

GLOBEC Report No.20

Background on the Climatology, Physical Oceanography and Ecosystems of the Sub-Arctic Seas

> Appendix to the ESSAS Science Plan



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Ecosystem Studies of Sub-Arctic Seas (ESSAS)

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LIST OF ACRONYMS

ACIA	Arctic Climate Impact Assessment
AFSC	Alaska Fisheries Science Center
AMAP	Arctic Monitoring Assessment Programme
AO	Arctic Oscillation
CIL	Cold Intermediate Layer
CPR	Continuous Plankton Recorder
CPUE	Catch Per Unit Effort
CZCS	Coastal Zone Color Scanner
ENSO	El Niño Southern Oscillation
ESC	East Sakhalin Current
ESSAS	Ecosystem Studies of Sub-Arctic Seas
GLOBEC	Global Ocean Ecosystem Dynamics
GSA	Great Salinity Anomaly
IAPRC	Interagency Arctic Research Planning Committee
ICES	International Council for the Exploration of the Sea
IPO	International Project Office
LME	Large Marine Ecosystem
NAFO	Northwest Atlantic Fisheries Organization
NAO	North Atlantic Oscillation
NEMURO	Northpacific Ecosystem Model Understanding Regional Oceanography
NMFS	National Marine Fisheries Service
NOAA	National Oceanic and Atmospheric Administration
NPFMC	North Pacific Fishery Management Council
NRC	National Research Council
PDO	Pacific Decadal Oscillation
PICES	North Pacific Marine Science Organization
SL	Standard Length
SLP	Sea Level Pressure
SSC	Scientific Steering Committee
SO	Southern Oscillation
SST	Sea Surface Temperature

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1. EXECUTIVE SUMMARY

The goal of the ESSAS Program is to compare, quantify and predict the impact of climate variability and global change on the productivity and sustainability of Sub-Arctic marine ecosystems.

The Ecosystem Studies of Sub-Arctic Seas (ESSAS) Program addresses the need to understand how climate change will affect the marine ecosystems of the Sub-Arctic Seas and their sustainability. The Sub-Arctic Seas support stocks of commercial fish that generate a major portion of the fish landings of the nations bordering them. They also support subsistence fishers along their coasts, and vast numbers of marine birds and mammals. Climate-forced changes in these systems, interacting with top-down removals by fisheries, will have major economic and societal impacts.

In recent decades, components of sub-arctic marine ecosystems have shown unexpected changes in abundance or distribution that, in many cases, correlate with physical variability. The high spatial and inter-annual variability of the Sub-Arctic Seas provide the opportunity for ESSAS scientists, within a ten-year program, to use short-term variability as a proxy for studying ecosystem responses to variability at longer time scales. Understanding the underlying processes responsible for ecosystem responses is the basis for providing good stewardship as these dynamic regions evolve.

The Science plan addresses three major areas of inquiry:

- 1. What are the external forcing functions that link global and regional climate processes to the physical oceanography of the Sub-Arctic Seas?
- 2. How does variability in the physical aspects of these marine systems affect ecosystem processes and structure?
- 3. How can we integrate across spatial and temporal scales to predict how changes in climate may affect the productivity and sustainability of the marine ecosystems of the Sub-Arctic Seas?

Role of External Forcing Mechanisms

ESSAS will investigate the connections between external forcing mechanisms and hydrographic structure and physical processes in the Sub-Arctic Seas. Two major external physical forcing mechanisms dominate the Sub-Arctic Seas, atmospheric forcing (solar insolation and winds) and transport of water between the temperate regions of the North Pacific and North Atlantic and the Arctic, both of which appear to be changing in recent years. Variability in these forcing mechanisms occurs on all spatial and temporal scales, including local episodic events (storms), interannual variability at the scale of basins, and decadal- and climatic-scale events at North Pacific/Atlantic- and global-scales.

Biophysical Coupling and Ecosystem Responses

ESSAS will investigate the connections between climate-forced changes in physical aspects of the marine environment and the responses of the biota of the Sub-Arctic Seas. Some factors affecting interaction that are important in these regions include:

- 1. Sea ice: affects light, water temperature, and the availability of substrate.
- 2. **Water temperature:** affects the rates of physiological processes, and directly influences behavior of top predators.
- 3. **Stratification of the water column:** affects the availability of light, turbulence levels, and nutrients needed to support primary production, as well as the vertical distribution of many of the smaller planktonic organisms.

Seasonal sea-ice cover is a dominant feature of the Sub-Arctic Seas, and ESSAS will provide a comparative framework for investigating how changes in sea ice cover impact Sub-Arctic marine ecosystems. Sea ice is pivotal to structuring the physical environment and, in some areas, affects the timing and fate of the spring bloom and hence, indirectly, the recruitment of important commercial fish species. Climate-driven changes in the mechanisms controlling fish populations would have important implications for fisheries management.

Without a better understanding of the effects of climate variability on processes that occur at the lower trophic levels, it is clear that any predictions that might be made concerning food web structure and dynamics in relation to future climate change scenarios will be of limited value.

On the continental shelves, pools of cold subsurface water are a signature feature of several Sub-Arctic Seas during spring and summer. ESSAS will investigate how changes in the size, duration and distribution of cold pools affect the circulation and ecology on the shelves. If warming of bottom waters allows expansion of the ranges of epibenthos-feeding fish, severe new competitive pressures could impact other benthic-foraging populations.

Forecasting Ecosystem Response: Integration through Modeling

ESSAS will also develop tools for integrating the effects of bottom-up forcing by climate change across spatial and temporal scales with top-down forcing by fishing. The goal will be to provide forecasts of how Sub-Arctic marine ecosystems might be expected to behave under different climate and exploitation scenarios. Althogh there are models that address regional climate variability and others that address large-scale circulation or fisheries management, there are presently no models that provide links from global climate forcing through physical oceanography to the impact on individual organisms and then back up to the ecosystem consequences of the responses of the organisms to bottom-up and top-down forcing. The ecosystems under investigation are large, complex and highly variable in space and time so that they cannot be understood and quantified by measurements alone. A series of linked models would have the prospect of providing not only intellectually exciting opportunities to investigate the ways in which the ecosystems might respond to climate change, they would also be valuable tools for management of fisheries in the Sub-Arctic Seas. Development of a model that would facilitate inclusion of ecosystem considerations in management models would be an important contribution toward sustainable management of the ecosystems of the Sub-Arctic Seas.

Comparative Approach

The ESSAS Program will leverage knowledge and resources from three important areas: 1) past and recently completed studies of the Sub-Arctic Seas, 2) ongoing national and international programs, and 3) international programs addressing global change. In particular, there will be exciting opportunities to develop comparisons between the results obtained in the Southern Ocean GLOBEC program and ESSAS. Important within ESSAS will be the comparative approach through which insights can be gained that would not be possible by examining a single Sub-Arctic region alone. It is vital to the future economic and social well being of the people who depend upon the Sub-Arctic Seas that we understand how processes controlled by climate influence their productivity. The ESSAS Program will focus on, and contribute to, developing the information necessary as a scientific basis for the wise use and stewardship of these important marine ecosystems.

Implementation

The ESSAS Program will consist of five major areas of activity: Ecosystem Summaries, Regional Studies, Comparative Studies, Prediction, and Synthesis. Modeling activities will be important components of all but the initial Ecosystem Summaries, and will, in addition to being imbedded in the Working Groups for each activity, have a separate Working Group to ensure the overall integration of modeling efforts across all activities. To manage these activities, there will be a Scientific Steering Committee consisting of representatives from the regional programs within ESSAS, as well as scientists from outside ESSAS. The SSC will guide the formation of Working Groups, including one for Data Management. Working Groups can be formed as needed to facilitate accomplishing the goals of ESSAS.

In association with a GLOBEC-sponsored multinational symposium on the Effects of Climate Variability on the Ecosystems of the Sub-Arctic Seas to be held in May 2005 in Victoria, British Columbia, there will be an open Implementation Workshop for the ESSAS Program where representatives of programs wishing to participate in or collaborate with ESSAS will be able to present their plans and to seek partnerships for integrated collaborative and comparative studies. This venue will provide the opportunity to assess the character and composition of the Working Groups needed to implement the ESSAS Program.

Ecosystem Summaries

The development of Ecosystem Summaries has commenced with the assembly of the Appendix to the Science Plan (ESSAS, 2005), and will be furthered by presentations of Regional Summaries at the GLOBEC symposium in Victoria. Publication of the Proceedings of this symposium will constitute the first science product of the ESSAS Program.

Regional Studies

It is expected that the Regional Studies will be undertaken mainly within national programs with emphasis on understanding climate variability and the responses of the ecosystems to this variability. The ESSAS SSC will work to ensure that the studies conducted in the various ESSAS regions are cognizant of each other and that the research is conducted in a fashion that facilitates comparison between regions. To this end, the Working Groups on Regional Studies and on Modeling will provide a vital integrative function. Collaboration with those studying the human dimension of these changes will be encouraged.

Comparative Studies

A central role for the ESSAS Program will be the development of studies that take advantage of the many Regional Studies programs by focusing on comparisons of the ESSAS regions. These Comparative Studies may include new field programs, collaborations comparing time series between regions and modeling efforts. The Working Group on Comparative Studies will have the primary responsibility to identify potential field studies that could resolve critical questions and to aid the Working Group on Modeling in focusing on promising avenues of comparative research.

Prediction

A major goal of the ESSAS program is furthering our ability to predict how the Sub-Arctic Seas will respond to climate change in the longer-term. Of interest is how climate variability will interact with fishing activities, and the relative role of bottom-up and top-down forcing of Sub-Arctic marine ecosystems. Developing predictive ability will require not only development of new modeling efforts, but also the assimilation of data from time series and on-going field studies. These efforts will require close collaboration between the Working Groups on Data management and Modeling, and those engaged with the field studies.

Synthesis

Synthesis will include the modeling efforts that will integrate much of the work of the ESSAS Program, and more. The legacy of ESSAS will be a variety of products such as scientific books, special volumes of refereed journals, and contributions to fisheries management plans that make a reality of the notion of ecosystem based management. Synthesis products can also be educational tools, such as books aimed at students at various levels from the elementary grades to graduate school, web sites that provide opportunities to interact with scientists or summaries of results. The Working Group on Synthesis will play an important role from the very beginning of ESSAS in ensuring that the work done by ESSAS reaches as wide an audience as possible and has a maximum impact. This will require development of scientifically sound products that are accessible to scientists and non-scientists alike.

FOREWORD

Recent, unprecedented changes in some Sub-Arctic marine ecosystems (e.g. Newfoundland/ Labrador Shelf, the eastern Bering Sea), and a lack of information about possible linkages between these changes and climate forcing, resulted in the convening of an international workshop in Laguna Beach, California, in September 2002, to assess the requirement for a large-scale, integrated study of the Sub-Arctic Seas. The Workshop participants agreed unanimously that there is an urgent need to improve our understanding of the linkages between climate variability and the responses of Sub-Arctic marine ecosystems and their productivity in the light of global change, as detailed in the Workshop Report: Ecosystem Studies of Sub-Arctic Seas: Results of a Workshop held in Laguna Beach, California, 4-6 September 2002 (http://www.arcus.org/bering).

Subsequently, the GLOBEC SSC at its meeting in Qingdao (2002) asked G. Hunt to develop a Science Plan for this activity, and allocated IPO resources to assist in the process. Under the auspices of GLOBEC, two planning workshops were convened, the first in May 2003, in Bergen, Norway, and the second in October 2003, in Seattle Washington. A draft Science Plan was presented to the GLOBEC SSC in Swakopmund (2003), and after peer-review and modification, in October 2004 it was given final approval by the GLOBEC Executive Committee as a GLOBEC Regional program. The Science Plan for the Ecosystem Studies of Sub-Arctic Seas (ESSAS) Program outlines a multi-year comparative research effort that will provide improved understanding of the effects of climate variability, at various temporal and spatial scales, on the ecosystems of the Sub-Arctic Seas. A successful GLOBEC program in the Southern Ocean was accomplished by cooperative, interdisciplinary research undertaken by the international community. In contrast, up to now, most research in the Sub-Arctic Seas has been undertaken by single nations within their territorial waters. A goal of ESSAS is to provide a framework for coordinated, interdisciplinary internationally cooperative studies of the effects of climate change on the Sub-Arctic Seas.

There is a need to develop a research program that will investigate how global change will influence the Sub-Arctic Seas and their ability to support resources of value to people. Fishing pressure and climate change are likely to cause major changes in the marine ecosystems of the Sub-Arctic Seas. To prepare for these changes, we need to understand better how these ecosystems function and how climate-driven processes may affect the flow of energy and species interactions that determine resource productivity in Sub-Arctic marine food webs.

The ESSAS Science Plan provides background information and frames science questions that serve as guidelines for integrated, interdisciplinary studies of Sub-Arctic marine ecosystems. The proposed studies focus on the mechanisms and processes that determine the biological production of the Sub-Arctic Seas and the fate of their production as it is transferred through the ecosystems to upper trophic level consumers, including humans. Thus, the ESSAS Program acknowledges, *a priori*, the need to understand the role of upper trophic level consumers, including humans and people, as agents that structure the marine ecosystems on which they depend.

Fully executed, the ESSAS Science Program will provide a major contribution to the understanding of how global change may impact ecosystem structure and productivity, and thus the future ability of the Sub-Arctic Seas to support commercial fisheries and subsistence harvests. In developing the ESSAS Science Plan, it is assumed that it is essential to conduct comparative studies of the Sub-Arctic Seas, including inputs and outputs of properties such as heat, kinetic energy, and nutrients. It is also acknowledged that measurements are needed in all seasons, including in the generally under-sampled winter. Thus, the ESSAS Program will be a major effort requiring, as part of integrated field programs, international, collaborative research among multiple institutions and disciplines, the deployment of *in situ* long-term instrument arrays, satellite-based remote sensing studies, and the deployment of multiple ships. Numerical modeling studies will be an integral part of the ESSAS Program from the outset, and they will provide frameworks for testing program hypotheses and developing sampling scenarios. Such an ambitious effort will of necessity require capacity building through targeted training programs, the involvement of social scientists, and strong public awareness and outreach efforts.

The creativity, enthusiasm, and hard work of many scientists, both during and after the workshops, have made possible this Science Plan. We thank the members of the International Planning Workshop who assembled in Laguna Beach. Their ideas and enthusiasm were of great importance in launching this endeavor. We also thank those who gathered in Bergen, and Seattle for the Science Plan Development Workshops. Finally, Erica Head and Astrid Jarre collaborated in addressing comments by the outside reviewers. Numerous members of the marine science community provided unsolicited suggestions and these added to the development of the Science Plan. In particular we thank I. Borkin, S. Drobysheva, P. Lyubin, O. Titov, and S. Zyryanov for contributions to the background sections on the ecosystems of the Sub-Arctic Seas. The staff at the GLOBEC International Project Office provided superb support before, during, and after the Planning Workshops, and in the editing and production of the Science Plan. Dr. Edward Urban and the Scientific Committee on Ocean Research aided in securing funds for the planning process. The strong support of the Arctic Section of the United States National Science Foundation and of the Norwegian Research Council is gratefully acknowledged.

For the Planning Group George L. Hunt, Jr. and Ken Drinkwater

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SECTION I. GENERAL BACKGROUND

The Barents Sea, Iceland and Greenland waters, the Newfoundland/Labrador Shelf, the Bering Sea, the Oyashio Shelf, and the Sea of Okhotsk are among the regions that support the most important fisheries of the Northern Hemisphere. They are located at the southern extreme of seasonal sea ice cover, and thus are likely to be exceptionally sensitive to variations in climate that impact the extent and duration of sea ice cover. Sea ice is a forcing mechanism that affects the timing, amount and fate of primary production and the survival of larval fish (Rey and Loeng, 1985; Hunt *et al.*, 2002a; Napp *et al.*, 2000). Sea ice influences the temperature and salinity of the water column, its hydrographic structure, the availability of light for photosynthesis, and the spatial distribution of fish and their predators. Changes in the dynamics of sea ice will have profound influences on the ability of a region to support fish, and fisheries (Skjoldal and Rey, 1989; Hunt *et al.*, 2002a; Schumacher *et al.*, 2003).

The fish biomass of the Sub-Arctic Seas is dominated by a few species of gadid fish, particularly species of cod and pollock. These species support immense fisheries, some of which are thriving (e.g. eastern Bering Sea walleye pollock, *Theragra chalcogramma*; Hunt *et al.*, 2002a), some of which cycle through periods of boom and bust (e.g. Barents Sea northern cod, *Gadus morhua*; Nakken, 1994), and some of which have had their stocks collapse (e.g. Labrador Shelf and Grand Banks, northern cod; Drinkwater, 2002). The importance of just a few species of gadoid fishes in each region suggests that there could be considerable value in developing studies that compare ecosystem function among the regions and provide mechanisms for sharing both basic scientific information and the means to incorporate this basic knowledge into the decision making process of fisheries management.

There is considerable concern that the combined effects of climate change and fisheries removals may shift marine ecosystems into alternative stable states which may have a lower yield of species valuable to people (Parsons, 1996; Scheffer *et al.*, 2001; Pauly *et al.*, 1998). Climate change can affect both the base of a marine food web and its productivity (Rey *et al.*, 1987), and the distribution and abundance of upper trophic-level consumers (Reid *et al.*, 1998; Hare and Mantua, 2000; Hunt *et al.*, 2002a; Hunt and Stabeno, 2002). In the North Atlantic, North Pacific and Southern Oceans, decadal-scale climate changes have impacted stocks of phytoplankton, zooplankton and fish (Murphy *et al.*, 1995; Reid *et al.*, 1998; Hare and Mantua, 2000; Pershing *et al.*, 2001). In the North Atlantic, climate plays a significant role in the population dynamics of the economically important cod (Loeng, 1989; Brander, 1994, 2001; Ottersen and Stenseth, 2001; Drinkwater, 2002).

There is the potential for climate change to cause shifts in the distribution and abundance of predators that in turn control the abundance of lower trophic level organisms such as small fish or zooplankton (top-down control) (Hunt *et al.*, 2002a; Hunt and Stabeno, 2002). Alternatively, changes in the primary or secondary production may affect the abundance of higher trophic level organisms that can be supported (bottom-up control). Fisheries affect top-down control by removing vast quantities of target species, as well as lesser amounts of non-target species. These removals alter the structure and function of marine ecosystems, and provide ecological space for the increase of non-target species (e.g. dogfish and skates on George's Bank; arrowtooth flounder in the Gulf of Alaska). Thus, the relative importance of natural variability and human factors in forcing change in the Sub-Arctic Seas is an issue of great scientific and management relevance.

Comparison of the forcing mechanisms among the Sub-Arctic Seas would be useful for learning more about these ecosystems, and the responses of their biological components, including commercially exploited fish stocks, to variation in physical forcing mechanisms. Gadid populations in the Sub-Arctic Sea ecosystems have been impacted both by natural variability and fisheries extractions. Comparative studies of these systems could be valuable to fisheries managers, perhaps enabling them to avoid repetitions of the population crash that devastated the cod fishery in the northwest Atlantic Ocean. The following paragraphs provide brief introductions to the Sub-Arctic Seas and their ecology.

SECTION II. NORTH ATLANTIC CLIMATE

The leading mode of variability over the North Atlantic region is the North Atlantic Oscillation (NAO). The NAO, which essentially is an indication of the relative strengths of the Icelandic Low and the Azores High, is the principal factor controlling air-sea interaction over the North Atlantic. It modulates the site and intensity of the sinking branch of the thermohaline circulation, and it controls the strengths and paths of the principal currents in the North Atlantic. The NAO influences water mass characteristics, volume fluxes and heat exchange (e.g. Hurrell *et al.*, 2003) that in turn influences marine ecosystems via effects on primary and zooplankton production as well as fish production, particularly cod (e.g. Drinkwater, 2002).

NAO interdecadal variability can probably be attributed to large-scale air-sea interactions south of Newfoundland and at the boundary between the Greenland and Norwegian seas, and result from large-scale oscillations of the Gulf Stream intensity and amount of ice discharged from the Fram Strait to the Greenland Sea (Smirnov and Smirnov, 1998; Smirnova and Smirnov, 2000). Periods of warm air and sea temperatures over the Labrador and Newfoundland shelf are out of phase with temperatures in the northeastern North Atlantic and in the Barents Sea (Ottersen *et al.*, 2003). In the northeast, notable warming and a reduction in ice cover during the 1920-1950s were followed by the drastic deterioration of environmental conditions in the 1960s. Conversely, in the northwestern Atlantic, the mildest recorded conditions were observed during the 1960s. There, recent decades were marked by a substantial cooling that culminated at the end of the 1980s and early 1990s. There are also indications of the influence of other large-scale climate indices, for example the Arctic Oscillation (AO) (Thompson and Wallace, 1998), the Euro-Siberian Oscillation (Kelly *et al.*, 1999), and Polar-Eurasian and Scandinavian Patterns. In the Arctic region, there are also examples of inter-decadal variability that indicate linkage to the earth's nutation (Yndestad, 1999, 2003).

Despite correlations between the NAO and various physical parameters in the ocean, there remains a need to determine the mechanisms by which the NAO affects ecosystem components. It is often difficult to determine the functional relationships to ecosystem change because of the wide range of effects of the various climate parameters. For example, a change in NAO index might be associated with changes in sea temperature, the wind pattern including wind-induced mixing, advection of Atlantic water, cloud cover, rainfall and light, and mixed-layer depth and heat exchange across the sea surface. All of these parameters will in various ways influence biomass production at each trophic level.

SECTION III. NORTH ATLANTIC SUB-ARCTIC SEAS

3.1 Barents Sea

3.1.1 Physical Oceanography

The Barents Sea is an open arcto-boreal shelf-sea with an area of about $1.4 \times 10^6 \text{ km}^2$ and an average depth of 230 m (Fig. 1) (Loeng, 1991; Sakshaug and Slagstad, 1992). Although located from about 70°N to nearly 80°N, sea temperatures are much higher than at similar latitudes in the western North Atlantic or Bering/Chukchi Seas due to the inflow of warm Atlantic water. The year-to-year variability in sea temperature is also strongly influenced by the change in the properties and volume of inflow in the highly productive southern part (Loeng, 1991; Ingvaldsen *et al.*, 2003), as well as by regional heat exchange with the atmosphere (Ådlandsvik and Loeng, 1991; Loeng *et al.*, 1992). Scenarios of regional climate change indicate a further increase in sea temperatures over the coming 50-100 years (Furvik *et al.*, 2002). However, these scenarios are uncertain, and the ecological effects even more so.

The Barents Sea receives both warm waters of the North Atlantic and cold waters of the Arctic Ocean (Figs. 1 and 2). The Atlantic waters enter the Barents Sea at its western entrance mainly through Bear Island Channel (Ingvaldsen *et al.*, 2004a). The most southern part of the Sea is under the influence of an eastward flowing coastal current, an extension of the low salinity Norwegian Coastal



Figure 1. Bottom topography of the Barents Sea. (Adapted from Loeng, 1991)



Figure 2. Frontal zones and water masses of the Barents Sea (Ozhigin and Ivshin, 1999):

T: thermal fronts S: haline fronts T,S: thermohaline fronts AW: Atlantic Water AMW: Atlantic Modified Water ArW: Arctic Water BSW: Barents Sea Water NCW: Norwegian Coastal Water MCW: Murman Coastal Water WSCW: White Sea Coastal Water PCW: Pechyora Coastal Water NZCW: Novaya Zemlya Coastal Water

Current with additional input of freshwater from several local rivers. The Arctic waters penetrate into the Barents Sea from the north through the straits between Spitzbergen and Franz Josef Land and from the northeast through the channel between Franz Josef Land and Novaya Zemlya. The cold waters flow westwards and southwestwards towards Bear Island where they eventually exit. The Polar Front separates the warm Atlantic waters and cold Arctic and Barents Sea waters. Figure 2 shows water masses and the frontal zones in the Barents Sea.

Observations of temperature, salinity and other oceanographic parameters in the Kola section (along 33°30'E) have a 100 year history. The time series of temperature in the 0-200 m layer at stations 3-7 (70°30' - 72°30' N) is considered to reflect temperature variability in the southern Barents Sea and serves as an indicator of marine climate variability in the region (Tereshchenko, 1997; Ingvaldsen *et al.*, 2003). The period of 1900-1920 was colder than normal (Fig. 3). Considerable warming started in the 1920s and lasted until the 1960s, with the 1930s being the warmest decade. The temperature varied substantially in the 1960s through to the late 1980s, but that period was generally colder than the long-term mean. During the most recent years warm sea temperatures prevailed over the southern Barents Sea, though the 1990s were colder than the 1930s (Ingvaldsen *et al.*, 2003).

Variations in the properties and volume transport of Atlantic water has a great impact on the oceanographic conditions of the Barents Sea. The fluctuations in the strength of the inflow, as measured at the eastern entrance between northern Norway and Bear Island during 1998 to 2001, depends mainly on the atmospheric circulation (Ingvaldsen *et al.*, 2004a,b). While there is a tendency for higher transport in the winter, not all years show this pattern.



Figure 3. Time series of yearly mean temperature anomalies in the layer 0-200 m in the Kola section (70° 30'-72° 30'N, 33° 30'E) in the Barents Sea (thin line) and their 11-year running means (bold line). Seasonal ice coverage has a minimum in late September or early October and a maximum in April, with the long-term annual mean close to 40% of the total area of the Barents Sea (Anon, 1990). The fastest retreat of ice is typically in July-August, and the interannual variability in these months exceeds 60% of the mean (Fig. 4). A magnitude of interannual variations of ice extent in March-April exceeds 40%. The extent of ice varies widely depending on whether the climate is cool or mild. For example, in the cold winters of the 1960s and late 1970s more than 80% of the sea area was ice-covered, while in mild winters of the mid-1950s, mid-1970s and early 1990s, about 50% of the sea area was ice-free. In August-September of extremely warm years there was no ice at all over the entire Barents Sea, in cold years 15-30% of the sea area was ice-covered.



Figure 4. Ice coverage of the Barents Sea (% of sea area) in March-April (upper thin line), in August-September (lower thin line) and yearly mean (middle thin line). Bold lines are their 5 year running means.

3.1.2 Ecosystem Properties

Large-scale climate fluctuations influence the population dynamics and community structure in the Barents Sea ecosystem through a number of different mechanisms (Loeng, 1989; Ottersen *et al.*, 2001; Stenseth *et al.*, 2002). Variations in properties and volume of Atlantic water inflowing from the Norwegian Sea produce both direct and indirect effects on the marine biota in the Barents Sea, including zooplankton abundance and the survival at early life stages, biomass, growth rates, and seasonal migrations of several fish species.

Of particular importance to the Barents Sea ecosystem is the dynamic between the three commercially valuable fish stocks cod, capelin and herring (Bogstad and Gjøsæter, 1994; Gjøsæter and Bogstad, 1998; Hamre and Hatlebakk, 1998). Also, the calanoid copepod *Calanus finmarchicus*, marine mammals, including ringed and harp seals and minke and fin whales, and sea birds are abundant and play important roles in the food web.

Primary production

Primary production begins in late March and April with increasing insolation (Olsen *et al.*, 2003). The initial blooms occur in Atlantic and coastal waters and near the ice edge in the southeast (Wassmann *et al.*, 1999). During this phase, the blooms tend to be sporadic (Sakshaug *et al.*, 1995), and a significant portion of phytoplankton settles to the seabed (Matishov *et al.*, 1994). By May-June stratification develops over a large part of the Barents Sea, and bloom activity peaks. During this period, the phytoplankton abundance increases much more rapidly in Arctic than in Atlantic waters. The decline in phytoplankton abundance after the peak is also faster in Arctic water (Rey and Loeng, 1985). In June-July, nutrient depletion occurs and phytoplankton growth in Atlantic water declines (Fig. 5). A sub-surface "bloom" develops in the nutricline, and the relative importance of production dependent on regeneration of nutrients increases. During June and July, a zone of spring "bloom" associated with the retreating ice edge spreads towards the north and northeast (Rey and Loeng, 1985).



Figure 5. Long-term mean seasonal variation of oxygen and phosphate at station No.5 of the Kola section (71°30'N, 33°30'E) in the surface layer (a) and near the bottom (b).

In the second half of summer and in the autumn, most of the nutrients in the photic layer are contained in the phytoplankton biomass. "New" primary production continues in the western part of the Barents Sea supported by an episodic supply of nutrients in Atlantic water that is mixed to the photic zone in frontal regions. In Arctic water, a bloom continues to follow the retreating ice edge until August-September (Rey and Loeng, 1985). During winter, production is low, and the distribution of nutrients in the water column becomes homogeneous.

In general, in Arctic waters, primary production is largely limited to the spring bloom while in Atlantic waters, a relatively large portion of primary production occurs in the summer and autumn. For this reason, annual primary production in Atlantic waters is approximately 3 times and "new" production is 2 times greater than in the Arctic waters of the Barents Sea (Table 1).

Water Mass	"New" Production	Total Primary Production		
Coastal Water	39	82		
Atlantic Water	83	174		
Barents Sea Water	86	172		
Arctic Water	42	66		
All Water Masses	60	111		

Table 1.	Mean	primary	production (g C	m ⁻² y ⁻¹)) in the	Barents Sea	(Titov,	1994))
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Zooplankton

The zooplankton community of the Barents Sea is characterized by the presence of both warmwater and cold-water species. *Calanus* dominates the zooplankton biomass in the Barents Sea (*C. finmachicus* in the Atlantic and boreal waters and *C. glacialis* in Arctic waters) although *Euphasiacea* are also important (Bogorov, 1974). The long-term mean biomass of the zooplankton is about 200 mg m⁻³ (Nesterova, 1990) and is fairly stable, changing interannually by no more than a factor of 2 or 3 (from 50 to 600 mg m⁻³; Fig. 6a) (Nesterova, 1990). The reason for this relative stability is that the abundant species are tolerant of a wide range of water temperatures and they are differentiated in space and time (Zelikman, 1977). Zooplankton production typically starts in the southwest of the Barents Sea in April and May, then spreads on to the northwestern, central and eastern areas in June-July and finishes in the northeastern part of the sea in August-September. The difference in the timing of growth in the north and in the south can be as much as 2 to 3 months (Drobysheva *et al.*, 1988). Accordingly, the feeding areas of capelin and cod shift northeastward over spring and summer, following the pattern of development of *Calanus* and *Euphausiacea* (Degtyareva, 1979). In the southwestern Barents Sea, *Calanus* begin spawning earlier in warm years. Thus, the mean zooplankton biomass for April-May equals 121 mg m⁻³ in cold years, while in warm years it is considerably higher (198 mg m⁻³) (Anon, 1992). In April, there is a significant correlation (r > 0.7) between temperature and zooplankton biomass in the upper 50 m layer in the southwestern Barents Sea (Degtyareva, 1979), but by June there is no longer any significant correlation (Ozhigin *et al.*, 2003).



Figure 6. (a) Biomass of *Calanus finmarchicus* in the 0-50 m layer at stations 3-7 of the Kola Section in June (thin line) and 5-year running mean (thick line); (b) Euphausid abundance in the southern Barents Sea in October-December (thin line) and 5-year running mean (thick line); (c) Euphausid abundance and capelin biomass. (from Ozhigin *et al.*, 2003)

The Atlantic inflow is thought to play an important role in advecting zooplankton, especially *C. finmarchicus* into the Barents Sea (Skjoldal and Rey, 1989; Skjodal *et al.*, 1992). They suggested that increased inflow could result in a higher influx of zooplankton but also greater amounts of warm water would also lead to elevated zooplankton production because of faster growth and, hence, lower mortality. However, an inverse relationship between temperature and zooplankton biomass (Skjoldal *et al.*, 1992; Tande *et al.*, 2000) was found but this may be explained by different faunal and seasonal succession in Arctic versus Atlantic water masses (Tande *et al.*, 2000). Indeed measurements taken on 2 different occasions in June and July 1998 indicate a net eastward flux of zooplankton into the Barents Sea in the Atlantic inflow but varying by 2 orders of magnitude between measurements (Edvardsen *et al.*, 2003).

Thysanoessa inermis and *Th. raschii* represent a major part of the Barents Sea euphausiids. *Th. longicaudata* is also found in the central and southwestern Barents Sea and reproduces there (Dalpadado and Skjoldal, 1996) but such species as *Meganyctiphanes norvegica* are scarce. In general, the long-term mean annual production by all euphausiids is about 20 x 10⁶ t. Interannually, their abundance varies from 50 to 1200 ind./1000 m³ (Fig. 6b) or from 9 to 50 x 10⁶ t, if converted to biomass (Fig. 6a) (Drobysheva, 1994). However, in the Barents Sea there is an out of phase variation in the abundance of warm-water and cold-water species. The total abundance of euphausiids is regulated through predation by fish, primarily, capelin (Fig. 6c).

Zooplankton-fish interactions

Calanus are the major prey of juvenile fish in the Barents Sea (capelin, cod and herring larvae). Capelin is a major predator on zooplankton, especially euphausiids (krill) and amphipods, with their importance varying with season and size of capelin. Predation by capelin can be as much as 26% of the available biomass of euphausiids (4 x 10^6 t y⁻¹, on average) and 10 times larger than the consumption by other fishes. Indeed, capelin probably exploits most of the zooplankton production during its main feeding season, a result supported by a statistically significant negative relationship observed between capelin stock size and zooplankton biomass in the Barents Sea (Dalpadado and Skjoldal, 1996; Dalpadado *et al.*, 2002).

Different age groups of cod feed on euphausiids and amphipods the whole year round. They are major prey of 0 and 1 group cod. In winter, juvenile cod depend on them for survival while in summer, mature cod enhance their growth rates, fatness and fecundity by feeding on euphausiids (Ponomarenko, 1984; Orlova *et al.*, 2001). Adult cod tend to switch their diet to euphausiids and amphipods especially when the capelin stock size is extremely low (Dalpadado and Bogstad, 2004).

Cod and capelin have different impacts on euphausiid populations. Capelin influence the formation of future generations of euphausiids, while cod consume post-spawners. Food relations between cod and capelin are also complex, as they have both direct and indirect links. The indirect link is that mature capelin consume large quantities of euphausiids in spring, and thus capelin can effectively influence the availability of euphausiids for cod in summer; the direct link is that cod, feed on capelin and their own juveniles. This contributes to conservation of euphausiid stocks by reducing predation by capelin. In the Barents Sea ecosystem, capelin plays a key role in trophic transformations. Zooplankton and capelin define the efficacy of utilization of primary and secondary production there, and thus impact the overall biological production.

Annually, the feeding areas of capelin and cod shift northeastward over spring and summer, following the pattern of development of *Calanus* and *Euphausiacea* (Degtyareva, 1979). In warm years, the feeding area of capelin is extensive and reaches as far north as Franz Josef Land (Fig. 7) (Ozhigin and Luka, 1985). In cold years the feeding area grows narrower and is displaced to the southwest.



Figure 7. Capelin feeding migrations in warm (a) and cold (b) years. 1) mature capelin; 2) immature capelin; 3) feeding area; 4) polar front. (after Ozhigin and Luka, 1985).

Benthos

Zoogeographically, the Barents Sea benthic fauna can be divided into boreal fauna (Atlantic and coastal waters in the southwest) and an Arctic fauna (the rest of the sea). The presence of sand or ooze at a site defines the composition of the dominant species of benthos, with an inverse relationship between depth and biomass (Antipova, 1975).

Benthic populations respond to long-term variations in marine climate rather than short-term fluctuations. Thus, climate change has the potential to cause change in these communities. For example, in the cold period of the 1960s, there was a decline of benthic biomass as compared to the 1930s which were warmer (Antipova, 1975). Alternatively, the reduction of biomass in the late 1960s may have been the result of the trawl fishery (Denisenko, 2001). In the 1960s, there was also a contraction of the distribution for boreal (warm-water) species and an expansion of Arctic (cold-water) forms that were not likely the result of trawling (Galkin, 1981).

Benthic organisms are important food for epibenthic fish (Miloslavskaya, 1958) and a number of valuable invertebrates (Gerasimova and Kochanov, 1997), such as a recently introduced species, the red king crab.

Fish

The Barents Sea is capable of maintaining large fish populations with approximately 150 species of fish in the area. Cod, capelin and herring are the key commercial species, but over-harvesting of fish resources has decreased their populations noticeably during the past few decades.

Climate also plays an important role in the changes in distribution and production of the major fish species. Cod and capelin generally move north and eastward during warm periods, such as in the 1930s and 1940s, and retract further south and westward in the Barents Sea during cooler periods (Blacker, 1957; Vilhjalmsson, 1997). During the warm 1930s a herring fishery developed along the Murman coast whereas previously this species was almost unknown in this region (Beverton and Lee, 1965).

The southern Barents Sea is the most productive region, and is home to the worlds largest cod stock, the Arcto-Norwegian (or Northeast Arctic) stock. Good recruitment of cod is dependent on higher than average temperatures (Sætersdal and Loeng, 1987; Ottersen and Sundby, 1995; Dippner and Ottersen, 2001; Ottersen and Stenseth, 2001; Sirabella *et al.*, 2001). The main reasons for this link has been suggested to be due to (i) higher primary production due to a larger ice-free area, (ii) a larger influx of zooplankton carried by the increased inflow of Atlantic water masses from the southwest and (iii) higher temperatures promoting higher biological activity at all trophic levels (Sakshaug, 1997; Drinkwater *et al.*, 2003). Warm conditions in the Barents Sea are related to a positive NAO phase and links between the NAO and cod recruitment have been demonstrated (Dippner and Ottersen, 2001; Ottersen and Stenseth, 2001).

Changes in climate patterns associated with the NAO also affect predator-prey interactions in the Barents Sea. An increase in the basic metabolic rate of cod, associated with higher temperature during years of high NAO index values results in an increase in the consumption of capelin (*Mallotus villosus*) by 100 thousand tonnes per degree centigrade (Bogstad and Gjøsæter, 1994; Drinkwater *et al.*, 2003).

Seabirds

Approximately 13 to 16 million seabirds of more than 20 species breed around the coasts of the Barents Sea. Consumption of fish by sea birds is estimated to be between 10% and 50% of the yearly catch of fish in the fisheries, or about 730,000 t y⁻¹ (Belopolsky and Shuntov, 1980; Mehlum and Gabrielsen, 1995). The most plentiful fish-eaters are Atlantic puffin (Fratercula arctica), Brünnich's guillemot (Uria lomvia), and common guillemot (Uria aalge). The largest colonies of Atlantic puffin and common guillemot are found on the coast of Norway and West Murman, where their major prey are herring, sand-eel, capelin, haddock and saithe. On Spitzbergen and Bear Island, polar cod predominate in the diet of Atlantic puffin. Major breeding colonies of Brünnich's guillemot are on Novaya Zemlya and Spitzbergen (more than 97% of the Barents Sea population). Brünnich's guillemot is the most important consumer of fish, of which polar cod (up to 95-100% on Novaya Zemlya) and capelin (up to 70-80% on Spitzbergen) are dominant in the diets. A strong anthropogenic impact on fish populations has indirect adverse effects on the communities of fisheating birds as their numbers are directly related to the availability of food (Erikstad, 1990). For instance, in the mid-1980s, the stocks of capelin and polar cod were severely depleted by the fisheries and seabird chicks in colonies on the coasts of Norway, Murman, and Novaya Zemlya suffered high mortality (Vader et al., 1990). In such years, guillemots in the Bear Island region of the Barents Sea switched to euphausiids (Mehlum, 2001).

Marine mammals

There are about 20 species of cetaceans and 7 species of pinnipeds in the Barents Sea. The majority of cetaceans are only present seasonally. Among the most common are minke whale (*Balaenoptera acutorostrata*), 85,000 individuals (Schweder *et al.*, 1997) and white-beaked dolphin, 60,000-70,000 individuals. Minke whale prey consumption is approximately 1,800,000 t, including

about 140,000 t of capelin, 600,000 t of herring, 250,000 t of cod, and 600,000 t of euphausiids (Bogstad *et al.*, 2000). Of the pinnipeds, the most common is the harp seal (*Phoca groenlandica*) whose abundance in the White Sea is 2,200,000 individuals (ICES, 1999). Abundance trends are largely unknown, though an upward trend has been noted for harp seal, walrus (*Odobenus rosmarus*), and common seal (*P. vitulina*). Ringed seal (*P. hispida*) in the western part the Barents Sea may be declining. Yearly food consumption by harp seals in the Barents Sea is estimated at a maximum of 3,500,000 t, including 800,000 t of capelin, 200,000 to 300,000 t of herring, and 100,000 to 200,000 t of cod. (Bogstad *et al.*, 2000; Nilssen *et al.*, 2000).

3.2 Iceland/Greenland Waters

3.2.1 Physical Oceanography

The Iceland Sea (Fig. 8) is the area between Iceland, Greenland and Jan Mayen (ca. 66°30'-71°00'N, 8°-28° W). Due to its location near the polar front, this region is particularly sensitive to climatic changes, which at the same time have a marked influence on the distribution and behavior of marine organisms (e.g. Malmberg and Blindheim, 1994; Astthorsson and Gislason, 1995, 1998; Astthorsson and Vilhjalmsson, 2002).

The general features of the current system and water mass distribution around Iceland have been described by Stefánsson (1962, 1999) and Valdimarsson and Malmberg (1999). The warm and saline Atlantic water (Irminger Current) flows along the south and west coasts of Iceland and splits into two branches off the Vestfirdir Peninsula. The larger branch turns west and southwards, meets the arctic East Greenland Current and forms a cyclonic eddy in the Irminger Sea. The other branch flows eastwards on to the shelf north of Iceland (southern Iceland Sea) as the North Icelandic Irminger Current (Fig. 9).



Figure 8. Bottom topography around Iceland. The 400 m depth contour is considered to mark the Icelandic shelf area.



Figure 9. Ocean currents around Iceland. (Modified from Stefánsson and Ólafsson, 1991).

In the northwestern part of the Iceland Sea the arctic East Greenland Current contributes to the East Icelandic Current that transports arctic water into the southern Iceland Sea. Southwest of Jan Mayen, an appreciable current is directed to the north or northwest, bringing relatively warm and saline water from the Norwegian Sea. The central part of the region between Iceland and Jan Mayen is characterized by a weak cyclonic circulation that feeds water to the East Icelandic Current (Fig. 9).

During recent decades, considerable variation has been observed in the relative magnitude of the of the North Atlantic Irminger Current and the East Icelandic Current north of Iceland and these variations have been reported to have considerable repercussions for the local marine ecosystem (e.g. Malmberg and Blindheim, 1994; Astthorsson and Gislason, 1995, 1998; Astthorsson and Vilhjalmsson, 2002).

A hydrographic section across the shelf in the Sub-Arctic waters north of Iceland (Siglunes section, 66°16′N, 18°50′W - 67°00′N, 18°50′W) has generally been used to characterize the volume of Atlantic water flowing into the region north of Iceland (Fig. 10). The period 1952-1964 was characterized by a strong inflow of Atlantic water, while during 1965-1971, the inflow was negligible. Since 1971, the inflow has been rather variable, often with 3-4 years of marked inflow and then a few years of limited inflow. During the most recent years, the Atlantic inflow has been relatively strong (Anon., 2002). To some extent, these fluctuations in the inflow of Atlantic water onto the northern shelf can be related to large-scale changes in the atmospheric circulation (e.g. NAO) over the North Atlantic Ocean (Malmberg *et al.*, 1999). The finer details of the hydrographic conditions on the shelf north of Iceland, however, appear to depend to a greater extent on local northerly and southerly winds than large-scale atmospheric features such as the NAO (Ólafsson, 1999).

The West Greenland marine system is considered to lie between about 60°N, the latitude of Cape Farewell, and about 70°N, the latitude of Disko Island. The near shore bottom topography is characterised by a continental shelf 60-200 km broad. The physical oceanographic conditions in West Greenland waters are controlled by the large-scale circulation in the North Atlantic: a branch of the warm North Atlantic current circles anti-clockwise in the Irminger Sea off southern east Greenland to join with the cold East Greenland current and round Cape Farewell to form the north-setting West Greenland Current. Under the influence of this relatively warm current, the West Greenland marine



Figure 10. Temperature and salinity deviations in late spring from the 1961-1980 average on the Siglunes section to the north of Iceland (the deviation is based on 5 stations between 2 and 46 nautical miles offshore and data from 0, 20, 50, 75, 100, 150, and 200 m. depth).

ecosystem is Sub-Arctic. Sea ice in winter usually extends no further south than about 66°N. The transport of heat, salt, and nutrients, as well as plankton, fish eggs and larvae, to Greenland waters by these dominant North Atlantic current systems and their fluctuations as a consequence of climate change are - together with runoff of fresh water from land - the major governing processes for the Greenland marine ecosystem.

For West Greenland there exists a continuous series of temperature and salinity observations spanning more than 50 years, but interdisciplinary research is needed to understand the physical, chemical and ecological processes that will be affected by climatic change and potentially cause changes in the marine ecosystem.

Investigations in other regions have documented that hydrographic fronts are important to plankton community structure and dynamics. Plankton production at fronts is transferred to higher trophic levels including commercially important fish stocks. Observation of fish catch and distribution of seabirds and marine mammals support the thesis that such sites are of key importance in understanding, as well as exploiting, the production from the West Greenland ecosystem. The coupling between frontal dynamics on the one hand, and ecosystem function and production on the other, along the banks at West Greenland has not previously been investigated, but in particular, knowledge about frontal dynamics and upwelling of nutrients from the deeper parts to the surface layer is needed if the pelagic production is to be understood.

3.2.2 Ecosystem Properties

Primary Production

On the Iceland shelf, interannual variation in primary productivity were mainly ascribed to changes in inflow of Atlantic water and its influence on stratification of the water column (Gudmundsson, 1998). During years of limited Atlantic inflow (cold years), the water column stabilizes after the initial spring bloom, nutrients become exhausted, the bloom ends abruptly, and biomass remains low throughout the summer. During warm years, the Atlantic inflow maintains mixing and leads to higher primary production (Thordardottir, 1977, 1984; Stefánsson and Ólafsson, 1991; Gudmundsson, 1998). This influence of the hydrographic conditions on the primary production is further demonstrated in Figure 11 that compares the Icelandic shelf stations of high salinity (> 34.5) with those of lower salinity (< 34.5).





Zooplankton

Calanus finmarchicus is the dominant member of the meso-zooplankton community on the northern shelf and commonly constitutes between 40 and 60% of the biomass in spring. Off the northern shelf, *C. finmarchicus* may dominate in numbers, but *C. hyperboreus* dominates in biomass (Astthorsson and Gislason, 2003). The spring zooplankton biomass in the upper 50 m over the north Icelandic shelf commonly ranges from 2-4 g dry weight m⁻². The highest biomass (8-16 g dry weight m⁻²) is attributed to large but slow-growing arctic species (*Calanus hyperboreus* and *Metridia longa*) that may have multi-year life cycles. These are usually found in the Arctic waters of the East Icelandic Current off the northeast coast (Astthorsson *et al.*, 1983; Astthorsson and Gislason, 1995). Due to the relatively long generation times of the Arctic species, advection may be relatively important in regulating their local biomass (Gislason, 2002). Studies on long term variations in zooplankton biomass was significantly higher in warm years than in cold years (Astthorsson and Gislason, 1994, 1995).

Advection of zooplankton is an important process, determined by the interaction between seasonal vertical migration and fluctuations in the ocean currents (Astthorsson and Gislason, 1995). Changes in the oceanic circulation will affect the transport of zooplankton, and therefore also the feeding conditions of pelagic predators.

The pelagic ecosystem off West-Greenland is poorly known, and baseline studies are therefore necessary before processes such as climate change can be addressed or scenarios modelled. Historically, most research in Arctic pelagic ecology has considered only the larger components of the food web, e.g. the diatoms and calanoid copepods. Research during the last century has documented the annual cycle and population dynamics of *Calanus* copepods and stressed the key role of these organisms in high-latitude ecosystems. This part of the food web is the direct link to the fish stocks. Several key seabird species also rely on *Calanus*.

The microbial food web in the Arctic has received relatively little attention. However, in highlatitude ecosystems the function of these small grazers in coupling primary production to the fish stocks has to be considered. Recent investigations in Disko Bay and Young Sound and on the Banks off West Greenland have documented that bacterioplankton and unicellular zooplankton play a prominent role (Rysgaard *et al.*, 1999; Levinsen and Nielsen, 2002). Judged on relative biomass distribution, a large part of the primary production may be channelled through these micro-organisms.

From a carbon sedimentation point of view the composition of the grazer community is also essential. Zooplankton influences carbon dynamics in several ways: by vertical migration, through grazing activity, and as accelerators of sedimentation of organic matter through production of fecal material. An efficient transfer of organic matter produced in the water column to the sea floor through a close pelagic-benthic coupling, together with low metabolism of benthic fauna, are among the reasons why high benthic biomass can be maintained in Arctic regions. Despite permanently low temperatures, near-shore Arctic benthic communities mineralize organic matter as efficiently and as rapidly as communities at lower latitudes. Although it represents the link between pelagic production and benthic animal production, virtually no measurements of vertical export exist from West Greenland waters. Furthermore, knowledge of distributional patterns and remineralization potential of the benthos along the West Coast of Greenland is absent. No studies have dealt with growth and production of individual species, and such studies are necessary in order to elucidate the ecological role of macrobenthos in the Arctic food chain.

Fish stocks

During recent years the fish catch from the waters around Iceland has been in the range of 1.5-2.0 million tonnes, with the fishery of pelagic fish stocks constituting about 1/2-1/3 of the total catch. The northern cod is by far the most important of exploited demersal stocks, and capelin is by far the most important pelagic stock. The deepwater shrimp *Pandalus borealis* is the most important of the invertebrates exploited in Icelandic waters (Fig. 12).

The main spawning grounds of the most important Icelandic fish stocks (e.g. cod, haddock, capelin) are located relatively close to the coast in the warm Atlantic waters off the south and southwest coasts (Jónsson, 1982). From the main spawning grounds the eggs and larvae drift with clockwise currents to the nursery and feeding grounds in the waters off the northwest, north, and northeast coasts.



Figure 12. The catch of pelagic fish in Icelandic waters during 1950-1998.

During their juvenile years, most of the demersal fish stocks occupying the waters to the north of lceland are confined to the shelf area. On the other hand during the summer as the ice in the lceland Sea retreats, capelin, which is the most important pelagic stock on the northern shelf, undertakes extensive pre-spawning feeding migrations further northwards. This northern part of the lceland Sea is virtually free of fish eating predators, except for humpback and minke whales, and by conducting these migrations the capelin are transferring large amounts of energy from the northern part of the lceland Sea to the north lcelandic shelf (Vilhjalmsson, 1994).

The year class strength (measured as numbers of 3 year olds) of Icelandic cod has been estimated as far back as 1920, including the component of the year class being immigrants from Greenland to Iceland (Schopka, 1994) (Fig. 13). All the largest year-classes include immigrants from Greenland, and the three largest year classes were to a great extent composed of immigrants from Greenland. During the whole period 1985-1997, recruitment was generally poor, with the 1996 year class consisting of only 54 million individuals, which was the poorest on record. With the exception of the 2001 year-class, since 1997, yearly cod recruitment has increased to *ca.* 200 million.





Drift of cod larvae from the spawning grounds at Iceland to Greenland waters extends the nursery area for cod of Icelandic origin, and thus both climate and fisheries around Greenland directly affect the state of the cod stock around Iceland. The warming of the northern North Atlantic in the early 1920s extended the distribution area of cod along the east, but particularly the west coast of Greenland. Combined with the drift of larval cod from Iceland to Greenland and the subsequent return of these fish as mature individuals, this warming is considered to be the main reason for the outburst of the superabundant year classes at Iceland in the early 1920s (Schopka, 1994).

Prior to 1970, this immigration took place more often than it has during the last three decades (only twice, 1973 and 1984). This is may be related to the reduced stocks of Icelandic cod stock in the last 3 decades compared to earlier, and the recent lack of successful reproduction by cod in west Greenland waters because of the cold marine climate. Further, there must have been a decline in the frequency of larval drift from the Icelandic ecosystem towards Greenland, possibly caused by

changes in the environment of the North Atlantic which took place during the late 1960s (Dickson *et al.*, 1988). Dickson and Brander (1993) suggested that increased larval exchange between Iceland and Greenland in warm years was connected to a strengthening of the Irminger/West Greenland Current system.

Capelin is a key species in the Icelandic ecosystem. It is the pelagic species with the largest biomass, the most important food for cod, and supports an extensive fishery. Capelin spawn off the south and southwest coasts of Iceland in February-March, and during summer the larvae drift to the nursery and feeding grounds northwest, north and northeast. During the months of June-September, most adult Icelandic capelin migrate north to feed in the deep waters of the Iceland Sea (Fig. 14), where they are out of reach of cod. This situation changes with the return of the capelin to the shelf area north of Iceland in late autumn. From then on and until spawning off the southwest coast, the adult capelin are eaten by the cod in large quantities (Pálsson, 1983; Magnússon and Pálsson, 1991). Furthermore, capelin is a major food constituent for other predators, such as Greenland halibut, saithe, seabirds and whales (Vilhjálmsson, 1994, 1997).

As mentioned earlier, influx of Atlantic water into the North and East Icelandic shelf area leads to increased primary production and zooplankton biomass, while the presence of polar water has the reverse effect. Astthorsson and Gislason (1998) have shown that zooplankton biomass in the waters north of Iceland is on the average higher during years when Atlantic inflow takes place than during years when it does not occur. Further, the mean weight-at-age and biomass of capelin were significantly larger in warm years than cold years. This influence of the hydrographic conditions on



Figure 14. Feeding areas and spawning grounds of adult Icelandic capelin. The feeding areas (grey) and spawning grounds (black). White arrows indicate feeding migrations and black arrows spawning migrations. (Redrawn from Vilhjálmsson, 1997)

both the primary and secondary production is also clearly reflected in the growth of capelin, which is better during years when the inflow of high salinity Atlantic water is strong. Magnússon and Pálsson (1991) showed that the Icelandic cod stock had lower stomach contents, reduced feeding levels and slower growth rate when the capelin stock was small. Vilhjálmsson (1997) reported that during the near-collapse of the Icelandic capelin stock in the early 1980s and 1990s, the weight at age in the Icelandic cod stock, decreased by about 25% (Fig. 15) for weight changes in 6 year old cod). It is quite clear that other available prey species cannot fully substitute for the loss of the capelin from the food resources available to cod in the Icelandic area.



Figure 15. Changes in capelin biomass and mean weight of Icelandic cod at age of 6 years. (Redrawn from Vilhjálmsson (1997) and additional data)

A conceptual model of how, during different regimes, climatic factors may through the food chain greatly affect the yield of cod in Icelandic waters is presented in Figure 16. The chain of events leading from fluctuating environmental conditions to different biomass of cod in warm and cold years may be simplified in the following way (Astthorsson and Gislason, 1998). The inflow of Atlantic water onto the shelf area north of Iceland (the southern Iceland Sea) is an important factor in maintaining mixing and renewal of nutrients and it also restricts the flow of arctic water from the north and thus hampers southward extension of ice. The higher nutrient levels and moderate mixing during warm years leads to a longer lasting phytoplankton bloom and probably also higher annual primary production compared to the cold years when the waters are more stratified and nutrients become rapidly depleted. Food availability for zooplankton is thus likely to be higher in warm years than in cold ones. A larger influx of Atlantic water may also result in greater advection of zooplankton biomass originating from the waters west and south of Iceland on the northern shelf area. Lastly, higher temperature conditions as such may favor faster growth. Both directly and indirectly, zooplankton production and biomass in the waters to the north of Iceland are thus likely to depend strongly on the hydrographic conditions. The higher zooplankton biomass is reflected in larger weight of individual capelin and larger biomass. Finally, during years of low capelin abundance the cod is growing slower and it appears not to be able to compensate for the lack of capelin by consumption of other food and which eventually leads to a lower yield from the cod stock.



Figure 16. A conceptual model of how climatic conditions in Icelandic waters may affect production at lower trophic levels and eventually the yield from the Icelandic cod stock

In spite of oversimplification, the model in Figure 16 suggests that the food chain in the Iceland Sea from phytoplankton-zooplankton-capelin and to cod is very much bottom up controlled and highly sensitive to climatic changes. The variations in inflow of Atlantic water on to the northern shelf appears to be a major forcing factor on the biology, and as it may vary form year to year, this may lead to great interannual variations in the dynamics of the whole ecosystem. How this compares to other Sub-Arctic systems is of great interest.

Exploitation of, and research on, offshore fish in West Greenland has been dominated by demersal species. The Atlantic cod fishery is episodic. For example in the 1960s, catches were up to 400,000 t y⁻¹, but in the 1990s they were close to zero. The most significant fishery since the 1970s has been that for northern shrimp, with catches up to 100,000 t y⁻¹ from a biomass estimated by trawl survey to be near to 1/3 Mt. Indications are that the stock has increased continuously over the last decade. Surveys in the area indicate that the composition of demersal fish species inhabiting the shelf and continental slope has changed fundamentally since the early 1980s. At the same time, there has been a dramatic change in biomass and size structure of ecologically and economically important species. Today, deep-sea shrimp and Greenland halibut are the only important offshore species fished in the area. In the past, the sand eel was a significant prey for other fishes, seabirds, seals and whales. Today there are indications that the sand eel is no longer as abundant, and its importance is uncertain. Unless the mechanisms underlying these past radical changes in the offshore demersal system can be better understood, the response of the ecosystem to a changing environment will remain unpredictable.

The pelagic fish community off West Greenland is poorly investigated. Arctic cod and capelin are probably the principal fish species, and with squids the most important pelagic macrofauna. However, juvenile redfish, distributed both demersally and pelagically on the slopes of the banks, compose a huge resource in the West Greenland marine ecosystem, and they probably come from stocks in waters east of Greenland. An important task is to examine the structure and function of the higher-level components of the pelagic system, and the implications of fishery exploitation on the internal stability of this sub-system

Seabirds

About 20 species of seabird breed at Iceland and the total number of breeding pairs is estimated in the range of 6.3-9.5 million. The largest populations are those of puffins and fulmar, 2-3 million and 1-2 million pairs respectively. The largest seabird colonies in Iceland are located on the Vestfjord Peninsula, Northwest Iceland. These colonies are situated along the drift route of fish larvae form the main spawning grounds in the Atlantic water south and southwest of Iceland to the nursery grounds to the north of the country. Therefore the seabirds could possibly have an impact on the fish larvae through predation. The summer food consumption of the six most common seabird species has been estimated to be about 184, 171 and 34 thousand tonnes respectively of sand eel, capelin and euphausiids (Lilliedahl and Solmundsson, 1997). The estimated seabird consumption of capelin is in the range of 11-17% of the total annual catch of capelin in recent years.

Seabirds constitute a conspicuous component of the West Greenland ecosystem in winter. At least 3.4 million birds are estimated to winter in the area, not counting unknown numbers, probably also in the millions, of little auks (*Alle alle*). The winter seabird community is dominated by pursuit-diving Alcidae - Brünnich's guillemot, black guillemot, little auk - and bottom-feeding eiders: king eiders on the banks and common eiders along the coasts. In summer, the offshore seabird density is lower and mainly consists of wide-ranging surface-feeding fulmars and gulls (kittiwake, glaucous gull and Iceland gull).

Seabird harvests in West Greenland have been high, in particular Brünnichs guillemot (>200,000/yr) and eiders (>80,000/yr), and declines in breeding populations both in Greenland and elsewhere in the Arctic have been ascribed to hunting in West Greenland. It is currently a major management problem to develop locally accepted and sustainable management regimes for seabirds in the West Greenland ecosystem, both in terms of harvest levels and in terms of ensuring that production is not reduced by disturbance in breeding and critical foraging areas.

Marine mammals

About 25 species of marine mammals inhabit annually, but for a variable length of time, the offshore and coastal waters around Iceland. There are 18 species of whales, which are generally most common in the coastal waters to the south, southwest and south east of Iceland (Sigurjonsson and Hauksson, 1994). Nearly all are migratory to some degree. The three largest baleen stocks that annually migrate to the seas between Iceland, Greenland and Jan Mayen are minke whales, 56,000, fin whales 19,000, and sei whales 10,000 (Víkingsson, 1999). The annual consumption by cetaceans is estimated to be about 6.3 million tones with crustaceans constituting about 50% and finfish and cephalopods comprising about 30% and 20%, respectively.

Two species of seals (common seal and gray seal) breed in Icelandic waters while 5 more species of pinnipeds regularly drift towards the northern shores from more arctic waters. The common seal stock in Iceland is estimated to be about 15,000 individuals while that of the gray seal is 6000 (Anon, 2002). Both species feed mainly on small fish and the total annual food consumption of both species has been estimated to be about 36,000 tonnes (Sigurjonsson and Hauksson, 1994).

The West Greenland marine mammal community reflects both Atlantic and Arctic influences. North Atlantic whale species occur in West Greenland: minke, fin, sei and humpback whales feed mostly on small schooling fish or on large invertebrates. Atlantic odontocetes include such cool-water species as the harbour porpoise, the Atlantic white-sided dolphin, the white-beaked dolphin, the killer whale, the long-finned pilot whale and the northern bottlenose whale. Among Arctic species, the bowhead occurs in West Greenland in winter but in low numbers; belugas and narwhals are also present in the more northerly parts of the West Greenland system in winter, associated with sea ice.

The north-west Atlantic stocks of harp and hooded seals are migratory, and pelagic in summer, and are then numerous in West Greenland; stock size for harp seals is of the order of 6 million, but it is not known what proportion come to Greenland waters. Ringed and bearded seals are restricted to areas with winter sea ice. Harbour seals and walruses are found in small numbers in West Greenland; both these species have been reduced in numbers by hunting and other disturbances.

3.3 Newfoundland/Labrador Shelf

3.3.1 Physical Oceanography

The Newfoundland/Labrador shelves were once home to the great northern cod stock that in the late 1980s and early 1990s fell to such low levels of abundance that a moratorium on cod fishing was imposed in 1992. The moratorium remains in place today with little to no signs of recovery of the cod stock. The region encompasses the area from Hudson Strait to the northern Grand Bank (Fig. 17). It is situated on the western side of the Labrador Sea and consists of numerous shallow offshore banks (typically 100-200 m deep) separated by a series of channels and gullies, often referred to as saddles (Fig. 17). In the southern half of the Labrador Shelf the banks are separated from the coast by deep (> 500 m) marginal troughs. Generally, sea-ice begins to form by December in the north and spreads southward, reaching a maximum extension by March (Prinsenberg *et al.*, 1997). On average, it reaches the northern Grand Bank but in heavy ice years it can cover the entire Grand Bank. In the southern regions, ice usually lasts from 1-2 months whereas at the northern end of the Labrador Shelf it lasts for an average of around 8 months.

The circulation pattern over the shelf is dominated by the southward flowing Labrador Current (Smith *et al.*, 1937; Greenberg and Petrie, 1988; Chapman and Beardsley, 1989; Fig. 17). The main branch is concentrated over the steep continental slope above depths of 400-1200 m with surface speeds of 0.3-0.4 m s⁻¹ and an estimated transport relative to 1500 db of 3.2 Sv (Lazier and Wright, 1993). These waters, at times, intrude onto the shelf through the saddles. The inshore Labrador Current (typical surface currents 0.15-0.25 m s⁻¹; transport of 0.6 Sv) flows along the inner half of the shelf. These two branches of the Labrador Current are separated by generally weak and directionally variable flows over the outer banks along the Labrador Shelf (Fissel and Lemon, 1991). The Labrador Current over the shelf is surface intensified and associated with the strong horizontal density gradients.



Figure 17. The Newfoundland/Labrador Shelf and Labrador Sea regions showing the topography and schematics of the near-surface circulation. The width of the arrows roughly represents relative transports.

The waters in the offshore branch are primarily an extension of the West Greenland Current that is steered by the topography across Davis Strait towards Labrador and the Baffin Current flowing southward along the western side of Davis Strait (Smith et al., 1937; Chapman and Beardsley, 1989; see also Fig. 17). The hydrographic characteristics of the waters over the shelf, however, originate in Hudson Strait (Iselin, 1927; Dunbar, 1951; Kollmeyer et al., 1967). They are formed from a mixture of cold Baffin Current waters, relatively warm West Greenland waters entering Hudson Strait from the east, and low salinity waters flowing westward from Hudson Bay and Foxe Basin (Smith et al., 1937; Sutcliffe et al., 1983). These water masses converge at the eastern entrance of Hudson Strait where strong tidal currents lead to intense vertical mixing (Drinkwater and Jones, 1987). The residual current carries the resultant mixture out onto the Labrador Shelf. The intense mixing results in a reduced range in temperature, salinity and stratification on the northern Labrador shelf relative to the Baffin Island Shelf north of Hudson Strait (Lazier, 1982; Sutcliffe et al., 1983). The mixing also elevates the surface nutrient concentrations during the summer and autumn within Hudson Strait, which subsequently flow onto the northern Labrador Shelf (Kollmeyer et al., 1967; Sutcliffe et al., 1983; Drinkwater and Jones, 1987). These lead to phytoplankton production, which is maintained at relatively high levels throughout the summer on the northern Labrador Shelf (Drinkwater and Harding, 2001).

Ocean temperatures tend to range from about 14°C in the surface waters in the southern areas of the region during the summer to near freezing below the ice-covered areas in winter. Near-bottom temperatures are strongly depth-dependent but generally cover the range from -1° on some of the shallower banks to 4°C in the deeper regions of the shelf and along the slope. An important hydrographic feature, especially on the southern Labrador and on the Newfoundland shelves, is the existence of a late spring to autumn subsurface temperature minimum. This gives rise to the Cold Intermediate Layer, or CIL, generally defined by waters of temperatures < 0°C (Fig. 18) (Petrie *et al.*, 1988). The CIL consists of winter-chilled waters that are sandwiched between surface solar-heated, upper-layer waters and the warmer offshore waters, which penetrate onto the shelf near bottom. Salinities range from <30 psu in the vicinity of Hamilton Inlet due to a freshwater outflow to near 35 psu in the deeper offshore waters with most waters over the shelf being 31-34 psu.



Figure 18. Temperature transects across the northeast Newfoundland Shelf showing the extent of the Cold Intermediate Layer (waters < 0°C) in 1965 and 1991.
Climate Influences

Seasonal variations in atmospheric forcing (e.g. air temperature and wind stress) and sea-ice extent lead to strong annual cycles in the water mass properties (Myers *et al.*, 1989; Petrie *et al.*, 1991). Peak temperatures in the surface layer occur in August but are delayed by a month or more as one descends in the water column. Minimum surface salinities generally occur in the late summer to early autumn in response to the melting of sea ice and subsequent advection. Little to no seasonal changes in hydrographic properties are detected below about 200 m.

Interannual changes in atmospheric forces, coupled with changing advection patterns, are responsible for the observed variations in the ocean climate on the Labrador and Newfoundland Shelves. In particular, the strength of the cyclonic atmospheric circulation over the North Atlantic, as reflected in the NAO index, can account for between 40-50% of the variance in sea-ice, ocean temperatures and shelf stratification off Labrador and Newfoundland (Fig. 19) (Colbourne *et al.*, 1994; Drinkwater, 1996). During decades when the NAO index is predominately negative, warm and generally saline ocean conditions prevail, and when the NAO index is positive, waters usually are colder and fresher. However, spatial variations in the positions and extent of the atmospheric pressure fields that define the NAO index can lead to exceptions to this pattern. For example, in the late 1990s, the eastward shift in the pressure cells maintained a high NAO index but weak winds and relatively warm conditions over Labrador and Newfoundland (Colbourne and Anderson, 2003).



Figure 19. The 5 year running means from the top are the winter NAO Index, the northwest wind stress for the Labrador Sea, the winter air temperature from Cartwright on the southern coast of Labrador, the ice area in February south of 55°N and the sea temperatures at the bottom (175 m) at a monitoring site off St. John's, Newfoundland. The plots show the strong association between the NAO and the atmospheric and oceanic variables (updated from Drinkwater, 2000).

The Labrador Current also undergoes variations in its volume transport. Annually, there is an approximate 4 Sv variation over the slope, being minimal in March-April and maximum in October (Lazier and Wright, 1993). It is not wind driven (Thompson et al., 1986), but rather is believed to be due to changes in steric height (Lazier and Wright, 1993; Han and Tang, 2001). Myers et al. (1989) were some of the first to examine interannual variability in the Labrador Current when they produced a time series of geostrophic currents over the Newfoundland/Labrador shelves. The volume flow in the Labrador Current, referenced to 100 m, tended to decrease during low NAO years while it increased in high NAO years. They also found that the geostrophic volume transport of the northward flowing West Greenland Current likewise increased during low NAO years, suggesting that this was at least a Labrador Sea-wide response. This relationship between the Labrador Current transport and the NAO was later confirmed by geostrophic estimates of velocity further south on the Grand Bank (Petrie and Drinkwater, 1993) and analysis of satellite altimeter data and hydrographic data (Han and Tang, 1999). The transport variations appear to be associated with changes of temperature/salinity structure over the lower continental slope, which in turn are related to large-scale atmospheric forcing through air-sea interactions and water mass transformation.

Dickson *et al.* (1988) described widespread freshening of the upper 500-800 m layer of the northern North Atlantic that they called the Great Salinity Anomaly (GSA). During the 1960s, an intense and persistent high-pressure anomaly became established over Greenland. As the northerly winds increased through to a peak in the late 1960s, there was a pulse of sea ice/ freshwater from the Arctic via Fram Strait with the result that the waters in the East Greenland and the East Icelandic Currents became colder and fresher. In addition, convective overturning north of Iceland and in the Labrador Sea was minimal, preserving the fresh characteristics of the upper layer. Beginning in the Greenland Sea in 1968, significant quantities of freshwater were advected via Denmark Strait into the sub polar gyre. The low salinity waters were tracked around the Labrador Sea and down the Labrador and Newfoundland shelves during the early 1970s before heading across the Atlantic. Dickson *et al.* (1988) further suggested the possibility of a similar event in the early 1900s. Low salinities in the mid-1980s off Labrador and Newfoundland were attributed to the advection of another low salinity anomaly that Belkin *et al.* (1998) suggested was formed in Baffin Bay.

Recent Changes

Warm conditions with above normal ocean temperatures, less sea ice and reduced amounts of CIL water dominated during the 1950s and 1960s. These were followed by a general decline in climate superimposed on three major cool periods, approximately a decade apart, in the early to mid-1970s, 1980s and 1990s and corresponded to peaks in the NAO index (Colbourne et al., 1994; Drinkwater, 1996). In the latter period, sea-ice was more extensive than anytime in the previous 30years, forming earlier and departing later than previously observed (Colbourne et al., 1997). The amount of CIL water was at a maximum and ocean temperatures were well below normal. Cold conditions continued through until 1996, when conditions warmed dramatically. After above-normal sea temperatures and reduced sea ice through most of the remainder of the nineties, conditions have been near the long-term (1971-2000) average in recent years. Salinity variability shows similar trends as temperature, with fresher-than-normal periods generally corresponding to the colderthan-normal conditions up to at least the early-1990s, although the phase of the salinity cycle tends to precede temperature by 1-5 years. In the 1990s salinities throughout the water column were significantly lower-than-average, with the largest anomaly in the surface waters. This produced the longest single period of fresher-than-normal salinities on record in the Newfoundland region (Colbourne, 2004). These low salinities may be a response to increased outflow of Arctic water through the Canadian Archipelago.

3.3.2 Ecosystem properties

Primary Production and Phytoplankton

Plankton dynamics on the Newfoundland/Labrador shelves are characterized by a strong and persistent seasonal signal, dominated at lower trophic levels by a dramatic spring phytoplankton bloom of diatoms (Prasad and Haedrich, 1993). Phytoplankton concentrations increase more than 100-fold during the spring bloom and inorganic nutrient concentrations in the upper mixed layer decrease to detection limits within 4-6 weeks (Deibel et al., 1992). Productivity estimates based on SeaWiFS data for the Newfoundland/Labrador region are 150-300 g C m⁻²y⁻¹. The bloom begins in March on the southern Grand Banks (Vladimirskaya, 1967), and during mid-April on the eastern banks near the Flemish Cap (Anderson, 1990). It appears progressively later as one proceeds northward along the Labrador Shelf. Physical forcing of the bloom is poorly understood, although mechanisms contributing to stabilization of the upper water column, such as melting ice, solar insolation and seasonally decreasing winds, all appear to be important (Prasad and Haedrich, 1993; Deibel et al., 1992). Indeed, there is some suggestion that the timing of spring bloom is linked to the retreating ice edge. Interannual variability in sea ice conditions and timing is thought to be a major physical factor affecting decadal scale variability of the blooms but no work has been undertaken to confirm or reject this hypothesis. Consistent with this hypothesis, however, the Continuous Plankton Recorder data show an increase in phytoplankton biomass, including an increase in winter blooms, off the Newfoundland Shelf and in the Labrador Sea through the 1990s. This corresponds to a period of rising temperatures and diminishing ice coverage. In addition there has been an increase in the warm water species Zoothamnium pelagicum in Labrador Sea that is speculated to have penetrated into the region through a northward extension of the North Atlantic Current loop (Edwards and Richardson, 2003).

Most areas off Labrador and Newfoundland show a similar seasonal trend in phytoplankton biomass, with the spring bloom, a summer low, a reduced peak in the autumn associated with increased storminess and then a winter low. On the northern end of the Labrador Shelf, however, phytoplankton production appears to remain high throughout the summer (Fig. 20) (Drinkwater and Harding, 2001). Intense tidal mixing results in high nutrient concentrations in Hudson Strait (Drinkwater and Jones, 1987), which are carried by the residual circulation onto the northern end of the Labrador Shelf (Kollmeyer *et al.*, 1967; Sutcliffe *et al.*, 1983). It is this process that maintains the high phytoplankton biomass at the northern end of the Labrador Shelf. Indeed, during the summer, phytoplankton productivity measurements suggest increasing values northward along the Labrador Shelf (Sutcliffe *et al.*, 1983). The relative importance of the summertime primary production on the northern Labrador Shelf compared to the overall annual production of the region is unkown.



Figure 20. A CZCS image showing average chlorophyll-a for July. Highest values are bright red and the lowest the light green. Note the high chlorophyll-a at the northern end of the Labrador Shelf. This high chlorophyll is maintained throughout the summer due to high nutrient fluxes from Hudson Strait. (Courtesy of G. Harrison, Bedford Institute of Oceangraphy, Dartmouth, N.S., Canada).

Zooplankton

The zooplankton in the waters over the Newfoundland/Labrador shelves are dominated by a mixture of Arctic species, Calanus hyperboreous, C. glacialis and Pseudocalanus spp., and the Atlantic species, especially C. finmarchicus (Drinkwater and Harding, 2001; Johns, 2001; Head et al., 2003). From samples taken in September of 1985, Drinkwater and Harding (2001) found that the abundance of the Arctic species generally decreased offshore over the Labrador Shelf, while Atlantic species increased in the more offshore samples. They also observed distinct zooplankton communities associated with the main oceanographic features, i.e. the inshore Labrador Current, the outer shelf consisting of banks and saddles, the offshore Labrador Current, and the Labrador Sea. Each region contained distinct dominant taxa at all trophic levels from the microplankton to nekton categories. There was also evidence that incursions of deep Labrador Sea water and its associated biota occurs through the outer saddles into the inner most shelf basins. Only on the northern Labrador were deep water organisms regularly found over shallow water, which is believed to be a result of the turbulent tidal mixing in Hudson Strait and subsequent advection onto the Labrador Shelf. Head et al. (2003) sampled across the Labrador Sea during the spring or early summer from 1995 to 2000. They also observed distinct community structure which corresponded to the Labrador Shelf, the Labrador Slope and the Labrador Sea but the boundaries between the regions varied spatially between years. While there was a general association of community structure with water mass characteristics, this was not always strictly observed.

The Labrador Sea is an important source of *C. finmarchicus* and is considered a centre of distribution of the species in the Northwest Atlantic (Weibe, 2001). The species overwinters there and surfaces in the spring in association with the phytoplankton bloom (Head *et al.*, 2000; Head and Harris, in prep.). *C. finmarchicus* has a one year life cycle over most of the Labrador Sea. Recent biophysical modelling studies have shown a latitudinally dependent emergence scheme, with earliest emergence to the south of Newfoundland (Tittensor *et al.*, 2003). Of particular importance, they found a temperature increase (decrease) of as small as 0.5°C produced a increase (decrease) on the order of 20% in *C. finmarchicus* abundance, due primarily to changes in growth rates. A decrease of 1°C reduced the abundance by 40%, but a increase of 1°C increased the abundance by as much as 60%. In recent years there has been an increase in *C. finmarchicus* abundance in the Northwest Atlantic, which includes the Labrador and Irminger seas, and is opposite to the trend in the Northeast Atlantic (Beaugrand *et al.*, 2002). This is believed to be a response to changes in the ocean climate.

Groundfish

Groundfish have traditionally dominated the Newfoundland/Labrador region, both in terms of biomass and in the commercial fishery, with Atlantic cod (Gadus morhua) the major species. Other commercially exploited fish species have included Atlantic haddock (Melanogrammus aeglefinus), American plaice (Hippoglossoides platessoides) (Fig. 21), redfish (Sebastes spp.), yellowtail flounder (Limanada ferruginea), Atlantic halibut (Hippoglossus hippoglossus) and Greenland halibut (Reinhardtius hippoglossoides). There was a rapid expansion of distant water fleets during the late 1950s, as well as an intensification of fishing effort, which lead to fisheries collapses (see Murawski et al., 1997). With the declaration of the 200-mile limit by Canada in 1977, the stocks began to increase. However, by the late 1980s the fisheries were in decline and a moratorium was imposed on cod in 1992 (Rice, 2002). While some argued that the collapse was entirely due to over fishing (Hutchings and Myers, 1994; Myers and Cadigan, 1995; Hutchings, 1996; Sinclair and Murawski, 1997; Bundy, 2001), there is increasing evidence that climate played a significant role (Rose et al., 2000; Drinkwater, 2002). This included environmentally induced changes in cod, including its distribution (deYoung and Rose, 1993; Rose et al., 2000), growth (de Cárdenas, 1996; Shelton et al., 1996; Drinkwater, 2002), condition (Drinkwater, 2002), and recruitment (Rose et al., 2000).



Figure 21. The catches of several of the main commercial fish and shellfish species in the Newfoundland/ Labrador region (courtesy of the Sea Around Us website: http://www.seaaroundus.org/).

These changes were not limited to cod, but were observed in many species (e.g. a general decline in demersal fish abundance (Atkinson, 1997), a southward shift and a decline in abundance of yellowtail flounder (Morozova, 1993), and a northward movement and increasing abundance with the advent of warmer waters in the late 1990s (Colbourne and Bowering, 2001); declines in the growth and abundance of American plaice (Brodie, et al., 1993); decline in abundance and change in the spawning time of capelin (Mallutus villosus) (Nakashima, 1996); a southward shift in distribution of polar cod (Boreogadus saida) (Lilly et al., 1994); and a general response of the ecosystem including southward movement and declining abundance of many species (Gomes et al., 1995). With a moderating climate in the late 1990s, the cod has remained low although there have been some minor increases in juvenile abundance (Anderson and Rose, 2001). This was due not only to a reduction in the number of eggs produced, but also due to increased mortality of the egg through juvenile stages. Since then, the numbers of 1-year old cod have begun to increase (Colbourne and Anderson, 2003), but they are still well below the estimates during pre-moratorium years. Other "warm-water" species such as yellowtail flounder have also increased their numbers. In contrast, the distributions of more "cold water' species, such as polar cod, have moved northward. During the 1990s, with the advent of cold waters and the disappearance of the groundfish, invertebrates such as snow crab (Chionoecetes opilio) and northern shrimp (Pandalus borealis) increased and their fisheries flourished. These stocks are still abundant, but snow crab, in particular, have undergone some declines in recent years, coincident with the warming of the waters in the region.

Marine Mammals

Seals are also an important component of the marine ecosystem in the Newfoundland/Labrador area. Except for the grey (*Halichoerus grypus*) and harbour (*Phoca vitulina concolor*) seals, seals in Newfoundland and Labrador migrate from Arctic waters on southward moving pack ice in early spring to pup. They retreat northward with the ice pack in late spring and summer. These include the hooded seal (*Cystophora cristata*), bearded seal (*Erignathus barbatus*), harp seal (*Phoca groenlandica*) and ringed seal (*Phoca hispida hispida*). The most abundant seal is the harp, with recent population estimates in the Northwest Atlantic, based on an extensive survey conducted in 1999, at around 5.2 million. This is up significantly from the early 1970s, when it was just under 2 million. Seals eat a tremendous quantity of food, mostly fish and shellfish, but how this is divided between species remains a hotly contentious issue and is as yet unresolved.

Seabirds

Seabirds also make up another vital component of the marine ecosystem in the Newfoundland/Labrador region. The species with the largest abundances include gulls, gannets, puffins and murres. There are significant numbers of summer migrants that nest along the coasts of Labrador and Newfoundland, as well as resident populations. The abundance and diets of many of these birds have undergone large variability, which directly reflect changes in the ecosystem (Montevecchi and Myers, 1995, 1996, 1997). Thus seabirds can be used as important samplers in detecting climate-induced ecosystem changes.

SECTION IV. NORTH PACIFIC CLIMATES

For the North Pacific Ocean, three well-studied indices of climate patterns are the Arctic Oscillation (AO), the Southern Oscillation (SO), and the Pacific Decadal Oscillation (PDO).

The AO is defined as the leading mode of sea level pressure variability north of 20°N, and consists of a pattern of zonally symmetric variability in the strength of the polar vortex (Thompson and Wallace, 1998). The AO has its largest variance in winter (January – March). A strong mode of variability in the AO is interannual, but it also varies at quasi-decadal scales, having changed sign in 1976 and again in 1989 (Thompson and Wallace, 1998; Overland *et al.*, 1999). The AO influences the Bering Sea through its effect on the Aleutian Low Pressure System (SLP), which is evident in the monthly or seasonal mean sea level pressures and is located over the North Pacific (Overland *et al.*, 1999). The value and position of the Aleutian Low reflects the strength and distribution of storm tracks in the southern Bering Sea and Sub-Arctic Pacific Ocean. These storms have great influence on the marine climate of the Bering Sea in winter.

The SO (and its associated El-Nino/Southern Oscillation or ENSO) has widespread influence on global climate variability at time scales of 2 - 7 years, and has its greatest influence in the tropics. Recently, the SO has been shown to have a small but significant influence on marine climate of the Bering Sea via atmospheric teleconnections (Niebauer, 1998; Hollowed *et al.*, 2001; Martin *et al.*, 2001; Overland *et al.*, 2001).

The PDO is defined as the leading mode of sea surface temperature variability in the North Pacific (north of 20°N), and has time scales of 50 - 60 years (Chavez *et al.*, 2003). Although the PDO is a major mode of variability, for the eastern Bering Sea it explains only 21% of the variance of the monthly SST and is primarily centered on the central North Pacific rather than the Gulf of Alaska and Bering Sea (Overland *et al.*, 2002).

Another index of atmospheric pressure, the North Pacific (NP) pattern, represents the leading mode in spring of the 700 mb height and is most prominent from March through July (Barnston and Livezey, 1987). The NP consists of a north-south pressure dipole, and its strong variance in spring relates to storminess in the Bering Sea (Overland *et al.*, 2002).

The most basic representation of atmospheric variability for the Bering Sea is the weekly to monthly average of the Siberian High SLP region and the Aleutian Low SLP region. The locations and intensities of these two pressure fields control the pressure gradient between them, which relates to the tracking and intensity of storms and other surface elements. Over the Bering Sea, there is a region of strong gradients in sea-level pressure between the Aleutian Low and the high pressure over the Arctic.

The close proximity of the Sea of Okhotsk to the cold (in winter) Eurasian continent results in severe climatic conditions, while a free exchange with the North Pacific determines rather moderate thermal conditions. In winter, the main features over the Sea of Okhotsk are the development of high pressure systems over Eurasia, which lead to a strong Siberian High and the development of lows over the Far East Seas and North Pacific resulting in the formation of the Aleutian Low (Dashko, 1979, 1998). From November to March, northerly winds prevail, and the mean airflow is from the continent to the sea (winter monsoon). In summer, the interaction of the North Pacific and Sea of Okhotsk Highs (over the relatively cold sea surface) with the Far East trough (over the warm continent) leads to establishment of the summer monsoon, i.e. advection of moist air from the sea to the continent.

The essential similarity between the climatic conditions of the Sea of Okhotsk and those of other subarctic and arctic seas is explained by its intensive cooling in the winter season, closeness to the "cold pole" located in East Siberia, and the presence of obstacles to the penetration of warm air and

water masses in the east and south (Chernyavsky, 1992; Dashko, 1998; Luchin, 1998). Seasonal and interannual variability in the climatic and synoptic flow patterns is very high in the Sea of Okhotsk. There is a paradox of prevalence of northerly flows in the warm season, which needs to be resolved. Comparative analysis is necessary for clarification of similarity and distinction of the present and the 1950s-1960s climatic regimes in the Sea of Okhotsk ecosystem. The teleconnections between the Sea of Okhotsk and other Large Marine Ecosystems (LME) in the North Pacific and Arctic require further investigation.

The prominent climatic regime shift in 1998 was reflected in changes of many meteorological and hydrological characteristics. Thus, there was an essential change in the atmospheric pressure patterns over the Far East Region. In winter 1997, the high-pressure cell was observed over the northern Sea of Okhotsk, while the atmospheric pressure low over the sea was lessened (Svinukhov and Shatilina, 1999). This situation was typical for the low-ice period of the early to mid -1990s. In 1998 there was a low pressure center that covered most of the whole Far East Basin, and the Sea of Okhotsk was invaded by cold air from Siberia. The situation was repeated in 1999 (Shatilina *et al.*, 2002). The invasions of cold air from Siberia caused high ice cover in the Sea of Okhotsk. The advection of cold Arctic air masses also increased ice cover in the Bering Sea. Compared with the previous warm climatic regime, the intensity of the winter monsoon increased in association with the intensification of the Siberian High. Moreover, the southerlies strengthened in the spring-summer period, and there was also an earlier development and termination of the summer monsoon (Glebova and Khen, 2002). As a result, negative water temperature anomalies started to predominate in the upper layer of the Sea of Okhotsk.

SECTION V. NORTH PACIFIC SUB-ARCTIC SEAS

5.1 Sea of Okhotsk

5.1.1 Physical Oceanography

The Sea of Okhotsk is a marginal sea that forms a deep indentation in the northeastern Asian continent centered near 54°N and 150°E (Fig. 22). It is mostly surrounded by Russia, although its southern part borders Japan. Its average depth is 821 m and most depths are generally less than 1,500 m but its deepest point, in the Kurile Basin, is 3,916 m (Leonov, 1960; Frolov, 1971; Dobrovolsky and Zalogin, 1982). The shelf zone occupies almost 40% of the total sea area and is widest in the north (up to 400 km), in Shelikhov and Sakhalinsky Bay). The western Kamchatka shelf is also wide (up to 100 km) and well known as a productive fisheries area. Southwards, the shelf is much narrower except for Terpeniya and Aniva Bays and the La Pérouse Strait area near Sakhalin Island. From the 200 m contour, the bathymetry deepens to a broad area with depths between 500 and 1500 m that occupies about 42% of the Sea of Okhotsk.

The Sea of Okhotsk is connected to the Pacific Ocean and the Japan Sea via relatively narrow passages. Two shallow straits connect the Sea of Okhotsk and the Sea of Japan: Tartar Strait is 10 km wide at its narrowest point and 10 m deep at its shallowest, and La Pérouse Strait is 40 km wide and 40 m deep (Fig. 23) (Leonov, 1960). The Sea of Okhotsk is connected to the Pacific Ocean by 30 large and more than 20 small straits through the Kuril Islands. The most important water exchange takes place in the Fourth Kuril Strait (depth 1700 m), Kruzenshtern's Strait (1400 – 1920 m), Bussol Strait (2500 - 3000 m), Freez's Strait (800 m), and Ekaterina's Strait (437 m) (Fig. 23). The exchange of water via these straits has a considerable impact on circulation and intermediate-water formation in the Sea of Okhotsk. The Amur is the only large Siberian river that drains into the Sea of Okhotsk.



Figure 22. Bathymetry of the Sea of Okhotsk. (Figure developed from the Large Marine Ecosystem website: http://www.edc.uri.edu/Ime)



Figure 23. Surface thermal fronts of the Sea of Okhotsk. (From Belkin and Cornillon, 2004)

Because the net annual heat exchange at the sea surface is negative (from the ocean to the atmosphere), the stability of the Sea of Okhotsk's ecosystem is largely dependent upon the advection of warm water from the Pacific Ocean through the Kuril Straits (West Kamchatka Current) and from the Japan Sea through La Pérouse Strait (Soya Current) (Fig. 24). Maximum advection of heat in the Soya Current occurs in summer although advection in winter has not been measured. There is indirect evidence that the maximum transport of Pacific water into the Sea of Okhotsk occurs in the autumn-winter period as a compensation for the intensive water flow from the western Sea of Okhotsk under strong and persistent northerly winds. In spring and summer, the winds slacken and hence water exchange and the circulation weaken. Interannual and long-term changes of the Sea of Okhotsk heat budget during the regime shifts and relatively stable years remain unclear.



Figure 24. Scheme of Sea of Okhotsk currents in the warm period of the year (Chernyavsky, 1981): 1) West Kamchatka Current; 2) Northern Branch; 3) Middle Current; 4) Penzhin Current; 5) Yamsk Current; 6) North Okhotsk Current; 7) Amur Current; 8) North Okhotsk Countercurrent; 9) East Sakhalin Current; 10) Northeast Current; 11) Soya Current; 12) East Sakhalin Countercurrent (from Figurkin, 2003).



Figure 25. Circulation patterns in the northern Sea of Okhotsk (a) after a mild winter and (b) after a cold winter. (From Figurkin, 2003)

Winter convection on shelf results in a substantial increase in water density. In turn, this leads to changes in the pattern of shelf currents from what is seen during the warmer parts of the year (Fig. 24). The difference between circulation patterns in summer-fall and winter-spring depends on the severity (area of ice cover) of the winter (Fig. 25) (Figurkin, 2000). Some of the dense shelf waters, with temperatures close to the freezing point and a salinity of 33.1, descend along the continental slope to depths that may reach 250-550 m. The descending shelf waters interact with advected Pacific waters, already transformed in the Kuril Straits, to form the cold Okhotsk Upper Intermediate water mass, the second deepwater temperature minimum, and one of the sources of Intermediate Pacific waters.

From the mid-1980s to mid-1990s, the 0-200 m layer in the West Kamchatka current at latitude 54°N weakened. The compensatory current was also weak. These two currents affect water exchange with the Pacific Ocean, and the result was weak advection of Pacific waters to the Sea of Okhotsk in the upper layers. From 1996, the West Kamchatka Current began to strengthen (Fig. 26) and its volume transport continues to be high (Khen, 2002). In the 500-1500 m layer during the last 5 years, a steady increase in water temperature and salinity occurred, i.e. opposite to those in the surface layer, and were associated with intensification of water exchange with the North Pacific Ocean. It is thus hypothesized that heat loss at the surface in the cold climatic regimes is compensated for partly or completely through strengthening of Pacific water advection, while during warm periods (for the surface layer), temperature and salinity in intermediate layers decrease (A. Krovnin, pers. comm.). This mechanism may be responsible for conservation of the heat and salt balance of the Sea of Okhotsk, which is important for the entire ecosystem.



Figure 26. Changes in volume transport of West Kamchatka Current and salinity in the 500-1000m layer in the Sea of Okhotsk. (From Khen, 2002)

The intensity of water exchange with the North Pacific Ocean is of ecological significance because the Sea of Okhotsk suffers a deficit of nitrate and silicate. The largest deficit is observed on the northern shelf. The compensation of nutrient loss is possible only through the inflow of Pacific waters. Hence, the present intensification of water exchange is favorable for primary production in the Sea of Okhotsk.

In the western Bering Sea, a sharp decrease in temperature of near-bottom water on the shelf occurred between 1997 and 1999 in the Navarin area, where bottom temperatures decreased by 1.5-1.8°C. On the other hand, in the Warm Intermediate Layer, in recent years the water temperature has been above normal (Khen and Petruk, 2000). But in contrast to the Sea of Okhotsk, the salinity of intermediate water has been below the long-term mean. This must have been associated with weakening of circulation in the deepwater basin, as evidenced by a decrease in volume transport of the Kamchatka Current (Fig. 27) and a corresponding elevation of the Warm Intermediate Layer (by 100-150 m from the 1980s to the 1990s).



Figure 27. Interannual variability of volume transport in the Kamchatka Strait in the 0-500 m layer during summer season, in Sv. (From Krovnin *et al.*, 2004)

Sea Ice

The Sea of Okhotsk is well known as one of the southernmost seasonal sea ice zones in the Northern Hemisphere. Although the Sea of Okhotsk is located to the south of the Bering Sea, and is only two-thirds the area of the Bering Sea, the volume of ice produced in both seas is similar. In the Sea of Okhotsk, ice cover, on the average, occupies about 73% of the total sea area, and in the coldest years, up to 98%. The large inter-annual variation in sea ice volume depends on the strength and duration of northerly winter winds. In winter, sea ice formation begins around Shantarsky Bay at the end of November, and it reaches its maximum extent in late February or March. Most of the sea ice disappears by May. Sea ice in the Sea of Okhotsk is generally advected southward by the prevailing northerly or northwesterly winds. In the southwestern part of the sea, the East Sakhalin Current (ESC) transports thick "first-year" ice to the southeast. Some of the ice is advected towards the offshore warm region and melted, freshening the surface layer. Some of this water is then frozen again by cooling. This process leads to formation of "new ice" at ice edges (Ohsima *et al.*, 2001). A conveyor mechanism of ice formation in the polynyas requires quantitative modeling.

Sea ice plays an important role in the physical structuring of the Sea of Okhotsk. The vertical profile of temperature in the Sea of Okhotsk is forced by intense winter cooling and a low salinity surface layer (Hays and Morley, 2003). In late fall and winter, strong, cold winds from Siberia mix the water column typically to around 70 m. For most of the Sea of Okhotsk, this results in a lowering of the temperature in the upper 150 m of the water column, to between –1.5 to 1.5°C, during winter and spring (Kitani, 1973; Tally and Nagata, 1995; Rogachev, 2000). With the beginning of the seasonal warming, the region between 50 and 150 m becomes the Cold Subsurface Layer or Cold Intermediate Layer (Hays and Morley, 2003; see also Moroshkin, 1966; Alfultis and Martin, 1987; Gladyshev *et al.*, 2000). The summer warming, advection of warm North Pacific waters and autumn wind mixing cannot destroy the cold layer of Sea of Okhotsk waters completely. Even in November-December, on the northern shelf there are the rather extensive areas called the "cold cores" where there is, under the surface cold waters, colder subsurface water formed in the previous winter with temperatures close to the freezing point. This "conservation" of temperature allows the forecast of water column temperatures throughout the Sea of Okhotsk based on the character of the previous winter (Chernyavsky, 1984, 1992).

In the 20th century there were at least two large-scale cycles in the extent of sea ice cover with a period of about 50 y (Fig. 28). During the last 50 years, two trends were distinguished: cooling from the mid-1950s to the 1970s, and warming in the 1980s-1990s. The latest warming, by its rate and intensity, exceeded substantially the previous warming of the 1940s-1950s (Khen, 1997).



Figure 28. Ten-year average of sea ice cover (% of the total sea area) in the Sea of Okhotsk. (From Khen, 1997)

Until the mid-1980s, the processes of ice cover development in the Bering and Sea of Okhotsk were opposite (Plotnikov, 1987). Later, this out-of-phase relationship was broken (Plotnikov, 1997; Khen, 1997), and the changes in development of ice cover were in phase in both seas. Beginning in 1998, the synchronous increase in sea ice cover in the Bering and Sea of Okhotsk was associated with a regime shift in the North Pacific (Minobe, 2002).

Over the last three decades there were several climate regime shifts in the North Pacific. The most famous and significant shift occurred in the second half of the 1970s (Minobe, 1997; Hare and Mantua, 2000). Data on ice cover show that, in the Bering Sea, the dates of the regime shifts coincided with that in the atmosphere over the North Pacific (Fig. 29). In the Sea of Okhotsk, the regime shift occurred in the first half of the 1980s. During the 1990s, both seas were very warm, in accordance with global warming.



Figure 29. Changes in winter (January-April) ice cover area (% from the total sea area) in the Bering Sea (upper panel) and the Sea of Okhotsk (lower panel) (from Ustinova *et al.*, 2002).

Water Temperature

Following changes in atmospheric pressure patterns, sea surface temperatures in the Sea of Okhotsk shifted between 1997 and 1998. In 1997, sea surface temperatures were above the long-term mean in the Okhotsk and in the western Bering Sea throughout the year. In contrast, in the first half of 1998, sea surface temperatures in the Sea of Okhotsk were below the long-term mean. In the western Bering Sea, the spring of 1998 was cold. In both seas, there was heavier sea ice cover than usual. In 1999, negative water temperature anomalies were more stable and extensive and 2001 was exceptionally cold (Radchenko *et al.*, 2001; Ustinova *et al.*, 2002). The marked differences between 1997 and 2001 were clear in the whole Northwest Pacific. During cold years in the northwestern Bering Sea, sea surface temperature does not exceed 6°C, while in warm years it reaches 7-8°C (Luchin *et al.*, 2000).

In the Okhotsk, the most significant changes in sea surface temperature are associated with the shelf zone. Thus, on the West Kamchatka shelf since 1997 a deep cooling has been observed (Fig. 30). Such cold conditions have not been recorded since the mid-1980s. The areas occupied by water with temperatures less than -1°C in the subsurface layer also show a considerable cooling in 1999 compared with 1997 (Fig. 31).



Figure 30. Changes in water temperature off the West Kamchatka: blue- Southwest Kamchatka shelf; red-central West Kamchatka shelf; yellow-Northwest Kamchatka shelf (From Figurkin, 2003).



Figure 31. Distribution of subsurface waters with T< -1° C in the core of the Cold Intermediate layer in the Sea of Okhotsk in September (from Khen *et al.*, 2002).

5.1.2 Ecosystem Properties

Nutrients

The Sea of Okhotsk is one of the most biologically productive regions in the world, and it supports high fisheries production (Shuntov, 1987). These high rates of biological productivity are the result of high concentrations of nutrients. In 1990, in ice-free waters before the spring algal bloom, phosphate concentrations were 1.3-2.2 μ g-atom/liter, silica concentrations were 30-65 μ g-atom/ liter and nitrogen concentrations were 17-27 μ g-atom/liter (Mordasova *et al.*, 1991). In general, the southern and eastern parts of the Sea of Okhotsk have higher nutrient concentrations than the northern and western regions (Shuntov, 2001). This pattern reflects the importance of the influx of Pacific water and vertical mixing in the Kuril straits (Luchin *et al.*, 1993). Silicate concentrations are also elevated in river discharge plumes, particularly in the plume of the Amur River.

Primary Production

In many Sub-Arctic regions, there are strong, ice-associated blooms that occur as sea ice melts and stabilizes the water column (e.g. the Bering Sea; Niebauer and Alexander, 1985; Stabeno *et al.*, 1999a). However, there are few studies (e.g. Matsumoto *et al.*, submitted) that discuss the effect of the sea ice on the spring bloom in the Sea of Okhotsk, and this remains an area for further investigation.

During the period 1978 until 1986, the spring bloom occurred between April and May (Saitoh et al., 1996). Chl-a concentration is lower (0-3 mg m⁻³) in autumn than during the spring bloom (2-10 mg m⁻³; Nishihama et al., 1989). Due to strong stratification in the summer and early autumn seasons, the photic zone is separated by both the thermocline and the Cold Intermediate Layer from the deeper waters enriched by nutrients. Therefore, the nutrient supply of the photic zone occurs in regions of intensive vertical mixing, upwelling or river runoff (Chernyavsky, 1981). Also likely important to this re-supply of nutrients to surface waters are mesoscale and small-scale eddies located above the outer shelf and continental slope (Arzhanova and Zubarevich, 1997a; Gruzevich et al., 1997). The role of these eddies on the vertical transport of nutrients is critical for the ecosystem productivity and requires further study. The Cold Intermediate Layer waters move up onto the outer shelf, where, once at the surface, they are warmed and transported offshore. Phytoplankton develop an intensive photosynthetic activity in these waters where there is a combination of high nutrient concentrations and vertical stratification of the water column. These blooms are most evident in the central zone of anticyclonic eddies (Fig. 32). Another important source of nutrients is recycling (Arzhanova and Zubarevich, 1997a). Maximal ammonia and minimal organic nitrogen concentration is observed immediately below the thermocline in the layer from 30-40 to 70-80 m. There is need for additional research on the cycling of nutrient and organic compounds, and their interannual and long-term dynamics.



Figure 32. Annual average primary production in the Sea of Okhotsk Large Marine Ecosystem. (Source: http://seaaroundus.org/lme/SummaryInfo.aspx?LME=52).

Estimates of total annual primary production in the Sea of Okhotsk are high and varied. Earlier estimates were in the range of 100-220 g C m⁻² (Nishimura 1983; Ivanenkov and Zemlyanov, 1985) as were some from recent years (Sorokin *et al.*, 1995; Sorokin, 1997; Nezlin *et al.*, 1997). However, others have estimated production in the Sea of Okhotsk to be 260-350 g C m⁻² per annum, which is equivalent to the fixation of 400-490 million metric tons of carbon per annum for entire area of sea (Arzhanova and Zubarevich, 1997b; Naletova *et al.*, 1997). An extremely high estimate of 450 g C m⁻² per annum was provided by Shuntov and Dulepova (1993, 1996, 1997) and recently accepted by Shuntov (2001). In contrast, Sorokin and Sorokin (1999) estimate non-grazed Sea of Okhotsk spring production at about 52 g C m⁻².

Diatoms constitute a major fraction of the phytoplankton in the Sea of Okhotsk (Hanzawa *et al.*, 1981). As in other Sub-Arctic seas, they determine the spring bloom intensity (Ohwada, 1957; Smirnova, 1959; Zenkevich, 1963; Mikhailov, 1990; Ventsel, 1997). Diatoms are most abundant in spring and least so in autumn (Ohwada, 1957; Hanzawa *et al.*, 1981). Cryophilic species predominate among the spring phytoplankton. Comparison of phytoplankton biomass in spring and summer showed that it decreases by a factor of 5-6 (Gorbatenko, 1997).

Zooplankton

Historically, a single pelagic zooplankton community was identified, based on the hypothesis that there was one single population of the common zooplankton copepod species, *Calanus glacialis*, throughout the northern shelf (Kun, 1975). However, distinct zooplankton communities were identified for the shallow northern and deepwater southern parts of the Sea of Okhotsk (Vinogradov, 1954; Kotlyar, 1967; Kun, 1975). The neritic community is distributed in a narrow belt along the northern Sea of Okhotsk coast, the Sakhalin and western Kamchatka coasts, and even around the Kuril Islands mostly out to depths of 40-60 m (Lubny-Gertsik, 1959; Shuntov, 2001). A significant portion of this community consists of meroplankton (polychaetes, bottom crustaceans and mollusks larvae) (Lubny-Gertsik, 1959; Volkov, 1996), with the inshore part (from coast to 15 m depth) being the most diverse. The zooplankton communities of the outer shelf zone contain many species in common with those of the deep water. Total zooplankton biomass was estimated at 325-410 x 10^6 t in the upper 200 meter layer in summer season of 1984-1987 and 250-325 x 10^6 t in autumn.

Euryphagous zooplankton are the main source of prey for the higher trophic level organisms, and they support elements of the nekton, benthos and predatory zooplankton. Predatory zooplankton consumes about 65% of secondary production, benthic organisms about 11% and nekton about 3% (Shuntov and Dulepova, 1997). Factors affecting zooplankton reproductive success and the fate of secondary production require further study. Research must include both the monitoring of planktonic community characteristics and the collection of appropriate physical data sets.

Fish and Fisheries

The 1980s were years of extremely high fish abundance in the Sea of Okhotsk ecosystem. Total fish biomass was estimated as 35×10^6 t and annual fish production was 17.5×10^6 t. The principal commercial fish species were walleye pollock ($10-15 \times 10^6$ t), and pelagic fish such as sardines and herring (2-3 10^6 t) (Fig. 33). A predominant role of walleye pollock in the Sea of Okhotsk epipelagic fish community was emphasized for those years (Shuntov *et al.*, 1993). Along with pollock, demersal gadids, such as cod and saffron cod, had a high biomass. In the epipelagic layer, Japanese sardine (labelled in Fig. 33 as South American pilchard) migrated into the Sea of Okhotsk in summer until the beginning of 1990s.



Figure 33. Fish and shellfish catches by species in the Sea of Okhotsk Large Marine Ecosystem. (Source: http://seaaroundus.org/lme/SummaryInfo.aspx? LME=52#)

In the 1990s, significant changes occurred in the Sea of Okhotsk pelagic fish community. Walleye pollock declined in biomass, and herring increased (Table 2). By the late 1990s, herring constituted a significant part of the pelagic fish community. The biomass of other pelagic fishes (for instance, capelin, cyclopterids, Sakhalin flounder *Limanda sakhalinensis*) also increased. But the large biomass losses from the walleye pollock stock were not compensated, and the total pelagic fish biomass decreased from 14 to 10.5×10^6 t in the epipelagic layer (Shuntov *et al.*, 1997).

Species	1988		1997		1998		1999	
	t×10 ³	%	t×10 ³	%	t×10 ³	%	t×10 ³	%
Pollock	9475.2	94.2	4391.9	57.0	3636.5	51.5	1278.0	17.4
Herring	497.2	4.9	2492.9	32.3	1209.7	17.1	1877.6	25.5
Capelin	11.3	0.1	31.0	0.4	1002.7	14.2	929.3	12.6
Sandlance	7.8	0.1	30.3	0.4	21.2	0.3	1.5	+
Cyclopterids	20.8	0.2	37.1	0.5	127.1	1.8	41.2	0.6
Other	46.9	0.5	727.7	9.4	1064.0	15.1	3223.9	43.9
Total	10,059.2	2 100%	7,710.9	100%	7,061.2	100%	7,351.5	100%

Table 2. Biomass (thousand metric tons) and ratio (%) of dominant fish species in the northern Sea of Okhotsk epipelagic layer in August – October of 1988, 1997 – 1999. (After Radchenko and Melnikov, 2001)

The biomass decline also affected the spatial distribution of common pelagic fish species in the offshore zone of the southern Sea of Okhotsk. In the 1980s, walleye pollock were widely spread there during their seasonal feeding migrations. In the 1990s, these areas became much more sparsely populated by fish and total late summer fish biomass in the Kuril Basin epipelagic layer decreased from 684,000 t in 1986 (Gorbatenko and Cheblukova, 1990) to 103,000 t in 1994 (Radchenko *et al.*, 1997). Over this period, the contribution to fish biomass by walleye pollock ratio decreased from 65.3% to 0.1%. In the 1990s, Pacific salmon and squids dominated the epipelagic nekton.

Walleye pollock, which have many local stocks with different habitats and spawning grounds, is one of the important species for trawl fisheries in the northern North Pacific. In the western Bering Sea and the Sea of Okhotsk, walleye pollock (and salmon) generally avoid areas of sea ice. An exception is the population of walleye pollock that spawn under the sea ice in the Kunashiri Strait, the southernmost corner of the Sea of Okhotsk.

The responses of pollock stocks to impacts from fisheries and environmental change seem to differ depending on location. For example, the walleye pollock stock in the northeastern shelf of the Korean Peninsula collapsed long before the start of intensive trawl fisheries. The Bering Sea Doughnut Hole stock, which was a major target for high sea trawlers, disappeared and never came back despite a long moratorium on fishing. Given these important differences in response, comparative studies among walleye pollock stocks are needed, especially in the context of response to climate change and resilience/ vulnerability to intensive fisheries.

About 61 species of mesopelagic fish belonging to 53 genera and 33 families have been recorded in the Sea of Okhotsk midwater layer (Balanov and Iljinsky, 1992). According to data collected in trawl surveys, in 1987-1991 the total mesopelagic fish biomass ranged from 19 to 30 x 10⁶ t (Lapko and Radchenko, 2000).

The Sea of Okhotsk shelf in general, and the western Kamchatka shelf in particular, are known to be productive areas for demersal fish, with about 309 species being recorded (Borets, 1997). The flatfishes, sculpins and cod were the most abundant. In the 1980s, these fishes contributed more than 90% of the total demersal fish biomass on the western Kamchatka shelf. More recently, the biomass and production of common bottom fishes throughout the shelf and continental slope zones began to decline, with flat fish biomass dropping from 1×10^6 t to 380 10^3 t on the western Kamchatka shelf during second half of 1990s. These declines included not only the piscivorous predatory fish, such as cod, halibut and Greenland turbot, but also common species that forage on the benthos. The causes of these declines remain poorly understood, but they may have resulted from a decrease in zooplankton standing crops.

Squids are a very important component in the food web of the Sea of Okhotsk ecosystem. Total squid biomass was estimated as $3.5-4 \times 10^6$ t in 1990s, and the annual consumption of squid is about 12×10^6 t.

Marine Birds and Mammals

The Sea of Okhotsk nekton production supports an abundant population of marine mammals and birds (Shuntov, 1999). Annual pollock consumption by predatory fish, marine mammals and birds (3.2×10^6 t per year in the 1980s) exceeds the average fishery harvest (1.8×10^6 t). Minke whale abundance is estimated at 25,000 in the Sea of Okhotsk and adjacent waters (Buckland *et al.*, 1992). These whales can consume about 0.9×10^6 t of food during the six warm months, assuming a diet ration of 4% of the mean body weight of 5 t. Total dolphin numbers were estimated to be greater than 100,000 (Shuntov and Dulepova, 1997).

Higher trophic communities should also be monitored. For example, Kitaysky and Golubova (2000) report that the reproductive success of marine birds breeding on Talen Island in the northern Sea of Okhotsk was sensitive to climatic fluctuations and the corresponding changes in oceanographic parameters. Reproductive success of piscivorous puffins was positively correlated with sea surface temperature whereas the reproductive success of planktivorous auklets was negatively correlated with SST. Macro-zooplankton, which were the main prey of the auklets were shown to be more abundant in the warm years. These results from monitoring seabirds suggest that the stock dynamics of commercially important fish and squid stocks must be specified separately for different climatic and oceanographic regimes.

5.2 Oyashio Current and Shelf Region

5.2.1 Physical Oceanography

The western Sub-Arctic Pacific, including the Oyashio shelf region, supports a wide range of commercially important marine species. These include not only gadids such as the walleye pollock, but also subarctic migratory pelagic fish such as salmon and herring. The western Sub-Arctic Pacific is also an important summer feeding ground for subtropical migrants like the Japanese sardine (*Sardinops melanostictus*), Pacific saury (*Cololabiss saira*), whales and sea birds. This region, from northern Honshu Island, Japan, to the Kamchatka Peninsula of Russia, has a narrow continental shelf (Fig. 34) and is dominated by the Oyashio Current, a western boundary current that flows southward from the Sub-Arctic North Pacific Ocean. The Oyashio current is fed by cold, nutrient–rich, upwelled waters from the western Sub-Arctic gyre. Its name, Oya (parent) shio (stream), reflects its great productivity (Qiu, 2001).



Figure AI-34. Bathymetry of the Sea of Okhotsk and the Oyashio Current regions. (Figure developed from the Large Marine Ecosystem website: http://www.edc.uri.edu/Ime

The western Sub-Arctic Pacific Ocean is characterized by the existence of a Sub-Arctic gyre, of which the Oyashio Current is the western boundary current. This gyre is formed by the westward flowing Alaska Stream, part of which enters the western Bering Sea between 168°E and 172°E. Here it circulates counterclockwise, with its western limb forming the East Kamchatka Current (Fig. 35) (Qiu, 2001). This southward flowing current, joined by the portion of the Alaska Stream that did not enter the Bering Sea, passes southward to the Kurile Islands. The East Kamchatka Current then splits, with some of its water passing into the deep Kurile Basin of the Sea of Okhotsk. There it forms a counterclockwise gyre, and subsequently leaves the Sea of Okhotsk through Bussol Strait, where it rejoins the East Kamchatka Current. South of the Strait, the East Kamchatka Current is renamed the Oyashio Current, which differs from the East Kamchatka Current in that the Oyashio Current is an admixture of east Kamchatka Current water and Sea of Okhotsk water (Qiu, 2001). The characteristics of the Oyashio Water result from processes of winter ventilation and sea ice formation in the waters east off Kamtchatka and in the northern part of the Sea of Okhotsk. The Oyashio Water is characterized by a shallow pycnocline caused by a shallow halocline, dichothermal water, and a mesothermal layer (Sekine, 1988). The water at the lower part of dichothermal water is the source water of North Pacific Intermediate Water. This water propagates in the subsurface layer of Subtropical circulation, which approaches the Equator and affects ENSO. Thus, the seasonal sea ice in the western North Pacific, especially that of the Sea of Okhotsk, has basin-wide influence, and is an important agent in global climate change. Although an important influence on the environment of the marine ecosystem, the seasonal sea ice and waters affected by it are not well elucidated, partly because of difficulties in accessing these regions for field survey, and partly for lack of sufficient effort toward the exchange of information.



Figure 35. Diagram of the relationship of the Oyashio Current to other currents in the Northwest Pacific Ocean (Modified from Qiu, 2001).

5.2.2 Ecosystem Properties

Plankton

The western Sub-Arctic Pacific, including the Oyashio shelf region, is one of the high-productivity zones of the world. Based on SeaWiFS global primary production estimates (> 300 g C m⁻² y⁻¹), it is a Class I, highly productive ecosystem (Fig. 36) (NOAA web site for Large Marine Ecosystemshttp://na.nefsc.noaa.gov/lme/text/oyashio-current.htm). The Oyashio Current system has "typical" spring bloom dynamics, with a strong burst of production in the spring (Kasai *et al.*, 1997). This in turn supports a high biomass of meso-/macro-zooplankton, on the order of 1.1-3.7 x10⁶ tons for the region as a whole (Odate, 1994). The biomass of zooplankton may have increased between 1951 and 1976, and it is believed that the presence of a high biomass of zooplankton depends upon the cold waters of the Oyashio Current. Recent study indicated interannual variations of mesozooplankton biomass in the Oyashio water using data and samples collected along a transect PH from 1972 to 1999 (Tadokoro *et al.*, submitted). In spring, mesozooplankton biomass, presumably mainly composed by *N. flemingeri* was high in the mid-1970s and decreased considerably in late 1970s and sustained low values until late 1990s (Fig. 37).



Figure 36. Annual primary production in the Oyashio Current Large Marine Ecosystem (Source: http://seaaroundus.org/Ime/SummaryInfo.aspx? LME=51#).



Figure 37. Interannual variations in total zooplankton biomass (mg m⁻³) in spring (squares) and in summer (diamonds) from 1972 to 1999. Lines show five-year running mean in spring (solid) and summer (broken). Bars denote ±SD. (From Tadokoro *et al.*, submitted)

Fish and Fisheries

The 530,381 km² Oyashio Current Large Marine Ecosystem supports a wide variety of fisheries, the most important of which are those for small pelagics such as pilchards, chub mackerel and Japanese flying squid. The life history characteristics, distribution and trends of abundance, and fisheries are described for resident and migrant species which constitute the largest fisheries: walleye pollock, Pacific cod (*Gadus macrocephalus*), chum salmon (*Oncorhynchus keta*), Japanese sardine, Pacific saury (Fig. 38), whales and sea birds.



Figure 38. Fish and shellfish catches by species in the Oyashio Current Large Marine Ecosystem. (Source: http://seaaroundus.org/lme/SummaryInfo.aspx? LME=51#)

Walleye Pollock (*Theragra chalcogramma*, hereafter referred to as pollock) is a demersal and semi-pelagic fish occurring in waters from 30 m to > 400 m deep, mostly on the North Pacific shelf, from the Southern Sea of Japan to Central California. Pollock make diurnal vertical migrations, sometimes reaching the surface. They reach sexual maturity at 3-4 years of age, at about 30-38 cm total length. Spawning takes place from December to March in the waters off southern Hokkaido, Japan. Pollock produce pelagic and separable eggs. Pollock spawn eggs at intervals of a few days over a month's time (Sakurai, 1989). In Oyashio waters, young pollock feed mainly on copepods and their eggs. Adults prey upon mysiids, euphausiids, silver smelt and capelin.



Figure 39. Biomass and Japanese catch of walleye Pollock (Pacific stock) (From FAJ, 2002).

In the Oyashio region, the pollock fishery stabilized at about 250,000 t in the mid 1970s to the mid 1980s (Fig. 39). After the late 1980's, the pollock catch decreased due to a decline of the stocks to 150,000 t in 1996. By 1998, the total pollock catch in the Pacific waters of Japan increased to 260,000 t, and then gradually decreased to 200,000 t in 2000.

The pollock off northern Japan is considered to consist of one stock for management purposes. Pollock are distributed on the shelf from the southern Kuril Islands to the Tohoku region (northeastern Honshu Island). The main spawning ground is around Funka Bay in southeastern Hokkaido. Spawning occurs mainly at depths of 100-150 m near the entrance of Funka Bay in January and February, and the eggs drift into the bay as they develop with intrusion of the coastal Oyashio. Some of the pollock eggs and larvae are transported by the Oyashio, which generally flows southward along the eastern coasts of Hokkaido and Tohoku.

The favorable temperature range for survival of eggs and larvae is estimated to be 2-7°C. Strong year-classes are believed to occur by the transport and aggregation of pollock eggs and larvae into Funka Bay as a nursery ground, where there is a high density of food organisms such as copepod nauplii. However, there is no information about the contribution to year class strength by offshore or southern transport of pollock eggs and larvae to the Tohoku area with the intrusion of the coastal Oyashio.

On the other hand, pollock catches off the Tohoku region have decreased drastically since 1993. Suzaki *et al.* (2003) examined how, between 1981-1995, annual variations in the abundance of age-0 pollock were related to variations in the Oyashio Current off the Tohoku region. During the 1980s, when the Oyashio flowed nearshore, pollock abundances were relatively high. However during the early 1990s, when it flowed further offshore and not as far south due to interactions with the Tsugaru Warm Current and the Kuroshio Extension, age-0 pollock abundances were lower. In addition, the nearshore flow was found to cause a decrease in the bottom temperatures over the continental shelf during the 1980s. When the coastal Oyashio flowed nearshore along southeastern Hokkaido and northeastern Honsyu (e.g. in 1989 and 1995), larval survival was enhanced, and year-classes were strong. However, when this flow occurred farther offshore (e.g. in 1991 and 1992), survival decreased and year-classes were weak. These results indicate that that the Oyashio plays an important role in determining the success of early life stages of pollock from Funka Bay.

Pacific cod (*Gadus macrocephalus*) is widely distributed in the northern part of the North Pacific Ocean and adjacent waters, in water temperatures from nearly freezing to 15°C. The fish lives mainly along the continental shelf and upper slope of the North Pacific in the areas bordered by

Korea and the western Chukchi Peninsula in the west, and Norton Sound and Oregon in the east. In all areas, the importance of cod in catches declines with depth. The bathymetric range of Pacific cod extends from shallow water (10 m) to about 550 m, but it is found mostly between 100 and 400 m. Age and size at first maturity vary geographically, with the southern stocks maturing at an earlier age. Sizes are, respectively, for males and females: 2-3 years and 40-44 cm standard length (SL) off Washington, USA, 3 years and 41-48 cm SL off Kinka-san in northern Japan, and 7-8 years and 60-63 cm SL off west Kamchatka. Fecundity is high, with 2 million eggs for a 4 kg female, and up to 4 million eggs for a 7 kg female in Mutsu Bay (northernmost Honshu, Japan).

Spawning is variable among the populations. It occurs mostly from winter to early spring; from January to May in the western Pacific, and from December to February in Mutsu Bay. Spawning migrations have been linked to annual changes in ocean temperature in various parts of the geographical range. Pacific cod inhabiting waters near northern Japan migrate to spawning grounds characterized by shallow bay waters (about 50 m), and silty or sandy bottoms with water temperatures of 4° to 8°C. The distribution of this stock extends widely from Kushiro in northeastern Hokkaido to Mutsu Bay off northern Honshu, and the seasonal migratory route has been documented by the tagging experiments of juvenile and adult cod.

Females spawn only once each season. The eggs are demersal and slightly adhesive. At spawning the size of the demersal eggs is from 0.9 to 1.0 mm (Sakurai and Hattori, 1996). Hatching takes place after 21 days at 5°C and after 15 days at 8°C. The size of the larvae ranges from 3.8 to 4.5 mm total length. The larvae are pelagic for 4 to 5 months, and then descend to the bottom. The growth rate is rather high, reaching 20 cm SL at the end of first year. Growth is similar in males and females. Pacific cod reach 40 cm SL at 2 years, and 77 cm SL at 6 years off the southern coast of Hokkaido. Longevity is up to 12 years. The food of the pelagic larvae of Pacific cod is mainly composed of copepod nauplii. The young cod eat euphausiids and benthic invertebrates. The diet of adults includes fish, octopus, and large benthic and bentho-pelagic crustacea such as crabs and shrimps.

In the Oyasho region off Tohoku, Pacific cod were estimated to be in low abundance during the late-1970s, but gradually increased during the 1980s, decreased during the early 1990s, and increased again after the late-1990s, particularly the 1996-1998 year classes. However, the local stock spawning in Mutsu Bay was drastically reduced after the early 1990s. In the western North Pacific, environmental conditions shifted to a cool regime in the late 1970s, and then back to a warm in the late 1980s. These regime shifts appear to coincide with variations in Pacific cod catches. The population biomass in the Oyashio region from Hokkaido to Tohoku areas is estimated to have peaked at 35,000 t in 1999 and has gradually declined to about half of the peak value in 2001.

Chum Salmon (*Oncorhynchus keta*) is produced by artificial propagation in Japan, with the number of adult chum salmon returning in 1998 being about 800 million fish. The Bering Sea and the Gulf of Alaska are important habitats for Japanese chum salmon during the ocean phase of their life history. After the mid 1960s, the number of fry released and adults returning increased until the early 1990s, but adult body size decreased and the age-at-maturity increased. After the1990s, the number of returning adults decreased drastically and the size of the adult became larger (Kawasaki, 2002). The change in biomass of Pacific salmon (*Oncorhynchus* spp.) indicates a 40- or 50-year periodicity in the North Pacific Ocean in connection with the long-term climate conditions (Kryashtorin, 1998). It was suggested that the carrying capacity in Pacific salmon will be closely related to the long-term climate change and density-dependent effects (Kaeriyama *et al*, 2004).

Japanese sardine (*Sardinops melanostictus*, hereafter referred to as sardine). The sardine population has fluctuated greatly over the last two decades; it began to increase in the mid-1970s, reached a peak in the mid-1980s, and has been declining since 1989. Total catch of sardine was 20,000 t in 1970 (Fig. 40). The sardine catch increased to 2,210,000 t in 1980, and reached a maximum of 4,490,000 t in 1988. The catch declined after 1989, falling to about 130,000 t in 2000. During the most abundant phase in the 1980s, the sardines, which spawn between coastal water and the Kuroshio Current in late winter-early spring, migrated toward the north across the Kuroshio-Oyashio transitional region and, in summer, fed on abundant zooplankton and phytoplankton in the Oyashio water. In autumn, they migrate south to the waters off Boso Peninsula in central Honsyu, Japan. It was suggested that the drastic changes of sardine stock during the last two decades changed both the structure and the function of the Oyashio ecosystem (Noto and Yasuda, 2003).



Figure 40. Japanese catch of sardine, anchovy, chub mackerel and common squid along the Pacific coast of Japan (From FAJ, 2002).

Japanese anchovy (*Engraulis japonicus*, hereafter referred to as anchovy) is divided into four stocks: northern Pacific, southern Pacific, East China Sea and Japan Sea. The north Pacific stock of anchovy is the most abundant. Annual landings were high (350-450,000 t) in 1950-1960s when the sardine biomass was very low, but landings of anchovies decreased rapidly after 1975 as the sardine population increased (Fig. 40). In the 1980s, the landings remained at low level (150-200,000 t). Since 1989, anchovy landings have recovered as the sardine biomass began to decline, and now the anchovy migration range extends to the Oyashio region during summer-autumn.

Pacific saury (*Cololabis saira*, hereafter referred to as saury) occurs throughout most of the northern Pacific. In the Western Pacific, saury is one of the major commercial species taken by Japanese, Russian and Korean fisheries. No estimation of the population size exists because the distribution of the larvae, juveniles and adults is continuous from the Western to the Eastern Pacific.

After World War II, a new fishing gear, the stitch-held dipnet (bouke-ami), was introduced in Japan. Total catch increased remarkably after its introduction and reached a peak during 1955-63 with a maximum catch of 575,000 t in 1958 (Fig. 38). The catch of saury decreased to 52,000 t in 1969. Annual fluctuation of the catch was quite large in 1970s ranging between 87,000-427,000 t. In the late 1980s, the catch stabilized because of landing regulations adopted by the saury fishermen association.

Saury spawn off the northern Honshu Islands in autumn and spring, and in the Kuroshio area in winter. Juveniles from different spawning seasons start migrating north in early summer to the Oyashio area where they feed on abundant zooplankton, especially *Neocalanus plumchrus* and euphasiids. The Western Pacific saury reaches a length of 30 cm in one year (Watanabe *et al.*, 1988) and their life span has been estimated to be 1.5-2.0 years (Suyama *et al.*, 1996). Fishing area in the Oyashio region in autumn varies with location of Oyashio and warm core rings derived from Kuroshio and Tugaru Warm Current.

Recently, a fish bioenergetics model (NEMURO.FISH saury version) coupled with an ecosystem model (NEMURO) was developed to analyze the influence of climate changes on the growth of Pacific saury (Ito *et al.*, 2004). The model was composed of three box oceans, which correspond to the Kuroshio, Oyashio, and inter-frontal zone (mixed water) regions. In this coupled model, three zooplankton densities that were derived from NEMURO were input to the bioenergetics model of saury as the prey densities.

Japanese common squid (*Todarodes pacificus*, hereafter referred to as *T. pacificus*) is a commercially important squid in Japan. Annual catches of *T. pacificus* in Japanese and Korean waters have markedly increased since the late 1980s, and catches of the late-1990s are equal to those of the 1960s (c.a. 400,000-700,000 t) (Fig. 40). Compared to the late 1970s and mid-1980s, paralarval abundances have also been higher since the late 1980s. In the western North Pacific, environmental conditions shifted from a warm regime, which began in the late 1940s, to a cool regime in the late 1970s, and back to a warm regime in the late 1980s (Minobe, 1997). The variations in *T. pacificus* catches coincided with these regime shifts, particularly during the early 1980s as catch decreased, and the late 1980s when catches increased. Sakurai *et al.* (2000, 2002) suggested that winter spawning areas in the East China Sea shrank when adult stocks decreased during the cool regime before 1988, and that fall and winter spawning areas extended and overlapped in the Sea of Japan and East China Sea when adult stocks increased during the warm regime after 1989. Also after 1989, the feeding area of the winter spawning stock expanded to the Oyashio region during summer-autumn. These squid feed on small fish and large zooplankton. It has also been suggested that they feed on juvenile walleye pollock on the Oyashio shelf region during autumn.

Marine Mammals and Seabirds

The Oyashio/Kuroshio regions contain a diverse assemblage of marine mammals and seabirds, including north temperate, and Sub-Arctic species. Thirty-three species from the orders Pinnipedia (sea lions, fur seal and seals), and Cetacea (whales, dolphins and porpoises) are present for varying times during the year (Hunt *et al*, 2000). Some species are resident throughout the year (e.g. harbor seal and Dall's porpoise) and others migrate into the Oyashio region during summer months on feeding excursions (e.g. minke, sei, and killer whales). About sixty species of seabirds are present in the Oyashio/Kuroshio regions, but information on their ecology and distribution is generally lacking.

The Steller sea lion (*Eumetopias jubatus*), a threatened species in Japan, annually causes more than US\$1,000,000 worth of damage to coastal fishing gear. To improve the coexistence of fishermen and Steller sea lions, and conservation of the sea lions, a better understanding is needed of sea lion behavior. The counts of sea lions wintering along the coast of Sea of Japan, Hokkaido were about 390 in 2000-2001, 135 in 2001-2002, and 200 in 2002-2003 (Sakurai *et al.*, 2004).

These relatively high numbers may to be due to ecosystem changes that have occurred in the neighboring Sea of Okhotsk (e.g. a decrease in abundance of walleye pollock). Since the late 1980s, some pelagic species such as anchovy, Japanese common squid, and arabesque greenling, *Pleurogrammus azonus*, have migrated to the Sea of Okhotsk during summer and fall, and to the Sea of Japan in winter. Sea lions are thought to have followed these prey into the Sea of Japan. Aerial surveys showed movement occurred between the Rishiri-Rebun Islands and Tsugaru Strait from February to April centering on the two haul-out sites: Cape Ofuyu during mid-November to early May, and Cape Kamui during mid-December to early March. Both sites appear to serve as winter haul-outs for Steller sea lions feeding on spawning schools of arabesque greenling and walleye pollock.

Common minke whale (*Balaenoptera acutorostrata*, hereafter referred to as minke whale) is widely distributed in the world. In the western North Pacific, two stocks have been recognized: one in the Sea of Japan-Yellow Sea-East China Sea (J stock) and the other in the Sea of Okhotsk-West Pacific (O stock) (Tamura and Fujise, 2002). In the western North Pacific, minke whales are opportunistic feeders with a board diet and with flexible feeding habits. The daily food consumption of a mature minke whale is 200 kg (Kasamatsu and Tanaka, 1992). The diet variability of minke whale was considered in relation to changes in food availability around Japan. Especially, in the Pacific side of Japan, they fed mainly on Japanese sardine, Japanese anchovy and Pacific saury (Tamura and Fujise, 2002).

Long-term research is essential to understand cetaceans, their prey and the oceanography. Furthermore, such research makes it possible to understand the food-web of marine organisms including marine mammals such as whales, dolphins, porpoises and pinnipeds, and their conservation in the world (Tamura and Kato, 2003).

5.3 Bering Sea

5.3.1 Physical Oceanography

The Bering Sea is a semi-enclosed Sub-Arctic sea that connects the North Pacific and Arctic Oceans. It is bounded by Bering Strait to the north and the Aleutian Archipelago to the south, and lies between 52° and 66°N, and 162°E and 157°W. The Bering Sea consists of a deep central basin, a northwestern shelf in the Gulf of Anadyr that reaches south along the Kamchatka Peninsula, and a broad eastern shelf that stretches from the Alaska Peninsular to Russia and the Bering Strait (Fig. 41). The sea area covers almost 3 x 10^6 km² and is divided almost equally between waters >200 m deep and shelf waters < 200 m in depth (ACIA, in press). The 500 km-wide eastern continental shelf is about 1,200 km from north to south, and encompasses about 40% of the Bering Sea. The Bering Sea shelves support extraordinarily rich marine resources of vital importance to the economic survival, subsistence, and cultural foundations of the many indigenous people of the Bering Sea coasts (IARPC, 2001). Marine resources of the eastern Bering Sea include fisheries equal to about one half of the United States' fishery production, about 80% of the seabirds found in United States' waters, and substantial populations of marine mammals (NRC, 1996; IARPC, 2001). Eastern Bering Sea fishery landings include walleye pollock (Theragra chalcogramma, a nodal species in the shelf ecosystem), salmon, halibut (Hippoglossus stenolepis) and crab, and generate over 2 billion dollars in revenue each year (IARPC, 2001). The western Bering Sea shelf, although supporting smaller stocks of fish and shellfish, is important for Russian fisheries.



Figure 41. The bathymetry of the Bering Sea. Source: Karen Birchfield at the NOAA Pacific Marine Environmental Laboratory, Seattle, WA, USA.

The eastern shelf can be sub-divided into the southeastern, central, and northeastern shelf (Schumacher and Stabeno, 1998). The divisions among these three regions have not been well delineated, but it is generally agreed that the central region is located between a line from St. Paul Island, Pribilof Islands, to Nunivak Island and an east-west line about half way between St. Matthew Island and St. Lawrence Island. The northeastern region of the shelf is dominated by advective processes and has relatively weak tides, whereas the southeastern region generally has relatively weak cross-shelf transport and strong tides. Little study has been devoted to the central region, but it is a transition area where cross-shelf transport may be important.

The southeastern Bering Sea shelf is differentiated into three bathymetrically-fixed domains, which include the Coastal Domain that extends from the shore to about the 50 m isobath, the Middle Shelf Domain, between the 50 m and 100 m isobaths, and the Outer Shelf Domain which ranges from 100 m to 200 m in depth (Fig. 42; Iverson *et al.*, 1979; Coachman, 1986; Schumacher and Stabeno, 1998; Stabeno *et al.*, 2001). The domains are separated by fronts or transition zones, with the narrow (5 to 30 km) Inner Front or Structural Front between the Coastal Domain and the Middle Shelf Domain, a wide (> 50 km) middle transition zone between the Middle Shelf Domain and the Outer Shelf Domain, and the Outer Front between the Outer Shelf Domain and the waters of the slope. In summer, the Coastal Domain is well mixed to weakly stratified, the Middle Shelf Domain is strongly stratified, and the Outer Shelf Domain has well mixed upper and lower layers with a zone of gradually increasing density between (Schumacher *et al.*, 2003). During summer in the Middle Shelf Domain, the temperature difference between the upper and lower layers can be greater than 8°C, and changes in density are dominated by temperature rather than salinity (Hunt *et al.*, 2002a). In the northeastern Bering Sea, changes in tidal energy and freshwater discharge from the Yukon River affect the location of the fronts.

Circulation

Water enters the Bering Sea through the passes of the Aleutian Islands and from the rivers of Siberia and Alaska. Water from the Alaska Coastal Current, a shelf current that originates in the Gulf of Alaska, passes into the Bering Sea primarily through Unimak Pass and Samalga Pass (Stabeno *et al.*, 2002; Stabeno *et al.*, in press). Water from the Alaska Stream, a shelf-edge current that is



Figure 42. Southeastern Bering Sea shelf showing isobaths, domains and the location of NOAA's biophysical Mooring 2. (Map courtesy of N. Kachel, NOAA Pacific Marine Environmental Laboratory, Seattle, WA, USA)

part of the North Pacific Sub-Arctic gyre, enters the Bering Sea through a series of deep passes from Samalga Pass westward to Amchitka Pass and beyond (Table 3) (Stabeno *et al.*, 1999a, in press). Water leaves the Bering Sea through Bering Strait and through Kamchatka Strait, though there is also some southward movement of water on the west side of each of the passes that is wider than the internal Rossby radius (Stabeno *et al.*, 1999a). Flow through Bering Strait is important for the northern shelf of the Bering Sea and for the Arctic Ocean, but it has virtually no effect on circulation in the Bering Sea basin. Inflow of fresh water from the Yukon (207 km³ y^{-1}), Kuskokwim (58 km³ y^{-1}) and the Anadyr Rivers (52-64 km³ y^{-1}) is important for establishing along-shore geostrophic flows in the eastern and western boundary currents (Alaska Coastal Current and Kamchatka currents, respectively) (Pavlov and Pavlov, 1996). There is evidence for variability in flow through the passes at time-scales of months to years, but the range of this variability is not known, and the causes and effects of the variable fluxes have yet to be resolved (Stabeno *et al.*, 1999a).

Table 3. Characteristics of some of the importa	nt passes and straits bordering the Bering Sea
(Pavlov and Pavlov, 1996; Stabeno et al., 1999a).	Minus transport indicates net transport out of
the Bering Sea.	

Strait or Pass	Width (km)	Max. Depth (m)	Average Depth (m)	Cross- Sectional Area (km²)	Net transport (10 ⁶ m³ s ⁻¹)
Bering Strait	88	58	38	3.4	-0.3-1.4
Kamchatka S.	191	4,420	1,758	46	-12
Near Strait	363	2,000	658	239	9
Buldir Pass	125	760	256	32	1
Amchitka Pass	138	1,082	398	55	2
Amukta Pass	74	446	314	23	0.5
Herbert Pass	26	635	268	7.0	?
Samalga pass	32	300	139	4.5	?
Unimak Pass	20	82	60	1.2	0.1

The Bering Sea basin is dominated by a cyclonic gyre, with the north-flowing Bering Slope Current forming the eastern boundary Current and the south-flowing Kamchatka Current forming the western Boundary Current (Fig. 43). The Oceanic Regime of the basin is influenced by Alaska Stream Water that enters the Bering Sea through many passes. That portion of the current that enters through Amchitka and Amukta Passes turns right to form the Aleutian North Slope Current (ANSC) (Reed and Stabeno, 1999) (Fig. 43). This current in turn provides the major source of water for the Bering Slope Current (BSC) that varies between following the depth contours of the eastern shelf northwestward with a regular flow, and becoming an ill-defined, variable flow characterized by numerous eddies and meanders (Stabeno *et al.*, 1999a). These eddies occur not only in water seaward of the eastern shelf (Schumacher and Reed, 1992), but also in waters as shallow as 100-122 m (Reed, 1998). These eddies are potentially important as habitat for larval and juvenile pollock, and they can carry these fish, as well as nutrient salts, from the Oceanic Domain into the Outer Shelf Domain (Schumacher and Stabeno, 1994, Stabeno *et al.*, 1999a).

The Kamchatka Current originates near Shirshov Ridge (about 175°E) and flows southward until it splits, and either enters the Okhotsk Sea or flows along the Kuril Islands to become the Oyashio Current (Fig. 43). The source of the Kamchatka Current is a combination of the westward continuation of the Bering Slope Current and water flowing northward through Near Strait (Stabeno and Reed, 1994; Khen, 1989).



Figure 43. Schematic diagram of major currents in the Bering Sea (From Stabeno et al., 1999a).

On-shelf Fluxes and Nutrient Replenishment

On-shelf fluxes of nutrients from the basin are critical for the long-term productivity of the Bering Sea shelves, but the mechanisms responsible for forcing these fluxes are still not well understood. In the northern Bering Sea, cross-shelf fluxes occur in the Anadyr Current and from the northward flow along the 100 m isobath (Fig. 43) (Stabeno *et al.*, 1999a). These waters then flow northward through Anadyr Strait and Bering Strait (Shuert and Walsh, 1993; Overland *et al.*, 1994). These are persistent currents during the summer months. The Anadyr Current is an important source of nutrients to the northern shelf, and its flow is, at least in part, a response to the northward flow through Bering Strait (Coachman *et al.*, 1975; Nihoul *et al.*, 1993). Nutrients in this water support the extraordinarily high rates of summertime production found in the Chirikov Basin and northward through Bering Strait (Springer and McRoy, 1993; Springer *et al.*, 1996). This process also transports large oceanic copepods onto the northern shelf, where they sustain immense populations of planktivorous seabirds (Springer and Roseneau, 1985; Springer *et al.*, 1987, 1989; Hunt and Harrison, 1990; Hunt *et al.*, 1990; Russell *et al.*, 1999). The exact connections to the Bering Sea basin, however, remain unclear.

Flow through the Bering Strait appears to be changing, but the effect of this change on heat balance, nutrient flux, and ecosystem structure on the northern Bering Sea shelf remains unknown. Net northward transport in Bering Strait results from the difference in the sea level heights between the Pacific and Atlantic Oceans (Overland and Roach, 1987). When strong winds blow southward in fall and winter, they can overcome the net northward flow through Bering Strait, causing a southward flow exceeding 1–2 10⁶ m³ s⁻¹ of cold, relatively fresh water from the southern Chukchi Sea into the northern Bering Sea (Roach *et al.*, 1995; Overland *et al.*, 1996). The likely impact of a long-term decrease (or increase) in flow through Bering Strait would be more localized than that of a decrease in flow through the Aleutian passes. Although the area most impacted would likely be the shelf region north of 63°N, reduced flow through Bering Strait would reduce on-shelf flow of nutrients, and thus primary production on the northern Bering Sea shelf. It would also modify the advection of nutrients and particulate carbon into the Arctic Ocean.

Mechanisms for on-shelf transport of nutrients include eddies that bring slope waters onto the shelf at least as far as the 150 m isobath (Stabeno *et al.*, 1999a; Stabeno and Van Meurs, 1999; Okkonen, 2001) and at times to near the 100 m isobath (Reed, 1998). The strongly flowing Kamchatka Current (40-77 cm s⁻¹) has numerous meanders and eddies which can be important for on-shelf advection of nutrient-rich water along the Kamchatka coast (Stabeno *et al.*, 1999a). However, eddies are

rare in water < 100 m deep, and other mechanisms are required to replenish nutrients in the Middle and Inner Domains of the wide southeastern shelf. Two regions of preferential on-shelf flow are Bering Canyon, which is just north of the Aleutian Islands near Unimak Pass, and the area south and west of the Pribilof Islands, where the shelf break narrows (Stabeno *et al.*, 1999a). On-shelf flow west of the Pribilof Islands can move into the Middle Domain where it is marked by a front to the northeast of St. Paul Island (Flint *et al.*, 2002), or it may be entrained around the islands by tidal currents (Stabeno *et al.*, 1999b). It is also hypothesized that the generally seaward movement of sea ice in winter may result in an onshore flow at depth that could contribute to replenishment of nutrients over the southeastern shelf, but this hypothesis has yet to be investigated (Schumacher and Alexander, 1999).

Stratification, Mixing and the Vertical Flux of Nutrients

Shelf waters of the southeastern Bering Sea, although well-mixed during winter by storms, stratify in late spring from solar heating (Eslinger and Iverson, 2001). This stratification inhibits the vertical flux of nutrients, and, once the spring bloom has exhausted them from the upper mixed layer, the lack of nutrients limits new production. These nutrients can be replenished when processes break down the stratification. Sambrotto *et al.* (1986) identified the importance of summer storms as a mechanism for deepening the pycnocline and stirring nutrients into the upper mixed layer. Analysis of wind speed cubed, a measure of the ability of winds to mix the upper water column, shows that summer winds have declined since the early 1980s (Fig. 44).

A second pathway for the movement of nutrients from depth to the surface layers is upward mixing in the vicinity of fronts (lverson *et al.*, 1979; Sambrotto *et al.*, 1986; Kachel *et al.*, 2002). For example, this upward mixing can result in regions of high productivity on the stratified side of the inner front (Hunt *et al.*, 1996a; Kachel *et al.*, 2002). In 1997 after the completion of the spring bloom, a severe storm in late May mixed the water column to depths of 65 m or more and resulted in renewed production. The result was a depletion of nutrients to 60 m or more, and a lack of availability of nutrients at the base of the inner front and at the pycnocline for mixing into the upper mixed layer (Stockwell *et al.*, 2001). This observation points to the importance of episodic events in structuring the ecology of shelf waters.



Figure 44. Wind speed cubed at St. Paul Island. Note that since the late 1970s winter winds have been less strong and in summer, there have been more periods of wind below the long-term average (those areas in light gray). From Hunt *et al.* (2002a).

Sea Ice

The Bering Sea is a marginal ice zone, which is now typically ice-free from June through October. Commencing in September, cold winds from the Arctic cool the water and begin the formation of ice on the northern and western shelves (Pavlov and Pavlov, 1996). Ice formation on the eastern shelf is delayed as compared to the western shelf because of the advection of heat in the Alaska Coastal Current (Pavlov and Pavlov, 1996; Stabeno *et al.*, 1999a, 2002b). Throughout winter, the prevailing winds advect the ice southward into warmer water where it melts, cooling and freshening the seawater (Pease, 1980; Niebauer *et al.*, 1999). The maximum southerly extent of the ice and the amount of ice melt affect fluxes of heat and salt, thereby influencing both baroclinic flow and the temperature at the bottom (the cold pool) in the Middle Shelf Domain (Ohtani and Azumaya, 1995; Schumacher and Stabeno, 1998; Wyllie-Echeverria and Wooster, 1998).

During cold winters, ice can cover most of the eastern shelf (Stabeno *et al.*, 2001). Alternately during warmer winters, ice does not extend much farther south than St. Matthew Island. Analysis of ice charts (Fig. 44) shows that decadal patterns of variability are evident (Niebauer, 1998; Hunt *et al.*, 2002a). In the period from 1977 to 1996, there was a 5% reduction of ice cover as compared to 1947-1977 (Niebauer, 1998). Interannual and decadal-scale variability in sea-ice coverage was greater at the southernmost edge of the ice field than farther north (Fig. 44).

One of the more readily observed impacts of climate change on the eastern Bering Sea ecosystem is the extent and duration of sea ice over the Bering Sea shelf (Niebauer, 1998; Stabeno et al., 2001; Hunt et al., 2002a). The seasonal variation in the position of the ice edge is about 1700 km, the most extensive of any Arctic or Sub-Arctic region (Niebauer, 1998). In an average winter, about 75% of the eastern shelf is ice covered, but the amount and duration of ice cover can vary interannually by up to 25% of the seasonal range, depending on the wind field (Niebauer, 1983, 1998; Schumacher and Stabeno, 1998). During the last two decades, the maximum ice extent over the eastern shelf occurred, on average, in March, but maximum ice extents have been as early as January (in 2000), and as late as the end of April (in 1976) (Stabeno and Hunt, 2002). Recently, Niebauer (1998) has found that the position and strength of the Aleutian Low has a significant effect on the sea ice cover of the Bering Sea, and that the effect of the Aleutian Low is linked to ENSO events. During the early and mid-1970s, ice arrived early over the southeastern shelf and persisted into spring (Fig. 45). Following this cold period, there was a warmer period when sea ice was less common. Finally, in 1989 there appeared to be a shift to cooler conditions although not as cold as observed in 1972–1976 (Stabeno et al., 2001). The average pattern of ice coverage has also changed since the early 1970s, when the maximum extent of the zone in which \geq 10% ice cover was present annually for > 2 weeks extended farther south and west than it did in the 1980s or the 1990s (Stabeno et al., 2001). Additionally, in the 1980s and 1990s, the zone where ice lasted for at least 2 weeks withdrew northeastward along the Alaska Peninsula. Most of the north side of the Peninsula has been ice-free since 1990. The 1989 regime shift did not result in a return to the extensive ice conditions present before 1977.

In the eastern Bering Sea, a proxy for sea ice extent is provided by the mean winter (January-April) surface temperature (Bond and Adams, 2002; Hunt, 2004). The 40 year record for the site of Mooring 2 shows a notably cold period in the early to middle 1970s, and a warm period in the late 1970s into early 1980s, but conditions during the 1990s are similar to those in the 1960s. The time series of atmospheric parameters directly related to sea ice indicate that the presence of sea ice is a function of not just the cross-shelf component of the wind, but is also strongly related to the net surface heat fluxes. Before the regime shift of 1976/77, below-normal ice cover in the eastern Bering Sea was associated with El Niño conditions, during which the center of the Aleutian Low shifted eastward, and resulted in warm air from the Pacific flowing over the southeastern Bering Sea (Niebauer, 1998). After the regime shift, the Aleutian Low was located even farther eastward during El Niño periods, and under these circumstances the southeastern shelf was subjected to north and east winds from the interior of Alaska, which resulted in increased ice cover. During the 1990s, sea ice has both extended farther south and it has retreated more quickly, resulting in the northern Bering Sea being ice free earlier than in previous decades (Stabeno and Overland, 2001). In addition, atmospheric temperature during May has increased by 3°C in the 1990s compared to the 1980s.



Figure 45. Percent ice cover for two latitudinal bands in the eastern Bering Sea. Note the decrease in ice cover in the southern region as of about 1977, whereas there is little evidence for a change in ice cover at this time in the more northerly region. From Hunt *et al.* (2002a).

Cold Pool Formation

The bottom waters over the Bering Sea shelves show considerable interannual variation in temperature. Over the northern parts of the shelf, cold, salty brine is rejected as sea ice forms in polynyas, and this dense water sinks to the bottom. Density flows to the north carry much of this salty bottom water through Bering Strait to the Arctic Ocean where it contributes to the halocline (Cavalieri and Martin, 1994; Schumacher and Stabeno, 1998). Over the central and southeastern Bering Sea shelf, cold bottom waters are formed when sea ice melts, and the cold, fresh melt water is mixed throughout the water column by storms (Stabeno et al., 1998). These melt waters can cool the entire water column to about -1.7°C. When the surface waters are warmed by solar radiation in spring, a thermocline forms, and the cold bottom waters are largely insulated from further heating (Coachman et al., 1980; Ohtani and Azumaya, 1995; Wyllie-Echeverria, 1995). Bottom temperatures in this "cold pool" warm slightly over the summer, but may remain below 2°C until storm-induced mixing occurs in fall. The extent and temperature of the southern cold pool is dependent on the amount of ice melt that occurs, and since ice is constantly melting as it is advected south, the amount of melt water generated is a function of the duration of time that ice is present (Pease, 1980; Overland and Pease, 1982). Winter conditions play an important role in determining the strength of the pycnocline, and hence the ease with which it could be eroded by storms.

5.3.2 Ecosystem Properties

Timing of Primary Production

In the southeastern Bering Sea, the timing of spring primary production is determined by a combination of the date of ice retreat, stabilization of the water column by solar heating, and the cessation of strong storm activity (Sambrotto et al., 1986; Stabeno et al., 1998, 2001; Eslinger and Iverson, 2001). The timing of the spring bloom is important because it determines the ambient water temperatures in which grazers of the bloom must forage. Data illustrative of the conditions that determine the timing of the spring bloom were obtained from Mooring 2, located in ~72 m of water in the middle domain (Figs. 42 and 46). If ice retreat comes before mid-March, there is apparently insufficient light within the portion of the water column through which algal cells are mixed to support net primary production (e.g. Fig. 46, 1996, 1998, 2000). If ice remains after mid-March, the spring bloom is delayed until May or June, after winter winds have ceased and thermal stratification stabilizes the water column (Fig. 46) (Stabeno et al., 1998, 2001; Eslinger and Iverson, 2001). If ice melt is delayed until April or May, there is an early, ice-associated bloom (e.g. Fig. 46, 1995, 1997, 1999). The pattern of late ice retreats with early icerelated blooms and early ice retreats with late blooms has held since the 1970s (Table 4). Although wind mixing of the water plays a role in determining when the bloom will occur, it is apparent that the timing of the last winter storm is less important than the date of ice retreat in determining the timing of the bloom. Thus, early blooms occur in cold water and are related to ice-edge blooms, whereas late blooms occur in relatively warm water and are not related to the ice edge (Fig. 46).





Table 4. Relationship between the timing of ice retreat and the type of spring bloom	. From Hunt
and Stabeno, 2002.	

Timing of Ice Retreat	Bloom Occurs at the lce Edge	Bloom in Open Water	
Ice Gone by mid-March	0	7	
Ice remains after late March	6	0	

Species Composition

The timing, species composition, and type of spring phytoplankton bloom appear to have changed in the southeastern Bering Sea. Observations in the 1970s showed the predominant bloom in the Bering Sea occurred along the ice edge in early spring as the sea ice retreated (Alexander and Niebauer, 1981; Niebauer, 1981). In the 1980s, the blooms in the southeastern Bering Sea were not tied spatially to the location of the ice edge, since the ice retreated early in the season. Peak primary productivity during this warm period took place mainly in May and June and consisted of different species assemblages than those found in the ice-edge blooms (Alexander et al., 1996; Alexander and Cooney, 1979; McRoy et al., 1986; Niebauer and Alexander, 1989). By the 1990s, the blooms again began appearing in March and April in association with the retreat of the ice edge. Yet, they were not as regular and intense as the ice-edge blooms of the 1970s (Stockwell et al., 2001; Stabeno et al., 1998, 2001; Napp and Hunt, 2001). The ecosystem effects of this variability in the timing and ice-association of the bloom have been hypothesized to include shifts in the fate of carbon between the pelagic and benthic components (Alexander et al., 1996; Walsh and McRoy, 1986), but this hypothesis has yet to be tested. At the least, the differences in species composition of the phytoplankton will affect the ability of zooplankton to graze the production effectively.

The species composition of sea ice algal communities in the Bering Sea has received little attention since the early work of Schandelmeier and Alexander (1981). Likewise, little is known about how the species composition of ice-associated blooms affects the fate of this production. The extensive pack and fast ice that forms in arctic regions provides a unique habitat for microbial assemblages. Sea ice provides a platform from which algae can remain suspended in the upper ocean where light is sufficient for photosynthesis and growth. Sea ice algae have been shown to sustain a wide variety of organisms through the winter months when other sources of food are lacking.





Figure 47. SeaWiFS false color images of coccolithophore blooms; left, in the Bering Sea on 20 July 1998 (from Napp and Hunt, 2001, processed by S. Zeeman, University of New England) and right, in the Barents Sea on 27 July 2004 (from http://www.redtailcanyon.com/items/3170071.aspx).

Coccolithophore Bloom

In the 1990s, there were marked anomalies in the species composition of phytoplankton in the eastern Bering Sea. Although diatoms typically dominate phytoplankton biomass in the eastern Bering Sea (Sukanova *et al.*, 1999), from 1997 to 2001, coccolithophore blooms dominated summer phytoplankton assemblages over much of the shelf (Fig. 47) (Sukhanova and Flint, 1998; Vance *et al.*, 1998; Napp and Hunt, 2001; Stockwell *et al.*, 2001).

Rates of Primary Production

The waters of the Bering Sea are rich in nutrients, and these support unusually high levels of primary production (Fig. 48). For the southeastern shelf of the Bering Sea, annual primary production rates of 200- 250 g C m⁻² y⁻¹ have been measured, and in the northern Bering Sea annual production rates of up to 540 g C m⁻² y⁻¹ have been reported (Springer *et al.*, 1996). Over the western shelf, maximum annual production (> 400 g C m⁻² y⁻¹) occurs over the continental slope (Arzhanova *et al.*, 1995).



Figure 48. Average summer surface chlorophyll-a concentrations estimated on the basis of satellite imagery. (From: http://mapper.edc.uri.edu/website/ Imeims/viewer.htm)

However, there is some evidence that the rates of new primary production, particularly in the northern Bering Sea, may be declining. Schell (2000), using stable isotope ratios from carbon sequestered in the baleen of bowhead whales during periods of feeding in the northern Bering Sea, estimated that primary production in the Bering Sea had decreased by as much as 30 to 40% since 1967, with almost all of the decrease coming since 1976. Cullen et al. (2001) questioned whether some of this effect was the result of anthropogenic CO₂ or changes in the species composition of the phytoplankton. However, Schell (2001) provided additional information, including data from stable isotopes of nitrogen, that corroborates the earlier findings. Grebmeier and Cooper (1994, 2002), Grebmeier and Dunton (2000), and Grebmeier (1992) have found evidence for declines in sediment oxygen respiration of as high as 73% over the period 1987 to 2002, with declines in benthic biomass of 89% over a longer period. In addition, they have documented changes in the species composition of benthic bivalves and other fauna. Taken together, these studies point to a decline in production levels for the northern Bering Sea, including in the Saint Lawrence Island Polynya region south of St. Lawrence Island. These reductions in production may be related to reduced northward flow through Bering Strait (Roach et al., 1995), and a consequent diminution of nutrient advection from the Bering Sea Basin onto the northern shelf.

In the southeastern Bering Sea, there appears to be no clear indication of a decrease in production, though Hirons *et al.* (2001) have attempted to extend the results of Schell (2000) to the remainder of the eastern Bering Sea and Gulf of Alaska by examining stable isotope ratios in the teeth of harbor seals (*Phoca vitulina*), northern fur seals (*Callorhinus ursinus*) and Steller sea lions (*Eumetopias jubatus*). For these species, when data from teeth from both the Gulf of Alaska and the Bering Sea were combined, they found a significant decline in the δ^{13} C in sea lions and similar, though non-significant, trends in harbor seals and fur seals.

In contrast, in 1997, estimates of primary production in the southeastern Bering Sea, based on the draw down of nitrate over the middle and inner shelf, suggested that new production may have been between 10 and 30% greater in 1997 than in the early 1980s (Stockwell *et al.*, 2001). Estimates for production levels in 1998 and 1999, however, do not appear to differ from those of the early 1980s (Whitledge, pers. comm.). In contradiction to these estimates of productivity in 1997, 1998 and 1999, sediment trap data supported the notion that productivity was higher in 1998 than 1997 (Smith *et al.*, 2002), as did data from the uptake of ammonium (Rho, 2000). However, δ^{13} C values from copepods in the 1997-1999 period were lower than found by Schell *et al.* (1998). Based on the sum of the above results and the high stable or increasing biomass of fish and invertebrates over the southeastern shelf (see below), it seems unlikely that there has been a marked reduction in primary production over the southeaster shelf since the 1970s (Hunt *et al.*, 2002a). However, this remains an area of contention and there is a clear need to determine whether there have been long-term changes in the rates of new production, and if so why.

Zooplankton

The species composition of the zooplankton of the Bering Sea is dominated by Copepoda (37% by abundance), Coelenterata (17%), and Amphipoda (12%) (Kun, 1975). Based on a faunistic analysis, Brodskiy (1955, 1957) and Brodskiy *et al.* (1983) identified four major epipelagic communities of calanoid copepods in the Bering Sea: southern Bering Sea oceanic, northern Bering Sea oceanic, eastern neritic and western neritic (Table 5). Based on numbers, the dominant species in these faunistic groupings differ somewhat from those that dominate the copepod biomass of these regions.

	Southern Bering Sea	Northern Bering Sea	Eastern Bering Sea	Western Bering Sea
Species	Oceanic	Oceanic	Neritic	Neritic
Pseudocalanus elongatus	35.0	65.5	61.6	69.5
Pseudocalanus spp.	0	<1	0	<1
Arcatia longiremis	<1	1.9	24.1	9.1
Calanus glacialis (marshallae)	0	3.1	2.0	<1
Centropages abdominalis	0	<1	2.7	11.5
Microcalanus pygmaeus	4	4.5	<1	0
Eurtemora kiefoeri and E. herdmani	0	0	<1	4.2
Tortanus discaudatus	0	0	2.6	<1
Eucalanus bungii	8.2	1.3	<1	<1
Metridia pacifica	45.6	24.2	<1	2.9
Neocalanus plumchrus	8.5	<1	<1	<1
Neocalanus cristatus	1.6	<1	<1	<1

 Table 5. Dominant species in the epipelagic copepod communities of the Bering Sea (After Brodskiy, 1957).
Traditionally, calanoid copepods have been believed to be the major agents of energy transfer between large-celled diatoms and upper trophic level consumers such as planktivorous fish (e.g. Hood, 1999). Although emerging data now suggest that in boreal oceans these large copepods have a large dietary component of microzooplankton (Capriulo *et al.*, 1991; Sherr and Sherr, 1992; Rivkin *et al.*, 1999), the large copepods are still important prey for fish, whales and seabirds. In the eastern Bering Sea, the copepod communities of the basin and outer shelf are dominated in spring by large species of *Neocalanus* (*N. cristatus, N. plumchrus, and N. fleminergi*) and *Eucalanus bungii*, and the middle and inner shelf by the smaller *Calanus marshallae, Pseudocalanus* spp. and *Acartia* spp. (Cooney and Coyle, 1982; Smith and Vidal, 1986). Based on Russian literature, the greatest biomass of plankton occurs in the northern Bering Sea (often > 2000 mg m⁻³) and up to 2000-3100 mg m⁻³), and along the narrow western shelf (1000-2000 mg m⁻³) and up to 2000-3100 mg m⁻³ in Karagin and Kamchatka bays (Coyle *et al.*, 1996). By contrast, the remaining deep-water area of the Bering Sea has a much lower biomass of plankton (500-1000 mg m⁻³).

The most complete time series of zooplankton abundances in the eastern Bering Sea depend on data gathered in summer by the T/S *Oshoro Maru*, which has documented declines zooplankton biomass from the basin between the late 1960s and the early 1990s (Fig. 49) (Sugimoto and Takadoro, 1997). In the basin, they also found a biennial fluctuation in zooplankton biomass that was negatively correlated with the catch of Asian pink salmon (*Oncorhynchus gorbuscha*). Sugimoto and Takadoro interpreted these two patterns as indicating a bottom-up control of the zooplankton on a decadal-scale, and a top-down control on an annual scale. In contrast to the results obtained from the basin, examination of *Oshoro Maru* data from the shelf showed neither a long term trend, nor evidence of biennial cycles in summer zooplankton biomass (Fig. 49) (Hunt *et al.*, 2002a; Napp *et al.*, 2000).



Figure 49. Changes in zooplankton biomass in the deep basin and in the outer, middle and coastal domains of the southeastern Bering Sea sampled by the Oshoro Maru Summer Cruises. Data from 1997 to 1994 from Sugimoto and Tadokoro (1998). Data from 1995 to 1999 from Dr. N. Shiga, unpublished. Means with standard errors. (From Hunt *et al.*, 2002a).

Effects of Water Temperature on Zooplankton

The ambient temperature is important for determining the rates of the physiological processes of organisms, and phytoplankton growth is less sensitive to water temperature than is zooplankton growth (see also Vidal, 1980; Vidal and Smith, 1986; Townsend *et al.*, 1994). Water temperature is often thought of as more important than food availability for limiting the growth rates of smallbodied copepods (McLaren, 1963; Corkett and McLaren, 1978; Vidal, 1980; Dagg *et al.*, 1984; Huntley and Lopez, 1992). Thus, in years with warm water, Walsh and McRoy (1986) hypothesized that zooplankton would capture more of the primary production than in cold years, and the greater production of zooplankton in warm years would support the pelagic community, e.g., fish such as pollock. In the middle domain, where interannual environmental variability is greatest, water temperature is likely to play a major role in interannual variation in copepod biomass.

For species of small copepods over the inner and middle shelf areas, June abundances in 1999 were reduced by up to 90% compared to the two warmer years (Coyle and Pinchuk, 2002b). Although Smith and Vidal hypothesized that differences in predation on the copepods as well as temperature might have affected the differences in abundance between 1980 and 1981, there was no indication in the data of Coyle and Pinchuk (2002b) that chaetognaths were responsible for the declines in copepod abundance observed in 1999. Coyle and Pinchuk (2002b) provide compelling evidence that, even on a station-by-station basis, there was a strong relationship between the numbers of copepods present and integrated water temperatures (Fig. 50). They estimated that secondary production of calanoids in spring 1999 was about 3-4% that which occurred in the warm years of 1997-1998. By August – September, there were no consistent significant differences in the biomass of small copepods between 1999 and the two warmer years (Coyle and Pinchuk, 2002b).



Figure 50. June abundances of *Pseudocalanus* spp. (top) and *Acartia* spp. (bottom) in relation to the integrated water temperatures at the stations where they were collected 1997-1999). Dashed lines are 95% confidence intervals around the regressions. K. Coyle, unpublished data.

The effect of temperature on euphausiids appears to be the inverse of its effect on copepods; in 1999, the acoustically measured biomass of adult euphausiids on the inner and middle shelf was significantly higher than in 1997 and 1998 (Coyle and Pinchuk, 2002a). This difference may be related to a delay in euphausiid breeding in the cold year, which would result in more adults remaining in the water column when they were sampled in June compared to a warm year when most adults would have spawned and died prior to June. Coyle and Pinchuk (2002a) noted that there were significantly higher densities of euphausiid eggs and larvae present in 1999 (the cold year) compared to the warm years of 1997 and 1998. If euphausiid spawning is completed in early spring and there is a reduced availability of late spawning adults in summer, this change in the timing of availability could have a negative impact on predators, such as short-tailed shearwaters (*Puffinus tenuirostris*) that depend on euphausiids for a significant portion of their diet (Baduini *et al.*, 2001a,b; Hunt *et al.*, 2002b).

Microzooplankton are protists and metazoan organisms smaller than 200µm that are present in the plankton (Dussart, 1965). Although microzooplankton are an abundant element in the food webs of the southeastern Bering Sea, we are only just beginning to investigate their role in this ecosystem (Howell-Kubler *et al.*, 1996; Olson and Strom, 2002). Microzooplankton were an important component of the southeastern Bering Sea food webs in the summer of 1999. For the shelf as a whole, grazing by microzooplankton accounted for 110% of the growth of cells > 10 µm and for 81% of the growth of cells < 10 µm. This preferential grazing on the larger cells may help to explain the persistence of the coccolithophore bloom and is contrary to the belief that microzooplankton are constrained to diets of nanno-phytoplankton (Olson and Strom, 2002). These findings emphasize the need for a thorough examination of the role of microzooplankton both in the summer, for which we have evidence that they may form an important link between phytoplankton and meso-zooplankton, and during the spring bloom, when their role has yet to be evaluated.

In the last three decades, gelatinous zooplankton, in particular large scyphomedusae, have gone through a remarkable increase in biomass and then crash (Fig. 51) (Brodeur *et al.*, 1999, 2002). The cause (or causes) of the outbreak of jellyfish is not known, though it has been hypothesized that changing climate and ocean temperatures may have been the trigger (Brodeur *et al.*, 1999). It has also been hypothesized that a decrease in forage fish over the southern portion of the shelf in the early 1980s may have contributed to the jellyfish increase by releasing them from competition (Brodeur *et al.*, 2002). Currently, there are no hypotheses to explain why they suddenly decreased. At the Pribilof Islands, the dominant scyphozoan, *Chrysaora melanaster*, was estimated to consume about one third of the standing stock of crustacean zooplankton and 4.7% of their annual production. Additionally, these jellyfish were estimated to consume about 3% of the standing stock of age-0 pollock in the vicinity of the Pribilof Islands (Brodeur *et al.*, 2002).



Figure 51. Biomass in thousands of metric tonnes of large medusae in the eastern Bering Sea (Courtesy of G. Walters, NOAA, AFSC, Seattle WA, USA).

Fish

The species composition and biomass of top predators in the Bering Sea differ greatly from what they were prior to exploitation by people. Not only have many marine mammal populations been severely reduced, but also the species composition and biomass of the fish and shellfish have been radically changed. Although some of these changes may, in part, result from climate forcing, many have been driven by fisheries removals. In the eastern Bering Sea, the removal of plankton-eating whales, herring and Pacific ocean perch (Fig. 52) may have opened the way for pollock to respond to the regime shift of 1976 with a burst of population growth that has resulted in the domination of the eastern Bering Sea pelagic ecosystem by pollock (Merrick, 1997; NRC, 1996). It is hypothesized that the removal of the whales and planktivorous fish released vast amounts of zooplankton from consumption, and that this newly available zooplankton resource then fuelled the expansion of the pollock population. Fish stocks in the Bering Sea are now being managed more conservatively, and as they rebuild, competitive and predator-prey interactions are evolving. These populations and communities are responsive to climate forcing of the marine environment (e.g. Hare and Mantua, 2000).



Figure 52. Commercial fisheries catch dynamics in the Eastern Bering Sea Large Marine Ecosystem (From http://seaaroundus.org/lme/SummaryInfo.aspx?LME=1#).

During the late-1970s and early 1980s, several stocks of eastern Bering Sea groundfish and non-crab invertebrates showed strong changes in biomass, with timing of changes in both commercially exploited and non-exploited species being similar (Conners *et al.*, 2002). Pacific cod and several species of flatfish showed increases of 300 to 600 percent, whereas the biomass of Greenland turbot decreased by 90 percent. These changes resulted in a marked shift in the species composition of ground fish and benthic invertebrates in shelf waters. Conners *et al.* noted that the timing of the change in CPUE in the trawls was consistent with the timing of the major regime shift of 1976/77, and that there was little evidence of responses to the later, weaker regimes shifts in 1989 and 1998.

For most species since 1975, the patterns of change in ground fish biomass have followed the availability of recruits, not the catch of the fishery. However, these stock changes greatly affected the fishery landings and sustainable yields. The most notable series of stock increases came after the 1976/76 regime shift that resulted in favorable ocean conditions north of the state of Washington. Although fishery takes have affected the total biomass of groundfish in the eastern Bering Sea, in recent years patterns of change appear to be driven by ecological determinants of recruitment. For example, decadal-scale variation in wind-forcing may have a strong impact on the recruitment of some flatfish species in the eastern Bering Sea. In the period 1980 to 1989, modeled near-surface, wind-forced fluxes were to the northeast, onto the shelf, whereas in the 1990s, winds flows originating in a major spawning area for these fish remained more offshore (Fig. 53) (Wilderbuer *et al.*, 2002). For three species of flatfish, year class strength had a strong negative relationship to a location index that factored in both the distance offshore and the water depth where eggs or larvae would be expected to be at the time of settlement (Fig. 54) (Wilderbuer *et al.*, 2002).





Figure 53. Modeled drift of surface waters from the spawning grounds of flatfish species in decades with different wind-forcing. (From Wilderbuer *et al.*, 2002)



Figure 54. The relationship between the estimated inshore drift of flatfish larvae and their recruitment. Depth x Distance is a proxy measure for location inshore. (From Wilderbuer *et al.*, 2002)

Walleye Pollock (*Theragra chalcogramma*) is the most abundant species within the Bering Sea and is widely distributed throughout the North Pacific Ocean in temperate and sub-Arctic waters (Shuntov *et al.*, 1993; Wolotira *et al.*, 1993). Pollock are a semi-demersal schooling fish that become increasingly demersal with age (ACIA, in press). They are a relatively short lived, fast growing fish. Females usually become sexually mature at age 4 and have a maximum recorded age of around 22 years.

Pollock currently support the largest fishery in U.S. waters and now comprise 75-80% of the annual catch in the eastern Bering Sea and Aleutian Islands (Fig. 50) (http://www.st.nmfs.gov/st1/ commercial/). Directed foreign fisheries first began in 1964, after which catches increased rapidly during the late 1960s and reached a peak in 1970-75, when they ranged from 1.3 to 1.9 million t annually (ACIA, in press). Since the advent of the US Exclusive Economic Zone in 1977, the annual average eastern Bering Sea pollock catch has been 1.2 million t and has ranged from 0.9 million in 1987 to nearly 1.5 million t in 1990. The stock biomass has ranged from a low of 4-5 million to highs of 10-12 million t. Pollock are also the most important component of the commercial fisheries catch in the western Bering Sea (Fig. 55). There, in the 1990s, pollock declined coincident with severe cooling of shelf waters and rising temperature contrasts between the shelf and basin zone (Radchenko *et al.*, 2001).



Figure 55. Commercial fisheries dynamics in the Western Bering Sea Large marine Ecosystem. (From http://seaaroundus.org/lme/SummaryInfo.aspx? LME=53#).

During the period from 1963 to 2001, estimated year-class strength of pollock in the eastern Bering Sea varied from a low of 3.6 billion age-1 fish in 1963 to a high of 63 billion in 1978 (Fig. 56). Hollowed and Wooster (1995) classified years into those warmer and colder than the long term mean for the North Pacific Ocean from 1946 to 1990. They found that during warm periods, the year-class strength of many stocks of groundfish were stronger, while during cool periods, the same stocks showed weaker year class strength. There were two or three banner year-classes of pollock per decade with intermediate years showing average to weak year classes (NPFMC, 2003). The biomass of age-3+ pollock increased strongly in the 1980s because of the growth and survival of the strong year-classes that started in 1978 (Fig. 57). The biomass continued to be above the long-term average during the 1990s because of the strong year-classes that followed the exceptionally strong 1989 year-class. The increases were apparently due to favorable ocean conditions. Walleye pollock was unique among eastern Bering Sea groundfish in its continued production of young through the decade of the 1990s.



Figure 56. Year-class strength of walleye pollock in the eastern Bering Sea in billions of fish (From NPFMC, 2003).



Figure 57. Estimated biomass of age-3+ walleye pollock in the eastern Bering Sea (mean and estimated 95% confidence limits). (From NPFMC, 2003)

What controls recruitment of walleye pollock?

In 1978, pollock produced an enormous year-class that numbered 63.5 billion age-1 fish in 1979 (NPFMC, 2003). The reasons for this spurt in population growth are not known. It is possible that this was a continuation of the ecological release of the pollock population subsequent to the removal of the whales and fish with which they are believed to have competed for prey. An alternative, but not mutually exclusive, hypothesis is that the strong year-classes of 1977 and 1978 were the result of the 1976/77 regime shift. This event resulted in earlier ice retreat and warmer water temperatures in spring, conditions favorable for zooplankton production that would have provided abundant prey resources for growing pollock (Francis *et al.*, 1998; Hunt *et al.*, 2002a). Indeed, there is a general acknowledgment that warm years are conducive to enhanced pollock recruitment (Walsh and McRoy, 1986; Bulatov, 1995; Hollowed and Wooster, 1995; Bailey *et al.*, 1995, 1996; Quinn and Niebauer, 1995; Blood, 2002). The cessation of the foreign fishery did not cause the exceptional year class of 1978. The increase was driven by exceptional early survival and recruitment.

Water temperature affects the timing of hatching and survival of pollock eggs. Blood (2002) found that the hatching periods for Bering Sea pollock eggs could vary as much as 13 days between the warmest and coldest years encountered between 1995 and 1998. Longer incubation means a greater exposure to predation and an increased risk of exposure to extreme low temperatures in the upper water column Malformation of pollock embryos occurs in eggs incubated at -1° C (Nakatani and Maeda, 1984), a temperature not infrequently encountered in the shelf waters of the Bering Sea shelf in late winter and early spring (Hunt *et al.*, 2002a).

Water temperature also influences the distribution of pollock, with adult pollock more sensitive to cold temperatures than juveniles. Juvenile pollock prefer to avoid waters < 2° C (Wyllie-Echeverria, 1996). When the near-bottom pool of cold melt water on the eastern shelf is of reduced size, these fish spread out over much of the middle domain in shelf waters not frequented by adult pollock. When the cold pool is extensive, juvenile pollock move toward the warmer waters of the outer domain and shelf edge, where they are subject to increased levels of cannibalism by adult pollock that reside in these outer shelf waters (Ohtani and Azumaya, 1995; Wyllie-Echeverria, 1995, 1996; Wyllie-Echeverria and Wooster, 1998).

Several additional hypotheses have been put forward as explanations for variation in pollock yearclass strength (Table 6). They can be divided into four groups. Group A focuses on the importance of primary or secondary production for the survival of young pollock. The abundance of small shelf copepods, varies significantly with integrated water temperature, and in cold years pollock may be limited by the scarcity of zooplankton. Group B focuses on the importance of cannibalism and mechanisms that result in the separation of adult and juvenile pollock. Cannibalism is recognized as a major source of mortality for young pollock (Dwyer et al., 1987; Wespestad, 1994; Balykin, 1996; Livingston and Lang, 1996; Livingston and Methot, 1998; Lang et al., 2000; Livingston and Juardo-Molina, 2000), and mechanisms for separating vulnerable individuals from cannibalistic older fish are likely to be of importance regardless of what other factors are at play. Group C includes a hypothesis that combines variation in risk of predation with variation in the abundance of zooplankton. For example, Cooney et al. (2001) found that in Prince William Sound, adult pollock would feed on large Neocalanus copepods in spring if the copepods were abundant, but if not, the adult pollock would prey upon juvenile salmon and herring. Presumably, if zooplankton prey were unavailable in the Bering Sea, adult pollock might increase their consumption of juveniles. Group D is an hypothesis that relates survival of young pollock to variation in the amount of turbulence when feeding. Variations in the amount of turbulence may influence foraging success of larval pollock be either enhancing the encounter rate with food particles at intermediate rates of turbulence, or depressing foraging success with either too much turbulence or insufficient turbulence (Megrey and Hinckley, 2001). It is also likely that, as pollock populations wax and wane, the mechanisms responsible for population control will shift (e.g. the Oscillating Control Hypothesis) (Bailey, 2000; Hunt et al., 2002a). Most of these hypotheses remain to be tested in the field, and it is likely that some combination of them together will provide the key to understanding the occurrence of strong year-classes.

H	pothesis	Citations	Tests	
A. Production-based hypotheses				
1.	Decreases in wind mixing negatively influence post-bloom primary production	Sambrotto <i>et al</i> . 1986 Hunt <i>et al</i> ., 2002a	Compare wind mixing in years with strong and weak year classes. Probably no significant relationship with summer mixing. Determine if there is strong coupling between spring and summer primary production, zooplankton abundance, and pollock year- class strength.	
2.	Late ice retreat results in cold water blooms and reduced zooplankton production	Stabeno <i>et al</i> ., 1998 Hunt <i>et al</i> ., 2002a Hunt and Stabeno, 2002	Compare zooplankton abundances in years with early and late ice retreat; Coyle and Pinchuk 2002b show significant differences Determine if zooplankton abundance limits age-0 or age-1 pollock survival	
B. Cannibalism-based hypotheses				
3.	When the cold pool is large, age- 1 pollock move to the shelf edge where adults abound	Dwyer <i>et al.</i> , 1987 Ohtani & Azumaya, 1995 Wyllie-Echeverria, 1995	Compare cold pool size in years with strong and weak year classes;	
4.	Favourable winds in early spring may transport eggs, larvae and small age-0 pollock deep onto the shelf thus separating them from adults	Wespestad <i>et al</i> ., 2000	Compare wind forcing in years with strong and weak year classes	
C.	C. Mixed production/cannibalism hypothesis			
5.	Adult pollock switch prey types such that when zooplankton are scarce in spring, they increase cannibalism	Cooney <i>et al</i> ., 2001	Since zooplankton are less abundant in cold years, compare the amount of cannibalism in years with cold and warm spring temperatures	
D. Mixing Process hypothesis				
6.	Intermediate levels of turbulence are required for optimal foraging conditions	Megrey & Hinckley, 2001	Compare turbulence levels in years with strong and weak year-classes	

 Table 6. Hypotheses for explaining variation in year-class strength of walleye pollock in the eastern Bering Sea.

Forage Fishes

In addition to work on the commercially important groundfish and salmon species, there have also been significant gains in our knowledge of the distribution, abundance, and ecology of forage fishes. These fish include both small species, such as sand lance (*Ammodytes hexapterus*), capelin (*Mallotus villosus*) smelts, and mesoplagic groups such as Myctophids (lanternfish) and Bathylagidae (deepsea smelts), as well as the young of larger species such as age-0 and age-1 walleye pollock. Also included is the commercially exploited Pacific herring (*Clupea pallasii*). Herring populations in the eastern Bering Sea have been depleted, and are showing little sign of recovery (Fig. 58). In the western Bering Sea, they apparently do best in cold years, when the biomass of pollock is reduced (Naumenko, 1996).



Figure 58. Herring numbers and biomass from the Togiak Bay region, Bristol Bay, Alaska. (From NPFMC, 2003).

Forage fish species are eaten by large fish, including Pacific cod, halibut and walleye pollock, and are also important components of the diets of marine mammals and seabirds. Brodeur et al. (1999) summarized data collected in 1987 in a joint program with Russian colleagues that resulted in a pair of surveys that covered most of the Bering Sea. They found that age-0 and age-1 pollock were more abundant on the eastern shelf than elsewhere in the Bering, that herring and capelin were most abundant on the northern and western shelves. They also compared the distribution of various species, as sampled in the National Marine Fisheries Bottom Trawl Surveys, in a warm year (1987) and in a cold year (1986). They found that some forage fishes, such as age-1 pollock, avoided regions with cold bottom temperatures, whereas others did not (e.g., capelin). As a cold water species, capelin may migrate in close association with the retreating ice edge. As a result, in the bulk of the summertime capelin biomass located in the northern Bering Sea, an area not covered by surveys and with very little commercial fishing. Capelin aggregations near the northwestern Kamchatka coast exhibit a stable distribution throughout the warm season. It is reported that the biomass of capelin and smelt grow in the transitional periods when the abundance of other common pelagic fish (walleye pollock and herring) are at a low level in the western Bering Sea (Naumenko et al., 1990).

Marine mammals

The Bering Sea contains a rich and diverse assemblage of marine mammals, including north temperate, arctic and subarctic species. Twenty-six species from the orders Pinnipedia (sea lions, walrus and seals), Cetacea (whales, dolphins and porpoises) Carnivora (sea otter) and polar bears are present for varying times during the year (Lowry and Frost, 1985). Marine mammals were heavily exploited early (ACIA, in press). From 1743 to 1823, 2,324,364 fur seals (*Callorhinus ursinus*) were taken from the Bering Sea (ACIA, in press). Between 1786 and 1862, the sea otter

(*Enhydra lutris*) harvest from the Aleutian Islands, eastern Bering Sea, and Gulf of Alaska totaled 201,403 animals. Other mammal harvests included 2 x 10³ Steller sea lions (*Eumetopias jubata*) yearly from St. George Island, Pribilof Islands and, until the population declined in the 1830s, an annual harvest of 300 to 2000 walrus (*Odobenus rosmarus*). Due to overexploitation, the fur seal breeding-grounds disappeared on the Pribilof Islands, Unalashka Island, and adjacent areas between 1830 and 1840. Additionally, 47.8 metric tons of baleen were harvested from Bering Sea whales. Removals of marine mammals of this magnitude must have caused major changes in the marine ecosystems of the Bering Sea.

Approximately 80% of the world population of northern fur seals breeds on the Pribilof Islands where population estimates have been conducted since the turn of the century, and with consistent methodology for the past 60 years (York and Hartley, 1981). There are currently an estimated 800,000 animals remaining from an estimated population of 2 million as recently as the 1950s. The species is listed as depleted under the Marine Mammal Protection Act (NMFS, 1993). Unlike most other apex predators in the Bering Sea, the pattern of decline among northern fur seals is one of steady to severe reductions in population numbers followed by some years of stability (Fig. 59). A steep decline began in the mid-1970s, the effect of either reduced pup production or decreased juvenile survival during their pelagic phase (York and Kozloff, 1986). Declines continued into the mid-1980's, after which the St. Paul Island population remained stable at 33% of its 1970's population, while the smaller population of St. George Island stood at 60% of its 1970's level and continued to decline incrementally into the 1990's (York *et al.*, 2000; Loughlin *et al.*, 1994). The most recent population count in 2002 indicates that an annual decline of 5% has been occurring on both islands since 1998 (NMFS, 2002).









Figure 59. Counts of fur seal pups on St Paul and St. George Islands, Pribilof Islands, eastern Bering Sea (From York *et al.*, in prep).

Fur seal diets in the eastern Bering Sea have changed since the 1960s when cold-water species such as capelin and Greenland turbot were important; by the 1980s, diets were dominated by pollock ≤ 2 years of age (Hunt *et al.*, 2002a). During the 1990s, analyses of scats on St. Paul and St George Islands have revealed that fur seals there take at least 4 species of squid and approximately 30 species of fish (Sinclair *et al.*, in prep.). Adult fur seals are typically specific to summer feeding locations (Robson, 2002) depending upon the rookery of their birth; adult females from St. George Island can be generally characterized as off-shelf feeders compared to those from St. Paul Island (Sinclair *et al.*, 1996). Off-shelf feeding is indicated by consumption of salmon, northern smoothtongue (*Leuroglossus schmidti*), and the Gonatid squid *Gonatopsis borealis/Berryteuthis magister*.

Steller sea lions are currently divided into two stocks. The western stock ranges from 144°W in the Gulf of Alaska westward across the Aleutian Island chain and includes Walrus Island in the Pribilof Island group. After a continual population decrease of 5% per year since the 1970's, the monitored portion of the stock in the Gulf of Alaska and along the Aleutian Islands chain showed an increase of 5% between 2001 and 2002. The western stock of Steller sea lions is currently listed as endangered under the US Endangered Species Act. The causes of the decline in western stock of Steller sea lions remains controversial (NRC, 2003).

In contrast to declines in pinniped and seabird populations (see below), populations of large baleen whales, which were almost extirpated in shelf waters of the eastern Bering Sea by the 1960s (NRC, 1996; Merrick, 1997), may be increasing. Although in the mid-1970s, it was rare to encounter any large cetacean over the eastern Bering Sea shelf (Leatherwood *et al.*, 1983; Brueggerman *et al.*, 1987), since the 1980s, whales have been encountered over shelf waters with increasing frequency (Baretta and Hunt, 1994). Significant numbers of large cetaceans are now present in shelf waters during summer (Tynan, 1999; Moore *et al.*, 2000).

Marine Birds

The Bering Sea supports some of the major seabird colonies of the Northern Hemisphere, and vast numbers of Southern Hemisphere shearwaters make annual, transequatorial migrations to forage in the Bering Sea during the Southern Hemisphere winter (Hunt *et al.*, 2000). In the Bering Sea, an estimated 57 million marine birds consume between 9.8×10^5 and 2.3×10^6 t wet weight of food each summer, with small fish and zooplankton (large copepods and euphausiids) being the principal prey (Hunt *et al.*, 2000). Sea ducks consume an additional, though unknown, amount of benthic prey during their use of the coastal waters of the Bering Sea as migratory corridors and wintering areas.

Over much of the eastern, northern and southern Bering Sea, marine bird populations have recently been stable (NPFMC, 2003), but in the Pribilof Islands, declines in piscivorous seabirds that started in the late 1970s to early 1980s have continued (Decker et al., 1995, Springer, 1998; Dragoo et al., 2001). These declines have been particularly severe on St. Paul Island, and can only be accounted for by emigration or adult mortality (Hunt, 2004). Diets of seabirds nesting on the two islands differ: birds nesting on St. George Island consume more invertebrates and a wider variety of fish than seabirds nesting on St. Paul Island (Springer, 1992; Decker et al., 1995; Hunt et al., 1996b, 2002a). In recent years on both islands, sand lance and age-0 pollock have been substituted for capelin and age-1 pollock formerly consumed. This change in diet has resulted in birds foraging on smaller, less energy-dense prey. There is a strong negative relationship (r = -0.68) between the reproductive success of black-legged kittiwakes on St George Island and the biomass of adult pollock on the eastern Bering Sea shelf (Livingston et al., 1999; Hunt and Stabeno, 2002). This may be the result of competition for prey, or it may be that when large, cannibalistic pollock are abundant, they cause age-1 pollock to leave the surface and seek refuge at depth (Sogard and Olla, 1993). After the biomass of adult pollock increased in the vicinity of the Pribilof Islands, the biomass of age-1 pollock there dropped precipitously (Hunt et al., 2002a). In 1997, high numbers of migrant shearwaters starved when they were unable to obtain euphausiids over shelf waters (Vance et al.,

1998; Baduini *et al*, 2001a, 2001b). The declines in the populations of several species of marine birds and pinnipeds in the shelf waters of the southeastern Bering Sea imply that the carrying capacity of the region for these birds and pinnipeds has decreased. Shifts in their diets indicate that the decrease in carrying capacity involves not just a reduction in the amount of preferred prey available, but also a change in the structure of the food webs that support these top predators.

Marine birds provide an inexpensive and immediate index of the availability of their prey (Cairns, 1987, 1992; Hamer *et al.*, 1993; Montevecchi, 1993; Ainley *et al.*, 1995, 1996; Hunt *et al.*, 1996a, b; Rindorf *et al.*, 2000; Sydeman *et al.*, 2001; Gill *et al.*, 2002). The strength of these relationships is the basis of their use as monitors of krill populations in the Southern Ocean (Croxall *et al.*, 1988). These same responses have also proved indicative of the effects of climate change on marine systems (Montevecchi and Myers, 1997; Gjerdrum *et al.*, 2003). In other cases, the survival of marine birds has been tied to decadal-scale climate variability (Veit *et al.*, 1996, 1997; Thompson and Ollason, 2001; Jones *et al.*, 2002). For example, in the western Aleutians, there is now evidence that annual adult survival of least auklets (*Aethia pusilla*) varies with large-scale climatic conditions in the North Pacific (Jones *et al.*, 2002).

SECTION VI. LITERATURE CITED

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