Gulf of Maine Ecosystem Overview Report

East Coast Aquatics

Ecosystem Management Branch
Maritimes Region
Fisheries and Oceans Canada
PO Box 1006
Dartmouth, NS
B2Y 4A2

2011

Canadian Technical Report of Fisheries and Aquatic Sciences 2946

Fisheries and Oceans Canada Pêches et Océans Canada

Canada

Canadian Technical Report of Fisheries and Aquatic Sciences

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Canadian Technical Report of
Fisheries and Aquatic Sciences 2946

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Gulf of Maine Ecosystem Overview

Prepared by:

East Coast Aquatics[1]

With contributions from:
Northeast Fisheries Science Center, National Marine Fisheries Service, National Oceanographic and Atmospheric Administration
St. Andrews Biological Station and Bedford Institute of Oceanography, Fisheries and Oceans Canada
Atlantic Cooperative Wildlife Ecology Research Network
Canadian Wildlife Service
University of New Brunswick

Oceans and Coastal Management Division
Ecosystem Management Branch, Maritimes Region
Fisheries and Oceans Canada
PO Box 1006
Dartmouth, Nova Scotia
B2Y 4A2

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[1] PO Box 129, 402 Granville Street, Bridgetown, Nova Scotia, Canada B0S 1C0

Cat No. Fs 97-6/2946E ISSN 0706-6457

Correct citation for this publication:

East Coast Aquatics. 2011. Gulf of Maine Ecosystem Overview. Can. Tech. Rep. Fish. Aquat. Sci. 2946: xvi + 203 p.

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ACKNOWLEDGEMENTS

The authors would like to thank the following people who made written contributions to various chapters of the Gulf of Maine Ecosystem Overview Report:

Alida Bundy, Fisheries and Oceans Canada - Introduction
Maria Buzeta, Fisheries and Oceans Canada - Introduction
John Chardine, Canadian Wildlife Service - Seabirds
Laurel Col, Northeast Fisheries Science Center, National Marine Fisheries Service (NMFS)
Tony Diamond, Atlantic Cooperative Wildlife Ecology Research Network - Seabirds
Michael Fogarty, Northeast Fisheries Science Center, NMFS
Kevin Friedland, Northeast Fisheries Science Center, NMFS
Robert Gamble, Northeast Fisheries Science Center, NMFS
Jonathan Hare, Northeast Fisheries Science Center, NMFS
Dvora Hart, Northeast Fisheries Science Center, NMFS
Peter Hicklin, Canadian Wildlife Service - Seabirds
Kimberly Hyde, Northeast Fisheries Science Center, NMFS
Catherine Johnson, Fisheries and Oceans Canada – Zooplankton
Jason Link, Northeast Fisheries Science Center, NMFS
Alan Logan, University of New Brunswick - Benthic invertebrates: non-commercial
Sean Lucey, Northeast Fisheries Science Center, NMFS
Keith McAloney, Canadian Wildlife Service - Seabirds
Gary Melvin, St. Andrews Biological Station (SABS), Fisheries and Oceans Canada - Pelagic fish, commercial
John Neilson, SABS, Fisheries and Oceans Canada - Pelagic fish, tuna
Janet Nye, Northeast Fisheries Science Center, NMFS
William Overholtz, Northeast Fisheries Science Center, NMFS
Anne Richards, Northeast Fisheries Science Center, NMFS
David Richardson, Northeast Fisheries Science Center, NMFS
David Robichaud, SABS, Fisheries and Oceans Canada - Benthic invertebrates, lobster
Rob Ronconi, University of Victoria - Seabirds
Rabindra Singh, Fisheries and Oceans Canada - Geological System, Introduction, Infauna, Oceanography, Groundfish
Kent Smedbol, SABS, Fisheries and Oceans Canada - Marine mammals
Sean Smith, SABS, Fisheries and Oceans Canada - Pelagic fish, mackerel
Maureen Taylor, Northeast Fisheries Science Center, NMFS
Jack Terhune, University of New Brunswick - Seals

East Coast Aquatics would also like to thank Heather Breeze, Alida Bundy, Steve Campana, Donald Clark, Cesar Fuentes-Yaco, Michelle Greenlaw, David Hardie, Glen Harrison, Erica Head, Glen Herbert, Jack Lawson, Cathy Merriman, Brian Petrie, Rabindra Singh, Stephen Smith, and John Tremblay of Fisheries and Oceans Canada, Kevin Friedland of National Marine Fisheries Service, Brian Todd of Geological Survey of Canada, Carina Gjerdrum and Gary Lines of Environment Canada, and John Kocik of NOAA, all of whom provided review and or comment to help ensure that a clear, current and accurate portrayal of research was presented in this document.

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LIST OF ACRONYMS AND ABBREVIATIONS

ATSW	Atlantic temperate slope water
AZMP	Atlantic Zone Monitoring Program
BoFEP	Bay of Fundy Ecosystem Partnership
BP	before present
CHC	Canadian Hurricane Centre
COOC	Coastal Ocean Observing Center
COSEWIC	Committee on the Status of Endangered Wildlife in Canada
CPR	continuous plankton recorder
CSRL	Canadian Shark Research Laboratory
DFO	Department of Fisheries and Oceans Canada
EEZ	exclusive economic zone
EMCC	eastern Maine Coastal Current
EOAR	*Ecosystem Overview and Assessment Report*
EOR	*Ecosystem Overview Report*
FMP	U.S. Federal Fisheries Management Plan
GIS	geographic information system
GM-WICS	Gulf of Maine–Watershed Information and Characterization System
GoM	Gulf of Maine
GSC	Great South Channel
iBoF	Inner Bay of Fundy
ICNAF	International Commission for Northwest Atlantic Fisheries
IPCC	Intergovernmental Panel on Climate Change
LSSW	Labrador sub-Arctic slope water
MCC	Maine Coastal Current
NAO	North Atlantic Oscillation
NEC	Northeast Channel
NEFSC	Northeast Fisheries Science Center
NHC	National Hurricane Center
NMFS	U.S. National Marine Fisheries Service
NOAA	U.S. National Oceanic and Atmospheric Administration
NPRI	National Pollutant Release Inventory
PCA	principal components analysis
PCB	polychlorinated biphenyl
PCI	phytoplankton color index
PM	fine particulate matter
POC	particulate organic carbon
PSU	practical salinity unit
SPM	suspended particulate matter
SSF	shelf–slope front
SST(s)	sea surface temperature(s)
TRAC	Transboundary Resources Assessment Committee
U.S.	United States
USGS	U.S. Geological Survey
WMCC	western Maine Coastal Current

ABSTRACT

East Coast Aquatics. 2011. Gulf of Maine Ecosystem Overview. Can. Tech. Rep. Fish. Aquat. Sci. 2946: xvi + 203 p.

The Gulf of Maine ecosystem has captured human interest since we first set foot on its shoreline and first ventured into and across its waters. It has been a source of food, with organisms being harvested from its shallowest intertidal zones to the deepest offshore basins. Researchers have studied its various living components, from the microscopic to the largest creatures on the planet. They have examined the geological history that lies under its waters and the relationship of the gulf with the climate and weather that passes through the atmosphere above. Tens of research institutes and organizations have been established across two countries around the gulf in order to study this ecosystem, and they have produced tens of thousands of documents. It is therefore no small task to try and summarize all that has been learned to date. It is important therefore to tell the reader what this document does not do by explaining some of the guidelines established to create this Ecosystem Overview Report of the Gulf of Maine.

This document focuses on offshore waters of the Gulf of Maine, including Georges Bank and the outer Bay of Fundy. It does not deal in detail with the inner coastal shelf and the complexities of the various bays and inlets along the Gulf of Maine coastline. The inner coastal shelf is described only as it relates to the processes of the offshore portion of the Gulf of Maine.

This document does not examine human uses, past or present, nor does it examine the influence of these activities on the natural resources of the Gulf of Maine. It does examine how biological communities have changed and the resilience of the ecosystem to changes, whether they are natural or human induced. An overview is provided of the reaction of components of the ecosystem to change, rather than the actions that may have driven those changes.

This document provides a limited amount of detail on historic trends and changes in the plants and animals that live within the Gulf of Maine ecosystem. Detailed scientific findings are not presented. Instead, the various living communities within the Gulf of Maine are described, as are the relationships that exist between those living organisms and the physical oceanography and habitats of the gulf, and the relationships that exist between living organisms within the ecosystem. We examine the most recent trends and knowledge (generally 1970 – present) regarding the state of the living biota, and the natural ecosystem mechanisms that influence their life cycle dynamics within the Gulf of Maine.

The oceanography of the Gulf of Maine is influenced by local climate and small scale circulation as well as by ecological changes that occur from north of Newfoundland, Canada south to the Gulf of Mexico. Because of variations that occur at scales much larger than the Gulf of Maine and that influence the physical habitats of the ecosystem, living organisms from vast distances travel to the gulf to benefit from the high productivity and diversity of habitats that exist. Still other aquatic and avian communities spend their entire life cycle within the Gulf of Maine, finding all they need to support every stage of development right here. The gulf is somewhat of a unique boundary for both northern species and southern species, and as large scale water currents flow into the gulf through the Northeast Channel and out through the Great South Channel, it influences what species may be found within the ecosystem. This document will provide the reader with an overview of the dynamic physical and biological components of the Gulf of Maine ecosystem.

RÉSUMÉ

East Coast Aquatics. 2011. Gulf of Maine Ecosystem Overview. Can. Tech. Rep. Fish. Aquat. Sci. 2946: xvi + 203 p.

L’écosystème du golfe du Maine a commencé à susciter l’intérêt des êtres humains dès qu’ils ont foulé le sol de ses côtes et qu’ils se sont aventurés dans ses eaux. Il constitue une source de nourriture, grâce aux organismes qui y sont pêchés, que ce soit dans les zones intertidales très peu profondes ou dans les bassins extracôtiers les plus profonds. Les chercheurs en ont étudié les diverses composantes vivantes, des créatures microscopiques aux êtres les plus gros de la planète. Ils ont examiné l’histoire géologique que recèlent ses eaux et le lien qui existe entre le golfe, d’une part, et le climat et le temps de l’atmosphère qui se trouve au-dessus, d’autre part. Des dizaines d’instituts et d’organismes de recherche se sont établis dans les deux pays qui bordent le golfe afin d’étudier cet écosystème, et ils ont produit des dizaines de milliers de documents. Ce n’est donc pas une mince tâche que d’essayer de résumer tout ce qui a été appris jusqu’à présent. Il est donc important d’informer le lecteur de ce que ce document n’est pas en expliquant certaines des lignes directrices sur lesquelles repose le présent Rapport d’ensemble sur l’écosystème du golfe du Maine.

Le document met l’accent sur les eaux extracôtières du golfe du Maine, y compris le banc Georges et la partie extérieure de la baie de Fundy. Il ne traite pas en détail la partie intérieure du plateau continental et les aspects complexes qui caractérisent divers passages et baies le long des côtes du golfe du Maine. La partie intérieure du plateau continental est décrite seulement en ce qui a trait aux processus de la portion extracôtière du golfe du Maine.

Le présent document n’examine ni les activités humaines, passées ou présentes, ni l’influence de ces activités sur les ressources naturelles du golfe du Maine. Il s’intéresse à la façon dont les communautés biologiques se sont transformées et à la résilience de l’écosystème face à ces changements, qu’ils soient d’origine naturelle ou humaine. On y présente un survol de la réaction des composantes de l’écosystème aux changements, plutôt que des actions qui ont pu motiver ces changements.

Ce document ne présente que quelques détails sur les tendances historiques et les changements observés dans les plantes et les animaux qui vivent au sein de l’écosystème du golfe du Maine. Il ne formule pas de conclusions scientifiques détaillées. À la place, les diverses communautés vivantes du golfe du Maine y sont décrites, tout comme les liens qui existent entre ces organismes vivants, l’océanographie physique et les habitats du golfe, ainsi que la relation entre les organismes vivants de cet écosystème. Nous examinons les tendances et les connaissances les plus récentes (généralement de 1970 à nos jours) concernant l’état du biote vivant ainsi que les mécanismes écosystémiques naturels qui influent sur les dynamiques des cycles de vie de ses composantes dans le golfe du Maine.

L’océanographie du golfe du Maine est marquée par le climat local et la circulation à petite échelle ainsi que par les changements écologiques qui ont lieu du nord de Terre-Neuve-et-Labrador (Canada) au sud du golfe du Mexique. En raison de variations qui se produisent à des échelles beaucoup plus grandes que le golfe du Maine et qui agissent sur les habitats physiques de l’écosystème, les organismes vivants situés à de grandes distances se déplacent jusqu’au golfe pour bénéficier de la productivité et de la diversité élevées des habitats qui y existent. D’autres communautés aquatiques et

aviaires passent toute leur vie dans le golfe du Maine, et y trouvent tout ce dont elles ont besoin pour soutenir tous leurs stades de développement. Le golfe tient en quelque sorte lieu de frontière unique entre les espèces du Nord et les espèces du Sud, et les courants d'eau de grande échelle qui se déplacent vers le golfe en passant par le chenal Nord-Est et le Grand chenal Sud ont une influence sur les espèces que l'on peut retrouver dans l'écosystème. Ce document donnera au lecteur un aperçu des composantes physiques et biologiques dynamiques qui forment l'écosystème du golfe du Maine.

INTRODUCTION

1. PROJECT DEFINITION

The following section provides a background on the driving factors to produce this report, the extent of content considered for its production, a description of the scope and perspective used.

1.1 Context and Purpose of Report

The Gulf of Maine-Bay of Fundy-Georges Bank marine ecosystem is a historically important international fisheries area. Due to its proximity to eastern cities and universities, this ecosystem is home to many marine institutes that have studied the system for well over 100 years. Acknowledgement of this ecosystem as functioning beyond political boundaries and deserving of a high management priority is highlighted through numerous activities involving Canada-United States collaboration in integrated oceans management, including the formation of a Canada/U.S. Oceans Working Group to complete a joint ecosystem overview. A joint National Oceanographic and Atmospheric Adminstration (NOAA)-Department of Fisheries and Oceans (DFO) work plan included activities of interest to both countries in the Gulf of Maine.

Canadian-U.S. collaboration in the Gulf of Maine is an important component of Canada's *Oceans Action Plan* (Fisheries and Oceans Canada 2005). In the U.S., both the U.S. Commission on Ocean Policy (2004) and the Pew Ocean Commission (2003) have issued calls for the development of an ecosystem approach to oceans management that parallels Canadian efforts. American and Canadian science is shifting to fulfill the need for ecosystem-based management measures. The U.S. *Oceans Action Plan*, in response to the Commission on Ocean Policy Report, has recommended a number of concrete steps to move towards an ecosystem approach that is consistent with U.S. and Canadian objectives in this area.

At a meeting of the Oceans Working Group of the Canada/U.S. Steering Committee in March 2006, it was concluded that a cooperative Canada-U.S. integrated assessment and ecosystem overview for the Bay of Fundy-Gulf of Maine area should be considered, focusing on offshore waters and living marine resources. The report was to generally follow the standard Ecosystem Overview and Assessment format developed by Canada with some modifications to reflect the interests of the working group. This document is the result of that agreement.

In March 2007, the DFO in partnership with the NOAA completed a scoping exercise to determine the feasibility and availability of information resources for completing a *Gulf of Maine Ecosystem Overview Report* (Parker et al. 2007b). This *Gulf of Maine Ecosystem Overview Report* (EOR) builds on the findings of that scoping exercise. This document has undergone peer review by both Canadian- and American-based scientists.

1.2 Boundaries of Study Area and General Features

The Gulf of Maine-Bay of Fundy-Georges Bank marine ecosystem is a macro-tidally influenced, semi-enclosed coastal sea, terrestrially bounded by three northeastern U.S. states (Maine, New Hampshire and Massachusetts) and two Canadian Maritime provinces (Nova Scotia and New

Brunswick) (see Figures 1.1 and 1.2). The terrestrial portion of the Gulf of Maine watershed encompasses much of Nova Scotia, New Brunswick, Maine, New Hampshire and Massachusetts, and a small portion of Quebec. The total land area of this watershed is 179 008 km^2 (69 115 square miles). Only one of the six jurisdictions, Quebec, does not have Gulf of Maine shoreline; and only one of the six, Maine, is located entirely in the watershed (Gulf of Maine Council on the Marine Environment 2004). However, for the purposes of this report, only the offshore marine areas within the Gulf of Maine are considered, including relevant areas within the Bay of Fundy to the north, Georges Bank to the south, and the gulf proper. The inner coastal shelf, from about the 60 m isobath landward, is only described as it relates to the processes of the offshore portion of the Gulf of Maine. Within the Bay of Fundy, the focus is on outer reaches of the bay and not the Minas Channel, Minas Basin or Chignecto Bay. Therefore, when the term Gulf of Maine is used in this report, we refer to the entire gulf, including the Bay of Fundy and Georges Bank. However, as some research has been conducted based on political boundaries, not all of the information described here covers the entire Gulf of Maine. We have strived to point out to the reader when this may be the case.

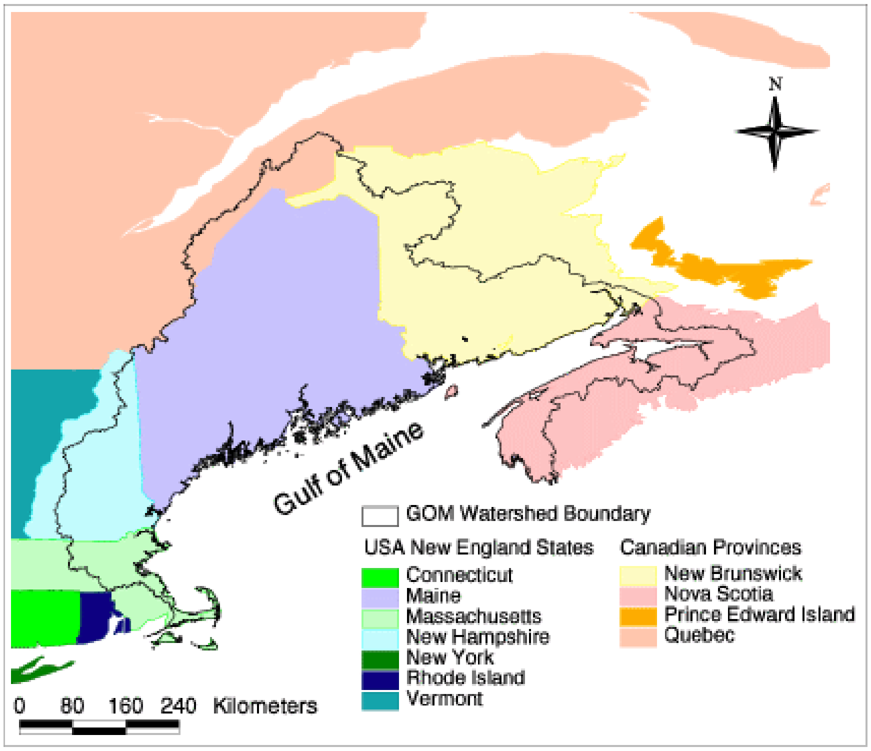

Figure 1.1: The Gulf of Maine Watershed encompasses much of Nova Scotia, New Brunswick, Maine, New Hampshire and Massachusetts, and a small portion of Quebec. The total land area of this watershed is 69 115 square miles, or 179 008 km^2. Only one of the six jurisdictions, Quebec, does not have Gulf of Maine shoreline; and only one of the six, Maine, is located entirely in the watershed.
Source: GM-WICS (2009).

Marine bathymetric features have loosely been used as the boundaries to define the Gulf of Maine for this report. However, physical features, such as marine geology, geomorphology and sedimentology are just a few of the habitat characteristics that influence aquatic flora and fauna of this ecosystem. Other features, such as oceanographic systems and climatic patterns, are also highly significant factors that do not always adhere to the physical boundaries of an aquatic system. So, although this report does not directly describe areas adjacent to our defined boundaries of the Gulf of Maine marine ecosystem, significant and critically important ecological linkages do exist with these neighbouring areas. Nevertheless, it is the larger-scale ecological characteristics of the open-water areas within the described boundaries upon which this report focuses. It is precisely these larger-scale characteristics, for example, that have caused scientists to frequently refer to the Gulf of Maine as a "sea within a sea" because its waters are separated from the Atlantic Ocean by the submerged plateaus of Georges Bank and Browns Bank, creating water temperature and salinity differences from the rest of the Atlantic Ocean.

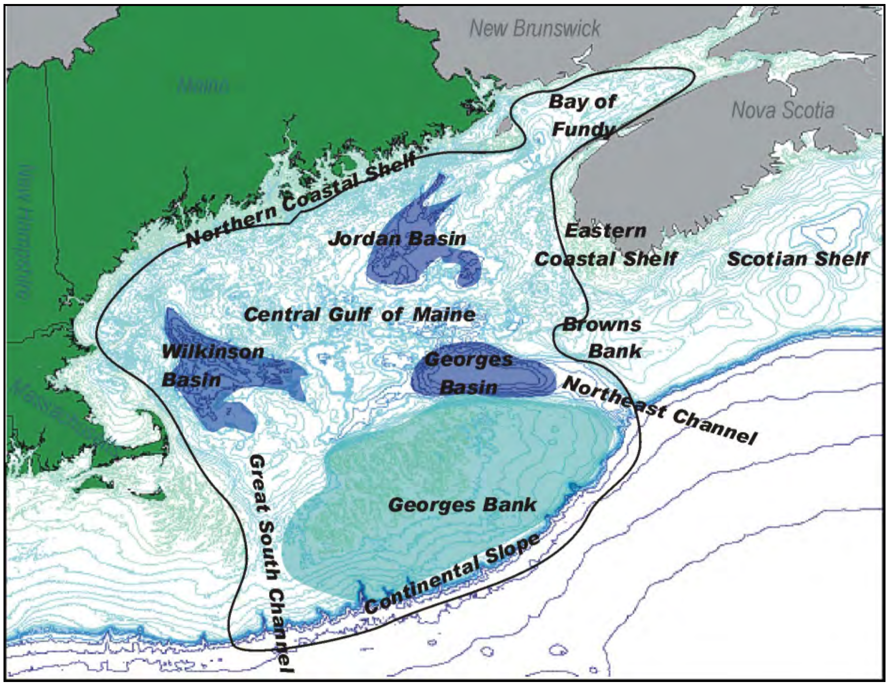

Figure 1.2: The physical boundaries and primary features for the *Gulf of Maine Ecosystem Overview Report*. The report does not address the complexities of the inner coastal shelf areas. The overview area runs along the Continental Slope from the Great South Channel to the Northeast Channel, and includes the Bay of Fundy in the north.
Source: Adapted from USGS (2007).

The Gulf of Maine area used in this report includes the Bay of Fundy, the Northeast Channel and Georges Bank, is bounded to the northeast by the Scotian Shelf and is separated from the waters to the southwest (i.e. the southern New England biogeographic area) by a boundary that extends from the southwestern end of Georges Bank towards the tip of Cape Cod, along the deepest part of the Great South Channel; in extent, it comprises 115 950 km^2 (Conservation Law Foundation –World Wildlife Foundation 2006). Georges Bank (28 800 km^2) is often considered its own biogeographic area. With its ovoid shape, the most southwesterly point of Georges Bank is bounded at the Great South Channel and its northeasterly tip is bounded at the Northeast Channel. The northern boundary separating this biogeographic area from the rest of the Gulf of Maine extends in a northeasterly direction from the Great South Channel at depths ranging from 50-100 m. The boundary shifts to an easterly course and extends to the western margin of the Northeast Channel, rounding the Northeast Peak and following the shelf edge (200 m isobath) back to the Great South Channel (Theroux 1998). Georges Bank is one of the most productive fishing areas of the northwest Atlantic (Backus and Bourne 1987).

The Bay of Fundy is a narrow funnel-shaped body of water that lies between Nova Scotia and New Brunswick. This large macro-tidal embayment and its oceanography are closely linked to the greater Gulf of Maine (Aretxabaleta et al. 2008, Chang et al. 2005, Desplanque and Mossman 2001, Xue et al. 2000). It is 270 km long and 60 km wide at its widest point, and encompasses offshore oceanic features with shallow banks and deep channels, as well as diverse coastal marine habitats (Willcocks-Musselman 2003). It is underlain by the Fundian Lowlands formation of Triassic sedimentary rocks (Pritchard 1955). The bottom contours largely follow the coastline and reflect its origin as a former drainage system originating in the Minas Basin-Truro area. The bay can be divided into two large regions, based on oceanographic parameters and biotic assemblages, with a transition zone between Point Lepreau and Musquash (Hunter and Associates 1982). The head of the bay, or the inner Bay of Fundy, shallows considerably and has extremely high tidal ranges that expose large expanses of mud flats. A description of the Minas Basin portion of the inner bay can be found in Parker et al. (2007a). The outer bay, also called the “mouth” of the Bay of Fundy, is the remaining portion that opens into the Gulf of Maine.

The outer bay is more oceanic than the inner Bay of Fundy, with cold summer and warm winter temperatures, high current velocities, high salinity and high water quality. It lacks the intertidal mud flats and salt marshes of the inner reaches; instead, its bottom consists of exposed bedrock and a coarse sand-and-gravel substrate winnowed by tidal currents (Davis and Browne 1996b). The defining characteristic of the Bay of Fundy is its gigantic tides, ranging from a mean height of 6 m (maximum 8 m) in the outer bay to a mean height of 11.9 m (maximum 16 m) in the furthest reaches of the inner bay, the highest in the world (Percy 2001, Cox 2007). The combination of strong tidal currents (7-18 km/hour in some areas) and complex bottom topography results in tidal rips, whirlpools, upwelling and intense mixing throughout the region. Productivity is exceptionally high and is greatest at the mouth of the Bay of Fundy due to tidal mixing. Certainly, the region’s unique topography and oceanographic conditions combine to promote highly productive phytoplankton and zooplankton populations that support high fish production (Sherman et al. 1987).

The Gulf of Maine, Georges Bank and Bay of Fundy regions are among the more diverse, productive and trophically complex marine temperate areas in the world (Link et al. 2002, Sherman and Skjoldal 2002, Overholtz and Link 2006). Piscivorous predators (carnivorous mammals and fish that consume primarily fish prey) and pelagic species are abundant (Read and Brownstein 2003, Brodziak et al. 2004), and include marine mammals such as humpback (*Megaptera novaeangliae*) and finback (*Balaenoptera physalus*) whales, harbour porpoise (*Phocoena phocoena*) and harbour seals (*Phoca vitulina concolor*), which are resident and abundant (Waring et al. 2002). The Gulf of Maine and Bay of Fundy region, furthermore, is critically important as a migratory staging area for millions of birds, and is also a significant summering and wintering area for them

Temperature and salinity conditions in the Gulf of Maine are determined by heat transfer between the ocean and atmosphere, inflow from the Gulf of St. Lawrence supplemented by flow from the

Newfoundland Shelf, exchange with offshore slope waters, local mixing, freshwater runoff, direct precipitation, and melting of polar sea ice (DFO 2008a). Year to year, water temperatures in the Gulf of Maine are among the most variable in the North Atlantic Ocean. Two currents dominate water circulation in the Gulf of Maine: the counter-clockwise gyre in the gulf and the adjacent clockwise gyre over Georges Bank (Link et al. 2008). Water circulating around the periphery of the gulf takes several months to make a complete rotation, and many parts of the gulf ecosystem are linked together by these circulating currents. Recent studies have shown that the inflow of relatively cool water of low salinity from the Scotian Shelf into the Gulf of Maine increased during the 1990s (Smith et al. 2001, Mountain 2004), causing salinity to decline on Georges Bank and throughout the surface waters of the northeastern U.S. continental shelf (Mountain 2004).

Several political boundaries separate states, provinces and nations in the Gulf of Maine and Bay of Fundy (see Figure 1.3); however, the natural processes that occur in the region pay no heed to these boundaries. Indeed, several species of fish, marine mammals and birds regularly migrate across these political boundaries in their life cycles and the gulf's currents ensure gulf-wide dispersion of the young of many sedentary species.

Figure 1.3: Location of the Gulf of Maine and Georges Bank off the eastern U.S. and Canada.
Source: Prepared by Stan Johnston, Fisheries and Oceans Canada.

2. METHODOLOGY OF STUDY

As with any report, the approach and methods used influence the resulting product. Therefore, the following section highlights some of the important methods employed during the writing of the *Gulf of Maine Ecosystem Overview Report* in order that the reader may better understand the perspective from which it has been written.

2.1 Sources of Information

Broad-scale electronic literary searches on the Gulf of Maine regularly produce 11 000-75 000 results, and it is likely that more than 30 000 documents relevant to the *Gulf of Maine Ecosystem Overview Report* exist (Parker et al. 2007b). In order to produce this EOR, a large number of overview, synthesis, review and summary-type documents have been synthesized for the marine subject areas covered. Those reviewed barely scratch the surface of the tens of thousands of study reports, monographs, mapping products, workshop proceedings and planning reports documenting various aspects of the geological, oceanographic and biological systems of the Gulf of Maine. However, they do represent existing synthesis of our knowledge on such topics as heat exchange, biogeochemistry and benthic infauna that are directly relevant to the *Gulf of Maine Ecosystem Overview Report*.

Early work on the Gulf of Maine-Bay of Fundy-Georges Bank marine ecosystem was conducted from the Marine Biological Laboratory in Woods Hole, Massachusetts, and the Biological Station at St. Andrews, New Brunswick, some of it by famous scientists such as Bigelow, Huntsman, Herrick, Steele, Pearce, Ketchum, Sherman, Hart and Hatchie. Today, there are over 50 institutes, including universities, conducting marine research around the Gulf of Maine. The region boasts world-renowned laboratories such as the Woods Hole Oceanographic Institution, the Northeast Fisheries Science Center, the Bedford Institute of Oceanography, and many others where research is conducted year round on all aspects of the ecosystem's geology and sedimentology, physical and chemical oceanography, biology and ecology, and fisheries and environmental issues. The gulf's offshore and coastal habitats, fisheries, wildlife and overall biological diversity are extensive, economically vital to the region, and an ecological treasure to sustain for future generations (Parker et al. 2007b).

Because of the great importance of the Gulf of Maine-Bay of Fundy-Georges Bank ecosystem to the residents of eastern North America, its physical, chemical, geological, and biological characteristics have been well studied for more than a century, and it is one of the most extensively researched marine areas in the world. With tens of thousands of publications spanning more than 100 years, it is not feasible to incorporate material from all of these, and the EOR provides only a snapshot of our knowledge of this system, drawing upon a wealth of knowledge. Sherman and others (1996), furthermore, cover many of the earlier U.S. studies. Some recent syntheses illustrate the extent of (Gulf of Maine) GoM literature, including Bigelow and Schroeder (1953, now republished), Thomas (1983), Gordon and Dadswell (1984), Backus and Bourne (1987), Thurston (1990), Conkling (1995), Sherman et al. (1996), Percy et al. (1997), Wallace and Braasch (1997), Lotze and Milewski (2002), Link and Brodziak (2002), Larsen (2004) and Pesch and Wells (2004). Organizations such as the Gulf of Maine Council on the Marine Environment (GOMC) have published extensively for many years, with many overview articles and technical reports (Cordes et al. 2006). There is also a variety of popular literature and many periodicals, such as the widely circulated *Gulf of Maine Times* and the *National Fisherman Magazine*. The reader is directed to the references section at the end of this EOR, and will find a number of other documents that cover particular areas of interest in greater detail.

2.2 Information Use and Reliability

As much as possible, this report relies on scientific literature and peer-reviewed information. However, where gaps exist, scientists familiar with the Gulf of Maine-Bay of Fundy watershed have been asked for personal comment, manuscript reports have been used and non-peer reviewed literature has been assessed (although an exhaustive search of all relevant collections at institutions around the Gulf of Maine or inquiry with all knowledgeable persons on the given field of expertise is not reflected in this document). These sources have been used with caution, and the most widely supported scientific understandings of the ecosystem are presented. The EOR, furthermore, has focused on material of an overview nature (on community rather than individual species scale) and does not provide a comprehensive summary of all works completed on the Gulf of Maine-Bay of Fundy-Georges Bank ecosystem. Reports that cover a limited spatial and time scale or subject matter, or that rely on pre-1980 research, were also limited in their inclusion in the *Gulf of Maine Ecosystem Overview Report*.

PART A – GEOLOGICAL SYSTEM

3. MARINE GEOLOGY

The processes that have taken place over millions of years to both create the very rock that underlies the Gulf of Maine waters, and to then shape those substrates into the physical contours (bathymetry) that exist, are extremely complex. The basic morphology of the Gulf of Maine that is visible today, including the numerous deep basins and the shallow banks, is thought to be the result of a complex sequence of marine deposition and subsequent river based deposition and erosion that was later altered by both glacial erosion and deposition (Backus and Bourne 1987). A large proportion of the offshore is overlain with metres to kilometres of sediments that form a relatively smooth and somewhat homogenous sea floor, at least at first glance. In this chapter we will provide an overview of both the broad aspects of the geology of the shallow banks, marine channels and deep basins of the Gulf of Maine, as well as an assessment of some of the important sedimentary features. This latter scale includes such things as modern sedimentation processes and the grain size of sediments, which influence where particular organisms may be found throughout the Gulf of Maine.

As the focus of this report is the offshore Gulf of Maine ecosystem, the complex coastal geology is addressed in a limited manner. However, other authors provide great detail on the various coastal geological processes of the gulf for the interested reader, e.g. Parrott et al. 2009; Costa et al. 2008; Uchupi and Bolmer 2008; Kelley et al. 1998; Barnhardt et al. 1996a-1996g; Fader 1996; Crossen 1991; Belknap and Shipp 1991; Belknap et al. 1988, 1989a, 1989b; Osberg et al. 1985; and Fader et al. 1977.

4. GEOMORPHOLOGY

Geomorphology is the study of landforms and the processes that shape them. On the broadest scales, the landscape is built up through uplift of the earth's plates (tectonics) and through volcanic activities. On progressively smaller scales, individual landforms are created by processes such as erosion and sedimentation. These geomorphic processes are influenced by such drivers as tectonics, climate, ecology, and human activity. The morphology of the Gulf of Maine is thought to have developed as a result of some bedrock types eroding more rapidly than others. Four major processes have been responsible for shaping the present morphology. These are preglacial erosion of areas exposed that were at one time above the oceans' surface; glacial erosion by bedrock scouring and melt water flows; late glacial and early post glacial sea level changes that were both relatively higher and lower on the landscape; and, a subsequent sea level rise relative to the land (marine transgression) (Fader 2007 unpublished).

The Gulf of Maine is part of the continental shelf, and the morphology of the gulf's seafloor is characteristic of glaciated continental shelf. It is therefore quite different than that of the U.S. shelf to the south, and more similar to the Canadian continental shelf that extends northward from the gulf. If you could easily look under the ocean's surface at the sea floor, you would see that the southern and western Gulf of Maine are characterized by relatively gentle bathymetric relief that is covered by a thick layer of sediments and glacial deposits. In contrast, the northern and eastern gulf has areas of exposed Paleozoic rocks (250+ million years old) that are formed into a series of irregular ridges, pinnacles, and channels, becoming thinly covered in sediments where the contours are less abrupt (Backus and Bourne 1987). The morphology of the Gulf of Maine consists of a 90 000 km^2 inner lowland area with an average depth of 150 m; the 28 000 km^2 Georges Bank, whose offshore crest is as shallow as 30 m below the ocean surface; and the Bay of Fundy, a narrow funnel-shaped body of water with an average width of 56 km and a length of 190 km (Willcocks-Musselman 2003, Tanner et al. 2006, Uchupi and Bolmer 2008, Todd et al. 2001). Although a number of deep basins exist within the Gulf of Maine, only 1.5% of the gulf is deeper than 300 m (Wolff and Incze 1998). On the seaward side of Georges Bank, the continental slope deeply cut by numerous canyons, forms the eastern boundary of the Gulf of Maine. Two large channels, the Northeast and Great South Channels, lie east and west of Georges Bank, providing passageways from the Gulf of Maine to the open Atlantic Ocean (Backus and Bourne 1987). Understanding the underwater landforms of the Gulf of Maine requires some understanding of the primary influencing processes that helped shape them. Here we provide an overview of geological processes that have influenced the gulf from the last glacial and post glacial periods.

The geological history of the seafloor that forms the structure of the inner continental shelf of the Gulf of Maine has both young and old components. The bedrock regions are the oldest and date back hundreds of millions of years to their formation. These hard crystalline rocks are primarily igneous or metamorphic (Stone and Borns 1986, Uchupi and Bolmer 2008). Ancient faulting and folding, and erosion of rocks with varied resistance occurred over millennia, and have resulted in the irregular shapes of the shoals, valleys and basins adjacent to the Maine and Bay of Fundy coastlines (Borns et al. 2004).

Figure 4.1: The most recent glacial episode brought the Laurentide Ice sheet eastward across the Bay of Fundy and much of the Gulf of Maine.
Source: USGS (2006).

Throughout history, the Gulf of Maine has been covered by ice a number of times. It has been above sea level, and has been below sea level. Multiple glaciations over the past 2 million years probably smoothed the landscape and seafloor without altering the overall bedrock influence on major morphology (Shaw et al. 2006, Butman et al. 2004, Valentine et al. 2001, Kelley 1987). The most recent glacial episode, the Wisconsinan Glaciation, began about 35 000 years ago. During this glaciation the Laurentide Ice Sheet spread south to New England, covering the Bay of Fundy and much of the Gulf of Maine (see Figure 4.1). The moving ice sheet would have scoured the crystalline basement rock of the gulf in a direction from land toward the open Atlantic, carrying with it tonnes of rock and sediment. Climatic warming forced the Laurentide Ice Sheet to start melting and receding as early as 21 000 years ago, soon after it reached Long Island, New York in the south (Sirkin 1986) and the Scotian slope to the east (Stea et al. 1998, Schnitker et al. 2001, Hundert 2003, Shaw et al. 2006, Parrott et al. 2008).

Although movement is comparatively slow, glaciers do move in a manner similar to rivers, generally flowing downhill through the lowest elevation within the topography. Within large sheets of ice, the areas of greatest movement are referred to as glacial “streams”. A conceptual model for the last deglaciation of Atlantic Canada shows how the ice margin lay close to the edge of the continental shelf at the last glacial maximum (Figure 4.2). Ice streams occupying continental shelf troughs in North America included secondary (less prominent) streams in the Bay of Fundy/Gulf of Maine region (Shaw et al. 2006). Repeated glaciations led to scouring of the sea floor by ice streams, and the formation of large transverse troughs across the Gulf of Maine. The largest of these troughs are the Northeast Channel and the Great South Channel (Hundert and Piper 2008). Glacial ice, moving southward in the area of the Great South Channel, sculpted the broad shallow depression, as well as deposited sediment to form low gravel mounds and ridges (Todd et al. 2001).

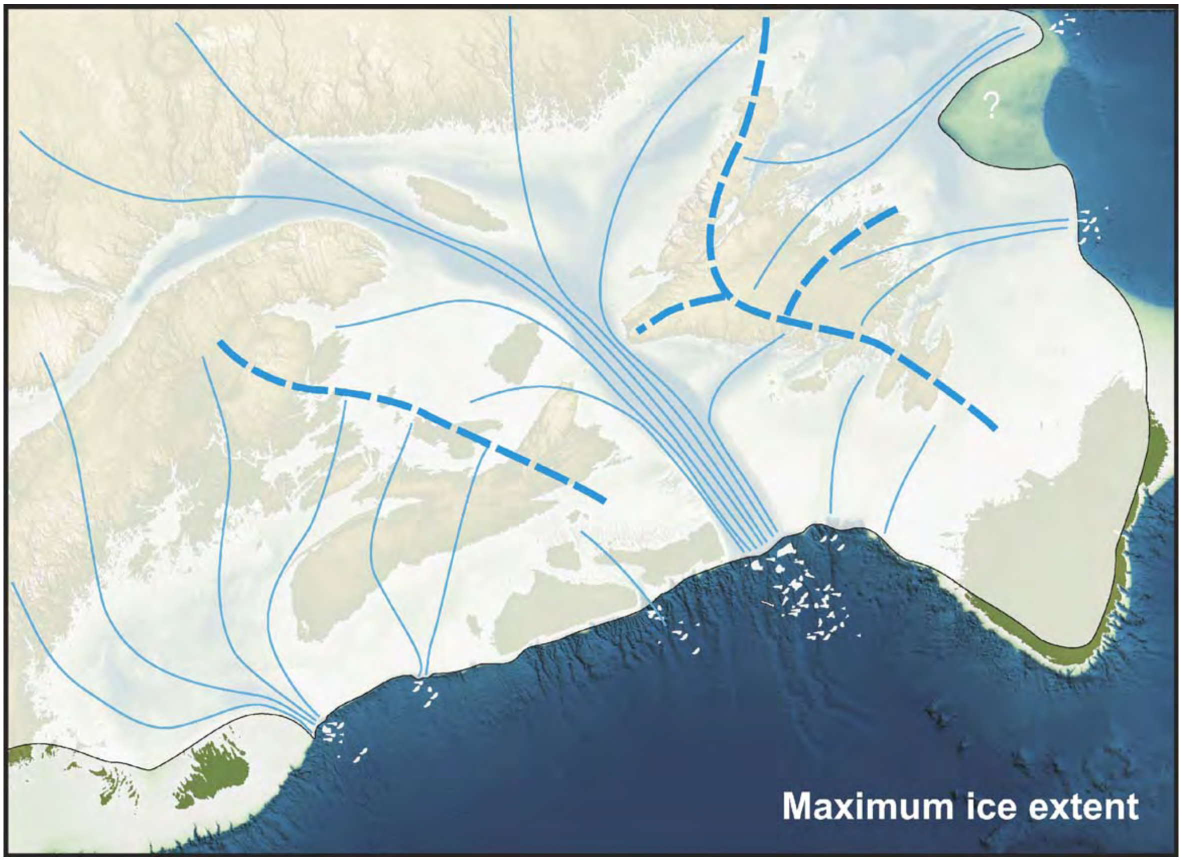

Figure 4.2: Maximum extent ice during the last glaciation. Thin blue lines are generalized flow lines; heavy blue dashed lines are major ice divides. The underlying digital elevation model shown here depicts the distribution of land and water at 13 000 years before present (Shaw et al. 2002), and is therefore an approximation only.
Source: Shaw et al. (2006).

The Northeast Channel was a major outlet for ice from the Gulf of Maine, and has been referred to as Fundy Ice Stream. It was fed by ice that converged within a large catchment area extending north into New Brunswick and New England. Rather than flowing directly south towards the ocean, however, the ice stream was contained within Northeast Channel, so that it flowed almost parallel to the edge of Georges Bank. Less-conclusive evidence for another ice stream is on unpublished multibeam bathymetric imagery of the north margin of Georges Bank. Multiple parallel ridges of acoustically incoherent material stacked against Georges Bank, where it slopes into Northeast Channel, are interpreted as ice-stream marginal moraines (Shaw et al. 2006).

By about 18 000 years ago (Figure 4.3) the delivery of large volumes of ice to the ocean was lowering ice elevations far inland of the margins, a process that would continue for many thousands of years. Ice streams occupied basins and troughs, and where the streams met the ocean large chunks would break off, or “calve” into the water. These areas became the quickest to retreat as the local climate began to warm. As deeper areas within the Gulf of Maine, having been scoured by glacial ice streams, became free of ice through calving, ice became stranded on the higher banks and intertidal areas where there was no mechanism for a similarly rapid removal of the ice (Shaw et al. 2006).

The ice margin withdrew from the Gulf of Maine to the present position of the Maine coast by 17 000 to 16 000 years ago (Borns et al. 2004), and grounded ice had disappeared entirely from the Gulf of Maine and Bay of Fundy by approximately 14 000 years ago (King and Fader 1986, Schnitker et al. 2001, Shaw et al. 2006, Parrott et al. 2008). In the Bay of Fundy, mapping based on multibeam bathymetry surveys and LiDAR (light detection and ranging) has been used to document geomorphological features formed during the Quaternary glaciation and deglaciation. Moraines and drumlins are topographically prominent. After grounded ice retreated from the area, icebergs scoured the seafloor in the waters east and south of Grand Manan Island near the mouth of the Bay (Parrott et al. 2009). The keels of icebergs similarly scoured furrows in the sea floor of the Northeast Channel (Todd et al. 2001). In the Stellwagen Bank area, in the west central portion of the Gulf of Maine, the most striking topographic features are the many long, narrow grooves that dominate the region. They typically are 50-100 m wide, 2-4 m deep, and up to 5 km long, and they have a dominant northeast-southwest orientation. These grooves are interpreted to be marks made by the jagged bottoms of icebergs that gouged the seabed by grounding here during the late stages of the last glaciation. The iceberg gouges are first observed at a water depth of 145 m and they disappear in the 70-75 m depth interval. The floors of many of the basins in this region (water depth greater than 120-125 m) are unmarked because icebergs would have grounded in the shallower surrounding area (Butman et al. 2004).

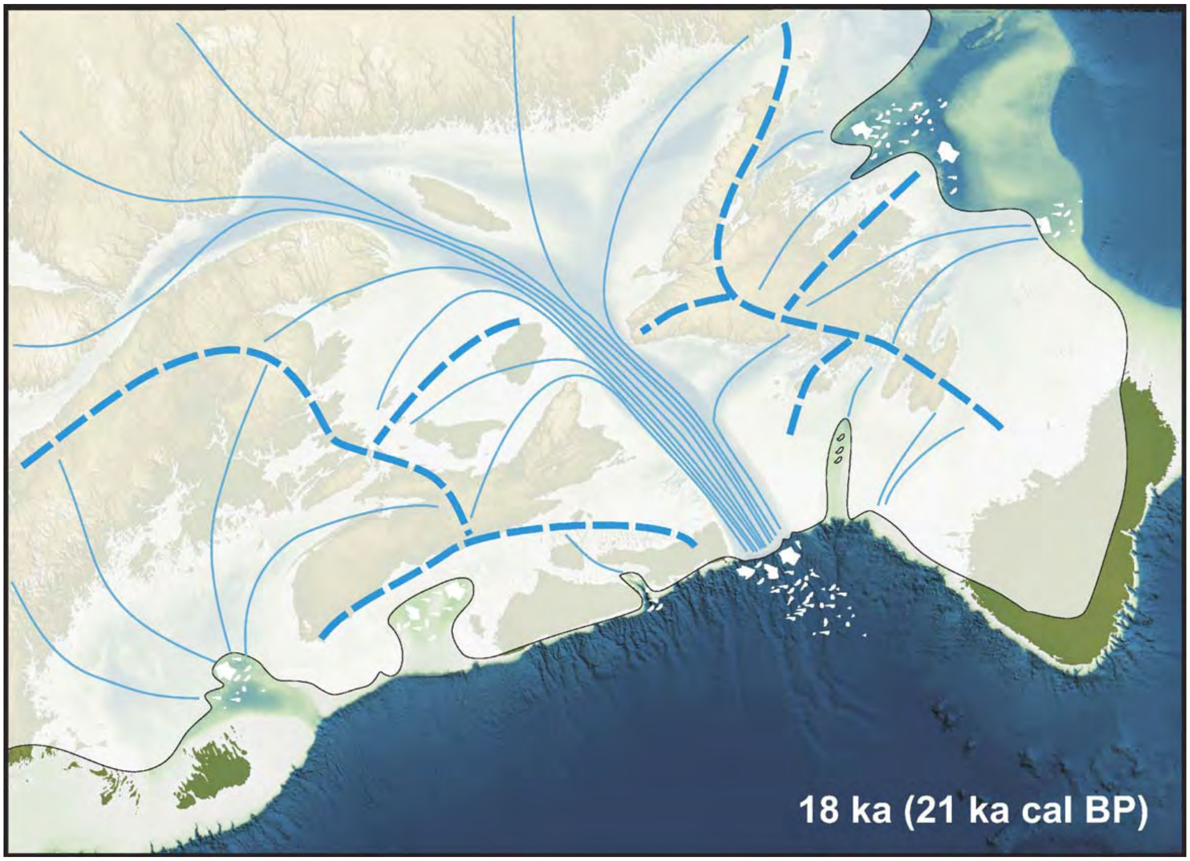

Figure: 4.3. Ice margins at 18 000 years ago. By this time there was a continued retreat of the calving margin into the Gulf of Maine and the area of Georges Basin.
Source: Shaw et al. (2006).

As the ice receded, tonnes of glacial till would have been left on what is now the Gulf of Maine seafloor. Further tonnes of till and glacial sediment would have been carried into the gulf by melt water. A vertical depression and rebound of the basement geology of the Gulf of Maine and eastern North America due to the weight and then melting of the Laurentide ice caused the shoreline of the Gulf of Maine to shift considerably during the last 14 000 years (Maine Geological Survey 2005). As a result, coastal processes associated with waves, tides, and currents reworked glacial deposits from elevations as high as 80 m above to as low as 60 m below the present shore (Kaplan 1999).

About 1000 years after glaciers retreated from the Gulf of Maine, low relative sea level allowed parts of the offshore banks to be emergent, forming islands (Figure 4.4). Georges Bank was an island, and there were likely some smaller islands between the bank and the mainland. These conditions continued along with increased emergence of southwest mainland Nova Scotia. Browns Bank to the north of Northeast Channel also became emergent. Farther southwest, the emergent George's Bank was separated from the mainland by only a narrow channel in the area of the modern Great South Channel. Through combining isobase maps with a digital terrain model of Atlantic Canada to map coastlines, Shaw et al. (2002) suggest that Georges Bank was connected to the continent by a peninsula in the west to Cape Cod as recently as 11 000 years ago. One thousand years later Georges Bank was an island once more, separated from the adjacent peninsula by nearly 100 km of open water. Georges Bank became submerged below the ocean about 8 000 years ago (Shaw et al. 2002).

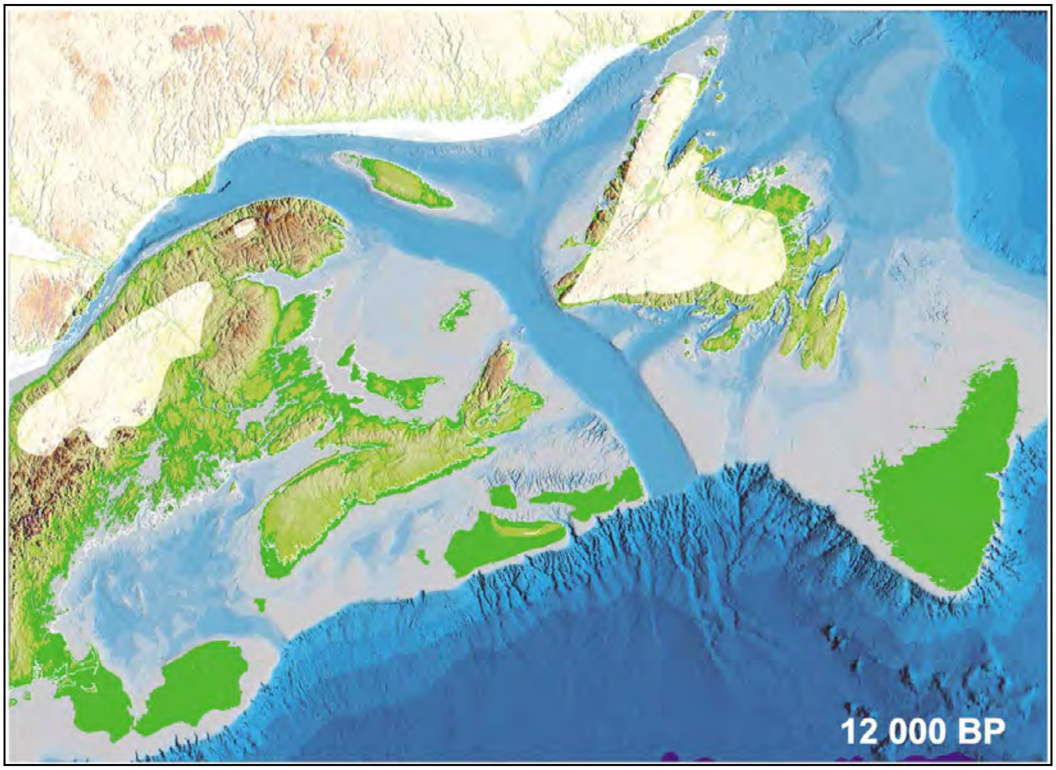

Figure: 4.4. The Gulf of Maine as it existed about 12 000 years before present. The current day coastline is shown with a white line, and highlights areas like Georges Bank that were emergent, and like coastal Maine that were submerged.
Source: Shaw et al. (2002).

Although scouring by glaciers had a significant influence on the shape of the ocean floor in the Gulf of Maine, bathymetry (the depth to the sea floor) has since changed substantially in some areas due to postglacial sedimentation and erosion. Thick deposits of postglacial mud (see Fader et al. 1982, King and Fader 1986, Shaw et al. 2002) in relatively deep basins created proportionally small changes in bathymetry. On the other hand, sediment thickness more substantially altered bathymetry in shallow areas. For example, 20 m high sand waves formed on Georges Bank in the postglacial period (Emery and Uchupi 1972 cited in Shaw et al. 2002), an area that is as shallow as 30 m (Backus and Bourne 1987). Along with deposition, there were processes of postglacial erosion. Large moraines may have existed on submarine banks, and may have been eroded during sea-level lowering. Erosion has significantly deepened the sea floor in places (Shaw et al. 2002). At the mouth of the Bay of Fundy, it is thought that the strong tidal currents associated with the large tidal range within the bay may have eroded older muddy sediment and prevented new material from accumulating (Maine Geological Survey 2005). Today, the surficial sediments and features are reworked and shaped by tidal and storm-generated currents, which erode and transport sediments from the shallow areas into the deeper basins. Over time, the shallow areas affected by these processes have become coarser as sand and mud are removed and gravel remains, and the deeper basins have been built up as they receive the winnowed sand and mud (Butman et al. 2004).

In summary, the geological processes of plate tectonics, faulting, sedimentation, and glaciation that have formed the basement rocks and primary geomorphology of the Gulf of Maine have been very complex. These processes formed the basic topographic structures that include modern day banks, basins and channels. The advance and retreat of several glaciations, including the most recent Wisconsinan glaciation, which covered the gulf between 21 000 and about 16 000 years ago, have largely been responsible for the deposit and shaping of sediment across the sea floor of the Gulf of Maine on top of the basement crystalline rock. Substantial quantities of fine-grained glacial-marine sediment were deposited along with till over virtually the entire gulf. Studies of terrestrial glacial movements and late Quaternary geology have been fundamental to establishing the nature of the sediment deposits found offshore in the Gulf of Maine region, as well as the timing of their deposition. Accumulations of river delta and littoral sediments on the inner continental shelf of the gulf contain a record of post-glacial sea-level changes and shoreline migrations (Barnhardt et al. 1997). Rivers in the region delivered large quantities of sandy and muddy sediment to the sea during the time of lower sea level (Kelley et al. 1992, Barnhardt 1994, Barnhardt et al. 1997, Uchupi and Bolmer 2008). The fine silts and clays, reworked from glacial deposits, collected in water depths generally greater than 60 m. Where enough sediment existed, relief associated with rock outcrops was smoothed or eliminated by burial (Maine Geological Survey 2005). The sand, gravel, and other unconsolidated sediments that today cover much of Maine and Nova Scotia are largely the products of glaciation, and continue to be eroded into the gulf along the coastlines and through the rivers. More modern marine sediments and land erosion continue to add to the extensive blanket of mud, sand, and gravel that covers the vast majority of the sea floor today. Localized tidal action, marine currents, and wave movement influence the sorting and distribution of the surface sediments, and create a complexity of smaller features such as shoals and sand waves. Shelf valleys, offshore canyons, pinnacles and rocky ledges further complement the bathymetry of the modern day Gulf of Maine.

4.1 Inner Shelf Bathymetry and Seascapes

Bathymetry is the measurement of depths of water and the information derived from such measurements (EEA 2011). Bathymetric (or hydrographic) charts usually show seafloor relief or terrain as contour lines called depth contours or isobaths. Bathymetric maps (a more general term where navigational safety is not a concern) may also use Digital Terrain Modelling and artificial illumination techniques to illustrate the depths being portrayed (Wikipedia 2011b).

The central and outer continental shelf areas of the Gulf of Maine are the primary focus of this report. This area, which includes the outer Bay of Fundy, begins at 60-80 m depth and extends to the eastern edge of the outer shelf. However, many biological and physical linkages exist between the inner continental shelf (landward of 60 m depth) and the central and outer regions. This is particularly true of geological erosive processes associated with streams and glaciers that have generally moved materials from upland and inner shelf regions toward the central and outer shelf. The inner continental shelf of the Gulf of Maine is a complex area. It includes the Eastern Coastal Shelf off southwestern Nova Scotian and the German Bank; the area northward across Lurcher Shoal through the inner Bay of Fundy; the area from Grand Manan Island along the coasts of Maine and New Hampshire; and, extends in a southerly direction from Cape Ann to Cape Cod.

The Maine Geological Survey (2005) identified three types of geomorphic compartments that extend from the coastline into the sublittoral zone. Based on bathymetry, sediment properties and geology of the inner continental shelf of the western Gulf of Maine, outer basins, rocky zones, and hard bottom plains dominate the seascape across much of the coastal shelf of the gulf (Figure 4.5). Although these compartments can be found in the inner continental shelf of the Gulf of Maine, they are also found offshore, and constitute a large portion of the transitional area between the inner and central continental shelf areas.

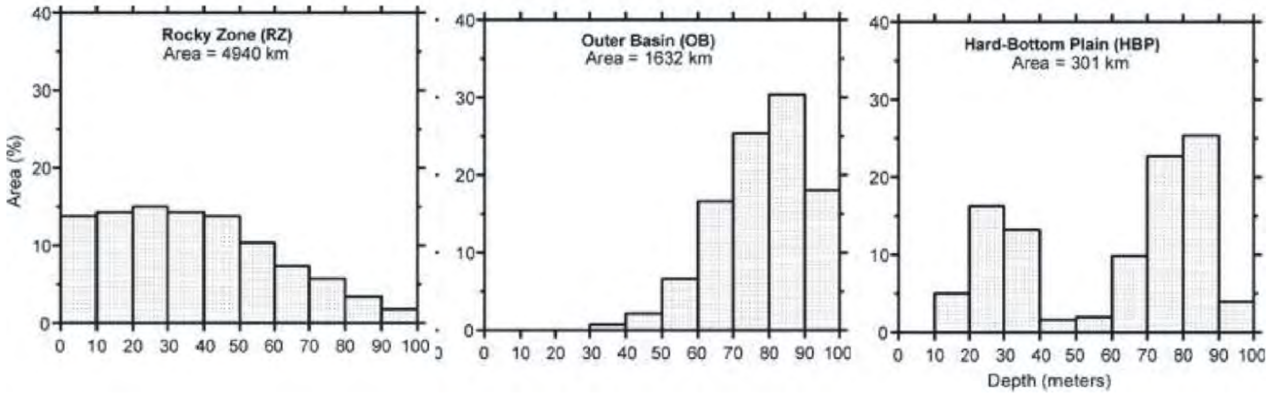

Figure 4.5: Area (%) graphs of the percentage of area of each of the three primary geomorphic zones found within the sublittoral zone of coastal Maine at various depths extending to 100 m. Although rocky zones show a symmetrical distribution centered on 30-40 m depth, outer basins comprise a larger portion of the deeper coastal water, and hard-bottom plains show a bimodal tendency, with abundances in both very shallow water and deeper water.
Source: Maine Geological Survey (2005).

The outer basins of the Gulf of Maine coastline are those that extend deeper than 60 m. These are not to be confused with deep central shelf basins such as Jordan and Wilkinson basins that extend well over 200 m. Instead, the outer coastal basins of the inner continental shelf have been described as generally having a subdued bathymetry, with 77% of their area covered by mud (see Figure 4.5), and with occasional outcrops of rock (Maine Geological Survey 2005). These inner shelf basins include Stellwagen Basin, Scantum Basin, Jeffrey's Basin, and Cashes Basin. In some areas there may be more than 50 m of sediment over the underlying bedrock of these basin features. The deep bowl shape of these inner shelf basins limits the influence of wind, waves and tidal currents, thereby allowing finer sediment particles to settle to the sea floor. Related structures are the many coastal shelf valleys that were completely excavated from overlying glacial-marine material by river flow, and that can be found along the seaward fringes of modern estuaries (Kelley et al. 1992). In some instances, linear bays along the coast of Maine clearly mark fault traces (Osberg et al. 1985) where fractures in bedrock were eroded by glacial and river processes. In some cases this erosion created what are now underwater valleys along the weaknesses in the bedrock (Kelley 1993), extending across the submerged coastal shelf deeper into the Gulf of Maine.

Rocky zones are a geomorphic feature that are generally found in less than 60 m of water along the inner shelf and that locally form shoals. Although bedrock dominates the substrate of rocky zones, sediment fills many fractures in the rock "ponds", and gravel aprons often form "halos" around more isolated bedrock outcrops and islands. Sediment in these ponds and halos is usually coarse grained and enriched (by as much as 100%) with shells from nearby encrusting organisms (see Kelley and Belknap 1991, Barnhardt and Joseph 1995, Barnhardt and Kelley 1995*)*. Despite the generally coarse nature of rocky zones, sediment samples from these regions contain the greatest range of particle sizes of any place on the inner continental shelf, and at least some muddy sediment occurs in most areas. Rocky zones can also be found further offshore, yet still on the inner continental shelf. For example, bedrock is exposed on German Bank off southwestern Nova Scotia (Todd 2009).

In the Bay of Fundy, the land surface rose rapidly following the retreat of glacial ice, causing the sea level to lower, so that the inner continental shelf is now less deeply submerged than that further to the east. Sambro Sand, a term used to describe a geological deposit that is mostly sand with silt and clay, is found at 120 m (and deeper) north of Browns Bank off the southern tip of Nova Scotia. Further into the Bay of Fundy, this deposit is found in shallower depths, at 37 m (and deeper) off Brier Island at the mouth of the Bay of Fundy. In the Bay of Fundy, increased current activity in the last few thousand years has modified the Sambro Sand deposits. It is actively being worked at the present time. Extensive sand waves, ripples and mega ripples with heights of up to 18 m have been mapped in these recent Sambro Sand deposits (Davis and Browne 1996a).

Hard-bottom plains are the vast areas on the coastal shelf of low bathymetric relief, and which are covered by gravel (83%), sand (14%) and rock (3%) (Maine Geological Survey 2005). The hard-bottom plains occupy a large area off eastern Maine (Dickson et al. 1994) and a smaller region off southern Maine at depths ranging from 60-90 m and 10-30 m, respectively.

In the eastern Gulf of Maine, near the Nova Scotian coast, bathymetric features of the inner continental shelf include German Bank, Trinity Ledge and Lurcher Shoal. Because these features are relatively shallow, their surface layers typically exhibit a variety of relief, including iceberg scours and pits as are visible on German Bank and Murr Ledges (Todd et al. 2004, Parrott et al. 2008).

The bathymetry of German Bank, off southwestern Nova Scotia, demonstrates a variety of moraines that were formed during the slow retreat of grounded ice during the last glaciation within the Gulf of Maine. Four regional moraines are apparent on the southwestern portion of the bank (Figure 4.6). They are 25-40 km long, curved segments concave to the northwest. They are roughly parallel, and traverse a wide range of water depths. The true moraine heights are likely appreciably greater than apparent heights, given they are buried under glaciomarine sediment. These larger moraines are indicative of halts in glacial retreat. There are also patterns indicative of re-advance. In between the larger moraines are smaller De Geer moraines several meters high and 2 to nearly 10 km in length, perhaps indicative of annual retreat (Todd 2009). Careful examination of multibeam bathymetry reveals that the moraines are superimposed on bedrock fluting indicating ice flow from the north and northwest (Shaw et al. 2006). Cobbles and boulders have been sampled from these moraines, while the smooth surface of the troughs between the moraines is composed of sand and pebble gravel (Todd 2009).

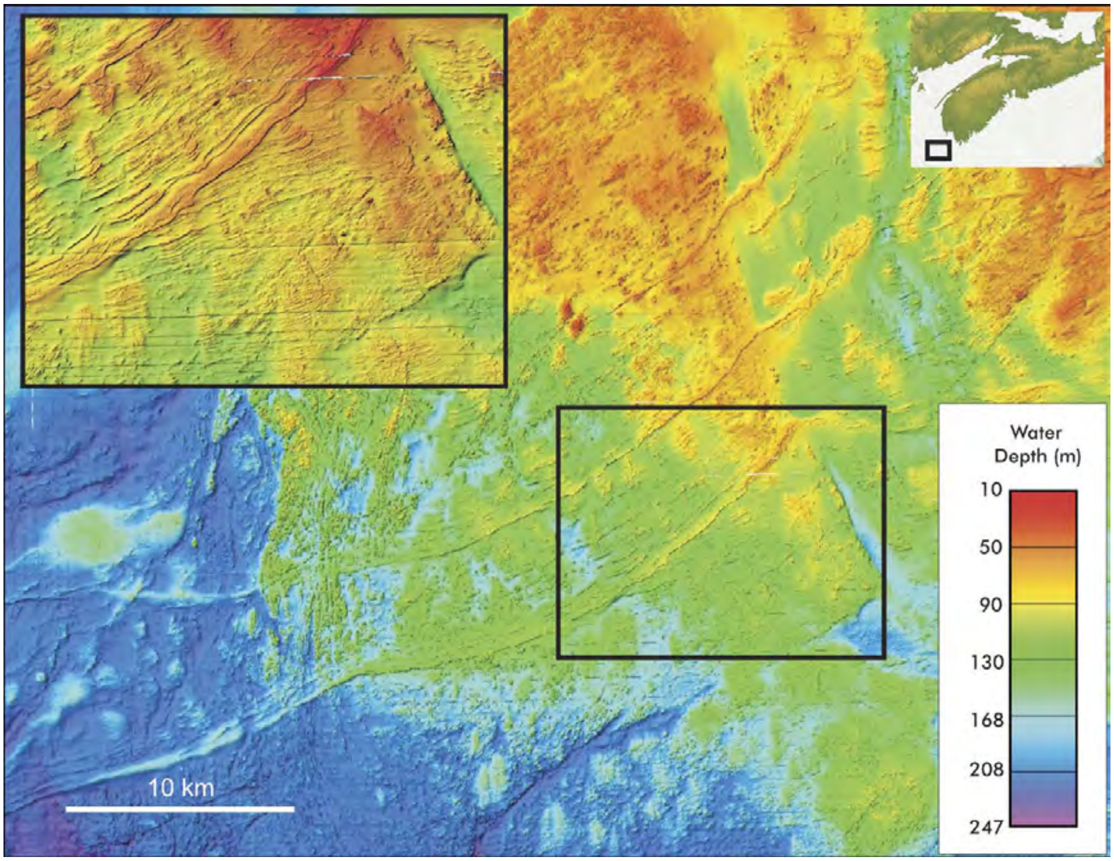

Figure: 4.6. Multiple moraines on German Bank, indicating gradual retreat of ice grounded in shallow water, punctuated by minor re-advances. The inset is an enlargement of the area within the box, showing large regional moraines and smaller DeGeer moraines.
Source: Shaw et al. (2006).

The geomorphology of northern German Bank is characterized by oval mounds of 500-800 m length and 100-300 m width, with long axes oriented northwest-southeast. They have elevations of 10-15 m above the surrounding seafloor. Assessed data indicate these features are till, deeply draped with glacimarine sand and silt. These were likely drumlins with their long axes parallel to the direction of ice flow. In some areas, megaflutes are interspersed with the drumlins. Similar to drumlins, megaflutes tend to be longer and narrower (Todd 2009).

4.2 Central Shelf Bathymetry and Seascapes

The central shelf covers the largest area of the gulf, consisting of broad open basins and shallow regions of complex morphology. Jordan, Wilkinson, and Georges basins, along with the central gulf that surrounds these features, are all part of the central continental shelf in the Gulf of Maine. It further includes the shallower Stellwagen Bank and Jeffrey's Ledge areas in the western gulf. As shown in Figure 4.7, the U.S. Geological Survey (USGS) Gulf of Maine Area Program (1998) has divided the region into a number of key features (known as physiographic areas) in order to classify the gulf's bathymetry and seascapes. The relatively flat central Gulf of Maine is a central continental shelf feature that covers some 59 000 km^2.

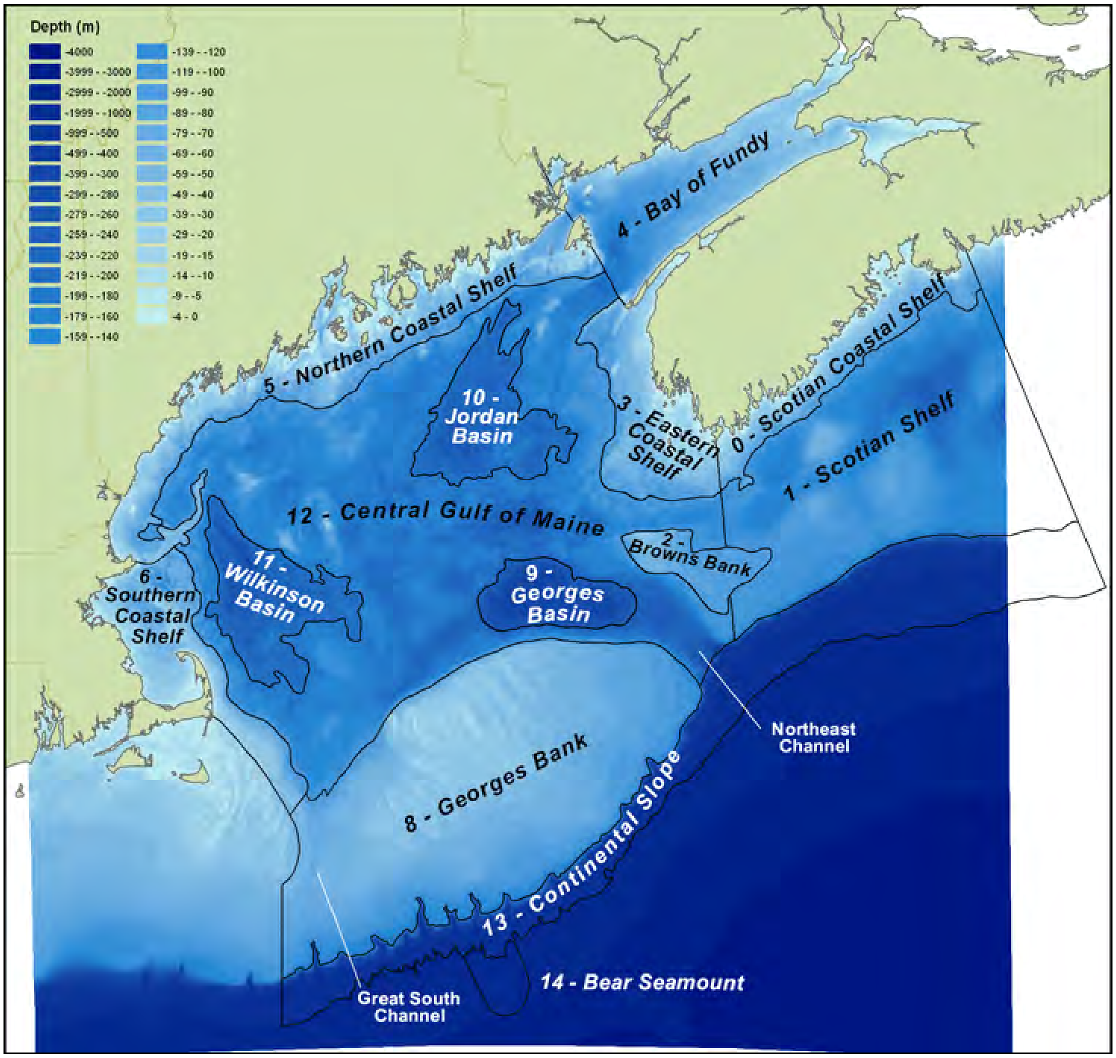

Figure 4.7: This bathymetric map that shows the relative location of large bathymetric features of the Gulf of Maine, including banks, basins and channels (feature numbers further correspond to data in Table 4.1). Complexity is added to each of these features by smaller morphological features such as canyons, shoals, and pinnacles.
Source: Wolff and Incze (1998).

The average depth of the Gulf of Maine is approximately 130-150 m (Wolff and Incze 1998, Backus and Bourne 1987). However, such a number is greatly misleading of the true offshore bathymetric diversity that exists within the Gulf of Maine. As shown in Figure 4.8, the surface area is significant at various depths within the gulf. The seafloor of the central Gulf of Maine is dominated by hummocky moraine topography over about half of the seafloor in water depths of 100-300 m. In other areas, covering about one-third of the 2 085 km that were seismically surveyed, a postglacial marine silty clay unit is up to 25 m thick. These marine silts and clays display a smooth, nearly level, surface except for apparent scour around bedrock promontories and V-shaped depressions suggestive of pockmark formation (McClennen 1989).

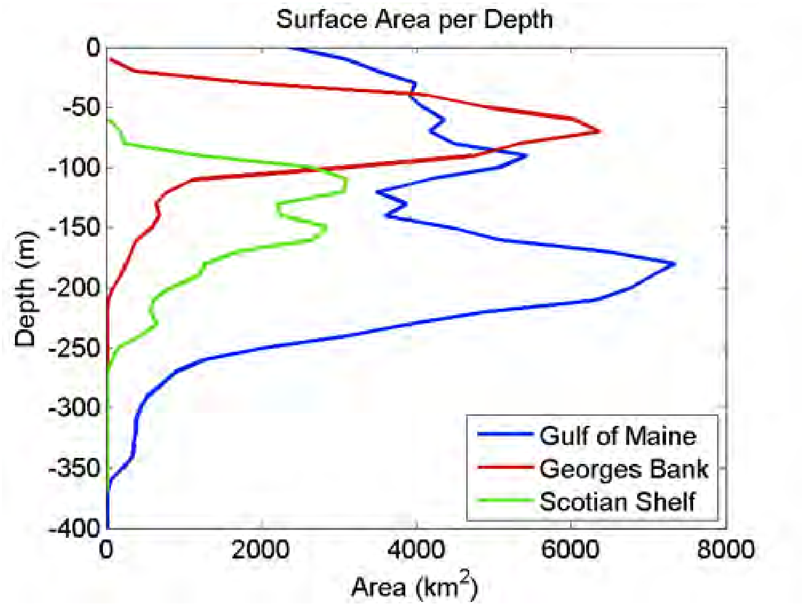

Figure 4.8: This image shows the approximate area (km^2) of the Gulf of Maine (which here includes the Bay of Fundy) and Georges Bank that exists at various depths, relative to area at depth for the Scotian Shelf. Note that Georges Bank has a significant area at depths <100 m, and the Gulf of Maine has a relatively large area at a wide range of depths.
Source: Wolff and Incze (1998).

There are a number of deep basins within the Gulf of Maine. However, Georges Basin, Wilkinson Basin, and Jordan Basin are the three largest (Table 4.1), and comprise approximately 11% of the area of the Gulf of Maine. They are more specifically located within the central continental shelf portion of the gulf. However, numerous other (20+) smaller basins also exist, including the Murray Basin, Grand Manan Basin, Rogers Basin, Howell Basin, and Crowell Basin. In total these basins make up about 30% of the floor area of the Gulf of Maine (Backus and Bourne 1987).

In contrast to the basins, Jeffrey's Ledge, Jeffrey's Bank, and Stellwagen Bank are a few of the more shallow bathymetric features found on the central continental shelf, and located a short distance offshore in the western Gulf of Maine. Stellwagen Bank, for example, is located some 40 km from the coast, and is a glacial deposit of sand, gravel and rock that today lies a mere 20 m below the surface (NOAA 2009). These features are similar in nature to the outer shelf banks.

Table 4.1: Surface area, total volume of water overlying the feature, and mean depth of the Gulf of Maine ecosystem bathymetric features (see Figure 4.7 for corresponding region numbers, which are classified according to depth). Total volume is all water below the surface for the area defined by each region.

Region	Name	Surface area (km^2)	Total volume (km^3)	Mean depth (m)
2	Browns Bank	2 951	268	-85
3	Eastern Coastal Shelf	7 760	481	-57
4	Bay of Fundy	12 544	920	-68
5	Northern Coastal Shelf	14 116	832	-54
6	Southern Coastal Shelf	8 203	457	-51
8	Georges Bank	41 934	3 353	-75
9	Georges Basin	4 110	1 246	-298
10	Jordan Basin	6 694	1 524	-222
11	Wilkinson Basin	7 078	1 655	-228
12	Central Gulf of Maine	59 041	10 357	-170
	Gulf of Maine	**164 431**	**21 093**	**-131**

Source: Wolff and Incze (1998).

The central Gulf of Maine consists mainly of a series of deep basins separated by glacial ridges. A large end moraine extends across the central and eastern Gulf of Maine onto the Scotian Shelf. Known as the Fundian Moraine, this feature forms a break between Georges Basin and Crowell Basin to the north. This moraine is part of a complex of such moraines that exist from the gulf across the Scotian Shelf (King and Fader 1986).

4.3 Outer Shelf Bathymetry and Seascapes

The outer continental shelf area of the Gulf of Maine consists of the area from Nantucket Shoals eastward across the Great South Channel and Georges Bank, and northeastward across the Northeast Channel. Northward across the Northeast Channel, Browns Bank is typically considered part of the Scotian Shelf that extends northward along the Nova Scotian coastline.

The Northeast Channel and the Great South Channel are unique offshore bathymetric features of the outer continental shelf. These channels were formed in part by freshwater erosion of glacially deposited sediments, and even today fulfill a “channel” function to circulate ocean water into and out of the Gulf of Maine. The Great South Channel has a sill depth (the shallowest cross section) of about 75 m, whereas the Northeast Channel is considerably deeper. The sill depth of the Northeast Channel, the primary inflow of ocean water to the Gulf of Maine, is 230 m below the ocean surface (Backus and Bourne 1987). Sand, transported by modern tidal and storm generated currents flowing north-south through the Great South Channel, form large east-west trending dunes and ridges typically 5-10 m in height (but ranging up to 20 m) (Valentine et al. 2002, Todd et al. 2001). During glacial and deglacial times, the sea floor of the Northeast Channel was extensively scoured by the keels of icebergs. Under the influence of strong tidal and storm generated currents, fine grained sediment has been winnowed from the coarse sediment of these relict iceberg furrows, leaving a gravel pavement with cobbles and boulders over much of the seafloor (Todd et al. 2001).

Between these two channels, the outer shelf consists of a large shallow bank (Hundert and Piper 2008) known as Georges Bank. Georges Bank is the shallowest part of the offshore Gulf of Maine, and has a more or less flat top shallower than the 100 m isobath. Approximately 50% can be found shallower than 60 m (Backus and Bourne 1987). Georges Bank is a bedrock cuesta, formed by gently tilted sedimentary rocks that have a steep slope on one side exposed as a cliff or escarpment. It is similar in this regard to other outer continental shelf banks off Nova Scotia (Davis and Browne 1996a). If the side slopes of Georges Bank are included in its area down to the "foot" of the bank, it covers nearly 42 000 km^2 (Wolff and Incze 1998). Although it averages a depth of about 75 m (Wolff and Incze 1998), Georges Bank rises to within 30 m of the ocean's surface on the northern edge at a location called Georges Shoal (Backus and Bourne 1987).

To provide a bathymetric overview of the Gulf of Maine, this document has described the physically dominant features across the continental shelf. However, each feature has additional complexity that contributes significantly to the ecosystem's habitat diversity. As an example, Georges Bank has a number of smaller "embedded" bathymetric or physiomorphic units that form a diverse seascape. On top of Georges Bank there are shoals. These are sand ridges that lie on the shallowest part of the bank, and run in a northwest - southeast trending direction (see Figure 4.9). The shoals of Georges Bank are as long as 75 km, and spaced some 10 km apart. In addition to the shoals, there are 20 m high sand waves superposed at 50-300 m spacing (Twichell et al. 1987 cited in Lynch and Naimie 1993, Uchupi and Austin 1987). Georges Bank had a layer of sediments deposited over it by glaciers during the Wisconsinan glaciation. These sediments were reworked by the subsequent sea level transgression that periodically exposed the bank, and by modern currents. Today, sand dominates the shallowest part of the bank and comprises sand sheets and sand wave fields oriented perpendicular to the predominant semidiurnal tidal flow. Gravel dominates the remainder of the bank (Todd et al. 2001). Sand wave fields exist around the Gulf of Maine where significant water movement aids in their formation. For example, they have also been identified in the Bay of Fundy where waves of 4-12 m height and 0.75 km length exist as part of the Margaretsville Dunefield in the south central portion of the bay (Percy et al. 1997). As earlier noted, at the same time that ice receded quickly away from lower areas along calving embayments, it was left stranded for a period of time on the shallow banks of the Gulf of Maine. These stranded ice margins were probably slowly retreating ice walls, and they produced parallel moraines on Georges Bank (Shaw et al. 2006). Further bathymetric variability exists on the seaward side of Georges Bank. A series of incisions lies between the outer edge of the bank and the open Atlantic that are known as submarine canyons. These canyons are part of the Atlantic Ocean fringe of the Gulf of Maine, and can be up to 1 km deep. Oceanographer and Lydonia Canyons are but two of the approximately eleven canyons that exist along the Atlantic side of Georges Bank between the Northeast and Great South channels (Backus and Bourne 1987). So, although Georges Bank's shape is typically described as a broad relatively flat feature, when examined at a larger scale it has canyons, sand waves, moraines, and shoal areas that provide a great diversity of habitats and seascapes.

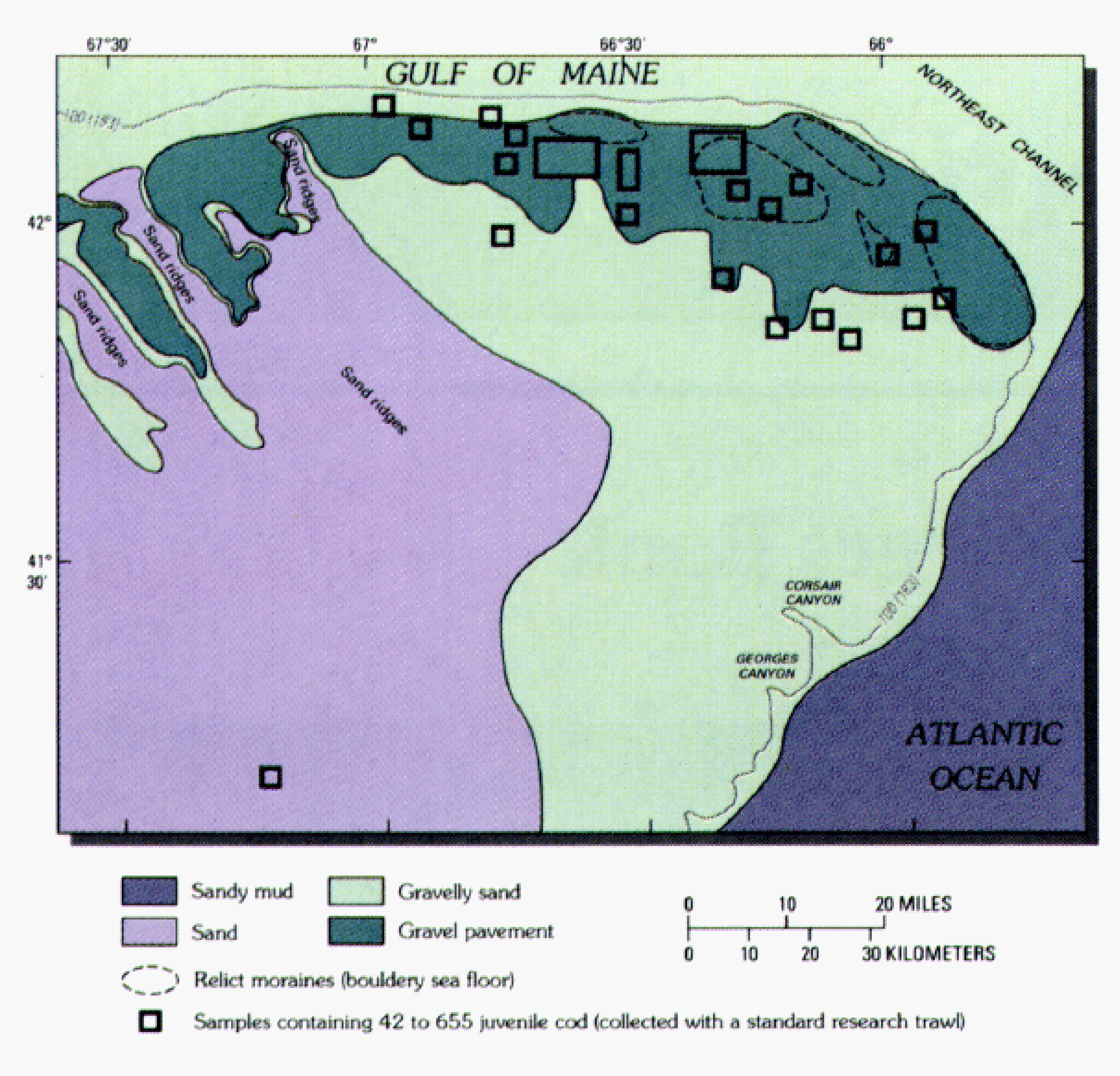

Figure 4.9: Georges Bank surface sediment map depicting the geographic distribution of sandy mud, sand, gravelly sand and gravel pavement along the northeast peak of the bank. Note the parallel sand ridges, or shoals, in the top left corner of the image, and the submarine canyons on the lower right.
Source: Valentine (1992).

5. SEDIMENTOLOGY

Sedimentology is the scientific study of sedimentary rocks and of the processes by which they were formed (EEA 2011). The aim of such study is to derive information on the conditions which acted to deposit a rock unit, and the sequence in which these units were deposited. In this way, each individual rock unit can be placed in geological history as a whole. The scientific basis (known as the principle of uniformitarianism) of sedimentology is that the sediments within ancient sedimentary rocks were deposited in the same way as sediments which are being deposited at the Earth's surface today (Wikipedia 2011c). This section provides an overview of the sedimentology of the Gulf of Maine, focusing on the more current processes such as marine deposition, shoreline erosion, and fluvial (river) erosion. Much of the sediment that exists within the Gulf of Maine, and that continues to be eroded into the gulf from the adjacent land is derived from glaciation. These glacial related processes were discussed previously in the section titled, Geomorphology.

A number of standards exist for naming sediment grain sizes. Wentworth scale or Picklwe-Wentworth scale are ones typically used in North America, although there are others such as Krumbein phi scale and Atterberg scale (Wikipedia 2011a). The sediment names used in this document are those used by the referenced authors, and although the units have not been standardized to one scale, Table 5.1 will allow the reader to understand the approximate size range to which a referenced name may refer. The term mud, for example, typically includes several grain sizes of material, including silt and clay.

Table 5.1: Particle size range and naming chart based on the Wentworth scale (1922).

Metric Size Range	Wentworth Range (inches)	Wentworth Name	Other Names
>256 mm	>10.1 in	Boulder	Boulder
64–256 mm	2.5–10.1 in	Cobble	Cobble
32–64 mm	1.26–2.5 in	Pebble	Gravel
16–32 mm	0.63–1.26 in		
8–16 mm	0.31–0.63 in		
4–8 mm	0.157–0.31 in		
2–4 mm	0.079–0.157 in	Granule	
1–2 mm	0.039–0.079 in	very coarse sand	sand
0.5–1 mm	0.020–0.039 in	coarse sand	
0.25–0.5 mm	0.010–0.020 in	medium sand	
125–250 µm	0.0049–0.010 in	fine sand	
62.5–125 µm	0.0025–0.0049 in	very fine sand	
31.25–62.5 µm	0.00015–0.0025 in	Silt	Mud
1/∞-3.9 µm	1/∞ –0.00015 in	Clay	
1/∞-0.97 µm	1/∞–0.000039 in	Colloid	

Source: adapted from Wikipedia (2011a).

Sediment mapping in the Gulf of Maine was conducted during the late 1980s by the Maine Geological Survey, the University of Maine, and the University of New Hampshire (Birch 1984a, 1984b, 1990), and recently, further mapping has been carried out by the Geological Survey of Canada (Todd 2009, Todd et al. 2004, Shaw et al. 2006) and the U.S. Geological Survey (Butman et al. 2004; Valentine et al. 2001, 2002). Reports defined broad-scale subdivisions within the gulf based on terrain texture, rock type, geologic structure and history (Kelley et al. 1989a, Kelley and Belknap 1991). Although, as shown in Table 5.1, there are a wide range of sediment particle sizes, three general classes of surficial sediments occur in the Gulf of Maine (see Figure 5.1).

- **Gravelly areas.** Gravel is a common feature of inner shelf sediment; but extensive areas of gravelly sediment cover only 12% of the seabed in the central and outer Gulf of Maine (Barnhardt et al. 1997). In many instances, the gravel has a rippled surface and may contain minor amounts of coarse sand (Maine Geological Survey 2005). In areas where scouring (scraping) of the seabed has occurred, a gravel-lag deposit covers the seafloor. Gravel also occurs in small linear bands where moraines exist on the seabed. Along the inner shelf of the Maine coast it is most abundant in the 20-40 m depth range, except in eastern Maine, where the hard-bottom plain is covered with gravel to depths of at least 100 m. In the Bay of Fundy gravels are concentrated in the central and southeastern bay (Hunter and Associates 1982).

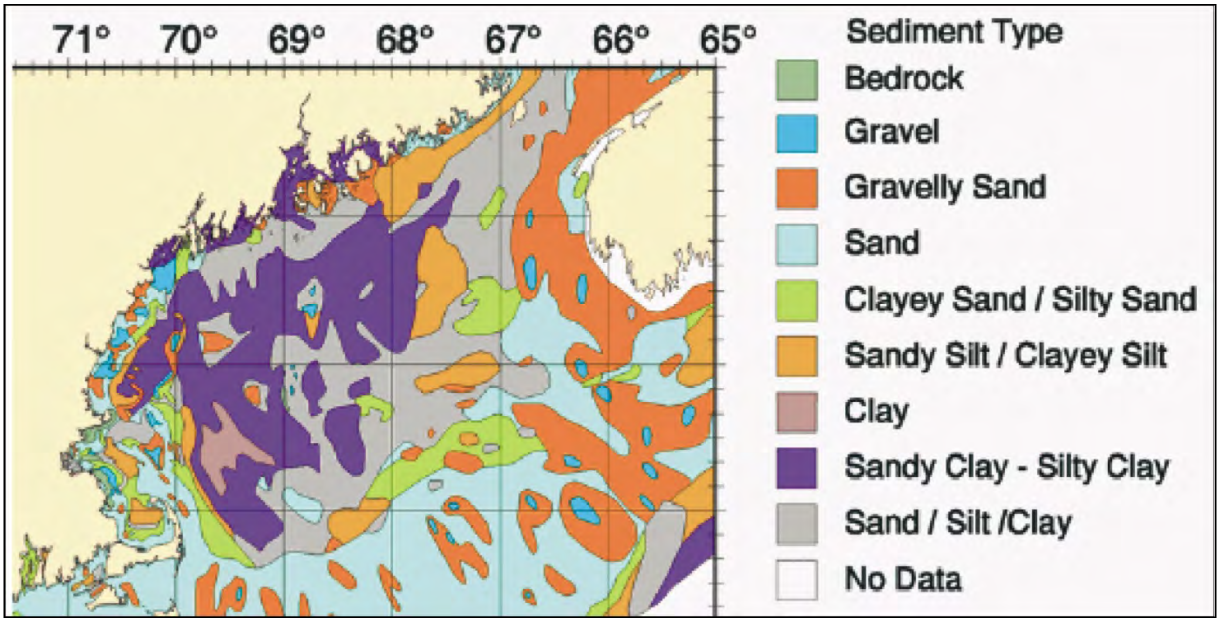

Figure 5.1: General spatial distribution of surface sediment classes within the Gulf of Maine. Mud, composed of silt and or clay, covers large areas of the gulf sea floor.
Source: modified from National Undersea Research Center as presented in Link et al. (2007).

- **Sandy areas.** Sandy areas are relatively rare along the inner shelf of the western Gulf of Maine, and occupy only 8% of the seafloor (Barnhardt et al. 1996a-1996g). The sandiest region is adjacent to southern Maine and New Hampshire. Further offshore, sandy areas exist on Georges Bank, where the sand forms ridges, shoals and waves at relatively regular intervals (Lynch and Naimie 1993), and the Great South Channel (Todd et al. 2001). These areas are visible in Figure 5.1. Sand is uniform in texture and strongly contrasts with bordering areas of gravel and rock. In deeper, lower energy areas, sand frequently is mixed with mud or gravel (Maine Geological Survey 2005).
- **Muddy areas.** Muddy regions are the most common areas on the continental shelf in waters deeper than 100 m (Barnhardt et al. 1996a-1996g), and poorly sorted silt (mud) can

be found in most Gulf of Maine basins (Backus and Bourne 1987). It is the dominant seabed material in all near-shore areas except for off southern Maine and near the Bay of Fundy (Maine Geological Survey 2005). Within the Bay of Fundy, mud deposits occur primarily on the northwestern side of the bay (Hunter and Associates 1982). Mud accumulates where there is an available supply of fine-grained sediment and still water conditions that favour the slow settling of small particles or their entrapment by sessile (slow-moving) organisms, such as polychaete worms. Deep-water mud is derived from the erosion of deposits in shallow water, as well as the organic remains of formerly living organisms.

5.1 Nature and Characterization of Surface Sediments

Any depression in a marine environment where sediments accumulate over time is known as a sediment trap. Major areas for deposition of generalized sediment types in the marine environment of the Gulf of Maine can include:

1. Beds of estuaries with deposits of mud.
2. Littoral (near-shore) zones for sands (e.g. beach sands, runoff river sands, coastal bars and spits) that are largely silicate minerals and rock fragments with little faunal content.
3. The continental shelf for silty clays, with significant marine faunal content.
4. The outer shelf margin with low terrigenous (land based contribution) sediment, instead consisting mostly of calcareous faunal skeletons.

Generally, thick sediments cover the central and outer continental shelf within the Gulf of Maine. These layers are up to 16 km deep in Georges Basin (Backus and Bourne 1987). Measurements in the inner shelf areas of the Gulf of Maine indicate that as much as 12 m of modern mud exists on the seafloor, which is abruptly underlain by older glacial-marine sand and mud (Kelley et al. 1992). As shown in Figure 5.1, the grain size of surface sediments varies spatially across the gulf.

In the sublittoral zone of the Gulf of Maine, an area generally described as lying between low tide and the edge of the continental shelf, collected bottom samples contain mostly sand and gravel, but also small amounts of mud (see Figure 5.2). The hard-bottom plain is associated with a large series of glacial moraine and till deposits. These were likely completely covered by sediment and later exposed by winnowing action of the modern current regime that has generally prevented the settling of finer grained silt and mud. Muds are dominant within the outer basins (Maine Geological Survey 2005).

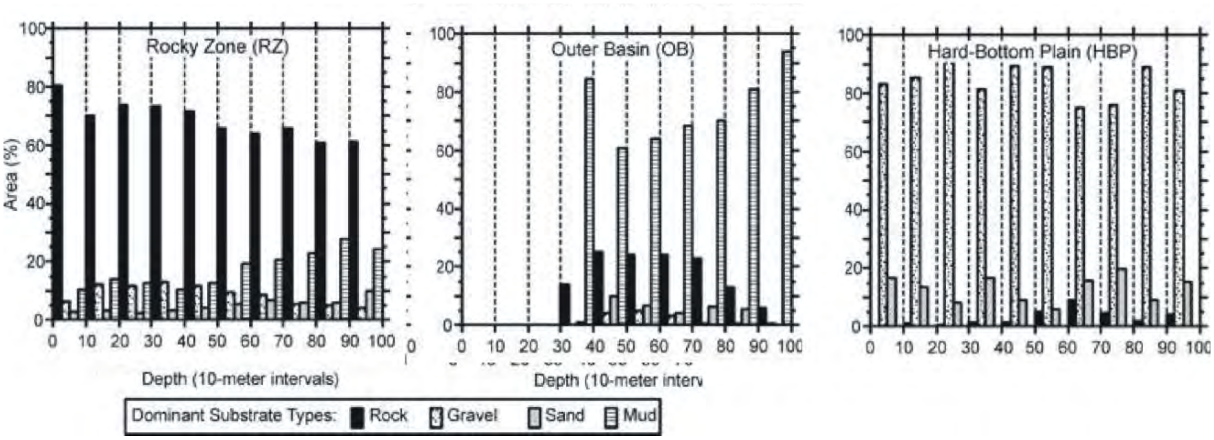

Figure 5.2: These histograms depict the percentage of area covered by rock, gravel, sand and mud for each of the three primary geomorphic zones found within the sublittoral zone of the coastal Gulf of Maine between the shoreline and 100 m depth. This demonstrates how rock dominates rocky zones at all depths; mud is most abundant in outer basins; and gravel is dominant in hard-bottom plains.
Source: Maine Geological Survey (2005).

Although large areas of the gulf can be generalized as muddy, gravelly, or sandy, it is important to note that at a finer resolution, a number of substrates can be found within a relatively small geographic area of the ocean floor. Using German Bank off southwestern Nova Scotia as an example, its surficial geology exhibits ice contact, with widespread deposits of glacial till. Some of this was reworked during sea level transgression to a gravel lag ranging in grain size from pebbles (2-64 mm) to cobbles (>64-256 mm) to boulders (>256 mm), while glaciomarine silt (sediments that result from fallout of glacial melt water plumes and ice rafted debris) is exposed at the seabed in small basins across the bank. Postglacial sediments, derived from current and wave reworking of earlier deposits, are predominantly sand with minor amounts of gravel. Although typically only a few meters thick, these can be found in broad sheets up to 20 m thick in deeper water (>100 m) on the western German Bank. There are also exposed bedrock outcrops with a rugged and fractured surface some 30 m below the gulf’s surface. (Todd 2009, Todd et al. 2004).

The dominance of glacial-marine sediment as an offshore deposit has been well recognized (Belknap et al. 1986, 1987; Kelley et al. 1986, 1989a, 1989b, 1989c). It typically fills depressions in bedrock and is often covered by more modern mud or sand. In areas of currents, however, this glacial-marine sediment may be exposed on the seafloor. The sediment supply to central and outer continental shelf areas has decreased since the last glacial maximum as the sea level has risen and land based sources of sediment are now further away (Hundert and Piper 2008). However, sedimentation and transport continue within the Gulf of Maine driven by ocean currents, waves, and river erosion and transport of sediments to the marine environment. Coastal erosion and land erosion by rivers are two major factors creating suspension of new sediment within the water column of the Gulf of Maine.

The most widespread recent sedimentary deposit to be made in much of the inner and central shelf regions of the Gulf of Maine is muddy glacial-marine sediment, locally known in Maine as the Presumpscot Formation (Maine Geological Survey 2005). The Presumpscot Formation ranges in texture from massive deposits of mud to well-layered beds of sand, silt and clay (see Figure 5.3). It probably entered the sea as rock sediment from glacial tunnels (Kelley 1989) and accumulated rapidly near these source tunnels 13 000-14 000 years before present *(*Dorion et al. 2001*)*.

Even far offshore it is possible for water movement to re-suspend ocean floor sediments, allowing these sediments to get redistributed to new locations. Suspended sediment concentrations reach a high of 500-1000 ug/l on the top of Georges Bank during the winter (Backus and Bourne 1987), likely the highest concentration in central and outer shelf regions of the Gulf of Maine. However, in comparison, large portions of the inner Bay of Fundy exceed 50 000-200 000 ug/l of suspended sediments during each tidal cycle (Greenberg and Amos 1983, Swift et al. 1971).

Figure 5.3: The Presumpscot formation of glaciomarine mud, which here changes colour from dark gray and brown upwards to a tan, silty sand at the top of the section, is typical of sediments that would have most recently been deposited in much of the Gulf of Maine.
Source: Weddle et al. (2001).

In terms of modern sedimentation, the Bay of Fundy is arguably the most currently active area in the Gulf of Maine. In the Bay of Fundy, glacially derived sediments comprise much of the seabed of the bay and show significant spatial differences (Amos and Long 1980, Amos 1984). The abundance of sand in the Bay of Fundy is the result of wave erosion of the Triassic sandstone cliffs that surround the shoreline, supplemented by the input of glacial outwash sand (Stea 2003). Amos (1984) suggests that a total of 3 x 10^6 m^3 of sand is introduced to the Bay of Fundy annually from erosion of the cliffs. Horizontal erosion of cliffs varies from 0.55-1.5 m per year. The cliff erosion supplies approximately 1 x 10^6 m^3 per annum of fine-grained sediment to the Bay of Fundy, while a further source of fine-grained material is from direct seabed erosion (Amos and Long 1980, Amos 1984, Amos et al. 1991). Recent estimates suggest that the conservative total volume of Quaternary sediment eroded from the trenches at Cape Split and Cape D'Or is 4 km^3 (Parrott et al. 2008).

Sediment transport within the Gulf of Maine is driven by currents, and occurs in areas such as Georges Bank, the Bay of Fundy, and the Great South and Northeast Channels where strong currents exist (See Section 7.3 - Water Currents and Masses). It is suggested that a current 1 m above the sea floor must exceed 0.25-0.35 m s^{-1} in order to move the fine sands on Georges Bank

(Backus and Bourne 1987). Waves on the surface of the Gulf of Maine primarily influence sedimentation of the modern day Gulf of Maine through coastal erosion; however, they can also influence transport and turbidity on the shallow banks and coastal shelf, particularly during storms (Backus and Bourne 1987). Nonetheless, waves are a much smaller influence on transport of sediments than currents. In shallow bank areas, where tidal or wave currents may influence fine sediments down to about 60 m depth, a series of superimposed sand structures known as ridges, waves, mega ripples and ripples (from largest to smallest) are formed. All are constantly moving features. In areas where the velocity of a current may not be strong enough to suspend sediment into the water column or create bedload movement, it will still influence what size particles settle to the seafloor in that area. In this way, deposition of sediments around the Gulf of Maine is strongly influenced by water currents. For example, fine silts and clays often get deposited in the deeper basins of the gulf where water movement is minimal.

In the Bay of Fundy sediments are not in equilibrium, and both the bottom and the shoreline of the bay are eroding and shifting. Redistribution of unconsolidated sediment takes place between the upper and lower bay, particularly during storms. Although it is suggested that the ebb tide is more turbid than the flood, and that residual currents slowly transport mud from the head of the bay toward the Gulf of Maine, primarily along the New Brunswick coast (Hunter and Associates 1982), the sedimentation budget of the bay, including its linkage to the rest of the Gulf of Maine, is not well understood (Percy et al. 1997).

Stellwagen Bank shows sharp transitions between sediment types and energy levels. Today, in the area of the bank, the sea floor is modified mainly by strong southwestward flowing bottom currents caused by storm winds from the northeast. These currents erode sediments from the shallow banks and transport them into the adjacent basins west of the bank. With time, the banks become coarser, as sand and mud are removed and gravel remains. Pebbles and cobbles in sand exist on the northeastern margin of the bank at 58 m depth, where storm wave currents expose gravel by transporting sand to the west. Coarse sand exists on the western edge of the Stellwagen Bank at 37 m depth. A muddy seafloor exists on the eastern edge of the Stellwagen Basin at 79 m depth, and is an example of a low energy and low deposition area (Todd et al. 2001, Valentine et al. 2001).

5.2 Habitat Classification and Physical–Biological Relationships

The Gulf of Maine ecosystem is a geologically complex coastal and ocean basin that gives rise to a great variety of habitats. Coastal habitat diversity and complexity, here, is greater than it is in more southerly temperate coastal regions (Costa et al. 2008). For this report, we have defined coastal as the inner continental shelf, from about the 60 m isobath landward, with the focus of the report being offshore of this area. Much of the geological influence differentiating between marine habitats of the offshore Gulf of Maine has to do with sediment particle size. There are also physically large geological features and areas of exposed bedrock that add to the complexity of habitats offered by the geological structure of the gulf. The large offshore geological features that create unique marine habitats include the banks, channels, and basins of the Gulf of Maine.

Basins are the deep areas of the gulf, and typically range from 60 m deep for coastal basins, and from 200 m for offshore basins. The deepest point in the Gulf of Maine is at the bottom of Georges

Basin, some 377 m (Backus and Bourne 1987). Because of their structure, basins tend to hold a deep stratified layer of cold saline water, have little to no current movement, have virtually no light penetration to the sea floor, and have very fine grained silt and mud surficial sediment. These characteristics are largely derived from the shape of the underlying geology, and support specific benthic communities that are described in greater detail in Section 9.2 - Benthic Communities. A second large physical habitat linked to the underlying geology is the deep channels that exist within the Gulf of Maine. Like basins, these areas are more than 100 m below the surface, and in some locations may be even deeper than the basins. However, deep offshore channels have the added feature of significant water velocities and areas of exposed bedrock or coarse geological substrates. The most notable deep channels within the Gulf of Maine are the Northeast and Great South Channels, which bookend Georges Bank, and which respectively serve as the primary inflow and outflow channels of marine waters to the gulf.

Finally, the Gulf of Maine banks, the most famous of which is Georges Bank, are shallow offshore areas. Large portions of Georges Bank lay a mere 40 m below the surface of the Atlantic Ocean, although the bank lies nearly 150 km from the nearest land (Backus and Borne 1987). There are a number of these bank areas in the Gulf of Maine, including Stellwagen Bank and Jeffrey’s Bank. Light typically penetrates to the sea floor through the water column above these shallow geological features. Waves and currents tend to keep the water over the banks well mixed, at least for periods of the year. The movement of water across the banks also tends to prevent the finest particles of sediment from settling on banks, instead exposing slightly more coarse sands and even gravel substrates. These surficial substrates, which form a variety of habitats, are a result of the basic geological structure of the banks and their interaction with ocean processes. Like basins and channels, the Gulf of Maine banks attract a unique variety of living organisms. These large geological features are further discussed in Section 4 - Geomorphology.

Bathymetric features are just one component of benthic habitat. It is important to note that adding the surrounding and associated oceanographic features with the bathymetric diversity further expands the number of different habitats available for the marine biota of the Gulf of Maine. One project identified a total of 36 unique pelagic and 77 unique benthic seascape classes within their three defined biogeographic regions: the Gulf of Maine (including the Bay of Fundy but excluding Georges Bank), Georges Bank, and the Scotian Shelf (see Table 5.2). These seascapes were defined by a combination of depth, substrate, and temperature-salinity zones. Many of the benthic seascapes were quite limited in their geographic extent; for example, those that were most extensive occupied 28% of the Georges Bank area and 14% of the Gulf of Maine-Bay of Fundy area (Conservation Law Foundation-WWF 2006). In contrast, the pelagic seascapes that were the most extensive occupied at least 20% of the Gulf of Maine-Bay of Fundy.

Although the large geological features and seascapes described above may be some of the most easily recognizable habitat types to the average person, the grain size of the sediments that blanket most of the offshore bottom of the Gulf of Maine is perhaps the most influential parameter on the distribution of marine biota. This geological influence is most strong in influencing the composition and distribution of benthic and demersal communities that live on, in, or near the sea floor (Conservation Law Foundation-WWF 2006). The distribution of marine worms, flatfish, lobster, scallops, and a number of other benthic organisms are influenced more by the content of silt, sand, gravel and pebble within the sea floor sediments than whether they occur on a bank or in a basin. Marine benthic communities, those organisms living on or near the bottom of the ocean, are commonly classified on the basis of whether they occur on hard or soft substrates, and on the basis of particle sizes ranging from large boulders to fine particles of mud. Grain size influences the size of organisms that may live amongst the grains, as well as which species might attach to, forage over, and spawn on the surface of the substrate (Etter and Grassle 1992). This is not to imply that oceanography is not important to these organisms, only that sediment particle size is a critical component of the equation. The size of these particles influences where some organisms can be found during a particular season and/or period of their life cycle, or may influence whether they will be found at a given location at all. A more complete examination of Gulf of Maine sedimentology is provided earlier in this chapter.

Table 5.2: Benthic and pelagic seascapes classified in the Gulf of Maine marine ecosystem (Gulf of Maine here includes the Bay of Fundy).

Number of benthic and pelagic seascapes classified					
Seascape	Unique	Gulf of Maine	Georges Bank	Scotian Shelf	Total
Benthic	77	29	22	57	108
Pelagic	36	14	14	19	47

Source: adapted from Conservation Law Foundation–WWF (2006).

Examples of relationships between sediment grain size and biological communities within the Gulf of Maine include the biogenic sand-gravel assemblage identified on Georges Bank (Thouzeau et al. 1991), the sand bottom community within the Bay of Fundy (Hunter and Associates 1982), the sublittoral hard substrate communities near Grand Manan Island (Ginn et al. 2000), the lamp shell community that has been reported by Kostylev et al. (2001) from immobile gravels at depths of 90-120 m in the southeast corner of the Gulf of Maine, important spawning areas for Giant Sea scallop *Placopecten magellanicus* on gravel lag areas of both German Bank and Georges Bank (Todd et al. 2001), and the various coral communities associated with the coarse gravel substrates of the Northeast Channel (Mortensen et al. 2006). Additional details on the relationship of Gulf of Maine biota and the ocean substrates can be found in Section 9.2.2 - Invertebrates: Infaunal communities.

PART B – OCEANOGRAPHIC SYSTEM

6. SEASONAL CLIMATIC PATTERNS

Two broad categories of oceanography consist of the study of the physical and the chemical characteristics of the ocean. While physical oceanography focuses on how the ocean moves through such mechanisms as tides, currents, upwelling/downwelling, waves, and stratification, chemical oceanography examines the make up of the water itself. Chemical oceanographers study such things as temperature, salinity, and nutrients. The climate of a region and individual weather events can have a significant influence on both the chemical and physical oceanography. In fact, in some cases the climate and events can have significant influence on oceanographic character in far removed areas if an oceanographic link exists between the two locations. Such is the case, for example, in the Gulf of Maine where climate around the Great Lakes can influence seasonal salinity within the gulf.

The following section describes key features of the seasonal climatic character of the Gulf of Maine region and how it influences the physical and chemical oceanography of the gulf.

6.1 Air Temperature

Annual average temperature for the Gulf of Maine and Bay of Fundy region shows considerable variability on interannual and longer time scales (see Figure 6.1) (Wake et al. 2006). For example, cooler years were recorded in 1904, 1917 and 1926; relatively warm years in 1949, 1953, 1990, 1998 and 1999. Extended warm periods are also evident, such as the middle of the last century and the 1990s. Cool periods occurred at the beginning of the 20th century and the late 1960s. However, an even more important observation is the long term air temperature trend for the region. During the 20th century there was a clear air temperature warming trend over the Gulf of Maine (Keim et al. 2003, Trombulak and Wolfson 2004). Based on the linear trend (represented by the red line in Figure 6.1), the region's average annual temperature has increased by about 0.8° C (1.4° F) since 1900 (an average temperature increase of 0.09° C (0.162° F) per decade).

Considering the information to 2002, the 1990s was the warmest decade on record in the Gulf of Maine region. Over the last 33 years in that time period, annual average temperatures increased 1.0° C (1.8° F) (an average temperature increase of 0.30° C (0.54° F) per decade), a rate three times higher than for the entire century (see Figure 6.2).

These longer term annual warming trends are also reflected in the seasonal data. Monthly air temperature data allows for the investigation of seasonal trends in temperature (Wake et al. 2006). Winter has shown the most significant warming over the last 100 years of the time series, with average December-February temperatures increasing by 1.4° C (2.5° F) (see Figure 6.3). Even more striking is the 2.4° C (4.3° F) increase in winter temperatures over the period 1970-2002. This amount of warming is comparable to the average wintertime temperatures of Halifax, Nova Scotia, being shifted more than 250 km, or 2 degrees of latitude, southward to the "average" wintertime temperatures of Boston, Massachusetts; or of the average wintertime temperatures in Boston being shifted southward to the "average" wintertime temperatures of Philadelphia, Pennsylvania (Wake et al. 2006). There is enhanced warming in the coastal regions, relative to inland locations. These warmer winter air temperatures represent one of the most significant changes in climate over the last three decades of the time series in the Gulf of Maine region and are consistent with other winter and spring trends, including decreasing snowfall and days with snow-on-ground, earlier lake ice-out dates and peak spring flow in unregulated rivers (see Keim et al. 2003, Trombulak and Wolfson 2004, Wake et al. 2006).

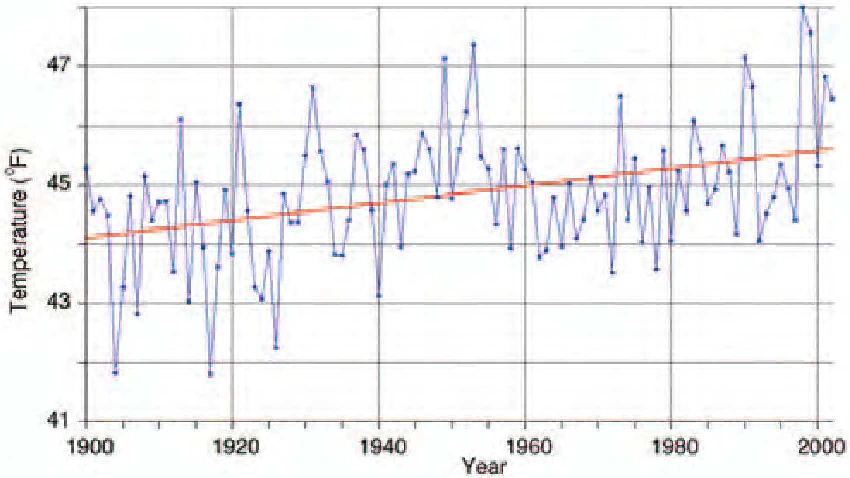

Figure 6.1: Average annual temperature for the northeastern U.S. and Maritime Canada cross-border region that includes the Gulf of Maine marine ecosystem, from 1900 through 2002. This time series is a spatially averaged temperature record from 136 stations in the region representing 92% of the region's climate zones. Note the warming trend over this time period (red line).
Source: Wake et al. (2006).

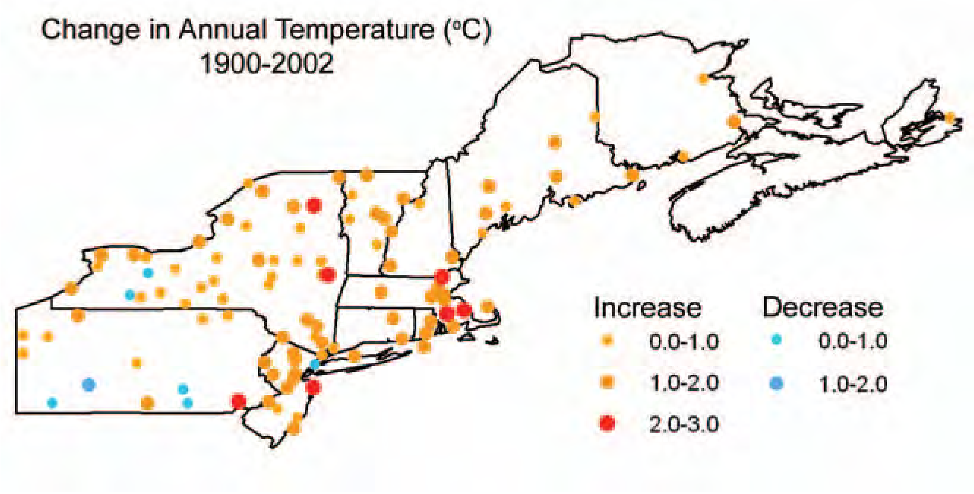

Figure 6.2: Map illustrating the linear trend in annual temperature (°C) for the northeastern U.S. and Maritime Canada cross-border region that includes the Gulf of Maine marine ecosystem, for approximately 100 years from 1900 through 2002. Cooling trends are shown with blue dots, while warming trends are shown with red dots. All areas around the Gulf of Maine reported increasing air temperatures.
Source: Wake et al. (2006).

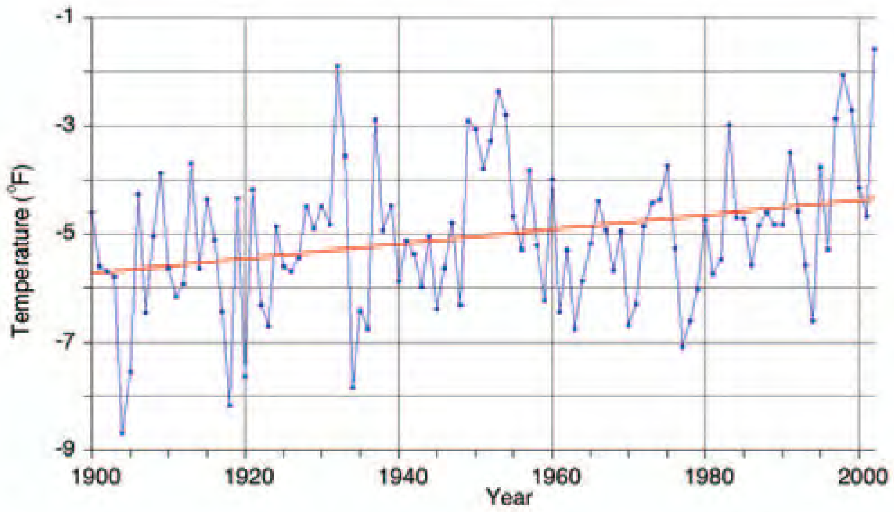

Figure 6.3: Average winter (December, January, February) temperature for the northeastern U.S. and Maritime Canada cross-border region that includes the Gulf of Maine marine ecosystem, from 1900 through 2002. This time series documents the long-term average temperature warming across the region (red line), and the annual variability in average regional winter air temperature (blue line).
Source: Wake et al. (2006).

Air temperature has a significant influence on the water temperatures in the Gulf of Maine because of the transfer of heat between the ocean and atmosphere (The other significant influence on marine water temperature is from source waters that flow into the gulf from the Scotian Shelf and through the Northeast Channel) (DFO 2008a). Because the water temperature within the Gulf of Maine is spatially and temporally varied, having large seasonal cycles, east-west and inshore-offshore gradients, and depth gradients (Petrie et al. 1996), summarizing when and where heat transfer with the atmosphere occurs is not a simple process. However, to provide some context of the variability of air temperature influence on the Gulf of Maine, we need only to examine the most dominant atmospheric pattern in the North Atlantic Ocean.

The North Atlantic Oscillation (NAO) is the dominant atmospheric pattern in the North Atlantic Ocean. The NAO is described as a large scale atmospheric alternation in the pressure difference between the subtropic atmospheric high-pressure zone centered over the Azores and the atmospheric low-pressure zone over Iceland. The NAO affects weather patterns in eastern North America and across the Gulf of Maine (Wake et al. 2006; Petrie et al. 2007a, 2007b; DFO 2008a). The most obvious and probably best-documented influence of the NAO on marine and terrestrial ecosystems is through air temperature. Global surface air temperatures reflect the interaction of several aspects of the Earth's climate system, including the exchange of energy between the ocean and the atmosphere (Wake et al. 2006). This air-sea heat energy exchange affects Gulf of Maine water properties and circulation. Over the period from 1970 to 2004, the NAO index has primarily been high, with relatively short cooling periods occurring in the last ten years of that time period (Petrie 2007). The increase in winter temperatures around the Gulf of Maine are associated with the positive phase of the NAO during recent years, and has resulted in relief from winter stress for many species and populations (Straile and Stenseth 2007). Within the Gulf of Maine this happens directly by the heat exchange between the marine waters and the overlying air. However, the NAO also has an indirect influence on the Gulf of Maine by altering air temperatures across the North Atlantic.

It has been suggested that the colder than normal winter air temperatures associated with a high NAO lead to colder than normal waters in the Labrador Sea. This leads to reduced transport of Labrador Current water southward and transported across the Scotian Shelf and into the Gulf of Maine (including the Bay of Fundy) (DFO 2008a). Instead warm slope water dominates the Scotian Shelf and Gulf of Maine continental shelf break. It has also been suggested that water temperature in the Labrador Sea is dependent on the strength of convection, which is driven in part by NAO influenced winds, but also by periodic freshwater anomalies at the surface (Curry and McCartney 1996). Therefore, the NAO and its resulting air temperature fluctuations not only have a direct effect locally on atmosphere-water heat exchange, but also indirectly affect water temperature change within the Gulf of Maine by warming or cooling distant source waters. More on NAO influence on Gulf of Maine circulation is discussed in Section 7.3 - Water Currents and Masses.

Annual air temperatures over the Scotian Shelf and the eastern Gulf of Maine were approximately 1.3-1.4° C above normal in 2006 (~1.0° C warmer than in 2005). The monthly anomalies were dominated by warmer than normal values throughout the year, but particularly in January, when air temperatures were approximately 4° C above normal at Yarmouth, Nova Scotia, and Saint John, New Brunswick (Petrie et al. 2007a, 2007b; DFO 2008a). These air temperatures contributed to the annual average sea surface temperature (SST) in 2006 at St. Andrews, New Brunswick, being 1.3° C above normal, making it the warmest in 86 years. Spatially across the Gulf of Maine, and vertically within the water column, the effect of changes in air temperature on the water will be varied because of local differences in such factors as stratification, mixing and salinity. Therefore, within the region, some areas may experience above normal, others normal, and still others below normal ocean temperatures all in the same year (DFO 2008a).

Over the last century, average global air temperature has increased by about 0.6° C, in part due to increasing greenhouse gases from human activities (IPCC 2001). Analysis of temperature trends in North America over the 20th century has found that the warming from 1950 to 1999 cannot be explained by natural climate variation (Karoly et al. 2003); rather, the observed temperature trends are consistent with human-induced forcing from increasing levels of greenhouse gases and sulphate aerosols. The average temperature of the Gulf of Maine ecosystem reflects these same global influences. Regional temperature is also affected by regional and local aspects of the climatic system, including the passage of different weather systems, storm tracks, fluctuations in the jet stream, topography, changing ocean currents and sea surface temperatures (SSTs), amount of snow on the ground, and the state of the NAO (Wake et al. 2006, Petrie et al. 2007b).

In sum:

- Average annual temperature in the Gulf of Maine region has increased 0.8° C from 1900 to 2002 – and 1° C over the 33 years before 2002.
- During the 20th century, average global air temperature increased by about 0.6° C.

- Average winter temperatures in the region have shown an even more dramatic increase (1.4° C) over the 20th century – and an even more striking 2.4° C increase between 1970 and 2002 (Wake et al. 2006).
- The NAO winter index has primarily been high in the last decades of the 20th century, indicating warmer winter air temperatures and warmer, more saline marine water in the Gulf of Maine (Fogarty and Trollan 2006).
- Annual air temperatures in 2006 over the Bay of Fundy and eastern Gulf of Maine were 1.3-1.4° C above normal, nearly 1° C warmer than in 2005.

6.2 Precipitation

Precipitation (in the form of rain, freezing rain and frozen precipitation) for the Gulf of Maine and Bay of Fundy regions has increased by an annual average of 129 mm (5 inches) (12%) during the 20th century (Keim et al. 2005, Wake et al. 2006) (see Figure 6.4). However, just as with temperature, there is significant year-to-year variability in the average annual amount of precipitation that falls in the region. For example, the most significant drought over the 20th century occurred during the early 1960s. By 1965, this drought reached critical levels and resulted in widespread forest fires, crop failures, fish kills, water shortages, harmful algal blooms, and heat-related deaths (Wake et al. 2006). Since the early 1960s, annual precipitation appears to have become increasingly variable. Despite a slight decreasing trend in annual precipitation between 1970 and 2002, this period also experienced the only four years on record with precipitation greater than 1400 mm (55.12 inches), and eight of the ten wettest years on record. Drought was also an issue during the summer of 2001 (Wake et al. 2006).

Considerable geographic variability also exists in the Gulf of Maine region's precipitation records over the twentieth century (see Figure 6.5). Some of the 133 stations in the region observed by the Climate Change Task Force adjacent to the Gulf of Maine experienced an increase of 200-300 mm (7.8 to 11.8 inches) or more of precipitation (representing an increase of 20% to 30%), while those in the interior sections of the region show lesser increases or decreases. It is important to note, however, that between 1970 and 2002, almost all of the stations experienced a slight decrease in annual precipitation (see Figure 6.6), contrary to the 100-year trend.

Intense precipitation events, such as those that result in more than 50 mm of rain (or water equivalent if the storm results in snowfall) during a 48-hour period, have the potential to significantly affect the region's streams and rivers. The average number of extreme precipitation events for the entire region is 2.6 events per year; however, this varies across the region, with more than four events per year occurring at several coastal sites in Massachusetts and Rhode Island, and some sites in upstate New York, New Brunswick and Nova Scotia (see Figure 6.7) (Wake et al. 2006). Climate change models produced by the Intergovernmental Panel on Climate Change (IPCC 2001) suggest that a warming planet will likely experience an increase in these extreme precipitation events.

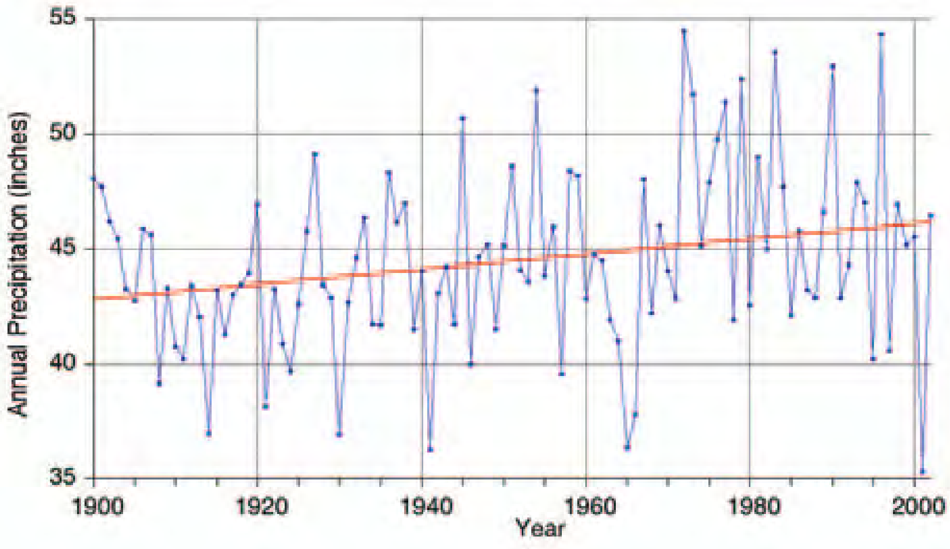

Figure 6.4: Average annual precipitation (mm) (red line) for the northeastern U.S. and Maritime Canada cross-border region, including the Gulf of Maine marine ecosystem, has increased from 1900 through 2002. The blue line represents the annual variability. The time series is an aerially weighted average of precipitation records from 133 stations in the region.
Source: Wake et al. (2006).

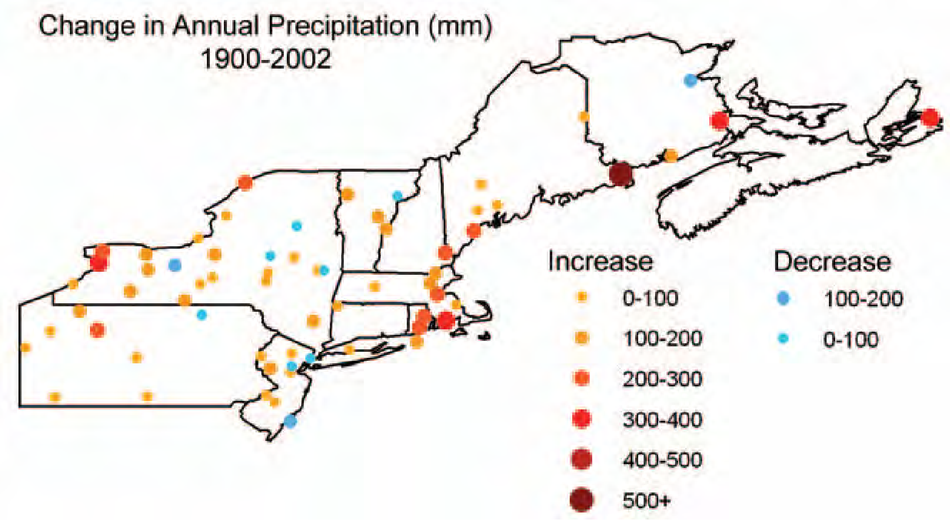

Figure 6.5: The long-term change in annual precipitation between 1900 through 2002 around the Gulf of Maine has been increasing, although significant spatial differences do exist. This map illustrates the linear trend in precipitation (mm) for the northeastern U.S. and Maritime Canada cross-border region.
Source: Wake et al. (2006).

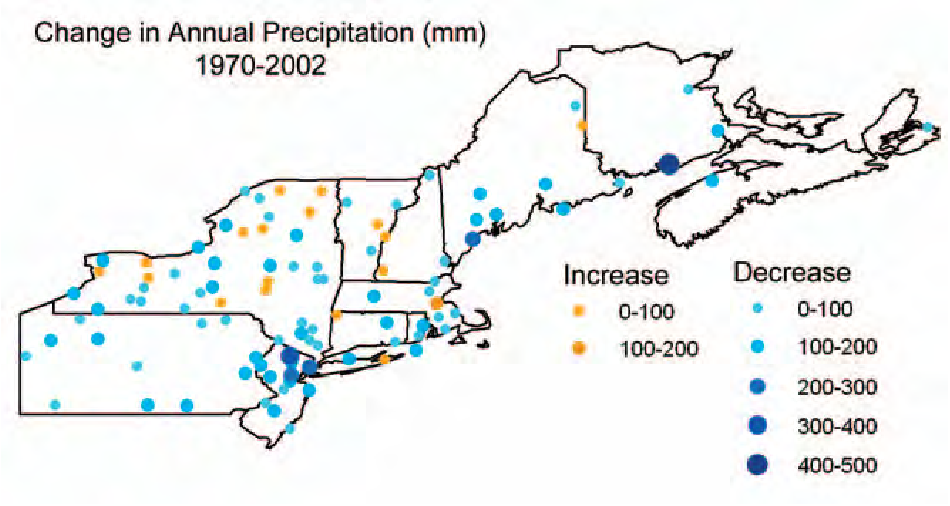

Figure 6.6: During the more recent 30-year period of 1970 through 2002, average annual precipitation around the Gulf of Maine and much of the northeastern U.S. and Maritime Canada cross-border region has been decreasing, contrary to the 100-year trend.
Source: Wake et al. (2006).

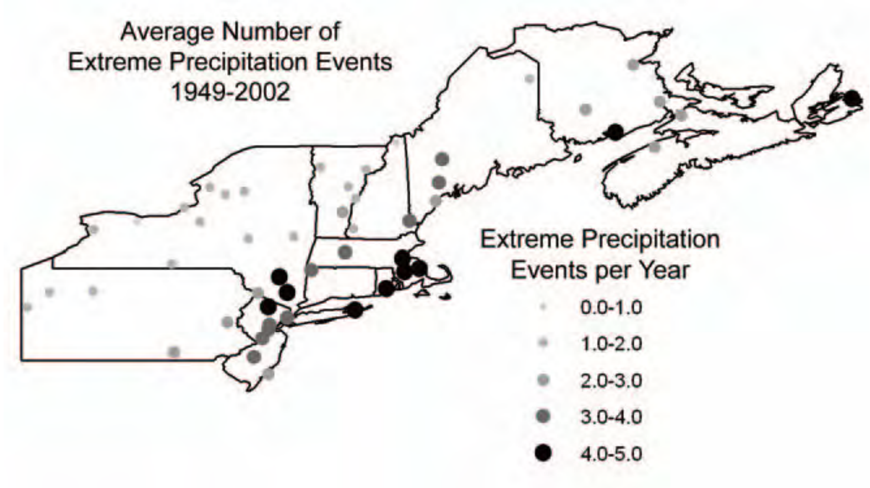

Figure 6.7: Map illustrating the average number of extreme precipitation events by station for the northeastern U.S. and Maritime Canada over a 54-year time period. Note the greater number of extreme events occurring along coastal areas relative to inland areas.
Source: Wake et al. (2006).

There is considerable variability in the trend in the number of extreme precipitation events per year across the Gulf of Maine region (see Figure 6.8). Of the 51 stations that contain data for greater than 90% of the years between 1949 and 2002 (Wake et al. 2006), 36 stations showed an increase of greater than 10% in the number of extreme events, while 8 stations showed a decrease of greater than 10%. Most of the stations showing a decrease are located in the northern part of the region around the Bay of Fundy. Conversely, most stations in the southern portion of the Gulf of Maine region showed a slight to moderate increase in extreme precipitation events. An examination of the records for each station (Wake et al. 2006) reveals a pattern of increasing extreme precipitation events during the 1980s and 1990s that is consistent with increases experienced in most of the U.S. and Canada (Groisman et al. 2004). For example, the contribution to the total annual precipitation by one-day storms that exceeded 50 mm of precipitation increased from 9% during the 1910s to 11% during the 1980s and 1990s (Karl et al. 1995). However, the frequency of storms in the 1980s and 1990s at many stations in the northeastern U.S. was comparable to the frequency of storms during the late 1800s and early 1900s (Kunkel et al. 2003). This suggests that the recent increase in intense precipitation may be due to natural variability, although the effect of human-induced climate change cannot be ruled out (Wake et al. 2006). Finally, research also suggests that when the NAO is high, as it has tended to be for much of the years 1970-2002, warm Gulf Stream waters influence the Gulf of Maine, and typically cause an increase in westerly winds and precipitation over the Gulf of Maine and the adjacent U.S. states and Canadian provinces (Fogarty and Trollan 2006). This may, at least in part, explain how long-term precipitation in the Gulf of Maine region has increased an average of 129 mm (5 inches) over the century, but decreased across the region over the years 1970-2002; as well as why during these last "drier" years between 1970-2002 we have documented record-breaking precipitation amounts in excess of 1400 mm (55 inches) and eight of the ten wettest years on record (Wake et al. 2006).

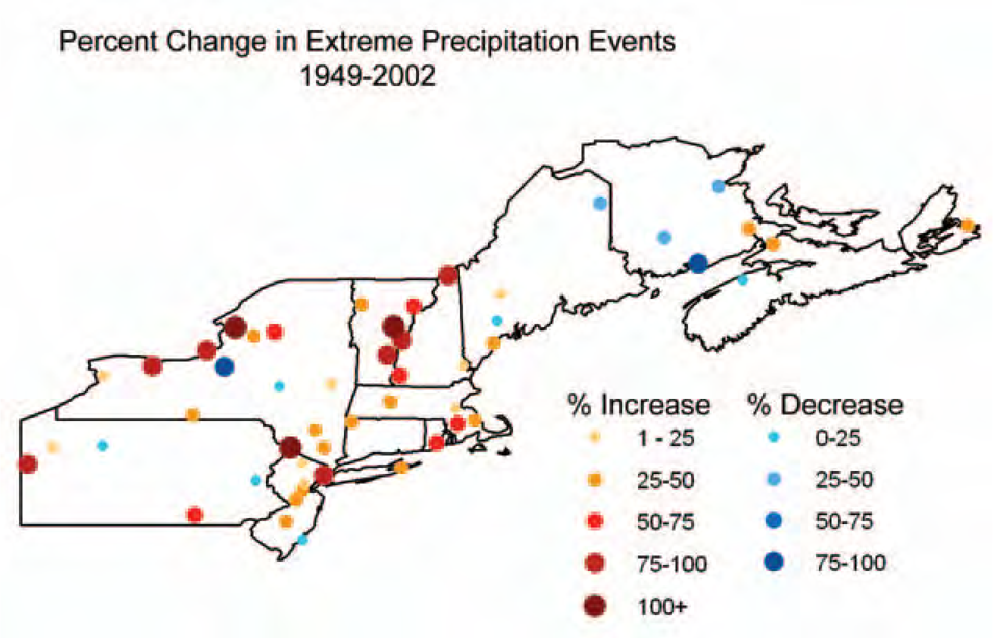

Figure 6.8: Map illustrating the linear trend in extreme precipitation events (percentage change over 54 years) from 1949–2002 for the Gulf of Maine region. Decreasing trends are shown with blue dots, while increasing trends are shown with red dots. Note that extreme events have generally decreased in the north and increased in the south.
Source: Wake et al. (2006).

Precipitation is critical for sustaining human populations and ecosystems around the world. The IPCC (2001) suggests that an increase in global surface temperatures will likely lead to changes in precipitation and atmospheric moisture, due to changes in atmospheric circulation, a more active hydrological cycle and increases in the water-holding capacity of the atmosphere since warmer air holds more moisture (see also Huntington 2006). Water vapour in the atmosphere is also a critical greenhouse gas; thus, temperature and precipitation are intricately linked in the global climate system. Over the 20th century there has been a 2% increase in global precipitation, although this change has not been uniform over time or geography (IPCC 2001).

6.3 Prevailing Wind and Storm Tracks (Influence on Mixing)

Tropical cyclones (hurricanes) have been a common feature of the Atlantic Basin for hundreds of years. Tracking and forecasting these tropical entities around the Gulf of Maine has been the responsibility of two organizations. The National Hurricane Center (NHC) not only tracks and forecasts these features through the U.S., but archives information on each storm (Wake et al. 2006). In 1985, Environment Canada formed the Canadian Hurricane Centre (CHC), co-located with the Storm Prediction Centre, in Dartmouth, Nova Scotia, to carry out similar functions on Canada's east coast.

Tropical cyclones have been tracked across the entire Gulf of Maine region since 1950 (Barks and Richards 1986, Wake et al. 2006). This area is prone to fairly intense northeast storm activity (Panchang et al. 1990, Petrie 2007), although cyclone and "northeaster" frequency is variable since 1900. Figure 6.9 depicts decadal storm variation from 1900-2000 in the Atlantic Basin, an area encompassing the Gulf of Maine ecosystem. While no specific trend can be extracted from the record, it is clear that the Atlantic Basin experienced an active period from 1990 to 2000.

Northwesterly winds dominate the Gulf of Maine in winter and southwesterly winds in summer. The transitions between these dominant winds generally occur in April and September. Monthly averaged winds are strongest in winter, weak during transition periods, and relatively strong again in summer, especially near the coast (Xue et al. 2000). In an assessment of strength, frequency and timing of large storms in Massachusetts Bay of the western Gulf of Maine, northeast storms were the major cause of large waves in Massachusetts Bay. This is in large part due to the long fetch (uninterrupted distance over open water) to the east (Xue et al. 2000). The long fetch allows for wind strength to build larger waves. The strongest 10% of storms (n = 38) ranked by wave size all had wind stress from the northeast. Based on the assessment of winds and waves, the Blizzard of December 1992, the Perfect Storm of October 1991 and a December 2003 storm were the strongest three storms between 1990 and 2006 - all were northeasters (Petrie 2007, Butman et al. 2008). However, winter storms such as these have decreased in frequency and intensity in the mid-latitude regions of North America, specifically in the area affecting the Northeast Shelf, including the Gulf of Maine. Conversely, autumn storm activity has increased (Freidland and Hare 2007). Autumn is a time of year when hurricanes tend to impact the Gulf of Maine. Atmospheric scientists are in agreement that the Atlantic Basin has returned to an extended period of heightened hurricane activity, as evidenced by the decade of 1995 to 2005 recording the highest frequency of tropical cyclones of any decade on record. These storms carry winds in excess of 63 knots (117 km/hour, or 73 miles/hour) (Wake et al. 2006). Based on data from 1953-2002, the NAO index appears to explain about 44% of the winter and 41% of the autumn cyclone activity variance along the east coast (Wang et al. 2006). Mid-latitude cyclones, also known as extra-tropical storms, may originate in a number of locations across North America and converge in an area associated with the Northeast Shelf. Many of these storms may track over the coast or over the continental shelf itself (Freidland and Hare 2007), including the Gulf of Maine. These storms can affect SST as they pass.

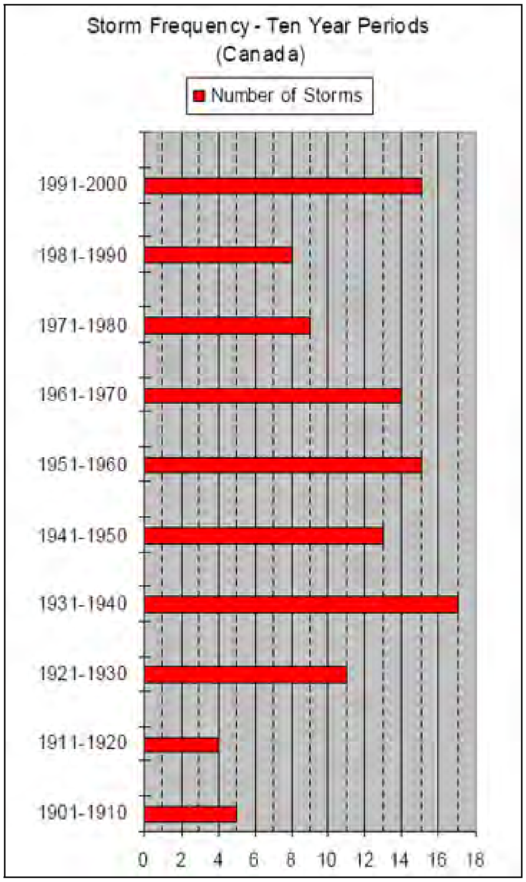

Figure 6.9: Decadal storm frequency over ten-year periods, Eastern Canada (area includes the Bay of Fundy and Gulf of Maine).
Source: Wake et al. (2006), derived from the Hurdat database of the National Hurricane Center (NHC) in Miami, Florida, and the Canadian Hurricane Centre (CHC), Dartmouth, Nova Scotia.

Prevailing winds are linked to the strongest along-coast velocities in the western Maine Coastal Current (WMCC). Strong southwestward wind stress produces these along-coast peak velocities (see Section 7.3 - Water Currents and Masses). Persistent changes in the wind field associated with the NAO are also responsible for much larger-scale changes in the direction and strength of oceanic surface currents across the North Atlantic. Larger-scale currents in shallow areas, such as the Gulf of Maine, are particularly influenced by these variable wind conditions (Ottersen et al. 2001).

Geyer et al. (2004) have noted that in the western Gulf of Maine, the wind stress commonly exhibits large fluctuations at time scales of one to three days and amplitudes of 0.1-0.2 Pa, with a small long-term mean. Wind and associated wind stress also influence mixing of the water column within the Gulf of Maine. In the western gulf, weak but significant wind-driven motions have been recorded to at least 27 m depth in the Maine Coastal Current (MCC) water column (Geyer et al. 2004), and during the summer, winds become predominantly southwesterly, a factor which may provide summer upwelling along the Maine coast (Xue et al. 2000). Additionally, the inward transport of continental slope waters through the Northeast Channel during winter has been noted to be episodic, but strong, and well correlated with alongshore winds (Xue et al. 2000).

Records indicate substantial inter-annual variability in wind stress on Georges Bank (Figure 6.10). Over the past two decades, there has been a general increase in the northward component of wind stress. Winds generally have been consistently from the west. These changes in wind stress may be linked to the NAO, as well as a northward shift in the location of the jet stream.

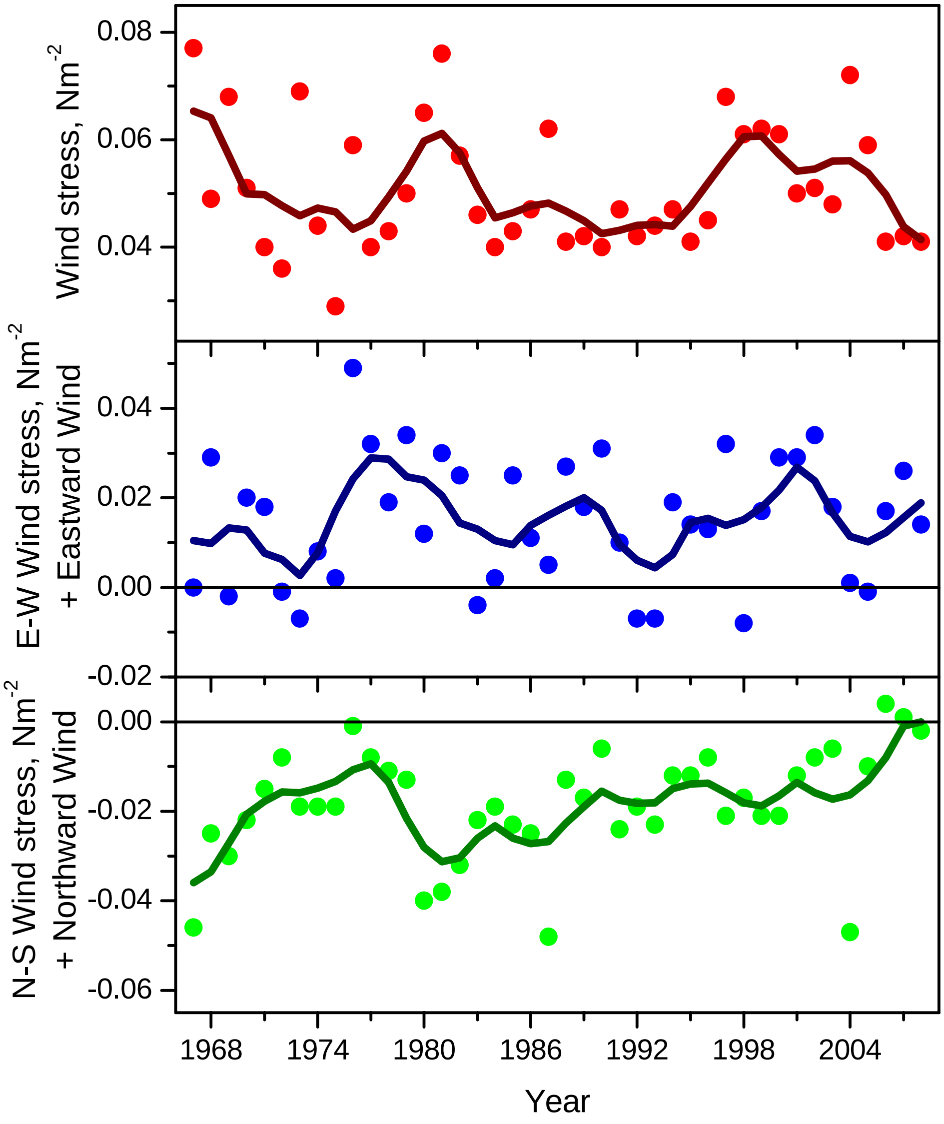

Figure 6.10: Annual averages of monthly mean wind stress for Georges Bank. Top panel shows the magnitude of wind stress; middle panel shows the east-west component of wind stress, and bottom panel shows north-south component of wind stress.
Source: adapted from EAP (2009).

7. PHYSICAL OCEANOGRAPHY

Physical oceanography is the study of the physical conditions and processes that occur in the ocean. A significant focus of physical oceanographers is to study movements within the ocean, such as waves, currents, tides, downwelling, and upwelling. In some cases, the boundaries of these movements are quite defined and even plainly visible. In other circumstances, the movements are very subtle and the boundaries very indistinct. Physical oceanography also includes evaluation of the temperature-salinity structure, which influences the density and movement of water bodies. Water masses are generally compartmentalized by density differences, and as will be discussed in Section 8, are primarily related to differences in temperature and salinity within the marine environment.

Understanding where and how water moves according to physical oceanographic principles and knowing where critical boundaries of temperature and salinity may exist provides a direct link to understanding marine biota. As many marine species are immotile (lacking the ability to move on their own), their distribution is influenced by ocean currents and circulation. All species have a range of salinity and temperature that they can tolerate, and the physical oceanography of an area can therefore cause a marine species to be limited or to flourish.

This section of the report will provide an overview of several of the key water body movements within the Gulf of Maine, describing some of what we know of where and why they move.

7.1 Freshwater Inputs

Freshwater sources to the Gulf of Maine include precipitation events of rain and snow, as well as flow from rivers along the coast and coastal runoff from rain and melting snow. Such water sources typically have < 0.5 PSU (practical salinity unit) of dissolved salts. In comparison, seawater tends to have a salinity of about 35 PSU. However, with a range of approximately 32-37 PSU some areas are more “fresh” than others. Seawater may be freshened by a large river inflow, or in northern climates, by seasonal melting of the polar ice cap.

There are two primary freshwater inputs to the Gulf of Maine. One is from the freshwater river systems that enter the coastline from the southern tip of Nova Scotia around the Bay of Fundy and along the U.S. coast to Cape Cod. The second is a slightly lower salinity oceanic current (Nova Scotia Current) that enters the Gulf of Maine from the north off the Scotian Shelf. This current brings water from both the Labrador Shelf and the Gulf of St. Lawrence into the Gulf of Maine. The Gulf of St. Lawrence water has a lesser salinity because of the freshwater flowing out of the Great Lakes through the St. Lawrence River system. The Labrador Shelf water is less saline because of the influence of Arctic sea-ice melt (Houghton and Fairbanks 2001). Because freshwater is less dense than seawater, these two sources flow somewhat like a river near the surface of the ocean and southwards across the Scotian Shelf and into the Gulf of Maine.

Freshwater discharges from the several large and numerous small rivers along the Gulf of Maine coastline play significant roles in circulation, mixing patterns, and nutrient regimes of the gulf. Freshwater discharge along the coastline of the gulf peaks during April and May due to spring runoff and rainfall flooding from a number of large rivers. The combined discharge of the four largest rivers (Saint John, Penobscot, Kennebec and Merrimack) entering the Gulf of Maine has been estimated at about 60 billion cubic metres of freshwater per year (see Table 7.1). This freshwater “plume” has a profound influence on water properties and dynamics not just in the estuaries, but also all along the Gulf of Maine Coast (Xue et al. 2000).

As one might expect, the freshwater inputs of the rivers entering the western gulf create a strong seasonal signal in salinity. However, this modification of salinity in the Gulf of Maine by river flow is primarily constrained to the surface water along the coastline from Saint John, New Brunswick to Boston, Massachusetts. Surface salinity within the MCC during the spring freshet is typically 2 PSUs below the local Gulf of Maine concentration. The freshwater plume that is created typically has a thickness of 10-20 m in water depths of 50-100 m along the coast, and is thus well isolated from the bottom over most of its areal extent. The along-coast freshwater transport within the plume varies considerably due to variations in wind stress; but on time scales of weeks to months, it follows the variations of riverine input, with a time lag consistent with the horizontal north-to-south movement of the current.

Table 7.1 The four largest rivers entering the Gulf of Maine contribute some 60 billion cubic metres of freshwater to the ecosystem every year.

River	Average discharge (m^3 s^{-1})	Average discharge (ft^3 s^{-1})	Annual average discharge ($m^3 \times 10^9$)	Annual average discharge ($ft^3 \times 10^9$)
Saint John River, New Brunswick	1 105**	39 020	34.8	1 230
Penobscot River, Maine	336	11 880*	10.6	375
Kennebec River, Maine	258[#]	9 110[#]	8.1	287
Merrimack River, New Hampshire	214[†]	7 560[†]	6.7	238
Total to the Gulf of Maine	1 913 m^3 s^{-1}	67 570 ft^3 s^{-1}	60.2 billion m^3 yr^{-1}	2 130 billion ft^3 yr^{-1}

Note: *102-year average from the University of Maine, http://www.pearl.maine.edu/windows/penobscot/research_hydrology.htm

Source: ** Xue et al. (2000); [#] en.wikipedia.org/wiki/Kennebec; [†] en.wikipedia.org/wiki/Merrimack_River.

The Saint John River constitutes some 70% of the freshwater entering the entire Bay of Fundy. There is a mean 1 105 m^3 s^{-1} discharge from this river, which flows towards the Gulf of Maine along the northern shore of the Bay of Fundy during ebbing tides (Hunter and Associates 1982). Much of this flow follows what is known as the MCC (see Section 7.3), parallel to the U.S. continental coastline. Freshwater transport calculations have indicated that more than half of the Saint John River discharge may be transported into the western Gulf of Maine through the MCC (Xue et al. 2000). The combined discharge of the Kennebec (including the Androscoggin), Penobscot and Merrimack rivers has a typical annual peak discharge of around 7 000 m^3 s^{-1} during the spring freshet. This occurs in about mid April, and accounts for more than 70% of the freshwater flow into the western gulf. However, the Saint John River in New Brunswick Canada, remains the largest river entering the Gulf of Maine, and discharges a comparable amount to the sum of the three American rivers (Geyer et al. 2004).

Interannual variability in river flow into the Gulf of Maine is relatively high (Figure 7.1), Complex long-term patterns have been identified. During the period 1950-1970 there appears to be one long cycle of 18-20 years. However, after the late 1970s, the period and magnitude of oscillations appeared to decrease. Visbeck et al. (2001) reported a connection between the NAO and river flow in the northeastern U.S. Recent years, 2006 and 2007, have had high river flows but freshwater inputs into the Gulf of Maine from riverine sources dropped in 2008.

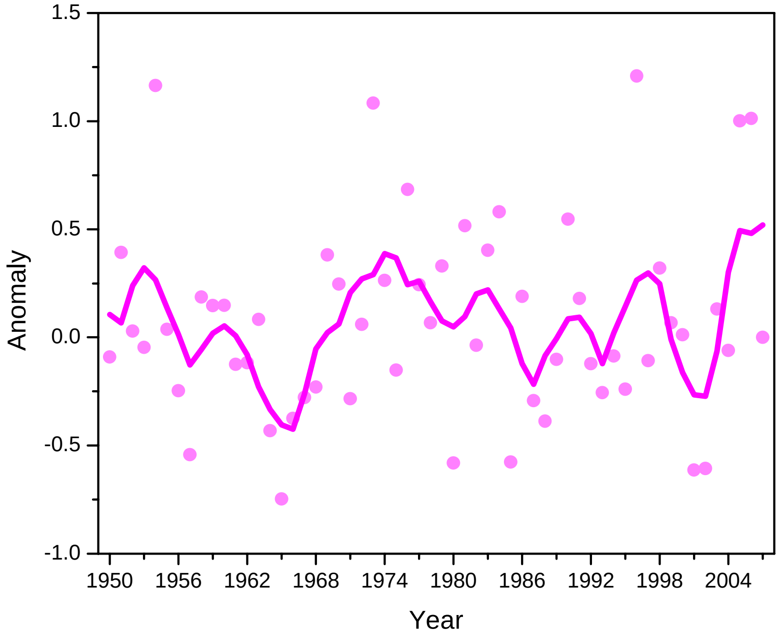

Figure 7.1: Trends in river flow from major rivers entering the Gulf of Maine, data presented as annual anomalies. **Source:** adapted from EAP (2009).

Spring river discharge to the Bay of Fundy has an important influence on near-surface circulation in the outer bay and the Bay of Fundy gyre, but only a small effect when averaged over the entire depth of the water column (Aretxabaleta et al. 2008). With the increase in freshwater discharge during the period of spring snow melt and high rainfall, the coastal current becomes slightly stronger. This occurs from April to June when less saline water creates density stratification in the water column, essentially flowing along the coastline on top of the denser and more saline marine water (Xue et al. 2000). However, measurements within the western Maine Coastal Current (WMCC) indicate that less than half of the transport of freshwater through the coastal current is explained by the local frontal gradients, such as the fresh river inputs and associated temperature differences. Instead, the primary year-round factors that influence movement within the Maine Coastal Current are the more uniform forcing elements associated with the larger-scale dynamics of the Gulf of Maine. These forcing elements, which include the relatively fresh oceanic water that enters the Gulf of Maine off the Scotian Shelf, account for about 60% of the transport along the U.S. continental coastline in the Gulf of Maine (Geyer et al. 2004).

In fact, the overall freshwater budget for the Gulf of Maine is dominated not by river inflow, but by the inflow of relatively cold low-salinity Scotian Shelf water (Smith 1983, and Brown and Irish 1993, cited by Pettigrew et al. 1998). As noted, rivers influence a relatively shallow surface lens of water flow along the MCC. However, the freshwater inputs from these rivers, along with precipitation falling on marine water surface, are about two orders of magnitude smaller

(0.005×10^6 m^3 s^{-1}) than the combined mean Northeast Channel and Scotian Shelf inflows (0.400×10^6 m^3 s^{-1}) (Mountain 1991). Although the salinity of the Scotian Shelf water is generally higher than the observed near-surface water along the Gulf of Maine coastline, its relative freshness will significantly contribute to the transport of deeper water with a salinity of 32-32.5 PSUs (Geyer et al. 2004).

The relatively fresh marine waters of the Labrador Current flow south down the continental shelf off Nova Scotia before entering the eastern Gulf of Maine. A small portion of this current enters the Scotian Shelf where it mixes with the Nova Scotia shelf waters, and then flows into the gulf. However, a greater portion continues along the continental shelf slope and enters the Gulf of Maine through the Northeast channel, even at relatively shallow depths of up to 50 m (Figure 7.2) (Hannah et al. 2001). Estimates of the percent contribution of Labrador Current water in the Gulf of Maine show a decline from the late 1970s through the early 1990s, followed by a reversal (Figure 7.3). The volume transport of the Labrador Current and the percent contribution of Labrador Slope Water in the Gulf of Maine show a steady increase since that time (EAP 2009).

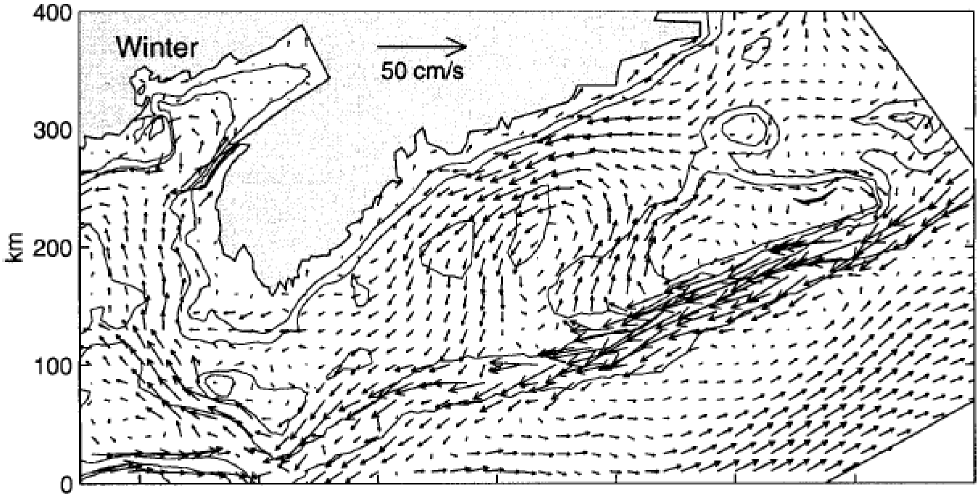

Figure 7.2: Circulation patterns at 20-50 m show how portions of the Labrador Current move southward along the continental slope before portions cross the Scotian Shelf to mix with shelf waters and portions directly enter the Gulf of Maine through the Northeast Channel.
Source: adapted from Hannah et al. (2001).

The properties of the water entering the Gulf of Maine from the Scotian Shelf do influence surface salinity seasonally, with minimum salinities occurring in February. This represents a nine-month lag in the peak outflow for the St. Lawrence River and indicates that the seasonal cycle of the Gulf of St. Lawrence freshwater sources persists downstream to the Gulf of Maine. It is estimated that the St. Lawrence River, although it is only about 6% by volume of the water that comes off Scotian Shelf and through the Northeast Channel into the Gulf of Maine, supplies 48% of the freshwater entering the Gulf of Maine at that point. The sea ice melt-freshened Labrador Shelf water makes up approximately 94% by volume of the flow entering the Northeast Channel, but only 52% of the freshwater (Houghton and Fairbanks 2001). Therefore, maximum inflow of freshwater to the Gulf of Maine occurs in the winter when the Scotian Shelf water is freshest, and a minimum occurs in the late spring when river runoff to the Gulf of Maine is greatest (Mountain 1991).

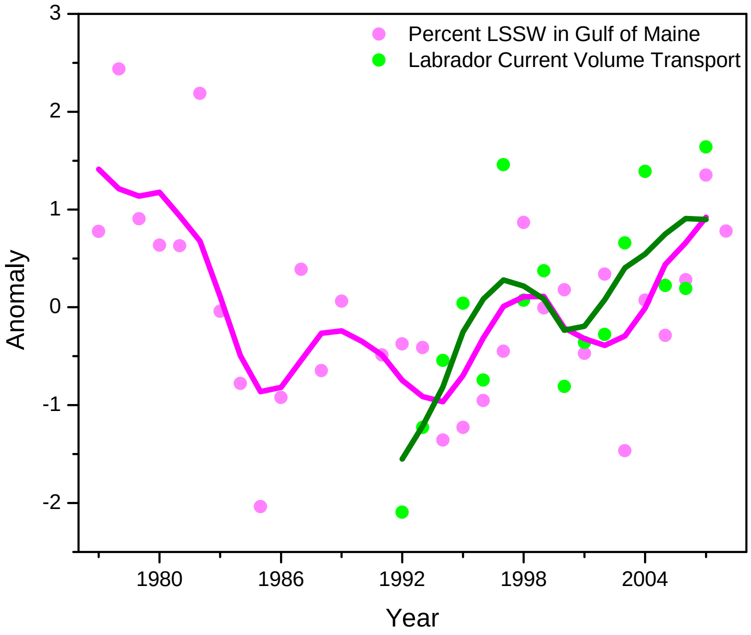

Figure 7.3: Trends in volume transport of the Labrador Current along southwest Newfoundland and the percent of Labrador Subarctic Slope Water in the Gulf of Maine (as an anomaly).
Source: adapted from EAP (2009).

At the eastward extent of the Gulf of Maine, the origin of Georges Bank freshwater sources is primarily the Gulf of St. Lawrence, although there is a small and variable amount of freshwater influence from Maine rivers that is delivered through the WMCC to central Georges Bank. However, the significant freshwater influence across the Gulf of Maine is the Gulf of St. Lawrence, consisting of Labrador Shelf water and St. Lawrence River water (Houghton and Fairbanks 2001).

7.2 Sea Level and Tides

About 2500 years ago the sea level was an estimated 7 m lower than present levels in the Gulf of Maine (Greenberg 1979, 1987, cited in Desplanque and Mossman 2001). Table 7.2 shows that the trend in sea levels has been positive up to 1980, although somewhat variable across the Gulf of Maine.

Table 7.2: Estimates trends in pre-1980 tidal amplitude from various stations around the Gulf of Maine.

Station	Trend in M2 tidal amplitude ($cm/century^{-1}$)	Trend in sea levels ($mm\ year^{-1}$)
Saint John, New Brunswick	8.5	2.9
Eastport, Maine	13.3	2.1
Portland, Maine	7.8	1.8
Boston, Massachusetts	4.3	2.6

Source: adapted from Ray (2006).

Eastern seaboard tidal characteristics are predominantly influenced by the diurnal (one tidal cycle per day) and semi-diurnal (two tidal cycles per day) tides, with the latter being the most influential

(Desplanque and Mossman 2001). The semi-diurnal tide is also scientifically referred to as the M2 (or M_2) tide. As tides move across Georges Bank, through the Gulf of Maine and into the Bay of Fundy, they become amplified (Davis and Brown 1996b). First the tidal swell becomes amplified as it moves from the open Atlantic Ocean and depths of over 3 500 m to the shallow continental shelf (about 200 m deep), and then it becomes further amplified as it pushes onto the coastal shelf that lies near 100 m depth. The oceanic tide moves predominantly through the Northeast Channel, the deepest entry point to the Gulf, and then across the entire Gulf of Maine. The primary tidal influence on circulation in the Gulf of Maine comes from water that flows in through the Northeast Channel (south of Nova Scotia).

As the tidal surge moves landward, it becomes higher with the shallower morphology. It is somewhat akin to taking a bucket of water and pouring it into a small diameter tube. The tube must be very tall to hold all of the water from the bucket. As the tidal surge (the bucket) approaches land, and the bottom morphology becomes more shallow (the tube), momentum forces the tides to become higher. Seaward of Georges Bank the tidal amplitude is roughly 0.5 m (Lynch and Naimie 1994). At Georges Bank the tidal range increases to about 1 m (3 feet) (Brooks 1992, Desplanque and Mossman 2001). Well into the Gulf of Maine, and closer to land, tidal range becomes approximately 3.1 m west of the Jordan Basin (Desplanque and Mossman 2001). At the mouth of the Bay of Fundy, near the Maine and New Brunswick border, tides of 7.6-8.5 m (25-28 feet) occur (Larsen 2004). In fact, across the Gulf of Maine, the range of the semi-diurnal tide increases exponentially at a rate of 0.35% per kilometre from Georges Bank and the continental shelf landward (Desplanque and Mossman 2001). However, through mathematical modelling, it has been suggested that 7 000 years ago the tidal range within the Gulf of Maine was only 20-50% of the present range. The tidal range grew with various large-scale oceanic and tectonic changes until the present tidal range was reached about 2500 years ago (Greenberg 1979, 1987, cited in Desplanque and Mossman 2001).

The tidal range in the whole Gulf of Maine-Bay of Fundy system is enhanced due to the natural period of oscillation (the time it takes for tidal water to flow into and then out of the gulf). This period of oscillation is a little over 13 hours and is nearly the same as the 12.4-hour tidal cycle of the North Atlantic (Garrett 1972). During a 24-hour 50-minute lunar day, some 584 km^3 of tidal water may move into and out of the Bay of Fundy. This is approximately four times the combined discharge of all the world's rivers (Desplanque and Mossman 2001). This tidal forcing results in the extremely high tidal amplitude in the Bay of Fundy (Figure 7.4) (Trites and Garrett 1983) and has led to the world record tidal amplitude being documented at Burntcoat Head, in the inner Bay of Fundy's Minas Basin. A major cross-sectional reduction occurs between the Grand Manan Channel and Saint John, reducing the area to about one quarter of the cross-section of the Gulf of Maine (Hagerman et al. 2006). The changing basin shape is a key factor that has driven the tidal range to as much as 16.27 m (53.38 feet) (BoFEP 2001) at the head of the Bay of Fundy.

Besides the shallow morphology and the natural period of tidal oscillation promoting high tides in the Gulf of Maine, there are other factors that also have an influence on the tidal range. Variations in atmospheric pressure and wind can create storm surges that result in changes in sea level. In the Bay of Fundy, these surges can result in a tide of up to 1 m (3 feet) higher than the regular high tide levels (Trites and Garrett 1983). In addition, on a daily basis, something known as the Coriolis force causes tides in the Bay of Fundy to move in a counter-clockwise direction. This force is driven by the rotation of the Earth. The strongest Bay of Fundy tidal currents occurring during the rising tide are located on the Nova Scotia side of the Bay, and the strongest outgoing tidal currents occur along the New Brunswick side.

As noted, all of the previously discussed features and characteristics promote high tides within the Gulf of Maine, and in particular, the Bay of Fundy. However, the strongest Bay of Fundy tides occur when four elements, scientifically known as perigee, spring tide, anomalistic and tropical monthly cycles, all peak simultaneously. The closest match occurs at intervals of 18.03 years, a time known as the Saros (Desplanque and Mossman 1999). With the approach of the ~18-year Saros tidal cycle in 2012-2013, the risks of storm surge and coastal flooding will increase throughout the Gulf of Maine, including the Bay of Fundy.

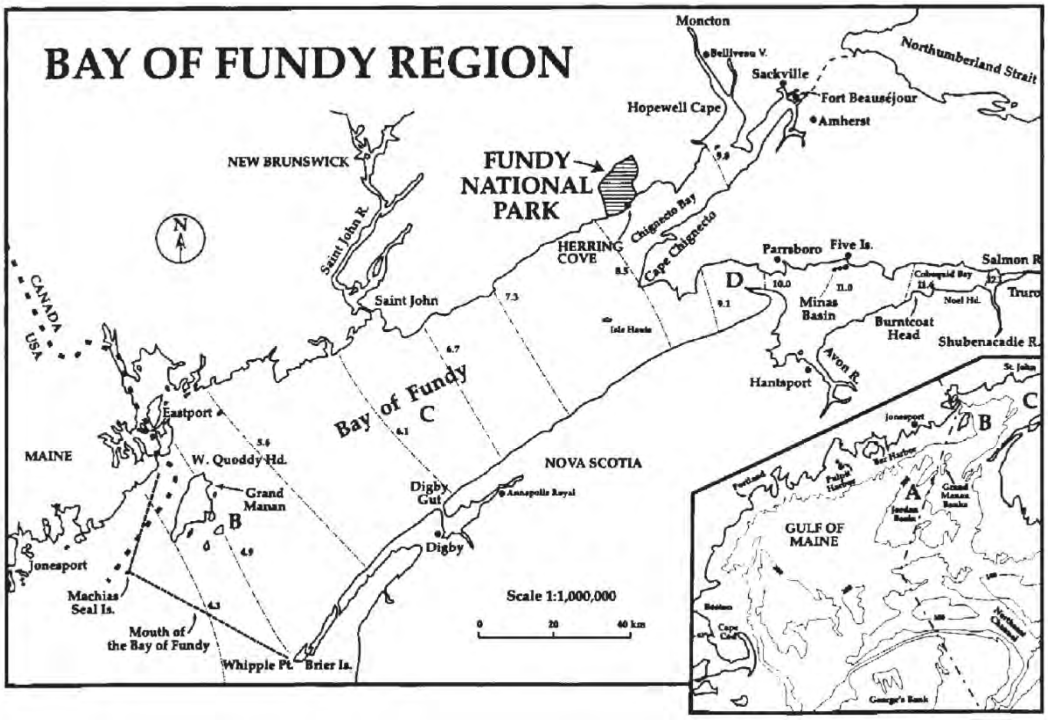

Figure 7.4: Approximate increase in tidal range progressing into the Bay of Fundy. A significant change in the cross-sectional area between the Gulf of Maine and the Bay of Fundy occurs between Grand Manan Island and Saint John, increasing the tidal range.
Source: adapted from Desplanque and Mossman (2001).

Analyses of the semi-diurnal tide (M2) in the Gulf of Maine (1896-present) reveal that the amplitude of the tide underwent a nearly linear long-term increase throughout most of the 20th century (Ray 2006). As shown in Table 7.3, tidal amplitude has been increasing over the years 1905-2004 at Saint John, New Brunswick. Godin (1992, 1995, cited in Ray 2006) showed that the long-term change in amplitude of the M2 tide at Saint John, New Brunswick has been increasing rapidly at an estimated 12.6 cm a century. However, late in the 20th century these long-term trends were broken.

During the early 1980s, the amplitude of tide abruptly dropped. Sea-level changes alone appear inadequate to explain either the long-term tidal amplitude trend or the recent discontinuity trend. Tidal models have predicted an amplification of the M2 tide, but much smaller than the currently observed trends. It appears likely that 20th century tidal trends, as well as the curious effect during the early 1980s, are caused by mechanisms related to or enhanced by the resonance nature of the Gulf of Maine; but they are not at this point well understood (Ray 2006).

Table 7.3: The long-term tidal amplitude of the semi-diurnal tide (M2) at Saint John, New Brunswick, demonstrates how tidal amplitude has steadily increased in the Bay of Fundy for most of the 20th century. However, an unexplained decrease has been observed since 1980 at Saint John and many monitored locations across the Gulf of Maine.

Time span	M2 tidal amplitude (cm)
1905–1923	299.78 ± 0.29
1924–1942	300.61 ± 0.56
1943–1961	302.13 ± 0.25
1962–1980	304.26 ± 0.25
1981–2004	301.18 ± 0.25

Source: adapted from Ray (2006).

7.3 Water Currents and Masses

Assessing an ecosystem is frequently a question of scale, as it has been in developing this *Gulf of Maine Ecosystem Overview Report*. However, regardless of the scale of the assessment, because of the the inherent physical-biological interactions upon which ecology is based, factors external to the chosen assessment scale will have significant influence over the observations that are being made. Examination of currents and water masses within the Gulf of Maine makes this point quite clear. There is large-scale coastal circulation influencing the Gulf of Maine that originates all the way from the Labrador Sea, north of Newfoundland, south to Cape Hatteras, North Carolina. This means that the circulation and water properties within the gulf may depend on influences on local processes originating over 1000 km away.

A seasonal variation in the gulf-wide circulation exists, strongest and most coherent in the summer and lacking a recognizable pattern in the winter (Bumpus and Lauzier 1965, cited by Xue et al. 2000). Although the summer circulation pattern in the Gulf of Maine is becoming increasingly clear, the circulation in winter, the transitions between seasons, and the factors that regulate the seasonal circulation are less certain (Xue et al. 2000). Tidal currents, which in part drive the changing circulation patterns, are seasonally stronger in winter and spring (Desplanque and Mossman 1999). It has been suggested that the circulation in the gulf is related to the evolving density structure of the water. Factors that influence the density distribution inside the Gulf of Maine include wind, winter cooling, river runoff, the periodic cooler and more fresh inflow from the Scotian Shelf, the deep warmer and more saline inflow of the slope water, and tidal mixing (Xue et al. 2000). These are all factors that influence salinity and/or temperature, and thus affect the density and circulation of the marine waters in the Gulf of Maine. This seasonal variation is discussed further in Section 8.0 - Seawater Temperature, Salinity and Density.

The Gulf of Maine near-surface circulation is generally characterized as a cyclonic (counter-clockwise) movement. The exception to this circulation is a clockwise pattern around Georges Bank. The Northeast Channel and Great South Channel provide pathways for sub-surface flow into and out of the Gulf of Maine, respectively. The shallower coastal shelf with its diverse morphology drives much of the detail we see regarding gyres and localized currents within such areas as the Bay of Fundy or along the Maine Coast. However, these patterns are arguably initiated by factors that occur far away from land and west of the continental slope, completely outside of the Gulf of Maine as defined in this report. The most significant of these factors appears to be the NAO.

The NAO influences the relative location within the Atlantic Ocean of warm Gulf Stream waters that approach the Gulf of Maine from the south, and the colder Labrador Current waters that flow toward the area from the north. The amount of these warmer and colder waters that move into the Gulf of Maine influences the currents and water masses of the gulf, including even the most landward areas such as the Bay of Fundy and the New England coastline. Small changes in the North Atlantic as a whole can produce large changes in the Gulf of Maine. Therefore, currents and water masses will be discussed at both the North Atlantic scale and the Gulf of Maine scale, and some of the ecological linkages will be provided from the larger scale to the more local scale.

Although it is not entirely clear how the NAO influences the position of the Gulf Stream within the Atlantic Ocean, the NAO is known to affect the distribution and fluxes of major water masses and currents in the Atlantic. How the NAO alters SST is one of the best understood mechanisms for its influence over marine currents, although NAO-influenced changes in wind, precipitation and atmospheric forcing also play a role in altering currents. The NAO affects not only surface water circulation but deep water circulation as well (Ottersen et al. 2001). Smoothed time trends of the NAO index, position of the North Wall of the Gulf Stream, and the relative contribution of Labrador Subarctic Slope Water reveal interesting associations among these indices (Figure 7.5). There is a positive relationship between the NAO and the Gulf Stream North Wall with a lag of 2 years, and there is a general inverse relationship between these indices and the Labrador Subarctic Slope Water index. For the Gulf of Maine, this means that a positive NAO eventually brings warm Gulf Stream water to the gulf while a negative NAO allows colder Labrador Subarctic Slope Water to influence the gulf. Changes in plankton community composition have been linked to these water mass dynamics (see Section 9.1.3).

Not only is the Labrador Current generally much colder than the southern-produced Gulf Stream waters, but it also is also less saline, less dense, and has lower nutrients (Fogarty and Trollan 2006). Temperature, salinity and nutrients are key water characteristics that influence what marine species will live where, and changes in the biological communities within the Gulf of Maine are not unexpected in relation to changes in the NAO. Several of these communities are discussed in Section 9. The change-over from water characteristics of a high NAO index to the greater influence of low-nutrient, cool, fresh Labrador Current waters associated with a low NAO index occurs within the Gulf of Maine on a time lag of approximately 18-24 months after the index changes.

Depending on the state of the NAO, water that enters the Northeast Channel tends to be more greatly influenced by one of two sources: warmer, saltier Atlantic temperate slope water from the open Atlantic, or cooler, fresher Labrador Current water moving south along the continental slope. For several years before 2009 (latest data available), the NAO has been high (EAP 2009), and the water entering the Gulf of Maine has been warm Atlantic slope water. This has a warming effect on the Gulf of Maine and is independent of the record warm air temperatures (COOC 2007c).

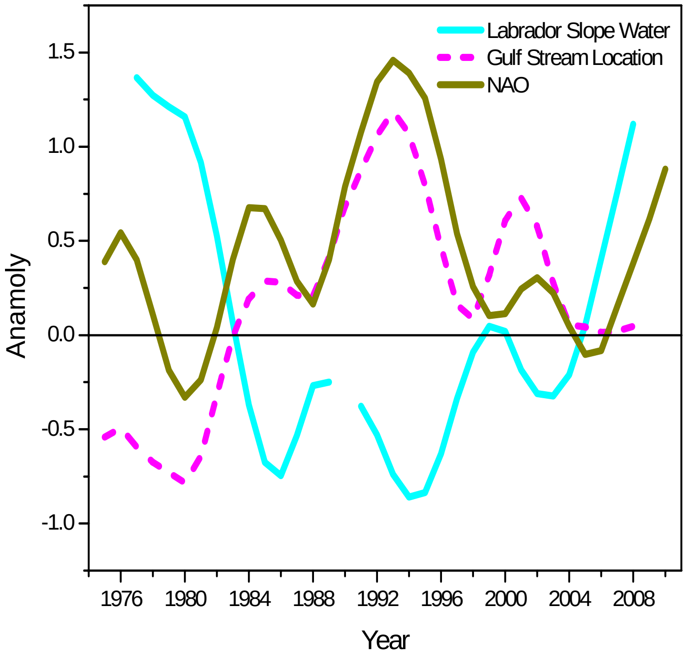

Figure 7.5: Trends in percent Labrador Slope Water, Gulf Stream location, and NAO. All data are presented as anomalies to standardize the y-axis scale and a 10 year smoother was applied to emphasize decadal trends. An anomaly is the deviation from normal, here shown as 0.0. A positive anomaly is above the norm, while a negative value is less than the norm. NAO was adjusted 2 years forward and shelf salinity was adjusted 3 years back based on a cross-correlation analysis.
Source: modified from EAP (2009).

When the NAO is low, the warm slope water coming through the Northeast Channel is met by increased volumes of relatively cold, nutrient poor and fresh water originating in the Gulf of St. Lawrence and entering the Gulf of Maine via the Nova Scotia Current flowing north of Browns Bank (Lynch 1996), near the southern tip of Nova Scotia.

As these offshore water sources enter the Gulf of Maine, they appear to drive the eastern portion of the counter-clockwise Gulf of Maine gyre, one of two main gyres in the gulf, and initiate the overall counter-clockwise direction of flow around the Gulf of Maine. The majority of the inflow turns southwestward near Grand Manan Island and the mouth of the Bay of Fundy; but part flows cyclonically into the Bay of Fundy before eventually leaving the bay to move along the New England coastline (Xue et al. 2000). The Gulf of Maine gyre is influenced not only by the Nova Scotia Current inflow around southwest Nova Scotia and by the inflow of dense deep water through the Northeast Channel (see Figure 7.6), but also by the spring runoff from the region’s rivers and daily tides (Van Dusen and Hayden 1989). Water circulates in the gulf gyre counter-clockwise around Jordan Basin, located at the mouth of the Bay of Fundy, and around Georges Basin, located at the head of the Northeast Channel. Vigorous tidal stirring keeps the water vertically well mixed in this eastern portion of the Gulf of Maine and the gulf gyre (Pettigrew et al. 1998).

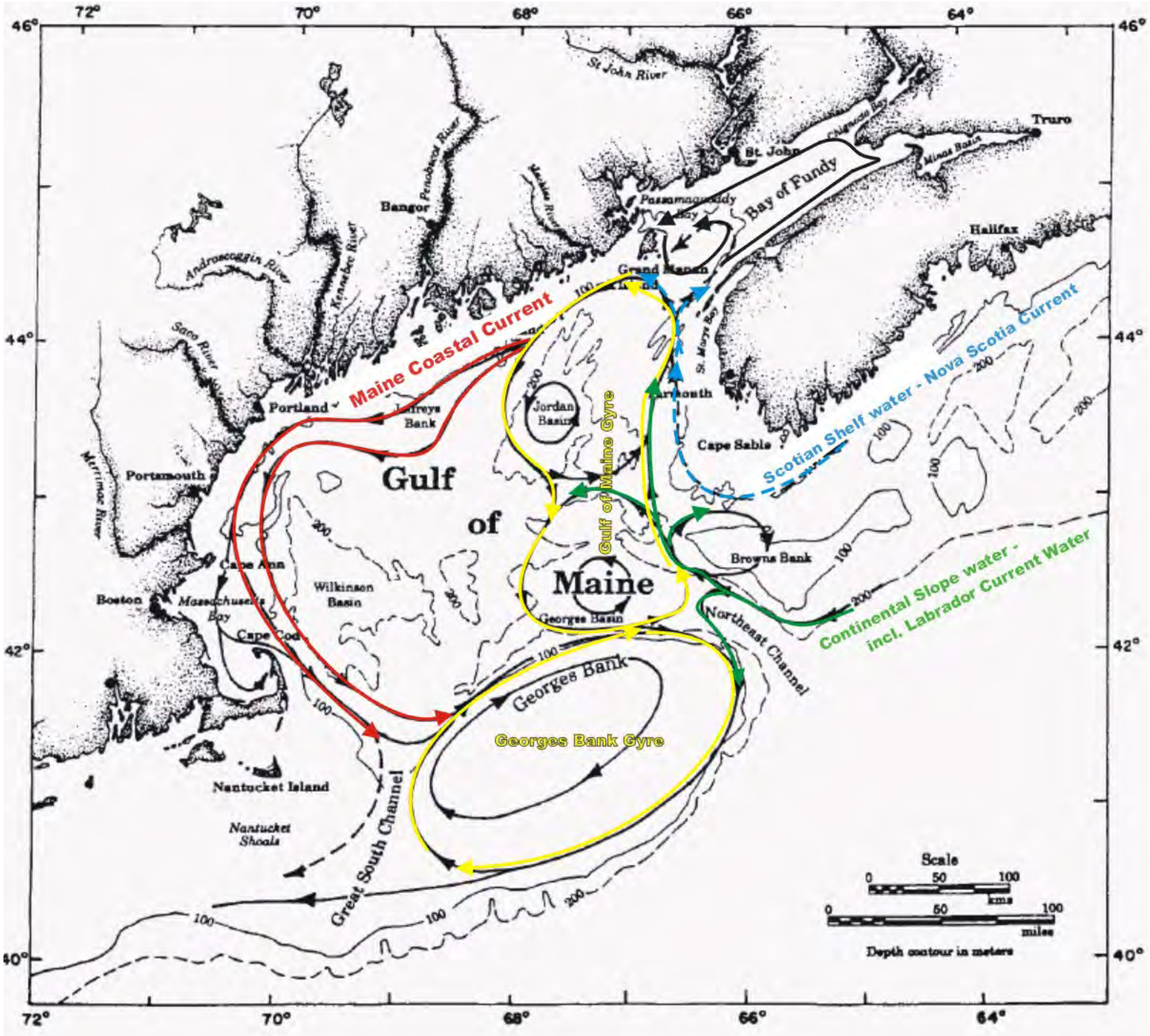

Figure 7.6: Schematic of springtime circulation in the Gulf of Maine based on 1994 observations. Circulation varies seasonally, annually and with depth; but the features highlighted here are typically present and dominant.
Source: adapted from Pettigrew et al. (1998), as cited in Xue et al. (2000).

The second main gyre in the Gulf of Maine exists over Georges Bank (Van Dusen and Hayden 1989). Like the gulf gyre, the Georges Bank gyre is also vertically well mixed due to tidal stirring (Loder and Greenberg 1986, cited in Xue et al. 2000). Unlike the gulf gyre, the Georges Bank gyre moves in a clockwise direction, picking up incoming slope circulation both directly from the Northeast Channel and from circulation that has moved south along the coastline of the gulf (referred to as the MCC) that gets pushed towards Georges Bank by the projection of the Cape Cod land mass. The Georges Bank gyre is also coupled with the southern extent of the gulf gyre that exists over Georges Basin. The Georges Bank gyre's strongest currents exist on the northward side of the bank during summer months (Xue et al. 2000). Near the sea bottom on Georges Bank, the tidal current 10 cm off the bottom has been estimated to be as little as 0.01-0.05 m s^{-1}, and at 1 m off the bottom it ranges from 0.07-0.24 m s^{-1} (Lough et al. 1989). However, higher in the water column, tidal currents of 1 m s^{-1} or greater are found (Xue et al. 2000). Eggs of fish species such as cod and haddock have been noted to drift 2-7 km/day in the clockwise gyre around Georges Bank (Lough et al. 1989). Two other significant and relatively constant circulation patterns exist within the Gulf of Maine. One is the counter-clockwise circulation in the Bay of Fundy, and the second is the MCC.

As noted earlier, Atlantic temperate slope water and, periodically, Labrador Current water moves toward the mouth of the Bay of Fundy. Some of this water then moves cyclonically (counter-clockwise) around the Bay of Fundy (Xue et al. 2000), entering along the Nova Scotian (southern) coastline of the bay. Another portion of this current turns west to feed the MCC (Aretxabaleta et al. 2008) and the gulf gyre. The stronger "ebb" tidal current velocity that moves out of the Bay of Fundy travels primarily along the New Brunswick (northern) side of the Bay of Fundy at a velocity of about 0.7 m s^{-1}. However, local extremes in Head Harbour Passage between Campobello Island and Deer Island have been recorded at 2-3 m s^{-1} (Hunter and Associates 1982). Typical depth-averaged tidal current magnitudes of 0.8-1.2 m s^{-1} have been noted over the deeper part of the Bay of Fundy Basin (Aretxabaleta et al. 2008). The counter-clockwise tidal circulation pattern in the Bay of Fundy ends with a portion of the circulation feeding the small Bay of Fundy counter-clockwise gyre that is found east of Grand Manan Island, as shown in Figure 7.7 (Chang et al. 2005, Aretxabaleta et al. 2008). The remainder of the Bay of Fundy tidal circulation pattern follows the coastlines of New Brunswick and Maine to join the MCC.

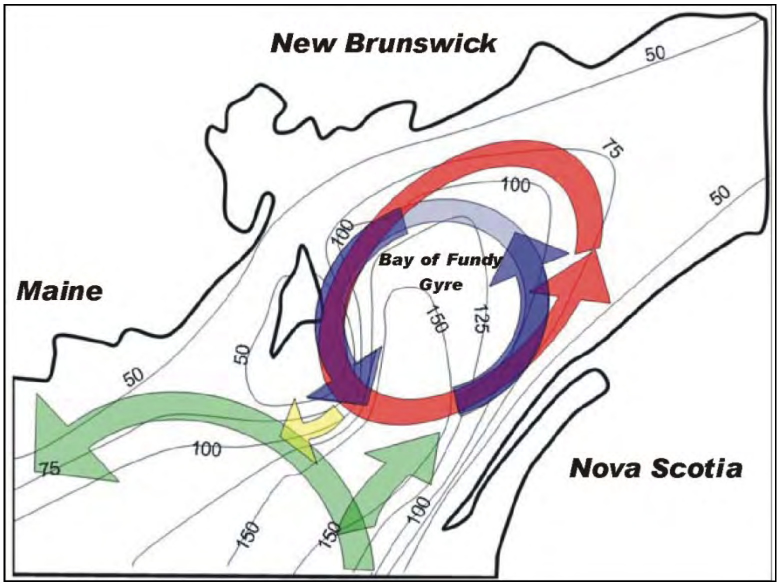

Figure 7.7: Basic schematic of the circulation associated with the Bay of Fundy gyre and its different forcing mechanisms. The strong tidal residual in both the east and west side of the mouth of the Bay is shown with dark blue arrows, while light blue represents the weaker north component of the tidal residual around the 125 m isobath. The red arrow indicates the effect of local fronts on circulation. The circulation in the Gulf of Maine, consisting primarily of inflows from the Northeast Channel and the Scotian Shelf, is presented with green arrows. The exchange between the gyre and the Maine Coastal Current around the 100 m isobath is shown with a yellow arrow.
Source: adapted from Aretxabaleta et al. (2008).

Large tidal vertical velocities are estimated for the Bay of Fundy gyre area (Aretxabaleta et al. 2008). This gyre is thought to be a major factor in the nutrient pump that brings deep water nutrients to the surface water where they reach the photic zone and contribute to primary production. The maximum vertical speed within the Bay of Fundy gyre is estimated on the order of 10^{-4} m s^{-1}, representing a vertical displacement of 10 m day^{-1} (Aretxabaleta et al. 2008). Productivity is exceptionally high in the Bay of Fundy and is greatest at the mouth of the bay (see Section 9.1).

The other dominant and large-scale circulation pattern within the Gulf of Maine is the MCC. The MCC is commonly referred to as a tidally mixed plume that arises from the discharges of fresh spring meltwater that enters the gulf through several land-based rivers (Xue et al. 2000). The MCC generally has a western and an eastern component (see Figure 7.8). Studies indicate that the current is primarily a pressure gradient-driven system with both principal branches increasing their transport in the spring and summer due to freshwater inflows, and flowing southwestward against the mean wind forcing during this period (Pettigrew et al. 2005). Although the main driving force behind the freshwater density gradient in the MCC appears to be the freshwater river input from the land base, it is also formed, in part, by the most southerly extent of the cold and relatively fresh Labrador Coastal Current (Friedland and Hare 2007) that flows across the Scotian Shelf east of Nova Scotia, into the western Gulf of Maine and Bay of Fundy, and, eventually, in a much diminished form as part of the MCC. Observations show strong seasonal and inter-annual variability in both the strength of the MCC and the degree of connectivity of its principal eastern and western branches (Pettigrew et al. 2005). Transport along the MCC increases sharply in early May, about two weeks after the peak spring freshet occurs. The low surface salinity produces the strongest along-coast velocities within the WMCC (Ottersen et al. 2001).

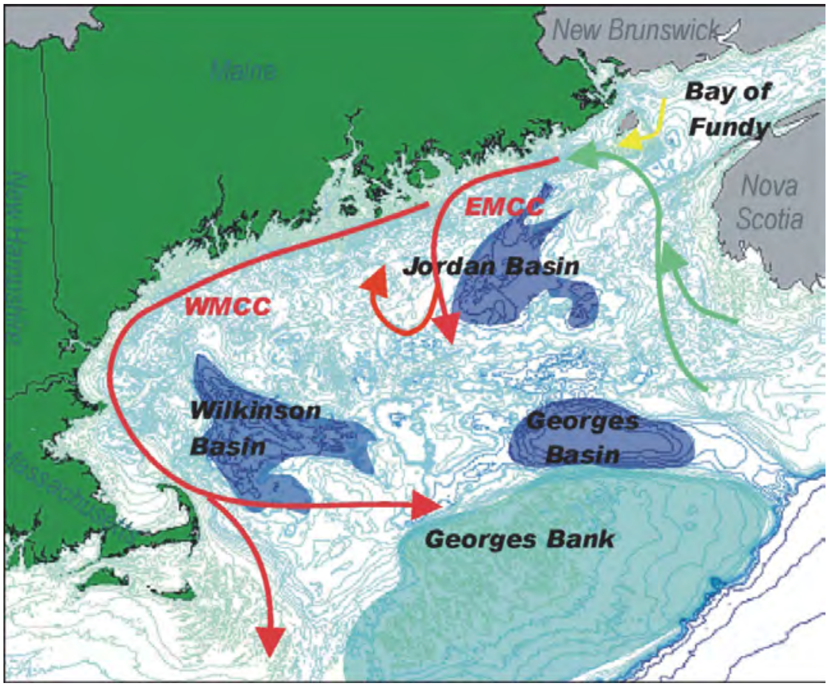

Figure 7.8: Source water for the Maine Coastal Current (MCC) originates from the Scotian Shelf, Northeast Channel, Bay of Fundy and coastal rivers. The MCC has two primary components – the western (WMCC) and the eastern (EMCC) – that are part of the general Gulf of Maine counter-clockwise circulation pattern.
Source: adapted from USGS (2007).

The western component is a plume of low salinity water some 10-30 km wide that travels more or less parallel to the continental shoreline from Maine all the way south past Cape Cod, Massachusetts. As shown in Table 7.4, a number of the physical characteristics of the WMCC have been quantified. The low surface salinity produces strong along-coast subtidal current velocities in the WMCC generally ranging in spring and summer from 0.05-0.15 m s^{-1} (Pettigrew et al. 2005). A May monthly average of 0.21 m s^{-1} and a maximum velocity of 0.55 m s^{-1} have also been documented (Geyer et al. 2004). This western component of the MCC appears to be broad and strong, having a large seaward movement that appears east of Massachusetts Bay. At Cape Cod the current separates near the northern end of the Great South Channel: part of it joins the clockwise Georges Bank gyre and the other part flows counter-clockwise in a southward direction around the Nantucket Shoals (Xue et al. 2000).

Table 7.4: Select key characteristics of the western Maine Coastal Current.

Parameter	Value
Typical freshwater discharge	3 000 m^3 s^{-1}
Coastal current salinity	29–30 PSUs
Ambient salinity	32–32.5 PSUs
Average thickness of coastal current	15 m
Width of coastal current	10 km (during downwelling) 30 km (during upwelling)
Width of mouth	0.5 km
Velocity in the plume	0.2-0.4 m s^{-1}

Source: Geyer et al. (2004).

The eastern component of the MCC quickly turns seaward just south of Bar Harbor, Maine. The eastern component helps to establish a counter-clockwise gyre over the Jordan Basin (COOC 2007b), previously described as the gulf gyre. The degree of summer offshore veering to the gulf gyre versus leakage into the WMCC along the coastline has been observed to vary strongly over a three-year period. It changed from nearly complete disruption in 1998 to nearly continuous throughflow in 2000 (Pettigrew et al. 2005). The eastern Maine Coastal Current (EMCC) occurs somewhat episodically as cold plumes of coastal current water that erupt from the eastern Maine shelf as offshore extensions. Some of the plume waters appear to become entrained within the cyclonic circulation of the gulf gyre over Jordan Basin, while a portion contribute to an anti-cyclonic eddy at the far end of the plume and west of Jordan Basin (Pettigrew et al. 1998). The spring and summer subtidal surface current component of the EMCC ranges from 0.15-0.30 m s^{-1} (Pettigrew et al. 2005), slightly stronger than the western current. On occasion, the EMCC has been observed to undergo a true reversal of its typical southwesterly direction, with average currents in the order of 0.1 m s^{-1} directed towards the northeast (Pettigrew et al. 2005), although the reversals are short lived and weak, even during strong northeasterly wind events (Geyer et al. 2004). Beneath the low salinity surface layer, the flow remains persistently southwestward, with velocities around 0.1 m s^{-1} (Geyer et al. 2004).

In summary, there are three primary sources of water to the Gulf of Maine. The marine inflow to the Gulf of Maine is the sum of two major sources of water. This portion of the continental shelf system receives inflow both from the Scotian Shelf around Cape Sable and through the deep Northeast Channel (Mountain 1991). These waters move predominantly in a counter-clockwise direction around the perimeter of the Gulf of Maine. It has been estimated that it takes about three months for water to circulate around the periphery of the gulf (Van Dusen and Hayden 1989). The third primary source of water to the Gulf of Maine is the relatively fresh water that forms the MCC. This current is driven by freshwater inputs originating primarily from the four largest rivers entering the Gulf of Maine: the Saint John River, Kennebec River, Penobscot River and Merrimack River. However, the freshwater inputs from these rivers, along with precipitation falling on marine water surface, is about two orders of magnitude smaller (0.005×10^6 m^3 s^{-1}) than the combined mean Northeast Channel and Scotian Shelf inflows (0.400 x 10^6 m^3 s^{-1}) (Mountain 1991).

7.4 Stratification and Mixing (Fronts, Gyres and Upwellings)

Sea water often has different properties spatially, either vertically from the top of a water column to the sea floor, or horizontally at different locations. These varying properties of temperature and salinity also vary the density of water and, as with any dense liquids, the heavier, more dense liquids will sink toward the bottom and lighter, less dense liquids will float on top. Stratification is the product of having both dense (cold and/or saline) water and less dense (warmer and/or less saline) water trying to occupy the same horizontal place at a given point in time. In such a case, the heavy water will sink to the bottom and the less dense water "floats" on top, creating a stratified water column. Several layers may exist vertically at one location. If there are adequate mixing mechanisms at the place where two or more water bodies of different densities exist, they get blended to a single density body of water, and the stratification is broken down.

The Gulf of Maine is typically a stratified three-layer system. The surface and intermediate layers may be mixed at certain times of the year and stratified at others. The contribution of Scotian Shelf water is to both Gulf of Maine surface water and intermediate layer water. Maine bottom water that is deeper than 115 m has a more complex origin than surface and intermediate waters. Continental slope water has been found on the bottom of the Wilkinson Basin at 220-270 m water depth; yet between the base of the intermediate layer water at 115 m water depth and the top of the slope water lens at 250 m depth there is a cluster of data with varying salinity and chemical signatures (Fairbanks 1982). The deep water layer of the Gulf of Maine is only located in a few deep basins and is rarely, if ever, vertically mixed with those layers above.

Spatially there are areas of the Gulf of Maine that are more likely to be vertically mixed than others. Water temperature and salinity are the two primary components of stratification because they alter the density of water. Cold salty water as a bottom layer is very dense and therefore quite stable when overlain with a less salty water of any temperature. However, if highly saline water flows on top of less saline water, or if the temperature of a very cold or very warm surface layer of water begins near that of the underlying waters during the change of seasons, the layers become unstable and prone to mixing. Finally, in areas of significant water movement with varied ocean bottom morphology, mixing will tend to occur more readily as the associated energy and turbulence of the water movement over a changing seafloor structure can break down the stability associated with stratified waters. Therefore, within the Gulf of Maine we expect to see stratified water where there is minimal bathymetric relief and circulation, and well-mixed waters where there is diverse bathymetry and relatively strong ocean circulation. The eastern and southern portions of the gulf, including the Bay of Fundy, Jordan and George's basins, the Northeast Channel and Georges Bank are vertically well mixed by vigorous tidal activity. The western portion of the Gulf of Maine, including Wilkinson Basin, is less well mixed as cold fresh water enters the gulf to form the MCC and rests on top of the more dense marine water in the western gulf. The result is a tidally mixed eastern region (Xue et al. 2000) separated from the stratified western region by a tidal front (see Figure 7.9).

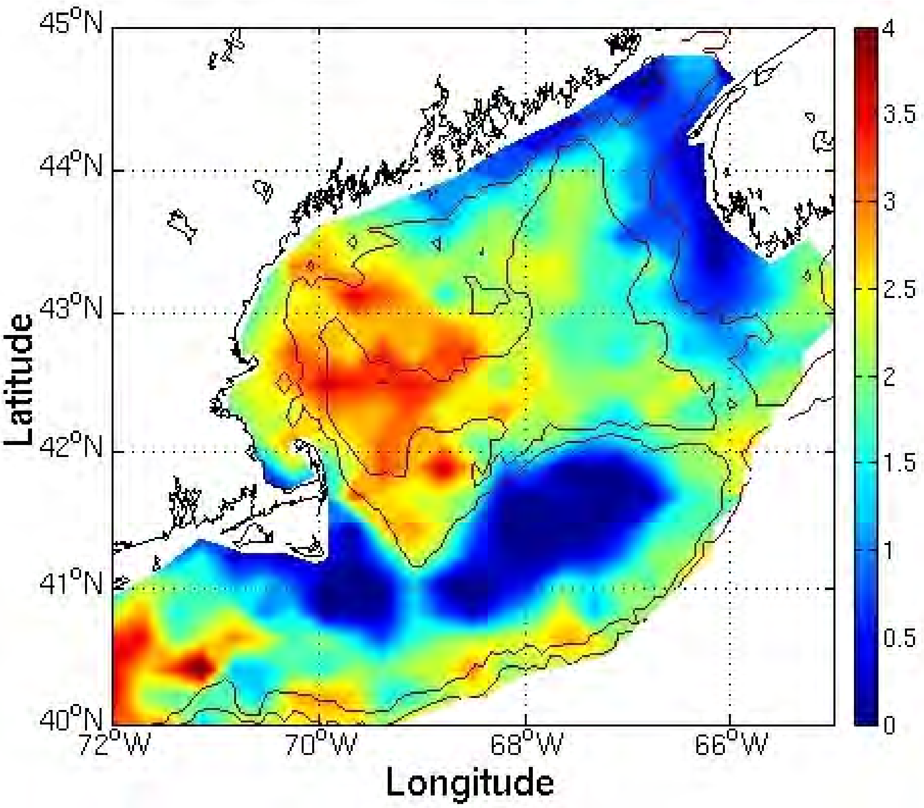

Figure 7.9: Summer stratification patterns for the Gulf of Maine and Georges Bank (sigma-t units). Warmer colours represent areas with higher stratification values.
Source: Maureen Taylor, Northeast Fisheries Science Center, NMFS, personal communication (2009).

Across the Gulf of Maine the annual cycle of the mixed layer depth follows a general pattern which can be described as follows. The mixed layer is deepest during the winter, followed by a shallower mixed layer during the spring. This layer reaches minimum depths during the summer (July to August) before a gradual return to deeper mixed layers during the autumn. Typically, the mixed layer depth is between 20-60 m during the winter (with occurrences reaching below 100 m), between 5-15 m during the summer, and between 20-40 m during the autumn (Casault et al. 2003). The variance of the mixed layer depth generally is larger during the winter than during the summer and the fall. Larger winter variances reflect, to a certain extent, movements of the mixed layer that are caused by the combined effects of storms and the weak stability conditions of the water column under surface cooling conditions of cold winds and snowfall. Such variability in the mixed layer depth does not tend to occur during the summer and the autumn because the energy from storms that initiates the movement must first overcome the stable stratified structure of the water column (Casault et al. 2003). However, across the Gulf of Maine there are exceptions to these observations, and these exceptions often occur in association with fronts, gyres and upwellings.

7.4.1 A Stratified Western Gulf: Primarily two scales of occurrences establish the amount of stratification within the Gulf of Maine waters. At a large multi-year scale, the NAO can affect a number of functions that ultimately influence water temperature and salinity. An increase in the inflow into the Gulf of Maine of cool, low salinity surface water from the Scotian Shelf during the 1990s has led to a general freshening of surface waters across the continental shelf. This freshening may have caused an increase in stratification, particularly during the summer months when the water column is typically highly stratified and has the increased potential to trap heat (Friedland and Hare 2007), becoming even more stable.

The second scale of occurrences that influences stratification is the change in seasons around the Gulf of Maine. As noted earlier, stratification occurs primarily in the western Gulf of Maine when cool, fresh and less dense water leaves the land base through spring river runoff and flows on top of the relatively warmer more saline marine water of the gulf. The salinity difference establishes the stratification, and summer warming of this layer enforces the stratification by having warmer water lying on top of the colder saltier layer. As winter approaches, the surface layer cools, eroding the stratification in the upper water column (Xue et al. 2000). During winter, the ocean releases heat to the atmosphere, and the net upward heat flux increases from near shore towards the open ocean. Although the air temperature is colder near the coastline, the outer Gulf of Maine air-to-sea temperature difference is larger because the continental slope water east of Georges Bank is much warmer. In March and April, the inner gulf begins to receive net downward heat flux from the atmosphere to the ocean (Xue et al. 2000). When less saline water volume from rivers and the Labrador Shelf increase in the Gulf of Maine, a rise in stratification may be expected. This is particularly true during the summer months when the water column is already highly stratified, and it is during the warm days of summer that there is increased potential to trap heat (Friedland and Hare 2007). In summer, solar radiation is the major contributor to the variability in heat flux and corresponds to a time when thermal stratification is strongest (Mountain et al. 1996).

Although the western Gulf of Maine is characterized as stratified, this does not mean that vertical mixing never occurs. Along the WMCC, downwelling-favourable winds (same direction as Kelvin wave propagation) squeeze the freshwater plume against the coast and accelerate its down-coast (southwestward) flow. Upwelling events have, at times, temporarily arrested or reversed the direction of surface flow in the WMCC as winds oppose the typical direction of wave propagation. It has been suggested that the mixing associated with observed upwelling events might, on occasion, weaken the density stratification of the MCC enough that it loses coherence after this point in time. A significant downwelling event may then be necessary to re-establish the coastal current stratified structure (Geyer et al. 2004). Based on analysis of 1980-2004 data, there were only two occurrences in the observed mixed-layer depth time series when there was nearly complete top-to-bottom winter mixing in Wilkinson Basin of the western Gulf of Maine, suggesting that full winter overturn of the basin is not a common event. The surface salinity in winter is dependent on change in contribution from the source waters of the Gulf of Maine (Taylor and Mountain 2009). However, the surface waters of the western Gulf of Maine freshen and stratify during the spring and summer due to both river runoff and increased solar heating (Taylor and Mountain 2009).

As described in Section 7.3, the WMCC, a predominantly stratified body of water within the Gulf of Maine, flow towards central Georges Bank. Therefore, some of the water column characteristics that influence stratification in the western Gulf of Maine are carried to Georges Bank. A modelling study of the long-term (1985-1995) monthly mean stratification on southern Georges Bank shows that the water column down to 60 m depth remains well mixed throughout the year with no stratification development. However, within the 60-80 m depth zone and 80-100 m depth zone at the edge of the continental slope, significant stratification begins to develop during May (60-80 m) and April (80-100 m). This stratification remains in place for the next few months, reaching a maximum during July and August. The interannual variability of this stratification is large (Bisagni 2000). The remainder of Georges Bank is similar to the eastern Gulf of Maine and is vertically mixed.

Important changes in stratification have been noted over time with increasing temperature and changes in salinity. Stratification increased steadily from the mid-1970s on Georges Bank and in the eastern Gulf of Maine (Figure 7.10). Increases were also noted in the western Gulf of Maine although these changes were less pronounced than in the other regions.

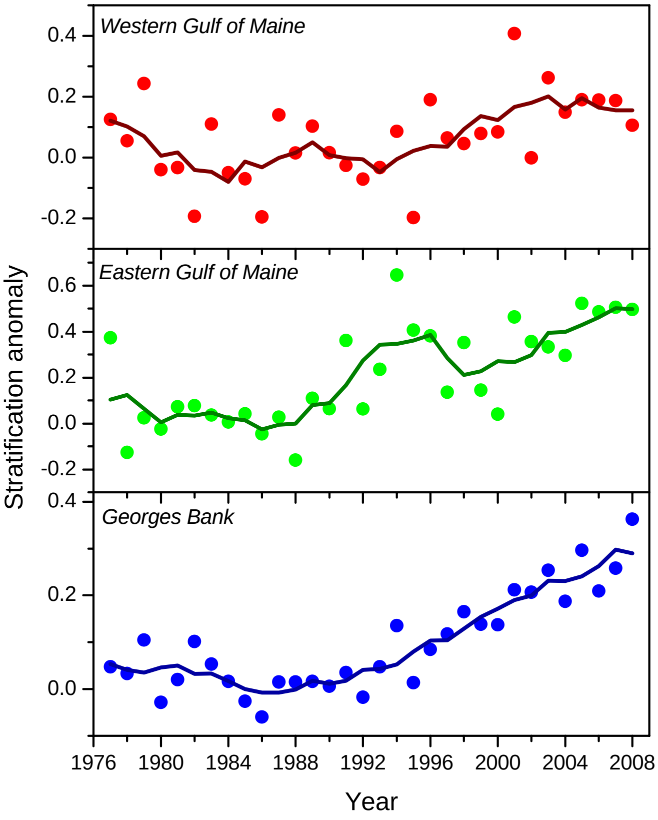

Figure 7.10: Trends in stratification for the western Gulf of Maine, eastern Gulf of Maine, and Georges Bank. Stratification was computed as the density difference (kg/m^3) between the surface and 50 m. The anomaly was derived using reference stratification annual cycles derived from standard MARMAP stations (time period = 1977-1987).
Source: unpublished data, Northeast Fisheries Science Center, NEFSC Oceanography Branch (2009).

7.4.2 A Vertically Mixed Eastern Gulf: In the southern and eastern Gulf of Maine there are a number of gyres and fronts that promote vertical mixing and inhibit strong stratification. The gulf gyre over Jordan Basin and Georges Basin, the Georges Bank gyre, the fronts on both the northwest and southeast slopes of Georges Bank, and the Bay of Fundy gyre northeast of Grand Manan Island all are recognized locations of strong vertical mixing within the Gulf of Maine.

The M2 tide, the large twice-daily tide, contributes to tidal mixing over the diverse bathymetry that exists at these various locations. For example, the velocity scale of the Jordan Basin gyre is approximately 0.1 m s^{-1} (Pettigrew et al. 1998); the maximum vertical displacement within the Bay of Fundy gyre is estimated at 10 m day^{-1} (Aretxabaleta et al. 2008); tidal currents of 1 m s^{-1} or greater are found on Georges Bank (Xue et al. 2000), 0.8-1.2 m s^{-1} over the deeper part of the Bay of Fundy Basin (Aretxabaleta et al. 2008). Tidal mixing reduces the vertical stratification and promotes a deep circulation that becomes strong earlier in the year (Xue et al. 2000) across the eastern Gulf of Maine.

Fronts, gyres, and upwellings are key places of mixing that typically pump nutrients up into the top of the water column where sunlight can reach them and the process of photosynthesis can take place. Phytoplankton generally thrives in these areas given the combination of nutrients and sunlight, and provides an abundant food source for the base of the food web. In estuaries and offshore areas near underwater banks, vertical upwelling brings cold, salty, nutrient-enriched bottom water to the surface. Vertical mixing occurs in such areas as off the southwestern coast of Nova Scotia between Cape Sable and Yarmouth adjacent to the Northeast Channel, and off the Maine coast from Grand Manan Island at the mouth of the Bay of Fundy south to Matinicus Island. The highly productive northwest edge of Georges Bank receives nutrient-rich deep water from the Gulf of Maine (Van Dusen and Hayden 1989). Nutrients washed off the land into rivers enrich the coastal waters and these mix with upwelling deep-ocean waters in many estuaries associated with the MCC. The Bay of Fundy gyre is a persistent feature in the mouth of the Bay of Fundy. The main mechanisms for the gyre's formation and existence are strong tidal flow and density-driven circulation that is formed during stratification related to spring freshwater runoff and summer solar heating. Stronger circulation of the gyre occurs during the latter part of the stratified season (July-August and September-October). Weak tidal mixing occurs in the deep basin in the central Bay of Fundy and strong tidal mixing exists on the shallow flanks around Grand Manan Island and western Nova Scotia. Residence times within the Bay of Fundy gyre are predicted to be longer than 30 days (Aretxabaleta et al. 2008).

Although some seasonal thermal stratification of near-surface waters on southern Georges Bank occurs, atmospheric cooling and wind mixing keep the entire Bank vertically well mixed during winter, and kinetic energy from either tidal or wind mixing is sufficient to prevent stratification due to surface heating across most of the bank year round (Mavor and Bisagni 2001). Over the shallow central region of Georges Bank, turbulent tidal mixing is sufficiently strong to keep the water column well mixed. The transition zone, or tidal mixing front, between the well-mixed area and the stratified region on southern Georges Bank is a persistent feature in hydrographic data from late spring until early fall (Mavor and Bisagni 2001).

The Gulf of Maine has temperature and salinity characteristics distinct from the adjacent offshore Atlantic Ocean. The front delineating these differences generally lies along the continental slope east of Georges Bank and typically moves farthest offshore in winter and farthest onshore in late summer and early autumn. Although this front has closely followed the edge of the continental shelf at the southern extent of Georges Bank, it lies slightly further offshore near the entrance to the Northeast Channel (Page et al. 2001).

A tidal mixing front separates the tidally stirred, well-mixed waters over central Georges Bank from the stratified water over the Bank's southern flank. Sea surface temperature fronts on the northeast peak of Georges Bank represent the boundary between very cold Scotian Shelf water and other water masses on Georges Bank. There is significant spatial and temporal variability of the tidal mixing fronts, as well as other frontal regions, on Georges Bank and therefore the use of a single bathymetric contour to describe the location of the fronts on Georges Bank is not possible (Mavor and Bisagni 2001).

7.5 Waves and Turbulence (Influence on Mixing)

In coastal areas waves play a significant role in near-shore mixing, sediment transport, erosion, seaweed establishment and many other ecosystem functions. However, in the areas that are the focus of this report (the more open water areas in the Gulf of Maine), waves have a more limited role and have therefore been less studied. Yet, in some areas, particularly the more shallow areas such as the outer edge of the coastal shelf, Georges Bank and portions of the Bay of Fundy, waves play an important role in mixing the surface water layer.

At 6-8 m heights, the large waves in the open Bay of Fundy are about three times as large as in the protected portions of the adjacent coastal shelf. However, waves in the open Gulf of Maine are generally about twice the height of waves in the Bay of Fundy (Chang et al. 2005). Similarly, at the edge of the coastal shelf, storm waves of 6 m occur near Massachusetts Bay and west of Wilkinson Basin (COOC 2007a). Offshore on Georges Bank, extreme wave heights have been estimated as high as 18 m, although typical mean wave height varies from about 1 m in the summer months to 2.8 m in the winter months (Backus and Bourne 1987). In April 2007, waves in this area had a strong mixing influence. The wave action was strong enough to break down the annual temperature stratification in the WMCC, where the surface layer is colder than the deeper water. The phytoplankton of the spring bloom was mixed down in the water column where light could not reach them, stopping short the production of chlorophyll that is characteristic of the spring bloom (COOC 2007a).

Kelvin wave propagation in the Northern Hemisphere is with the shore to the right of the direction of travel. This means that the natural (Kelvin) wave direction along the western Gulf of Maine coastline is in the same southwesterly direction as the MCC (Geyer et al. 2004). In an assessment of strength, frequency and timing of large storms in Massachusetts Bay between 1990 and 2006, northeast storms were the major cause of large waves. This is in large part due to the long fetch (uninterrupted distance over open water) to the east across the Gulf of Maine and into the open Atlantic (Butman et al. 2008). Within the Bay of Fundy, approximately 30% of the waves propagate into the bay from the Gulf of Maine (Chang et al. 2005).

7.6 Ice (Seasonal Coverage)

Within the Gulf of Maine, ice has long been noted as a significant force in tidal estuaries of the Bay of Fundy where it plays a significant role in moving sediments and changing morphology.

Estimates exist that nearly 85 275 tonnes of tidal mud might be encased in ice and moved on a change of tide in a single estuary in the upper Bay of Fundy (Hind 1875). More recently, it has been noted that ice may also play a critical role in propagation of tidal marsh grasses through the potential to rip out marsh vegetation and their roots and transport them to new areas (van Proosdij 2005). Ice occurs in the upper reaches of the Bay of Fundy from December to April and is typically composed of two types. Drift ice forms on the seawater surface and, because of almost constant movement in tidal currents, is composed of small rounded pieces. Shorefast ice develops from the stranding of drift ice between the neap and spring high water levels, and may be up to 5 m in thickness. A frozen crust ice may also form up to 0.5 m thick on exposed intertidal sediments (Gordon and Desplanque 1983). Similar ice formations can be found along the intertidal area of virtually the entire coastline bounding the Gulf of Maine. However, all of these ice forms are generally limited to intertidal areas that are not considered in depth within this report. The Canadian Ice Service (2008) indicates that the 30-year frequency of sea ice in the Upper Bay of Fundy is only 1-15% and is contained in the outer extent of the Minas Basin and Chignecto Bay.

In the deeper, more open waters of the Bay of Fundy and inner gulf, where salinity increases and tidal currents are strong, there is little winter ice. The open Gulf of Maine waters rarely see coastal pack ice or the icebergs that occasionally move south of Newfoundland with the Labrador Current. The long-term annual mean for the number of icebergs south of Newfoundland is 483 (International Ice Patrol 2009). However, they tend to also follow currents east of the continental shelf, well outside of the Gulf of Maine. The cold meanders of the Labrador Current support icebergs commonly to the same latitude as the southern Gulf of Maine. When icebergs encounter the warm temperatures of the Gulf Stream, they usually melt very rapidly. However, in 1926, the southernmost-known iceberg reached about 150 nautical miles from Bermuda (International Ice Patrol 2009), and Wisconsinan-age iceberg furrows are preserved in silt on parts of German Bank in the eastern Gulf of Maine (Todd et al. 2004), and the Murr Ledges near the mouth of the Bay of Fundy (Parrott et al. 2008).

The greatest effect of ice within the Gulf of Maine is related to the transport of relatively fresh water, achieved in part from melting ice north of the gulf, through the Labrador Current and into the Gulf of Maine. The Labrador Current is the single greatest source of freshwater to the Gulf of Maine (Mountain 1991, Pettigrew et al. 1998, Houghton and Fairbanks 2001). An estimated 48% of the freshwater carried into the Gulf of Maine with the Nova Scotia Current comes from St. Lawrence River outflow and 52% from the Labrador Current north of Newfoundland and Labrador (Houghton and Fairbanks 2001). Studies have not been carried out to directly relate the annual ice coverage and melt in these two areas to the supply of freshwater to the gulf. The long term maximum annual ice coverage for the areas immediately north of the Gulf of Maine do provide a potential indication of years in which fresher water may have been delivered to the gulf (see Figure 7.11)

The maximum ice coverage to have occurred between 1968 and 2007 north of the Gulf of Maine occurred on March 12, 1990. As indicated in Figure 7.12, the areal extent during this maximum coverage did not extend to the Gulf of Maine or onto the Scotian Shelf northeast of the gulf (Canadian Ice Service 2008).

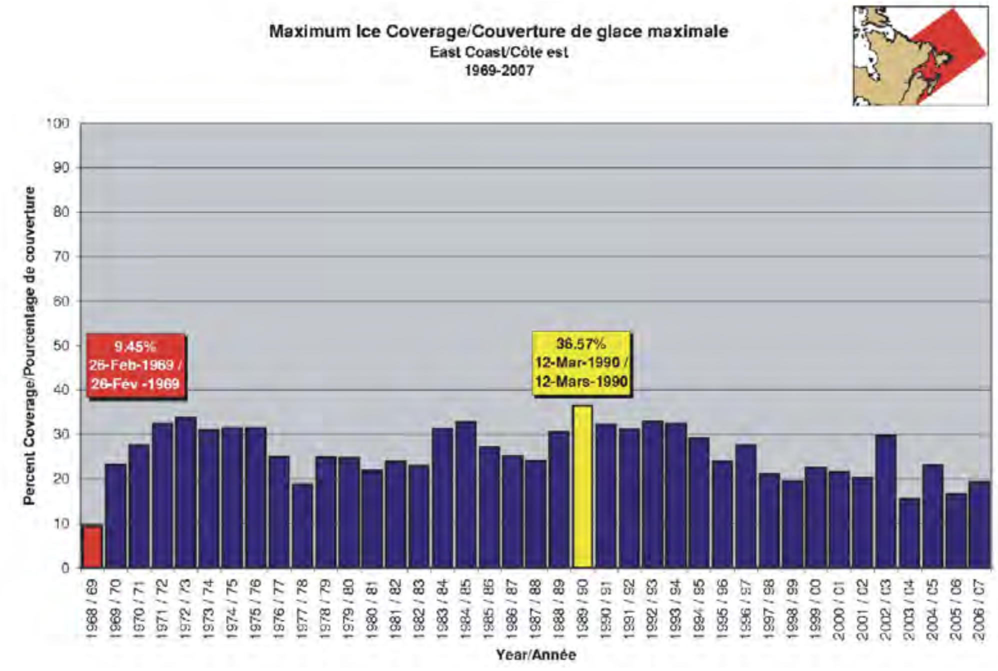

Figure 7.11: Maximum annual ice coverage in percentage between 1968-2007 for the area between the Gulf of Maine and northern Labrador. Ice coverage and subsequent melt in this area influences the salinity within the gulf.
Source: Canadian Ice Service (2008).

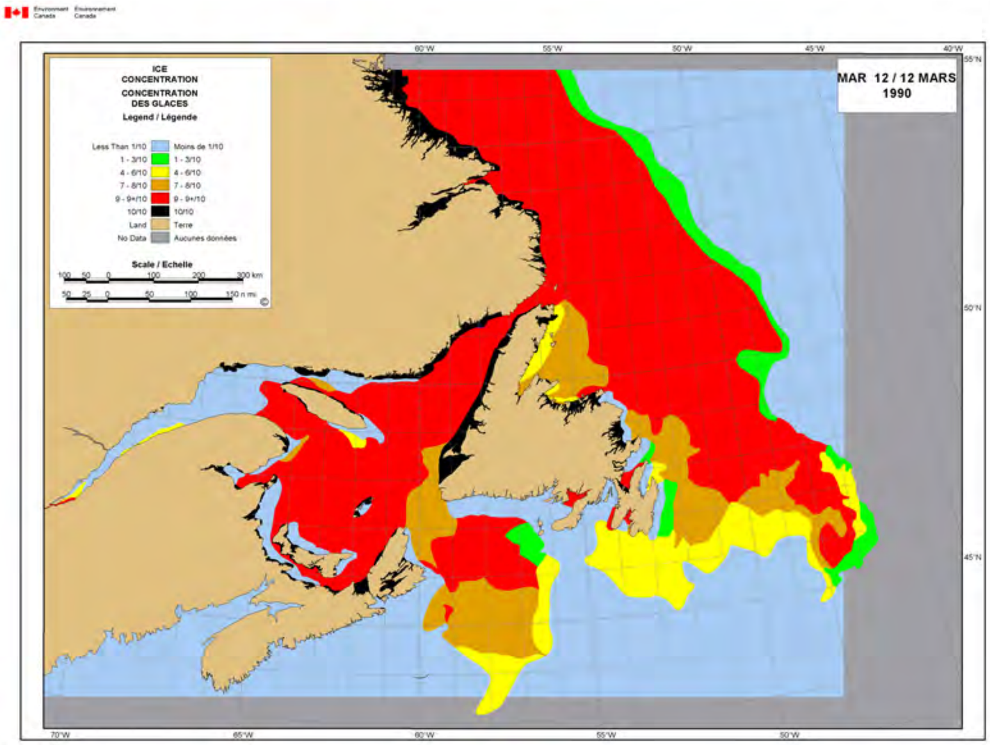

Figure 7.12: Between 1968 and 2007, the maximum ice coverage in the Canadian North Atlantic occurred on 12 March 1990. This map shows the extent of ice coverage at that time, distant from the Gulf of Maine.
Source: Canadian Ice Service (2008).

8. SEAWATER TEMPERATURE, SALINITY AND DENSITY

The temperature, salinity, density and nutrient content of the water across the Gulf of Maine vary enormously depending on the location, time of year and water depth. For example, based on daily air temperature, water temperature and wind speeds for the period of 1979 to 1987, it has been found that the interannual variability in water temperature in the western Gulf of Maine is significantly correlated with the variation in the rate of heat exchange between the gulf waters and the atmosphere. However, in the eastern gulf, no relationship is found in the exchange of heat between the water and the air, and the temperature variability is thought to be dominated by flows into and out of the eastern area of the gulf (Mountain et al. 1996). The water temperature of the North Atlantic ranges from -1.7°C in the Labrador Current to 20°C in the Gulf Stream (International Ice Patrol 2009). Both of these large-scale currents periodically find their way into the eastern Gulf of Maine, influencing seasonal and interannual temperature, salinity, density and nutrient characteristics around the gulf. A final example of the variability in key water parameters is how the M2 tide contributes seasonally to changes in temperature and salinity (and, therefore, density) of Gulf of Maine waters through tidal mixing that reduces the vertical stratification. This tidal mixing tends to increase the salinity along the shallow coastline of the Gulf of Maine (Xue et al. 2000). Furthermore, since nutrients vital for growth tend to become trapped in deeper waters, in locations where the mixing of bottom and surface waters due to tides, currents and bottom topography occur, biological productivity is highest (Van Dusen and Hayden 1989).

The following sections highlight some of the better understood changing characteristics of the seawater in the Gulf of Maine.

8.1 Temperature

There are two primary mechanisms that create water temperature variability in the Gulf of Maine. One is the exchange of heat between the water and the atmosphere. The second is the exchange of different temperature waters with neighbouring areas through water currents and circulation. In the Gulf of Maine, the between-year variability in the heat exchange between the water and the atmosphere is largest in winter, a time when the upper 100 m of the water column is generally well mixed. In summer, solar radiation is the major contributor to the variability in this heat flux and corresponds to a time when thermal stratification is strongest (Mountain et al. 1996). This atmospheric–water exchange is spatially more pronounced in the western Gulf of Maine where stratification of the water column is stronger. Studies indicate that surface heat flux can account for the characteristic seasonal change in the heat content of the upper 100 m of the water column in the western and central Gulf of Maine and upper 65 m in the eastern gulf (Mountain et al. 1996). Approximately 80% of the interannual stratification variability on southern Georges Bank appears related to heat flux (Bisagni 2000). In the eastern gulf, water temperature variability does not appear correlated with atmospheric temperature variability, but is thought to be dominated by the variability of warm slope water and cold shelf water into the eastern portion of the Gulf of Maine (Mountain et al. 1996). Gulf Stream and warm slope waters that may enter from the edge of the continental shelf through the bottom of the Northeast Channel are typically 10-16°C at depths >100 m, whereas the cold Labrador Shelf water that enters the Gulf of Maine's upper water column as it flows off the Scotian Shelf and around the southern tip of Nova Scotia is closer to 0°C (Houghton and Fairbanks 2001).

Most often, ocean temperatures are measured within the upper 1 m of the water column, a temperature recorded as the SST. The mean annual SST cycle shows that maximum SST in the Gulf of Maine, as well as the entire U.S. continental shelf area, is usually achieved in August (Figure 8.1). Minimum SST usually occurs during March in the Gulf of Maine regions (Friedland and Hare 2007), and the gulf tends to have the lowest summer and winter SSTs of the U.S. northeastern continental shelf.

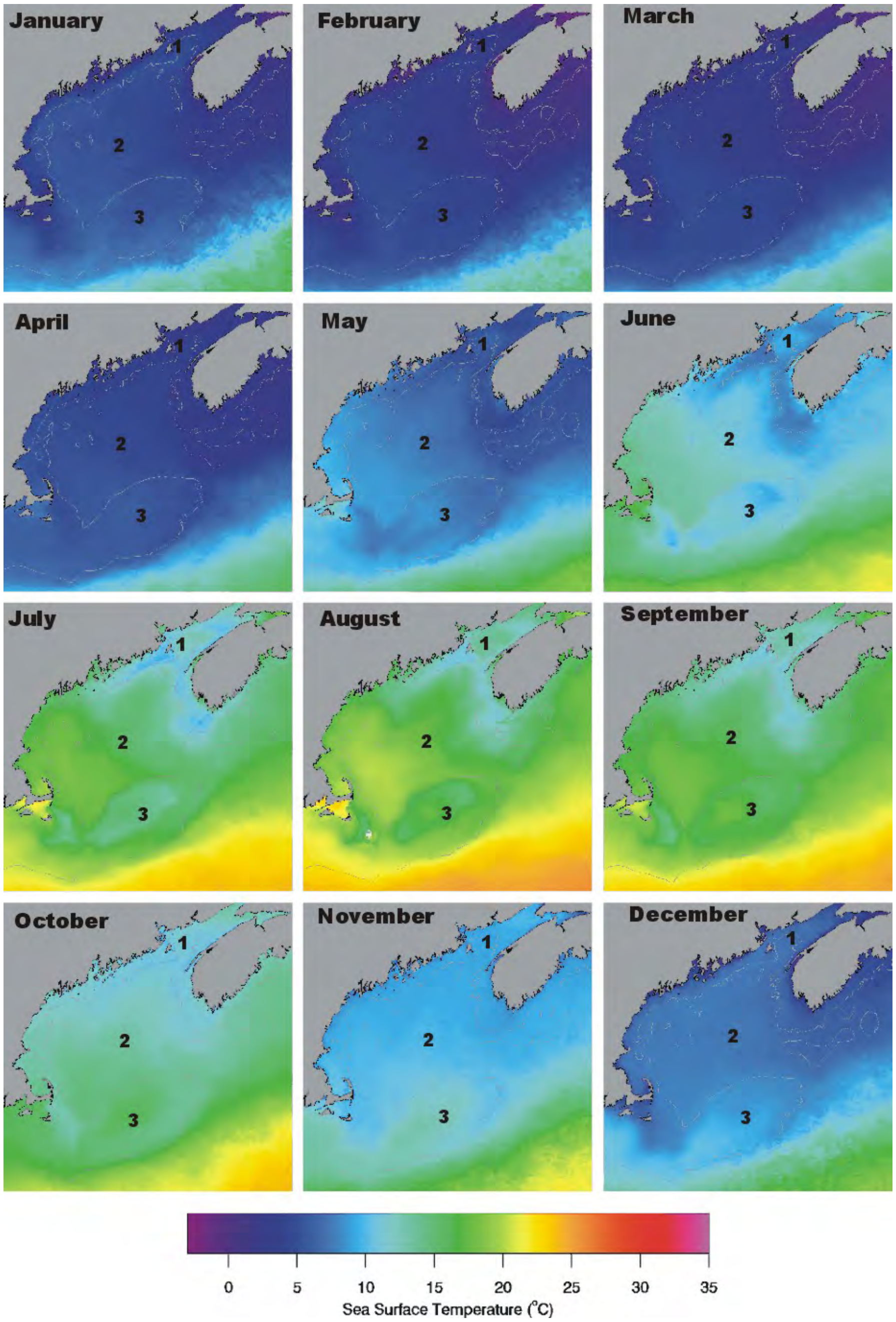

Figure 8.1: Composite of mean monthly sea surface temperature patterns for the Bay of Fundy (1), the central Gulf of Maine (2), and Georges Bank (3) for the period 1998-2008.
Source: K. Hyde, NMFS, Woods Hole, personal communication (2009).

In general, 10-30 year monthly temperature trends indicate periodic short period fluctuations of 1-2°C above or below the long term mean (DFO 1997a). There is some indication that SST has increased during the most recent decade. However, the levels associated with this most recent SST regime remain lower than the temperature levels associated with the warm conditions of the 1940s and 1950s (Friedland and Hare 2007) and during the late 1990s. In many years during the 1980s and 1990s, SSTs during the winter and spring seasons on Georges Bank exceeded 6°C, whereas they have cooled about 1°C in recent years (NOAA 2008). Overall, the late-winter Gulf of Maine SSTs recently are about 4°C, while spring temperatures are near 5°C (NOAA 2008). Long-term averages show that late winter surface water temperatures will cool to near 3°C in the coastal shelf area of the Gulf of Maine, while Georges Bank will be warmer in winter and summer, even approaching 20°C in August. It has also been shown that between 1854 and 2005, SST began declining at the beginning of the 20th century, followed by increases through to 1950, and then rapidly decreased between 1950 and the mid 1960s, with somewhat warmer SSTs thereafter to 2005 (Friedland and Hare 2007).

An analysis of nearly 60 years of annual temperature anomalies[2] at depth shows that temperatures fell to 1-2°C below normal from the late 1950s through the early 1970s. The drop occurred at depths of both 50 m and 200 m in the vertically mixed waters of Georges Bank and Georges Basin (see Figure 8.2; DFO 2008a).

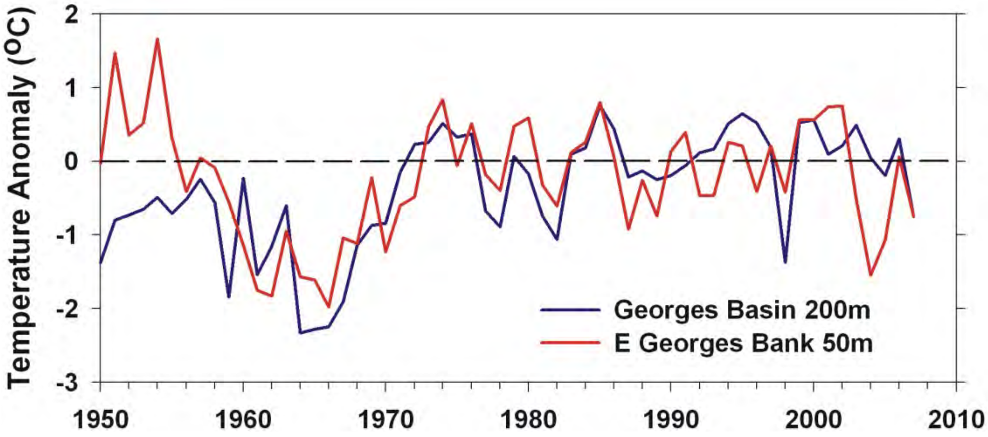

Figure 8.2: Annual temperature anomalies between 1950 and 2008 at two different depths and locations in the Gulf of Maine show temperatures 1-2°C below normal from the late 1950s through the early 1970s.
Source: adapted from DFO (2008a).

The Bay of Fundy is the largest body of cold water in the Gulf of Maine. However, during the summer months the outer Bay of Fundy exhibits a local surface temperature maximum. The region of high surface temperature occurs over the deepest part of the Bay, where tidal mixing is insufficient to vertically mix a relatively fresh surface lens associated with discharge from the Saint John River, and solar warming occurs more rapidly (Pettigrew et al. 1998). This warmer zone can be seen in Figure 8.3, just west of Grand Manan Island. Although the Bay of Fundy is the largest body of cold water in the Gulf of Maine, the coldest surface waters appear in a band roughly 30 km wide along the Maine coast, from Grand Manan Island to just east of Mount Desert

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[2] A temperature anomaly is the difference between the observed temperature and the long-term average.

Island. This is the beginning of the MCC. The cold 4-5°C surface temperatures observed in this region are, at least in part, a consequence of the vigorous tidal mixing that occurs in the vicinity of Grand Manan Island (Pettigrew et al. 1998). The near-surface waters of the core of the EMCC in June 1998 had an approximate temperature range of 6.9-7.6°C (Pettigrew et al. 2005).

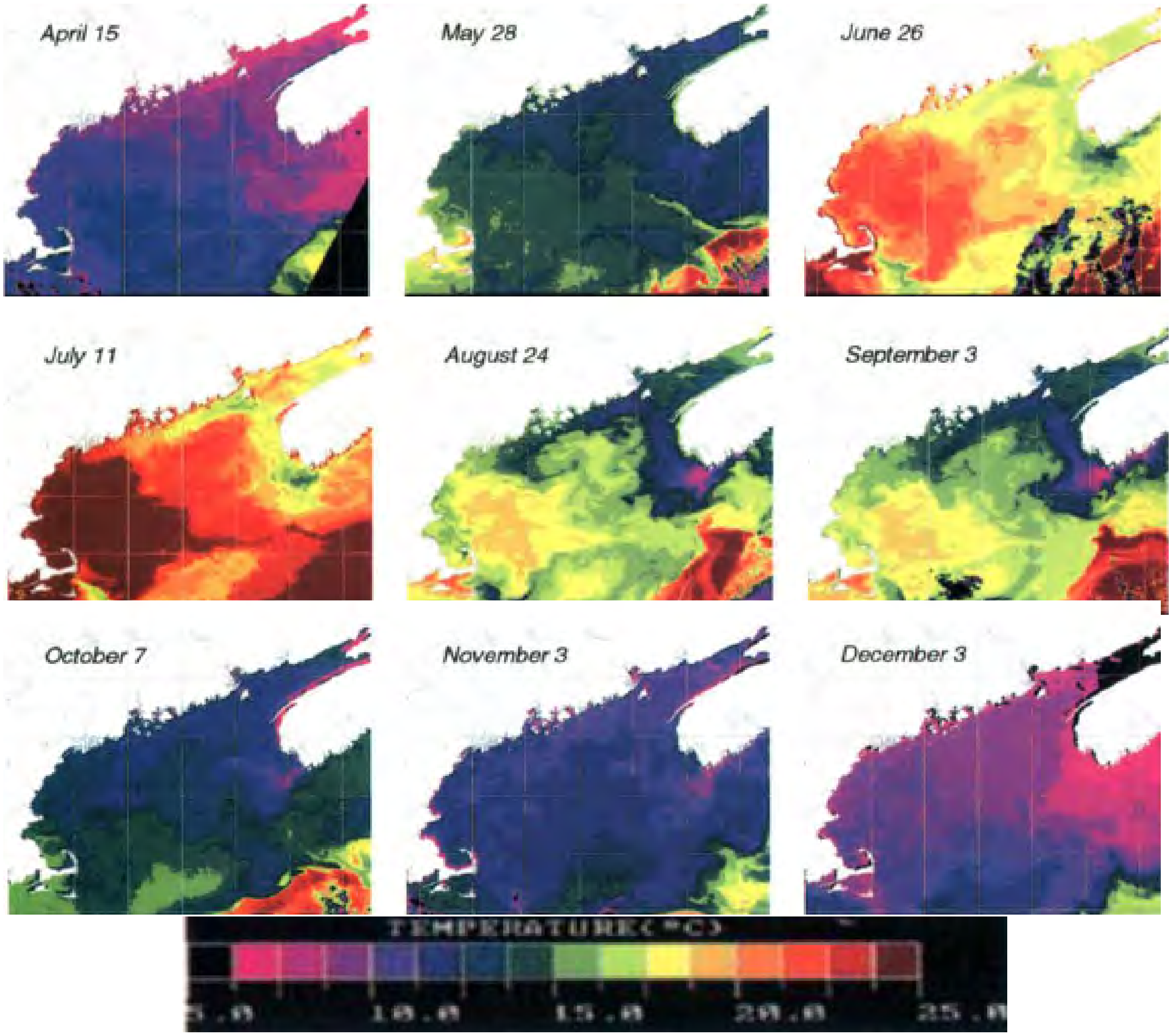

Figure 8.3: Point-in-time sea surface temperatures from April-December (1994) generally highlight both colder areas (Bay of Fundy, eastern Maine Coastal Current and the southern tip of Nova Scotia) and warmer areas (western Gulf of Maine, Wilkinson Basin and, seasonally, Georges Bank) within the Gulf of Maine.
Source: adapted from Pettigrew et al. (1998).

Over time, SST difference has increased in a latitudinal pattern from south to north along the U.S. coastline (with warmer waters moving northward along the coast over time). A regime shift (a significant change in temperature from one relatively stable state to another) occurred during the late 1980s in the eastern Gulf of Maine. More recent data indicate that a regime shift may have started during the last few years in the western Gulf of Maine and on Georges Bank (Friedland and Hare 2007).

Although maximum, minimum and mean temperatures are key components to monitor, another key temperature measure also provides scientist with insight into changing conditions. Temperature range, the difference between the maximum and minimum temperature, does not always remain the same. A change in temperature range can have significant implications regarding how quickly seasonal change occurs. If a greater temperature range exists, it is likely that the rate of change between two seasons must also increase. Such seasonal changes have significant biological implications, such as when and how long conditions may be able to support a spring phytoplankton bloom, or how long a particular temperature-sensitive species can inhabit the Gulf of Maine. Georges Bank experiences the widest range of SSTs in the gulf, a characteristic that is greatly narrowed in areas further offshore and, to some extent, inshore of the Bank (Friedland and Hare 2007). On Georges Bank, long-term data sets for bottom temperatures (1987-2001) indicate a range of 3-14°C, with the warmest temperatures located along the southern flank of the bank and the remaining areas being 3-8°C (Page et al. 2001).

Although the patterns in mean annual SST on the northeast U.S. shelf mirror global patterns, a recent observed increase in SST *range* is novel and significant. Even though recent SSTs are still less than during the mid-20th-century warming regime, the range between the maximum and minimum is currently greater than during the 1940s and 1950s. Mean annual SST range has increased on the continental shelf to the highest levels seen during an 1875-2005 time series, suggesting that we have entered a new regime of SST variability (Friedland and Hare 2007). Annual SST range decreases in a seaward direction from the coastal shelf to the continental shelf to the open Atlantic Ocean. During the most recent observed summer warming trend, there has not been a matched increase in winter SST. Instead, winter SSTs have remained cool. This explains why range has increased, while mean annual SST has remained below historical levels (Friedland and Hare 2007). However, the cause of this recent change in range of sea surface temperatures (SSTs) is unexplained.

Jordan Basin, Georges Basin and Wilkinson Basin are the three deepest areas of the Gulf of Maine. Jordan and Georges basins are in the eastern gulf and are linked through the circulation of the gulf gyre. As can be seen in Figure 8.4, these two eastern basins' bottom temperatures are warmer than the western gulf's Wilkinson Basin, which is influenced by the MCC. The eastern basins exhibit a single season minimum bottom temperature around May-June, whereas Wilkinson Basin in the western Gulf of Maine demonstrates both a spring minimum (April) and a second cool autumn period (October). Oceanic heat transfer is frequently driven by density differences due to varying salinity. It is possible for relatively warm saline water to sink, and for colder fresher water to rise, reversing the normal transport of heat. Observations of nearly three decades of data suggest that the interannual variability of wintertime convection in Wilkinson Basin is related to the variation in the surface layer salinity in the western Gulf of Maine. When the winter convection is stronger (weaker), the resulting deep-layer temperatures are colder (warmer), and the likelihood of deep winter mixing is greater when the salinities are high in the western Gulf of Maine (Taylor and Mountain 2009).

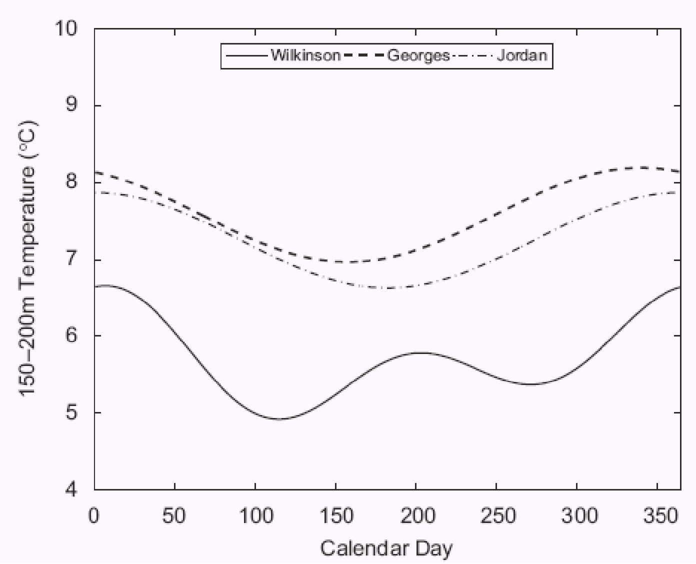

Figure 8.4: Mean bottom temperatures during the years 1978-1987 for the three deepest basins of the Gulf of Maine (Jordan's, Georges and Wilkinson) show that during winter, the deep layer temperatures in the western Gulf of Maine (Wilkinson Basin) are much colder than the eastern Gulf of Maine basins.
Source: Mountain (2004), as cited in Taylor and Mountain (2009).

8.2 Salinity

The primary source waters to the Gulf of Maine have great influence on local salinity, just as they do on temperature. The continental slope water that enters through the Northeast Channel is warm and saline, whereas the water that comes off the Scotian Shelf and is fed, in large part, by the Labrador Current is cool and relatively fresh. Salinity of slope water is generally estimated at 35.2 PSUs (Fairbanks 1982), whereas the shelf water salinity is a fresher <32 PSUs (Bisagni et al. 1996). These waters mix with the existing Gulf of Maine water at various intensities and depths depending on location in the gulf, and thereby provide a range of salinities around the Gulf of Maine.

At the mouth of the Bay of Fundy, where the MCC begins southwest of Grand Manan Island, the surface salinity is about 21 PSUs during high freshwater discharge season (April) and increases to approximately 30 PSUs during the low discharge season (September) (Xue et al. 2000). The near-surface waters of the core of the EMCC in June 1998 had a salinity range of approximately 31.7-32.0 PSUs (Pettigrew et al. 2005). Continental slope water has been found on the bottom of Wilkinson Basin at 220-270 m, and is generally >33.5 PSUs (Fairbanks 1982). Approximately 100 km offshore in Jordan Basin, low salinities of less than 32.4 PSUs have been observed at depths of 80 m (Pettigrew et al. 1998). Changes in the salinity of the Gulf of Maine may be influenced remotely by shifts in atmospheric forcing on the Arctic Ocean, resulting in atypical salinities moving through the Labrador Current and into the Gulf of Maine (Greene and Pershing 2007). Just as there is spatial variability in salinity around the Gulf of Maine, there is also seasonal variability. For example, during the month of February, maximum salinities will be observed for the western Gulf of Maine, whereas minimum annual salinity will be measured in the eastern gulf (Taylor and Mountain 2009).

The St. Lawrence River water and the Labrador Shelf water have relatively similar contributions of freshwater entering the Gulf of Maine despite varied salinities and total volume (Houghton and Fairbanks 2001). The Labrador Shelf water is typically <34 PSUs and is usually estimated to be between 32.5 and 33.5 PSUs (Mountain 1991) whereas the St. Lawrence River water at its origin is essentially 0 PSU (Houghton and Fairbanks 2001) and as low as 28-29 PSUs in late August off the Laurentian Channel, where it mixes with the Labrador Shelf water. The annual August low salinity corresponds with the pulse of the spring freshet that occurrs in the St. Lawrence River watershed, finally reaching the northern tip of Nova Scotia. Winter salinities of the St. Lawrence River water near northern Nova Scotia approach 31.5 PSUs (Chassé 2001). Gulf Stream and warm slope waters that may enter the Gulf of Maine from the edge of the continental shelf through the Northeast Channel are typically >35.5 PSUs (Houghton and Fairbanks 2001). As noted in Section 7.1 – Freshwater Inputs, a significant contribution of low salinity St. Lawrence estuary water also reaches the Gulf of Maine via the Nova Scotia Current through a channel that lies between Browns Bank and the southern tip of Nova Scotia.

Within the WMCC, surface salinity of 29-30 PSUs is generally about 2 PSUs below the surrounding marine waters during spring freshet, although it may vary by as much as 10 PSUs, particularly near the Kennebec River estuary. At 50 m depth, the salinity of the WMCC shows a slow seasonal decrease, dropping about 0.5 PSUs over the summer months as freshwater inputs from land decrease (e.g. river flow and precipitation run-off). A zone of low salinity water has been documented during spring freshet as extending 20-30 km offshore along some 250 km of coastline in the western gulf (Geyer et al. 2004) (see Figure 8.5).

The general circulation of the MCC is subject to strong interannual, seasonal and shorter-term variability, all of which may strongly affect the horizontal spatial distribution of planktonic species around the Gulf of Maine. The data suggest that the degree of connectivity between the eastern and WMCC is highly variable, and that the variability is, in part, the result of changes in water density (Pettigrew et al. 2005). Changing densities in the eastern and western MCC is related to varied salinity, where less saline freshwater riverine input contrasts with various dense saline marine sources.

Offshore, the primary source of freshwater on Georges Bank is waters from the Gulf of St. Lawrence. Entering the Gulf of Maine at the Northeast Channel, this freshwater consists of 5.6% St. Lawrence River water and 94.6% Labrador Shelf water by volume (Houghton and Fairbanks 2001). The water on central Georges Bank consists of a mixture of this freshwater source as well as a small volume of Maine coastal river water that is transported to the bank via the WMCC. However, there has been no observed relationship between the salinity on Georges Bank and the volume of local Maine river outflow. Instead, it appears that the interannual fluctuations of salinity on Georges Bank are driven by variations in upstream Scotian Shelf sources and mixing of these waters onto the bank (Houghton and Fairbanks 2001).

Surface salinity (0 to ~20 m depth) on northeastern Georges Bank has a distinct late summer minimum associated with the arrival of an annual pulse of Scotian Shelf water, and another relative minimum in March. Minimums approach 32.3 PSUs while maxima are near 32.8 PSUs (Bisagni and Smith 1998). Analysis of historical data collected between 1912 and 1987 indicates the occasional occurrence of low-salinity (less than 32.0 PSUs) water on southern Georges Bank

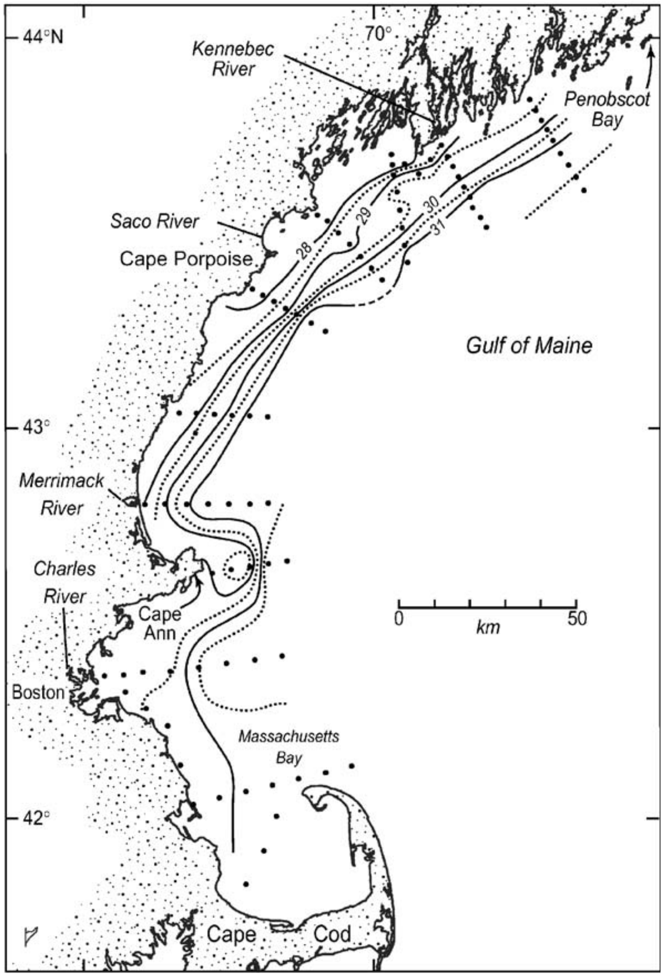

Figure 8.5: Near surface salinity from April 1993, is typical of when the spring freshet has the greatest influence on the salinity of the western Maine Coastal Current. Here reduced salinity occurs for 20–30 km offshore along 250 km of Gulf of Maine coastline.
Source: Geyer et al. (2004).

during the month of May, and the southwestern Scotian Shelf appears to be the immediate upstream source of this low salinity water (Bisagni et al. 1996).

8.3 Nutrients

Across the Gulf of Maine, the same processes that bring variable salinities to different areas also tend to drive local nutrient regimes. In locations where mixing brings highly saline water to the surface, it also brings marine nutrients from deep within the water column. Where stratification prevails and relatively fresh low salinity water occurs on the surface, fewer nutrients are generally observed within the productive upper levels of the water column. Freshening can impede vertical nutrient exchange between surface and deep waters, reducing the overall spring primary productivity throughout the region as it creates a shallower mixed layer depth and a more stable water column (Ji et al. 2008). Nitrates that come to the surface of the water column during winter mixing periods often drive the spring phytoplankton bloom as seasonal water temperatures warm.

As shown in Figure 8.6, bottom nitrates are high along the Northeast Channel where inflowing warm, nutrient-rich continental slope water comes into the Gulf of Maine. However, the presence of nutrients at the bottom of the water column does not necessarily mean that they are mixed to the surface where they can be used in phytoplankton production. Bottom nitrate levels decrease from the Northeast Channel into the Bay of Fundy. However, the long-term average winter maximum nitrate inventories for the upper 50 m of the water column in the Bay of Fundy are about 400 millimolar (mmol) m^{-2}. Long-term summer levels are slightly more than half (~200 mmol m^{-2}) the winter maximum. Overall, large-scale annual nitrate inventories around the Canadian portion of the Gulf of Maine continue to be greatest in the Bay of Fundy (DFO 2006a). Annual chlorophyll inventories that were collected in the Bay of Fundy in 2005 were the lowest on record and the biomass maxima were later in the year than usual (DFO 2006a).

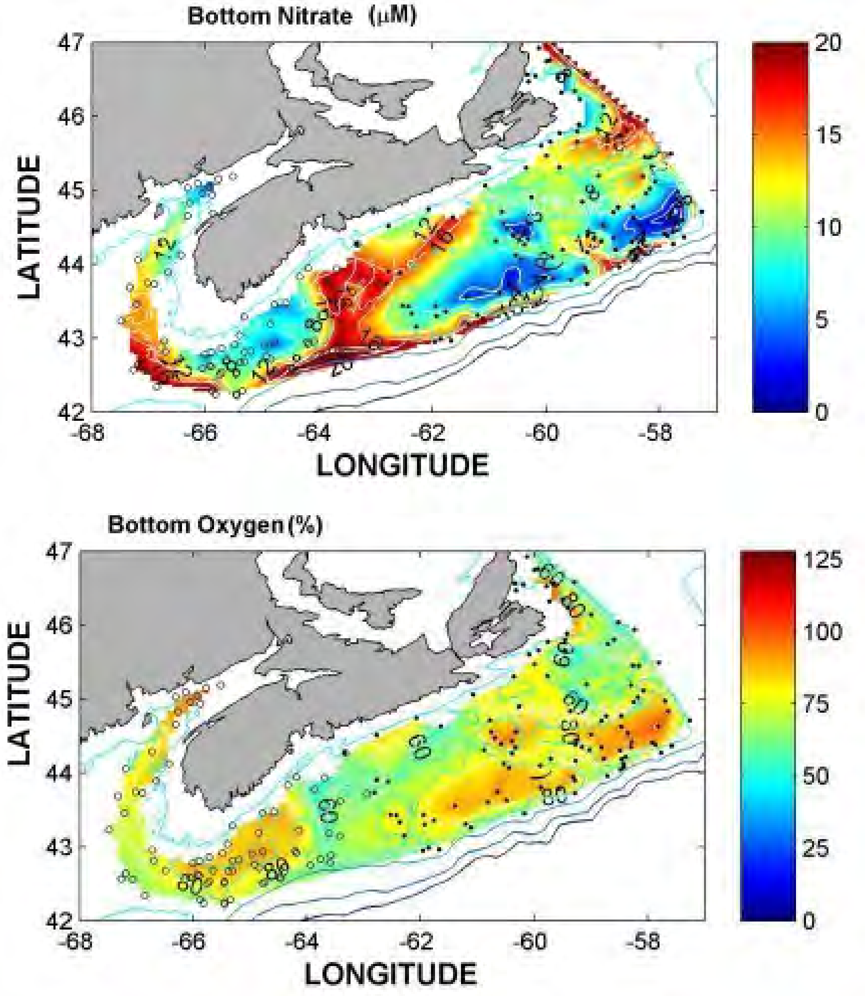

Figure 8.6: Images from data collected during the July 2005 groundfish survey data show that bottom nitrates decrease from the Northeast Channel towards the Bay of Fundy, while dissolved oxygen at the bottom appears to slightly increase.
Source: DFO (2006a)

The MCC system and its rich load of inorganic nutrients are of great importance to the biological productivity of the Gulf of Maine. Transport of the high-nutrient waters from the cold vertically mixed EMCC towards both the WMCC and offshore into Jordan Basin represents significant contributions to these areas. These nutrients are especially important to the offshore regions that are normally nutrient depleted during the late spring and summer (Pettigrew et al. 2005), while the WMCC will derive some nutrients from early season land-based river discharge.

The EMCC and its offshore extensions, which appear episodically as cold plumes, are thought to export significant quantities of nutrients to offshore regions that are generally nutrient depleted during spring and summer (Pettigrew et al. 1998). A flux of approximately 5 kg of nitrate s^{-1} has been estimated for this small plume. This nitrate flux is of the same order as both the flux estimated for the coastal current in the vicinity of Grand Manan Island (a vertically well-mixed area) and for the influx through the Northeast Channel (derived from nutrient-rich continental slope water). These EMCC plumes have great potential biological significance because of the episodic and spatially variable nature of the plumes, which could result in alteration of the type and magnitude of primary production in the western, central and eastern Gulf of Maine (Pettigrew et al. 1998).

Chlorophyll concentration, a surrogate measure of nutrient levels and primary production generally ranges from 1-5 ug L^{-1} on Georges Bank. The annual maximum on Georges Bank typically occurs in late March and peaks progressively later in a northward direction (Page et al. 2001). More information on chlorophyll and primary production can be found in Section 9.1.2.

8.4 Seasonality

Fairly significant temperature, salinity, and density differences exist seasonally in the Gulf of Maine. As is apparent from the previous sections, spatial variability within the salinity and temperature regimes of the Gulf of Maine are closely tied to the source waters of the gulf. Similarly, much of the seasonality that is observed in the various areas of the Gulf of Maine are also driven by the seasonality of these source waters and the time lags associated with their transport both to the Gulf of Maine and around the Gulf of Maine. Other seasonal patterns, such as local spring freshet and river discharge, have local seasonal influence on particular areas of the Gulf of Maine. However, it is the large-scale seasonal patterns of the source water on the Scotian Shelf that determines much of the monthly variation observed in the Gulf of Maine oceanography.

The following is an overview of unique seasonal temperature and salinity observations across and around the Gulf of Maine. Year to year, water temperatures on the Scotian Shelf and in the Gulf of Maine are among the most variable in the North Atlantic Ocean (DFO 2008a).

8.4.1 Winter Observations: The salinity cycle of the Gulf of Maine originates in large part with the strong seasonal pattern of the Scotian Shelf inflow that has a minimum surface salinity during the winter (Figure 8.7). As this low salinity water slowly circulates around the Gulf of Maine with the typical counter-clockwise circulation of the gulf, it creates minimum salinities in the eastern Gulf of Maine during February (associated with the newly arriving “fresh” Scotian Shelf water), while the western Gulf of Maine exhibits maximum salinities at the same time of year (not having yet received the “fresh” Scotian Shelf water) (Houghton and Fairbanks 2001, Taylor and Mountain 2009). The maximum salinities in the gulf occur at depth with the inflow of saline slope waters through the Northeast Channel (Figure 8.7). The highest winter temperatures also occur at depth with the inflow of slope water through the channel. In winter, virtually all areas of the gulf appear to have a positive temperature-salinity relationship (high temperature/high salinity, low temperature/low salinity) throughout the water column, based on the ten year data set from 1977-1987 (Mountain and Taylor 1998).

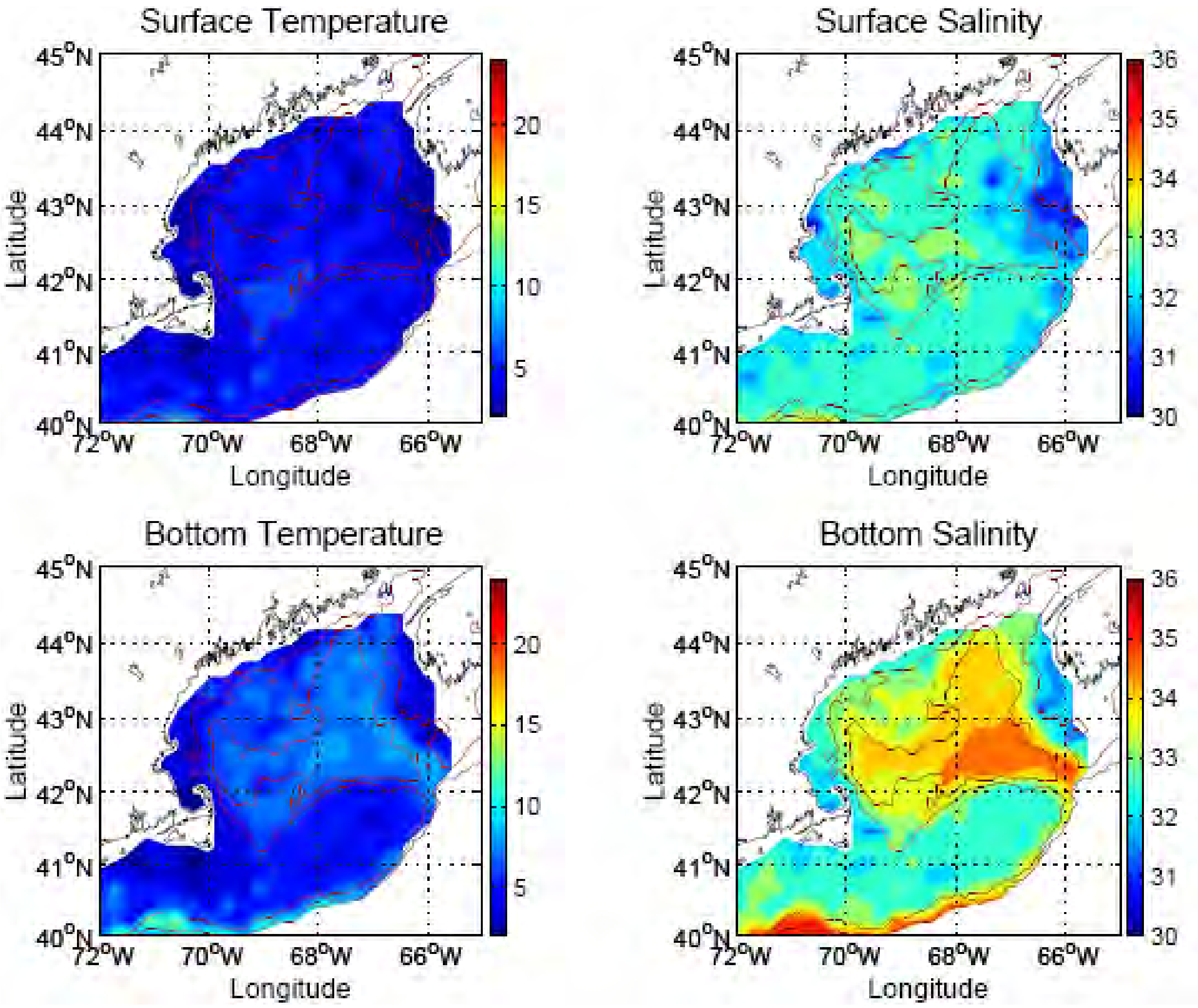

Figure 8.7: Winter temperature (°C) (January-March) and salinity (PSUs) for surface (upper) and bottom (lower) waters in the Gulf of Maine based on NEFSC research vessel surveys (1986-2008).
Source: Maureen Taylor, Northeast Fisheries Science Center, NMFS, personal communication (2009).

Long-term mean annual SSTs for the eastern gulf, western gulf and Georges Bank highlight that all regions have a minimum temperature usually occurring during March. In fact, the Gulf of Maine regions have the lowest winter SSTs observed on the northeast U.S. continental shelf (Friedland and Hare 2007). In the Gulf of Maine, the between-year variability in the heat exchange between the water and the atmosphere is largest in winter, a time when the upper 100 m of the water column is generally well mixed (Mountain et al. 1996). Georges Bank has the warmest winter water temperatures within the Gulf of Maine (Friedland and Hare 2007). Sea surface temperature spatial patterns identified from the assessment of a 12-year time series reveals the winter occurrence of fronts on the northeast peak area of Georges Bank, which is most likely associated with Scotian Shelf water flow across the Northeast Channel. These tidal mixing fronts on Georges Bank have been shown to move as much as 5 km per month and are not permanent year-round features (Mavor and Bisagni 2001).

8.4.2 Spring Observations: There are strong seasonal changes in salinity and along-shore velocity of the MCC, caused by the freshwater inputs of the rivers entering the western gulf (Geyer et al. 2004). River discharge helps to establish a clear annual cycle in surface salinity along the Gulf of Maine coastline. Surface salinity of the MCC decreases by as much as 2-3 units immediately after the high discharge season in April and May (Xue et al. 2000). Within the WMCC, surface salinity of 29-30 PSUs is generally about 2 PSUs below the surrounding marine waters during spring freshet (Figure 8.8), although it may vary by as much as 10 PSUs, particularly near the Kennebec River estuary (Geyer et al. 2004). Again, maximum salinities occur at depth with the transport of saline slope water through the Northeast Channel and penetrating into the deep water basins of the gulf. Surface temperatures begin to show increases on Georges Bank and in the western Gulf of Maine while higher temperatures are apparent at depth on Georges Bank and in areas affected by the inflow of warmer slope water (Figure 8.8).

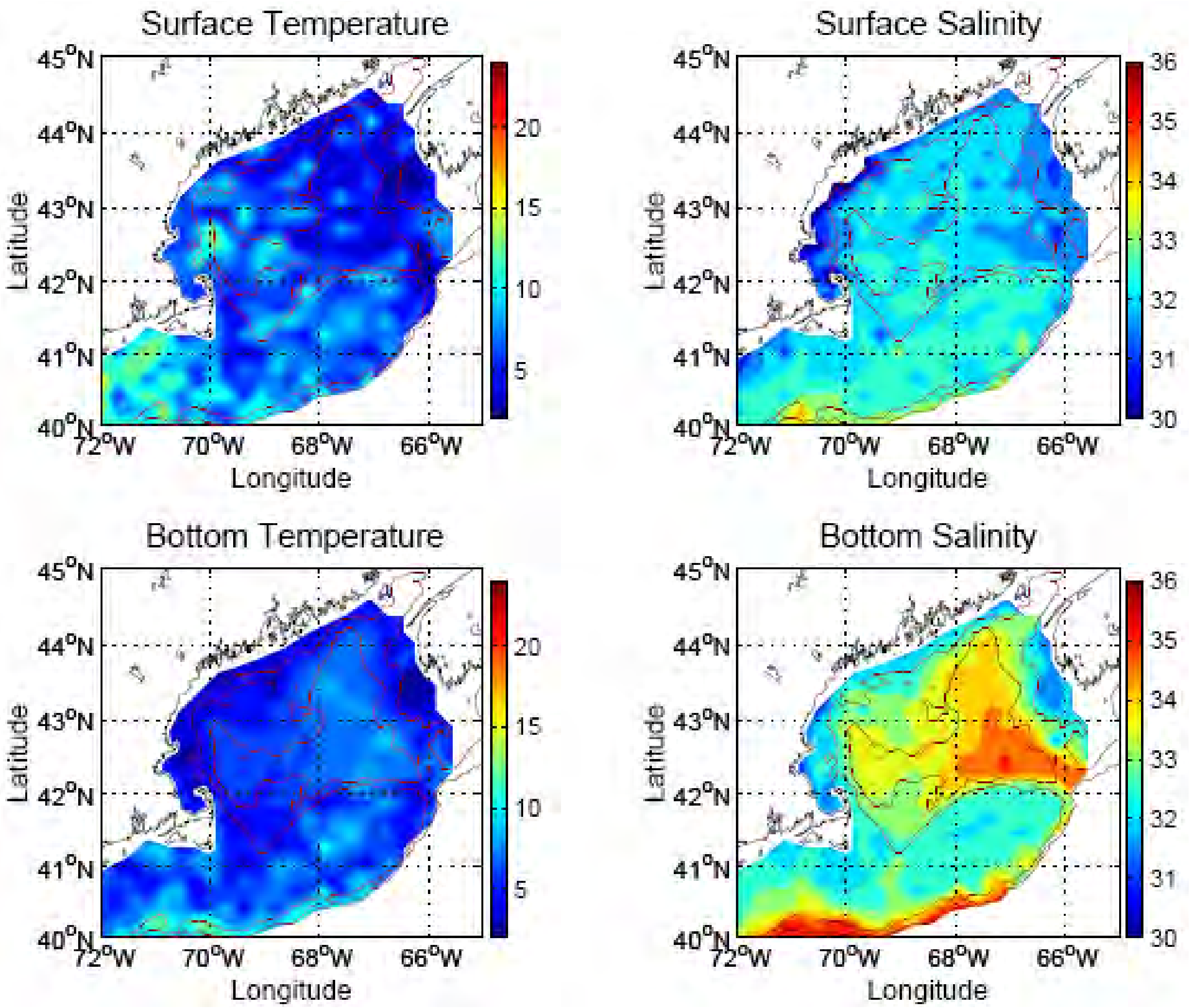

Figure 8.8: Spring temperature (°C) (April-June) and salinity (PSUs) for surface (upper) and bottom (lower) waters in the Gulf of Maine based on NEFSC research vessel surveys (1986-2008).
Source: Maureen Taylor, Northeast Fisheries Science Center, NMFS, personal communication (2009).

The annual maximum chlorophyll concentrations, an indicator of the spring bloom, typically occur on Georges Bank in late March (Page et al. 2001). However, during the late spring and summer, most of the offshore regions are normally nutrient depleted (Pettigrew et al. 2005). March is also the time for a relative minimum salinity, although not an annual minimum that occurs in late summer (Bisagni and Smith 1998).

Wilkinson Basin, the deepest portion of the western Gulf of Maine, demonstrates a spring minimum (April) bottom temperature, whereas the two deep eastern basins (Jordan and Georges) exhibit minimum bottom temperatures around May to June (Taylor and Mountain 2009).

8.4.3 Summer Observations: The summer period in the Gulf of Maine is characterized by the development of thermal and density stratification in the upper layers. In summer, solar radiation is the major contributor to the variability in the flux of heat between the atmosphere and the water, and corresponds to a time when thermal stratification is strongest (Mountain et al. 1996). Areas of the western Gulf of Maine exhibit negative correlation between the summer surface or bottom temperature and salinity (i.e. high temperature/low salinity or low temperature/high salinity) (Mountain and Taylor 1998).

A “hot spot” forms on the shallowest portion of Georges Bank in the late summer-early autumn period (Figure 8.9). This area becomes very warm at depth relative to the rest of the Gulf of Maine (Mavor and Bisagni 2001). The bottom temperatures in the eastern gulf are relatively warmer during summer than those of the central and western gulf. Little of the seasonal spring runoff from the Gulf of St. Lawrence and Labrador Shelf reaches the eastern gulf, and deep waters are relatively warm due to the influence of warmer Gulf Stream and continental slope water.

Long-term mean annual SSTs are shown in Figure 8.10 for the western gulf, eastern gulf and Georges Bank. The cycle shows that in all regions, maximum SST is typically achieved in August. An analysis of data spanning the years 1854-2005 showed that the Gulf of Maine regions had the lowest summer SSTs observed on the northeast U.S. continental shelf (Friedland and Hare 2007).

Georges Bank exhibits the warmest non-coastal water temperatures within the Gulf of Maine, approaching 20°C in August (Friedland and Hare 2007). The surface water in the Bay of Fundy is the coolest within the gulf during the summer, likely because of strong tidal mixing that works against stratification of the water column (Casault et al. 2003).

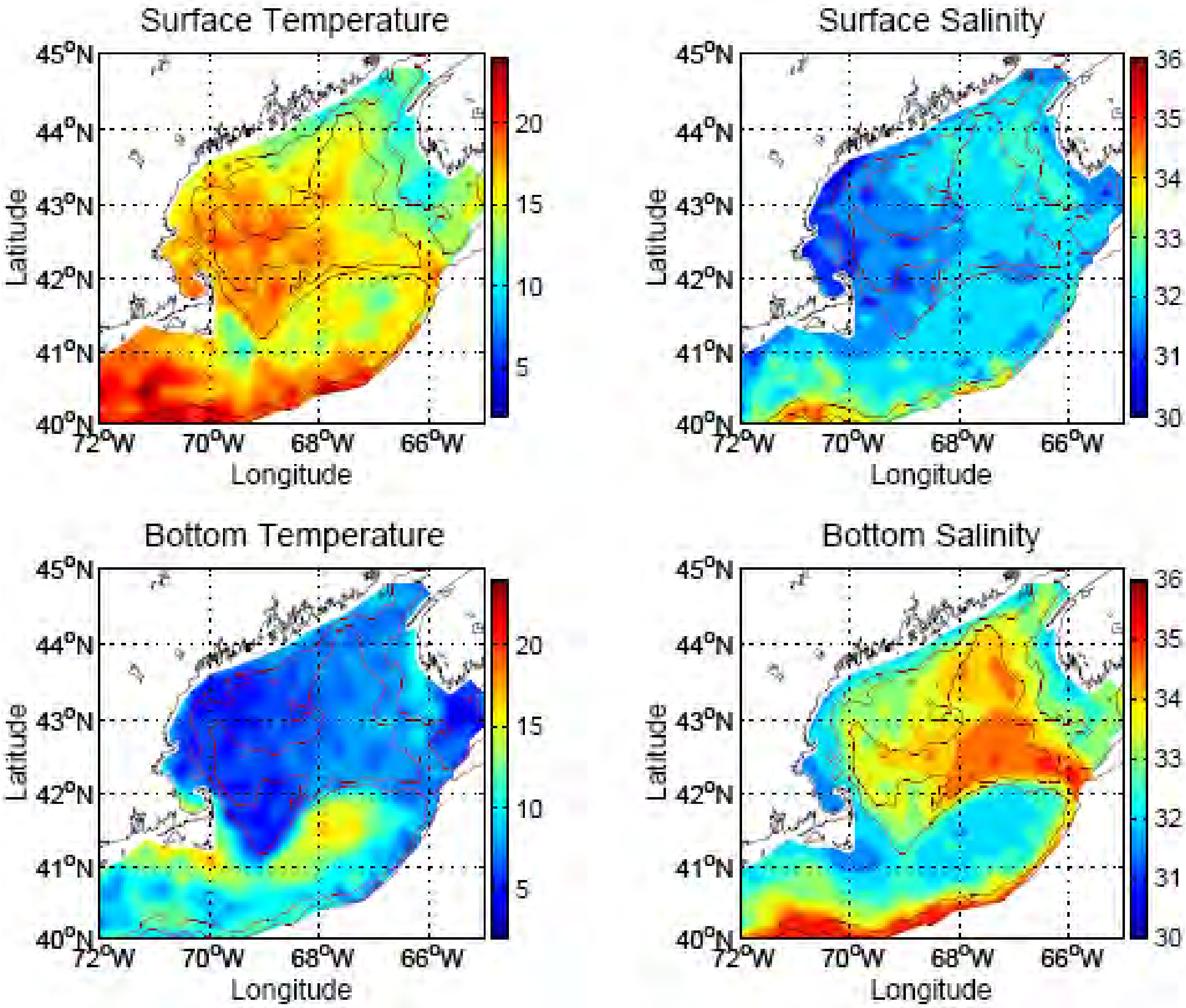

Figure 8.9: Summer temperature (°C) (July-September) and salinity (PSUs) for surface (upper) and bottom (lower) waters in the Gulf of Maine based on NEFSC research vessel surveys (1986-2008).
Source: Maureen Taylor, Northeast Fisheries Science Center, NMFS, personal communication (2009).

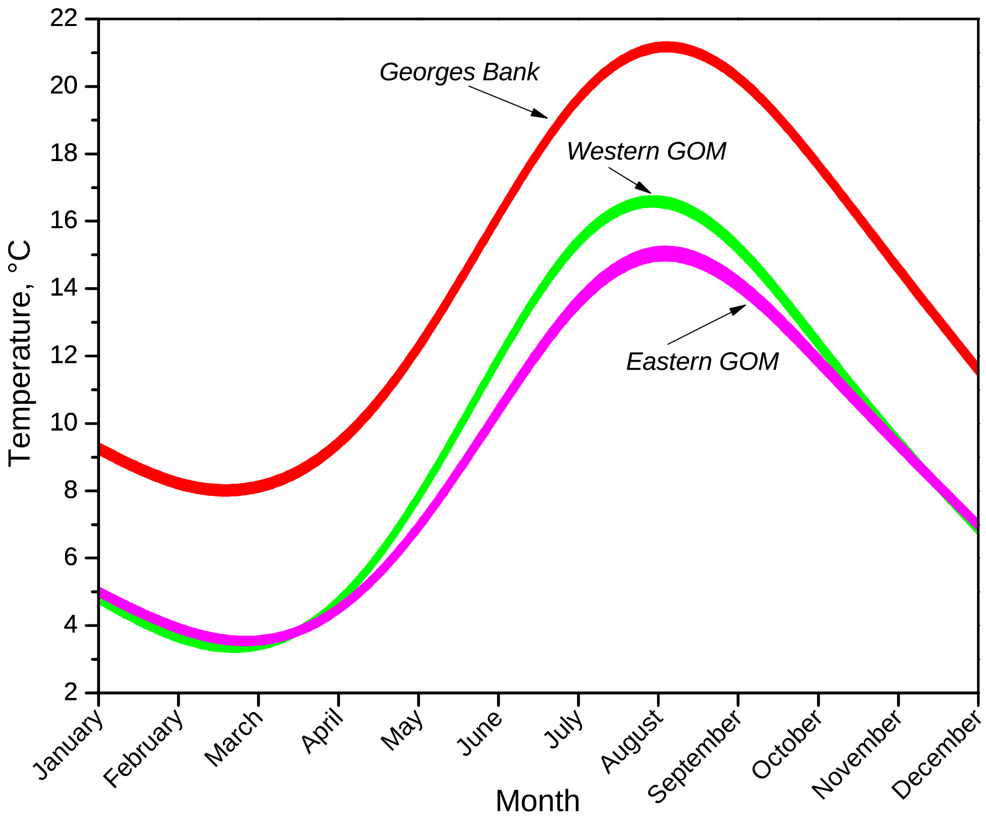

Figure 8.10: Monthly sea surface temperature curves for various locations in the northwest Atlantic, including Georges Bank, the eastern Gulf of Maine, and the western Gulf of Maine. These curves demonstrate the long-term seasonal sea surface temperature cycle.
Source: adapted from Friedland and Hare (2007)

The salinity cycle of the Gulf of Maine originates, in large part, with the strong seasonal pattern of the Nova Scotia Current inflow that has a maximum salinity occurring as it enters the gulf in late summer. Minimum surface salinities in the Gulf of Maine typically occur in February (Smith 1983). Relative to most of the gulf, surface salinity (0 to ~20 m depth) on northeastern Georges Bank has a distinct late summer minimum associated with the time lagged arrival of an annual pulse of Scotian Shelf water (Bisagni and Smith 1998) and the within-gulf scale circulation patterns (Houghton and Fairbanks 2001). There is also a high likelihood that a tidal mixing front will develop on the northwestern edge of Georges Bank during June and July annually (see Figure 8.11).

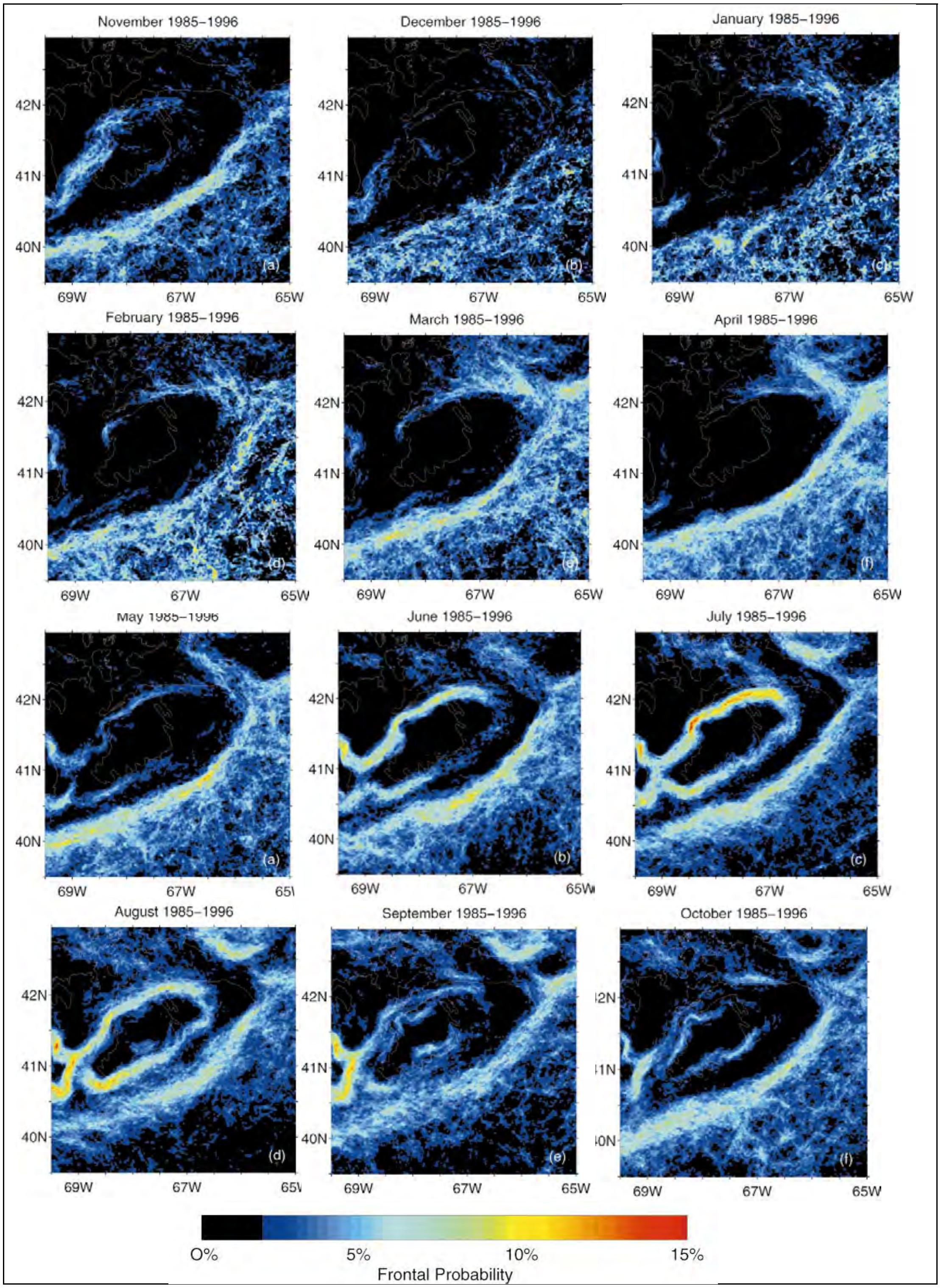

Figure 8.11: Frontal zones in water are not permanent temporally or spatially, so monthly probabilities of various fronts around Georges Bank have been calculated based on 12 years of data. The most persistent frontal region is at the continental shelf break on the southeastern flank of Georges Bank, while a very strong probability of a July tidal mixing front on the northwestern flank of the bank exists.

Source: adapted from Mavor and Bisagni (2001)

8.4.4 Autumn Observations: The area known as the "hot spot" that forms on the shallowest portion of Georges Bank in the late summer will dissipate during the autumn period (compare Figure 8.9 with Figure 8.12). Unlike the other two deep basins located in the Gulf of Maine, the western Gulf of Maine's Wilkinson Basin exhibits two yearly cool-bottom temperature periods. Although the minimum occurs in spring, a second cool period typically occurs in fall (October) in Wilkinson Basin (Taylor and Mountain 2009).

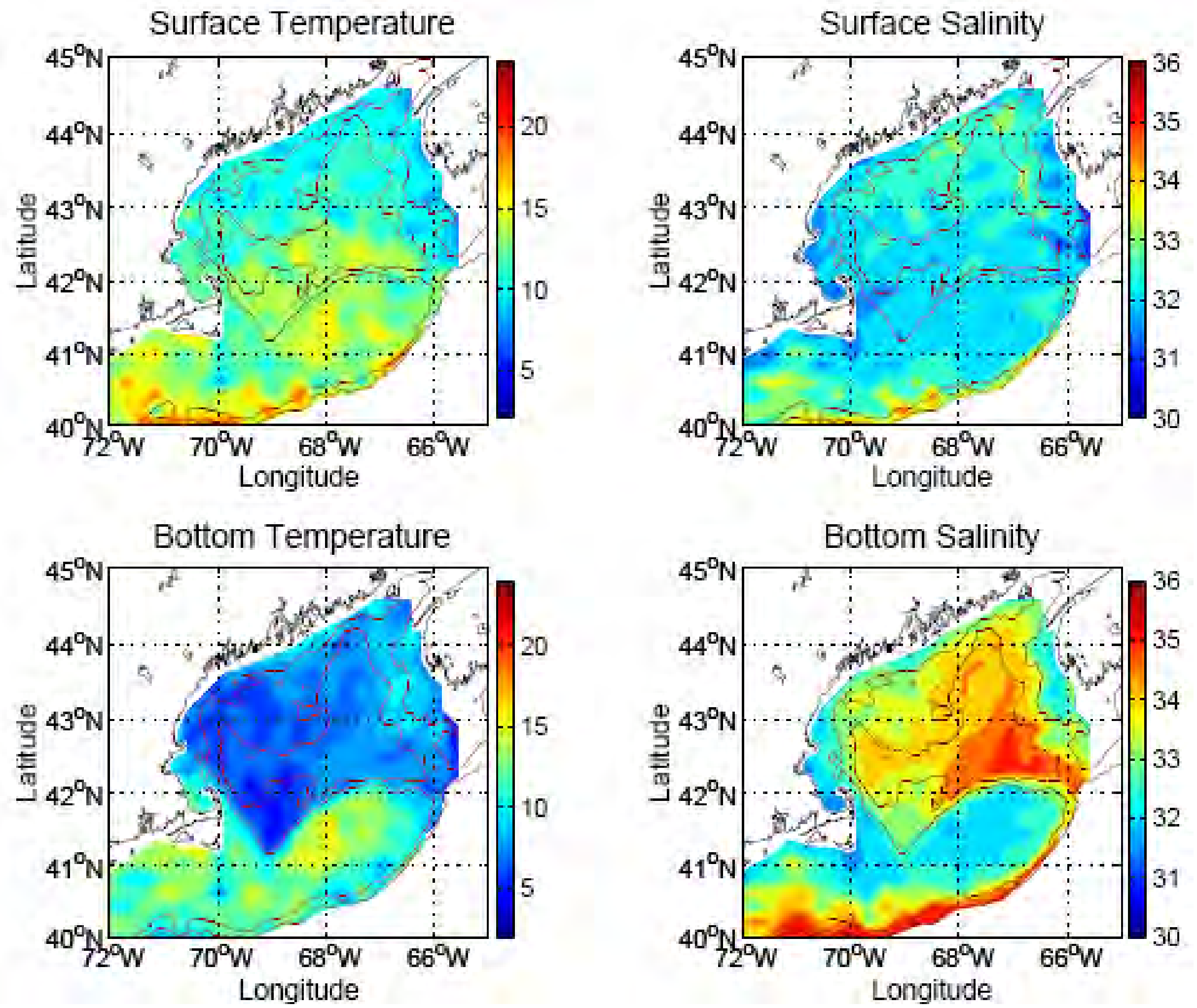

Figure 8.12: Fall temperature (October-December) and salinity for surface (upper) and bottom (lower) waters in the Gulf of Maine based on NEFSC research vessel surveys (1986-2008).
Source: Maureen Taylor, Northeast Fisheries Science Center, NMFS, personal communication (2009).

8.5 Major Spatial Patterns

Many, although not all, of the temperature and salinity spatial patterns can be compartmentalized based on the degree of stratification/mixing that occurs in an area, and its relative position along the predominant counter-clockwise circulation pattern that originates near the Northeast Channel. As noted in Section 7.4, the eastern Gulf of Maine is generally well mixed vertically and the area west of the Gulf gyre has a tendency to be more strongly stratified for at least portions of the year.

The eastern gulf is the first to receive inflow water from the Scotian Shelf and continental slope, while the western gulf and southern Georges Bank are influenced by the character of the inflow some three months after it first enters the gulf.

Based on a ten-year data set from 1977-1987, interannual changes in the temperature and salinity of the surface layer (0-50 m) has indicated that the variations in the western Gulf of Maine are significantly correlated with those on Georges Bank and in the Middle Atlantic Bight (south of the Gulf of Maine) (Mountain and Taylor 1998). The salinity variability of the western gulf and Georges Bank appears to be more greatly influenced by local precipitation and coastal runoff, and temperature variability appears to be associated with the local surface heat exchange with the atmosphere (Mountain and Taylor 1998). In fact, the variability in water temperature is significantly correlated with the heat flux variations. Generally, annual SST range decreases in a seaward direction across both the Gulf of Maine and the Northeastern U.S. Shelf (Friedland and Hare 2007). However, in the eastern gulf, no relationship is found and the temperature variability is thought to be dominated by variability in source water temperatures that flow into the gulf from the Scotian Shelf and the continental slope (Mountain et al. 1996). The southern side of Georges Bank, an area relatively far from sources of coastal runoff, shows little seasonal variability in salinity, although relatively large interannual variability does exist (Mountain and Taylor 1998).

Both the winter minimum and the summer maximum temperatures in the Gulf of Maine show important spatial variability. On the one hand, the winter surface water is coolest in the eastern sub-regions of the Gulf of Maine. On the other hand, the summer surface water is coolest in the northern sub-region of the Bay of Fundy, where tidal mixing appears to work against stratification of the water column. Finally, the most easterly boundary of the Gulf of Maine, the shelf break/slope sub-regions, exhibits both the warmest winter and summer surface water due to the presence of horizontal eddies, resulting in mixing of shelf water with warmer water from the Gulf Stream (Casault et al. 2003).

As shown in Figure 8.13, much of the western gulf and portions of Jordan Basin exhibit negative summer temperature-salinity relationships where cool water is more saline than warm water measurements. This is particularly true for surface waters, but in some limited locations has also been observed at depth. No such relationship is apparent in the winter when cool waters are less saline than warm waters around the Gulf of Maine. The negative summer correlation is consistent with variability driven by coastal upwelling, which would bring cooler, more saline water from depth offshore into the coast (Mountain and Taylor 1998).

Friedland and Hare (2007) have further documented that there are long-term spatial variances in monthly SSTs between the vertically more well-mixed eastern gulf water temperature and the more strongly stratified western gulf water, particularly during the summer months (as shown in Figure 8.9). However, both areas are considerably cooler than Georges Bank, where a greater influence of moderate continental slope waters exists.

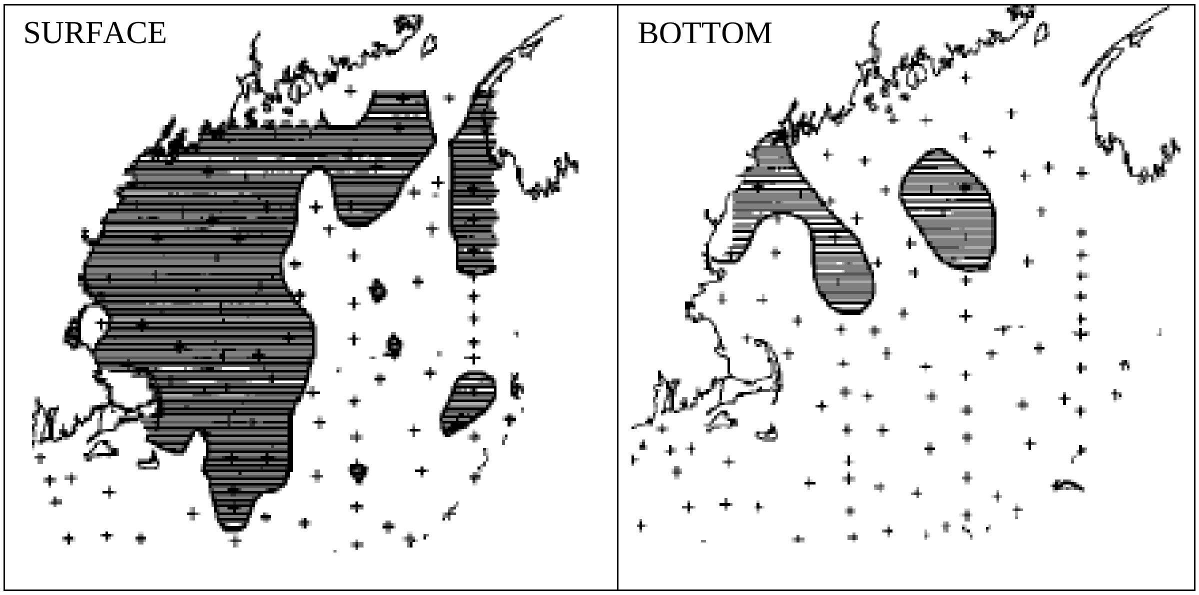

Figure 8.13: Shading indicates the Gulf of Maine regions with negative correlation between the summer surface (L) or bottom (R) temperature and salinity anomalies (i.e. high temperature/low salinity or low temperature/high salinity). In winter, all areas appear to have a positive temperature salinity relationship (high temperature/high salinity, low temperature/low salinity) based on the ten-year data set from 1977-1987.
Source: adapted from Mountain and Taylor (1998)

8.6 Long-term trends

There have been major decadal-scale changes in both the water properties and the seasonal currents in the Gulf of Maine region during the past century, and these changes appear to be a common occurrence. Subsurface ocean temperature and salinity data show evidence of extended periods with abnormal cool and fresh ocean conditions from the late 1930s to the early 1940s, and from the late 1950s to the mid 1960s. During a decadal-scale cooling and freshening of upper ocean waters in the Gulf of Maine region around the 1960s, temperatures dropped an estimated 4.63°C and salinities were up 0.7 PSUs (Loder et al. 2001).

During the 1990s, surface salinity freshened (dropped) by about 0.5 PSUs across the Gulf of Maine and Georges Bank relative to the earlier decade, and appears to have occurred independently of the NAO, a typical driving factor in Gulf of Maine salinity. An increase in the inflow to the Gulf of Maine of cool, low-salinity surface water from the Scotian Shelf appears to be responsible for the freshening. The volume of shelf water in the Middle Atlantic Bight was about 1000 km^3 greater, on average, during the 1990s compared with the previous decade. The cause of this decadal change is not known. It was also noted that the deep waters of the western Gulf of Maine (Wilkinson Basin) exhibited warming during the same 1990s timeframe. This warming is thought to have occurred because of reduced winter cooling exchange with the atmosphere, a response to the freshening of the surface layer that increased the stratification that inhibited convection (Mountain 2004).

Regional-scale fluctuations in sea surface and bottom water temperatures on the northeast U.S. shelf have been associated with trends in the NAO. For example, long-term analysis of mean annual SST between 1854 and 2005 shows declining temperatures at the beginning of the last century, followed by increasing SST through 1950, and then rapidly decreasing between 1950 and the mid 1960s, with somewhat warmer SST thereafter to 2005 (Friedland and Hare 2007). Several of these periods of transition correspond with changes in the NAO. During the 20-year period of the 1950s to the 1970s, the NAO index was low (see Figure 8.14). When the NAO index is low, it can be expected to be accompanied by warmer than normal winter air temperatures and waters in the Labrador Sea. These waters are still relatively cold, but can subsequently be transported into the Gulf of Maine with the influx of Labrador Slope water through the Northeast Channel, affecting the region's ocean conditions (DFO 2008a). However, over the past 30 years the NAO index has primarily been high. This allows warmer, more saline marine water from the continental slope to enter the Gulf of Maine as cold Labrador Slope water is largely excluded. There have only been two major cooling periods over the decade (1996-2006), both relatively short (Fogarty and Trollan 2006). It is estimated that 75% of the climatic variance in the NAO has been in shorter than decadal time scales (Ottersen et al. 2001). This means that NAO related trends in salinity, temperature, and water density have typically changed on a time scale of less than ten years from a warmer more saline to a colder more fresh water influence, or vice versa.

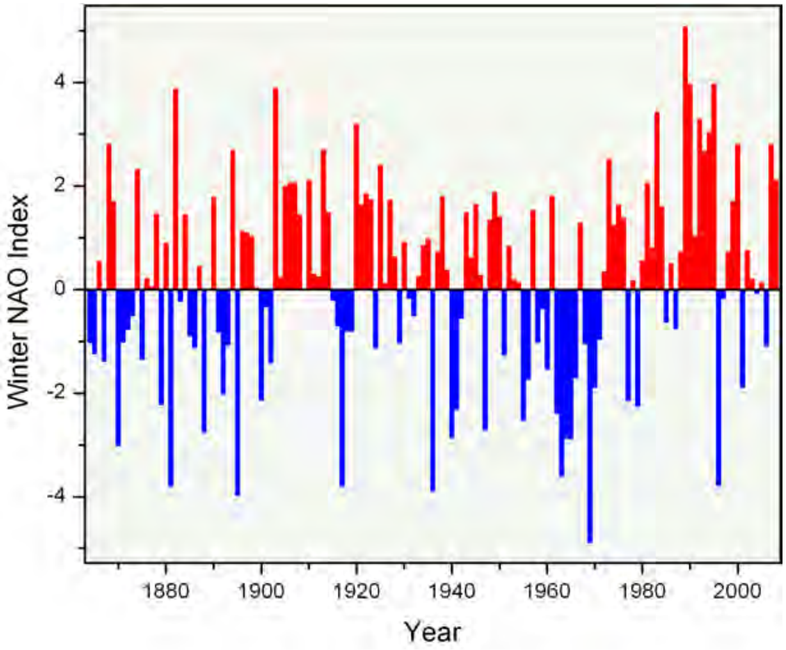

Figure 8.14 North Atlantic Oscillation (NAO) index (1900–2008). The bars show each winter's mean NAO index as being positive or negative. The index influences the position of major oceanic currents around the Gulf of Maine, and thereby alters temperature and salinity in the gulf.
Source: EAP (2009) using data released to the public domain by J.W. Hurrell, NCAR

There has also been a long-term trend in the range of SSTs. A decreasing range was observed at the beginning of the last century, followed by an increase in range from 1920 to the late 1980s. Range has remained high through to the present, with some spatial variability across the Gulf of Maine. Although the mean annual SST in the Gulf of Maine is currently trending below historical levels (1854-2005), the intensity of summer warming is at or near its highest levels, and winter SSTs are remaining relatively constant and cool (Friedland and Hare 2007). Spring warming rate has increased during the last half of the 20th century in the order of 0.5°C per month. A regime shift in spring warming rate was identified around 1940 in the eastern Gulf of Maine, although not in the western gulf or on Georges Bank. Conversely, autumn cooling rates have decreased over the time series in the order of 0.5°C month^{-1}. Notably, a fall regime shift occurred around 1987 in five regions of the northeastern continental shelf, including the western gulf, suggesting a relatively widespread phenomenon. A second contemporary shift was identified in 2002 that included the eastern gulf and Georges Bank (Friedland and Hare 2007), but not the western gulf.

PART C – MAJOR ECOSYSTEM COMPONENTS

9. FLORA AND FAUNA

Some 3317 species of flora and fauna have been inventoried from the Gulf of Maine (Valigra 2006). Approximately 2350 of those are also found in the Bay of Fundy (Census of Marine Life 2009). More than 652 species of fish have been documented living in or migrating through the Gulf of Maine. It is estimated that 87 (13%) of these species of fish are resident (live their whole lives) within the Gulf of Maine (Valigra 2006).

This part of the *Gulf of Maine Ecosystem Overview Report* examines some of the plants and animals that live in offshore areas of the Gulf of Maine. The focus of Part C of the report is on the communities of organisms, changes in community structure, their use of the available habitats, and their relationships with the physical oceanography of the Gulf of Maine. Although communities is the focus here, species-level study has long been the norm, and only more recently are communities such as benthic, pelagic or spatially constrained organisms being assessed and reported as a group. Furthermore, the historic focus of studies has been dominated by those species that have had commercial significance; these species do not necessarily correlate with the keystone species of an ecosystem. Because of these limitations within the available literature, communities are discussed as comprehensively as possible, although a species-oriented focus still prevails.

9.1 Planktonic Communities

Oceanic planktonic communities are composed of single and multicelled plants (phytoplankton), animals (zooplankton), and bacteria (bacterioplankton). All are drifting organisms with limited to no directional motility, moving about with the oceans currents. As shown in Table 9.1, Gaichas et al. (2009) estimated that the lower trophic level biomass in the Gulf of Maine and Georges Bank was roughly composed of 50% zooplankton, 40% primary producers, and 10% bacteria. Fish larvae and eggs that are not yet developed enough to undertake directional self propulsion (ichthyoplankton) may also be considered part of the planktonic community.

Table 9.1: Modeled (Link et al. 2006) estimates of biomass and production for various plankton community constituents on Georges Bank, and the Gulf of Maine excluding Georges Bank.

	Biomass		Production	
Planktonic Community	**Gulf of Maine ($t\ km^{-2}$)**	**Georges Bank ($t\ km^{-2}$)**	**Gulf of Maine ($t\ km^{-2}$)**	**Georges Bank ($t\ km^{-2}$)**
Bacterioplankton	5.5	6.5	500	595
Phytoplankton	22.1	25.7	3 609	4 270
Zooplankton	33.2	30.6	1 205	1 430

Source: adapted from Gaichas et al. (2009)

Although many plankton are microscopic, not being visible to the naked eye, some can be much larger. For example, jellyfish are considered part of this community (gelatinous zooplankton). However, not all gelatinous zooplankton are jellyfish, and other commonly encountered representatives include ctenophores (comb jellies), medusae, salps (tunicate) and Chaetognatha (predatory worm). Based on at-sea surveys of the Wilkinson and Georges Basins and four submarine canyons on the seaward side of the continental shelf in the Gulf of Maine that were conducted during 2002-2004, eighty one species of gelatinous zooplankton were identified. Some 75% were either siphonophores (e.g. corals, hydroids, and true jellyfish) or hydroidomedusae. The numbers of mollusc and salp species were low (Pages et al. 2006). Siphonophores are colonies of organisms that together often look like a jellyfish. The best-known species is the dangerous Portuguese man o' war (*Physalia physalis*). This species, although not common in the Gulf of Maine, has been found in the gulf (Census of Marine Life 2009), and are known to occur in the North Atlantic in Gulf Stream waters.

Although a diverse array of organisms constitute the planktonic community of the Gulf of Maine, our discussion here is focused on the small organisms that so profoundly influence the productivity of the ecosystem.

Spring blooms are associated with the sudden growth of phytoplankton. These plants undergo photosynthesis, deriving their energy from the sun, and fixing it into their carbon based form. This energy production process is referred to as primary production, and is the basis for virtually all marine foodwebs. Therefore, changes in phytoplankton abundance can influence energy production and the entire marine foodweb that it supports. Figure 9.1 shows the typical annual cycle of primary production on the Northeast Continental Shelf, including the Gulf of Maine. The area has a pronounced spring peak associated with the spring phytoplankton bloom followed by an annual maximum during summer. As a result of summer solar energy, higher rates of primary production can be maintained, even as phytoplankton biomass. The summer maximum in primary production is a consequence of greater available solar radiation that limits photosynthesis at other times of the year. A peak in zooplankton abundance often follows the spring phytoplankton bloom, as the single to multi-cell animals proliferate, grazing on the suddenly plentiful microscopic plants and each other. A description of the distribution of phytoplankton and zooplankton is important biologically, as these organisms form the base of the marine food web. An understanding of the production cycles of plankton is an essential part of an ecosystems approach to fisheries management (DFO 2006a).

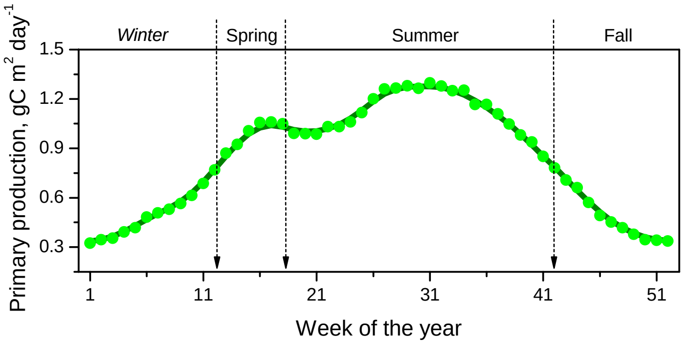

Figure 9.1: Typical annual cycle of primary production on the Northeast Continental Shelf, as measured by satellite-derived ocean colour measurements.
Source: adapted from EAP (2009).

Based on long-term plankton data collection (1961-2000), it appears that plankton abundance and bloom timing changed significantly in the Gulf of Maine around 1991. Phytoplankton generally increased and some zooplankton species decreased in abundance, while the spring bloom occurred earlier in the year (Sameoto 2004, Head and Pepin 2010). The mechanisms for this changed timing appears to be different in the eastern Gulf of Maine, compared to the western gulf (Head and Pepin 2010; Ji et al. 2008, 2007).

The plankton community has been studied within the Gulf of Maine using two primary methods: capture of organisms directly from within the water column, and by data interpretation through remote sensing. The longest running data sets are derived from the Continuous Plankton Recorder (CPR). Several sampling programs have monitored long-term changes in Gulf of Maine zooplankton abundance. The United Kingdom’s Sir Alister Hardy Foundation for Ocean Science CPR program has sampled lines across the central Gulf of Maine and Georges Bank since 1961. The CPR is towed from ships-of-opportunity and collects plankton at about 10 m depth. Two CPR routes are operated on the U.S. side of the Gulf of Maine: the Gulf of Maine line (1961-present), and the Georges Bank line (1992-present) (EAP 2009). On the Canadian side of the gulf, a portion of the western Scotian Shelf CPR sample path (1961-1976, 1991-present) extends across the Northeast Channel toward Georges Bank. This western Scotian Shelf CPR data is considered representative of the eastern Gulf of Maine because ocean currents carry western Scotian Shelf waters into the region (E. Head personal communication 2011).

Along with the CPR program, other direct plankton sampling programs have been undertaken within the Gulf of Maine. Between 1977 and 1987, the U.S. National Marine Fisheries Service (NMFS) conducted intensive surveys of plankton within the Gulf of Maine as part of the Marine Resources Monitoring, Assessment and Prediction program (MARMAP). Samples were collected every 1 to 2 months at approximately 25 km intervals using 333 µm bongo nets. The nets were towed obliquely to within 5 m of the bottom or to 200 m in deeper areas (Pershing et al. 2009). Since 1999, DFO has collected zooplankton samples in February and July by means of vertical net hauls throughout the entire water column at the mouth of the Bay of Fundy, on Georges Bank, and in the eastern Gulf of Maine. These direct sampling programs have helped answer a wide array of questions regarding the plankton community of the Gulf of Maine, including those around species diversity, abundance, and spatial distribution.

Remote sensing is a more recent means of assessing plankton communities. NASA's Moderate Resolution Imaging Spectroradiometer (MODIS) (2005-present) and Sea-viewing Wide Field-of-view Sensor (SeaWiFS) ocean color data (1998-present) are satellite derived imaging tools that pick up the color of the ocean and interpret it as chlorophyll. As phytoplankton are the primary chlorophyll producers in the off shore marine environment, these images have been particularly useful for determining such community characteristics as bloom timing, duration, peaks, and spatial variability across the Gulf of Maine. They provide a measure of near surface phytoplankton biomass. The images have a resolution of approximately 1 km for anywhere within the Gulf of Maine ecosystem, and produce one image every day for which there is good visibility (GoMOOS 2011).

9.1.1 Bacterioplankton: Bacterioplankton refers to the microbial component of the plankton community that respire carbon dioxide and regenerate inorganic nitrate. Remineralization, the transformation of organic molecules into inorganic forms by bacteria and microplankton, plays an important role in the recycling of nutrients in the Gulf of Maine and Scotian Shelf ecozone (EAP 2009). Many bacterioplankton species obtain energy by consuming organic material produced by phytoplankton and found in dissolved form. Others live and grow in and near the bottom where dead and dying plankton and other particulate detritus, known as marine snow, slowly accumulate. Yet other bacterioplankton species derive energy from either photosynthesis or chemosynthesis. This diverse means of obtaining energy allows bacterioplankton to fill a number of ecosystem niches, and facilitates important roles in energy pathways through processes such as nitrogen fixation, nitrification and denitrification. The biomass of bacteria in the Gulf of Maine and Georges Bank has been estimated at 5.5 t km^{-2} and 6.5 t km^{-2} (Gaichas et al. 2009). Bacterioplankton may be preyed upon by some zooplankton species.

9.1.2 Phytoplankton: Primary production is the rate at which dissolved inorganic carbon is photosynthetically fixed by plants into organic carbon (carbohydrates). In a marine ecosystem, photosynthesis takes place only to the depth that solar energy can effectively penetrate the water column, a depth known as the euphotic zone. Although phytoplankton are not the only photosynthetic organisms in the Gulf of Maine (large seaweeds and some bacteria also carry out photosynthesis), they are the main primary producers in the ecosystem. Despite this fact, the annual cycle of primary production on the Northeast Continental Shelf (shown in Figure 9.1) does not mirror the typical annual cycle of phytoplankton abundance (shown in Figure 9.2) because phytoplankton photosynthesize at different rates at different times of the year.

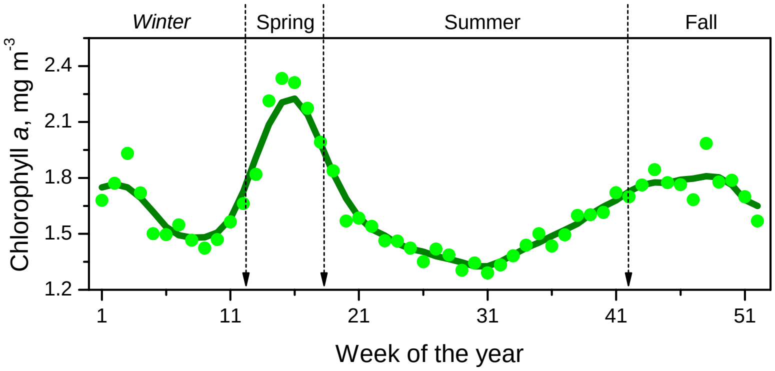

Figure 9.2: Annual cycle of phytoplankton abundance as measured by chlorophyll concentration on the Northeast Continental Shelf showing typical spring bloom and a lower fall bloom. Chlorophyll is produced by phytoplankton that grows quickly during the bloom.
Source: adapted from EAP, Northeast Fisheries Science Center (2009).

The Gulf of Maine annual cycle of phytoplankton production begins in earnest as light levels increase in spring, triggering an increase in biomass. The summer maximum in primary production is a consequence of greater available solar radiation that limits photosynthesis at other times of the year. However, as production peaks in the summer, phytoplankton biomass is moving toward an annual minimum. This minimum is influenced primarily by the depletion of nutrients by the phytoplankton in stratified surface layers. Nutrient depletion leads to lower growth rates, especially for large phytoplankton, such as diatoms, which cannot compete effectively for scarce nutrients (Head and Pepin 2010). Grazing by zooplankton also puts a negative pressure on phytoplankton abundance through the summer. Although some fall recovery of phytoplankton abundance occurs as stratification breaks down and nutrient supply from depth increases, reduced solar energy typically limits the magnitude of this recovery. The fall phytoplankton abundance is much smaller in magnitude than during the spring bloom. Despite the lower phytoplankton abundance during the fall, this bloom period is an important and sometimes overlooked part of the primary production cycle. In some areas of the Gulf of Maine and Georges Bank, the fall bloom production is a distinct event of equal or greater size than the spring bloom (EAP 2009). As winter begins, downward pressure on the phytoplankton community abundance continues in the form of poor solar energy availability and continued zooplankton grazing. These factors promote late winter low phytoplankton abundance. However, this low abundance time frame allows the nutrient load in the surface water to build until the cycle reinitiates sometime in the following spring.

Stratification Role: Nutrient level is the main factor that affects the magnitude of the spring bloom, but has almost no effect on bloom timing (Song et al. 2010). Although increased primary production begins with the increased solar intensity of spring, the timing of the spring bloom (the rapid growth of phytoplankton) usually follows the seasonal stratification that occurs during the winter-spring transition period. Stratification in the Gulf of Maine is influenced by solar warming (thermal stratification) and source water salinity (density stratification) mechanisms. Recent numerical modeling experiments suggest that salinity is the main factor influencing the bloom timing and magnitude in the Nova Scotian Shelf – Gulf of Maine region, especially for the timing of spring phytoplankton blooms. The impact of surface heating (thermal stratification) and surface wind stress on the blooms variability is much weaker than the influence of vertical salinity gradients (Song et al. 2010).

Spring is a time when nutrient concentrations are high throughout the water column, having been brought towards the surface during strong winter mixing. The spring sun heats the surface water causing it to expand and gets less dense. This warm layer sits on top of the denser water below, leading to stratification. The warm surface layer remains stable unless vertical mixing occurs (e.g. due to high winds, tidal turbulence etc.). This stratification in turn allows the phytoplankton to flourish by holding them near the surface in nutrient rich waters where they experience high light levels. The high nutrient and light levels provide ideal growing conditions, leading to a proliferation of phytoplankton cells, i.e. a bloom (Friedland and Hare 2007).

In areas where the salinity of the surface water is low, “density-driven” stratification can occur. Low salinity water has a lower density than high salinity water, regardless of temperature. In the eastern Gulf of Maine there has been a greater contribution of low salinity (less dense) arctic water since the early 1990s. This has led to increased stratification during the fall and winter. Increased freshening enhances the spatial gradients in bloom timing by stimulating earlier blooms in the eastern Gulf of Maine and western Scotian Shelf, but it has less impact in the western Gulf of Maine. Strong spatial gradients (increasing westward) of mean chlorophyll concentration and net primary productivity during post-bloom months (May–June) indicate that lower sea surface salinity in the eastern gulf can likely impede nutrient fluxes from deep water and therefore affect overall productivity (Ji et al. 2007).

As the primary mechanism of control of spring phytoplankton bloom timing in the Gulf of Maine, stratification controls the rates of development and seasonal cycles of species dependent on these blooms, such as zooplankton (Friedland and Hare 2007).

Intra Gulf Bloom Timing: Since chlorophyll is essential for photosynthesis, it is present in all phytoplankton species. Along with direct organism sampling (CPR data), chlorophyll concentration may be measured as a positively correlated indicator of phytoplankton biomass.

Chlorophyll can be measured directly from water samples, or color interpreted from satellite imagery. Although remotely sensed chlorophyll concentrations can not detail phytoplankton abundance in the same manner that CPR data does, these concentrations do help us understand the spatial timing and relative intensity of phytoplankton blooms within the Gulf of Maine at a given point in time.

There is a general pattern that the spring phytoplankton bloom progresses westward as the season progresses, and this occurs along a corresponding gradient of increasing sea surface salinity from the western Scotian Shelf/eastern Gulf of Maine to the western Gulf of Maine (Ji et al. 2007). However, the waters in the western Gulf of Maine do not show the same positive correlation between spring phytoplankton bloom and sea surface salinity that exists in the eastern gulf. For instance, the blooms in 1998 and 1999 in the western Gulf of Maine appear to have been much later than expected given that a shallower mixed layer depth resulting from more intense freshening at those times would be expected to cause earlier blooms. One possible explanation for the east/west Gulf of Maine difference is that the stability of the water column in the western zones is not controlled by sea surface salinity alone (although it is a very important factor). Rather, the variability of local wind forcing (hence heating) and deep water properties might contribute to the variability of water column stability, thus confounding the direct correlation between sea surface salinity and bloom timing that is observed in the eastern gulf. Another possible explanation is that prior to arriving in the western Gulf of Maine, the surface water nutrients are already depleted as a result of the earlier blooms upstream in the eastern gulf and western Scotian Shelf, leaving a nutrient-poor but vertically-stable water column in the western Gulf of Maine. Either way, the spring phytoplankton bloom in the western Gulf of Maine would be expected to show less interannual variability since the impact of external water inflows could be significantly dampened. This appears to be the case as the timing of the spring phytoplankton bloom in the most western portion of the gulf (Wilkinson Basin area) is less variable (<20 days between 1998 and 2006), than that in the upstream zones (~30 days) (Ji et al. 2007).

Although there is strong interannual variability in phytoplankton-produced chlorophyll in the Gulf of Maine, the typical North Atlantic seasonal cycle is present over the deeper basins of the Gulf of Maine. This cycle includes low chlorophyll concentrations in winter, an annual maximum in March-April, reduced concentrations in summer, and a secondary autumn bloom beginning as early as September in Jordan Basin, but in October-November over other regions (Figure 9.3). In contrast to this pattern, relatively low concentrations are evident over the deeper basin at the mouth of the Bay of Fundy from October through March (Thomas et al. 2003).

Peak spring chlorophyll concentrations occur earliest over Georges Bank and progressively later over Wilkinson Basin (late March), eastern Gulf of Maine (March/April), Jordan Basin, throughout the WMCC, and latest within the EMCC and Bay of Fundy (early May) (Head and Pepin 2010, Thomas et al. 2003). This progression can be seen in Figure 9.3. In Jordan Basin, the spring phytoplankton bloom that occurs from early-April to late-May has a relatively longer duration than other areas of the Gulf of Maine (Song et. al. 2010). The appearance of maximum abundance of diatoms within the Gulf of Maine during the months of March or April is also the earliest of three representative regions of the Northwest Atlantic Shelf (Newfoundland Shelf, Eastern Scotian Shelf, and Western Scotian Shelf) (Head and Pepin 2010).

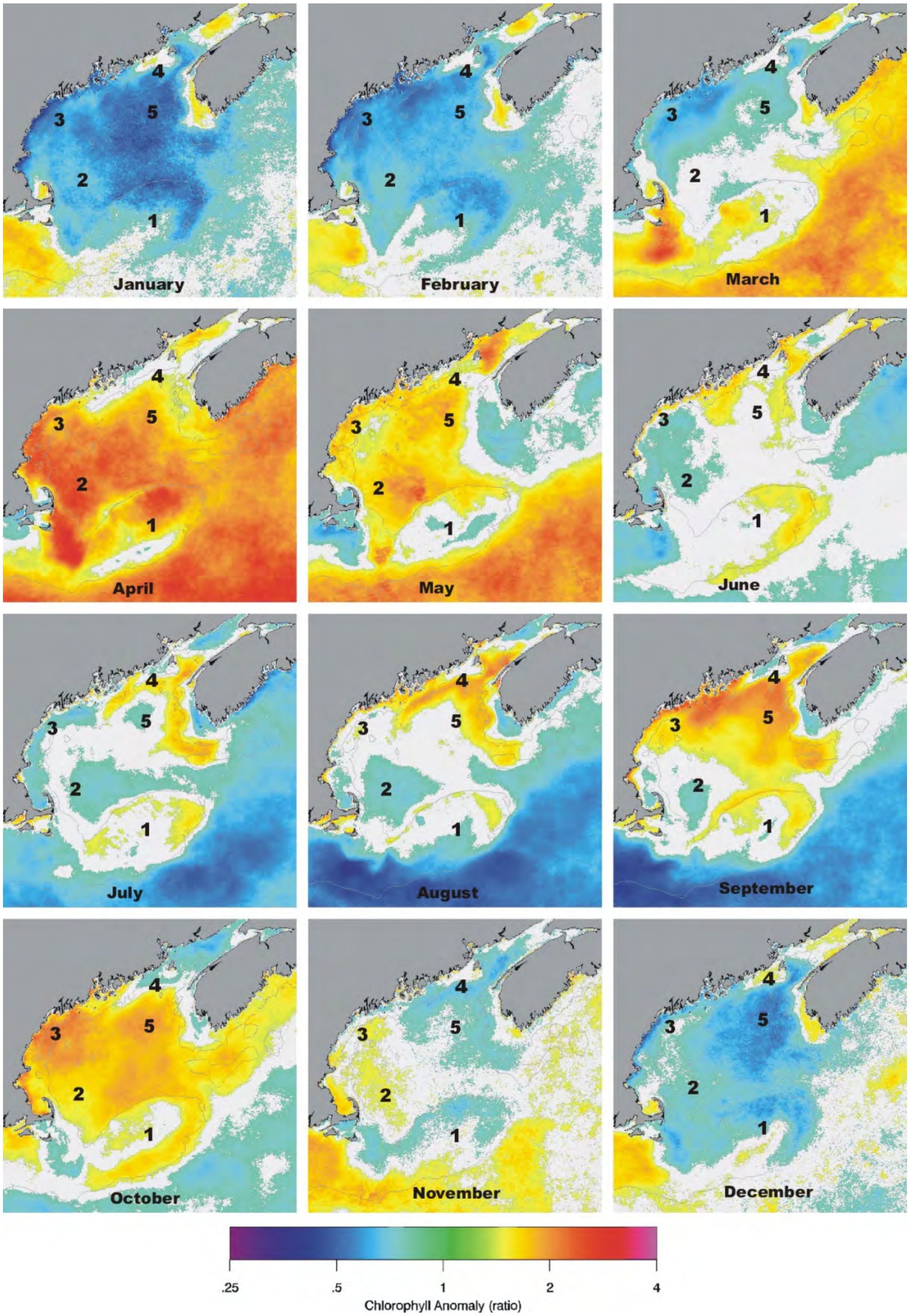

Figure 9.3: Monthly mean chlorophyll levels in the Bay of Fundy, Gulf of Maine, and Georges Bank measured as ratios of the monthly to annual mean from the 1998-2007. Numbered locations: (1) Georges Bank, (2) Wilkinson Basin, (3) Western Maine Coastal Current, (4) Eastern Maine Coastal Current, (5) Jordan Basin. The images are a combination of all available SeaWiFS (1998-2008) and MODIS-Aqua (2002-2008) chlorophyll images.

Source: K. Hyde, Northeast Fisheries Science Center, personal communication (2011).

Remotely sensed Sea-viewing Wide Field-of-view Sensor (SeaWiFS) ocean color data, collected by satellite between 1998-2008, along with numerical modeling, have been used to study the periodic life cycle events of both spring and fall phytoplankton blooms in the Scotian Shelf/Gulf of Maine region and how these are influenced by seasonal and interannual variations in climate. The ocean color data support the previously noted general pattern of westward progression of the spring phytoplankton bloom, but further highlight an apparent eastward progression of the fall phytoplankton bloom. Interannually, there is a weak but significant tendency for years with earlier (delayed) spring bloom to be followed by delayed (earlier) fall bloom, but the mean chlorophyll concentrations during spring blooms are not correlated with those during fall blooms (Song et al. 2010).

Distinct differences within the Gulf of Maine are evident in both the timing and the duration of the fall chlorophyll increase, which peaks first during September in the Bay of Fundy, on Georges Bank and EMCC, a little later over Jordan Basin and the WMCC (early October), but progressively later over Wilkinson Basin (mid November) and offshore (late November) (Thomas et al. 2003, Song et al. 2010). The peak timing of the fall phytoplankton bloom in the eastern gulf/Scotian Shelf can occur as late as December (Song et al. 2010).

By examining the mean surface chlorophyll and monthly averaged net primary productivity across the Gulf of Maine in later spring (May–June), it is clear that the mean surface phytoplankton biomass and productivity during the post-bloom season exhibit a general spatial gradient, where both chlorophyll and primary productivity in the western Gulf of Maine have been almost doubled that of areas further to the east (during the 1998-2006 study period). This pattern is consistent with the assumption that there is greater mixing of surface waters in the western zones with nutrient-rich deeper waters in the Gulf of Maine, increasing the nutrient supply and thus enhancing the integrated productivity (Ji et al. 2007). The spatial distribution of the mean chlorophyll during the fall phytoplankton bloom has a similar pattern to that of spring phytoplankton bloom, with a slightly lower mean chlorophyll concentration in fall than that in spring (Song et al. 2010).

As shown in Figure 9.4, the fall phytoplankton bloom over the Jordan Basin reaches its peak earlier (about October 1) and with the strongest magnitude among seven zones assessed in the Gulf of Maine/Scotian Shelf region. On the Northeast Peak of Georges Bank, there is a major spring phytoplankton bloom but no distinctive fall bloom (Song et al. 2010).

Blooms end abruptly once nutrient concentrations are depleted in surface waters, but their actual duration may be influenced by weather events, self-shading and zooplankton grazing pressure (Ji et al. 2008). Nitrogen is generally the nutrient in shortest supply, and it may limit the growth of phytoplankton, particularly in summer (DFO 2006a).

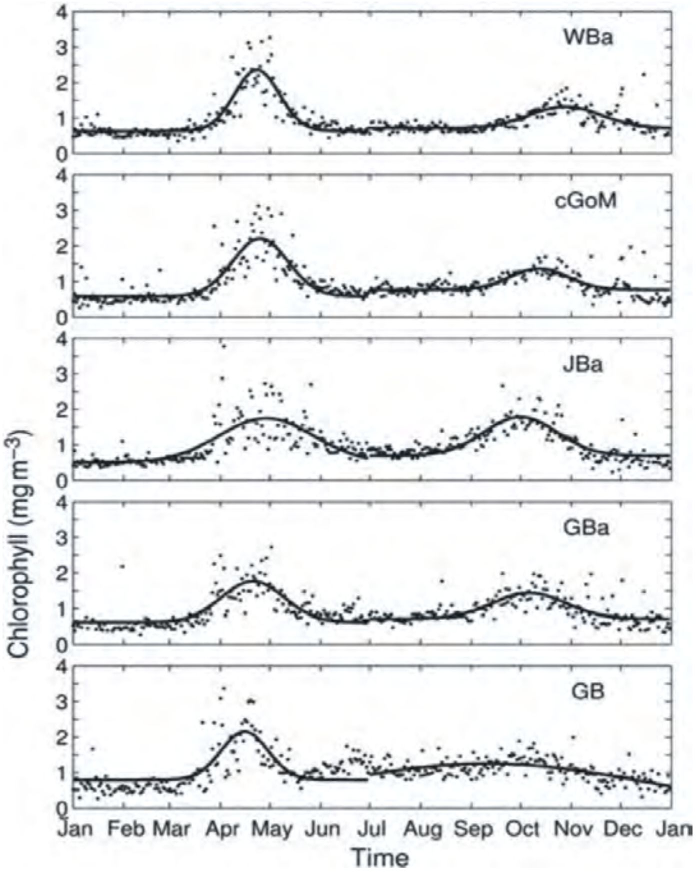

Figure 9.4: Time series of climatological daily chlorophyll concentration in the Gulf of Maine. The black dots represent the zonal mean chlorophyll from SeaWiFS, and the lines show the Gaussian fit. (Wba – Wilkinson Basin, cGoM –central Gulf of Maine, JBa – Jordan Basin, GBa – Georges Basin, GB – Georges Bank)
Source: adapted from Song et al. (2010)

Phytoplankton Composition: A typical seasonal evolution of the phytoplankton community composition in the Gulf of Maine has been winter, spring and late autumn dominance by diatoms, and post-bloom and summer dominance by flagellates (DFO 2006a). As summer nutrient levels diminish in the Gulf of Maine, small phytoplankton species can compete better for scarce nutrients than the larger diatoms. However, dinoflagellates, despite their large size, can compete for nutrients in well-stratified waters by swimming to the depth of the nitracline at night to absorb nutrients, and returning to the surface layers to grow during the day. For this reason, they are generally abundant in summer and early autumn, before stratification breaks down. This likely explains why the observed decadal annual average abundance for dinoflagellates is more closely related to the decadal annual stratification (anomaly) than that of diatom abundance (Head and Pepin 2010).

Unlike the Gulf of Maine proper, the phytoplankton community in the Bay of Fundy is almost exclusively comprised of diatoms (>90%) year round (DFO 2006a). Surveys during 1979-1980 identified 113 species of diatoms, 12 dinoflagellates species, and one species of green algae (Prouse et al. 1983). In total, some 310 species of phytoplankton have been identified throughout the Gulf of Maine (Census of Marine Life 2009).

Carbon production and chlorophyll concentration: Production by marine phytoplankton refers to the creation of organic carbon through photosynthesis, and it is measured as a weight of carbon produced in every unit of area of ocean. The more productive phytoplankton is within an area, the greater the weight of carbon produced. Since chlorophyll is required for photosynthesis, measures of chlorophyll provide an indicator of how much mass of phytoplankton is in an area of ocean. Although measures of chlorophyll are not a direct measure of production of carbon by photosynthesis, the higher the concentration or production of chlorophyll in an area, the more likely that a larger abundance of phytoplankton, which would be producing carbon through photosynthesis, exists in that area of ocean.

Mixing processes and thermal stratification vary across the Gulf of Maine, and so too does the intensity of the phytoplankton bloom. Regardless, the Gulf of Maine/Georges Bank ecosystem is estimated to have one of the highest primary production rates in the North Atlantic (Gaichas et al. 2009). Average annual phytoplankton production levels have been estimated for the U.S. portion of the Gulf of Maine (290 g C m^{-2}) and Georges Bank (between 300-470 g C m^{-2}) (O'Reilly and Busch 1984, cited by Kenney et al. 1997). Gaichas et al. (2009) estimated primary production to be 360 g C m^{-2} and 427 g C m^{-2} in the gulf and on Georges Bank respectively. Annual phytoplankton production rates in the open waters of the inner Bay of Fundy have been estimated at 27 g C m^{-2}, and in the outer bay at some 133 g C m^{-2}. The outer bay accounts for 85% of the total annual production of the bay, and 96% of the total is derived from phytoplankton. The remaining 4% is derived from seaweeds, benthic microalgae and salt marshes. High production in the outer bay is largely attributed to the less turbid, more stratified nature of the water column, which allows better light penetration (Prouse et al. 1983).

The 1998-2008 satellite derived mean surface chlorophyll concentration during the spring phytoplankton bloom in the Gulf of Maine was about 1.25 mg m^{-3}, but observed to be much higher on Georges Bank and in the nearshore waters (~2.5 mg m^{-3}) (Song et. al. 2010). However, an unknown portion of this satellite derived signal is undoubtedly contributed by resuspended sediment and/or colored dissolved organic matter, factors that cause an overestimate of chlorophyll and phytoplankton, particularly in coastal areas (Thomas et al. 2003). Over a four-year assessment (1997-2001) mean chlorophyll concentrations along the more shallow MCC, Georges Bank and Browns Bank typically ranged between winter and summer lows of 1-2 mg m^{-3} to spring and fall bloom highs between 2 and 4 mg m^{-3} (Thomas et al. 2003). Summer surface chlorophyll concentrations of >2 mg m^{-3} have recently been observed in the eastern Gulf of Maine near the coast of southwestern Nova Scotia, as well as in the approaches to the Bay of Fundy (DFO 2006a). Maximum mean chlorophyll concentrations within the Gulf of Maine of 4.8 mg chl m^{-3} have been recorded on Georges Bank during the spring (mid March) bloom. In contrast, the deeper basins have lower year round chlorophyll concentrations. The range of satellite derived 4-year mean chlorophyll concentration in Wilkinson and Jordan basins generally ranged from a late summer low of approximately 0.6 mg chl m^{-3} to a spring maximum of around 1.7 mg chl m^{-3}. At least two mechanisms have been postulated that link the interannual variability of deepwater properties to the surface chlorophyll interannual variability. First, the connection between deepwater nutrient concentrations and surface availability to phytoplankton is through strong vertical mixing and the vertical flux of subsurface water within the Gulf of Maine over the year. This is especially true within the EMCC region and over shallow bathymetry. At times when deep water sources are colder and less saline they also exhibit reduced nitrate/nitrite and silicate concentrations.

Therefore, it is suggested that, despite mixing, such water would support lower phytoplankton biomass than when deep source water to the Gulf of Maine is warmer and more saline. A second mechanism linking deepwater variability to chlorophyll variability is the argument that upward doming of dense deep water and the subsequent formation of a warm saline pycnocline (vertical density gradient) within the upper 75 m is one mechanism by which the spring bloom can be initiated over deeper basins of the Gulf of Maine, as nutrient rich water gets pushed into the euphotic zone despite lack of mixing to the surface. In contrast, if deep source waters are cooler and fresher, it appears there is an associated lack of upper water column stability capable of delaying or reducing the spring bloom, with elevated near-surface nutrient concentrations still present (Thomas et al. 2003).

Long Term Trends and Recent Changes: Three indices of phytoplankton abundance are measured by the CPR: diatoms, dinoflagellates, and phytoplankton color index. CPR collected data have demonstrated shifts in long term mean abundance for diatoms (+2.07%), dinoflagellates (−2.07%) and phytoplankton colour index (−0.81%) for the western Scotian Shelf/eastern Gulf of Maine between the 1960s and 2006 (Head and Pepin 2009). The phytoplankton color index, recorded from CPR collected data, is best viewed as a measure of the abundance of larger phytoplankton (e.g. diatoms and large dinoflagellates). It has been used since the early 1960s, providing a longer time series than satellite measures of chlorophyll concentration. Since the late 1970's, the phytoplankton color index from the western Gulf of Maine CPR data has shown an overall decline in color (and by proxy larger phytoplankton) over the series (Figure 9.5). This decline in larger phytoplankton has important implications for food webs in the ecosystem and may indicate a shift to smaller phytoplankton in recent decades (e.g. smaller dinoflagellates) (EAP 2009).

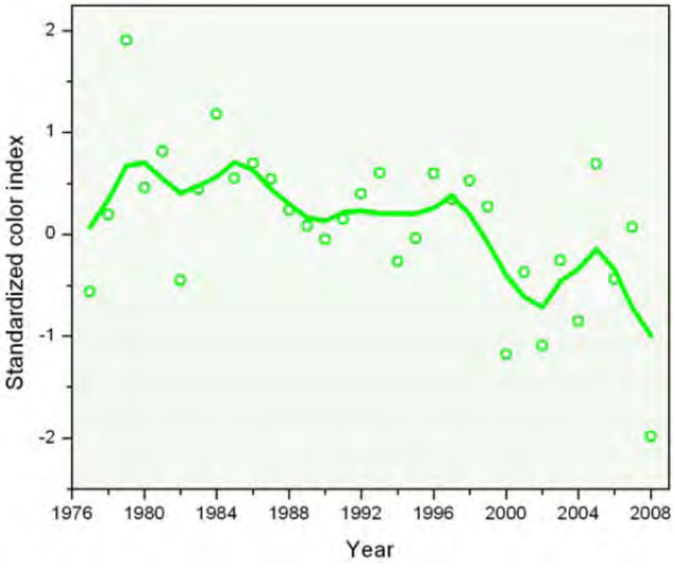

Figure 9.5: Standardized color index from three Continuous Plankton Recorder routes on the northeast U.S. shelf ecosystem: across the Gulf of Maine, from New York to Bermuda, and across Georges Bank
Source: EAP (2009).

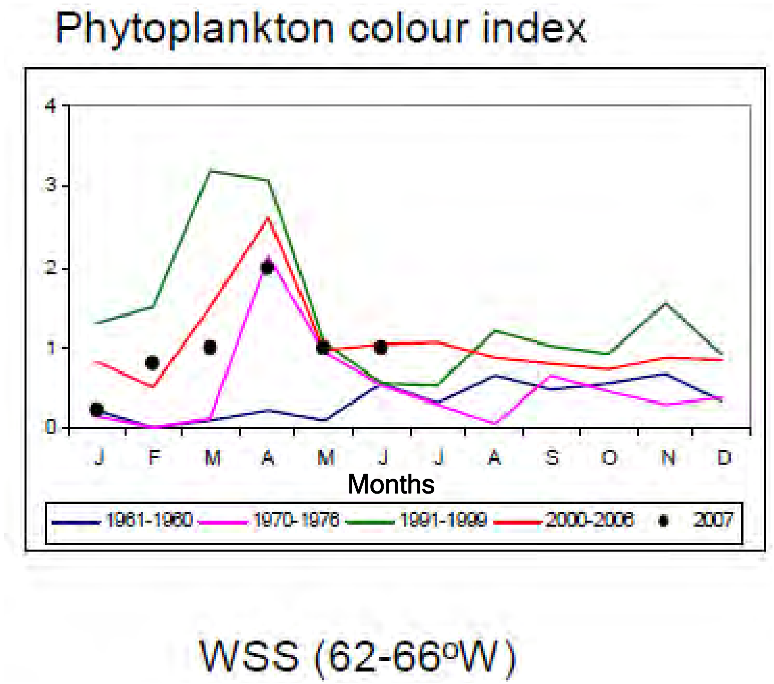

Figure 9.6: Seasonal cycles of the phytoplankton colour index by decade and with data for the months sampled in 2007 west of 45°W, for the western Scotian Shelf, an area inclusive of the eastern Gulf of Maine, shows a decadal increase during winter months.
Source: Head and Pepin (2009)

From an assessment of CPR data collected between 1959 and 2000, it appears the 1990's were a unique period of large and persistent change in abundance and timing of phytoplankton blooms. The bloom periods for diatoms and dinoflagellates occurred progressively earlier on the western Scotia Shelf/eastern Gulf of Maine in this period when compared to years prior (Sameoto 2004). Diatom and dinoflagellate abundances, and the phytoplankton color index, increased significantly on the western Scotian Shelf/eastern Gulf of Maine between the 1970s and the 1990s, and then remained largely unchanged in the 2000s (Head and Pepin 2010). Although the peak of the spring bloom has generally been in April in all decades, both diatom abundance and the phytoplankton colour index of the eastern Gulf of Maine (see Figure 9.6) showed increases in the winter months (January-March) in the 1990s and 2000s compared with earlier decades (Head and Pepin 2009). Furthermore, the dinoflagellate bloom on the western Scotian Shelf/eastern Gulf of Maine showed less change to earlier months than did the diatoms (Sameoto 2004).

Head and Pepin (2009) suggest that decadal patterns of change in annual abundance and seasonal cycles in the plankton are clearly very different on the Canadian continental shelf when compared with the deep Northwest Atlantic, reflecting regional differences in changes in environmental conditions over the years. The Gulf of Maine, for example, was subjected to an increased contribution of fresh arctic water during the 1990s that had a dramatic impact on the plankton community. Modelling by Ji et al. (2008) suggested that the blooms in the eastern Gulf of Maine have occurred earlier when the surface salinity of Nova Scotian Shelf inflow was lower, in association with a shallower mixed layer depth and more stable water. More recent data further support the premise that increased stratification has led to higher annual phytoplankton abundance and earlier blooms in the eastern Gulf of Maine. The increase in abundance in the 1990s and 2000s was most obvious in May, as the spring bloom was ending (Head and Pepin 2010).

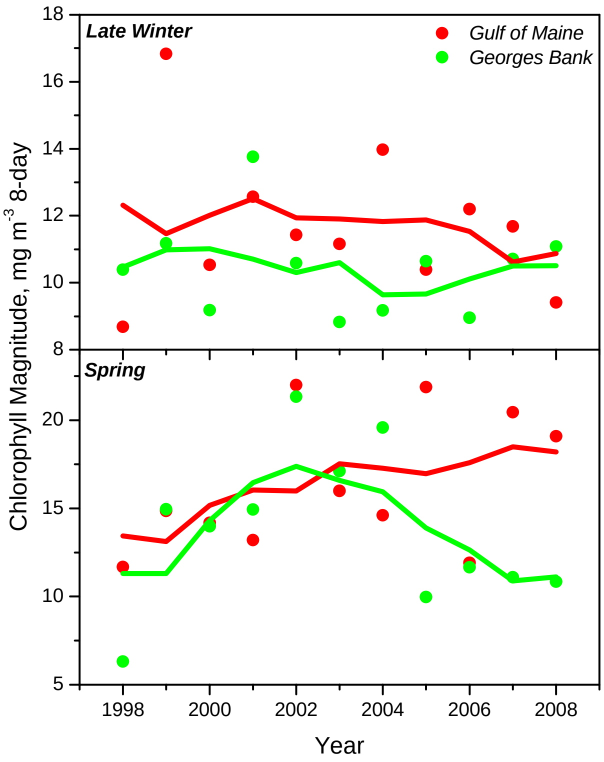

Figure 9.7: The chlorophyll magnitude of late winter and spring for the Gulf of Maine and Georges Bank.
Source: K. Friedland, Northeast Fisheries Science Center, personal communication (2009)

Peak chlorophyll production summed over 8-day blocks during the spring blooms, recorded as chlorophyll magnitude, has increased overall in the Gulf of Maine since the late 1990s. As shown in Figure 9.7, levels rose from <15 mg m^{-3} to approximately 18 mg m^{-3}. On Georges Bank, the magnitude of the bloom in spring has recently declined from a peak in 2002, suggesting that the spring blooms on the bank have more recently been of short duration, which results in low magnitude blooms. Chlorophyll production levels have remained more constant in late winter across the entire Gulf of Maine (NOAA 2008).

Toxic algae: Some 733 different species of microscopic plants, including algae, have been identified in the Gulf of Maine to date (Valigra 2006). A large number of these are microscopic plants, known as phytoplankton, which includes the micro-algae. A few species of micro-algae can create what are referred to as harmful algal blooms or red tides. Of the micro-algae present in the Gulf of Maine, *Alexandrium fundyense* is one of the most studied and of greatest concern. This dinoflagellate is a common cause of toxic "red tide" that causes shellfish poisoning. *A. fundyense* algae derive from germinated cysts that exist in bottom sediments for nearly 500 km alongshore in the Gulf of Maine, primarily from the Bay of Fundy south to Cape Cod. Embedded within this area are several distinct accumulation zones or "seedbeds," each 3000-5000 km^2 in area, with maximal cyst abundances ranging from 2-20 ×10^6 cysts m^{-2} (Anderson et al. 2005). Cyst germination flux from deep-water (>50 m) cyst seedbeds is 14 times the flux in shallow waters. Cysts germinate within the Bay of Fundy seedbed, causing localized recurrent blooms that are self-seeding and "propagatory" in nature, supplying cells that populate the eastern and, eventually, the Western Maine Coastal Currents. It is suggested that without the localized "incubator" characteristic of the

Bay of Fundy bloom zone, *A. fundyense* populations in the Gulf of Maine would diminish through time (Anderson et al. 2005). It is likely that *A. fundyense* populations in the western Gulf of Maine are habitually nitrogen limited each season, which may partially explain why relatively small cell concentrations are usually recorded in the region (Love et al. 2005). Through analysis of a two-year data set it appeared that consumption of *A. fundyense* by zooplankton during strong toxic algal bloom periods was an important cause of mortality of the toxic blooms (Campbell et al. 2005), although other studies indicate that this effect may actually be a rare occurrence in nature (Turner and Borkman 2005).

Alexandrium ostenfeldii is a less well known phytoplankton species found in the Gulf of Maine that has recently been linked to a novel suite of toxins called spirolides. Spirolides are also found in *A. ostenfeldii* in waters off southern Nova Scotia. The hydrographic forcings controlling the distribution of *A. ostenfeldii* in the Gulf of Maine are quite similar to those acting on the *A. fundyense* population. The highest concentrations of *A. ostenfeldii* are observed nearshore, adjacent to the junction of the eastern and western MCC near Mount Desert Island. Lower concentrations are generally found in deeper water, except at locations where the pooling of lower-salinity water at the surface may have led to the downward movement of the population flowing in from the east (Gribble et al. 2005).

9.1.3 Zooplankton: Zooplankton are small animals that feed on both phytoplankton and, in some cases, other zooplankton. They are a key link in the marine food web, transferring energy from primary producers such as phytoplankton to larger organisms such as fish, seabirds, and marine mammals. By definition zooplankton are weak swimmers, but many can strongly influence their own transport by vertical migration. Their distribution, abundance, and community structure are influenced by transport in ocean currents, interactions between their behaviour and ocean physics, their reproductive and physiological responses to the physical and biological environment, and mortality. Zooplankton are generally divided into three size classes: microzooplankton (0.02-0.2 mm) that includes single-celled protozoa and the early life stages of other organisms; mesozooplankton (0.2-20 mm) that includes late stages of crustaceans such as the numerically dominant copepods, larvae of benthic organisms, small gelatinous taxa, chaetognaths (“glass worms”) and fish eggs; and macrozooplankton (2-20 cm) that includes larger gelatinous taxa, amphipods and krill. Sampling efforts in the Georges Bank/Gulf of Maine region have primarily targeted the mesozooplankton, particularly their upper size range, and the reporting here focuses on this size class.

Zooplankton Composition: Bigelow (1926) first recognized that the offshore mesozooplankton community of the Gulf of Maine is dominated in biomass by the large omnivorous copepod *Calanus finmarchicus*. Bigelow observed that this copepod was associated with a community that included the small, abundant copepod *Pseudocalanus* spp. (his *P. elongatus*), the large, deep-water copepod *Metridia lucens*, the arrow worm *Parasagitta elegans* (his *Sagitta elegans*), the amphipod *Themisto compressa* (his *Euthemisto compressa* and *E. bispinosa*), krill of the genera *Meganyctiphanes* and *Thysanoessa*, the pteropod (pelagic mollusc) *Limacina retroversa*, the comb jelly *Pleurobrachia pileus*, and the large but relatively uncommon predatory copepod *Euchaeta* spp.

Corey and Milne (1987) identified a similar core group of species in the waters off southwest Nova Scotia, including *Calanus finmarchicus*, *Metridia lucens*, *Parasagitta elegans* (their *Sagitta elegans*), and *Pseudocalanus* spp. Sampling efforts by the Atlantic Zone Monitoring Program (AZMP), using smaller mesh nets (200µm), have identified several additional species of small copepod as numerically dominant where Scotian Shelf water enters the eastern Gulf of Maine. With some seasonal variations, the copepod *Oithona similis* (a small ambush-predator), *Calanus finmarchicus*, *Pseudocalanus* spp., the pelagic tunicate *Fritillaria* spp., which feeds on very tiny particles, *Metridia lucens*, the shallow-water copepod *Temora longicornis*, the small deep-water copepod *Microcalanus* spp., and the tiny copepod *Paracalanus* spp. are dominant (Harrison et al. 2008). Other spring taxa in the eastern Gulf of Maine region are pteropods (*Limacina*), barnacle larvae and *Calanus hyperboreus*, an Arctic copepod.

During any given season, over 80% of the total zooplankton abundance in the Georges Bank area of the Gulf of Maine is accounted for by just six copepod species. These are: *Calanus finmarchicus*, *Pseudocalanus* spp., *Paracalanus parvus*, *Centropages typicus*, *Centropages hamatus*, and *Oithona similis (*HBOI 2011).

Corey and Milne (1987) identified a core zooplankton community in the Bay of Fundy that includes the arrow worm species *Parasagitta elegans* and *Serratosagitta tasmanica* (their *Sagitta tasmanica*), along with *Meganyctyphanes norvegica*, *Calanus finmarchicus*, *Metridia lucens* and *Euchaeta norvegica*. This is a community similar to the Gulf of Maine *Calanus*-associated community identified by Bigelow (1926). DFO sampled zooplankton along the long axis of the Bay of Fundy in July of 1999 to 2006. When clustered based on zooplankton community composition, inner bay and outer bay groups were apparent (Johnson 2008). Species typical of the outer bay community include *Calanus finmarchicus*, *Metridia lucens*, *Microcalanus* spp., *Meganyctyphanes norvegica*, and euphausiids eggs and larvae, all abundant in the Gulf of Maine. The inner bay zooplankton community includes near-shore and small estuarine species, including *Eurytemora herdmani*, *Acartia tonsa*, *Temora longicornis* and *Pseudodiaptomus coronatus*, the near-shore cladoceran *Podon leuckardii*, and larvae of bivalves, barnacles and echinoderms that live on the bottom as adults (meroplankton) (Brylinsky et al. 1997, Daborn 1984, Garrett et al. 1978). The spatial distribution of the outer and inner bay communities corresponds approximately to the stratified outer and tidally well-mixed inner regions of the bay (Garrett et al. 1978).

Spatial and Seasonal Distribution: Zooplankton biomass data collected during groundfish surveys of Canadian Gulf of Maine waters show that biomass is generally highest in the deep basins and deep waters off the edge of the shelf areas or in channels (e.g. Northeast Channel and eastern Georges Bank) (DFO 2006a), although there are spatial and seasonal variations. The primary circulation pattern in the Gulf of Maine is counter-clockwise from the Northeast Channel around to the Great South Channel. Therefore, the Gulf of Maine zooplankton community, particularly in the east through Georges Basin and into the Bay of Fundy, is influenced by inflow from the Scotian Shelf (Loder et al. 1998). The hydrographic link between the Gulf of Maine and the Scotian Shelf is important to the population dynamics of *Calanus finmarchicus*, the biomass-dominant zooplankton species within the gulf. Overall it has been estimated that >60% of the annual net production of *C. finmarchicus* on the Scotian Shelf is exported to the southwest. A portion is retained along the shelf edge, but most is transported to overwinter in the deep basins of the Gulf of Maine. *C. finmarchicus* that mature on the Scotian Shelf resurface to seed populations that grow and develop in the Gulf of Maine and on Georges Bank (Zwanenburg et al. 2006). In the temperate North Atlantic, *C. finmarchicus* is generally known as a winter/spring cold-water species that gives way to warm-water species whose abundance peaks in summer/autumn. This relationship has also been confirmed on Georges Bank (Kane 2007).

The relatively warm and diverse Georges Bank sub-region is unique in the Gulf of Maine in that it is very shallow, but well offshore. Some Scotian Shelf water crosses over the Northeast Channel and onto Georges Bank, transporting zooplankton directly onto the northeast peak of Georges Bank (Smith et al. 2001, Wishner et al. 2003). However, the northeast peak is more typically influenced by transport onto the bank from the southwest and central Gulf of Maine. Warm-water, oceanic zooplankton species are transported into the region intermittently via intrusions of warm slope waters through the Northeast Channel or onto Georges Bank (Colton et al. 1962, Brown et al. 2005).

The copepods *Calanus finmarchicus* and *Pseudocalanus* spp. are the numerically dominant species in the early spring to early summer zooplankton assemblage across the Gulf of Maine. As the season progresses, *Paracalanus parvus* and the two *Centropages* species dominate the zooplankton community toward the late summer and fall. *Oithona similis* is common throughout the year (HBOI 2011). Although *Calanus finmarchicus* is not numerically dominant in the second half of the year, it is typically in its largest fifth copepod stage and therefore still biomass dominant in the late summer and throughout the autumn.

At the mouth of the Bay of Fundy near St. Andrews, New Brunswick, seasonal variability in zooplankton abundance and community structure has been measured by the AZMP since 1999 (at the monitoring station “Prince 5”) and is a mixture of near-shore and Gulf of Maine species (Harrison et al. 2008). Despite the mixed origins of zooplankton species at this station, the community exhibits some patterns of seasonal variability that are typical of the western Scotian Shelf and the Gulf of Maine. In springtime, *Calanus finmarchicus*, *Oithona similis* and barnacle larvae (infraclass Cirripedia) are numerically dominant (see Figure 9.8), while *C. finmarchicus* is dominant in terms of biomass. *O. similis* remains a numerically dominant species throughout the year. *Pseudocalanus* spp. and euphausiids (krill) are among the dominant species in summer. The warmer water coastal copepods *Acartia* spp. and *Temora longicornis* are dominant in the summer and early autumn, and the warm water shelf copepod *Centropages typicus* is an autumn-dominant species.

The annual abundances of a complex community of several small copepod species found in the central Gulf of Maine have varied from year to year. On an interannual basis the abundances of these species has been negatively correlated with salinity and positively correlated with autumn phytoplankton abundance (Pershing et al. 2005, Greene and Pershing 2007). A similar pattern was observed on Georges Bank for *Centropages typicus*, *Oithona* spp., *Pseudocalanus* spp. and *Metridia lucens,* and for two less abundant groups, Larvacea and hyperiid amphipods (Kane 2007). Survival of these species through the autumn may be enhanced when low salinity waters move into the eastern Gulf of Maine from the Scotian Shelf and act to stabilize the water column at a time when autumn storms would otherwise cause strong vertical mixing. Reduced mixing may allow phytoplankton to grow during the autumn and winter (Durbin et al. 2003, Pershing et al. 2005, Kane 2007). This is a hypothesis, but is supported by the observation of much higher abundances

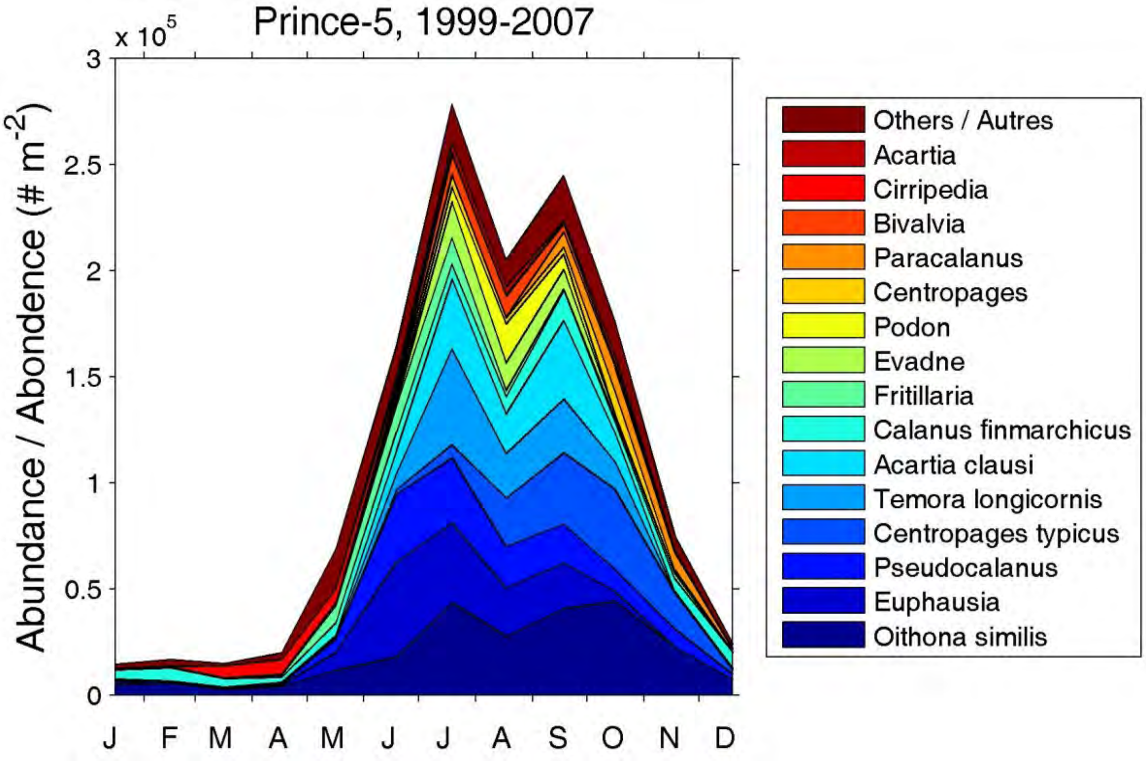

Figure 9.8: Seasonal variability of dominant zooplankton taxa just north of Grand Manan Island at the mouth of the Bay of Fundy (Prince-5) from 1999 to 2007. The top 90% of taxa by abundance are shown individually; other taxa are grouped as ‘others’.
Source: adapted from Harrison et al. (2008)

of *Centropages typicus*, *Oithona* spp., *Pseudocalanus* spp., *Metridia lucens*, and late-stage *Calanus finmarchicus* in the central Gulf of Maine in the winter of 1999, a year when colder low-salinity water was present in the gulf and a winter bloom occurred. This was in stark contrast to the winter of 2000 when conditions were more typical, having higher surface salinities, and there was no winter bloom and low copepod abundance (Durbin et al. 2003).

Calanus finmarchicus: Monitoring of *Calanus finmarchicus* within the Gulf of Maine has been important, as it is the dominant zooplankton species in terms of biomass throughout the year, and is an important component of the foodweb. Despite the higher abundance of small copepods, *C. finmarchicus* dominates zooplankton biomass for most of the year due to its large size and relatively high abundance.

Like all free-living copepod species, *Calanus* individuals hatch from eggs and proceed through several stages before they become adults. Recent modelling of remotely sensed data predicts that based on the chlorophyll patterns, *C. finmarchicus* egg production should be limited over most of the Gulf of Maine until mid-March (Pershing et al. 2009). In the Gulf of Maine region, either one (Georges Bank) or two (Gulf of Maine proper) generations are produced between March and July (HBOI 2011). The rapid increase in both temperature and food after mid-March are expected to support a corresponding increase in the *C. finmarchicus* population. In all decades since the 1960s, the seasonal cycle of *Calanus* stages I–IV in the eastern Gulf of Maine/western Scotian Shelf region has had broad abundance peaks during early to mid-summer (Head and Pepin 2010). The life cycle of *Calanus* exhibits an interesting twist, in that the final copepodid stage (C_5) can enter a state of diapause. Diapause is a period of delayed development or growth and reduced metabolism that provides a mechanism for surviving adverse environmental conditions. Most *C. finmarchicus* that enter diapause in the Gulf of Maine migrate into the deep (300-400 m) basins (Wilkinson, Jordan, Georges) prior to the onset of the warmest months of late summer (HBOI 2011).

In the winter months, only the deep basin habitats of the Gulf of Maine contain large numbers of *C. finmarchicus*, all of which occur at that time as diapausing C_5 copepodids. They remain there through the fall and winter (HBOI 2011). In the western Gulf of Maine, after an early peak in abundance during January, modelling indicates the *C. finmarchicus* populations in the outer Massachusetts Bay and Wilkinson Basin regions decline toward a minimum around mid-February and then increase rapidly through mid-May (Pershing et al. 2009). The diapausing C_5 copepodids molt into adults by early spring and then migrate vertically to feed in the phytoplankton-rich upper water layers. Large numbers of newly emerged adult *C. finmarchicus* are also transported into the Gulf of Maine each spring with cold oceanic currents that flow into the gulf, both through the deep Northeast Channel and in shallower currents that flow from the western Scotian Shelf (HBOI 2011).

Long Term Trends and Recent Changes: CPR survey data between 1961 and 2000 shows that significant changes have occurred in the abundance and seasonal timing of the blooms of North Atlantic zooplankton taxa, a period over which phytoplankton increased and zooplankton decreased. Spatial variances indicate that changes might have been related to changes in the Labrador Current system (Sameoto 2004).

Calanus finmarchicus abundance is correlated with sea surface temperature in the Gulf of Maine; higher abundances occur during cold years. Conversely, the copepods *Centropages typicus* and *Centropages hamatus* have typically been more abundant in years when surface waters are warm (Meise-Munns et al. 1990, Licandro et al. 2001, Kane 2007). Data from the 1960s to 1980s based on the CPR program indicated that *C. finmarchicus* abundance was correlated to the NAO index, but lagged the NAO by four years (Conversi et al. 2001) (see Sections 7.3 and 8.3 for discussion of NAO). During this period, *C. finmarchicus* abundance was low during the 1960s and early 1970s and peaked in abundance in the 1980s (Page et al. 2001). More recently, the correlation between the NAO and *C. finmarchicus* has broken down (post-1995): limiting the time-series to a recent 22-year period (1981 to 2002) shows that the NAO is no longer correlated to *C. finmarchicus* abundance (Kimmel and Hameed 2008). Nevertheless, changes in ocean circulation in the northwest Atlantic have occurred since the early 1990's, and these changes appear to have had an important impact on the zooplankton community of the Gulf of Maine (Greene et al. 2003).

On the Scotian Shelf, the peak in young stage abundance (*Calanus* I-IV) has occurred earlier in the year since the 1990s, which may be linked to the fact that high phytoplankton concentrations are also found earlier in the year than in previous decades (Head and Pepin 2009). Modelling for the Gulf of Maine, based on satellite-derived measurements of SST and chlorophyll concentration used to determine the developmental and reproductive rates of *C. finmarchicus*, suggests that temperature has the largest effect on growth rate of the species. Elevated chlorophyll during the late winter can lead to increased *C. finmarchicus* abundance during the spring, but the effect of variations in chlorophyll concentrations is secondary (Pershing et al. 2009). Head and Pepin (2010) highlight that, if the increases in phytoplankton concentrations in the eastern Gulf of Maine in the 1990s are attributable to increased stratification, then the negative relationships between the abundances of zooplankton and phytoplankton abundance are not the result of the release of grazer control, but rather are reflections of a new, alternative, ecosystem state where there will be higher annual phytoplankton levels and (slightly) lower annual abundances for some zooplankton taxa.

In partial contradiction to the CPR data, an analysis of Northeast Fisheries Science Center (NEFSC) plankton monitoring program data has shown a general decline in annual mean *Calanus* abundance from 1977 through the mid 1990s in the western and central Gulf of Maine and on Georges Bank. Abundance then followed the trend of the eastern gulf with an increase over the next decade (Figure 9.9).

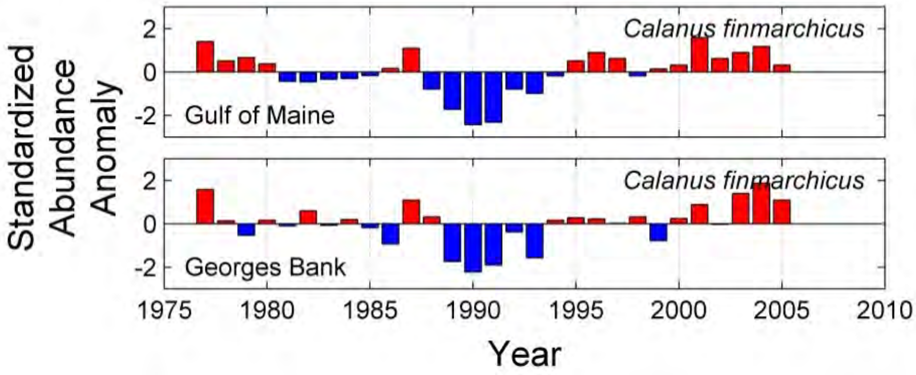

Figure 9.9: Mean annual abundance of *Calanus finmarchicus* in the Gulf of Maine and on Georges Bank based on NEFSC plankton monitoring sampling using bongo gear.
Source: M. Fogarty, Northeast Fisheries Science Center, personal communication (2009).

Sameoto (2004) suggested that after 1991, concentrations of *C. finmarchicus* early life stages (copepodites 1 to 4) decreased in abundance in the Gulf of Maine (up to the study end date of 2000), but mainly during July to September, with the later life stages showing little change. The studied data also indicate that *C. finmarchicus* tended to bloom earlier in the year since 1991 (to 2000) corresponding to an observed earlier start in the spring phytoplankton bloom. More recently (to 2006), young stage *C. finmarchicus* abundance has returned to relatively high values since 2004. The patterns are similar for late stage *C. finmarchicus* abundances on the Scotian Shelf, except that in this case the recovery from low values in the 1990s began at the beginning of the 2000s (Head and Pepin 2009).

Historic zooplankton biomass in the Bay of Fundy has been generally <10g wet wt m^{-2}; yet recent observations in late autumn have approached 40g wet wt m^{-2}. Zooplankton biomass in the Bay of Fundy is typically quite low (10% to 20%) relative to levels at other sites around Nova Scotia, and peak levels occur later in the year than at the other sites. The contribution of *Calanus* spp. to the zooplankton community in the Bay of Fundy has increased steadily since the AZMP observations began in Canadian waters in 1999. Species such as *Calanus finmarchicus* have increased, at least periodically, to levels well above the long-term average (DFO 2006a).

A complex of taxa, including *Centropages typicus*, *Oithona* spp., *Pseudocalanus* spp., and *Metridia lucens* (all small bodied zooplankton) followed a common pattern of interdecadal variability characterized by a dramatic increase in these taxa around 1990, followed by a rapid decline in 2002. All of these taxa shifted from low abundance through most of the 1980s with a large proportional increase in winter abundance across the Gulf of Maine up to the 1990s. The increased abundances for these species in Continuous Plankton Recorder samples after 1991 reflected an apparent increase in community diversity and a shift away from *C. finmarchicus* towards smaller-sized taxa (Pershing et al. 2005, Greene and Pershing 2007). NEFSC plankton monitoring program results also indicate decadal-scale shifts in abundance of some small bodied copepod species during the same time frame. The species *Centropages typicus*, *Centropages hamatus*, *Oithona* spp., and *Temora longicornis* in particular all exhibited increases during the late 1980s through the very early years of the 2000s both in the Gulf of Maine and on Georges Bank (Figure 9.10). Winter, early spring and spring zooplankton biomasses on Georges Bank were at intermediate levels during the early 2000s. There is some evidence for increasing zooplankton in the winter (January/February), but decreasing zooplankton in the spring (March/April) (NOAA 2008).

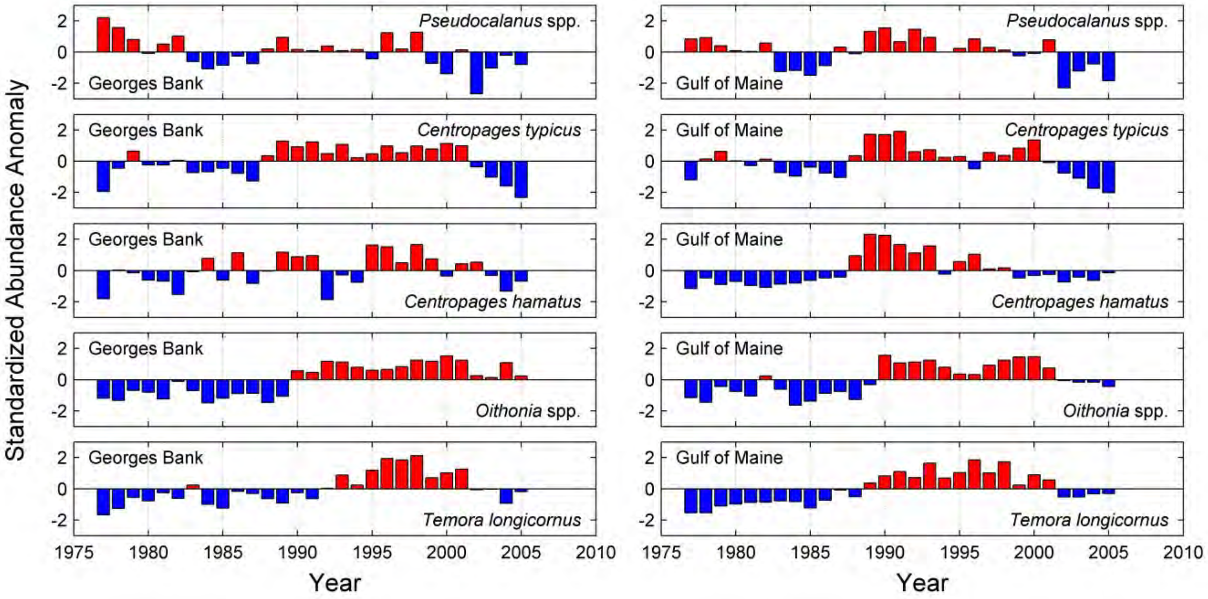

Figure 9.10: Mean annual abundance of *Pseudocalanus* spp., *Centropages typicus*, *Centropages hamatus*, *Oithona* spp., and *Temora longicornis* in the Gulf of Maine and on Georges Bank based on NEFSC plankton monitoring sampling using bongo gear.
Source: M. Fogarty, Northeast Fisheries Science Center, personal communication (2009).

The species that increased around 1990 have very different life histories and phenologies and occupy a range of ecological niches. Despite their significant biological/behavioural differences, the taxa represented in the community shift were similar in that they all had large proportional changes in their seasonal cycles during the winter - spring period. Pershing et al. (2005) suggest that the concentration of the taxon-specific changes near the beginning of the year strongly indicates that the community shift was driven by processes during this portion of the year. The period of high abundance of smaller copepod species on Georges Bank coincides with strong negative salinity anomalies on Georges Bank (Link et al. 2008).

During the 1990s, zooplankton increases were observed in the central Gulf of Maine (Pershing et al. 2005), eastern Gulf of Maine (Sameoto 2004), and Georges Bank (NOAA 2008). However, unlike the central and eastern gulf, the increase in the Georges Bank zooplankton community was not seasonally restricted, nor did it end in 2002. The abundance of some dominant taxa declined, but that of others increased or continued at high levels through 2004 (Kane 2007). In contrast to the central Gulf of Maine/Georges Bank areas, the abundance of small copepods in the eastern Gulf of Maine/western Scotian Shelf has been relatively low in winter (January-March) throughout the decades, but otherwise the seasonal cycle shows no obvious pattern (Head and Pepin 2009).

Following an increase in abundance of small copepods in the 1990s, they have remained relatively high through much of the 2000s. There is some indication of an inverse relation between the abundance of small copepods and that of early *Calanus* (copepodites 1 to 4) (Head and Pepin 2009).

A new way to present CPR data collected in the Northwest Atlantic for reporting to the AZMP has been developed. Results for the Scotian Shelf, including the eastern Gulf of Maine, show that *Calanus finmarchicus* have made a comeback in the 2000s, two arctic *Calanus* species (*C. hyperboreus* and *C. glacialis*) increased in abundance in the 1990s and stayed high in the 2000s, while krill (euphausiid) levels decreased and remained low over the same time periods (Head and Pepin 2009). The increased abundance of the arctic *Calanus* species (*C. hyperboreus* and *C. glacialis*) during the 1990s and 2000s is likely the result of increased transport from the Arctic via the Gulf of St. Lawrence (Head and Sameoto 2007, Head and Pepin 2010). The eastern gulf euphausiid abundances, which had been highest during summer and fall, saw a decrease in summer abundances during the 1990s and 2000s such that the seasonal abundance peak shifted to later in the year (Head and Pepin 2009).

Despite increasing and decreasing trends for some species abundances over time, other zooplankton populations appear to have remained stable. For example, based on long term CPR data available for the eastern Gulf of Maine (1961-2006), no discernable changes in the abundance of the acid-sensitive taxa *Limacina* spp. have been noted. These predatory sea snails have been monitored to assess changes in pH. Head and Pepin (2010) suggest that the abundances documented to date should be regarded as baselines against which effects of ocean acidification can be judged in future.

9.1.4 Ichthyoplankton: Ichthyoplankton is composed of fish eggs and larvae in various stages of development (Figure 9.11). These stages of fish development cannot actively move by themselves and typically float in the water column, drifting with the currents for a period of several weeks to months until they have hatched and yolk sacks have been absorbed. At this point, the developing fish begin to become actively mobile and forage for prey. Larval fish are very dependent on phytoplankton and zooplankton for food during their early life history. If a larval cod hatches too early or in a region that is low in food concentration, it will starve within several days of yolk sac absorption. Environmental conditions that affect the timing and magnitude of the spring bloom and the subsequent zooplankton production have the ability to strengthen or weaken whole year class recruitment success of commercially important species such as haddock. The offset of spring bloom timing by a few weeks can have a many-fold effect on recruitment of larval fish into the population (UNH 2009).

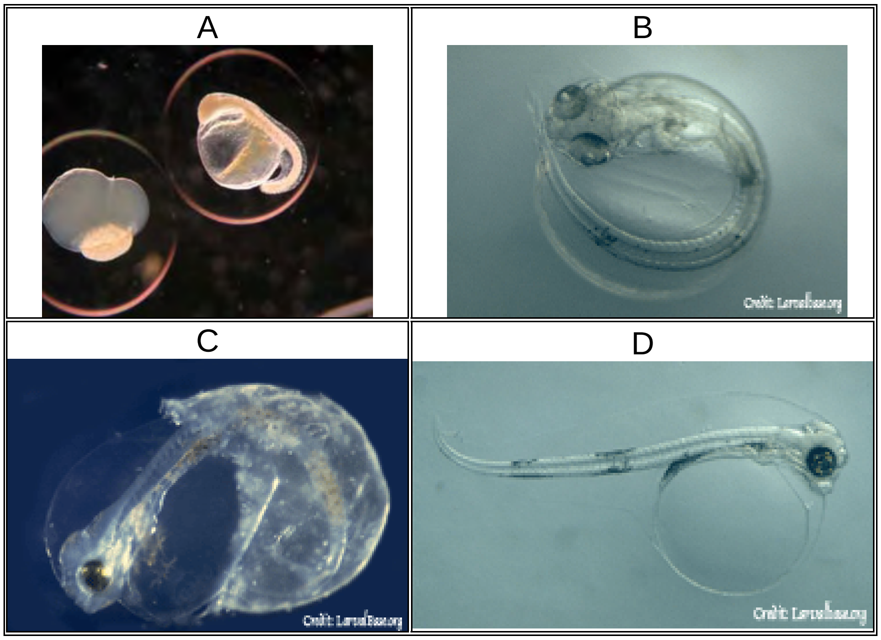

Figure 9.11: Several species of ichthyoplankton common to the Gulf of Maine: (a) American plaice eggs within early stages of embryonic development; (b) Atlantic cod egg in a late stage of development just before hatching; (c) Atlantic cod larva in the act of hatching; and (d) newly hatched Atlantic cod larva with yolk sac still attached.
Source: UNH (2009).

The eggs of some fish species start out on the ocean bottom. For example, herring spawn from June through November in the Gulf of Maine. The eggs are adhesive and stick to the substrate; however, within a period of two weeks the 4 mm to 6 mm larvae emerge to spend several months in the water column as ichthyoplankton before metamorphosing into juvenile herring at 60 mm (TRAC 2006, DFO 2007a). The eggs of other species are pelagic and begin their lives drifting through the ocean. Eggs of fish species such as cod and haddock have been noted to drift 2-7 km day^{-1} in the clockwise gyre around Georges Bank (Lough et al. 1989).

Data obtained through ichthyoplankton surveys better represent several species of economic (e.g. Atlantic herring and Atlantic mackerel) and ecological importance (e.g. sand lance and Gulf Stream flounder) than do fish trawl surveys because they estimate long term trends in species abundance and estimate the short term abundance of spawning biomass for species for which other reliable abundance indices are unavailable. These surveys also provide information on the entire finfish biomass with the exception of a few species that do not have pelagic eggs or larvae (NOAA 1988). Ichthyoplankton surveys can also be used as indication of adult fish activity. For example, plankton surveys conducted between 1979 and 1984 show that finfish spawning was at a minimum level during November through March, increased during April to July and then declined again in August to October. Spatially, peak egg production varies. Although Georges Bank exhibited some of the highest egg densities on the northeast U.S. continental shelf during the survey period, the Gulf of Maine, as a whole, consistently produced the fewest eggs (NOAA 1988).

Recent modeling of ichthyoplankton dispersal in coastal areas of the Gulf of Maine shows that dispersal of early planktonic life stages of fish and invertebrate species is highly dependent on the regional dynamics and its variability. It appears that although factors such as tidal forcing and current variability do not change the general pattern of connectivity between spawning locations and the nursery areas to which eggs tend to drift in the western Gulf of Maine, they do tend to increase within-site retention (Huret et al. 2007).

Huret et al. (2007) have noted that there is a high potential for cod larvae arising from spawning grounds in the western Gulf of Maine coastal areas to be exported along currents out of the sub-region to the Nantucket Sound and Shoals or beyond and to Georges Bank. It is unknown whether surviving juveniles that undergo such transport are still connected to western Gulf of Maine stocks, returning to spawn in their natal locations, or whether they become part of the new stocks to which they have drifted, and thus are lost to the reproductive pool of the western gulf (Huret et al. 2007).

Ichthyoplankton surveys of spawning intensity on Georges Bank and in the Gulf of Maine indicate that the peak period for all species of spawned eggs on the bank varied by year from early July to late August (NOAA 1988). Relative ichthyoplankton abundance is lower and more temporally varied across the Gulf of Maine proper (Figure 9.12).

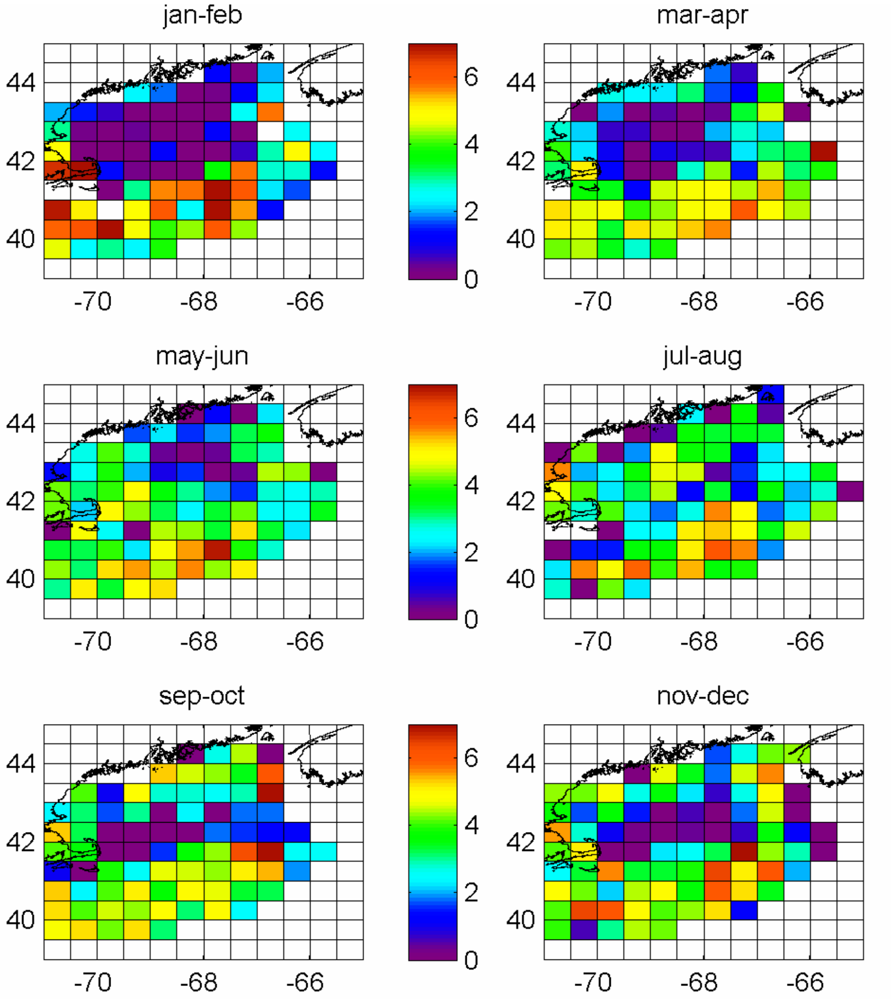

Figure 9.12: Average spatial and intra-annual temporal patterns of relative ichthyoplankton abundance in the Gulf of Maine and on Georges Bank based on NEFSC plankton monitoring sampling (1977-2007) using bongo gear.
Source: David Richardson, Northeast Fisheries Science Center, personal communication (2009).

A study of fisher's knowledge of local stocks documented several spawning locations for commercial species in the Bay of Fundy (Graham et al. 2002). The location of spawning was inferred from catches of fish releasing eggs or milt in the areas where they were caught. There were changes over time in the spawning locations; some areas were no longer used and appeared to be lost spawning grounds. The relationship of the small and relatively inshore spawning areas to offshore areas in the rest of the Gulf of Maine is not clear. However, one of the conclusions was that spawning location and time can be highly variable, even among relatively well-known commercial species.

9.2 Benthic Communities

Macrobenthos, excluding groundfish, dominate the intermediate trophic-level biomass, production and consumption in the Gulf of Maine, and therefore have significant influence over the energy flow through the system as a whole (Gaichas et al. 2009). Although we tend to focus on the fish within a system that are of commercial and dietary significance to us, and because they are important in supporting the top trophic levels of the ecosystem, it is the macrobenthos such as sea grasses, starfish and shellfish that transfer the greatest proportion of energy through the system. This section will provide an overview of three trophic levels of the benthic community, but will focus on the intermediate level that has such great influence on the ecosystem. Benthic communities are further categorized as epifauna and infauna. Epifauna are those organisms that live *on* the sea floor, while infuana are those that live *within* the mud and other substrates of the sea floor.

Animal communities may also be categorized as vertebrates (with a backbone) and invertebrates (without a backbone). There are some 1410 species of invertebrates making up approximately 60% of the known marine species of plants and animals within the Gulf of Maine. Many invertebrates are part of the infauna community. Two orders of Polychaetes (a class of worm), along with one order of Hydroida and one Amphipoda (an order of crustacean), dominate the species richness of documented invertebrates within the gulf (Census of Marine Life 2009). In terms of mean biomass distribution, molluscs and echinoderms (such as sea urchins and starfish) are dominant in sand and sand-silt habitats, while the dominants in gravel are molluscs, and in silt-clays echinoderms are the dominant species (GOMC 2004). The distribution of a number of invertebrate species in the Canadian portion of the gulf has been mapped (Tremblay et al. 2007).

9.2.1 Macrophytes: There have been 271 species of macrophytes identified in the Gulf of Maine (Census of Marine Life 2009). These are marine algae that are large enough to be seen with the naked eye. They may be free floating, grow fully below the water surface, or only be rooted in the water and grow primarily above the surface. Although many types of macrophytes are subtidal, most live in coastal areas, not the area of focus for this ecosystem overview. Important coastal species include eelgrasses (*Zostera* spp.), brown algae (*Fucus* spp.), and the commercially important Irish moss (*Chrondrus crispus*). Although most macrophytes within the Gulf of Maine grow in relatively shallow water, some species can be found in shallow offshore bank areas, and more deeply along the outer coastal shelf. Kelps, a brown algae found in the Gulf of Maine, can be found attached to rocks from the lower intertidal zone to about 40 m depth if the water is very clear. The most common species in this region are sugar kelp (*Laminaria saccharina*), oarweed, edible kelp (*Alaria esculenta*) and shotgun kelp (*Agarum clathratum*). The precise distribution and abundance of kelp beds in the Gulf of Maine are poorly known. In general, kelps require clear, cold water and a firm substrate for attachment (Tyrrell 2005). The extreme lower littoral and sublittoral zones of the Bay of Fundy are dominated by the kelps *Laminaria digitata*, *Laminaria longicruris*, *Alaria esculenta* and *Agarum cribrosum* (Prouse et al. 1983).

Three depth zones of algal dominance are apparent in the Gulf of Maine consisting of leathery macrophytes (to 40 m), foliose red algae (to 50 m) and crustose algae (to 63 m). The three zone structure of algal morphologies observed in the Gulf of Maine appears to be a global phenomenon (Vadas and Steneck 1988). Representing the third group, *Peyssonnelia* spp. and *Leptophytum laeve* were the deepest occurring algae with fleshy organisms (to 55 m) and calcareous crusts (to 63 m), respectively. The occurrence of these algae at record depths for the Gulf of Maine and for cold water marine environments may be the result of an absence of large herbivores and the high productivity potential of the benthos in these relatively clear waters.

9.2.2 Invertebrates: Infaunal communities: Gulf of Maine infauna is composed of those species that live *within* the bottom substrates of the gulf, typically buried in the mud. Those that cannot be seen with the naked eye are referred to as meiofauna. The meiofauna are a source of food for many macroinfauna, as well as other organisms that live on the surface of the ocean substrates (epifauna). Studies have shown that the bacteria associated with sediments are essential food for many infaunal species (Tunnicliffe and Risk 1977). The habitat requirements and trophic importance of these meiofauna are not fully understood (GOMC 2004). The larger organisms are referred to as macroinfauna (typically up to about 0.5 mm) and mesofauna. This last group includes organisms such as some marine worms and bivalves.

Relatively common infaunal invertebrate bivalves in the Gulf of Maine include the American cupped oyster (*Crassostrea virginica*), Atlantic razor clam (*Ensis directus*), Atlantic surf clam (*Spisula solidissima*), European flat oyster (*Ostrea edulis*), Iceland scallop (*Chlamys islandica*), northern quahog (*Mercenaria mercenaria*), Ocean quahog (*Arctica islandica*), sand gaper (softshell clam, *Mya arenaria*) and Stimpson's surf clam (*Spisula polynyma*) (Heymans 2001).

Substrates made up of clay, silt and sand provide suitable habitat for infauna, while hard surfaces provide little habitat for infauna that burrow into the substrate, except where sediment has accumulated in cracks and under rocks and boulders (Davis and Browne 1996a). The bottom habitat type and primary productivity in the overlying water are key factors influencing the biomass and abundance of the benthic macrofauna and meiofauna (GOMC 2004). In gravel and sand bottom areas of the Gulf of Maine, infauna abundance is dominated by annelids and arthropods, while molluscs become more dominant in the softer (sand-silt and silt-clay) bottoms. Annelids, the segmented worms, represent a greater portion of the biomass in sand-silt and silt-clay habitats. All of these groups consist mostly of organisms that feed passively on particles transported by currents or deposited on sediments. However, other trophic groups such as predators and scavengers do exist, and actively search for their food (Wildish 1983).

Over 200 infaunal species have been identified in the lower Bay of Fundy alone (Peer et al. 1980). There, the deposit-feeding polychaete worms have the widest distribution, followed by crustaceans and molluscs (Wildish and Peer 1983). Infaunal monitoring studies done on Georges Bank demonstrated that there was a strong relationship between faunal composition and both sediment type and water depth (Maciolek-Blake et al. 1985). There is a strong correlation between benthic invertebrate (including infauna) production and fish feeding (Collie and Curran 1985), which is an indication of the significance of this group of organisms in supporting higher trophic levels within the Gulf of Maine food web.

9.2.3 Invertebrates: Key commercial species: Important commercial invertebrate species within the Gulf of Maine include large crustaceans like the American lobster (*Homarus americanus*) and large crabs such as the Atlantic rock crab (*Cancer irroratus*), Jonah crab (*Cancer borealis*) and red crab (*Geryon quinquedens*), as well as a number of shellfish such as American sea scallop (*Placopecten magellanicus*) and blue mussel (*Mytilus edulis*). The biomass of large crustaceans within the gulf has been estimated at approximately 5.5 g wet weight m^{-2} (Heymans 2001). The American lobster and the rock crab are among the most common and abundant macroinvertebrates in coastal zones of the Gulf of Maine (Palma et al. 1998). Although the bivalve sea scallop is also a significant commercial species in the gulf, the lobster fishery is the most lucrative coastal fishery in the Gulf of Maine, now comprising more than 80% of total commercial landings of all species of fish and shellfish in the state of Maine (Xue et al. 2008), and a significant component of the global lobster (*Homarus* sp.) catch (Pezzack et al. 2006). This commercial significance also leads to it being one of the most studied species of commercial benthic invertebrate.

The spawning and early post-settlement preferences of lobster and rock crab are on substrates of cobble and coarse sand (Palma et al. 1998, Wahle 2006). These are areas that tend to be quite shallow and exposed to significant water movement, and therefore are predominantly found in shallow coastal areas of the Gulf of Maine. However, there are areas where greater depths are either approached or used in some portions of the life cycles of these animals.

Lobster: Although American lobster (*Homarus americanus*) is fished primarily in the shallower waters of the coastal shelf, lobsters can be found in deeper waters beyond the inner shelf (Fogarty 1995). Various physical oceanographic properties of the deeper water areas of the Gulf of Maine further influence this key commercial species. As this report is focused on the offshore features of the Gulf of Maine, our discussion regarding lobster will focus primarily on those areas.

Lobsters are located across the Gulf of Maine, including on the Atlantic side of Georges Bank. That lobster population seems to be genetically separate from a relatively homogenous more northern population, and is part of a relatively heterogeneous number of populations centered on the Gulf of Maine (Kenchington et al. 2009). Genetically, the similarity that does exist within the Gulf of Maine may be in part due to the manual relocation of individuals associated with the commercial catch and propagation (Harding et al. 1997).

The lobster populations in the Gulf of Maine have become viewed as a metapopulation, meaning that there are a number of sub-populations linked in various ways by movements of larvae and adults (Fogarty and Botsford 2007). The full number and distribution of these sub-populations remain unknown (Lawton et al. 2001, Pezzack et al. 2006, Robichaud and Pezzack 2007).

To grow, lobsters must shed their shell, a process called molting. Very young lobsters molt three to four times a year, increasing 50% in weight and 15% in length with each molt. Larger lobsters molt less often, with a 1.4 kg (3 lb) lobster molting every two to three years. The largest lobster ever reported in the Gulf of Maine was 20 kg (44 lb), estimated to be 40 to 65 years old (D. Robichaud, pers. comm. 2009). At an estimated 104 mm carapace length, Bay of Fundy lobsters have the largest 50% size of maturity across the entire range of the lobster (not just within the Gulf of Maine) due to the colder waters that they experience within the Bay (Waddy and Aiken 1995).

Most lobsters in the Gulf of Maine make seasonal migrations, moving to shallower waters in summer and deeper waters in winter. Typically across the Atlantic region these movements amount to a few kilometres for most lobsters. However, in the Bay of Fundy, Gulf of Maine and offshore regions of New England, lobsters can undertake long-distance migrations of tens to hundreds of kilometres (DFO 2007d). Tagging studies have also shown that at least some of these lobsters return to the same areas each year (Campbell and Stasko 1985, 1986; Campbell 1986, 1990; Robichaud and Lawton 1997). Temperature-dependent, seasonal deep-shallow migration may explain both the local returns and the long-distance migrations of mature lobsters in the Bay of Fundy and the Gulf of Maine (Campbell and Stasko 1986).

Commercial lobster fishing began during the mid 1800s and annual lobster landings in the Gulf of Maine were first recorded in 1892 (Williamson 1992). Lobster landings in the State of Maine averaged 5000 tonnes per year during the period 1897-1945 (Figure 9.13) and 9110 tonne per year during 1946-1986. Over the following two decades, Maine lobster landings tripled (Figure 9.13). In the Bay of Fundy, landings remained relatively constant, averaging ~680 tonnes seasonally for the 40 years from 1946-1986. However, during the 1980s the increase in landings observed in Maine and over most of the range of lobsters in the western Atlantic was observed in the Bay of Fundy. During the 2006-2007 Bay of Fundy season landings reached 3997 tonnes. During the last five years (2003-2008), landings have levelled off at a historically high plateau. Lobster Fishing Area (LFA) 34, off Southwest Nova Scotia, includes the mouth of the Bay of Fundy, offshore to the eastern edge of Jordan Basin and the Northeast Channel and onto the western edge of the Scotian Shelf. This area recently had the highest landings of any LFA in Canada, accounting for 40% of Canadian landings and 23% of the world landings of *Homarus* sp. (Pezzack et al. 2006). As shown in Figure 9.13, recent landings have been well above historic means.

Two studies of lobster have been maintained since the early 1990s, forming a 16-year+ time series of observations of recruitment and spawning area use in the Bay of Fundy and New England states (Figure 9.14). The settlement densities of new lobster at study sites along the New England states have typically ranged between 1 to 2 lobster/0.25 m^2 (Wahle et al. 2004, Wahle 2006). Northeastern Maine has historically received a relatively poor supply of settlers when compared to western Maine. The predominant direction of larval movement follows the cyclonic Gulf of Maine Coastal Current. Modelling suggests that larvae originating around Grand Manan Island at the mouth of the Bay of Fundy contribute fewer post-larvae to the eastern Maine coast than to the western Maine coast. In years when the eastern branch of the MCC turns offshore over Jordan Basin, the model predicts more lobster larvae will accumulate just downstream of the branch point (Xue et al. 2008).

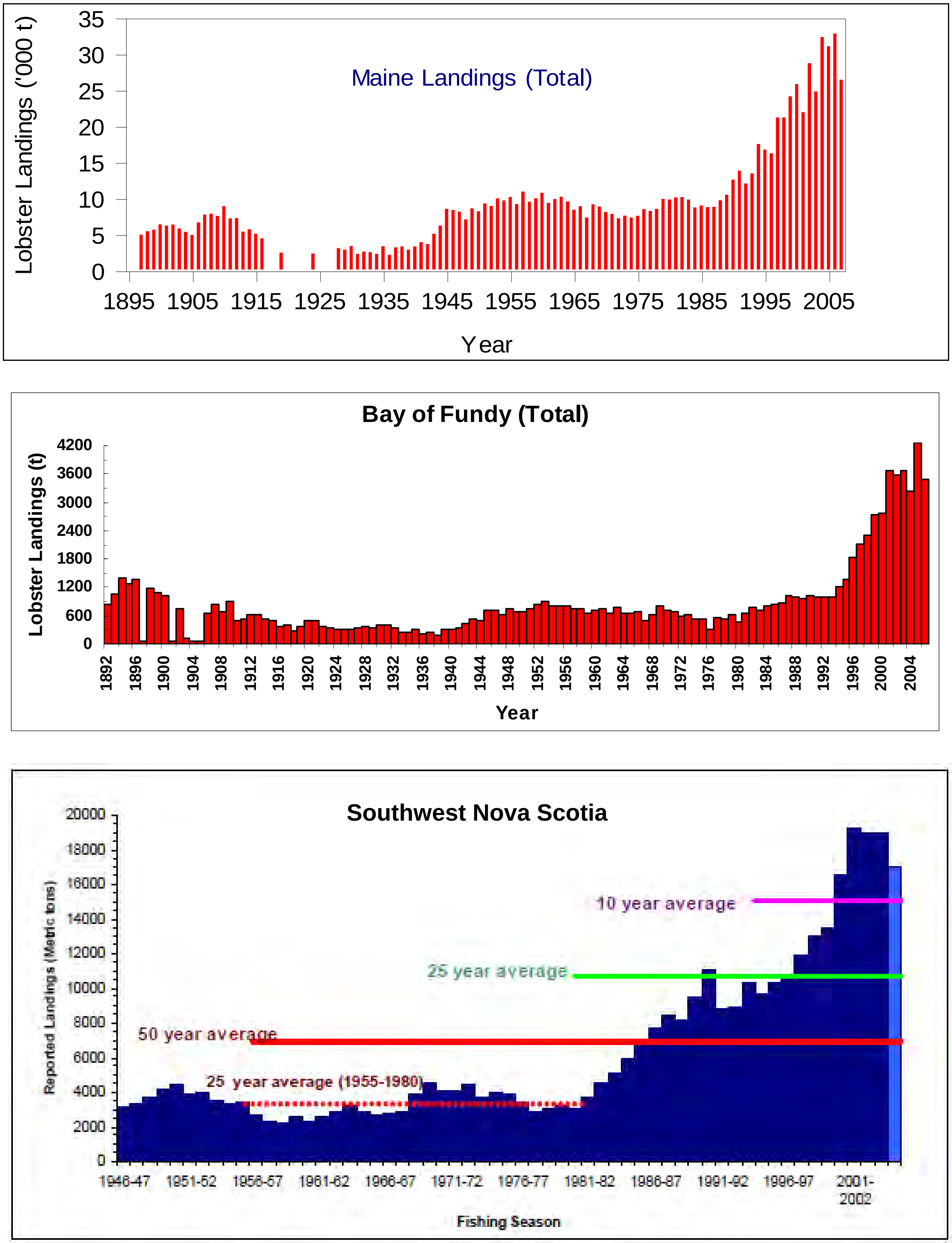

Figure 9.13: Yearly lobster landings in tonnes (t) for the State of Maine, the Bay of Fundy, and Southwest Nova Scotia document the observed increase that occurred over much of the western Atlantic since the 1980s.
Source: D. Robichaud (2009), DFO Science lobster landing information and Northeast Fisheries Science Center, Pezzack et al. (2006).

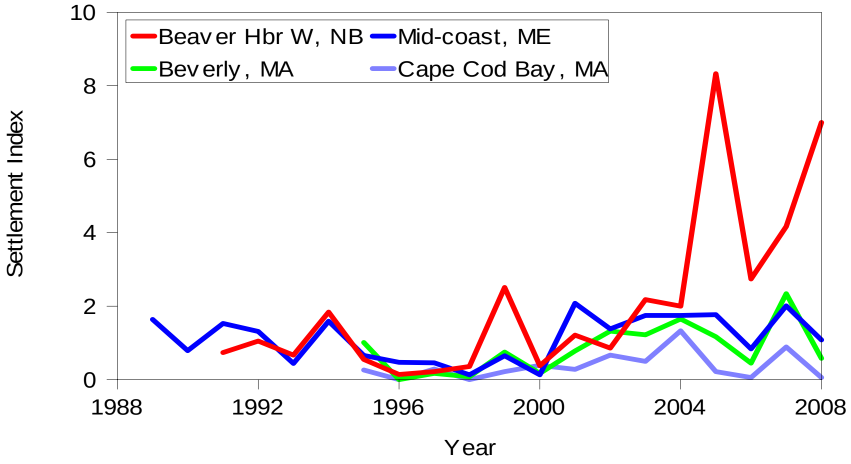

Figure 9.14: Patterns of lobster settlement in the longest running monitoring sites in the Gulf of Maine and Bay of Fundy.
Source: Rick Wahle, Darling Marine Centre, personal communication (2009).

Although there are obvious large-scale variances in various lobster population dynamics observed in the Bay of Fundy, some generalizations can be made. Since 1992, pre-recruit abundance (one-year prior to the fishery) has been high. As well, at-sea sampling and dive surveys indicate that berried females are generally more abundant from the late 1990s to the present, compared with the 1980s and early 1990s (DFO 2007d).

In distinct contrast to the restricted movements of coastal stocks of lobsters, those inhabiting the outer continental shelf undertake extensive seasonal migrations. The distribution of lobster from tagging studies demonstrated shoal-ward migration in spring and summer and a return to the edge of the shelf in autumn and winter. There is generally little evidence for return movement to the nearshore following offshore dispersal (Pezzack et al. 2009). Deep-sea lobsters have a faster rate of growth than coastal lobsters; growth increments at molting and the frequency of molting are greater (Cooper and Uzman 1971). Female lobsters found offshore in the Gulf of Maine and from Georges Bank have been shown to mature at a larger size than those from the middle and southern New England continental shelf. This development lag appears to be temperature related, but the mechanism of how temperature affects their development is not clear (Little and Watson 2005). In the Canadian offshore areas of Georges Bank, Georges Basin and Crowell Basin, the size structure of the lobster population has remained stable except for an apparent decrease in median size in Crowell Basin. Abundance indicators for these areas suggest lobster abundance has been either stable or has trended higher since 1999 (Pezzack et al. 2009).

Within the Gulf of Maine there are offshore lobster hatching sites in water up to 224 m deep. It is estimated that these larval lobster can be suspended in the water column for up to 38 days and are transported as much as 180 km. This offshore reproduction may be linked to inshore recruitment (Incze and Naimie 2001). Through modelling, areas off Cape Cod, Massachusetts, and off Penobscot Bay, ME appear the most likely sources of lobster larvae observed on Georges Bank, but coastal Maine or even Georges Bank itself could be the source (Harding et al. 2005).

Surveys for lobster larvae in offshore waters of the northeastern Gulf of Maine in the mid to late 1980s confirm that local hatching occurs mainly at depths <100 m over the banks, including

Georges Bank. Detailed studies in the vicinity of Georges Bank in late July indicated that early development stages of larval lobster were located primarily in the waters on top of the bank, whereas later development stages were collected both over and off the bank. At times, stage IV lobsters (those that are large enough to begin settling on the bottom) were more abundant off the bank than over it. The condition of these late-stage larval lobsters was better than the condition of those found over Georges Bank. This indicates a possible physiological advantage to being off the bank (Harding et al. 2005).

Other Commercial Benthic Invertebrates: Sea scallops (*Placopecten magellanicus*), ocean quahog (*Arctica islandica*) and Atlantic surfclams (*Spisula solidissima*) are fished both offshore on Georges Bank and in other areas within the Gulf of Maine. The macrobenthos biomass that includes these species is considerably higher per unit area on Georges Bank than in the rest of the gulf (Heymans 2001). Sediment type, tidal current speed, turbulent mixing and food availability appear to be major influencing factors on megabenthos distribution in the 55-105 m depth range offshore on Georges Bank. Total biomass and total density are consistently dominated by a small number of organisms. Three commercial bivalve species (surf clams, ocean quahog and scallops) made up to 71% of total sampled biomass (Thouzeau et al. 1991).

Scallops are concentrated in persistent, geographically discrete aggregates or “beds”. Within the Bay of Fundy such beds are primarily found offshore. Scallops in different beds, and in different areas of large beds, show different growth rates and meat yields, the cause and consequence of which are not well understood. Unlike many commercial scallop species, the sea scallop has separate sexes. Spawning begins in late August to early September, and the larvae drift in the water for almost a month before settling to the bottom in October (Tremblay et al. 1994). Scallops prefer a sandy, gravel bottom (DFO 2008b), part of the reason they are found in significant numbers on the northeast peak of Georges Bank (see Section 4.2 – Central Shelf Bathymetry and Seascapes). Sea scallops typically occur at depths ranging from 18-110 m, but they may also occur in waters as shallow as 2 m along the coast, and some deep water beds have been found in the Gulf of Maine down to 180 m (NOAA 1999). In Canadian coastal areas, the German Bank, Lurcher shoals, and the lower Bay of Fundy have scallop beds (DFO 1997b, Davis and Browne 1996b). Although there are offshore concentrations of scallops within the Bay of Fundy, there appears to be few scallops southwest of Grand Manan (DFO 2007e).

Georges Bank has recently supported the world’s largest natural sea scallop resource (Marino and Stokesbury 2005); however, in the past scallops have also been estimated to constitute only 0.1% of the total biomass on the bank (Backus and Bourne 1987). Recent studies appear to indicate that such offshore scallop populations may be distinct from inshore populations. Based on a 1996-2007 data set of the Lurcher Shoal in the eastern Gulf of Maine, scallops within 30 km of the shore appeared to be from a separate population than offshore scallops. The notion of limited spatial exchange is consistent with an earlier study that noted that although there is some transport of larvae within the Bay of Fundy most scallop larvae either remained in, or were returned to, the area of major spawning (Tremblay and Sinclair 1986). Additionally, a second study also indicated no large-scale exchange between Georges Bank and the Scotian Shelf occurred (Tremblay and Sinclair 1992). However, there is the potential for exchange among major scallop aggregations on Georges Bank (Tremblay et al. 1994).

With the 1994 establishment of three fishery closure areas on the U.S. side of Georges Bank, the sea scallop biomass in those areas increased dramatically (Figure 9.15). During 1994-2005, the biomass of sea scallops in the U.S. sector of Georges Bank increased by a factor of about 18. These increases were primarily due to the area closures. Biomass in the Georges Bank closed areas was 25 times higher in 2005 than in 1994, and the 2005 level constituted over 80% of the biomass in the U.S. portion of Georges Bank (Hart and Rago 2006). Higher sea star mean densities have also been found in the closed areas, and the higher concentration of sea scallops may be drawing an aggregation of sea stars that prey on the scallops (Marino and Stokesbury 2005). Sea star predation is not unique to scallops but also impacts other commercial bivalve species such as oysters and mussels (Barkhouse et al. 2007).

Landings of sea scallops from Georges Bank and the Gulf of Maine have undergone a classic boom-bust pattern (NOAA 1999, see Figure 9.16). Landings from Georges Bank are currently at an historic high while those from elsewhere in the Gulf of Maine are among the lowest on record. The Canadian commercial catch rates of the scallop wetfish fleet on Georges Bank reached historically high levels during 2000 to 2002, declined to near average levels between 2003 and 2006, and in 2007 were the third highest in the 1981-2007 time series. Freezer trawler scallop catch rates increased dramatically between 2006 and 2007 and were at the highest level since those vessels began fishing in 2002. Recent scientific survey catch rates on the Canadian portion of Georges Bank for pre-recruits, recruits, and commercial size scallops peaked between 1998 and 2001. All three indices were at or above their respective long-term median values in 2007 (DFO 2008b).

From 2004-2009, U.S. scallop landings on Georges Bank were above the long term mean. In 2006 they were more than three times the mean. During the same time frame U.S. catches throughout the rest of the Gulf of Maine have been well below the long term mean (1975-2009). Historically, Georges Bank was the dominant component of the U.S. sea scallop resource. Despite the strong recent landings, the Mid-Atlantic Bight has become more productive than Georges Bank, an occurrence which is unprecedented (NOAA 2010).

Since 1976, landings in the southwest Bay of Fundy have shown two large peaks: one in 1989 and a more recent one in 2003 with landings currently declining. The 1989 peak was seen throughout the Bay (DFO 2007e). There was, however, a subsequent drop in landings virtually every year from 1989 to 1996.

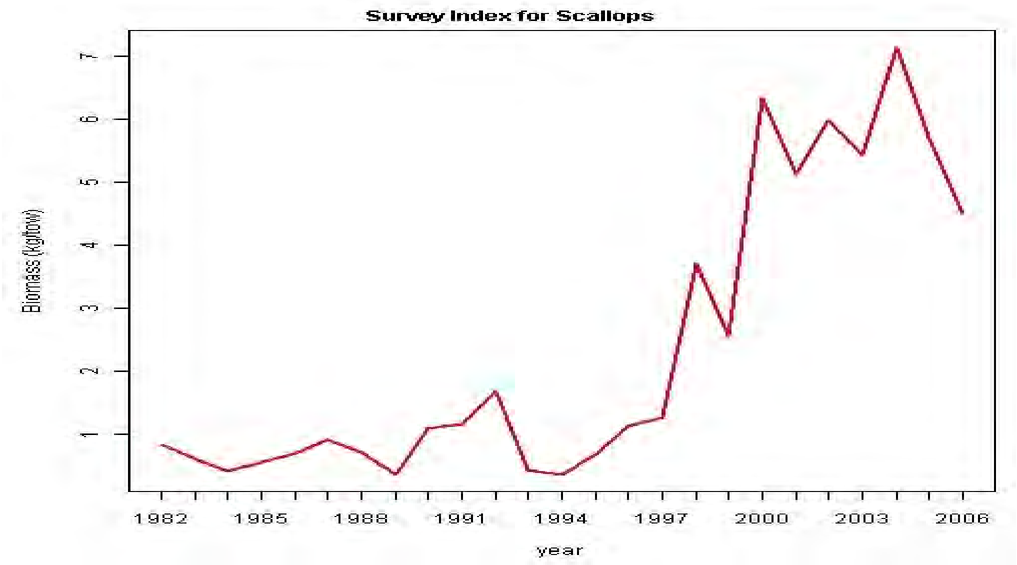

Figure 9.15: Relative biomass (kg/tow) of sea scallops on the U.S. Northeast Continental Shelf based on NEFSC research vessel dredge surveys.
Source: D. Hart, Northeast Fisheries Science Center, personal communication (2009).

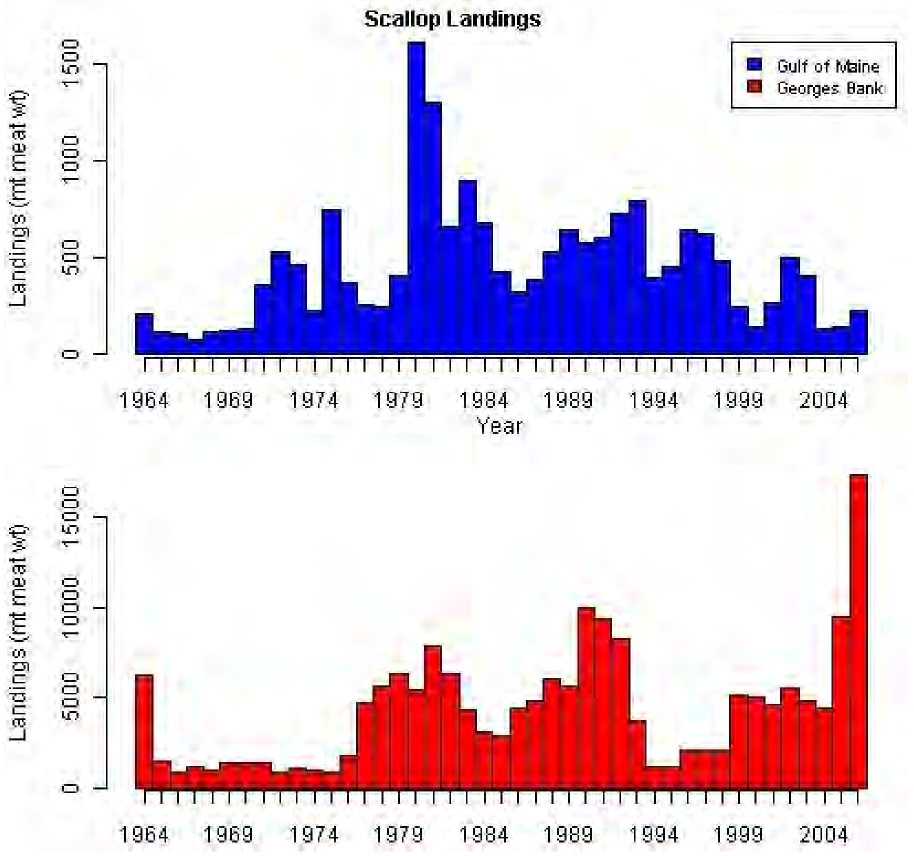

Figure 9.16: U.S. landings of sea scallops (metric tonnes meat weight) on Georges Bank and the rest of the Gulf of Maine. Landings for the gulf include coastal areas.
Source: D. Hart, Northeast Fisheries Science Center, personal communication (2009).

The softshell clam, *Mya arenaria*, has the highest landed value of Maine bivalves. It is estimated that as little as 0.01% of the larvae spawned inshore are retained long enough to set. As populations inshore are significantly harvested, this offshore flushing pattern becomes a significant reason that “only rarely, indeed, is a substantial set obtained”. If larvae do not “set” on appropriate substrate, they will not survive to populate an area. Tidal flushing moves clam larvae away from the mud flats where they are spawned (Congleton et al. 2006). Soft shell clams are predominantly harvested in the intertidal zone; but they are also found subtidally to depths of 100 m to 199 m along the Atlantic coast of the Gulf of Maine. Spawning peaks from mid to late summer, and typically only occurs once north of Cape Cod, although the clams are known to spawn twice in warmer waters to the south (Newell and Hidu 1986).

Commercial fisheries for Jonah crab, *Cancer borealis* and rock crab, *Cancer irroratus* were established during 2004 in the Bay of Fundy and much of the eastern Gulf of Maine (Robichaud and Frail 2006). Jonah crab is caught in a number of locations including Crowell Basin, Georges Basin and deeper water around the edge of Georges Bank. Abundance indicators suggest a decline has occurred in these areas between 1995 and 2009. Such a trend has not been observed in other adjacent areas of the Canadian Gulf of Maine (Pezzack et al. 2011). Although the rock crab typically inhabits a slightly wider range of water depths than the Jonah Crab, both species would inhabit the depths of the central and outer continental shelf found within the Gulf of Maine. However, substrate is also a critical component of preferred habitat for each of these species that limits distribution despite appropriate water depth. Rock crab prefer sandy or mud bottom, but are commonly found on coarse gravel or mixed rocky bottom. Jonah crab has been found on a range of substrates such as rocky areas along the coast of Maine (Krouse 1980 cited in Robichaud and Frail 2006), to silt and clay. In the Gulf of Maine, male rock crab reach a maximum of only 150 mm carapace width (CW) while female rock crab rarely reach 110 mm CW while male Jonah crab (222 mm) and female Jonah crab (150 mm) may grow considerably larger (Robichaud et al. 2000). In the Gulf of Maine, male Jonah crab can reach a maximum of 222 mm carapace width (CW) while female Jonah crab can grow to 150 mm, in contrast female rock crab rarely reach 110 mm CW while male rock crab can reach a maximum of only 150 mm (Robichaud et al. 2000).

9.2.4 Invertebrates: Non-commercial epifaunal communities: Epifauna are those organisms living on the sea floor. Current velocities are an important factor for epifauna distribution, typically promoting high abundances of deposit feeders in areas with low current velocities and positive deposition, and supporting high abundances of suspension feeders in areas of higher current velocities where deposition and erosion are low or absent (Wildish and Peer 1983).

On Georges Bank, sediment type was found to have significant effect on species diversity, total abundance and total biomass. Thouzeau et al. (1991) found that maximum megafaunal richness was found in biogenic bottoms (those in which marine invertebrates contributed to the formation of the habitat), while minimum richness was observed in underwater sand dunes. They found six megafaunal associations related to two major assemblages (biogenic sand-shell and sand-gravel fauna). The typical fauna of the sand-shell assemblage extends over most of the southern half of Georges Bank from 75-90 m depths. *Arctica islandica* and *Echinarachnius parma* are the leading species of this assemblage, while *Actinothoe gracillima*, *Epizoanthus incrustatus*, *Pagurus* *arcuatus*, *Spisula solidissima*, *Clymenella torquata*, *Aphrodite hastata*, *Dentalium entale*, *Phascolion strombi* and *Cerebratulus* spp. are other typical components (Thouzeau et al. 1991).

The biogenic sand-gravel assemblage is the second major megafaunal grouping identified on Georges Bank. Adapted to this bottom type are an abundance of suspension-feeding organisms that stay in one place (i.e. barnacles - *Balanus hamen*, tunicates, poriferans, epifaunal bivalves and tube-dwelling polychaete worms). A number of species are exclusive to the biogenic substrate, such as *Ophiura sarsi*, *Chlamys islandica*, *Hiatella arcfica*, *Natica clausa*, *Margarites costahs*, *Calliostoma occldentale*, *Halocynthia pyriformis*, *Pandalus montagui* and *Lebbeus groenlandicus* (Thouzeau et al. 1991).

On eastern Georges Bank, a total of 140 species of mega-invertebrates representing 10 phyla have been identified. Some 76% are part of the epibenthic taxa, or organisms living on the surface of the sea floor. Molluscs, crustaceans, annelids and echinoderms were best represented, with bivalves ranking first in abundance (55%) and biomass (86%). Dominance of suspension feeders among Georges Bank megafauna (70% of total density; 89% of total biomass) reflects Georges Bank having virtually the highest annual total primary production on the U.S. northwest Atlantic shelf (Thouzeau et al. 1991).

Although there is an abundance of epifauna on Georges Bank, all taxa identified by Thouzeau et al. (1991) showed sharp decreases in density and biomass below 100 m; therefore, it might be expected that their distribution throughout the Gulf of Maine area considered within this report is limited to areas such as the coastal shelf and Georges Bank.

Like Georges Bank, in the coastal shelf area in the southwestern region of the Bay of Fundy, especially in the Quoddy-Western Isles area, substrates play an important role in the epifauna community. Hard substrates of bedrock, boulders, gravels and shell predominate in the upper part of the sublittoral zone and exert a strong influence on the composition of epifaunal communities. The high tidal range and associated strong currents in this area result in relatively clear waters most of the year and the hard bottoms support a very abundant and diverse epibiota. In shallow water, where sufficient light reaches the sea floor, encrusting coralline algae colonize exposed rock surfaces, together with occasional stands of fleshy algae (seaweeds); but with increasing depth this plant-dominated community is gradually replaced with an animal-dominated community as light is reduced.

The recognition of distinctive sublittoral hard substrate communities in the Quoddy region is based mainly on studies in the Deer Island-Campobello Island area (Noble et al. 1976; MacKay et al. 1978; Logan et al. 1983, 1984; Logan 1988; Hatfield et al. 1992; Singh et al. 1999; Ginn et al. 2000). Three epifaunal communities are generally recognized and include the encrusting algae-urchins community, the lampshell (*Terebratulina septentrionalis*) community and the sea anemone (*Tubularia-Tealia feline*) and bivalve (*Modiolus modiolus*) community. However, only the latter community has the ability to be widespread in the deeper waters of the Gulf of Maine away from the coastal shelf (i.e. >100 m) (see Table 9.2).

In most parts of the Quoddy region, hard substrates are replaced by finer sediments below about 30 m. However, the bottom of the deep, narrow, ravine-like Eastern Channel in Head Harbour

Table 9.2: Zonal scheme for sublittoral hard substrate epibenthic communities in the Deer Island-Campobello Island area, southwestern New Brunswick, Bay of Fundy.

Zone/ subzone	Depth range (m)	Type of hard substrate	Community	Key biota
Circa-littoral	30-140 m	All rock surfaces, coarse gravels, shell beds	*Tubularia-Tealia Felina-Modiolus modiolus* community	*Tubularia* spp.,*Tealia felina*, *Modiolus modiolus*, sponges, hydroids, molluscs, arthropods, echinoderms, tunicates, some brachiopods

Source: adapted from Logan (1988).

Passage, between Deer Island and Campobello Island, is scoured free of fine sediments by strong tidal currents and has substrates of coarse gravel and shells covering bedrock down to depths of just over 140 m (Logan 1988). Below 30 m depth there is a highly diverse and abundant faunal community of sponges, hydroids, anemones, polychaetes, brachiopods, molluscs, arthropods, echinoderms and tunicates present down to a depth range of ~140 m. This biota, mainly suspension feeders, is dominated in terms of abundance by tubularian and campanularian hydroids, the anemone *Tealia felina* and the bivalve *Modiolus modiolus* (see Figure 9.17). Attached to the latter species is the colonial tunicate *Didemnum albidum* (Hatfield et al. 1992). The brachiopod *T. septentrionalis* and the sea urchin *Strongylocentrotus droebachiensis* show a gradual reduction in abundance with increasing depth, as do stalked tunicates, while tubularian and campanularian hydroids, anemones and mussels increase in abundance. However, where substrate stability is attained at patches of coarse gravels, the typical *T. septentrionalis* community is found. Similar isolated occurrences of this lamp shell community have been reported by Kostylev et al. (2001) from immobile gravels at depths of 90-120 m on Browns Bank at the southeast corner of the Gulf of Maine.

In certain parts of the Bay of Fundy, dense concentrations of horse mussels (*M. modiolus*) form large reefs. They play an important role in pelagic-benthic coupling, consuming phytoplankton and excreting nutrients used by the plankton (Wildish and Fader 1998). The biodiversity of these reefs has not been studied in detail; however, in other parts of the world many different species are associated with horse mussel reefs (Holt et al. 1998, Lindenbaum et al. 2008).

Although several species of crab, small fish and marine worms will feed on various life stages of the softshell clam (Newell and Hidu 1986), the aquatic invasive green crab, a relative newcomer to the Gulf of Maine, is thought to be a major predator of shellfish from newly settled juveniles to adults (Congleton et al. 2006). However, their preference for habitats within shallow water (<10 m) limits their impact on shellfish of the central and outer shelf areas of the Gulf of Maine. Tagging and recapture studies of the invasive green crab estimated a population of 10 000 crabs per acre in coastal areas of southern Maine in 1953. More recent studies vary in their estimation of green crab abundance to being similar or less than these early study results. These crabs are presently being harvested in southwest Nova Scotia and used as bait in the lobster fishery. During the autumn/winter of 2003/2004, fishermen in eastern Maine reported moderate to numerous live crabs in their traps in the autumn, but numerous dead green crabs in their spring hauls after a

Figure 9.17: Abundant anemones (*Tealia felina*) and sponges on living and dead shells of horse mussels (*Modiolus modiolus*) and gravels at 95 m, Head Harbour Passage, southwestern Bay of Fundy. Although this community is typically found in more shallow water, given appropriate stable substrates it has been documented to depths of over 140 m off the edge of the coastal shelf in the Gulf of Maine.
Source: A. Logan, personal communication (2008).

particularly severe winter with an average water temperature of 2.81°C. These water temperatures were one of the lowest winter temperatures in 60 years. It is suggested that these temperatures were approximately the critical limit to create winterkill of the green crab, which has been expanding its northward range (Congleton et al. 2006).

Another invertebrate living on the surface of the sea floor is the corals. There have been 14 species of coral identified in the Gulf of Maine. Two or three species of soft corals exist off the southwest coast of New Brunswick in the Bay of Fundy. Others exist around the Gulf of Maine, particularly in the deep basins such as Jordan Basin and the Northeast Channel (DFO 2006g, Mortensen et al. 2006). Cup corals (*Flabellum* spp.) are found in soft sediments in the basins of the Gulf of Maine.

The Northeast Channel is an area identified as having significant concentrations of octocorals within the Gulf of Maine (Figure 9.18), and a portion of the channel was designated in 2002 as the Northeast Channel Coral Conservation Area. This area has the highest known density of large octocorals *Primnoa resedaeformis* (seacorn) and *Paragorgia arborea* (bubblegum coral) in Atlantic Canada. Both are found in deep waters (see Table 9.3) (DFO 2006g). These gorgonian corals are more abundant on the western side of the Northeast Channel, presumably due to a combination of favourable environmental factors, including higher concentration of food particles in circulating water. Concentrations of cold water coral species are also found at the edge of the continental shelf (Figure 9.18).

Table 9.3: Taxon, abundance (colonies/100 m^2) and depth range for deep water coral in the Northeast Channel of the Gulf of Maine.

Order	Taxon	Specimens	Abundance	Depth
Gorgonacea	*Acanthogorgia armata*	212	0.5	231–364 m
	Paragorgia arborea	322	0.6	235–498 m
	Primnoa resedaeformis	2 663	4.8	196–498 m

Source: Mortensen et al. (2006).

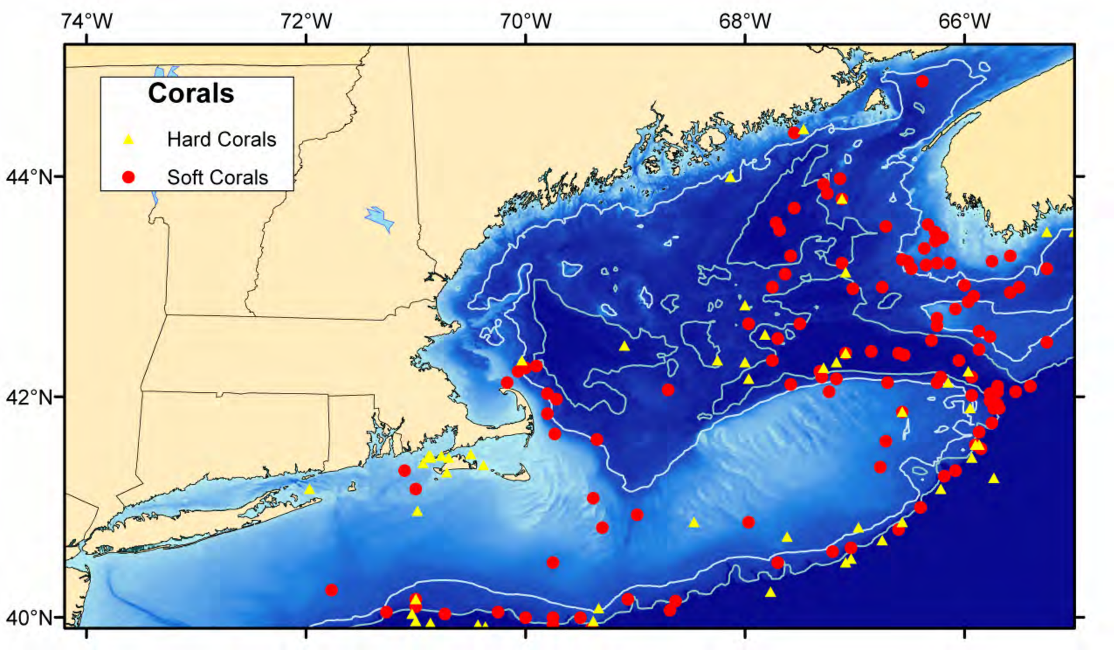

Figure 9.18: Distribution of hard and soft coral species in the Gulf of Maine, Scotian Shelf and Georges Bank based on NEFSC dredge samples.

Source: D. Packer, Northeast Fisheries Science Center, personal communication (2009).

In a study of corals off Nova Scotia, the highest abundance of corals were characterized by a depth greater than 400 m, a maximum water temperature less than 9.2°C, and a relatively high percentage coverage of cobble and boulders. High temperatures probably control the upper depth limit of the corals (Mortensen et al. 2006). The height of *Paragorgia arborea* colonies observed range from as small as 5 cm to as tall as 180 cm, greater than that of *Primnoa resedaeformis* colonies. The height of *P. arborea* colonies was positively correlated to the size of the boulders to which they were attached. Based on calculated growth rates, the largest *P. resedaeformis* colony observed was about 61 years old, while the largest *P. arborea* colony was between 45 and 180 years old (Mortensen et al. 2006).

Deep-water corals provide a variety of habitats for other organisms. The *Paragorgia arborea* and *Primnoa resedaeformis* colonies located in the Northeast Channel of the Gulf of Maine host a rich associated fauna dominated by suspension feeders that use the coral colonies as a substrate on which to fasten themselves or as a refuge against predators. One hundred and fourteen invertebrate species were recently found associated with the corals, including a new genus and species of a gall-forming parasitic copepod (*Gorgonophilus canadensis*) that was discovered on specimens of *Paragorgia arborea* collected in the Northeast Channel. The most frequently occurring associated community of species in the Northeast Channel included an unidentified encrusting white sponge, and three anemones (*Bolocera tudiae*, *Actinauge verrilli* and an unidentified species). In the Northeast Channel, redfish were almost four times more common in video sequences with corals than in sequences with boulders but no corals (Metaxas and Davis 2005, Mortensen et al. 2006).

9.2.5 Groundfish: Key commercial and non-commercial species: This section presents two approaches to identifying groundfish communities within the Gulf of Maine. An overview of a few of the key commercial groundfish species within these communities is then provided. There are 652 species of fish that have been listed in the *Gulf of Maine Register of Marine Species*, including those found on the slope and the southern part of Georges Bank. Benthic fish communities that live on or near the bottom of the ocean are typically referred to as groundfish if they are commercially harvested or (generically) as demersal fish. These fish fall primarily under three taxonomic orders in the Gulf of Maine. Two of those, the Gadiformes (cods, burbot, hake, pollock and rocklings) and Pleuronectiformes (flatfish such as flounder, halibut, plaice and sole), constitute the majority of commercially valuable groundfish. Scorpaeniformes, which include fish such as sculpins and ling cod, are part of the benthic community but are not as commercially valuable. Together these three orders of benthic fish account for approximately 31% of all 120 fish species found in the Bay of Fundy (Census of Marine Life 2009). The gadids in the bay consists of 11 species of cod, burbot, hake and rockling.

Recently, an assessment was conducted of biomass surveys that had been carried out separately on the Canadian and U.S. portions of the Gulf of Maine. Assessment of the time-series (>35 yrs) of 19 representative fish species collected during 7 different surveys showed that some species, such as Atlantic cod, Atlantic herring, haddock, thorny skate, and goosefish, had comparable trends across the gulf regardless of survey location. Conversely, species such as longhorn sculpin and spiny dogfish showed differing survey trends and event timing, suggesting that their population dynamics differ spatially across the Gulf of Maine (Nye et al. 2010). Population trends for economically important and non-harvested groundfish species for the Bay of Fundy, Georges Bank and the rest of the Gulf of Maine, based on standardized research vessel surveys conducted by the Department of Fisheries and Oceans Canada and the Northeast Fisheries Science Center are shown in Figure 9.19.

Groundfish Communities: A recent study based on a 35-year time series of data (1968-2002) of a 24-species assemblage of groundfish for the Gulf of Maine found that fish distribute according to habitat parameters of depth and temperature, rather than according to substrate type in both autumn and spring (Methratta and Link 2007). The results further indicate that four separate demersal “communities” exist within the Gulf of Maine, as shown in Table 9.4.

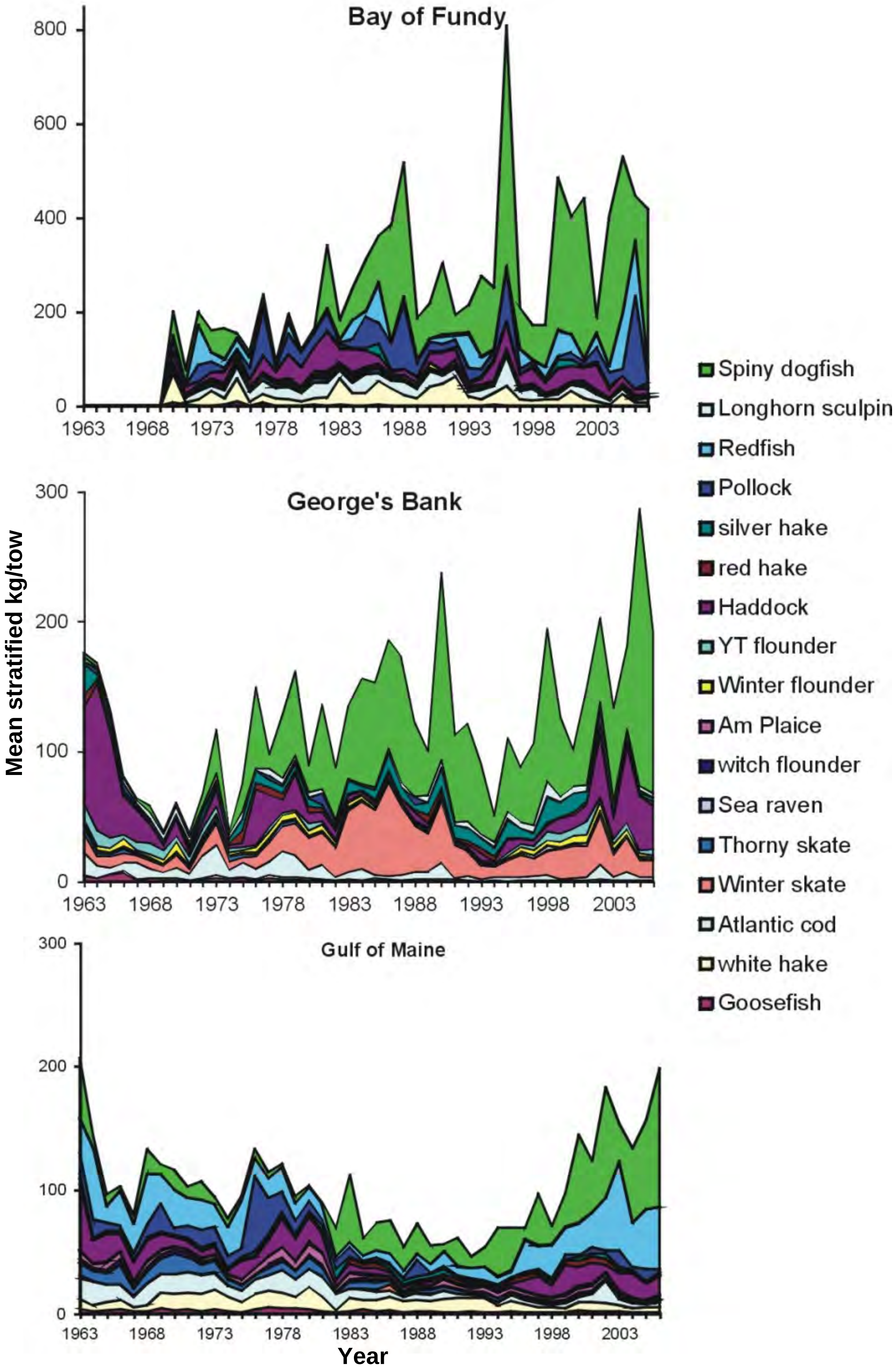

Figure 9.19: Population trends (mean stratified kg/tow) for fish species based on research vessel surveys conducted by the Department of Fisheries and Oceans Canada in summer and the Northeast Fisheries Science Center in autumn. Gulf of Maine and Georges Bank are based on U.S. surveys, and the Bay of Fundy based on Canadian surveys.

Source: J. Nye, Northeast Fisheries Science Center, personal communication (2009).

Table 9.4: Four “community” groups have been identified from a 35-year time series study of 24 demersal fish species within the Gulf of Maine. These groupings indicate a seasonal preference for temperature and depth over substrate type.

	Seasonal habitat keys	**Demersal species**
Community 1	➢ **Remained in relatively deep waters** in both autumn and spring. ➢ Experienced the relatively **cooler** portion of the region in the autumn and the relatively **warmer** portion of the region in the spring.	White hake, silver hake, Acadian redfish, goosefish, witch flounder, thorny skate and pollock.
Community 2	➢ **Remained in relatively shallow** habitats in both seasons. ➢ Experienced **wide temperature fluctuations**.	Winter flounder, yellowtail flounder, winter skate, little skate, windowpane, longhorn sculpin and sea raven.
Community 3	➢ Moved from **shallow areas in the autumn to deep areas in the spring**. ➢ Maintained relatively **warm waters**.	Spiny dogfish, summer flounder, fourspot flounder, barndoor skate and red hake.
Community 4	➢ Travelled from the **deep portion of the region in the autumn to the shallow portion of the region in the spring**. ➢ Maintained relatively **cool waters**.	Atlantic cod, haddock, American plaice and ocean pout.

Source: adapted from Methratta and Link (2007).

The four communities of Gulf of Maine demersal fish can be described based on their seasonal preference for temperature and depth. First, some species remained in relatively deep waters in both autumn and spring. By remaining in relatively deep habitats in both seasons, the species in this group experienced the relatively cooler portion of the region in the autumn and the relatively warmer portion of the region in the spring. Second, there were some species that remained in relatively shallow habitats in both seasons. Species that remained in relatively shallow waters in both seasons also experienced wide temperature fluctuations on a seasonal basis, with warmer temperatures in the autumn and cooler temperatures in the spring. A representative species from this group, winter flounder (*Pseudopleuronectes americanus*), was most abundant in coastal southern New England and the northern portion of Georges Bank, where it experienced temperatures primarily between 7°C and 17°C in the autumn and between 3°C and 8°C in the spring. Third, some species moved from relatively warm shallow areas in the autumn to relatively warm deep areas in the spring. Spiny dogfish (*Squalus acanthias*), for example, was most abundant in the northern portion of the region during the autumn and the more southerly portions of the region during the spring, migrating to maintain a surrounding temperature primarily between 4°C and 17°C. Fourth, some species travelled from relatively cool deep portions of the region in the autumn to relatively cool shallow portions of the range in the spring. As a representative of this group, Atlantic cod (*Gadus morhua*) was more abundant around Cape Cod and in the Gulf of Maine during the autumn and on Georges Bank during the spring, where it experienced a temperature range of 3°C to 15°C. Although Atlantic cod occupied some of the coolest temperatures in the region during the autumn, these temperatures were still warmer overall than those experienced by this species in spring due to warmer overall temperatures in the autumn compared to spring (Methratta and Link 2007).

A second approach to identifying demersal fish communities across the North Atlantic relied more on depth alone to establish assemblages. As shown in Table 9.5, Mahon et al. (1998) identified five assemblages of demersal fish that exist in the Gulf of Maine based on data from between 1975 and 1994. The assemblages were derived from the 108 most abundant demersal species in the North Atlantic and were based, in part, on the depth of water in which they were found. None of these five assemblages were unique to the Gulf of Maine. However, the gulf did appear to be the northern extent for two assemblages (southern deepwater and southern bank/slope). Similarly, the Gulf of Maine appears to be the southern extent for two other assemblages (temperate deepwater and north temperate bank/slope). Figure 9.20 shows the long-term distribution of individual species representing the temperate deepwater and southern bank/slope assemblages both in and around the Gulf of Maine. Only one assemblage, the south-temperate bank/slope assemblage found in waters <200 m deep, extended both north and south of the Gulf of Maine (Mahon et al. 1998). Others have noted that the generally cool waters of the Gulf of Maine and Georges Bank predominantly support a temperate and cold water fish community, but that immediately to the south of the Gulf of Maine, the Mid-Atlantic Bight is dominated by subtropical and temperate species (Fogarty and Trollan 2006). Therefore, the southern Gulf of Maine could be described as a boundary between subtropical and cold-water communities, and is within the heart of the temperate fish community. Being the spatial boundary for several assemblages is a reflection of the diversity of habitat and water conditions found in the Gulf of Maine. It is also arguably an indicator that a small shift in circulation and associated water conditions could preclude the future presence of one or more assemblages within the gulf.

Through an assessment of the available data (a multivariate analysis process called principal components analysis, or PCA), it appears that only 56.3% of the changes in distribution of the species over the time series could be explained. Mahon et al. (1998) therefore suggest that the demersal fish assemblages in the Gulf of Maine should be interpreted as quite loose in nature, and as potentially adaptable entities rather than rigid ecological constructs. The assemblages that were identified (see Table 9.5) were persistent in composition through time, but appeared to shift in location (Mahon et al. 1998).

Groundfish Species: As noted, assemblages and communities of fish are likely to vary over time. Water is an extremely dynamic habitat property that, in the Gulf of Maine, can be influenced by large-scale changes such as the NAO and the size of the spring freshet from the Great Lakes and the St. Lawrence River. Water can also be influenced locally by storms and tidal circulation/mixing. So, although fish and fish assemblages undoubtedly have a preference for a particular depth, variability in other habitat parameters means that they can be expected to be spatially dynamic. Add to the spatial changes anticipated population changes due to natural predator-prey cycles and human influenced changes in population, and it is difficult to determine if an assemblage has spatially moved or simply changed in composition. Therefore, an overview of some well-studied groundfish species found within the Gulf of Maine is presented.

Pollock (*Pollachius virens*) are found in “fishable” concentrations throughout the Gulf of Maine, including Georges Bank (DFO 2006b). Pollock eggs are buoyant, floating in the water column for about seven days at 7°C before they hatch. Based on egg collection, spawning locations include areas off southwest Nova Scotia and Georges Bank. Egg release occurs earlier than is the case for haddock and, unlike cod, there is only one peak in spawning activity during December to January.

Table 9.5: Deepwater and shelf/slope fish assemblages found in the Gulf of Maine.

Depth class	Demersal fish assemblage	Boundary relevance to the Gulf of Maine	Primary assemblage species	
>200 m	Temperate deepwater	From the GoM northwards; the GoM is approximately southern in extent.	Marlin-spike Black dogfish Atlantic argentine	Longfin hake Barracudinas Roughnose grenadier
>200 m	Southern deepwater	From the GoM southwards; the GoM is approximately northern in extent.	Blackbelly rosefish Offshore hake Shortnose greeneye Shortfin squid	Buckler dory Beardfish Slatjaw cutthroat eel Armoured searobin
<200 m	North-temperate bank/slope	From Georges Bank northward; the GoM is approximately southern in extent.	Northern wolffish Spotted wolffish Atlantic sea poacher Arctic cod Greenland halibut Polar sculpin	Greenland cod Fourline snake blenny Threebeard rockling Atlantic spiny lumpsucker Atlantic hookear sculpin
<200 m	South-temperate bank/slope	Extends to both north and south of the GoM.	Red hake Goosefish (angler) Spiny dogfish Silver hake White hake Pollock Cusk Yellowtail flounder Winter flounder Ocean pout	Longhorn sculpin Winter skate Northern sand lance Atlantic hagfish Fourbeard rockling Haddock Atlantic soft pout Wrymouth Threespine stickleback Sea raven
<200 m	Southern bank/slope	From the GoM southwards; the GoM is approximately northern in extent.	Fourspot flounder Butterfish Spotted hake Fawn cusk-eel Gulf Stream flounder Summer flounder Scup Black sea bass Northern (common) searobin	Smooth dogfish Windowpane flounder Little skate Bigeye scad Rough scad Round scad Plainhead filefish Smallmouth flounder

Source: adapted from Mahon et al. (1998).

In contrast to many other species in the order Gadiformes (e.g. cods, burbot, hake and rocklings), young pollock are closely associated with nearshore habitats before moving to the offshore at around age two. Pollock spend the least amount of time on the bottom of all the cod-like fish, and show strong schooling behaviour. Similar to other groundfish species, the length and age of pollock at maturity has followed a declining trend recently (DFO 2004).

U.S. studies published in 1993 indicate that the lengths at maturity were 41.8 cm and 39.1 cm for males and females, respectively. This result contrasts with a study for the Bay of Fundy published in the 1960s that indicated that females attained maturity at 62.5 cm and males at 58 cm (DFO 2004, 2006b).

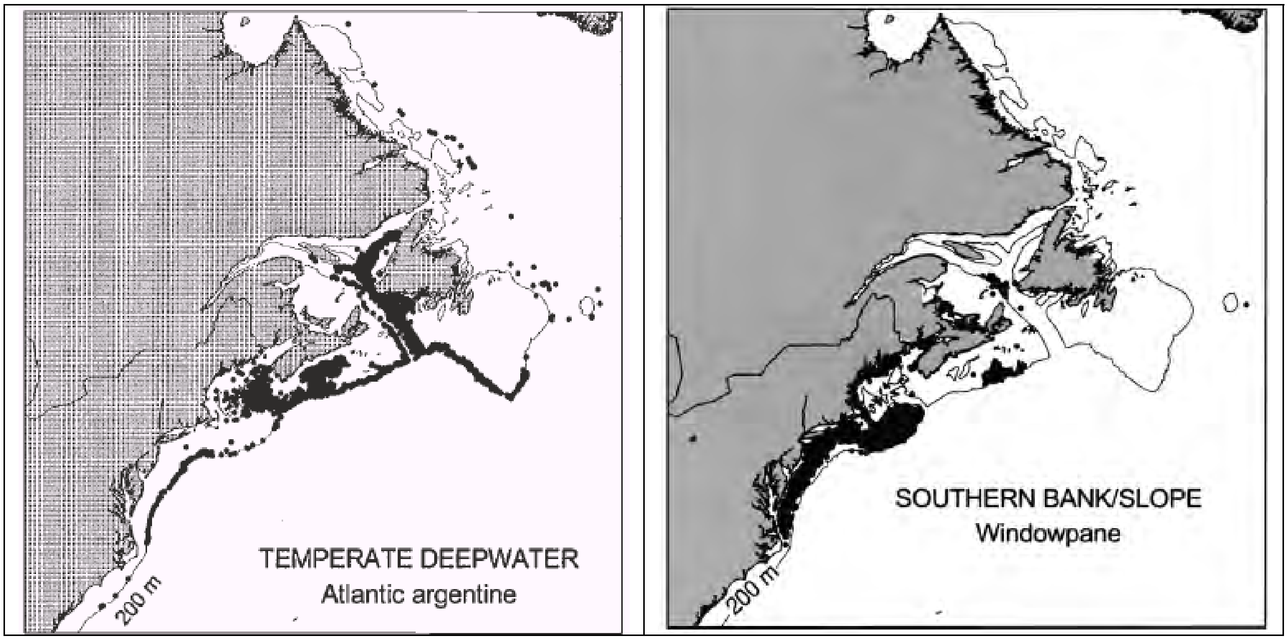

Figure 9.20: The Gulf of Maine is the approximate southern boundary for the temperate deepwater demersal fish assemblage and approximate northern extent of the southern bank/slope assemblage. The long-term distribution data for respective representative species of these two assemblages, Atlantic argentine and windowpane flounder, are shown.
Source: Mahon et al. (1998).

Pollock has been one of the key groundfish predators in the northeast U.S. continental shelf ecosystem, and has changed its targeted prey species accordingly over the last three decades to focus on the available prey at a given point in time (Tyrrell et al. 2007). Pollock's average total annual consumption rate over a 33-year timespan (1973-2005) was approximately 3.4% of the annual consumption attributed to all finfish in the Gulf of Maine and Georges Bank system (Link et al. 2006, cited in Tyrrell et al. 2007), which is similarly proportional to pollock's abundance as a fraction of total finfish biomass. Seasonally, the highest pollock biomass density in the Gulf of Maine has been recorded in December to January, a time when very dense aggregations can extend up to 30 m off bottom. These aggregations can form during night and disperse during the day. Physical bathymetric features such as "sea-mounds" seem to be a focus for pollock schools (DFO 2004, 2006b). In terms of long-term fluctuations, pollock abundance on the Northeast Shelf dramatically increased during the late 1970s and early 1980s, and then dropped during the late 1980s and early 1990s. Pollock abundance has been recovering in the last decade. Pollock population fluctuations have been synchronous with those of the larger finfish community (Tyrrell et al. 2007).

Atlantic cod (*Gadus morhua*) is a bottom-dwelling North Atlantic fish that was long a cornerstone of the commercial fishing industry. Cod are found throughout the Gulf of Maine. There are several concentrations of cod within its North Atlantic range, including those adjacent to the Gulf of Maine on the southern Scotian Shelf, and those within the Gulf of Maine in the Bay of Fundy. Seasonal movements associated with spawning occur and a number of spawning areas exist in the gulf. Cod in this area reach, on average, 53 cm by the age of three years and increase to 72 cm by the age of five, and 110 cm by the age of ten. Growth rates, however, vary, with more rapid growth noted for cod in the Bay of Fundy (DFO 2006c). On Georges Bank, the median date for spawning is mid-March (Page et al. 2001). The estimated survival to age one for fish in 2003 was 5 million, the first above-average cohort since 1990 on Georges Bank (see Figure 9.21). However, the 2002 and 2004 year classes were 1 million each, the lowest on record. The adult population biomass (ages 3+) on Georges Bank declined from an estimated 43 800 tonnes in 1990 to 8 500 tonnes in 1995. The population biomass since 1995 has fluctuated between roughly 5000 and 10 800 tonnes. In absolute numbers the population age structure displays a low proportion of ages 7+ compared to the 1980s. Productivity on eastern Georges Bank is currently poor due to the low weight of individual cod and a generally low recruit/spawner ratio (TRAC 2010a).

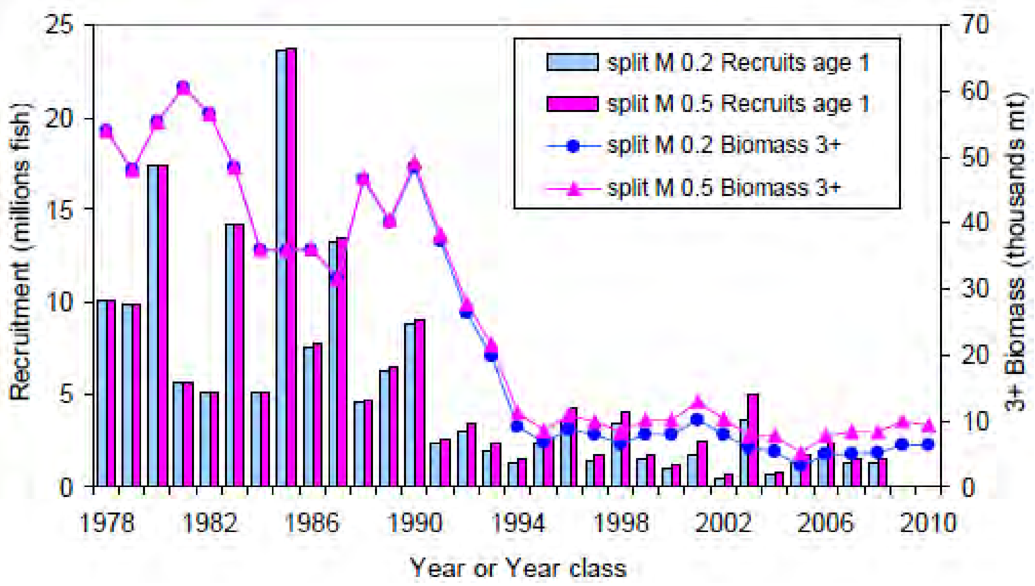

Figure 9.21: Adult cod (3+) biomass and young of the year recruitment to the age 1 class for Georges Bank, 1977-2009.
Source: TRAC (2010a).

Over a 25-year time series study (1973-1998), data collected from Cape Hatteras, North Carolina to southwestern Nova Scotia, indicated that the majority of North Atlantic cod could be found in the Gulf of Maine, Georges Bank and the Scotian Shelf regions. This indicates the historic importance of the Gulf of Maine to the entire North Atlantic cod population. Cod abundance declined across the time series, with much lower values observed during the 1990s than the 1970s. During this current period of low abundance on the U.S. continental shelf, fewer cod have been found south of the Gulf of Maine, implying an effective contraction of the distribution of cod over the past three decades (Link and Garrison 2002).

Haddock (*Melanogrammus aeglefinus*) is another commercial groundfish found on both sides of the North Atlantic. A major stock exists in the southern Scotian Shelf and Bay of Fundy area, while there are two other haddock stocks in the region; one on Georges Bank and another elsewhere in the Gulf of Maine. Although seasonal migrations are evident within the stock area, there is relatively little exchange between adjacent haddock stocks. Haddock is most common at depths of 46 m to 228 m and in bottom temperatures above 2°C. As with cod and pollock, haddock in the Bay of Fundy grow more rapidly than those in other areas of the Gulf of Maine.

Approximately 50% of female haddock are mature by the age of three; however, the number of eggs produced by a female of this age is low, but increases dramatically with age. Major local spawning grounds are found on Browns Bank just north of the Northeast Channel, and peak spawning occurs in April/May (DFO 2006d). On Georges Bank, the median date for haddock spawning is earlier, about mid-March (Page et al. 2001). Unlike the rest of the large commercial species from the order Gadiformes, overall haddock biomass on the Scotian Shelf remains fairly high. However, this is not the case in the eastern Gulf of Maine and Bay of Fundy areas where biomass is low (Clark and Perley 2006). In contrast, haddock biomass on Georges Bank is currently high (Clark et al. 2010).

Adult biomass of eastern Georges Bank haddock increased, with some fluctuation, from a near historic low of 8 500 tonnes in 1993 to an estimated 157 300 tonnes in 2009. The latter is higher than the 1931 to 1955 maximum biomass of about 90 000 tonnes. Georges Bank haddock had an exceptional 2003 survival to one-year-olds, estimated at 293 million fish, but has otherwise fluctuated without trend about an average of 9 million fish since 1990. The 2003 recruitment was the largest observed in the assessment time series (1931 to 1955 and 1969 to 2005). As the large 2003 year class passes through the population, adult biomass is expected to decline from the recent 2009 high to about 68 000 tonnes by 2012. Overall resource productivity is high, negatively affected only by recent reductions in fish weight at age. Both length and weight at age have declined since about 2000. While size at age increased in 2007 for most ages, weights remained about 40% to 50% below the average during the 1986 to 2000 period (TRAC 2007b, 2010b).

As noted previously, there are well over 100 species of benthic or demersal fish within the Gulf of Maine. Haddock, cod and pollock are only a few of the more significant commercial species. Like these three, in the early 1990s many species were very low in numbers. There have been some wild swings in abundance of a number of species since the early 1990s. Recruitment of winter flounder on Georges Bank initially improved from the mid 1990s, averaging 23.6 million fish at the age of one during 1998 to 2001, but has since declined, with the exception of the 2006 value of 62.9 million fish, which is near the highest value in the time series. Adult biomass of winter flounder (over the age of three years) increased from a low of 2 200 tonnes in 1995 to 11 400 tonnes in 2003 and then declined to 6 200 tonnes at the beginning of 2007. A truncated age structure of the winter flounder currently exists, where few older fish are found in the population. This, along with changes in distribution, indicates that current population productivity may be limited relative to historic levels (TRAC 2007c). Similarly, during recent surveys of the Canadian portion of the Gulf of Maine and Bay of Fundy, halibut were widely caught and biomass reached a record high in 2007 and remained high in 2008. The catches of Atlantic cod and argentine in the same areas were the lowest in the series (1970-2006) (Clark and Perley 2006, Clark and Emberley 2009). Yet other species of fish have exhibited opposing trends. Of 24 species of demersal fish assessed in the Gulf of Maine over a 35-year time series, spiny dogfish, fourspot flounder, summer flounder, spotted hake and barndoor skate were all relatively more abundant later in the time series (Methratta and Link 2007).

9.3 Pelagic Communities

Pelagic communities are those flora and fauna that live above the sea floor. Here we provide an overview of a few animals found in the deeper waters of the Gulf of Maine, or above the offshore

Georges Bank. Because of the trophic interactions between the benthic fish communities and the pelagic communities, changes observed in one group of fishes are often tied to the other. Whereas a significant number of commercial benthic fish have exhibited recent abundance declines, several key pelagic species have increased over their historic means. The pelagic-to-demersal biomass ratio also drives fish production and consumption patterns across systems, and pelagic fish have greater biomass, production and, particularly, consumption over demersal fish in the Gulf of Maine (Gaichas et al. 2009).

9.3.1 Pelagic Invertebrates: This section provides an overview of some of the macropelagic invertebrates within the Gulf of Maine. Although many zooplankton would technically fall within this category, our discussions here focus on the largest invertebrates, and those organisms not addressed previously in this report under Section 9.1.

Northern (pink) shrimp (*Pandalus borealis*) inhabit soft mud bottoms at depths of approximately 1 m to 300 m, most commonly in cold waters. The Gulf of Maine is the southern limit of the species' distribution in the North Atlantic. Although they spend time in the benthic mud, as much as 70% of their feeding is assumed to occur in the pelagic environment (Heymans 2001). In a recent assessment of North Atlantic Shrimp stocks, the Gulf of Maine experienced the warmest bottom temperatures (~6°) during hatching, and had the shortest egg development periods (~6 months) of all stocks assessed (Koeller et al. 2009).

Distribution sampling within the Gulf of Maine during 1965 revealed that shrimp were primarily found in the western portion of the gulf. Abundance was highest in moderate depths in the vicinity of Jeffrey's and Cashes Ledges and southeast of Mount Desert Island, Maine. It was lowest in the deeper offshore areas in the west-central part of the gulf. Shrimp were present year round at these locations and at two isolated localities southeast of Nova Scotia (Haynes and Wigley 1969). However, abundance in the eastern Gulf of Maine is relatively low, and there is no evidence of a relationship between the Gulf of Maine population and populations on the Scotian Shelf (Clark et al. 2000). Distribution based on catches during DFO groundfish surveys (1970-84) and exploratory catches (1965-70, 1992-93) includes moderate numbers within the outer Bay of Fundy (Koeller 2000). Haynes and Wigley (1969) initially suggested that the distribution of Northern shrimp within the Gulf of Maine depended primarily on the type of bottom sediment and its organic content, rather than on temperature or salinity range. More recent study seems to indicate temperature as being a significant influencing factor on seasonal movements of the northern shrimp within the gulf (Clark et al. 2000). It is the only stock in which egg-bearing females are known to migrate during winter from offshore waters into shallow, colder nearshore water. It is suggested that this migration may be a behavioral adaptation to warm bottom water temperatures that delays egg development and brings hatching closer to the spring bloom (Koeller et al. 2009). The stock of northern shrimp in the Gulf of Maine collapsed during the late 1970s (Figure 9.22). After a moderate recovery, average shrimp biomass varied between 15-20 thousand tonnes during 1984 to 1997 before undergoing another decline and subsequent recovery starting around 2000 (Clark et al. 2000).

In the Gulf of Maine, shrimp spawning begins in offshore waters in late July (Clark et al. 2000). In August and September, egg-bearing females move from the offshore areas towards the inshore and estuary areas (Haynes and Wigley 1969). After shrimp larvae hatch, spent females immediately

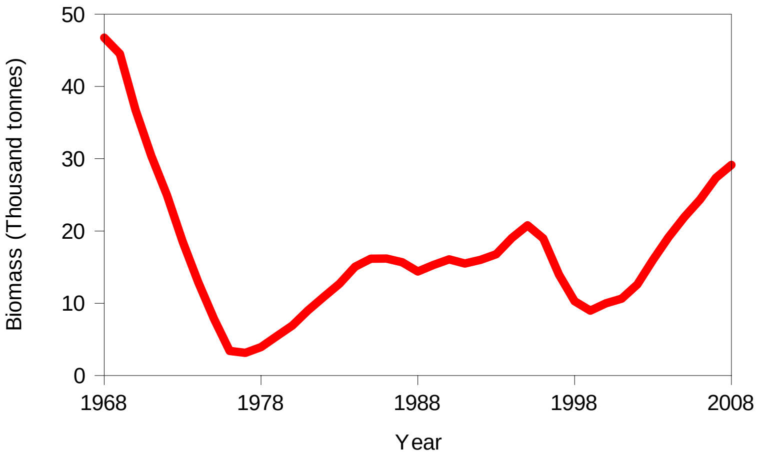

Figure 9.22: Estimated biomass of northern shrimp in the Gulf of Maine based on surplus production model analysis. **Source:** Data from Atlantic States Marine Fisheries Commission (2009).

move back offshore in February to April. Juveniles move to deeper water after about one year. As shown in Figure 9.23, maturation, spawning and transition from male to female form all take place offshore in deeper waters of the Gulf of Maine (Clark et al. 2000). Haynes and Wigley (1969) reported that the growth rate of shrimp aged two and older was greater in the Gulf of Maine than had been reported for any other population of this species to date. Most groundfish feed on crustaceans at some point in their life history, and shrimp are often identified as an important component of their diet. Although the influence of predation appears to have increased more recently, water temperature likely explains more of the variation in shrimp abundance within the Gulf of Maine than does predator abundance (Koeller 2000).

Squid are an important member of the pelagic invertebrate community within the Gulf of Maine. Two species are common in the gulf. The longfin inshore squid (*Loligo paeleii*) is managed as one stock from Georges Banks to Cape Hatteras, and the highly migratory northern shortfin squid (*Illex illecebrosus*) is considered a unit stock from Cape Hatteras to Newfoundland. The biomass of the longfin squid stock was approximately 42 000 tonnes in 1999, an amount thought to be similar to the 1977-1986 estimated average. A biomass measurement of northern shortfin squid could not be established (Heymans 2001). These species are a significant part of the food chain, being preyed on by birds, fish and cetaceans.

On Georges Bank, squid has been a particularly important prey of bluefish and fourspot flounder. Consumption of shortfin and longfin squid by 12 predator fish species across the northeastern U.S. shelf averaged 24 000 tonnes and 46 000 tonnes respectively during 1977 to 1997 (Overholtz et al. 2000). It appears that consumption of longfin squid by piscivores increased during the period, and may have approached or exceeded the estimated maximum sustainable yield (Overholtz et al. 2000). Squid themselves feed intensively on small fish such as cod or capelin, shrimp and/or other squid for most of their life (NOAA 2000).

Over the period of 1963 to 1974, virtually all commercially important finfish species in the Gulf of Maine showed a marked decline in abundance. At the same time, both longfin and shortfin squid showed significant increases. Shortfin squid appeared more abundant across the entire gulf, and both species were more abundant around Georges Bank (Clark and Brown 1977). Seasonally,

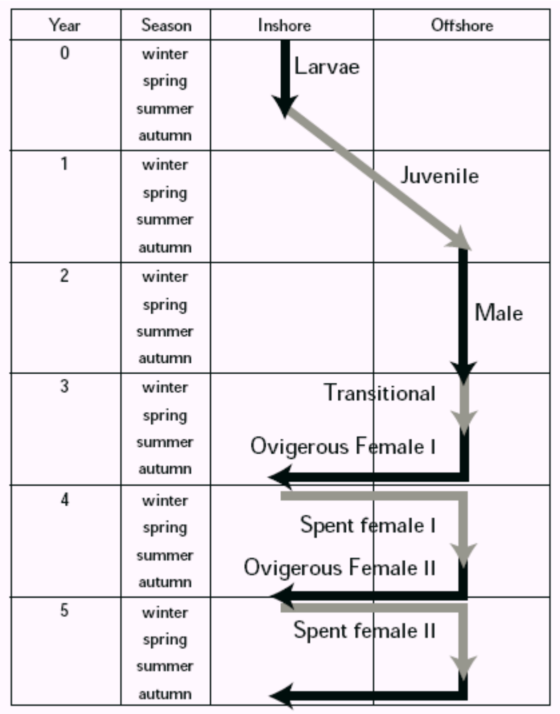

Figure 9.23: Significant periods of time and life-cycle development of the northern shrimp occur offshore in the Gulf of Maine. These shrimp begin life as males before transitioning into females at age three.
Source: Shumway et al. (1985), as cited in Clark et al. (2000).

shortfin squid are not found during the spring on Georges Bank, but become widely distributed throughout the gulf in the autumn. Some spawning is thought to take place on Georges Bank (Azarovitz and Grosslein 1987). During the period of 1977-1997, both squids were generally more abundant during the late 1970s and early 1980s, but did not fluctuate to any great degree during the entire period (Overholtz et al. 2000).

Longfin squid males within the Gulf of Maine are typically a little larger than females. Although the majority of male longfin squid live to about two years of age, it appears likely that only a few will live to three years, and that females rarely reach 20 months of age. At two years of age, females sampled in the gulf tended to be about 27 cm in length and males approximately 32 cm (mean dorsal mantle length) (Summers 1971).

Certainly, a large number of other pelagic invertebrates are found within the Gulf of Maine, and several are important as prey to fish communities. A recurring pulse of echinoderm (star fish and sea urchins), barnacle larvae, and krill is observed during the spring and summer in the Bay of Fundy, and occasionally a pulse of jellies and free-swimming tunicates may be seen (DFO 2006a). Jellyfish are a pelagic invertebrate that is often classed as a gelatinous zooplankton (discussed further in Section 9.1.3). During the 2008 summer research vessel surveys of the Bay of Fundy and Canadian Gulf of Maine, the most frequently captured invertebrates were the shrimp (*Pandalus montagui*), short-fin squid, and sponges, while sea cucumbers, shortfin squid, American lobster, and Northern shriimp (*Pandalus borealis*) contributed most to the weight of the invertebrate catch (Clark and Emberley 2009).

9.3.2 Marine turtles: Two sea turtle species, loggerhead (*Caretta caretta*) and leatherback (*Dermochelys coriacea*) are documented as regularly occurring in the Gulf of Maine (Census of Marine Life 2009). However, Kemp's ridley (*Lepidochelys kempii*) and the green sea turtle (*Chelonia mydas*) have also been reported around Cape Cod at the southern extent of the Gulf of Maine. All sea turtles in the Gulf of Maine are considered migrants, coming to forage or passing by in order to forage at other more northerly areas along the shelf (Shoop 1987).

There is little focused study on these marine reptiles within the Gulf of Maine; but many relevant observations have been made as part of studies focused on the southern U.S. continental shelf and the Scotian Shelf to the north. The patterns of distribution and concentration of sea turtles in forage areas of the North Atlantic differ greatly from nearly all marine mammals, suggesting that the turtles have little overlap in resource utilization with whales, dolphins and seals (Shoop and Kenney 1992). Atlantic leatherback sea turtles migrate annually from foraging grounds off eastern Canada and the northeastern U.S., including the Gulf of Maine, to southern foraging and breeding areas (Sherrill-Mix et al. 2008). Tag recoveries from 25 leatherbacks captured off Canada reveal nesting origins throughout South and Central America, and the Caribbean (James et al. 2007).

In forage grounds of the northern Gulf of Maine and on Nova Scotia's Scotian Shelf, it has been found that there is a significant female-biased sex ratio (1.86 females: 1 male) among mature leatherback turtles. It is expected that this may vary by geographic area in which foraging populations exist, reflecting breeding period, distance from nesting areas and associated migration patterns (James et al. 2007). Leatherback turtles feed almost exclusively on jellyfish while in the Gulf of Maine (Shoop 1987).

Based on visual surveys between 1998 and 2005, most leatherback sea turtles in the northern forage grounds were reported inshore from the continental shelf break and associated with mean sea surface temperatures of 16.6°C. Concentrations of leatherback turtles in Canadian waters of the Gulf of Maine have been documented near the northeastern point of Georges Bank and the eastern extent of the Northeast Channel, as well as in the Brier Island area of the mouth of the Bay of Fundy. However, data suggest that the Bay of Fundy may provide less suitable habitat for leatherbacks relative to other areas in Canadian waters, and that observer effort bias associated with a tourist whale-watching industry accounts for the higher numbers of observations made in the Bay (James et al. 2006). Leatherbacks and loggerheads can be expected on Georges Bank between May and October (Shoop 1987), and concentrations of leatherbacks are found in the central and eastern Gulf of Maine region (Shoop and Kenney 1992). It is predicted that annually 50% of the leatherbacks have departed Georges Bank by November 13 and that 95% have left a little less than a month later in mid-December (Sherrill-Mix et al. 2008).

Through aerial surveys, loggerhead densities ranged seasonally from 1.6×10^{-3} to 5.1×10^{-1} km^{-2} across the northeast U.S. shelf, and leatherbacks from 2.09×10^{-3} to 2.16×10^{-2} km^{-2} (Shoop and Kenney 1992). More recent data suggest that abundances of leatherback are likely higher than these estimates (James et al. 2006). Although there is little data available directly for the Gulf of Maine, the population of loggerhead turtles from Texas to Maine appears to have been stable throughout the 1980s (Thompson 1988).

9.3.3 Pelagic fish: Key commercial and non-commercial species: Perciformes (perch, bass, mackerel and tuna) are the most diverse order of pelagic fish found in the Bay of Fundy, with 28 species having been identified. A similar abundant representation of this order would be expected across the Gulf of Maine where 132 Perciformes have been documented (Census of Marine Life 2009). Therefore, this overview of the pelagic fish of the gulf will centre on several of these families, along with several shark species. The species discussed have great significance as prey, as a commercially targeted resource, and/or as an apex consumer within the Gulf of Maine ecosystem.

The overall pelagic (herring and mackerel) fish biomass in the Gulf of Maine has slowly risen through the time series of 1990 to 2003. A sharp rise in 2000 has been followed by steady, modest increases (see Figure 9.24). This pattern has been positively correlated to surface layer temperature, and negatively related to salinity (Kane 2007).

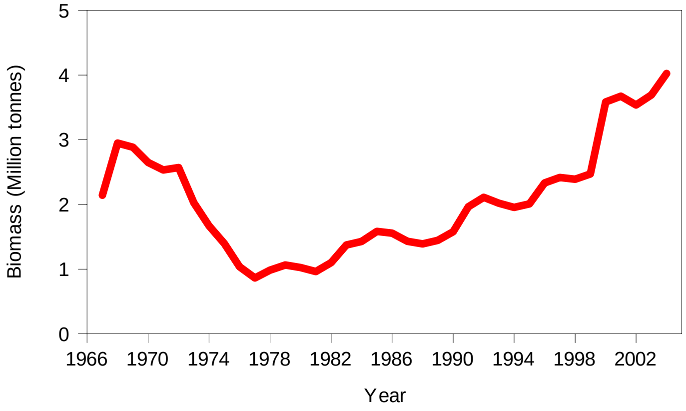

Figure 9.24: The combined total biomass (million tonnes) of Atlantic herring and mackerel in the Gulf of Maine and Georges Bank indicates the general increasing trend of pelagic fish within the ecosystem.
Source: EAP (2009).

Swordfish and Tuna: Swordfish (*Xiphias gladius*) are members of the family Xiphiidae. They can reach a maximum size in excess of 500 kg. They are distributed widely in the Atlantic Ocean and the Mediterranean Sea. Swordfish undertake extensive daily vertical migrations and feed throughout the water column on a wide variety of prey, including groundfish, pelagic fish, deep-water fish and invertebrates. Although they spawn in tropical and subtropical waters, during summer and autumn months they are found in the colder temperate waters and reside in the Gulf of Maine from April to December, primarily on the edge of Georges Bank. Like many pelagic species, North Atlantic swordfish biomass has recently improved, possibly due, in part, to strong recruitment during the late 1990s (ICCAT 2007, Figure 9.25).

There are seven tuna species from the family Scombridae found within the Gulf of Maine (Census of Marine Life 2009). Albacore, bigeye and yellowfin tunas are at the northern edge of their range in Canada, and they are found along the edge of the Gulf Stream and Georges Bank throughout the year. Yellowfin tuna (*Thunnus albacares*) is distributed mainly in the tropical and subtropical oceanic waters, with spawning and rearing occurring in tropical waters. However, it does migrate seasonally into the Gulf of Maine. Growth rates have been described as relatively slow initially, increasing when the fish leave the nursery grounds. Smaller fish (juveniles) form mixed schools with skipjack and juvenile bigeye, and are mainly limited to surface waters, while larger fish form schools in surface and sub-surface waters. Reproductive output among females has been shown to be highly variable.

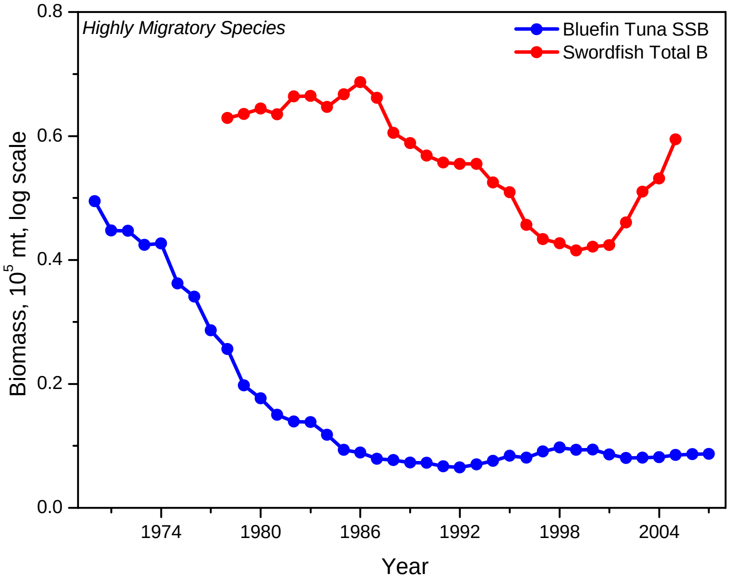

Figure 9.25: Population estimates for bluefin tuna and swordfish in the North Atlantic.
Source: EAP (2009).

Bigeye tuna (*Thunnus obesus*) are distributed throughout the Atlantic Ocean. This species swims at deeper depths than other tropical tuna species and exhibits extensive vertical movements with clear daylight time patterns when they are found much deeper than at night. Spawning and nursery phases take place in tropical waters, after which juvenile fish tend to diffuse into temperate waters as they grow larger. Bigeye tuna exhibit a relatively fast growth rate and become mature at about three years old. The Atlantic stock has stabilized in recent years (ICCAT 2007). Young bigeye tuna form schools, mostly mixed with other tunas such as yellowfin and skipjack. These schools are often associated with floatting objects and sea mounts. This association appears to weaken as bigeye grows larger (ICCAT 2007).

Albacore (*Thunnus alalunga*) is a temperate tuna widely distributed throughout the Atlantic Ocean. In the North Atlantic, the spawning stock size has declined and in 2007 was about one quarter of the peak levels estimated for the late 1940s. The most recent recruitment is estimated to be large, albeit uncertain, and over the next few years, the spawning stock is expected to decline (ICCAT 2007).

Atlantic bluefin tuna (also known as the Northern bluefin) (*Thunnus thynnus*) are a major apex predator in the Gulf of Maine ecosystem. Estimates of the bluefin tuna population in the North Atlantic indicate a steady overall decline in abundance since the 1970s and 1980s to lower values in the 1990s and 2000s (Figure 9.25). It is estimated that bluefin tuna consume 58 000 tonnes of Atlantic herring in a year across the gulf region (Overholtz 2006). The bluefin is also the largest of the tuna (see Figure 9.26) and can reach a length in excess of 4.5 m (15 feet), and a weight of 650 kg (1 400 lbs). The Northwest Atlantic bluefin stock migrates into the region and distributes throughout the waters of the Gulf of Maine during July to October. During this time bluefin tuna are actively feeding on prey fishes that probably follow temperature frontal zones in areas of high productivity (Schick et al. 2004, cited in Overholtz 2006). Research appears to indicate that two populations of Atlantic bluefin tuna overlap on the foraging grounds of the Gulf of Maine, but spawn in separate locations well removed from the Gulf of Maine in either the Gulf of Mexico or the Mediterranean Sea (Block et al. 2005).

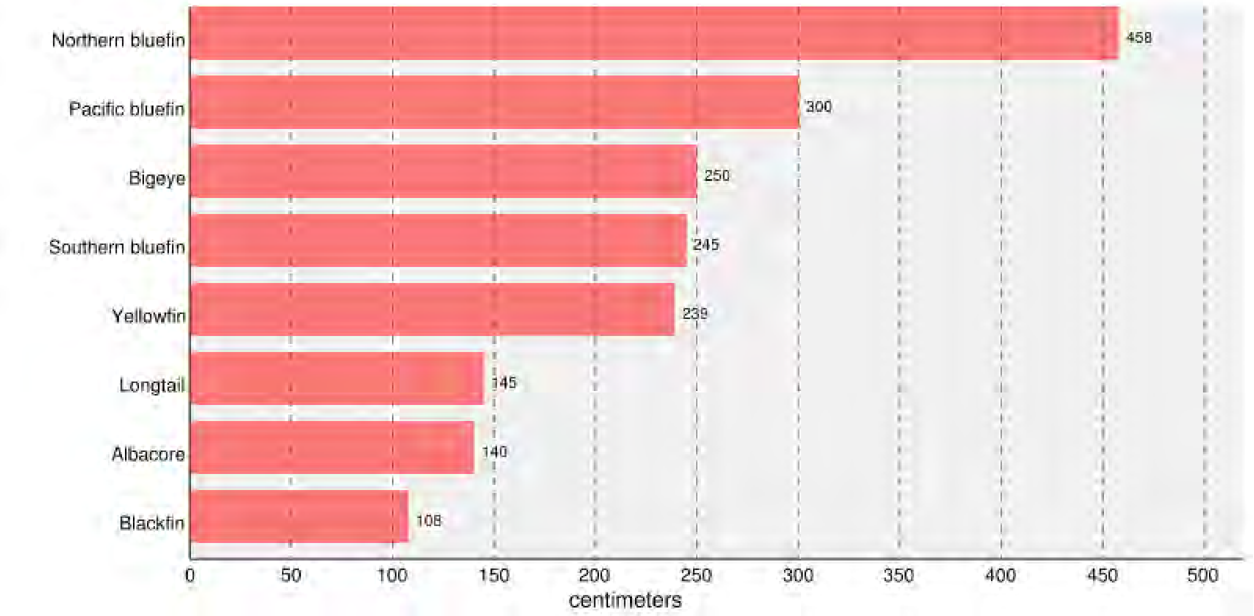

Figure 9.26: Maximum reported sizes (centimetres) of various *Thunnus* (tuna) species: All but the Pacific and longtail tunas may be found in the Gulf of Maine.
Source: public domain by Peter Halasz through Wikipedia, http://en.wikipedia.org/wiki/Tuna.

An examination of catch data from 1950 to 1999 suggests that, on average, about half of the adult Atlantic bluefin tuna stock comes to the Gulf of Maine-Georges Bank region during the summer feeding season (Overholtz 2006). Some of the stock move into the Bay of Fundy (Overholtz 2006, ICCAT 2007). However, a congregation of bluefin tends to form in the area of the Northeast Channel known as the Hell Hole, and along the northern edge of Georges Bank. The spatial presence of bluefin tuna within the Gulf of Maine was compared against environmental variables of SST, distance to a SST front, frontal density, bottom depth and slope. The relationship between bluefin tuna schools and SST fronts was inconsistent, and there was no significant correlation with any of the measured environmental features, suggesting that other untested features, such as prey density, may be important predictors of their distribution in the Gulf of Maine (Schick et al. 2004).

An assessment of fat and oil content of bluefin tuna caught in the Gulf of Maine between 1991 and 2004 indicates a decline in marketable quality, and is also reflective of a significant change in the cellular condition of these fish. Northern bluefin tuna are now arriving in the Gulf of Maine in a leaner condition, and are not increasing their fat stores while here on the feeding grounds as they did during the early 1990s, despite a long residency in the area. Herring are a primary food for tuna in the Gulf of Maine, and herring abundance is at historically high levels. However, a reduction in the energy density of herring itself is a possible reason for the observed condition decline in bluefin tuna. A coincident decline in Northern bluefin tuna and Atlantic herring condition in the

Gulf of St. Lawrence indicates that similar changes are occurring not only in the Gulf of Maine, but also in other Northwest Atlantic shelf systems (Golet et al. 2007).

Herring and Mackerel: Atlantic herring (*Clupea harengus*) is a pelagic species found on both sides of the North Atlantic. It is an important prey species within the Gulf of Maine, feeding not just a community of predator fish species, but also mammals and birds. Therefore, the herring has been considered a keystone prey species in the Gulf of Maine ecosystem (Overholtz and Link 2006). Annual consumption of Atlantic herring by four groups of predators – demersal fish, marine mammals, large pelagic fish and seabirds – averaged just 52 600 tonnes during the late 1970s, but rose to as much as 281 200 tonnes during the years of 1998 to 2002. Demersal fish consumed the largest proportion of this total, followed by marine mammals, large pelagic fish and seabirds (Overholtz and Link 2006).

In the Gulf of Maine-Bay of Fundy region, two stock complexes of herring are recognized: the Gulf of Maine/Georges Bank stock, and the Southwest Nova Scotia/Bay of Fundy stock (TRAC 2006, DFO 2007a). Although morphometric analyses suggest that discernable phenotypic differences exist among herring from the Gulf of Maine and Georges Bank, there is currently no genetic evidence to suggest that these two components are separate stocks (Overholtz 2006). The herring stock complex in the Gulf of Maine declined by ~85% between the early 1970s to mid 1980s (Overholtz 2002). However, more recent Atlantic herring spawning stock assessments in the Gulf of Maine and Georges Bank indicate historically high levels (Overholtz et al. 2004). As shown in Figure 9.27, there has more recently been a better balance across the age structure for this stock.

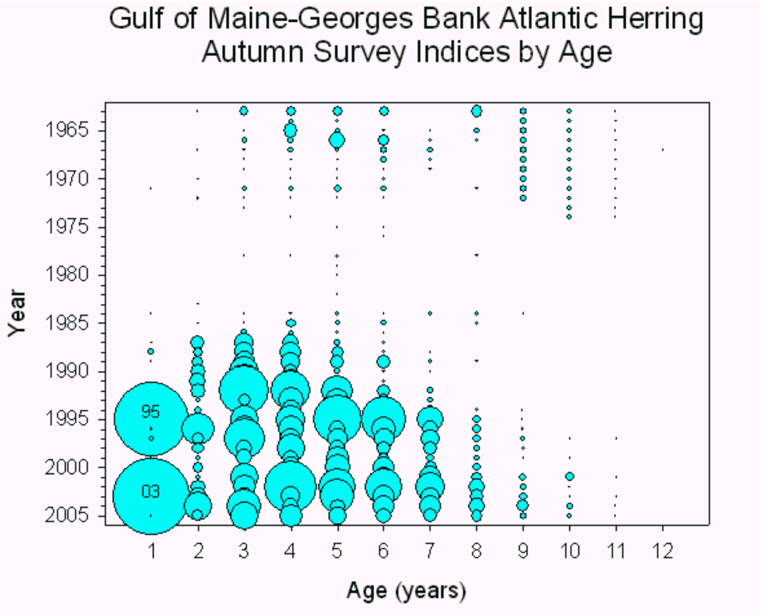

Figure 9.27: Since the herring collapse during the 1970s to 1980s, there has been a greater balance within the age structure in the Gulf of Maine-Georges Bank region. The size of the bubbles in the graph corresponds to the magnitude of the catch at age.
Source: Overholtz (2006).

Herring spawn in discrete locations from June to November in the Gulf of Maine, and they have a strong affinity to those spawning locations. Primary spawning locations off the northeastern United

States are located on the Maine coast, Jeffreys Ledge, Nantucket Shoals and Georges Bank (Overholtz 2006), while Trinity Ledge, Lurcher Shoals, German Bank, the southwest shore of Grand Manan and Scots Bay are important spawning areas within the Canadian portion of the Gulf of Maine (Reid et al.1999). The area around the Fundy Isles near the mouth of the Bay of Fundy is a major juvenile nursery area. Dense aggregations of fish are formed at summer feeding, overwintering and spawning locations. Generally, the large spawning areas are offshore, and the smaller spawning grounds more localized, sometimes very near to shore or in small embayments (TRAC 2006, DFO 2007a).

Herring migrate long distances, although some unknown portion of the Gulf of Maine-Georges Bank stock is known to overwinter in the Gulf of Maine and just south of Cape Cod. Conversely, an unknown portion of the Gulf of Maine-Georges Bank stock is known to move northward into the Bay of Fundy/Southwest Nova Scotia during the summer for feeding. In the U.S., the Gulf of Maine stock complex was reported to be healthy in 2005 (see Figure 9.28), especially for the offshore Georges Bank spawning component. The inshore component is not doing as well. Over the last few years serious concern has been expressed about the status of the coastal spawning areas of Maine and Massachusetts (TRAC 2006, DFO 2007a).

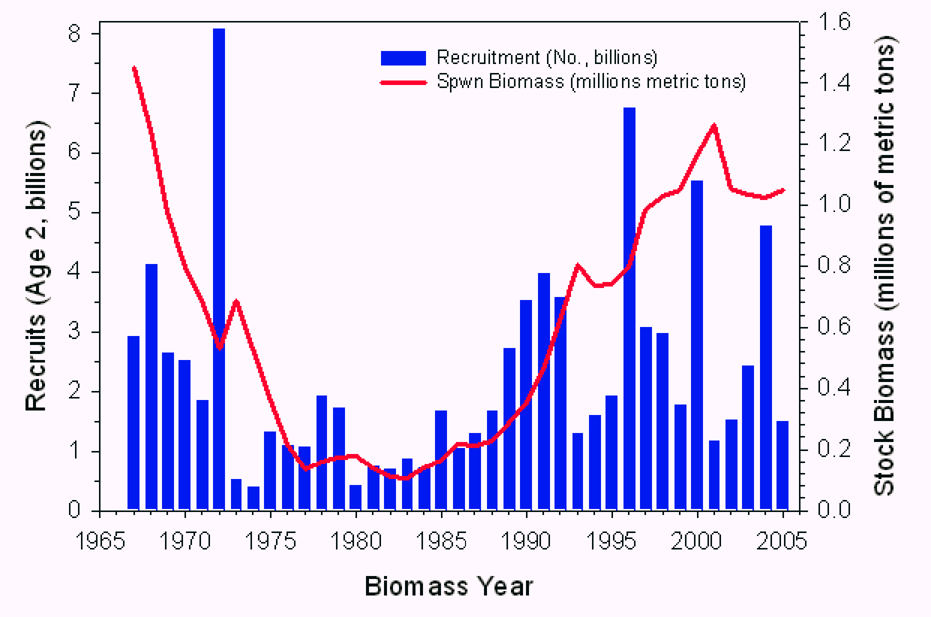

Figure 9.28: Herring stock biomass in the Gulf of Maine-Georges Bank area has recovered significantly since the collapse that occurred between the early 1970s and mid 1980s based on spring and autumn research vessel tows.
Source: Overholtz (2006).

The interpretation of trends in abundance for the herring stock complex in the Bay of Fundy and Canadian side of the Gulf of Maine is not clear. While the 2006 research survey catches remain an order of magnitude higher compared to the 1980s and early 1990s, the assessment indicates that this does not reflect trends in abundance (Clark and Perley 2006). As noted earlier, another point of concern that tempers some of the observations of increased herring numbers in large portions of the Gulf of Maine ecosystem is the apparent decline in energy density and condition of the fish (Diamond and Devlin 2003, Golet et al. 2007).

The year-to-year energy density (i.e. kCal/100 g) of larval herring is often considered a constant. However, assessment of fish at the mouth of the Bay of Fundy indicates significant variability (>135 to <95 kCal/100 g, Figure 9.29). This variability influences the productivity of predators that rely on the young herring as a food source to aid in their own development. It has also been noted that a strong negative correlation exists between the number of herring found in the diet of terns and the abundance of larval herring in the previous autumn.

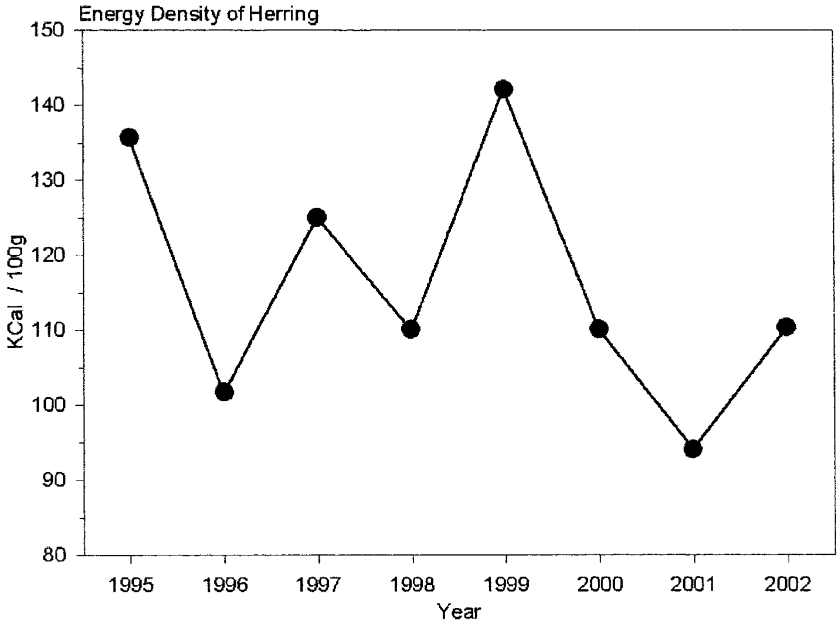

Figure 9.29: The variability in the energy density of herring larvae (a preferred seabird prey item) at the mouth of the Bay of Fundy.
Source: Diamond and Devlin (2003).

When herring are more abundant, they are not being consumed in corresponding amounts by terns. It is suggested that there may be a strong density-dependent competition occurring among herring larvae such that more survive from small spawnings than from large ones (Diamond and Devlin 2003).

Atlantic mackerel (*Scomber scombrus* L.) is widely distributed in the waters of the North Atlantic. It does not have a swim bladder, requiring it to swim continually in order to maintain its hydrostatic balance. This biological feature, along with its high swim speed, helps it to change position rapidly, making it difficult to catch compared with other pelagic fish species. During long annual migrations in the spring and fall, mackerel sometimes travel in very dense schools composed of similar-sized individuals travelling at the same speed. In the spring and summer, mackerel are found in inshore waters; but from late autumn into winter, they are found in warmer, deeper waters at the edge of the continental shelf. In the Northwest Atlantic, two known spawning areas characterize its distribution, and mackerel may leave the Gulf of Maine and Georges Bank area in early spring to reach either the northern spawning grounds in the southern Gulf of St. Lawrence or the southern spawning grounds between the coast of Rhode Island and Virginia (DFO 2007b).

Sharks: The U.S. Federal Fisheries Management Plan (FMP) identifies three management groups of sharks: large coastal sharks, small coastal sharks and pelagic sharks on the North Atlantic Shelf. The focus of this discussion is on the pelagic shark community that includes ten species (ICCAT 2007), of which the shortfin mako (*Isurus oxyrinchus*), porbeagle (*Lamna nasus*), thresher (*Alopias vulpinus*), blue (*Prionace glauca*) and oceanic whitetip (*Carcharhinus longimanus*) can be found on the Canadian continental shelf (CSRL 2008). The 1993 FMP classified the status of pelagic sharks as unknown because no stock assessment had been conducted for this complex (ICCAT 2007). The blue shark (*Prionace glauca*), porbeagle shark (*Lamna nasus*), mako shark (*Isurus oxyrinchus*) and the spiny dogfish (*Squalus acanthias*) are four shark species that are common in the Canadian Maritime region (CSRL 2008).

The porbeagle shark (*Lamna nasus*) occurs in the Bay of Fundy and the Gulf of Maine. It is common in pelagic and littoral zones, and is found as deep as 370 m. Off eastern Canada, it is most commonly found on the continental shelf or near the shelf edge, but is sometimes found inshore. It prefers cool water and is usually found in temperatures between 5°C and 10°C. It is the second most commonly observed large shark in Atlantic waters. Adult porbeagle can grow to 3 m in length. The porbeagle undertakes extensive migrations in the North Atlantic from Massachusetts up along the Scotian Shelf to Newfoundland. The porbeagle is often seen inshore and around mouths of estuaries in Nova Scotia and New Brunswick in late summer. Based on population dynamics analysis, it appears that the porbeagle population in the Northwest Atlantic has collapsed and remained low since the 1990s (Campana et al. 2008). Recently, a porbeagle mating area was identified on Georges Bank, where a concentration of shark will amass during June and July (Campana, pers. comm. 2009).

Shortfin mako (*Isurus oxyrinchus*) is one of two shark species in the genus *Isurus* (Family Lamnidae, or mackerel sharks). Longfin mako are rare in Canadian waters, while shortfin mako are typically associated with warm waters such as those of the Gulf Stream that enter the Gulf of Maine through the Northeast Channel. Shortfin mako are known to migrate over long distances and have been recorded from Georges Bank and even further north. However, the Gulf of Maine is generally considered the northern extent of their range (COSEWIC 2006a). Population estimates for the shortfin mako population in the Northwest Atlantic indicate an increase in the mid-1980s from a low during the previous decade and subsequent fluctuations including another decline followed by a partial recovery (Figure 9.30). They can be found in association with other large pelagic fish such as swordfish and bluefish, two species on which they will prey (Campana, pers. comm. 2009). They prefer temperate to tropical waters with temperatures between 17°C to 22°C and occur from the surface to 500 m depths (DFO 2006e). Their preference for warm waters is likely the reason that the majority of tagging and recaptures around the Gulf of Maine have been located near the continental slope at the eastern extreme of the Gulf of Maine. However, they can also be found in the eastern Gulf of Maine and the Bay of Fundy (COSEWIC 2006a). The Council on the Status of Endangered Wildlife in Canada has identified the shortfin mako as a threatened species in Canadian waters since 2006 (DFO 2006e).

The blue shark, *Prionace glauca*, has a cosmopolitan distribution, occurring principally in warmer waters throughout the world's oceans. Blue sharks are found during summer months in the Gulf of Maine but may avoid the colder waters of the Bay of Fundy (Collete and Klein-Macphee 2002). Blue sharks prey principally on cephalopods and pelagic fishes. Population estimates for blue sharks in the Northwest Atlantic indicate a general decline from a recent peak in the mid-1980's (Figure 9.30). Like porbeagle and mako sharks, blue sharks are caught incidentally in long-line and other fishing operations.

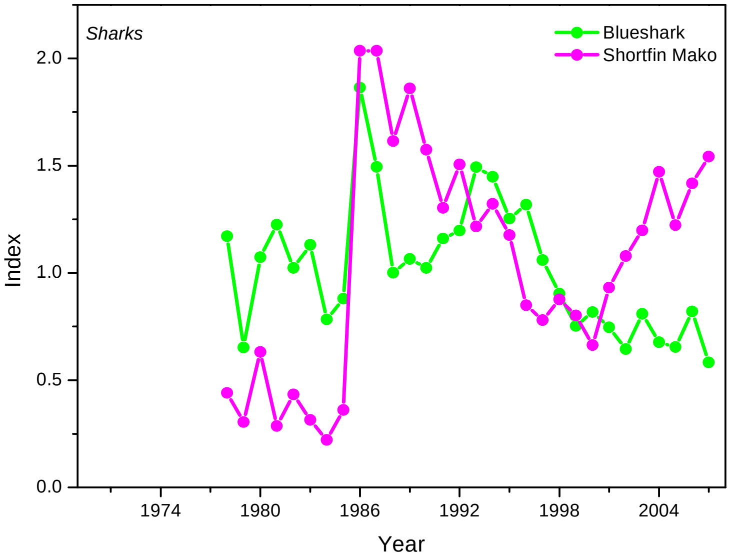

Figure 9.30: Population index for shortfin mako and blue shark in the Northwest Atlantic.
Source: adapted from EAP (2009).

Spiny dogfish (*Squalus acanthias*) are small squaloid sharks common both on the bottom and in the water column of coastal temperate oceans around the world. Dogfish in Atlantic Canada are usually associated with bottom water temperatures between 0°C and 12°C throughout the year. The species is commonly observed at depths of 50-200 m, but may be found to 350 m. In Canadian Gulf of Maine waters they are abundant in the Bay of Fundy; largest concentrations likely occur in U.S. Gulf of Maine waters off Cape Cod (Campana, pers. comm. 2009). Large aggregations of mature females occur in deep warm waters off the edge of the continental shelf east of the Gulf of Maine in the winter when it is presumed pupping occurs. It appears likely that the small juveniles remain east of the Gulf of Maine and pursue a largely pelagic existence for the first few years of their lives before moving onto the continental shelf. Study of the age structure of Canadian Atlantic dogfish indicates a mean longevity of 31 years (DFO 2007c). It appears that the Gulf of Maine is likely central to the home range of the spiny dogfish, and that various areas of the gulf support all life cycle stages for at least a portion of the fish found within the gulf (Campana, pers. comm. 2009).

Through tagging of dogfish, it is known that they seasonally migrate from as far as the inner Bay of Fundy to Cape Cod, and from Georges Bank south to North Carolina. However, most stay relatively local to their place of tagging. In the Gulf of Maine, 87% of U.S. tagged fish and 80% of Canadian tagged fish remained within their host country waters (see Figure 9.31). Large-scale annual migrations do occur along the east coast of the U.S., but are primarily limited to the area between North Carolina and the Gulf of Maine. About 10% of the stock within the Gulf of Maine will mix cross-border. Overall, the data collected suggest that there are both migratory and resident components to the stock (DFO 2007c).

In approximately 1992, a Georges Bank dogfish stock component disappeared. These dogfish apparently moved to another area, since the abrupt decline cannot be explained by fishing or discarding (DFO 2007c).

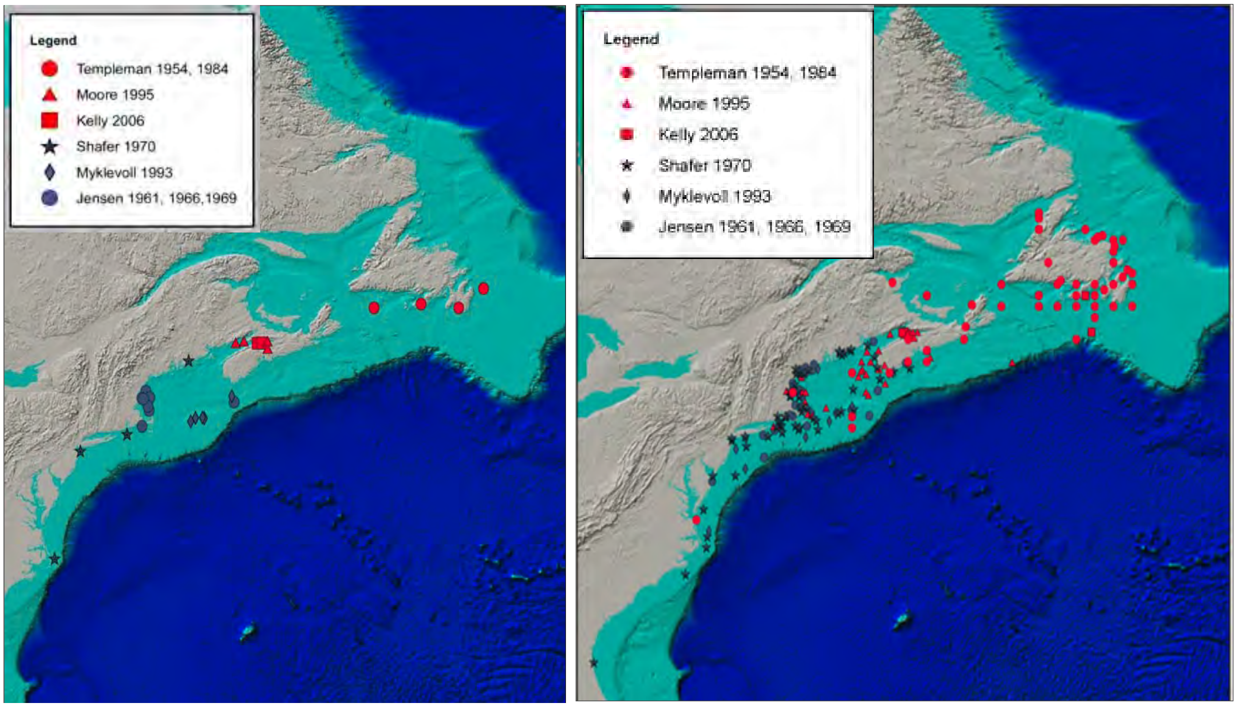

Figure 9.31: Distribution of spiny dogfish tag recaptures from various studies. Tags applied in Canadian waters are shown in red, while those applied in U.S. waters are shown in blue. The results indicate that only about 10%-20% mix outside the country of tagging, and that the Gulf of Maine is the primary mixing location.
Source: DFO (2007c).

Several other species of shark can be found in the Gulf of Maine, including two that are generally recognizable by the public, the white shark and the basking shark. Although rarely observed in the Gulf of Maine, "great" white sharks (*Carcharodon carcharias*) may be seen during the months of August and September (DFO 2006f). There are only 32 records over 132 years for Atlantic Canada, and most of the Gulf of Maine records come from the Bay of Fundy area (COSEWIC 2006b). White sharks undergo long migrations and they inhabit coastal and offshore waters from the subarctic to tropical regions. They range from surface waters down to depths as great as 1280 m and tolerate a wide range of water temperatures (5°C to 27°C). An area just south of the Gulf of Maine in the Mid-Atlantic Bight, between Cape May and Cape Cod, is thought to be a mating area for the single Atlantic Ocean population of white sharks. In the North Atlantic, there was a sharp decline (between 59% and 89%) in the abundance of this species between 1986 and 2000. In April 2006, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) designated the Atlantic population of white sharks as endangered (DFO 2006f).

The basking shark (*Cetorhinus maximus*) is the second largest fish in the world and can attain lengths of at least 10 m, with an average of about 7-9 m. They may live up to 50 years. The basking shark is often seen during the summer and autumn (May to September) near and around the coastline, and can be found throughout the Gulf of Maine and the Bay of Fundy (CSRL 2008).

Often, basking sharks will be found in association with right whales within the Gulf of Maine, although the significance of this relationship is not fully understood (Campana, pers. comm. 2009). The basking shark is a pelagic animal, occurring in both coastal and oceanic waters from 200 m to 2000 m deep, but often straying inshore. In offshore areas, it is often found near oceanic fronts at temperatures between 7°C to 16°C (CSRL 2008).

Atlantic Salmon: Another pelagic species found in the Gulf of Maine is perhaps more familiar to the general public than any other, primarily due to its excursions up the coastal rivers that feed into the gulf. Atlantic salmon (*Salmo salar*) is known for its anadromous life history, spending considerable time in both freshwater and marine environments. It is in the ocean environment that most of the growth, potential fecundity and a substantial portion of overall mortality for this species occur. Since the late 1980s and 1990s, Gulf of Maine salmon populations have diminished at an unprecedented magnitude and once again have drawn attention to our lack of knowledge of life history during the marine phase. Migration routes, distribution and abundance for specific stocks are completely unknown. Furthermore, the reason(s) behind the current high mortality rates for Atlantic salmon, which are known to be occurring at sea, have no specific known cause(s) (Reddin 2006). Atlantic salmon in the inner Bay of Fundy were plentiful only 30 years ago, being found in some 48 different rivers. However, their numbers have dropped dramatically to the point where they are in danger of being extirpated. The analysis of specific rivers from the inner bay indicates that annual mortality of immature salmon at sea increased from 0.83 (pre-1990) to 0.97 (post-1990), and mortality of post-spawning adults increased from 0.49 to 0.64. These results, along with the known availability of freshwater habitat, suggest that declines of the iBoF salmon lie almost exclusively with marine survival (Trzcinski et al. 2004).

It does appear that within the Gulf of Maine, Atlantic salmon have two different migration strategies. Ritter (1989, cited in Reddin 2006) concluded that inner Bay of Fundy salmon remain as adults in the Bay of Fundy and surrounding areas, such as the Jordan Basin. All other salmon from the Bay of Fundy and around the Gulf of Maine migrate to overwintering areas on the Grand Banks and in the Labrador Sea (Reddin 2006).

9.4 Marine Mammals

More than 32 species of marine mammals have been inventoried in the Gulf of Maine (Valigra 2006), although at least 18 are known to only spend a part of the year in the waters of the gulf (*Science Daily* 2006). Twenty-four of these species of marine mammals have been confirmed within the Bay of Fundy (Census of Marine Life 2009). There are three general communities for which overall patterns of population trends and habitat use are similar, with a few differences among species. These marine mammal communities include the large cetaceans, the small cetaceans and the seals. Cetaceans are the whales (large), and dolphins and porpoises (small).

9.4.1 Large cetaceans: In the Gulf of Maine, large cetaceans are dominated by the suborder *Mysticeti*, or baleen whales. In fact, the Gulf of Maine has high baleen whale biomass (0.5-0.6 t km^{-2}) when compared to a number of ecosystems around the world (Gaichas et al. 2009). This group includes the commonly seen, though globally endangered, North Atlantic right whale (*Eubalaena glacialis*), humpback whale (*Megaptera novaeangliae*), fin whale (*Balaenoptera physalus*), sei whale (*Balaenoptera borealis*) and minke whale (*Balaenoptera acutorostrata*)

(Smedbol, pers. comm. 2008). As shown in Table 9.6, the fin whale dominates the large cetacean biomass within the Gulf of Maine at all locations in virtually all seasons during 1979-1982, ranging from 34% to 67% of the total standing stock of all cetaceans (large and small) (Kenney et al. 1997). The exception is autumn on Georges Bank, when a greater proportion of the standing stock is represented by humpback and sei whales.

Seasonally, the Gulf of Maine has its greatest standing stock of cetaceans during the summer when several species come to the area to feed. The whales also show strong seasonal patterns, remaining relatively high in the water column during the warm part of the year and deeper during the colder seasons. The Gulf of Maine also has the maximum annual regional cetacean standing stock for the whole U.S. northeastern shelf area, with some 134 300 tonnes or 2055 kg km^{-2} during the summer (Kenney et al. 1997).

Table 9.6: Seasonally dominant cetacean species of the Gulf of Maine (GOM) and Georges Bank (GBK) for those comprising more than five percent of the cetacean standing stock by mass based on data from 1979-1982.

Region	Season	Dominant Species (% of total standing stock)
GOM	Winter	White-sided dolphin (85.3), Harbour porpoise (8.0), Common dolphin (6.6)
	Spring	Fin whale (60.2), Minke whale (15.8), Right whale (10.4), Humpback whale (7.6)
	Summer	Fin whale (67.7), Minke whale (11.7), Humpback whale (11.2), Right whale (6.8)
	Autumn	Fin whale (60.4), Minke whale (31.3), White-sided dolphin (5.7)
GBK	Winter	Fin whale (55.9), Sei whale (25.0), Sperm whale (11.5)
	Spring	Fin whale (34.2), Minke whale (25.3), Sei whale (21.3)
	Summer	Fin whale (51.4), Sperm whale (20.2), Pilot whale (8.4), Sei whale (7.4)
	Autumn	Humpback whale (27.3), Sei whale (27.3), Fin whale (22.6), White-sided dolphin (7.9)

Source: adapted from Kenney et al. (1997).

As shown in Table 9.6, fin whales are the biomass dominant cetacean in three of the four seasons. However, in the winter, dolphins and porpoises comprise the largest single percentage of cetacean standing stock. Although fin whales make up the largest percentage of the cetacean standing stock in the Gulf of Maine at virtually all times of the year, they only constitute 33% to 69% of the total Northeast Shelf abundance in any one season. As shown in Table 9.7, for the other whale species that enter the Gulf of Maine, a high percentage of their population on the Northeast Shelf is resident in the gulf at the same time. Although most species leave the gulf for a portion of the year, typically winter, nearly 100% of the year-round sei whale population in the U.S. Northeast Shelf is located in the Gulf of Maine, primarily on Georges Bank (Kenney et al. 1997).

Although rarely sighted, blue whales (*Balaenoptera musculus*), sperm whales (*Physeter macrocephalus*), northern bottlenose whales (*Hyperoodon ampullatus*) and Cuvier’s beaked whales (*Ziphius cavirostris*) may be seen on occasion in the Gulf of Maine. The baleen whales are known to occupy Canadian waters in the Gulf of Maine and Bay of Fundy, mainly during the summer and autumn months. However, most species may be sighted sporadically year round (Smedbol, pers. comm. 2008).

In general, populations of western North Atlantic large whales have declined greatly. With a few notable exceptions, these species are thought to be recovering from whaling given the North American prohibition on hunting. However, information concerning long-term whale trends is relatively poor. Several species that use the Gulf of Maine for some of their life history are listed

Table 9.7: Seasonal estimates of abundance of the five large cetacean species for the U.S. Gulf of Maine and the relative percentage of the Gulf of Maine abundance to the total U.S. Northeast Shelf abundance for each species. These mammals are some of the top predators in the Gulf of Maine food web.

Species	Season	U.S. Gulf of Maine abundance estimate	Percentage of the total U.S. Northeast Shelf
Right whale	Winter	–	–
	Spring	361	92
	Summer	251	100
	Autumn	–	–
Fin whale	Winter	596	33
	Spring	3 174	63
	Summer	4 181	69
	Autumn	1 263	63
Sei whale	Winter	616	100
	Spring	2 156	100
	Summer	291	100
	Autumn	524	100
Minke whale	Winter	–	0
	Spring	9 929	74
	Summer	4 289	87
	Autumn	3 709	100
Humpback whale	Winter	–	–
	Spring	429	90
	Summer	703	100
	Autumn	320	100

Source: adapted from Kenney et al. (1997).

under Canada's *Species at Risk Act* due to their low abundance. These include North Atlantic right, blue and the Scotian Shelf population of northern bottlenose whales (endangered); and the fin, humpback and Sowerby's beaked whales (special concern). Population estimates range from about 473 right whales (Right Whale Consortium 2010) to approximately 4000 for the western North Atlantic humpback whale population (COSEWIC 2003).

North Atlantic right whales migrate into Gulf of Maine waters to feed and congregate in the summer and autumn in the lower Bay of Fundy, mainly east of Grand Manan Island. A portion of the population may be resident year round in the Gulf of Maine region. The survival of these whales is clearly at risk, and published models indicate that the population may be heading towards extinction (Caswell et al. 1999, Fujiwara and Caswell 2001). A large number of North Atlantic right whales have been seen in the Gulf of Maine in December 2008. Whale researchers at NOAA's Northeast Fisheries Science Center sighted 44 individual right whales on December 3 in the Jordan Basin area, when three to five are more typical numbers to be observed at that time of year (*Science Daily* 2009). The significance of this observation is not yet understood.

The humpback whale within the Gulf of Maine has been identified as a discrete subpopulation of the western North Atlantic population (NOAA 2006). This is considered a feeding population, as virtually all humpbacks from the North Atlantic mate and calve at one location in the West Indies. Many hundred humpback whales will come to the Gulf of Maine, with virtually 100% of the North Atlantic shelf whales being located on the gulf during most of the summer and autumn (Kenney et al. 1997). As shown in Figure 9.32, key humpback habitats tend to be located in banks and shoals in and around the gulf (Provincetown Center for Coastal Studies 2009). Population estimates of humpback whales for the Gulf of Maine-Bay of Fundy have ranged from 497 in 1992 to 902 in 1999. Overall, the North Atlantic population increased 3.1% for the period of 1979 to 1993 (NOAA 2006).

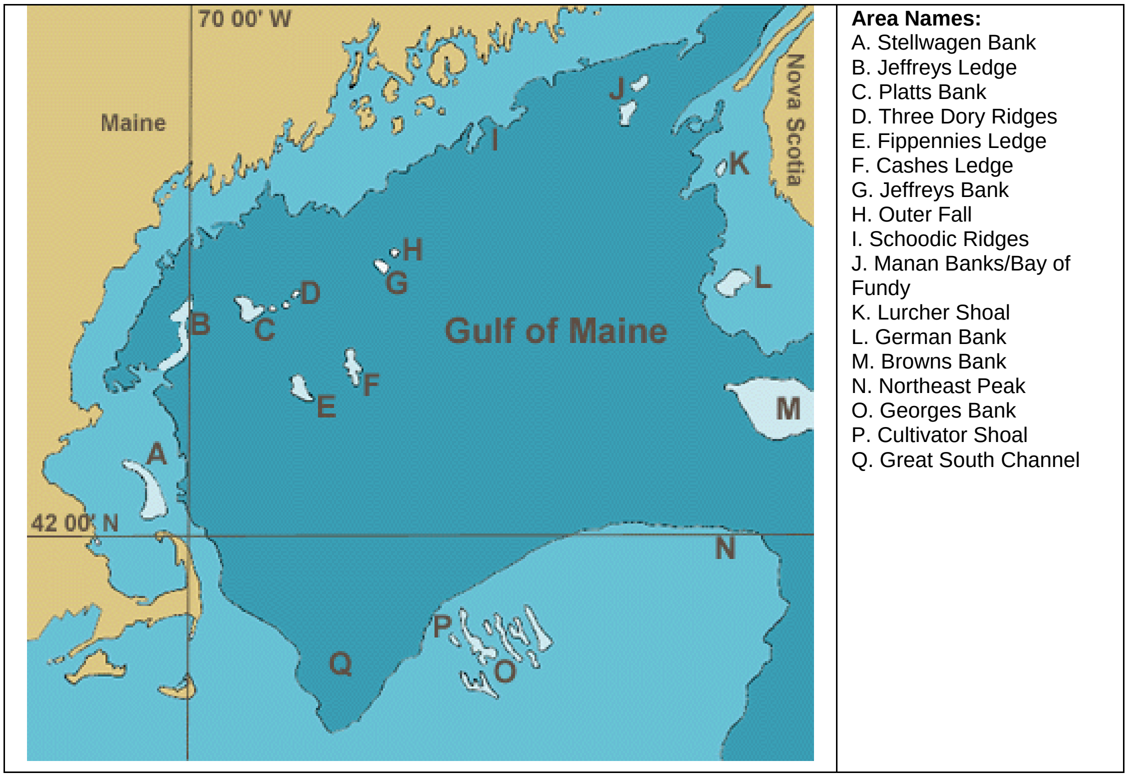

Figure 9.32: Humpback whale habitats in the Gulf of Maine.
Source: Provincetown Center for Coastal Studies (2009).

<u>9.4.2 Small cetaceans</u>: Related to the large whales, this group includes species of dolphin and porpoise. In Canadian waters of the Gulf of Maine, the main species sighted (in descending order of abundance) are harbour porpoise (*Phocoena phocoena*), white-sided dolphin (*Lagenorhynchus acutus*), two species of pilot whales (long-finned - *Globicephala melas*; and short-finned - *Globicephala macrorhynchus*), and the common dolphin (*Delphinus delphinus*). Two other dolphin species, Atlantic bottlenose (*Tursiops truncates*) and white-beaked (*Lagenorhynchus albirostris*) are seen occasionally. Risso's dolphin (*Grampus griseus*) and killer whales (*Orcinus orca*) are rarely sighted. Overall, there is little or no information on abundance trends in Canadian waters of the Gulf of Maine. All abundance estimates for the Gulf of Maine area have been derived from surveys undertaken by the U.S. National Marine Fisheries Service, which have not centred on Canadian waters (Smedbol, pers. comm. 2008).

Significant numbers (~40 000) of both white-sided dolphin and harbour porpoise reside in the U.S. Gulf of Maine year round, with virtually all of the Northeast Shelf population located in the gulf (see Table 9.8). Considerably fewer pilot whales and common dolphins are found in the gulf, and a smaller proportion of their Northeast Shelf populations are located in the gulf ecosystem at any one point in time (Kenney et al. 1997).

Table 9.8: Seasonal estimates of abundance of four small cetacean species for the U.S. Gulf of Maine and the relative percentage of Gulf of Maine abundance to the total U.S. Northeast Shelf abundance. These mammals are some of the top predators in the Gulf of Maine food web.

Species	Season	U.S. Gulf of Maine abundance estimate	Percentage of the total U.S. Northeast Shelf
Pilot whale	Winter	974	44
	Spring	6 722	58
	Summer	4 890	55
	Autumn	768	8
White-sided dolphin	Winter	12 310	99
	Spring	38 187	96
	Summer	38 016	100
	Autumn	42 019	99
Common dolphin	Winter	11 827	26
	Spring	5 435	28
	Summer	831	20
	Autumn	16 182	53
Harbour porpoise	Winter	3 050	100
	Spring	46 872	95
	Summer	18 934	100
	Autumn	548	100

Source: adapted from Kenney et al. (1997).

It appears from research that the Gulf of Maine-Bay of Fundy population of harbour porpoise is one of four in the western North Atlantic (NOAA 2006), and individuals move around the gulf (COSEWIC 2006c). Nearly all of the individuals in the U.S. Northeast Shelf reside in the Gulf of Maine year round (Kenney et al. 1997). Harbour porpoise is listed as a species of special concern under the Canadian *Species at Risk Act*, and is the only member of this group of small cetaceans that is a federally listed species as of 2006 (COSEWIC 2006c). During the summer, harbour porpoises are concentrated in the northern Gulf of Maine and southern Bay of Fundy region, generally in waters less than 150 m deep, with a few sightings in the Upper Bay of Fundy and on the northern edge of Georges Bank. During autumn and spring, harbour porpoises are widely dispersed from New Jersey to Maine (NOAA 2006). There does not appear to be a temporally-coordinated migration or a specific migratory route to and from the Bay of Fundy region, and harbour porpoises can be sighted in this area throughout the year (Smedbol, pers. comm. 2008). In 1999, NMFS conducted a survey for harbour porpoise that covered the known range for the Gulf of Maine-Bay of Fundy stock. Resulting population estimates rose from 37 500 harbour porpoises in 1991 to 89 700 in 1999. However, statistically, there are insufficient data to determine population trends for this species (NOAA 2006).

In the winter, dolphins and porpoises comprise the largest percentage of cetacean standing stock in the Gulf of Maine (see Table 9.6). However, this is not the period of their peak abundance throughout the course of the year, but, instead, a time of year when virtually all the whales leave the Gulf of Maine (Kenney et al. 1997).

9.4.3 Seals: Harbour (*Phoca vitulina*), hooded (*Cystophora cristata*), and grey seals (*Halichoerus grypus*) are listed on the Gulf of Maine species census (Census of Marine Life 2009). However, records do exist for harp seal as well (McAlpine et al. 1999). One other pinniped, the walrus (*Odobenus rosmarus)*, has historically been found on occasion within the Gulf of Maine (Census of Marine Life 2009), although the Northwest Atlantic population from which these individuals likely strayed is now considered extirpated (COSEWIC 2006d). Harbour seals are the most numerous in the Gulf, followed by grey seals, while other species are only present in relatively low numbers (NOAA 2006). In general, there is evidence that the seal populations in the Gulf of Maine have increased substantially over the last 20 years (Terhune, pers. comm. 2008).

Harbour seals are a year-round inhabitant of the Gulf of Maine, with most pupping and breeding occurring along the coastline from Maine northwards. Seasonal movement patterns include a general southward movement from the Bay of Fundy to southern New England in autumn and early winter (Jacobs and Terhune 2000), and a northward movement from southern New England to Maine and eastern Canada prior to the pupping season, which takes place from mid-May through June (NOAA 2006). Harbour seals have been sporadically surveyed on haul-out sites from low-flying aircraft in areas of the Bay of Fundy and Gulf of Maine. In Maine there appears to have been an increase in observed harbour seal numbers from around 10 000 seals and 600 pups in 1981 to just over 38 000 adults and juveniles and 9 000 pups in 2001 (Gilbert et al. 2005). After correcting for the seals in the water during the surveys, it is estimated that the Maine harbour seal population is likely to number just under 100 000 individuals. During the early 1990s, Canadian scientists counted some 3500 harbour seals in the Bay of Fundy, although a population estimate has not been made (NOAA 2006). In addition to the increase in numbers in Maine, the proportion of pups in the population and the numbers of haul-out sites has also increased over the past two decades (Gilbert et al. 2005). The majority of these seals are found in waters less than 100 m on the coastal shelf, and not in the deeper waters of the Gulf of Maine. There is insufficient current data to determine if the population growth of the harbour seals in Maine is slowing (Gilbert et al. 2005).

Aerial surveys were conducted along much of the New Brunswick coast of the Bay of Fundy in 1984, 1987 and 1998. The high count of just over 1 000 harbour seals in the late summer or early autumn was similar for each survey (Jacobs and Terhune 2000). Interestingly, the counts did not change over the 14 years. Gilbert et al. (2005) note that the counts made near Cobscook Bay, close to the New Brunswick border, also did not change very much between 1986 and 2001. This suggests that the Bay of Fundy harbour seal populations may not have increased over the past two decades (Jacobs and Terhune 2000).

Grey seal numbers in Maine have increased from a few animals reported in the mid 1970s to aerial counts of almost 600 in 1993 to over 1 700 in 2001 (Gilbert et al. 2005). Along the New Brunswick coast of the Bay of Fundy, single grey seals were occasionally observed on haul-out sites in the 1980s and 1990s; more recently, two to three grey seals were observed throughout the summer of 2007 (Emery, pers. comm. to J. Terhune 2009). This increase in sightings is expected, in part because of the large increase in grey seals at Sable Island, Nova Scotia, and tagged seals from Sable Island have been spotted in the Bay of Fundy (Terhune, pers. observ.). Grey seal pup production on the island has increased from a few hundred per year in the 1960s to an estimated 41 500 in 2004. However, Bowen et al. (2007) report that the rate of increase of the grey seals on Sable Island is slowing. The current numbers of grey seals breeding near the mouth of the Bay of Fundy and along the Maine coast are unknown. However, an abundance estimate of approximately 7300 adults in U.S. waters of the gulf (1999-2001) was dominated by nearly 77% being located in the Great South Channel (NOAA 2006). Furthermore, as shown in Figure 9.33, it would appear that grey seals from Sable Island spend relatively little time in the Gulf of Maine, and primarily limit their presence to the Northeast Channel, across Georges Bank to the Great South Channel (Zwanenburg et al. 2006). During the late 1990s, a year-round breeding population of approximately 400+ animals was documented on outer Cape Cod and Muskeget Island (NOAA 2006), near the Great South Channel.

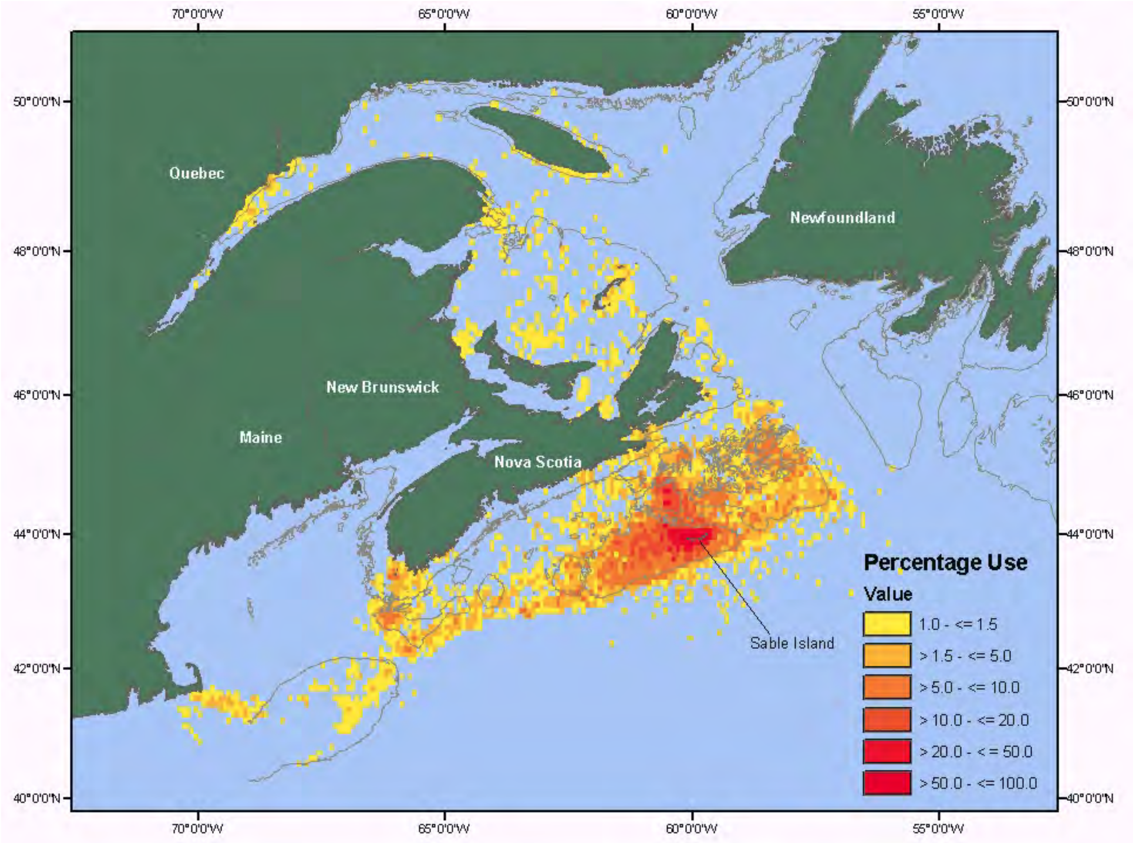

Figure 9.33: Annual distribution of adult grey seals based on locations of 70 animals fitted with Argos satellite tags on Sable Island demonstrates limited use by the species in the Great Southern Channel, Georges Bank and the Northeast Channel areas of the Gulf of Maine.
Source: Zwanenburg et al. (2006).

McAlpine et al. (1999) report an increase in the numbers of extra-limital observations of both harp (*Pagophilus groenlandicus*) and hooded (*Cystophora cristata*) seals in the Gulf of Maine and Bay of Fundy region. The numbers of sightings are low; but there was a noticeable increase after 1994. As with the grey seals, the populations of both of these ice-breeding seals have increased substantially over the past two decades. Over the two years of 2002 and 2003 there were 156 documented strandings of harp seal along the U.S. coastline of the Gulf of Maine (NOAA 2006). The northeast Atlantic population of hooded seals extends southwards during the spring; therefore, their appearances in the Gulf of Maine usually occur between January and May (NOAA 2006).

9.5 Seabirds

The Gulf of Maine is rich in avian diversity and abundance. There are more than 184 species of marine birds that have been documented within the Gulf of Maine (Valigra 2006) and 177 in the

Bay of Fundy (Census of Marine Life 2009). Seabird biomass in the Gulf of Maine and Georges Bank has been estimated at 0.004 t km^{-2}, with a consumption rate of 0.015-0.019 t km^{-2} (Gaichas et al. 2009). The Gulf of Maine has several features that attract pelagic birds, including ice-free winters and areas of high marine productivity that ultimately produce food supplies at the top of the food chain. The Gulf of Maine ecosystem components support breeding, migrating/staging and non-breeding populations of waterfowl, seabirds and shorebirds.

Regardless of the acknowledgement of the diversity and abundance of seabirds in the gulf, little is known regarding details of their pelagic existence in the offshore areas. Most studies have focused on the coastal areas where breeding and nesting take place. However, the importance of some offshore locales to individual species is apparent (see Table 9.9).

Table 9.9: Some important marine areas within the Gulf of Maine for select seabirds.

Species	Status of bird	Time of year/location	Environmental characteristics
Northern Gannet	Immature	Winter - Cape Cod Breeding - Grand Manan Post-breeding - Grand Manan and Cape Cod	Shallow and mixing regime Strong tidal currents Strong tidal currents
Greater Shearwater	Moulting	June - Georges Bank	Shallow waters
Black-legged Kittiwake	Juvenile	Post-breeding - Grand Manan	Shallow and mixing regime
Herring Gull	Immature	Winter - Cape Cod Breeding - Cape Cod Post-breeding - Cape Cod, Grand Manan and Georges Bank	Mixing regime Strong tidal currents Strong tidal currents and shallow waters
Great Black-backed Gull	Immature	Winter - Cape Cod and Georges Bank Breeding - Cape Cod Post Breeding - Georges Bank	Shallow and mixing regime Currents and shallow waters Shallow waters

Source: adapted from Huettmann and Diamond (2000).

9.5.1 Breeding Marine Birds: The coastal areas around Cape Cod in the southern gulf and Grand Manan at the mouth of the Bay of Fundy are significant breeding grounds for a number of species of marine birds in the Gulf of Maine. The small islands of offshore New Brunswick provide predator-free habitat for breeding marine birds. Breeding species include Leach's Storm-Petrel (*Oceanodroma leucorhoa*), Double-crested Cormorant (*Phalacrocorax auritus*), Herring Gull, Great Black-backed Gull and Ring-billed Gull (*Larus argentatus*, *L. marinus* and *L. delawarensis*), Common Eider (*Somateria mollissima*), Common and Arctic Tern (*Sterna hirundo* and *S. paradisaea*), Razorbill (*Alca torda*), Atlantic Puffin (*Fratercula arctica*), Common Murre (*Uria aalge*) and Black Guillemot (*Cepphus grille*) (Canadian Wildlife Service Atlantic Waterbird Colony Database, Mawhinney et al. 1999, Diamond and Devlin 2003, Ronconi and Wong 2003, McAlpine et al. 2005). Leach's Storm-Petrel is the only true pelagic species nesting in the Bay of Fundy (Ronconi and Wong 2003). Small numbers of Black-legged Kittiwakes (*Rissa tridactyla*) (Kehoe and Diamond 2001) and Northern Gannet (Corrigan and Diamond 2001) have also been documented breeding in the Bay of Fundy. This is a remarkable diversity of breeding marine birds and atypical of the Canadian Maritime provinces as a whole.

The most important single breeding colony for marine birds in the Bay of Fundy is Machias Seal Island. There, Common and Arctic Terns are found along with Leach's Storm-Petrels, Common Eiders, Razorbills, Atlantic Puffins and Common Murres and, in 2008, Black Guillemots. The Razorbills, Atlantic Puffins and Common Murres are more typical breeders in cold-water areas to the north of the Gulf of Maine. Atlantic Puffins monitored at two Gulf of Maine colonies off the state of Maine coastline for 11 years (1992-2003) exhibited a high constant survival of 0.95 ± 0.01 (SE), consistent with other estimates for Atlantic Puffin and other long-lived seabirds. Furthermore, it appears that these puffins may have overlapping territory in the non-breeding period (autumn, winter and spring), although they return to their natal colonies during breeding season (Breton et al. 2005).

9.5.2 Non-Breeding Marine Birds: Non-breeding marine birds consist of those species that carry out non-breeding activities within the Gulf of Maine, as well as those species of birds that migrate through or overwinter in the gulf. It is for these functions that an overview is provided of sea bird activity in the offshore areas of the Gulf of Maine.

The migration patterns and concentration areas of seabirds in the northwest Atlantic are not well known (Huettmann and Diamond 2000). Staggering of migration and different feeding strategies may decrease some of the competition among pelagic seabirds using the Bay of Fundy. However, two coastal areas of the Bay of Fundy host significant populations of stop-over migrant marine birds: the head of the bay, and the outer bay. At the head of the bay are found significant stretches of mud flats in which a rich community of intertidal invertebrates live - in particular, the mudshrimp *Corophium volutator* (Hicklin and Smith 1984; Hamilton et al. 2003, 2006; Sprague et al. 2008). The invertebrates on the mud flats form the food base for over 2 million migrant shorebirds (Hicklin 1979), most of which are Semipalmated Sandpipers (*Calidris pussila*). This shallow intertidal area, although of great ecological significance, generally falls outside the scope of this ecosystem overview report. Of note, however, is that the shorebird population that uses the Bay of Fundy has experienced a decline of 5% per year between 1982 (about 800 000) and 2004 (about 260 000) (Hicklin and Chardine 2006).

In the deeper outer Bay of Fundy, tidal upwellings drive nutrients and plankton to the surface, where they are fed upon by phalaropes (*Phalaropus* spp.) and gulls. Hundreds of thousands of Red-necked (*Phalaropus lobatus*) and Red Phalaropes (*P. fulicaria*), and tens of thousands of Bonaparte's Gulls (*Chroicocephalus philadelphia*) stop over between mid-July and September or later to feed on surface plankton (Braune and Gaskin 1982, Mercier and Gaskin 1985, Brown and Gaskin 1988) in the gyre north of Grand Manan and other turbulent areas along the continental coast. One of the key plankton species, which is fed upon by phalaropes, is the large copepod *Calanus finmarchicus*. Bonaparte's Gulls target northern krill and the young age classes of herring.

Each spring, Black Scoters (*Melanitta nigra*), Surf Scoters (*M. perspicillata*) and White-winged Scoters (*M. fusca*) pass through the Bay of Fundy in daytime on their northward migration to the sub-Arctic breeding grounds. Between 1996 and 2004, some 6% to 18% and 28% to 37% of the North American breeding populations of Surf Scoters and Black Scoters, respectively, utilized this northward migration route annually. The low numbers of White-winged Scoters (0.4%-0.6%) suggested that larger numbers of this species employed a different migration route in spring or migrated undetected at night. Over all years, approximately 88 000 ± 10 000 (SE) Black Scoters were estimated to pass by the mouth of the Bay of Fundy each spring, by far the greatest average abundance of these three species. In terms of migration timing through the Bay of Fundy, Black Scoters arrive first, followed by Surf and White-winged Scoters arriving together. However, the migration of White-winged Scoters extended for a period almost 20 days longer than the other scoters in some years (Bond et al. 2007).

The Bay of Fundy hosts marine birds from the Southern Hemisphere that spend the austral winter in Bay of Fundy waters during the summer, as well as over-wintering Northern Hemisphere species. These species stay at sea during this phase of their annual cycle, some remaining well offshore (pelagic) and some inshore, within sight of land. Information regarding pelagic seabirds in the Bay of Fundy is poorly documented. The abundance of pelagic seabirds varies seasonally with respect to migratory patterns. During the summer and autumn, the most common pelagics include Great Shearwater (*Puffinus gravis*), Sooty Shearwater (*P. griseus*), Wilson's Storm-petrel (*Oceanites oceanicus*) and Leach's Storm-petrel (Ronconi and Wong 2003). Autumn migrants, likely post-breeding adults and juveniles, include Northern Gannet (*Morus bassanus*), Great Skua (*Catharacta skua*), Jaegers (*Stercorarius* spp.) and terns (*Sterna* spp.) (Huettmann 1998). Regular winter pelagics include Northern Fulmar (*Fulmarus glacialis*), Iceland Gull (*Larus glaucoides*), Glaucous Gull (*L. hyperboreus*), Black-legged Kittiwake (*Rissa tridactyla*) and Razorbill (*Alca torda*) (Huettmann 1998, Huettmann et al. 2005). Several other members of the auk family are winter visitors to the Bay. Rare and vagrant pelagics include Cory's Shearwater (*Calonectris diomedea*) and Yellow-nosed Albatross (*Thalassarche chlororhynchos*).

Spatially, there are several regions of the Bay of Fundy where pelagic seabirds are regularly found. Greater and Sooty Shearwaters frequently forage in areas off Brier Island (Brown et al. 1981) where tidal upwellings contribute to daytime surface swarming of northern krill (Brown et al. 1979). Recent satellite telemetry studies of Great and Sooty Shearwaters also found tidal upwelling areas around Grand Manan to be important to this species (Ronconi and Wong 2003). These areas are also important for wintering Razorbills (Huettmann et al. 2005), and Storm-Petrels (Ronconi pers. observ., L. Murison, pers. comm.). Northern Gannets across the central Bay of Fundy show habitat associations with the shelf area off Digby, Nova Scotia (Huettmann 1998).

During moult, some seabirds are vulnerable since they cannot fly; their moulting locations therefore constitute key areas for conservation of the full life cycle of these birds. Based on a long-term dataset (1966-1992), Huettman and Diamond (2000) indicate that Georges Bank has been identified as August moulting grounds for the Greater Shearwater and Northern Fulmar. Large numbers of Northern Fulmar have also been reported far at sea in the Gulf of Maine between January and April. Moulting Greater Shearwaters may be found in the Gulf of Maine during August. Although they are also observed in great numbers at the mouth of the Bay of Fundy, they do not appear to be moulting there. High Northern Gannet concentrations occur in the lower Bay of Fundy and Georges Bank; it is suggested that these are non-breeding birds, which are not tied to colonies. After the breeding season, high densities of immature gannets can be found in the Lower Bay of Fundy and off Cape Cod, locations well removed from established breeding colonies (Huettman and Diamond 2000).

The Great Black-backed Gull post-breeding season includes four concentration zones in the Canadian North Atlantic, with the Gulf of Maine being one of those zones. The winter distribution of immature birds in the gulf is characterized by a high-concentration area off Cape Cod (Huettman and Diamond 2000). Although a limited number of Razorbills will breed in the Gulf of Maine, their main breeding areas are further north. They are mainly found in the Gulf of Maine during winter around Georges Bank and in the outer Bay of Fundy (Chapdelaine et al. 2001, cited by Diamond and Devlin 2003), diving 30-60 m deep into the water column to obtain prey. In the breeding season, immature Herring Gulls are distributed through the breeding areas that are located mainly in coastal waters throughout the southern Gulf of Maine. Outside of the breeding season, Herring Gulls will be found widely distributed around the Gulf of Maine (Huettman and Diamond 2000).

PART D – INTEGRATING CONCEPTS

10. ECOSYSTEM STRUCTURE AND DYNAMICS

Understanding an ecosystem means not just understanding the physical and chemical environment as described in the previous sections of this report, but also understanding the interaction of living things both with their environment and with each other. When examining ecosystem linkages within an area, most, if not all, relationships can fit into one of two general categories:

- physical-biological linkages; or
- biological interactions.

The following are a series of examples of both the physical-biological linkages and the biological interactions that are found in the Gulf of Maine, and these examples provide an overview of the dynamics and structure of the ecosystem.

10.1 Physical-Biological Linkages

Most marine species are found within a “range” of habitats that are defined by physical characteristics such as water chemistry, temperature, substrates (the environment) that they can tolerate or even prefer. Any changes or shifts in these physical and chemical characteristics can be expected to shift the suitability of a habitat for a particular species. Such a shift may be significant enough to alter the presence of a plant or animal in an area, or simply affect what life-cycle activities it undertakes within the altered area. If the change is small enough, the shift in habitat suitability may not cause any shift in species activity, but simply change it from “preferred habitat” to “within the tolerable range”. Understanding the physical-biological linkages for most life stages of most species is crucial to effective management at an ecosystem level. The following are several examples from current studies that demonstrate some of the physical-biological linkages that exist within the Gulf of Maine ecosystem.

There are many mechanisms by which physical habitat characteristics affect biological resources. For example, the distribution of macrobenthic organisms is influenced by sediment type, depth, bottom structure, temperature, salinity, dissolved oxygen concentrations and human influences such as levels of bottom-trawling fishing activity (GOMC 2004). However, the most important linkages at the ecosystem scale (rather than at the species or group of organism scales) are those that influence energy flow within the ecosystem. Physical characteristics influence both the amount of primary and secondary production available to planktivorous animals (Gaichas et al. 2009), and therefore the amount of energy available to move to higher trophic levels within the food web. Such physical-biological linkages have been demonstrated within the Bay of Fundy. There, a large volume of marine water pushes into the Bay of Fundy (Desplanque and Mossman 2001) where it is influenced by the physical funnel shape of the bay and the rotation of the Earth (Coriolis effect) to create the highest tides in the world (BoFEP 2001), the counter-clockwise circulation that exists, and localized high tidal velocities (Hunter and Associates 1982). These physical attributes promote vertical mixing in the Bay of Fundy gyre near Grand Manan Island (Aretxabaleta et al. 2008). The mixing “pumps” nutrient-rich water from deep in the water column towards the surface of the bay and sunlight (Pettigrew et al. 1998, cited in

Xue et al. 2000). This mixing is sometimes referred to as a benthic pump (Aretxabaleta et al. 2008, Van Dusen and Hayden 1989). As the nutrients reach the daily sunlight, they are taken up by phytoplankton, thus promoting growth at the base of the food chain. In this manner the physical attributes of the outer Bay of Fundy are linked to its biological productivity, supporting a diverse intermediate (TRAC 2006, DFO 2008a) and top trophic level community (NOAA 2006).

Not all physical-biological interactions are necessarily positive in terms of maintaining ecosystem stability or growth. Related to the Bay of Fundy's benthic pump and the resulting biological diversity found around the Bay of Fundy gyre is a second physical-biological relationship that has apparent widespread negative influence on the Gulf of Maine. The Bay of Fundy gyre forms because of a number of physical attributes (see Section 7.4 of this document for a further description of the gyre). The circular movement of the gyre has a tendency to retain particles within its boundary for extended periods of time. One such particle is an organism known as *Alexandrium fundyense*, a toxic dinoflagellate that is a common cause of red tide and shellfish poisoning within the Gulf of Maine. The dormant stage is a cyst. According to Aretxabaleta et al. (2008), the retentive nature of the gyre favours the self-sustainability of the Bay of Fundy population of this dinoflagellate and creates the possibility of the cyst bed located in the bay acting as a long-term source for the wider Gulf of Maine. Water from the Bay of Fundy gyre eventually follows other pathways out of the bay; it follows the Eastern Maine Coastal Current to Jordan and Georges Basins, and the WMCC southward all along the U.S. coastline. The physical retention characteristics of the Bay of Fundy gyre may sustain a concentration of *A. fundyense* cysts that, when they bloom during summer, can be carried out of the gyre and distributed by various other currents around a vast area within the Gulf of Maine (Pettigrew et al. 2005). This distribution then provides the opportunity for a variety of shellfish to feed on the toxic dinoflagellate, exposing both shellfish and potentially higher trophic levels to its poisoning effect (Campbell et al. 2005).

Physical-biological linkages exist all across the Gulf of Maine, and some of those that occur in more localized areas are better understood. On Georges Bank, an 11-year time series study of water column stratification has shown that, each year, the mean date of first transient stratification at the 80-100 m depth coincides with the historical maximum abundance of early-stage (<6 mm) cod larvae and copepod nauplii. In addition, the historical maximum abundance of haddock larvae occurs on Georges Bank at the same time that seasonal stratification is established at that same depth (Bisagni 2000). These results suggest another physical-biological interaction is at play. Water density stratification may play a role in causing variability of zooplankton and ichthyoplankton (eggs and larval fish) recruitment to southern Georges Bank. Increased concentrations of chlorophyll and zooplankton are often associated with the rapid vertical changes in density that result from the development of seasonal stratification on southern Georges Bank during the spring (O'Reilly et al. 1987, O'Reilly and Zetlin 1998, Meise and O'Reilly 1996, cited in Bisagni 2000). If the physical stratification of the Georges Bank water column promotes a concentration of potential prey organisms for zooplankton, such a linkage is likely an important factor controlling growth, survival and recruitment of copepods and larval fish at lower trophic levels of the food chain. While many of the biological processes occurring on Georges Bank may be linked in some way to physical processes and hydrography of the larger Gulf of Maine and adjacent continental slope region, much more work needs to be completed before exact mechanisms can be proven (Mavor and Bisagni 2001).

The previous examples show that physical-biological linkages exist across both small geographic areas of the gulf, and on short time scales (seasonally). The following example indicates how some physical-biological linkages may occur over a much longer time scale and larger geographic area. Petrie and Yeats (2000) noted that a potentially major influence of decadal variability on marine populations may occur through associated changes in chemical oceanographic properties. Significant changes in nutrients and dissolved oxygen in the Gulf of Maine region during the cold 1960s have been noted, with potentially important biological implications. Such implications include change in distributions, migrations, spawning times and even survival of various species (Loder et al. 2001).

Physical linkages to the biological communities of the Gulf of Maine do not have to originate within the gulf in order to effect change. For example, on a much larger scale, the NAO and a number of associated physical oceanographic changes have significant biological influence within the Gulf of Maine. Straile and Stenseth (2007) have outlined a wide array of known ecological relationships with the NAO, including the abundance and production of phytoplankton and the thermal habitat in oceanic waters for Atlantic salmon. Ottersen et al. (2001) have shown that the North Atlantic and surrounding regions display a biological response to NAO influenced climatic variability not just at the individual level, but also at the population and community levels. They have demonstrated how NAO influenced changes ripple through trophic levels of the ecosystem from primary production to herbivores to predators; influencing growth, life history traits, and population dynamics along the way. For example, timing of egg laying by Atlantic puffins (*Fratercula arctica*) at the mouth of the Bay of Fundy followed sea surface temperature variation at neither the local (Machias Seal Island) nor regional scales, but at the scale of the North Atlantic (Diamond and Devlin 2003). Another example has become apparent based on the analysis of 40 years of plankton data collection. Data indicate that plankton abundance and bloom timing within the Gulf of Maine changed significantly around 1991. It has been suggested that these changes are related to changes in the Labrador Current (Sameoto 2004), a water mass known to be influenced by the NAO. Loder et al. (2001) suggest that the large change in southward movement of cold water along the edge of the continental shelf in the vicinity of the Gulf of Maine can be expected to lead to increased transport of organisms along the shelf edge, reductions in their residence times in the vicinity of the shelf edge, and increased occurrence of major inter-stock exchange events. This is particularly true for species with spawning distributions concentrated near the shelf edge for which there could be major and even catastrophic influences (Loder et al. 2001). Such predictions demonstrate the potential large scale biological influence that physical-biological linkages can have, affecting biota not just locally, but across the entire gulf.

Although the physical-biological linkages here have focused on physical water quality influences on biological organisms, physical structure has much the same influence. For example, Thouzeau et al. (1991) identified a megafaual grouping that was associated with the biogenic sand-gravel areas of Georges Bank. This assemblage of organisms is adapted to this bottom type of sands, gravels, and old shells to which they generally attach themselves. The solid substrates allow them to hold their position within a current and filter food particles that may pass by in the water column. A number of species are exclusive to the biogenic substrate, and are not found in other locations, which highlights the physical-biological linkage between the substrate type and the individual species' life cycle functions.

As is apparent in the previous examples, many physical-biological linkages exist within the Gulf of Maine ecosystem. However, fully understanding the mechanisms associated with these relationships and the extent of change that may occur is not always well understood. Such limitations provide significant challenges to the management of human interactions with the natural resources of the Gulf of Maine.

10. 2 Biological Interactions

A second, and equally important, category of ecosystem linkages are “biological interactions”. This category describes how one living organism depends on or interacts with another. These relationships identify an organism’s place within the food web and trophic structure of an ecosystem. Biological interactions are an area of ecosystem science for which there are significant information gaps. These gaps in information provide challenges for resource management, industry development, and marine resources planning. Such gaps include the complexities of the food chain, which support our knowledge of the nature and extent of the ramifications that a change in a single species’ abundance may have throughout the entire food web. Section 10.3 further examines some of the biological linkages related to the food web of the Gulf of Maine, and the relationships both within and between the various trophic levels.

Although the following sections focus on predator-prey relationships, a number of types of biological interactions exist, including mutualistic relationships, where both organisms realize a benefit. Biological interactions may also be commensal, where one organism benefits but the other is neutral, receiving no harm or benefit. For example, within the Gulf of Maine, barnacles can be found attached to the jaw area of baleen whales that feed at the mouth of the Bay of Fundy. This allows the barnacle to be carried to food-rich areas by their host whale. A more general example of a commensal relationship has been found through the study of corals, such as those found in the Northeast Channel. Dozens of other organisms are found to live in association with the protective cover that the corals provide, a three-dimensional biogenic habitat (Metaxas and Davis 2005, Mortensen et al. 2006). Our gulf-specific knowledge of such non-predator-prey type biological interaction is relatively limited, although it is known that such important relationships likely exist throughout the Gulf of Maine ecosystem.

10.3 Trophic Interactions (Food Webs)

Trophic-level analysis within the Gulf of Maine has been conducted using three, four and five levels (Kenney et al. 1997, Link et al. 2008, Gaichas et al. 2009). Each approach reveals different insights into the biological interactions of the Gulf of Maine ecosystem. Marine ecosystems typically span five trophic levels ranging from primary producers and grazers to upper level predators and include detrital and other feedback loops (Zwanenburg et al. 2006). In order to provide an overview of the ecosystem, the general approach of low, intermediate and high trophic levels (Figure 10.1) as aggregated by Gaichas et al. (2009) has been followed in this report. The Gulf of Maine trophic interactions are undoubtedly more complex, yet this approach allows the reader to begin to see some of that complexity without introducing an intricate level of detail. As shown in Table 10.1, the highest levels of production and consumption within the gulf occur in the plankton communities (low trophic level). However, the greatest biomass exists at the intermediate trophic levels.

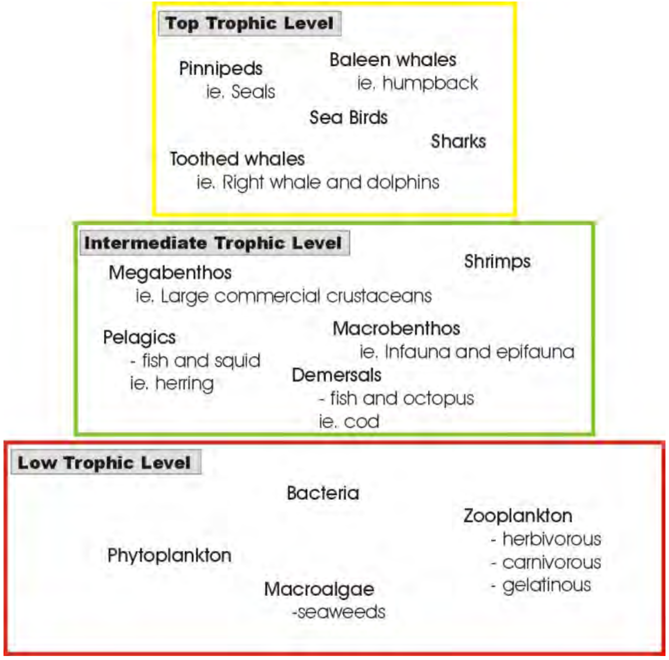

Figure 10.1: A simplified three level trophic structure for the Gulf of Maine based on groupings made by Gaichas et al. (2009).

Table 10.1: Biomass, production and consumption (t km^{-2}) for each trophic level in the Gulf of Maine (GoM) and Georges Bank (GB).

Aggregation	Biomass		Production		Consumption	
	GoM	GB	GoM	GB	GoM	GB
Total low trophic level	61	62	5 316	6 296	6 272	6 583
Total mid trophic level	79	108	154	208	945	1486
Total high trophic level	0.71	0.58	0.03	0.03	2	3.482

Source: adapted from Gaichas et al. (2009).

How growth occurs in particular organisms at a trophic level, and how much and from which trophic level an organism chooses to consume, determines how energy flows through a system. The flow of energy begins with the uptake of sunlight and nutrients by phytoplankton, and follows a path where it is transferred through growth (production) and consumption both up and down the trophic structure of the Gulf of Maine. Energy flow is often considered to end by supporting the top predators in the ecosystem. However, various other linkages exist that return energy to the food web through detritus and decay. Efforts have been made within the Gulf of Maine ecosystem to quantify the biomass and, therefore, the potential energy associated with a number of marine communities and organisms (Link et al. 2006, Link et al. 2008, Gaichas et al. 2009). Realizing that all trophic levels are interconnected (e.g., as a group whales will feed on plankton at the lowest level, fish at the intermediate level, and seals or seabirds periodically at the top level) highlights the challenging complexity of mapping the energy flow within the Gulf of Maine.

Understanding the intricacies of food webs and how energy flows through the ecosystem are lofty goals, but worthy targets if our objective is to try to manage our own relationship with the Gulf of

Maine ecosystem. The following sub-section provides an overview of some of the trophic-level relationships that regulate energy flow through the Gulf of Maine ecosystem.

10.3.1 Low Trophic Level: As described here, the low trophic level of the Gulf of Maine ecosystem primarily includes the plankton communities. This level is comprised of not just the primary producers (phytoplankton), but also zooplankton, and bacterioplankton. At 61-63 t km^{-2}, the lower trophic level biomass in the Gulf of Maine, including Georges Bank, is estimated to be roughly comprised of 50% zooplankton, 40% primary producers and 10% bacteria (Gaichas et al. 2009).

There is little known about the meiofauna and microfauna of the Gulf of Maine. Yet, most benthic biodiversity lies within these smaller size classes (<~0.5 mm) of animals, as does a significant fraction of secondary production. The habitat requirements and trophic importance of meiofauna/microfauna, both on the sea floor and in the water column of the Gulf of Maine, are not fully understood (GOMC 2004). These small organisms are a source of food for many larger organisms that live within or on the sea floor. Studies have shown that one such group, the bacteria associated with sediments, is an essential food source for many larger organisms living in the sand and sediments of the sea floor (Tunnicliffe and Risk 1977).

The importance of primary producers (photosynthetically active organisms) to the food web has long been acknowledged. For example, stable isotope analysis of fish scales has indicated that changes in the Georges Bank food web at the level of the primary producers can be detected throughout the food web (Wainright et al. 1993). However, it has recently been found that lower trophic levels in general (not just phytoplankton) can be important in balancing energy fluxes (Link et al. 2006). It further appears that non-living dissolved organic carbon may be the largest biomass node in the ecosystem by several orders of magnitude, and that significant bacteria and microzooplankton biomass have a large role in trophic energy transfer. It is now known that a significant portion of the ecosystem’s energy goes to detritus, such as dead organisms and fecal wastes, and to bacteria in ocean sediments. This represents a major change in thinking and philosophy of how energy flow in the oceans works compared with even 10 to 20 years ago (Link et al. 2006). The significance of this microbial community to the transfer of energy through Georges Bank has recently been demonstrated (Link et al. 2008).

Despite recent findings that bacteria and microzooplankton may play a significant role in energy transfer within the Gulf of Maine, phytoplankton is most often considered the base of the marine food web and the primary food source for the animal component of plankton (zooplankton). Both phytoplankton and zooplankton, in turn, are food for larval fish and invertebrates of the intermediate trophic level, and influence the survival rate of these larger organisms (DFO 2006a). As shown in Table 10.2, and as an example of within trophic level interaction, the herbivorous zooplankton species are estimated to be the greatest consumers in the low trophic level of the Gulf of Maine ecosystem. These herbivorous species in turn support a considerably smaller biomass of carnivorous zooplankton, also in the low trophic level.

Zooplankton is well studied as an energy source (prey) for the intermediate trophic level organisms. The early stages of *Calanus finmarchicus* and *Pseudocalanus* are important prey for larval fish, and the late stages of *C. finmarchicus* are prey for planktivorous fish. Several taxa, including arrow worms, amphipods, ctenophore and the carnivorous copepod *Euchaeta*, are voracious predators of these copepods, as well as other zooplankton and ichthyoplankton. *Metridia lucens* is an omnivorous copepod with a preference for small zooplankton (Bigelow 1926, Haq 1967), and provides an example of a within trophic level predator-prey relationship.

Table 10.2: An estimate of biomass, production and consumption (t km^{-2}) for low trophic level organisms in Georges Bank (GB) and the rest of the Gulf of Maine (GoM), excluding the Bay of Fundy.

Aggregation	Biomass		Production		Consumption	
	GoM	GB	GoM	GB	GoM	GB
Gelatinous zooplankton	1.3	1.4	45	53	187	188
Carnivorous zooplankton	4.9	3.8	698	54	178	138
Herbivorous zooplankton	27	25	1 091	1 324	3 822	3 777
Phytoplankton	22	25	3 609	4 270	NA	NA
Bacteria	5.5	6.5	500	595	2 085	2 478

Note: NA = not available.
Source: adapted from Gaichas et al. (2009) based on data from Link et al. (2006).

Another example of an observed predator-prey relationship within this low trophic level grouping is the grazing of the micro-algae *Alexandrium fundyense* by zooplankton species such as *Acartia hudsonica* (Campbell et al. 2005). This alga is largely responsible for paralytic shellfish poisoning in the Gulf of Maine, and zooplankton grazing has been observed to increase during strong toxic algae bloom periods. It has therefore been suggested that this trophic interaction may be an important source of mortality to the toxic bloom. Furthermore, toxin levels accumulated in zooplankton tissues through grazing on the micro-algae appear to be sufficient to pose risks to higher trophic levels, such as fishes and marine mammals (Campbell et al. 2005). However, these are relatively recent investigations and concurrent offshore Gulf of Maine field studies found maximum ingestion of *Alexandrium* accounted for only up to 3.2% of total cells ingested by zooplankton. Therefore, it is thought that increased grazing during toxic blooms may only rarely occur in nature (Turner and Borkman 2005).

Although within-trophic-level biological interactions exist at the low trophic level, low trophic level organisms may also be directly preyed upon by top level consumers, including seabirds such as phalaropes and dovekies, and North Atlantic right whales. However, a greater number of biological interactions likely occur between the low and intermediate trophic levels. Abundances of low trophic level prey organisms may affect abundances of higher trophic level predator organisms. Observed changes in zooplankton production in the Gulf of Maine appear to have affected recruitment patterns in the gulf’s fish community. Community abundance of a group of copepods went through a low period (the 1980s) and a high period (the 1990s) that is significantly positively correlated with yellowtail and witch flounder stocks. Weaker yet statistically significant interactions between the copepod *C. finmarchicus* and Gulf of Maine yellowtail flounder, witch flounder, and Georges Bank haddock have also been observed. These biological linkages between the zooplankton abundances and the recruitment of certain fish stocks suggest that the zooplankton data reflect large-scale changes in the Gulf of Maine ecosystem (Pershing et al. 2005).

10.3.2 Intermediate Trophic Level: Following Gaichas et al. (2009), the pelagic fish, demersal fish, megabenthos, shrimp and macrobenthos groups are included in the intermediate trophic level. The Gulf of Maine has a relatively high percentage of intermediate trophic level species when compared to some other global marine ecosystems (Norwegian/Barents Seas, the eastern Bering Sea, and the Gulf of Alaska) (Gaichas et al. 2009). Spatially within the gulf, total fish biomass is higher on Georges Bank than in the Gulf of Maine proper. As shown in Table 10.3, macrobenthos, not fish, make up the largest component of intermediate trophic level biomass, production, and consumption across the entire ecosystem (Gaichas et al. 2009). Macrobenthos are the larger organisms, excluding fish, which live at the bottom of the water column and in association with the sea floor. These organisms include, but are not limited to, crustaceans (crabs, shrimp and lobster), sponges, worms, starfish, oysters, clams and corals.

Table 10.3: Estimated biomass, production and consumption (t km^{-2}) for intermediate trophic-level groupings in the Gulf of Maine proper (GoM) (excluding the Bay of Fundy) and Georges Bank (GB): Note the dominance of macrobenthos in all categories. Data were derived from Link et al. (2006), and were predominantly based on stock assessments. Some values may have been modelled as necessary.

Aggregation	Biomass		Production		Consumption	
	GoM	GB	GoM	GB	GoM	GB
Pelagic fish	7.6	18	7.06	17	23	65
Demersal fish	7.4	10	3.79	4.69	7	12
Megabenthos	6.4	7.58	8.37	25	67	136
Shrimp	0.39	0.09	0.79	0.18	1.9	0.4
Macrobenthos	57	72	134	160	845	1 272

Source: adapted from Gaichas et al. (2009) based on data from Link et al. (2006).

Given the simplified three-level trophic structure described here, and the consequent numerous and varied species included at each of the levels, there are both within-level predator-prey relationships, as well as external trophic level interactions with organisms from the low and high trophic levels. Bundy et al. (2011) have noted that some within-level predator-prey relationships changed when growing fish (of the ten intermediate trophic level species studied) reached about 20 cm length. This developmental related shift in diet changed from one focused on invertebrates to a more piscivorous (fish as prey) diet. The diet of mackerel, a pelagic species, includes prey at low trophic levels such as small and large zooplankton (copepods, planktonic crustaceans, euphausiids, hyperiid amphipods and chaetognaths). It also includes prey at intermediate trophic levels including capelin (*Mallotus villosus*) and northern shrimp (*Pandalus borealis*) (DFO 2007b). The main cause of mortality for mackerel is predation by cetaceans, large cod (*Gadus morhua*), and other large pelagic and demersal fish (DFO 2007b). This variety of mackerel predators opens both benthic and pelagic pathways to the top trophic level.

The intermediate trophic-level species present in the ecosystem have significant influence on whether energy moves along a benthic or a pelagic pathway from the lowest to the highest trophic level of the Gulf of Maine ecosystem. Furthermore, organisms at the intermediate level function both as predators and as prey within the marine food web. The following examples of intermediate trophic level biological interactions within the Gulf of Maine demonstrate the roles as prey, predator, and important energy conduit that species within the level provide.

As a predator, adult pollock (*Pollachius virens*) live throughout the water column feeding on both pelagic krill and fish, such as herring, and benthic species like sand lance and silver hake. Pollock and silver hake eat similar foods and are thus also competitors (Bundy et al. 2011). The role of pollock as one of the key groundfish predators in this ecosystem has changed over the last three decades relative to the availability of prey species. Tyrell et al. (2007) suggest that pollock diet may have shifted from euphausiids (krill), squid and sand lance early in the 30-year (1973-2005) time series to depend on decapod shrimp, herring and hake in recent years. Both small and large size classes of pollock have shown an increased proportion of fish in their diet through time. Pollock has at times exerted notable predatory removals on squid (early 1980s) and, to a lesser extent, on herring (1990s to 2005) and mackerel (late 1990s). However, the total amount of prey removed by pollock has principally followed fluctuations in the number of pollock within the gulf. Changes over time in the diet composition of these fish have largely reflected changes in the relative abundance of prey (Tyrrell et al. 2007).

As the description above has shown, pollock, in its role as predator from the intermediate trophic level, draws energy from both the low and intermediate trophic levels. Additionally, pollock also draws energy both through benthic and pelagic pathways by consuming a variety of prey. As well, pollock has shifted its prey preference over time. The varied strategies of this single species highlight the complexities that face scientists in understanding marine food webs.

As a category of intermediate trophic level organisms, macrobenthos fulfill a role as prey for both within level and high trophic level fauna. Lobster is a reasonably well studied species of macrobenthos in the Gulf of Maine. For the first two to three years of benthic life, lobsters remain in or near their shelter to avoid the small fish that feed on them. As they grow and have less chance of being eaten, they begin to move about in a wider range of habitats (Lawton and Lavalli 1995).

Soft-tissue macrobenthos, largely made up of deposit feeders that wait for food to drop out of the water column above them, is the preferred food of groundfish species (Tyler 1973, Mills 1975). While the influence of the relatively recent decline in abundance of bottom-dwelling fish species on the predator-prey interactions between fish and their benthic fauna prey is not well understood, areas that have been closed to commercial finfish harvest have seen increased abundance and size of benthic species like scallop (GOMC 2004). Additionally, there is a demonstrated strong correlation between benthic invertebrate production and fish feeding within the Gulf of Maine (Collie and Curran 1985).

Atlantic herring is an important prey species for a number of intermediate trophic level consumers in the Gulf of Maine, and therefore they have been considered a species that has a disproportionate influence on the ecosystem. Changes in the herring population could be anticipated to have important consequences for a number of other species. Annual consumption of Atlantic herring by four groups of predators (demersal fish, marine mammals, large pelagic fish and seabirds) increased more than five fold between the late 1970s and the period of 1998 to 2002. The intermediate trophic level demersal fish consumed the largest proportion of this total, followed by top trophic level groupings of marine mammals, large pelagic fish and seabirds (Overholtz and Link 2006). Given its position in the food web, herring is an important component of energy transfer between the low trophic level and the top trophic level of the Gulf of Maine ecosystem.

Using the Gulf of Maine cod as an example, the challenges in understanding the complexities of trophic status, trophic interactions, and energy transfer of even a single species becomes apparent. First, cod, like some other species, feed at different trophic levels of the food web during their various life history stages. Adults are typically considered top predators in the ecosystems, but for discussions here, cod are classed as an intermediate trophic level organism, recognizing that younger (smaller) cod play a significant role as prey of other species. A 25-year study of cod in the northeast U.S. shelf ecosystem indicates that early juveniles consume more pelagic than benthic invertebrates (pelagic energy transfer and intermediate trophic level role), that medium cod consume benthic invertebrates and fish (benthic energy transfer and intermediate trophic level role), and that larger cod consume larger amounts of fish (top trophic level role) (Link and Garrison 2002, DFO 2006c). Secondly, it has also been noted that the diet of cod has shifted significantly over a period of three decades, concurrent with changes in forage species' abundance and distribution. The targeting of prey when they were abundant during the same time and space as cod indicates opportunistic feeding by cod. However, Gulf of Maine cod prefer sand lance, *Cancer* spp. crabs, and herring, regardless of the abundance or space/time overlap with these prey species. This is indicative of selective feeding habits. This shifting of feeding habits by cod inherently implies that the significance of biological interactions within individual prey species can shift over time. Thirdly, cod were a dominant fish consumer prior to the collapse of cod stocks in the Gulf of Maine. Although there has been a general trend toward more fish prey within the Gulf of Maine, cod diets continue to be relatively diverse (Link and Garrison 2002) and facilitate both benthic and pelagic energy transport through the Gulf of Maine ecosystem.

Despite the presence of both benthic and pelagic energy pathways through the Gulf of Maine trophic structure, preliminary energy modelling results show that small pelagic fishes clearly are keystone species in the current ecosystem. In terms of biomass, production, energy flows and importance for upper trophic levels, the pelagic community is more prominent than the benthic community. In particular, consumptive demand is quite high for small pelagics such as herring, squid and mackerel, which indicates that these are a keystone group (Link et al. 2006). These small intermediate trophic level pelagics appear to be more significant (high standing biomass, more prominent) in the Gulf of Maine than in other regions of the northeastern U.S. shelf (Link et al. 2006). Although the intermediate trophic level across the Gulf of Maine is dominated by the macrobenthos, the pelagic fish are also a prominent within-level consumer (see Table 10.3). This is driven, in part, by increased abundance of juvenile dogfish and small pelagic species such as herring and mackerel (Link et al. 2002). The increased abundance of these small fish may be important for energy transfer through pelagic pathways within the Gulf of Maine.

10.3.3 Top Trophic Level: An apex predator is one that is at the top of the food chain, having no natural predators. In our simplified three trophic level system, an apex predator (such as a shark) belongs within the top trophic level. However, not all top trophic level organisms are apex predators. For example, baleen whales are not considered an apex predator, but they are certainly an apex consumer within the ecosystem, and draw much of their energy source from the low trophic level.

The Gulf of Maine has a relatively low percentage of top predators when compared to some other global marine ecosystems (Norwegian/Barents Seas, the eastern Bering Sea, and the Gulf of Alaska) (Gaichas et al. 2009). Cetaceans (whales, dolphins and porpoises) have few predators, and as such they function as apex consumers in many marine ecosystems, including the Gulf of Maine. The diet of this group of top trophic level animals includes a wide variety of prey species, such as pelagic and demersal fishes, euphausiids (krill), copepods and other zooplankton, shrimp, crabs, squid, octopods, birds, and other marine mammals. As a result, they draw energy through both the benthic and pelagic pathways of the ecosystem, and from virtually every trophic level. In the Gulf of Maine their prey can generally be categorized as fish, squid or zooplankton. Using a simple five-level trophic model and 10% estimated trophic energy transfer of efficiency, Kenney et al. (1997) calculated that a significant fraction of the total net primary production (20.4% in the Gulf of Maine proper) was required to support cetacean apex consumption. This amounts to phytoplankton primary production requirements of some 111 tonnes of carbon per km^2 each year to support cetaceans within the gulf. Although cetaceans do not directly feed on phytoplankton, this measure gives us an idea of how much phytoplankton is required to support cetaceans.

Humpback whales, a baleen species found in the Gulf of Maine, are frequently piscivorous when in these waters, feeding on herring, sand lance and other small fishes (NOAA 2006). It is estimated that a large humpback whale may need to eat one ton of herring daily (about 5 000 fish). Each herring has fed on hundreds of zooplankton (particularly krill), and each krill has fed on as many as 130 000 diatoms (phytoplankton). Therefore, one meal for a humpback may represent more than 400 billion diatoms (Cerullo 1999, cited in *Science Daily* 2006). This example further highlights the manner in which baleen whales come to dominate the consumption of biomass within the food web of the Gulf of Maine, as estimated in Table 10.4.

Table 10.4: Estimated biomass, production and consumption (t km^{-2}) for top trophic-level organisms in the Gulf of Maine proper excluding Bay of Fundy (GoM) and Georges Bank (GB): Baleen whales are dominant in all three categories. Data were derived from Link et al. (2006), and were predominantly based on stock assessments. Some values may have been modelled as necessary.

Aggregation	Biomass		Production		Consumption	
	GoM	GB	GoM	GB	GoM	GB
Toothed whales	0.034	0.113	0.001	0.005	0.286	1.559
Sharks	0.009	0.048	0.003	0.007	0.016	0.032
Pinnipeds	0.063	0.000	0.004	0.000	0.306	0.000
Baleen whales	0.602	0.417	0.025	0.016	1.385	1.875
Birds	0.004	0.004	0.001	0.001	0.019	0.015

Source: Gaichas et al. (2009).

Baleen whales feed at a comparatively low trophic level compared to other top trophic organisms. They annually consume an estimated 1.3-1.8 t km^{-2} of biomass within the Gulf of Maine ecosystem, excluding the Bay of Fundy (Gaichas et al. 2009). Baleen whales (such as humpback, sei and right whales) filter plankton and small crustaceans out of the water by swimming with their mouths wide open, and collecting these low trophic level organisms with their long tightly-set gill rakers. The water then exits the body via the gill slits, leaving the prey captured in the rakers. Most of the plankton that is ingested by baleen whales consists of copepods and other crustaceans, fish eggs and larvae (CSRL 2008). In the Gulf of Maine, the spring and summer zooplankton consumption by this group is considerable. Right and sei whales are the primary cetacean consumers of zooplankton. Consumption by cetaceans remains high year round on Georges Bank (Kenney et al. 1997). Like the fish-eating cetaceans, baleen whale consumption is primarily a pelagic energy pathway. As shown in Figure 10.2, baleen whales are the single most significant natural consumer of biomass within the ecosystem, although several other marine mammals register significant consumption at the top trophic level within the gulf. Even though baleen whales are the top natural consumer within the Gulf of Maine, it is important to note that commercial fisheries are the most significant consumer overall.

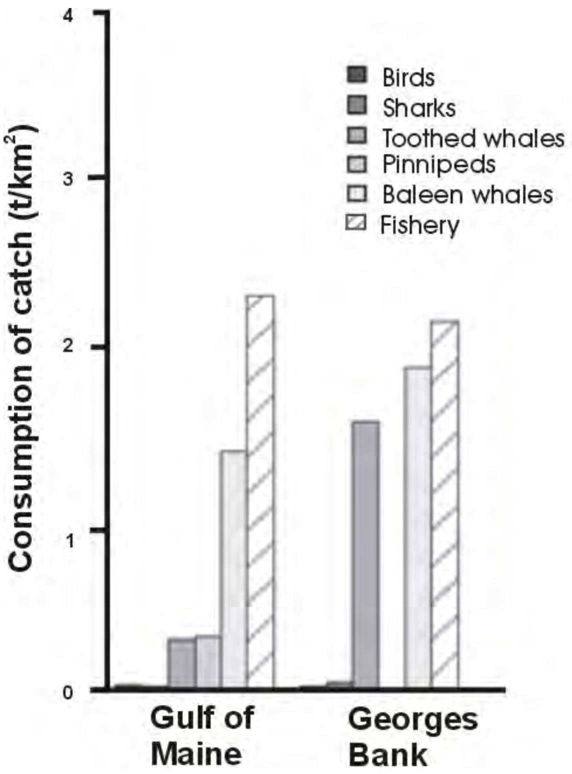

Figure 10.2: Consumption of high trophic-level functional groups of birds, sharks, toothed whales, pinnipeds and baleen whales, compared with fishery catch in the Gulf of Maine proper and Georges Bank. Baleen whales are the largest natural consumer.
Source: adapted from Gaichas et al. (2009).

Although the cetaceans draw food from numerous trophic levels, it is estimated that their consumption of fish dominates in most seasons (see Table 10.5), primarily because of the widespread distribution and high relative abundance of large piscivorous fin whales. Secondary consumption comes from the presence of humpback and minke whales, as well as some of the smaller toothed whales (Kenney et al. 1997). Stomach analysis of harbour porpoises collected between 1989 and 1994 indicated that Atlantic herring were the most important prey to this species, although pearlsides (*Maurolicus weitzmani*), silver hake, and red and white hake were other common prey species (NOAA 2006). As indicated by these examples of cetacean predation on fish, energy transfer from the intermediate trophic level to these top level predators may primarily be through a pelagic pathway given the predominately pelagic nature of the prey species.

Bluefin tuna are another top trophic level consumer and an apex predator in the Gulf of Maine ecosystem. Atlantic herring are an important prey item in the diet of the bluefin. It is estimated that bluefin tuna consumed a peak of 58.0 kt of herring within the Gulf of Maine in 1970, and a series (1970 – 2002) low of 2.2 kt in 1982. Only fin whale, humpback whale, silver hake and spiny dogfish consume more herring from this ecosystem than the bluefin tuna. The current impact of bluefin tuna on herring is about 7% of the total herring consumption in the region (Overholtz 2006). Along with herring, sand lance, mackerel, squid and bluefish accounted for 88% of consumed biomass in bluefin tuna sampled between 1988 and 1992. Dominant bluefin prey appears to vary spatially across the Gulf of Maine, such that sand lance dominates in the Great South Channel and herring at Jeffreys Ledge (Chase 2002). A recent observation adds to our understanding of energy transfer within the food web and reflects the importance of not just the abundance, but also the quality of prey items. Recently observed condition deterioration for bluefin tuna in the Gulf of Maine (Golet et al. 2007) may be related to lower observed energy density of herring (Diamond and Devlin 2003). Within the gulf there is considerable (~50%) interannual variation in the energy density (fat content) of juvenile herring. Furthermore, this may be part of a larger observed coincident decline in northern bluefin tuna and Atlantic herring condition in the Gulf of St. Lawrence, and an indication that similar changes are occurring in other Northwest Atlantic shelf systems (Golet et al. 2007).

Table 10.5: Estimated seasonal consumption of prey in tonnes by cetaceans (whales, dolphins and porpoises) in the Gulf of Maine proper and Georges Bank.

Region	Season	Fish	Squid	Zooplankton	Total
Gulf of Maine	Winter	5 269	695	0	5 964
	Spring	142 230	2 795	30 283	175 308
	Summer	241 300	2 513	35 860	279 673
	Autumn	107 270	2 720	7 645	117 635
Totals		469 069	8 723	73 788	578 580
Georges Bank	Winter	31 820	9 640	16 050	57 510
	Spring	173 275	30 835	71 587	275 697
	Summer	58 980	37 177	12 081	108 238
	Autumn	36 730	13 131	15 394	65 255
Totals		300 805	90 783	115 112	506 700
Grand total		**769 874**	**99 506**	**188 900**	**1 085 280**

Source: adapted from Kenney et al. (1997).

A number of seabird species are top trophic level consumers within the Gulf of Maine. Similar to a majority of apex predators and piscivorous fish, seabirds feed on herring within the gulf (Overholtz 2006). Juvenile herring are the main seabird prey, and breeding success of both Arctic and Common Tern at the mouth of the Bay of Fundy have (when herring has been the dominant prey) been positively correlated with the energy density of juvenile herring (Diamond and Devlin 2003). Younger age classes of herring are also an important food source for Bonaparte's Gull (Clarke et al. 2008).

More typical of public perception of a top predator, porbeagle sharks are both a top trophic level species and an apex predator, preying predominantly on intermediate trophic level organisms. Within the gulf they are known to feed mainly upon pelagic fishes such as herring, lancetfish and mackerel. However, they also eat cod, redfish, haddock, squid and shellfish, and therefore utilize both pelagic and benthic energy pathways. They do not feed upon marine mammals (CSRL 2008).

10.4 Natural Variability (Seasonal, Inter-Annual and Long-Term Changes)

Natural variability within the ecosystem occurs on seasonal, interannual and multi-year scales. Variability in ecosystem drivers leads to ecosystem responses, and the terms "drivers" and responses" are highlighted throughout this section in order to demonstrate this relationship. Understanding natural variability, and what extends beyond the typical range of fluctuations, is a key component to understanding an ecosystem such as the Gulf of Maine. Unfortunately, study of variability requires a good, consistently collected, continuous time series of comparable data. Such data is not always available, and determining which measures are statistically outside of the norm is not always possible. The following examples provide an overview of some of the driver variability within the Gulf of Maine ecosystem and the associated biological responses. Some of the noted trends and patterns of variability are statistically significant and others are qualitative or quantitative observations based on available data.

A recent study on energy transfer through the various trophic levels of the Gulf of Maine ecosystem indicates a notable influence of primary producers throughout the system (Link et al. 2008). This structure is indicative of strong bottom-up forcing where primary producers of the system can have widespread effects on the ecosystem at various trophic levels. Therefore, it can be expected that factors that alter levels of primary production (drivers) can also create significant variability within a portion of the biological community (response).

A number of drivers influence both the seasonal and interannual variability of primary production in the Gulf of Maine ecosystem. These include SST, circulation, and climate. Changes that affect stratification of the water column may ultimately prove very important in nutrient dynamics and primary production processes. Such changes may effect significant ecosystem structural change (Link et al. 2008) on a seasonal, interannual or long term basis.

The phytoplankton biomass on the U.S. northeast continental shelf (between Cape Hatteras north to and including the Gulf of Maine) follows seasonal temporal and spatial patterns that reflect a number of ecosystem drivers including stratification of the water column, increases in light intensity, the dynamics of the currents and water masses, and the introduction of nitrogen into the surface waters from depth during the well-mixed periods. Table 10.6 shows the normal seasonal spatial patterns in phytoplankton biomass and primary production that reflect the natural, but variable, ecosystem response to these drivers. Highest and earliest annual values occur in the mixed region of western Georges Bank, and lower values in nearshore and deep basin areas of the Gulf of Maine proper and eastward at the shelf edge (GOMC 2004). There can be significant variability within the expected annual pattern (See Figure 9.2 in Section 9.1.2 for typical annual cycle of phytoplankton abundance). For example, in 2007, a mid-April storm broke down the stratification that facilitates the spring bloom on the inner continental shelf of the western Gulf of Maine. As shown in Figure 10.3, large waves associated with the storm appear to have created an ecosystem response by arresting the spring bloom in mid-April, as measured by phytoplankton chlorophyll production (COOC 2007a). Although this was an abrupt change in the typical spring bloom pattern, it was still likely a “normal” variance.

Table 10.6: Seasonal peak and annual phytoplankton biomass and primary production within the Gulf of Maine proper and Georges Bank.

Region	Peak biomass (ug/L Chlorophyll a)	Annual production (g C $m^{-2}yr^{-1}$)
Georges Bank		
Well-mixed areas	8-16 (March–April)	455
Stratified areas	1-2 (April–May)	285
Gulf of Maine		
Nearshore areas	1-8 (April–May)	260
Deep basin areas	1-4 (May–June)	270

Source: O’Reilly and Zetlin (1998), cited in GOMC (2004).

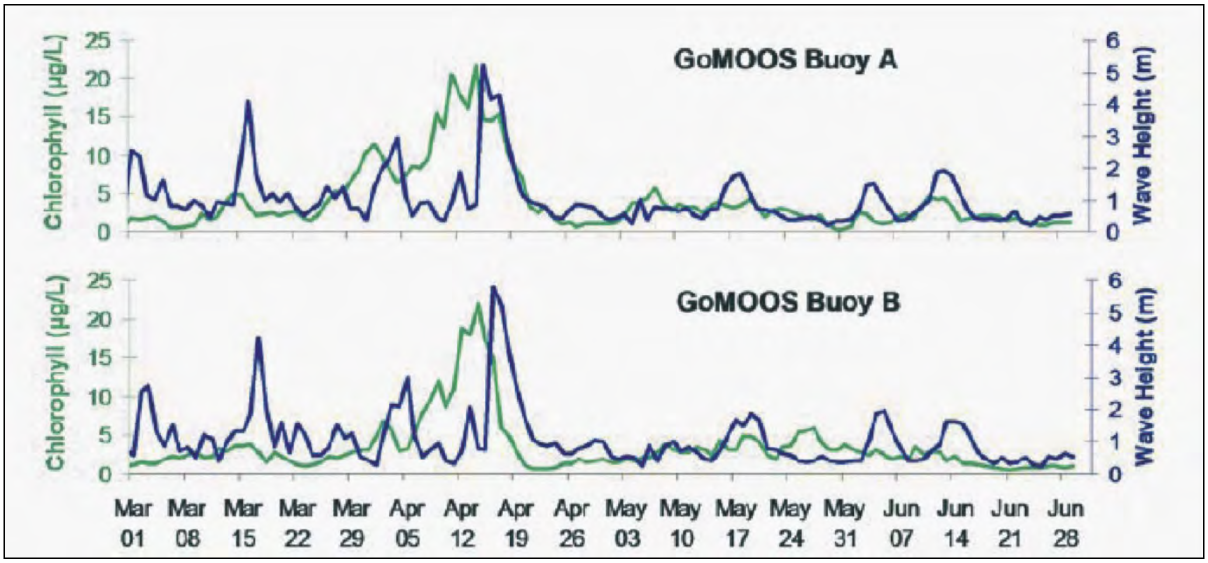

Figure 10.3: Chlorophyll (green line) and wave height (blue line, indicative of mixing) during the spring of 2007 demonstrates how phytoplankton abundance was still increasing when a storm hit in mid April. Following the storm there was no re-establishment of the spring phytoplankton bloom.
Source: COOC (2007a).

From an ecosystem standpoint, the seasonal changes in phytoplankton abundance/composition, along with the levels of primary production in different areas, are critical in determining the seasonal abundance/composition of the next trophic level. In this way, phytoplankton abundance/composition becomes a driver of ecosystem response at higher trophic levels. This next consumer level, the zooplankton community, blooms after a time lag, and even higher trophic levels of the benthic community respond following a longer lag period. The abundance and secondary production of these subsequent trophic levels is dependant in part on the character and magnitude of the phytoplankton bloom within the Gulf of Maine. The extent to which the bottom-up driven biomass and production of pelagic herbivorous fish and marine mammal species are controlled by the availability of zooplankton prey is not well known. This is because top-down selective predation by piscivores also plays a role in structuring the herbivore community (GOMC 2004).

Ten predator species from the intermediate trophic level had stomach contents assessed over the entire Gulf of Maine area (including the Bay of Fundy) during the spring, summer and autumn seasons for the period of 1998-2007 to determine both seasonal and spatial variation in diets. The results suggest that there are (1) minimal differences in diet across seasons for the species assessed, (2) minimal differences in diet are seen geographically for these species and (3) differences across species, as expected, are important (Bundy et al. 2011). Bundy et al. (2011) suggest there are several reasons why minimal differences in diet were observed across season or area within the Gulf of Maine. First, it is possible that for some predators, there is little seasonal variation in their prey distribution, thus their diet does not appear to change considerably from season to season. Benthic predators such as haddock and winter flounder were among the species for which similarity across season and area was greatest, and which fed primarily on relatively sedentary prey, such as brittle stars, worms, and amphipods.

Second, at the other end of the feeding and mobility spectrum, seasonal differences in feeding for species like white hake and silver hake may be minimized due to their relatively narrow prey spectrum. The top 80% of the silver hake diet and the top 90% of the white hake diet comprised only five prey items. In each case, all five species were present in all three seasons assessed, but in varying amounts (Bundy et al. 2011).

As the previous examples show, seasonal variability can be comparatively large for some organisms and processes (phytoplankton production), but relatively minimal for others (some predator fish diets).

As might be expected, different organisms can have different responses to the same ecosystem driver. For example, in the temperate North Atlantic, the copepod *Calanus finmarchicus* is generally known as a winter/spring cold water species that gives way to warm water species whose abundance peaks in summer/autumn. Although abundance response of *C. finmarchicus* is negatively correlated with temperature trends, *Centropages typicus* and *Centropages hamatus* are both positively related to temperature as a driver. Therefore, abundance trends are reversed, with cool years enhancing *C. finmarchicus* production and warm ones being more favorable for the two species of *Centropages*. As the production of these three species is sensitive to temperature fluctuations, they are candidate indicator species of climate warming; monitoring future abundance trends of these species could be critical in assessing the impact of climate variability (Kane 2007). Limited CPR data for the 1980s indicates that it was a period of high abundance for *Calanus* (stages 1 to 4) and euphausiids, arguably among the most important prey organisms in the Gulf of Maine (Zwanenburg et al. 2006).

Traditionally, scientific study has tended to focus on individual species and, in the case of commercial groundfish, long term data sets have been collected on certain parameters related to these species. From these data we can, for example, observe population variability for a species. However, a species’ variability is in response to one or more ecosystem driver(s). From the perspective of integrated concepts, species population data do not help identify the driver or explain the linkages (physical-biological and biological interactions) between the driver and associated response.

As an example of long-term variability, fishing is one driver within the Gulf of Maine that has produced a response within the ecosystem. Not only has fishing driven variability in a single species within the Gulf of Maine, but also within a whole community of species. During the early 1980s there appeared to be a regime shift (response) in the offshore fish community on Georges Bank, as it changed from being dominated by demersal species (cod, haddock and yellowtail flounder) to pelagic species (Atlantic herring and mackerel) (see Figure 10.4). This shift appears to be a consequence of commercial fish harvesting (the driver) (GOMC 2004). Even though many of the pelagic fish species that are now dominating fish biomass on Georges Bank (Gaichas et al. 2009) are planktivores, there does not appear to have been a corresponding decrease in the zooplankton abundance levels or changes in the zooplankton species composition that may have been expected. Shifts in dominant species within the pelagic planktivorous fish community from sand eels to herring may also have been a driver of changes in the distribution patterns of fish-eating whales, dolphins and porpoises, as well as changes in the diets of piscivorous fish species (secondary responses) (GOMC 2004). This example demonstrates how long-term variability at one level (demersal fish community) can influence an assortment of biologically linked species or groups or organisms within the Gulf of Maine.

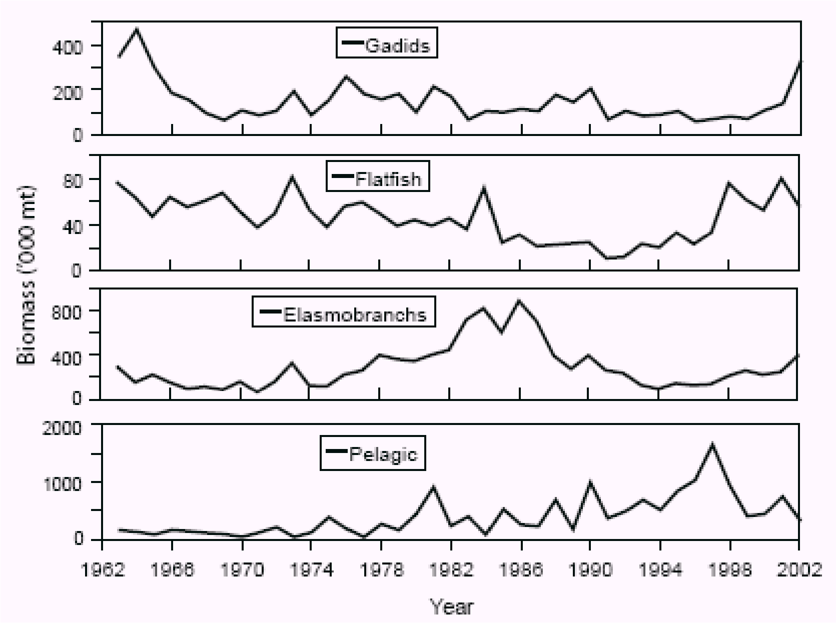

Figure 10.4: Since the 1960s, biomass of demersal fishes such as the gadids and flatfish generally declined on Georges Bank, replaced by an increase in pelagics.
Source: Link et al. (2008).

Another example of long-term variability within the Gulf of Maine has been documented through monitoring of SST. The long-term trend in mean annual SST *range* has been increasing on the northeast U.S. continental shelf, including the Gulf of Maine. Range is the difference between the high and low SST's, and therefore one measure of how variable SST is over the year. The increased range is the highest level seen over the existing 150-year time series, suggesting that we have entered a new regime of SST variability, with seasonal warming and cooling rates that have not been observed before (Friedland and Hare 2007). This seasonal temperature variability is an ecosystem driver that has the potential to affect the biological foundation of the Gulf of Maine ecosystem and its trophic structure. Because rapid warming is critical to the formation of spring blooms in the Gulf of Maine, in part through the associated change that it causes to the density structure and thermal stratification of the water column, changes in the rate of warming would likely affect the timing of the bloom and, thus, species dependent on these blooms (Friedland and Hare 2007).

One of the more studied long-term broad-scale drivers influencing ecosystem variability within the Gulf of Maine is the NAO (see Section 6.1 for further description of the NAO). Variability in the NAO has been linked to the population dynamics of marine species from algae to whales (Straile and Stenseth 2007). Alteration in the geography of weather patterns linked to the NAO also seems to be a driver affecting the spatial distribution of species. For example, the size of the thermal habitat of Atlantic salmon within the ocean has decreased during the years of positive NAO and expanded during negative phases of the oscillation (Ottersen et al. 2001). Warmer winter temperatures associated with the recent shift in the NAO towards its positive phase has allowed for the northward expansion of many warmer water species into the gulf. With further warming, summer heat stress might become an increasingly important determinant of the response of species to climate warming (Straile and Stenseth 2007). Changes in climate patterns associated with the NAO also affect a response in predator-prey interactions. Even the predator-prey interactions between crustaceans and algae have been linked to NAO (Straile and Stenseth 2007). Complex responses to the NAO generally involve a direct physiological response by an organism to some NAO-related environmental process (driver) such as temperature or salinity change. For example, low (negative) NAO may cause the water temperature in the gulf to cool, and thereby force some organisms to move, at least for a portion of the year, to a place with warmer water. Such a movement in one species may cause changes in species' interaction in the wider community, possibly creating competitive interactions or predator-prey interactions that might not otherwise have occurred. The complexity of these relationships is often difficult to characterize – that is to say, the variability of some responses of the ecosystem appears to be statistically linked to variability in the NAO, but it is not clearly understood what the mechanisms (drivers) are that cause the variability (Ottersen et al. 2001).

As noted, ecosystem drivers that affect the base of the food chain, creating variability in phytoplankton production, are likely to have significant influence on the wider biological community within the Gulf of Maine. However, it has also been noted that the macrobenthos in the gulf constitutes the largest biomass component of the intermediate trophic level (Gaichas et al. 2009), and species included in this community can likewise influence a significant portion of the Gulf of Maine biota through their variability. Sometimes we observe changes in ecosystem drivers but cannot fully predict the pending ecological response because of a lack of information on the physical-biological linkages that may exist. For example, tides play a major role in the complex interactions among the Bay of Fundy physical and biological processes. Recent observations on mud flat grain-size alteration, deepening of the sea bed, and benthic community changes indicate changing environmental conditions in the bay, possibly caused by increased hydrodynamic energy in the system (Desplanque and Mossman 2001). The potential result of such changing benthic habitats includes changes to the benthic community (GOMC 2004) that lives within these areas.

Variability need not always be directly related to a change in a physical driver resulting in a biological response. Due to complex biological interactions among species, a change in one species can drive an ecological response in another species. Such biological interactions can create trophic variability. For example, Wainright et al. (1993) have demonstrated that there is long-term variability not only in the abundance of particular species within the Gulf of Maine, but also with the trophic status of a species over time, and even trophic status for a single species spatially within the Gulf of Maine. The trophic status of haddock on Georges Bank shifted toward feeding at two-thirds of one trophic level lower by 1987 than the species had in 1929. A long-term decrease in haddock's trophic level status may be driven by a change in prey availability, a decrease in the abundance of fish prey in recent years, or even a shift towards invertebrate prey that occupy lower trophic levels. Regardless of the specific driver, it appears likely to be biological in nature rather than physical.

The interactions of predators (top-down) and resource availability (bottom-up) control the variability in community structure of aquatic food webs. Much evidence exists for bottom up drivers in the Gulf of Maine. For example, recent analysis suggests that bottom-up processes influence the abundance and species composition of the pelagic food web on Georges Bank (Kane 2007). Pelagic fish biomass and abundance of several zooplankton taxa were positively correlated, indicating that both populations depend on ecosystem drivers that regulate primary productivity. The spawning biomass of the two major planktivores on Georges Bank, Atlantic herring and Atlantic mackerel, has slowly increased since lows in the 1980s (Overholtz et al. 2004). As the biomass increase of these fishes parallels an increase in zooplankton levels, it appears their recovery was fuelled, at least in part, by the high density of prey during the 1990s, indicating predominantly bottom-up controls on the Georges Bank food web (Kane 2007).

Link et al. (2002) assessed a large number of ecosystem metrics for the Gulf of Maine that covered a long time series. It was noted that there was consistent change in multiple metrics, indicating that there was likely a large event or series of events disturbing the system during the late 1970s to early 1980s. Such examples show how species-oriented monitoring can allow us to learn about an ecosystem response, in this case evidenced by change in multiple metrics and population trends, but may not provide answers on which ecosystem drivers created the change. Table 10.7 highlights a selection of various biota trends (responses) that have been noted by scientists for the Gulf of Maine, and that cover all trophic levels. In some cases, the time frames noted by Link et al. (2002) for apparent disturbance event(s) (drivers) within the ecosystem correspond to periods of observed variability in biota. As previously noted, such changes in biota (responses) can act as drivers of still more change in the ecosystem because of biological interaction between species. Clear drivers of variability in biota have not always been apparent, and identifying them continues to challenge scientific research within the Gulf of Maine.

10.5 Resilience of the Ecosystem

Holling (1973) defined ecosystem resilience in terms of drivers and responses, such as we have used in this report throughout the previous section on natural variability (Section 10.2). He states, “Resilience determines the persistence of relationships within a system and is a measure of the ability of these systems to absorb changes of state variables, driving variables, and parameters, and still persist. In this definition, resilience is the property of the system and persistence or probability of extinction is the result.” Holling further contrasts resilience with the concept of stability, defining the later as “…the ability of a system to return to an equilibrium state after a temporary disturbance. The more rapidly it returns, and with the least fluctuation, the more stable it is. In this definition, stability is the property of the system and the degree of fluctuation around specific states the result” (Holling 1973). For the purposes of this report, we will address with examples the Gulf of Maine’s ability to ***absorb***, ***resist or recover from disturbances*** or ***to adapt to change*** while continuing to maintain essential functions and processes (The Nature Conservancy 2011) as evidence of its ecological resilience. Empirical observations are used to assess the resilience (or lack thereof) of ecosystems. However, this approach is limited to those parts of the system that we measure.

As noted, resilience is, in part, the ability to adapt to change while continuing to maintain essential functions and processes. During the late 1990s there was a dramatic shift in species composition from a demersal fish community to a pelagic fish community across both the Gulf of Maine and much of the North Atlantic shelf. Although there has been a great decline in the abundance of many benthic fish species within the Gulf of Maine ecosystem, particularly for commercial groundfish species, the resilience of the ecosystem is reflected in how it has adapted to these changes. Invertebrates such as lobster, mammals such as the harbour seal, and several small pelagic fish have thrived throughout the 1990s (GOMC 2004; Link et al. 2006, 2008; NAMA 2006; NOAA 2006; Overholtz and Link 2006; Gaichas et al. 2009) in response to such factors as release from predation and decreased competition for food that were driven in part by the decline of demersal fish. Despite the reduction in demersal fish, which had been a large component of overall Gulf of Maine biomass prior to the 1990s, overall biomass has remained comparable over 60 years of studies (Link et al. 2008), indicating the ecosystem's resilience and ability to adapt to change.

Table 10.7: Select observations of recent trends in Gulf of Maine biota.

Trophic level		**Community**	**Recent trend* and time scale**	**Source**	**Approximate size of most recent change**
Low Trophic Level	1	Phytoplankton	Chlorophyll magnitude during the spring bloom for the Gulf of Maine (excluding Georges Bank) increased during the period 1998-2008 from <15 to 18 mg m^{-3}; 8-day composite average.	(NOAA 2008)	1.2x
			Data recorded up to 2000 indicate that the spring phytoplankton bloom in the Gulf of Maine has shown a trend towards occurring earlier than prior to the 1990s.	(Sameoto 2004)	NA
	2	Zooplankton	*Calanus finmarchicus* abundance was low during the 1960s, early 1970s, and peaked during the 1980s and has been declining ever since (data to 2000).	(Page et al. 2001)	NA
			Historic zooplankton biomass in the Bay of Fundy has been ~ <10 g wet wt m^{-2}; yet recent observations have approached 40 g wet wt m^{-2}.	(DFO 2006)	4X
Intermediate Trophic Level	3	Forage fish - small pelagics	Herring numbers declined by ~85% between the early 1970s to mid 1980s, but have climbed relatively steadily since (data up to 2002).	(Overholtz 2002, 2006)	10X
	4	Piscivores - demersal, groundfish	The adult cod biomass on Georges Bank declined from an estimated 43 800 tonnes in 1990 to 8 500 tonnes in 1995, and increased to 20 200 tonnes at the beginning of 2007.	(TRAC 2007)	2.4X
			Adult biomass of eastern Georges Bank haddock increased from a near historic low of 8 500 tonnes in 1993 to ~145 300 tonnes in 2007.	(TRAC 2007b)	17X
			Winter flounder adult biomass on Georges Bank was 11 400 tonnes in 2003, and declined to 6 200 tonnes at the beginning of 2007.	(TRAC 2007c)	–1.8X
High Trophic Level	5	Apex predators - seals and sharks	Grey seal numbers in Maine waters increased from a few individuals in the mid 1970s to over 1 700 in 2001.	(Gilbert et al. 2005)	17X
			Harbor porpoise numbers increased from 37 500 in 1991 to 89 700 in 1999.	(NOAA 2006)	2.4X
			Bluefin tuna biomass declined during 1970-2002 from ~65-20 kT.	(Overholtz 2006)	–3.25X

Note: *Trends may be observed and/or statistical.

One of the key components of resilience, and the ability of current ecosystem relationships to persist despite change in ecosystem drivers, is associated with the range of tolerance of individual species. For example, despite changes in salinity and temperature beyond the long-term norms on Georges Bank, they have still remained within the range normally associated with demersal stages of cod and haddock (Page et al. 2001). Being able to tolerate a range of temperatures, depths, habitats, etc. is what allows species to be adaptable or resilient to change. When 1975 to 1994 demersal fish data for the gulf was assessed, it was found that assemblages of fish had not been distributed consistently within accepted biogeographical boundaries, and that principal components analysis (PCA) could explain only 56.3% of the variance in distribution of the species. This highlights that demersal fish assemblages in the Gulf of Maine should be interpreted as indeterminate and potentially adaptable entities, rather than as rigid ecological constructs. Even though assemblages may be persistent in composition through time, they are likely to shift in location. Furthermore, there is an apparent looseness about the assemblages of demersal fish within the Gulf of Maine, and these assemblages have shown persistence through time in spite of severe impacts from fishing (Mahon et al. 1998).

Another component of our definition of resilience is the ability to recover from a disturbance. It has been long understood that energy is transferred through the food web from the smallest organisms to the top predators. However, it is only with more recent understanding of the food web itself and the energy pathways (both benthic and pelagic) associated with it that scientists have learned why the removal of a key intermediate benthic assemblage, the groundfish, has not had more widespread repercussions within the Gulf of Maine ecosystem. Scientists have documented a high degree of throughput and interconnectedness of all the biota within the Gulf of Maine. This means that if one biomass flow pathway (either benthic or pelagic) is altered, another pathway compensates so that overall changes in standing stock biomass at a given trophic level are minimized. These conditions are all indicative of a highly productive and highly resilient system (Link et al. 2008). Recent studies have revealed that energy transfer to the highest trophic levels within the Gulf of Maine is often through pelagic pathways (Chase 2002, Diamond and Devlin 2003, GOMC 2004, Overholtz 2006, CSRL 2008), despite the fact that demersal fish biomass, and the associated benthic energy pathway, were a large overall component within the gulf prior to the 1990s (Link et al. 2008).

Ecosystem resilience also comes from not only the interconnectedness of biota within the Gulf of Maine providing multiple energy pathways, but also from its interconnectedness with other ecosystems. For example, in addition to water properties introduced by Scotian Shelf water flowing into the Gulf of Maine, the water is also thought to carry significant quantities of plankton and early life stages of gadoid fish from Browns Bank, particularly toward Georges Bank (Bisagni and Smith 1998). In this way the large-scale circulation serves to restock fish populations in the Gulf of Maine despite changes or disturbance that may occur there. Similarly, the Northeast Channel inflow from the continental slope and the Great South Channel that flows to the Mid-Atlantic Bight provide connections to other ecosystems. When seawater temperature changes are observed (DFO 1997a, Page et al. 2001, Pettigrew et al. 2005, NOAA 2008) or when temperature range changes (Friedland and Hare 2007) it can be expected that such change may exert pressure on fish and fish populations in a number of ways. For example, longer and more intense (warmer) summers would be expected to raise the metabolic demand and, thus, food consumption for a number of pelagic and demersal species. If food is not available, diminished growth and a cascade of effects dependent on growth, such as reproduction success, could be expected. However, it is also likely that many of the effects of elevated temperature will not be realized in natural populations simply because these populations will move to more suitable environments (Friedland and Hare 2007) through connections with neighbouring ecosystems north and south of the Gulf of Maine. This mobility of biota and interconnectedness with other ecosystems provides further resilience by allowing populations of biota to adapt to change in the Gulf of Maine.

Ecosystem resilience is also inherently linked to the concept of keystone species. These are species that influence the ecological composition, structure, or functioning of its community far more than their relative abundance would suggest (EEA 2011). The ability of a keystone species to absorb, resist or recover from disturbance influences the resilience of the ecosystem within which it is found. Monitoring and managing keystone species is considered one way of determining changes in the greater ecosystem. Herring is a key prey item for the majority of apex predators, seabirds and piscivorous fishes in the Gulf of Maine ecosystem (Overholtz 2006) and has therefore been considered a keystone prey species in the Gulf of Maine-Georges Bank ecosystem (Overholtz and Link 2006). In 1984, a list of keystone marine fishes was identified for the Bay of Fundy. This list includes the spiny dogfish, American shad, Atlantic herring, rainbow smelt, Atlantic cod, haddock, pollock and winter flounder (Dadswell et al. 1984). Although that list was limited to marine fishes, birds, seaweeds, benthic invertebrates and marine mammals may also be keystone. In fact, keystone species from several groups of organisms have been identified for the Bay of Fundy (Bredin et al. 2001). It is important to note that a keystone species for Massachusetts Bay may not be a keystone species for the Bay of Fundy, or for the wider Gulf of Maine. Which species are identified as a keystone is, in part, dependant on the spatial scale being considered. At this point in time, Atlantic herring appears to be one of the most consistently identified species as a potential keystone species across the Gulf of Maine. In terms of biomass, production, energy flows, and importance for higher trophic levels in the Gulf of Maine, Link et al. (2006) have identified small pelagics in general (including herring) as a keystone group in the ecosystem.

Finally, it should be noted that our limited understanding of the physical-biological linkages and biological interactions in the Gulf of Maine provides a number of challenges regarding ocean management. Further challenges also arise since these two classes of ecosystem relationships do not exist independently of one another, and their complex interconnectedness directly influences ecosystem resilience. This is perhaps most apparent with Atlantic cod, an organism that has historically been culturally, economically and ecologically important in the Northern Hemisphere. It is perhaps the most studied marine organism in and around the Gulf of Maine and, as such, there are known effects of over-fishing, environmental change (physical-biological linkages), fish community dynamics (biological interactions) and other factors that have altered the trophic ecology of the cod. However, these factors, even for a single well studied species, are not fully understood (Link and Garrison 2002).

10.6 Information Gaps

One of the challenges of ecosystem management is having enough information about ecosystem functions to understand how the ecosystem is resilient and fragile, and therefore make sound management decisions. Although the Gulf of Maine is perhaps one of the most studied marine ecosystems in the world, and is the subject of tens of thousands of scientific publications

(Parker et al. 2007b), there is still a significant amount that remains unknown. A number of potential information gaps have been identified in Table 10.8.

Table 10.8: Knowledge matrix for the deep water areas of the Gulf of Maine that have been the focus of this ecosystem overview report.

Region	High	Moderate	Poor	None
Coastal ocean				
Biota		X		
Water transport			X	
Water quality		X		
Habitat quality			X	
Offshore linkages		X		
Onshore linkages			X	
Offshore ocean				
Biota		X		
Water transport		X		
Water quality		X		
Habitat quality			X	
Offshore linkages			X	
Onshore linkages			X	

Source: adapted from GOMC (2004).

The availability of information on biota, water quality and habitat quality is greatest for the coastal watersheds and decreases with distance towards to the outer continental shelf area of the Gulf of Maine. The level of information on water quality appears to be better than that on water transport and habitat quality. Information on the functional value of various habitats is absent and habitat quality is defined on the basis of association with particular organisms or qualitative changes in the abundance/distribution of organisms following habitat loss/degradation. There are numerous biological and chemical measurements used to operationally define water quality, but the relationship of these physical parameters to biological integrity is generally only understood qualitatively (GOMC 2004).

As previously noted, resilience in the Gulf of Maine ecosystem is primarily documented by empirical observations. Our poor understanding of the physical-biological-chemical interactions within the Gulf of Maine lead to observations of ecosystem response that we do not always anticipate. It has been suggested that this is particularly true within the offshore ecosystem, where coupling between the far field ocean forcing/migration and inshore coastal areas is not well understood. These knowledge gaps prevent scientists from developing predictive models of the offshore ecosystem (GOMC 2004), and remain the challenge for current and future management of the Gulf of Maine ecosystem as we strive to further enhance our already significant knowledge of the Gulf of Maine ecosystem.

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