and Oceans, Canadian stock assessment secretariat research document 99/160. Department of Fisheries and Oceans, Ottawa, Ontario, Canada.

Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology and Evolution **14**:483–488.

Paerl, H. W., and D. R. Whitall. 1999. Anthropogenically-derived atmospheric nitrogen deposition, marine eutrophication and harmful algal bloom expansion: is there a link? Ambio **28**:307–311.

Palumbi, S. R. 2001. The ecology of marine protected areas. Pages 510–530 *in* M. D. Bertness, S. D. Gaines, and M. E. Hay, editors. Marine community ecology. Sinauer, Sunderland, Massachusetts, USA.

Pauly, D. 1995. Anecdotes and the shifting baseline syndrome of fisheries. Trends in Ecology and Evolution **10**: 430.

Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F. Torres, Jr. 1998. Fishing down marine food webs. Science **279**:860–863.

Perley, M. H. 1852. Reports on the sea and river fisheries of New Brunswick. Second edition. Simpson, Fredericton, New Brunswick, Canada.

Pettingill, S. O. 1939. The bird life of the Grand Manan archipelago. Proceedings of the Nova Scotian Institute of Science **19**:293–439.

Rangeley, R. W. 1994. The effects of seaweed harvesting on fishes: a critique. Environmental Biology of Fishes **39**:319–323.

Rangeley, R. W. 2000. Aquatic macrophytes as foraging and refuging habitats for fish. Pages 18–23 *in* R. W. Rangeley and J. Davies, editors. Gulf of Maine rockweed: management in the face of scientific uncertainty. Huntsman Marine Science Centre occasional report 00/1, St. Andrews, New Brunswick, Canada.

Rees, R. 1995. St. Andrews and the islands. Nimbus Publishing, Halifax, Nova Scotia, Canada.

Reeves, R. R. 2001. Overview of catch history, historic abundance and distribution of right whales in the western North Atlantic and in Cintra Bay, West Africa. Journal of Cetacean Research and Management (special issue) **2**:187–192.

Robichaud, D. A., P. Lawton, and M. B. Strong. 2000. Exploratory fisheries for rock crab, *Cancer irroratus*, and Jonah crab, *Cancer borealis*, in Canadian lobster fishing areas 34, 35, 36 and 38. Canadian Science Advisory Secretariat research document 2000/051:1–27. Department of Fisheries and Oceans, Ottawa, Ontario, Canada.

Roman, J., and S. R. Palumbi. 2003. Whales before whaling in the North Atlantic. Science **301**:508–510.

Sanger, D. 1986. An introduction to the prehistory of the Passamaquoddy Bay region. American Review of Canadian Studies **16**:139–159.

SCEP (St. Croix Estuary Project). 1997. St. Croix estuary area: a profile. St. Croix Estuary Project, St. Andrews, New Brunswick, Canada.

Schulte-Oehlmann, U., J. Oehlmann, B. Watermann, B. Bauer, I. Ide, and P. Fiorino. 1996. Effekte von Tributylzinn (TBT) aus Antifoulinganstrichen auf Schneckenpopulationen in der Ostsee. Pages 176–179 *in* J. L. Lozán, R. Lampe, W. Matthäus, E. Rachor, H. Rumohr, and H. von Westernhagen, editors. Warnsignale aus der Ostsee. Parey, Berlin, Germany.

Shackell, N. L., and K. T. Frank. 2003. Marine fish diversity on the Scotian Shelf, Canada. Aquatic Conservation: Marine and Freshwater Ecosystems **13**:305–321.

Shelden, K. E. W., and D. J. Rugh. 1995. The bowhead whale, *Balaena mysticetus*: its history and current status. Marine Fisheries Review **57**:1–20.

Simon, J. E., and P. A. Comeau. 1994. Summer distribution and abundance trends of species caught on the Scotian Shelf from 1970–1992, by research vessel groundfish survey. Canadian Technical Report of Fisheries and Aquatic Sciences **1953**:1–145.

Smith, G. J. D., C. L. Jovellanos, and D. E. Gaskin. 1984. Near-surface bio-oceanographic phenomena in the Quoddy Region, Bay of Fundy. Canadian Technical Report of Fisheries and Aquatic Sciences **1280**:1–124.

Spiess, A. E., and R. A. Lewis. 2001. The Turner farm fauna: 5000 years of hunting and fishing in Penobscot Bay, Maine. Occasional Publications in Maine Archaeology **11**:1–177.

Spiess, A. E., E. Trautman, and T. Kupferschmid. 1990. Prehistoric occupation at Reversing Falls. File report. Maine Historic Preservation Commission, Augusta, Maine, USA.

Statistics Canada. 1984. Historical statistics of New Brunswick. Statistics Canada, Ottawa, Ontario, Canada.

Steneck, R. S. 1997. Fisheries-induced biological changes to the structure and function of the Gulf of Maine ecosystem. Regional Association for the Research on the Gulf of Maine (RARGOM) report 91-1, Hanover, New Hampshire, USA.

Steneck, R. S., and J. T. Carlton. 2000. Human alterations of marine communities: students beware! Pages 445–468 *in* M. D. Bertness, S. D. Gaines, and M. E. Hay, editors. Marine community ecology. Sinauer, Sunderland, Massachusetts, USA.

Thain, J. E., P. Matthiessen, and S. Bifield. 1990. The toxicity of dichlorvos to some marine organisms. Pages 1–15 *in* International Council for the Exploration of the Sea (ICES), editor. Council meeting, ICES, Copenhagen, Denmark.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of earth's ecosystems. Science **277**:494–499.

Walters, C., and J. F. Kitchell. 2001. Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. Canadian Journal of Fisheries and Aquatic Sciences **58**:1–12.

White, A. W. 1981. Sensitivity of marine fishes to toxins from the red-tide dino-flagellate *Gonyaulax excavata* and implications for fish kills. Marine Biology **65**:255–260.

White, A. W. 1982. Intensification of *Gonyaulax* blooms and shellfish toxicity in the Bay of Fundy. Canadian Technical Report of Fisheries and Aquatic Sciences **1064**:1–15.

Whitehead, H. 2002. Estimates of the current global population size and historical trajectory for sperm whales. Marine Ecology Progress Series **242**:295–304.

Whitehead, R. H. 1991. The protohistoric period in the Maritime Provinces. Pages 235–266 *in* M. Deal and S. Blair, editors. Prehistoric archaeology in the Maritime Provinces: past and present research. Council of Maritime Premiers, Maritime Committee on Archaeological Cooperation, Halifax, Nova Scotia, Canada.

Whoriskey, F., J. Carr, G. Lacroix, and M. Stokesbury. 1998. A review and update of aquaculture impact studies carried out on the Magaguadavic River, Southern Bay of Fundy, New Brunswick. Canadian Stock Assessment Secretariat research document **98/155**:1–37.

Wilson, G. A. C. 1956. St. Croix River. Resource Development Branch, Fisheries Service Maritimes Region, Canada, manuscript report **56-10**:1–30.

Wootton, J. T. 1995. Effects of birds on sea urchins and algae: a lower-intertidal trophic cascade. Ecoscience **2**:312–328.

Worm, B. 2000. Consumer versus resource control in rocky shore food webs: Baltic Sea and NW Atlantic Ocean. Berichte aus dem Institut fuer Meereskunde Kiel **316**:1–147.

Worm, B., and H. K. Lotze. 2000. Nutrient pollution, low-trophic level harvesting and cumulative human impact on coastal ecosystems. Pages 40–41 *in* R. W. Rangeley and J. Davies, editors. Gulf of Maine rockweed: management in the face of scientific uncertainty. Huntsman Marine Science Centre Occasional Report 00/1, St. Andrews, New Brunswick, Canada.

Worm, B., H. K. Lotze, C. Boström, R. Engkvist, V. Labanauskas, and U. Sommer. 1999. Marine diversity shift linked to interactions among grazers, nutrients and dormant propagules. Marine Ecology Progress Series **185**:309–314.

Worm, B., H. K. Lotze, H. Hillebrand, and U. Sommer. 2002. Consumer versus resource control of species diversity and ecosystem functioning. Nature **417**:848–851.

Worm, B., H. K. Lotze, and R. A. Myers. 2003. Predator diversity hotspots in the blue ocean. Proceedings of the National Academy of Sciences USA **100**:9884–9888.

Worm, B., H. K. Lotze, and U. Sommer. 2001. Algal propagule banks modify competition, consumer and resource control on Baltic rocky shore. Oecologia **128**:281–293.

Worm, B., and R. A. Myers. 2003. Meta-analysis of cod–shrimp interactions reveals top-down control in oceanic food webs. Ecology **84**:162–173.

APPENDIX

A complete list of references used to determine occurrence, abundance, and change of species over time is available online in ESA's Electronic Data Archive: *Ecological Archives* A014-030-A1.