GLOBEC Report No.19

Ecosystem Studies of Sub-Arctic Seas (ESSAS)

Science Plan

ISSN 1066-7881

GLOBAL OCEAN ECOSYSTEM DYNAMICS

GLOBEC Report No.19

Ecosystem Studies of Sub-Arctic Seas
(ESSAS)

Science Plan

The Results of Planning Workshops held 26-28 May 2003 at the
Havforskningsinstituttet/Institute of Marine Research Bergen, Norway

and

30 October – 1 November 2003 at the
Edgewater Hotel Seattle, Washington, USA

GLOBEC is a Programme Element of the International Geosphere-Biosphere Programme (IGBP).
It is co-sponsored by the Scientific Committee on Oceanic Research (SCOR) and the
Intergovernmental Oceanographic Commission (IOC).

The GLOBEC Report Series (Ed. Manuel Barange) is published by the GLOBEC International Project Office and includes the following:

No. 1. Towards the development of the GLOBEC Core Program (CP). A report of the first International GLOBEC planning meeting. Ravello, Italy, March 31- April 2, 1992.

No. 2. Report of the first meeting of an International GLOBEC working group on Population Dynamics and Physical Variability. Cambridge, United Kingdom, February 1-5, 1993.

No. 3. Report of the first meeting of the International GLOBEC working group on Sampling and Observation Systems. Paris, France, March 30–April 2, 1993.

No. 4. Report of the first meeting of the ICES/International GLOBEC working group on Cod and Climate Change. Lowestoft, England, June 7–11, 1993.

No. 5. Report of the first meeting of the International GLOBEC working group on Development of an International GLOBEC Southern Ocean Program. Norfolk, Virginia, USA, June 15–17, 1993.

No. 6. Report of the first meeting of the International GLOBEC working group on Numerical Modelling. Villefranche-sur-Mer, France, July 12–14, 1993.

No. 7. Southern Ocean Implementation Plan. Bremerhaven, Germany, June 6–8, 1994.

No. 7a. Report of the meeting of the Southern Ocean Planning Group, San Diego, California, 1-3 August 1997.

No. 8. Report of the first planning meeting on Small Pelagic Fishes and Climate Change Program. La Paz, Mexico, June 20-24, 1994.

No. 9. IGBP Report No. 40. Global Ocean Ecosystem Dynamics Science Plan.

No. 11. Small Pelagic Fishes and Climate Change Programme Implementation Plan.

No. 12. Report of the first SPACC Modelling workshop. Ispra, Italy, 14-16 October 1996.

No. 13. IGBP Report No. 47. Global Ocean Ecosystem Dynamics Implementation Plan.

No. 14. Report of a Workshop on the Use of the Continuous Underway Fish Egg Sampler (CUFES) for Mapping Spawning Habitats of Pelagic Fish.

No. 15. Report of a GLOBEC-SPACC/APN Workshop on the Causes and Consequences of Climate-induced Changes in Pelagic Fish Productivity in East Asia, 25-27 October 2001, Kobe, Japan.

No. 16. Report of a GLOBEC-SPACC/IDYLE/ENVIFISH Workshop on Spatial Approaches to the Dynamics of Coastal Pelagic Resources and their Environment in Upwelling Areas, 6-8 September 2001, Cape Town, South Africa.

No. 17. Report of the GLOBEC Workshop on Optical Plankton Counters, 17-20 June 2001, Tromsø, Norway.

No. 18. CLimate Impacts on Oceanic TOp Predators (CLIOTOP). Science Plan and Implementation Strategy.

No.19 Ecosystem Studies of Sub-Arctic Sea (ESSAS) Science Plan.

No.20 Background to the Climatology, Physical Oceanography and Ecosystems of the Sub-Arctic Seas. Appendix to the ESSAS Science Plan.

Cover images courstesy of James Lovvorn, NASA SeaWiFS, National Snow and Ice Data Center and Southampton Oceanography Centre, UK.

GLOBEC Special Contributions

No. 1. Predicting and Monitoring of the Physical-Biological-Chemical Ocean. A.R. Robinson (Ed.)

No. 2. An Advanced Modeling/Observation System (AMOS) For Physical-Biological-Chemical Ecosystem Research and Monitoring (Concepts and Methodology). GLOBEC International Working Groups on Numerical Modeling and Sampling Observational Systems.

No. 3. GLOBEC Workshop on the Assimilation of Biological data in Coupled Physical/ Ecosystems Models. A.R. Robinson and P.F.J. Lermusiaux (Eds.)

No. 4. Report on the GLOBEC National, Multi-National and Regional Programme Activities 2001. H. Willson (ed).

No. 5. Report of the first meeting of the SPACC/IOC Study Group on 'Use of environmental indices in the management of pelagic fish populations', 3-5 September 2001, Cape Town, South Africa.

No. 6. Report of the second meeting of the SPACC/IOC Study Group on 'Use of environmental indices in the management of pelagic fish populations', 9-11 November 2002, Paris, France.

No. 7. Update of the GLOBEC National, Multinational and Regional Programme Activities, 2004. D.M. Ashby (Ed.)

Additional copies of these reports are available from:

GLOBEC International Project Office
Plymouth Marine Laboratory
Prospect Place
Plymouth PL1 3DH
United Kingdom

Tel: +44 (0)1752 633401
Fax: +44 (0)1752 633101
e-mail: GLOBEC@pml.ac.uk
Homepage: www.globec.org

This report may be cited as:
Hunt, G.L., Jr and K.F. Drinkwater (Eds.). 2005. Ecosystem Studies of Sub-Arctic Seas (ESSAS) Science Plan. GLOBEC Report No.19, viii, 60pp.

Planning of ESSAS and printing of this report have been made possible by SCOR, NSF, The Research Council of Norway and GLOBEC.

The GLOBEC Report Series is partially supported by the US National Science Foundation under grant OPP-0330758. Any opinions, findings and conclusions or recommendations expressed in these reports are those of the authors and do not necessarily reflect the views of the US National Science Foundation.

GLOBEC is a Programme Element of the International Geosphere-Biosphere Programme (IGBP).
It is co-sponsored by the Scientific Committee on Oceanic Research (SCOR) and the
Intergovernmental Oceanographic Commission (IOC).

LIST OF ACRONYMS

ACIA	Arctic Climate Impact Assessment
AMAP	Arctic Monitoring Assessment Programme
AO	Arctic Oscillation
ASOF	Arctic-Subarctic Ocean Flux
BaySYS	Hudson Bay System Study
BEST	Bering Ecosystem Study
CCC	Cod and Climate Change program
CCCC	Climate Change and Carrying Capacity program
CLIVAR	Climate Variability and Predictability program
DMS	Dimethyl sulphide
ECOBE	Effects of North Atlantic Climate Variability on the Barents Sea Ecosystem
ECOGREEN	Ecosystem West Greenland
ENSO	El Niño Southern Oscillation
ESSAS	Ecosystem Studies of Sub-Arctic Seas
GCM	General Circulation Model
GLOBEC	Global Ocean Ecosystem Dynamics
GOOS	Global Ocean Observing System
ICES	International Council for the Exploration of the Sea
IBM	Individual Based Model
IPCC	Intergovernmental Panel on Climate Change
IPO	International Project Office
LTL	Lower Trophic Level
MERICA	étude des MERs Intérieures du CAnada
MIZ	Marginal Ice Zone
MSVPA	Multi-Species Virtual Population Analysis model
NAFO	Northwest Atlantic Fisheries Organization
NAO	North Atlantic Oscillation
NOAA	National Oceanic and Atmospheric Administration
NPFMC	North Pacific Fishery Management Council
NPZ	Nutrient-Phytoplankton-Zooplankton model
OGCM	Ocean General Circulation Model
PDO	Pacific Decadal Oscillation
PICES	North Pacific Marine Science Organization
PNA	Pacific/North American
SSC	Scientific Steering Committee
SST	Sea surface temperature
SEARCH	Study of Ecosystem Arctic Change
SPACC	Small Pelagics and Climate Change program
UVR	Ultra-Violet Radiation

TABLE OF CONTENTS

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 (Hunt and Drinkwater, 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 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 asses the requirement for a large-scale, integrated study of the Sub-Arctic Seas (Appendix I). 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 (Appendix II), and the second in October 2003, in Seattle Washington (Appendix III). 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 marine mammals 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 (Appendix I). 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 (Appendix II and III). 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 (Hunt and Drinkwater, 2005). 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 Draft 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

Sub-Arctic Seas are affected by decadal-scale and secular changes in climate. These regions are especially sensitive to climate change because they experience seasonal ice cover, and they have strong seasonal cycles of insolation, temperature and production. The extent and nature of the seasonal ice zone impacts all levels of the physical and biological systems of these seas. The last few decades of modern ocean observation have recorded significant year-to-year variations in both the seasonal ice and the ecological dynamics of these regions (e.g. Stabeno and Overland, 2001; Hunt *et al*., 2002a; Drinkwater, 2002; Stern and Heide-Jorgensen, 2003; Buch *et al*., 2004). However, the critical processes linking these important aspects are not well known, and thus our ability to predict and prepare adequately for fluctuations in biological resources caused by regional, short-term climate variability is limited. Predictive ability is almost non-existent for more pervasive, larger-scale climate changes that would alter ice-extent for extended periods. This lack of process-level predictive capability for a system that is important to commercial and subsistence harvests, as well as to non-harvested marine life, is a powerful motivation to learn more about how climate change will affect Sub-Arctic marine ecosystems and their connections to the North Atlantic, North Pacific and Arctic Oceans.

Climate variability has profound impacts on the structure and function of Sub-Arctic marine ecosystems. In recent years, major changes in phytoplankton and zooplankton stocks and the abundance and productivity of commercially important groundfish, marine mammals and seabirds have been correlated with temporal shifts in physical forcing. In particular, seemingly small shifts in the long-term mean values of atmospheric variables, at least when compared to their interannual variability, may result in major changes in the productivity or standing stocks of fish populations (Hare and Mantua, 2000; Drinkwater *et al*., 2003). Climate variation that affects the mechanisms (e.g. bottom-up or top-down) controlling fish populations may result in a given rate of harvest having different impacts on fish stocks under different climate regimes.

Variations in sea ice cover provide a potential linkage between climate-induced changes and the timing, amount and fate of primary production, and hence the recruitment of commercially important fish in the Sub-Arctic Seas. Small changes in air or sea temperatures or wind patterns can create large changes in the timing, extent, and duration of ice cover. Recent studies in the Bering Sea suggest that spring sea ice melt-back in the northern region now occurs 2-3 weeks earlier than in the past (Stabeno and Overland, 2001). Changes to the spring melt-back have direct effects on the timing and fate of primary production (e.g. Rey and Loeng, 1985; Thordardottir, 1986; Stabeno *et al*., 1999a; Hunt *et al*., 2002a), and the amount of melting sea ice affects bottom temperatures and benthic ecosystems (e.g. Grebmeier and Dunton, 2000). Sea ice is a critical habitat for several species of seals and walrus, and the persistence and location of sea ice affects the migratory routes of cetaceans. Thus, sea ice cover is one of the most important climate-related variables and it directly impacts the ecology of all of the Sub-Arctic Seas. Climate change, and in particular global warming, will have an immense impact on these regions, and this may first be apparent in the sea-ice record, considered a sensitive indicator of a warming climate (IPCC, 2001, p.124).

The Sub-Arctic Seas are important to people. There are great social and economic incentives to understand how the biological resources of the Sub-Arctic Seas should be managed in a period of rapid environmental change. The resources of Sub-Arctic Seas are important for the local economies and subsistence harvesters throughout the north. Thus, understanding how climate change will interact with fisheries removals to impact the exploitable resources of the Sub-Arctic Seas is critical for predicting responses of the fish stocks to environmental change so that depletion of the fisheries, as happened in eastern Canada (Rice, 2002), can be avoided or mitigated. The ESSAS Program will work towards development of the information necessary to facilitate the wise use and stewardship of these most important marine ecosystems.

1.2 Opportunities Afforded by ESSAS

ESSAS offers the opportunity to test crosscutting hypotheses that can best be examined with coordinated, concurrent research in several regions. This approach effectively increases the sample size of study years and takes advantage of the often-negative relationships between climate conditions in different Sub-Arctic regions (e.g. the eastern and western North Atlantic). Testable hypotheses of importance include:

- Forcing mechanisms and biological processes controlling energy flow are similar across all of the Sub-Arctic Seas. Lessons learned in one system can be transferred to other areas.
- Temperature controls the direction of energy flow within the pelagic/benthic subcomponents of the ecosystem.
- Physical and anthropogenic forcing mechanisms determine the relative importance of top down vs. bottom up control of energy flow in the ecosystem.

The Sub-Arctic Seas are amenable to understanding. The ESSAS Program's goal of characterizing processes that link climate related variables to biological structure and function on the Sub-Arctic Seas is ambitious. However, **the ESSAS goal is attainable due to the convergence of several important features:**

1. Many of the Sub-Arctic regions now have many decades of modern oceanographic observations to draw on.
2. The biological signals are large and dynamic. The short growing season produces some of the highest primary production levels in the world ocean, and dramatic changes between diatom-dominated and coccolithophore-dominated communities have been recorded. Large changes in fish, bird and mammal populations have also been observed.
3. The Sub-Arctic Seas occupy the region of the phase change between the permanently open water of the north temperate region and the Arctic pack ice. Modest changes in atmospheric and oceanic forcing produce large changes in sea ice distribution. Large year-to-year changes have already been recorded and have a high probability of re-occurring during ESSAS fieldwork.

The ecosystems of the Sub-Arctic Seas are relatively simple, with linear food chains, distinct trophic levels and low species diversity. They are usually dominated by one or two species at each of the upper trophic levels. These characteristics facilitate modeling of these systems. The high spatial and inter-annual variability of the Sub-Arctic Seas provides, within the lifetime of a field program, a proxy for studying the responses of these systems to variability at longer time scales. The high amplitude variability also provides a strong signal-to-noise ratio and the potential for detecting threshold phenomena that characterize non-linear relationships in ecosystems. Thus, the Sub-Arctic Seas are excellent laboratories for studying the effects of climate change on ecosystems. **To take advantage of this short-term variability for building predictions of long-term responses to climate change, ESSAS will be a ten-year program, thus giving it an opportunity to observe a series of short-term fluctuations in climate patterns, ice cover and fish recruitment.**

There is an opportunity for comparison with the Antarctic Southern Ocean GLOBEC program. The importance of the distribution, timing and duration of sea ice in the marginal ice zone (MIZ) in both the Arctic and a Sub-Arctic invites comparison with processes and studies in the Southern Hemisphere as well as among sites in the Northern Hemisphere. Do these MIZ systems behave similarly, or are the Sub-Arctic Seas with their broad, shallow shelves and strong benthic-pelagic coupling fundamentally different from Antarctic systems?

The Sub-Arctic Seas are already changing. Some of the Sub-Arctic Seas appear to be changing from a system dominated by coldwater, Arctic species to a temperate system in which a new set of species may come to dominate. For example, in the eastern Bering Sea, a coldwater amphipod (*Themisto libellula*), once common in seabird diets at the Pribilof Islands, is now absent from the southeastern Bering Sea (K.O. Coyle, pers. comm.), and Greenland turbot (*Reinhardtius hippoglossoides*), a coldwater species once an important component of eastern Bering Sea commercial fisheries, is in severe decline (NPFMC, 2003). Warming of the northern Bering Sea allows northward range shifts of benthic-feeding species of fish (Wyllie-Echeverria, 1995), and this may accelerate the decline in amphipod beds necessary for gray whales (*Eschrichtius robustus*) and other benthic-foraging species (Coyle and Highsmith, 1994; Moore *et al*., 2003). Similarly, the distribution of several Icelandic fish stocks (e.g. haddock, *Melanogrammus aeglefinus*, blue whiting, *Micromesistius potassou*, and whiting, *Merlangius merlangus*) have shifted northward in response to increasing temperatures since the late 1990s. Also, capelin (*Mallotus villosus*), a Sub-Arctic species that during past years has been subjected to extensive summer/autumn fishery in the Iceland Sea at around 68°N, has more recently been very difficult to locate by both fishing and research vessels, probably due to a more northward distribution related to a marked shift in the physical environment of the Iceland Sea (Vilhjálmsson, 2002).

1.3 Connections with Other Sub-Arctic Seas Programs

The ESSAS Program will leverage knowledge and resources from three important areas:

1. Recently completed studies of the Sub-Arctic Seas,
2. Ongoing national and international programs, and
3. International programs addressing global change.

ESSAS will capitalize on data from long-term hydrobiological and fisheries investigations, from recent syntheses of regional ecosystems (e.g. Dagg *et al*., 2002; Macklin *et al*., 2002a,b; Skjoldal, 2004), planned syntheses of the ICES Cod and Climate Change (CCC) and the PICES Climate Change and Carrying Capacity (CCCC) programs, and reports from AMAP (1998) and ACIA (in press). These and other recently completed studies will provide ESSAS with a solid basis on which to build its science program. Principal Investigators from many of these programs have helped to construct the ESSAS Science Plan. In addition, members of the ESSAS Science Plan Team are active members in PICES and serve on working groups and advisory panels of the CCCC and the CCC programs.

ESSAS will benefit from information developed in the Global Ocean Observing System (GOOS), including ARGO, Arctic-Subarctic Ocean Fluxes (ASOF), the Climate Variability and Predictability (CLIVAR) and Study of Ecosystem Arctic Change (SEARCH) programs, particularly as ESSAS synthesizes its results and attempts to develop models of what future global change may bring to the Sub-Arctic Seas. In return, ESSAS will be able to provide ASOF and SEARCH with information on how the quality of the water flowing from the Sub-Arctic into the Arctic Ocean will change given different climate scenarios. There should also be opportunities to share logistics with ASOF in the North Atlantic and Barents Sea, as the areas of operation will overlap. ESSAS will complement ASOF with its focus on physical and chemical aspects of flux between the Arctic and Sub-Arctic. Another international program is the West-Nordic Ocean Climate program of the Scandinavian countries, which includes not only physical oceanography but also work on recruitment of living marine resources. The ongoing Norwegian project, Effects of North Atlantic Climate Variability on the Barents Sea Ecosystem (ECOBE) is expected to be an integral part of ESSAS, as will be the Bering Ecosystem Study (BEST) Program, a SEARCH-affiliated program, which is being developed through support by the United States National Science Foundation, and is planned as a multi-year, multi-ship program. Other equally important developing national programs include the Oyashio-pollock project in Japan and Ecosystem West Greenland (ECOGREEN). The ESSAS Program would also be expected to interact closely with PICES, ICES and NAFO. A central role of ESSAS will be to facilitate communication between scientists and those institutions or organizations representing the social and economic interests of local communities.

SECTION II: WHAT ARE THE IMPORTANT PHYSICAL PROCESSES AFFECTING SUB-ARCTIC SEAS?

One of the aims of ESSAS is to elucidate the physical processes that force large-scale changes in Sub-Arctic marine ecosystems and to understand the mechanisms through which these changes occur. Two external physical forcing mechanisms that tend to dominate in Sub-Arctic Seas are atmospheric forcing (e.g. winds, heat fluxes) and advective fluxes at the boundaries. Important internal physical processes include those associated with sea ice, tides, oceanic fronts and freshwater discharge. The temporal scales of the physical processes of primary interest to ESSAS span from hours to multi-decadal, and spatial scales from tens of meters to hemispherical (Fig. 2).

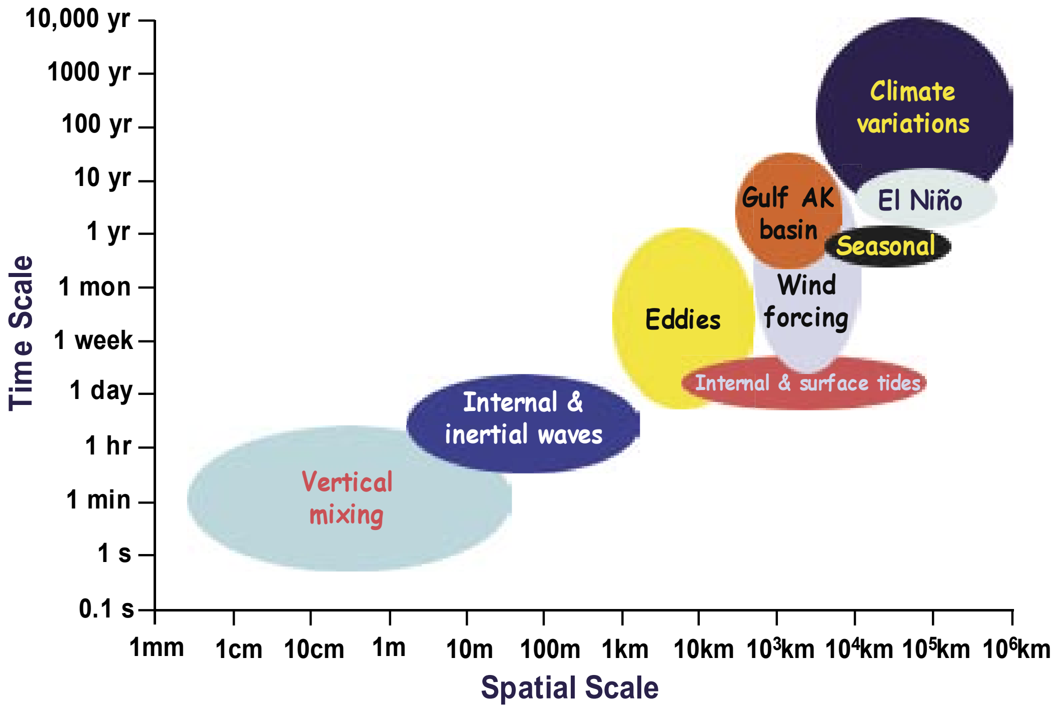


Figure 2. Physical Oceanographic Time and Space Scales (Adapted from D. Chelton, Oregon State University, Corvallis, OR)

2.1 Atmospheric Forcing

Atmospheric forcing, through winds and air-sea exchanges, greatly affects marine ecosystems. Winds influence small-scale turbulence and mixing in the upper levels of the ocean, which in turn determine vertical nutrient fluxes, primary production, and the feeding success of zooplankton, fish, seabirds, and marine mammals. Winds drive horizontal currents in the upper layers of the ocean by direct forcing and throughout the water column through influences on the sea surface slopes. Currents transport zooplankton and fish larvae into or out of areas where they can achieve high survival and good recruitment. Winds also drive vertical motion such as upwelling, which can lead to higher primary production through nutrient enrichment, and can influence the formation, duration and breakup of sea ice. Atmospheric heat exchanges determine near-surface ocean temperatures, the potential for thermally driven convection, and the rates of ice formation and melting, all of which have important biological consequences. However, **our present understanding of the processes linking atmospheric changes to their effect on the physical oceanography and biology of Sub-Arctic Seas is insufficient to make reliable quantitative statements about the effects of predicted future climate change. It is our intent that the suites of observations and models to be developed during the program will improve our predictive capacity in these areas.**

In Sub-Arctic Seas, strong winter winds tend to deliver cold, dry Arctic air masses from the north and contrast with the weaker summer winds, often from the south, that carry relatively warm moist air from the Atlantic or Pacific Oceans (Fig. 3). The seasonal winds undergo large interannual variability, which is reflected in the temperature and moisture content of the air masses over Sub-Arctic Seas. These changes in air masses, in turn, affect the heat exchanges between the ocean and the atmosphere and control sea surface temperatures (Battisti *et al*., 1995).

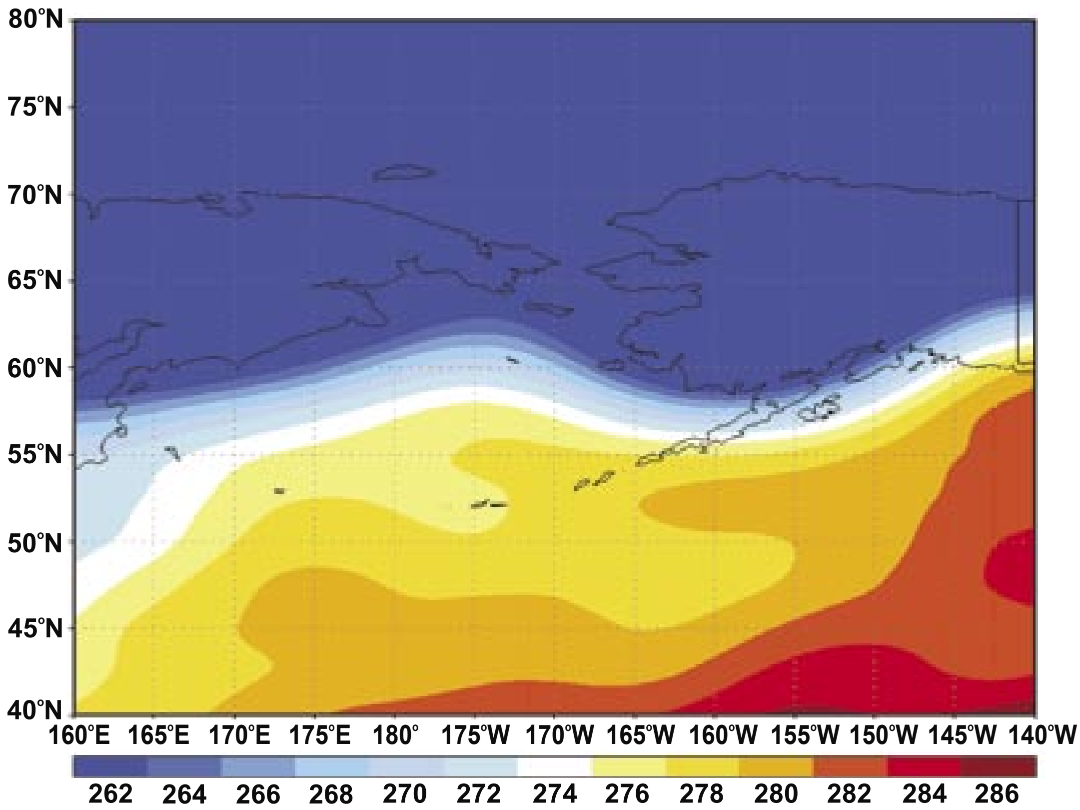


Figure 3. Temperature in degrees Kelvin at 1000 Pascals, 1 January 2003 showing the frontal zone between warm air from the North Pacific meeting cold air from the Arctic. These air masses serve as proxies for the regions of control by the Arctic Oscillation (AO) and the Pacific Decadal Oscillation (PDO). Illustration courtesy of J. Overland, NOAA, PMEL, Seattle, WA, USA.

Given the strong links between air and sea temperatures on monthly to decadal scales that have been observed in most Sub-Arctic Seas, the general atmospheric warming predicted by global models is expected to be accompanied by increases in water temperatures and reduced ice coverage (IPCC, 2001; ACIA, 2004). However, the fate of other atmospheric variables, such as winds, or precipitation and evaporation in the global models are less clear, and sometimes even contradictory between models. Flux of sensible heat from the atmosphere to the ocean is expected to increase, although the amount is uncertain given our lack of information on winds. Little is known of what will happen to latent heat and hence the change in the overall heat fluxes (ACIA, in press). These large uncertainties are confounded by the lack of regional models at the geographic scale of the Sub-Arctic Seas.

It is critical to understand how the various physical processes associated with wind events interact to influence the ecosystems of Sub-Arctic Seas. For example, strong winter winds mix water in the Sub-Arctic Seas to depths of ~100 m (Coachman, 1986). In addition, winter wind-driven currents can result in strong cross-shelf exchanges of water. The offshore waters transported onto the shelf tend to be rich in nutrients, and this wind-driven cross-shelf flux is thought to be a major mechanism for re-supplying nutrients in some Sub-Arctic Seas, e.g. the eastern Bering Sea shelf (Stabeno *et al*., 2001, 2002a). During summer, the weaker winds reduce such cross-shelf transport. In several Sub-Arctic Seas, the winter mixed-waters lay above warmer, saltier waters that originate deep offshore (e.g. Petrie *et al*., 1991). Solar heating through the spring and the summer forms a shallow warm layer on top. Thus in these seasons, the cold, winter waters are sandwiched between warmer layers (Petrie *et al*., 1988). In most Sub-Arctic Seas, there is a limited understanding of the processes that determine the extent and formation of these cold layers and their impact on the ecosystem.

Upwelling of deep, nutrient-rich water with a resultant elevated primary production may be generated in those areas of the Sub-Arctic Seas where prevailing winds generate Ekman transport offshore. Upwelling in the vicinity of cross-shelf canyons has also been found to generate hot spots of nutrients and primary production (Moseidjord *et al*., 1999). When these processes are prominent in early summer prior to strong surface stratification, there is an enhanced nutrient supply to surface waters, and downstream an elevated productivity is anticipated.

Changes in the location, strength and timing of storms are likely to be critical to Sub-Arctic ecosystems, but their effects are not well understood. Any long-term warming of the climate will almost certainly be accompanied by a change in the number, intensity and tracks of storms (ACIA, in press). Fewer and weaker winter storms could reduce vertical mixing, thereby producing a shallower mixed layer and ultimately lower nutrient concentrations at the end of winter, prior to the spring bloom. Lower concentrations of nutrients could reduce primary production, and that in turn could impact upon the rest of the food web, such as survival of first feeding fish larvae (Walsh and McRoy, 1986). On the other hand, if such winds were accompanied by reduced ice coverage, there could be more vertical mixing during the winter and hence higher nutrient concentrations. A change in the number and/or strength of summer storms might also impact post spring bloom primary production (Sambrotto *et al*., 1986). More storms could lead to greater cloud cover, in turn modifying insolation, and thus decreasing sea surface temperature (Stone, 1997) and primary production. A change in the winds and wind stress curl would modify currents in the Sub-Arctic Seas. In general, the effects of changes in storms are difficult to predict.

Sub-Arctic Seas exhibit strong decadal changes in wind forcing, much of which can be linked to basin-scale atmospheric changes. The Sub-Arctic Seas come under the influence of large-scale atmospheric patterns. For example, the Barents Sea, West Greenland and the Labrador/Newfoundland shelves reflect changes in the North Atlantic Oscillation (NAO) index (Fig. 4) (Ottersen *et al*., 2001; Buch, 2000; Colbourne *et al*., 1994; Drinkwater, 1996). Typically 40-50% of the variance in oceanographic variables such as sea temperatures and sea ice in these regions can be accounted for by the NAO index, including the strong decadal variability since the 1960s. In the Labrador Sea, the strengthening of the Icelandic Low associated with a high NAO index results in stronger northwest winds and hence colder conditions over both West Greenland and Labrador, while in the Barents Sea, increases in the southwest winds bring warmer conditions. Ocean climate variability around Iceland, which lies mid-way between the Labrador and Barents seas, is less influenced by the NAO than either of the two other areas.

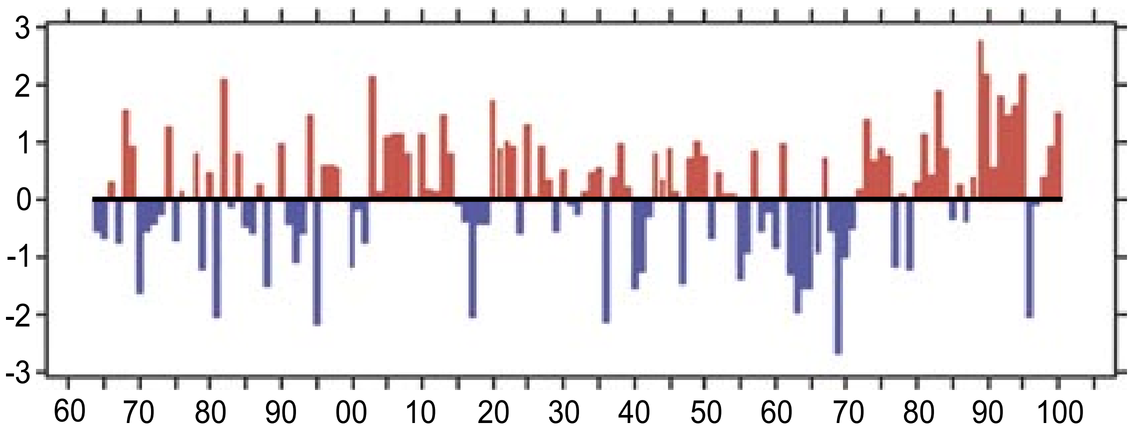


Figure 4. The North Atlantic Oscillation index (1864-2001) of Hurrell

In the North Pacific, the years of the 20th century can be divided into four main groups based on basic differences in large-scale modes of oscillation. The wintertime physical climate indices, in conjunction with indices of biological responses in marine ecosystems, have been used to identify abrupt shifts in climatic forcing and ecosystem response at decadal time scales (e.g. Trenberth and Hurrell, 1995; Mantua *et al*., 1997; Francis *et al*., 1998; Hare and Mantua, 2000; McFarlane *et al*., 2000; Hollowed *et al*., 2001). Two of these regime shifts have been identified in the past thirty years. One followed the winter of 1976-1977, in which the PDO and the AO both shifted (Fig. 5). A second shift, of just the AO, occurred after the winter of 1988-1989 (Ebbesmeyer *et al*., 1991; Hare and Francis, 1995; Sugimoto and Tadokoro, 1998; Beamish *et al*., 1999; Brodeur *et al*., 1999; Hare and Mantua, 2000). There is some evidence of a third shift in the winter of 1998-1999 (Schwing and Moore, 2000; Peterson *et al*., 2002). Although the ENSO appears to alternate between two states that are repeatedly visited, that does not appear to be the case for regime shifts in the southeastern Bering Sea, where the few regimes documented so far have each had unique characteristics (Bond *et al*., 2003). An important aspect of the AO is its trend toward a more persistent positive state since the late 1960s (Thompson and Wallace, 1998). The influences of the North Pacific (NP) and AO modes in spring have resulted in an increase in southerly winds over the Bering Sea (Overland *et al*., 2002). Atmospheric teleconnections also result in influences from more distant regions, such as the equatorial Pacific Ocean (e.g. ENSO; see Overland *et al*., 2001).

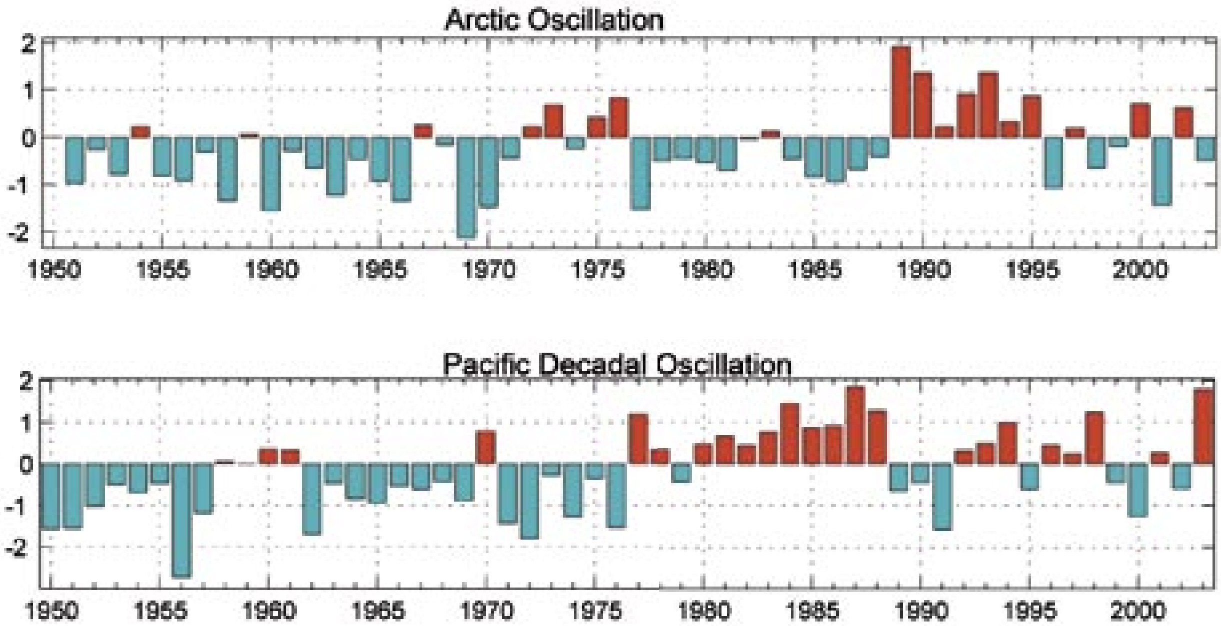


Figure 5. Time series of the Arctic Oscillation (top) and the Pacific Decadal Oscillation

In the northeastern Pacific Ocean, as the wintertime Aleutian low-pressure system deepens, the winds driving the Alaskan gyre strengthen, so that the gyre becomes more energetic (Mann and Lazier, 1996). This intensification, in turn, leads to more Ekman upwelling in the center, so that more nutrients are brought to the surface and ocean productivity increases. This process was most active in the 1940s and 1980s with particularly rapid change in the system being recorded in 1976-1977 (Mann and Lazier, 1996). Many fish stocks have shown strong recruitment during the years when the Aleutian low was deep and extensive and poor recruitment when it was shallow and limited.

Observations indicate **that there are also longer-term trends in the atmospheric forcing of most Sub-Arctic areas**. For example, significant atmospheric warming over the North Atlantic in the 1920s and 1930s resulted in an approximate 30-year oceanic warm period that affected the Labrador/Newfoundland shelves, Greenland, Iceland and the Barents Sea. Associated with this warm water, cod and other warm-water species spread north along the coast of western Greenland

(Jensen and Hansen, 1931; Jensen, 1939). Migration patterns were also altered as the species associated with more temperate waters arrived earlier and left later. More recently, Arctic air masses that impact the Bering Sea show a long-term upward trend in springtime temperatures (Stabeno and Overland, 2001). In contrast, over the Labrador Sea temperatures in all seasons have generally decreased over the past 40 years, although the last half of the 1990s did show a return to warmer temperatures (Colbourne and Anderson, 2003). During the period of low temperatures, the cod stocks of the Labrador Shelf and northern Grand Bank succumbed to heavy fishing pressure, so that the fishery had to be closed in 1992. It is strongly suspected that the presence of cold, low-salinity waters also contributed to the collapse (Rose *et al*., 2000; Drinkwater, 2002).

In summary, large-scale changes in atmospheric circulation lead to changes in oceanic circulation and hydrographic properties which in turn lead to biological responses, including distributional changes in species, changes in the timing of migrations, and differences in the recruitment survival, growth, condition and maturity of commercial fish species (Drinkwater, 2000; Drinkwater *et al*., 2003; Ottersen *et al*., 2004). **These large-scale temporal and spatial variations in physical and biological components clearly impose major signals onto the Sub-Arctic Seas,** and are superimposed on top of locally-forced atmospheric responses.

Quantitative estimates of the magnitude of Sub-Arctic responses to atmospheric changes at these scales are often uncertain because of our lack of understanding and proper parameterization of the processes involved. One of the goals of modeling within the ESSAS program will be the development of predictive models to address the issue of the influence of atmospheric forcing on the physical oceanography.

2.2 Advection

Most **Sub-Arctic Seas are subject to strong advective fluxes within and at their boundaries,** e.g. the Atlantic inflow into the Barents Sea, the Irminger Current off southwestern Greenland, the Labrador Current off Labrador and Newfoundland, the Alaska Stream and the Kamchatka Current in the Bering Sea and the Oyashio Current off northeastern Asia (Fig. 6). Most of the major residual currents in Sub-Arctic Seas, while influenced by local processes, are part of larger regional circulation patterns and thus are influenced by processes and events outside the bounds of the Sub-Arctic Seas. The effects of changes in distant ocean regions can be advected into the Sub-Arctic regions, sometimes from thousands of kilometers away (Dickson *et al*., 1988; Belkin *et al*., 1998; Belkin, 2004). **The relative importance of local versus remote forcing of currents and their hydrographic properties are often not well resolved. This question will be addressed within the ESSAS program by the use of a combination of observational and modeling approaches.**

In spite of the importance of advective fluxes within and on the boundaries of Sub-Arctic Seas, estimates of their mean volume transports are usually based on few or scattered measurements and have high uncertainty. Knowledge of the variability in transport is even less. Measuring this variability is crucial to determining its causes. Measurements of the transports between the Arctic and the Sub-Arctic are taking place within the Arctic-Subarctic Ocean Flux (ASOF) program, however, and these results will become available to ESSAS. This will allow ESSAS to concentrate upon what such variability in advection means to the Sub-Arctic Seas and their biology.

Advective fluxes play a major role in controlling the heat and salt budgets in Sub-Arctic Seas. The near-surface circulation of the Sub-Arctic Seas is composed of two major different water bodies (Arctic and temperate) with a variable zone of mixed water masses (Fig. 6). This is clearly evident in the case of the heat content, where Sub-Arctic Seas receiving warm water from the south are much warmer than equivalent bodies of water at similar latitudes, while those that receive Arctic Waters from the north are much colder.

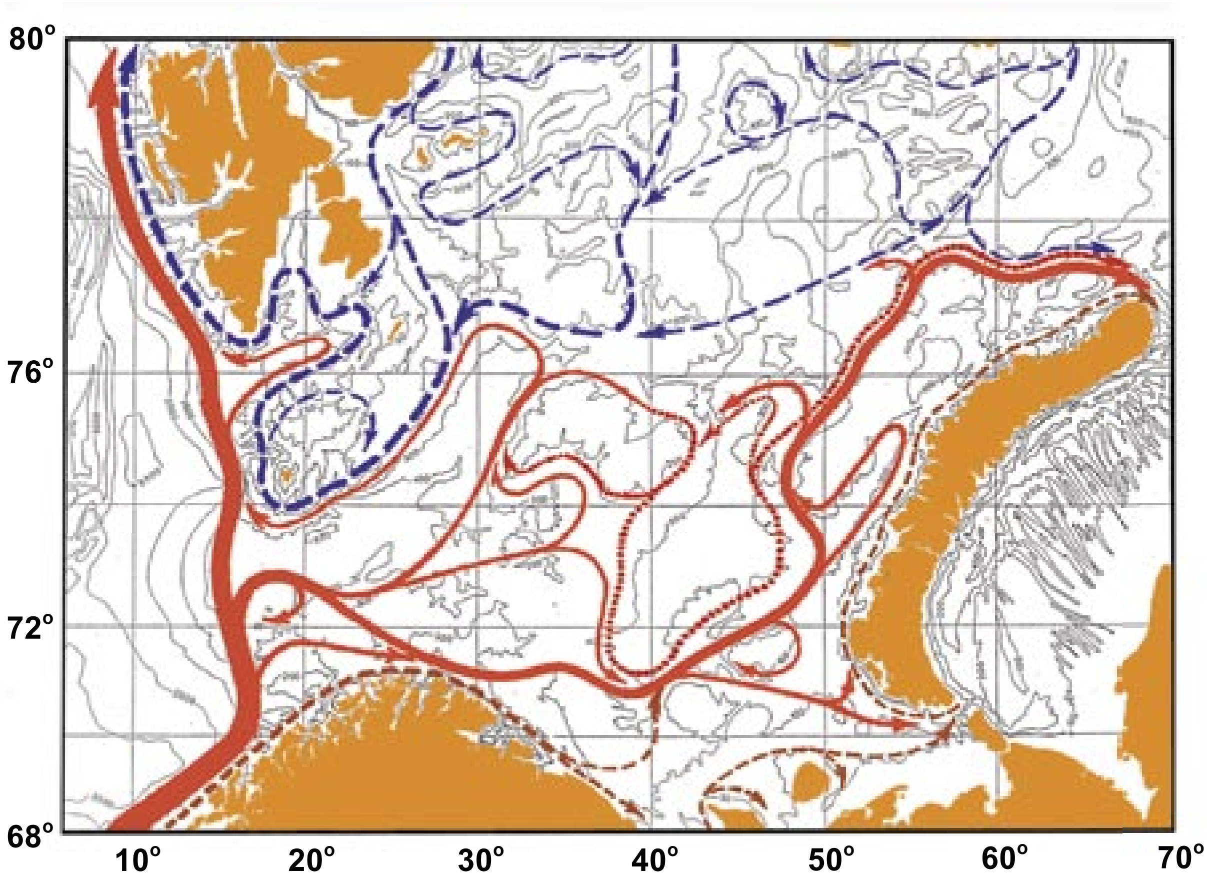


Figure 6. Map of currents in the Barents Sea (after Ozhigin *et al.*, 2000). Blue indicates water of Arctic origin, red indicates water of North Atlantic origin.

The Sub-Arctic Seas also export water to neighboring ocean basins. For example, in the southern Barents Sea and the eastern Bering Sea currents transport relatively warm salty water to the Arctic from the Atlantic and the Pacific, respectively. Other Sub-Arctic Seas, as well as the northern Barents Sea and the western Bering Sea, contain currents that carry Arctic water towards the large ocean basins (Fig. 6; Hunt and Drinkwater, 2005). The similarity in the Oyashio Current in the Pacific and the Labrador Current in the Atlantic carrying Arctic-type waters southward and the Bering and the Barents Seas where warm temperate waters are transported northward offer great potential for comparative research.

Also important is the modification of water masses as they are transported through the Sub-Arctic on their way to or from the Arctic. For example, the transformation of Atlantic Water as it passes through the Barents Sea is important for the ventilation of the Arctic Ocean (Aagaard and Woodgate, 2001). The Barents Sea also provides intermediate water to the Arctic Ocean to a depth of 1200 m (Rudels *et al*., 1994; Schauer *et al*., 1997, 2002).

There is considerable variability in the concentrations of nutrients available in the Sub-Arctic Seas, and advective fluxes play an important role in determining the regional abundance of nutrients, and thus the resultant levels of new production. For example, the waters of the warmer, southern regions of the Barents Sea contain higher initial nutrient concentrations than do the more northern regions, because North Atlantic waters are richer in nutrients than Arctic waters (Sakshaug and Slagsted, 1991; Hegseth, 1998). In addition, mixed-layer depths in southern regions are generally deeper than those generated by ice-melt induced stratification in northern regions. Thus, the Arctic waters of the Barents Sea support an annual primary production of 66 g C m^{-2} y^{-1}, with 42 g C m^{-2} y^{-1} fuelled by nitrate (new nitrogen) *vs*. ammonia (re-cycled nitrogen), while for the Atlantic waters the corresponding rates are 174 and 83 g C m^{-2} y^{-1} (Titov, 1994). For the south-eastern 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 540 g C m^{-2} y^{-1} have been reported (Springer *et al*., 1996). Annual primary production in the Sea of Okhotsk has been estimated to be on the order of 260-350 g C m^{-2} y^{-1} (Arzhanova and Zubarevich 1997a,b; Naletova *et al*., 1997) and may be up to 450 g C m^{-2} y^{-1} (Shuntov and Dulepova, 1997). The annual primary production rate over Labrador/Newfoundland is estimated from satellite imagery to be between 150-300 g C m^{-2} y^{-1}. **However, in many regions of most Sub-Arctic Seas, we know little about the relative importance of local remineralization as compared to advection in determining spring nutrient concentrations.**

In addition to influences on the nutrients, heat and salt within Sub-Arctic Seas, currents also transport biological material. For example, in the Barents Sea, zooplankton (especially *Calanus finmarchicus*) are transported by the Atlantic inflow, with a higher influx of zooplankton-rich water from the Norwegian Sea into the Barents Sea in years of higher inflows (Ottersen and Sundby, 1995). Also, the distribution of capelin, the single most important food species for Arcto-Norwegian cod, is known to vary from year to year, dependent on the inflow of Atlantic water (Sakshaug *et al*., 1992).

Some of the major signals of advected biomass occur during the summer when plankton and nekton are found in the surface water. Model runs from the northeast Atlantic demonstrate that the origin of the advected biomass of copepods found in the Barents Sea is winter habitat hundreds of km upstream in the Lofoten Basin (Halvorsen *et al*., 2003). The seeding from these winter habitats is considered to be extremely important for determining the available biomass of zooplankton and nekton on the feeding grounds of herring, capelin and cod. The variability in the intrusion of zooplankton from the northeast Atlantic to the Barents Sea is clearly prominent, and is coupled to the size of the over wintering stocks of plankton, the magnitude of the current at the time of their upward migration in late winter, and the wind pattern during spring and early summer responsible for the direction of surface currents into the Barents Sea proper (Skjodal and Rey, 1989; Skjodal *et al*., 1992). In the other Sub-Arctic Seas, we know less about the role of seeding from southerly regions.

In addition to advection of biota from southerly regions, northern currents transport Arctic biota southward into conditions that are gradually translating into a different physical environment. Such changes do not favor the Arctic endemic biota, and with the anticipated global warming, a decline in their growth and production is expected. On the other hand, elevated temperatures will increase the success of temperate species, which are being advected from the south. **The future prospect for marine production in the Sub-Arctic Seas will depend on the scale of change in the currents and hydrography.**

What is the role of the mesoscale circulation features in maintaining or dispersing populations of zooplankton and fish larvae? Advection occurs at the mesoscale level by eddies and circulation features associated with banks and basins within the Sub-Arctic Seas. **Relatively little attention has been directed towards mesoscale circulation features in Sub-Arctic Seas.** Currents tend to be anticyclonic around banks and small islands in the Northern Hemisphere, and cyclonic around basins. These circulation patterns tend to result in longer residence times of the water and materials there than in those regions with strong along-shelf flows, such as near the coast or along the continental slopes (Loder *et al*., 1988). Eddies have been observed from satellite imagery of temperature and ice along the Labrador and West Greenland shelves and in the Barents and Bering seas. These are believed important in generating cross-shelf transport of water properties, nutrients and biological material, although this has yet to be quantified. Models of mesoscale circulation currently under development within other programs will be used by the ESSAS program to investigate these processes, with a view to developing a predictive capacity under a climate change scenario.

2.3 Sea Ice

Most shallow regions of the Sub-Arctic Seas experience seasonal sea ice, although the duration and severity of ice is spatially dependent (Fig. 7). In winter, relatively heavy ice is observed in the northern Bering Sea, the Sea of Okhotsk, the northern Barents Sea, Hudson Bay and on the Labrador and northeast Newfoundland shelves. The duration of sea ice can extend upwards to 8-10 months in the northern parts of these regions. Much reduced ice concentrations and shorter ice seasons are observed on the southern Greenland shelves and in the Gulf of St. Lawrence. While ice has been observed along the north coast of Iceland, this is not a regular occurrence and indeed has only been observed sparingly over the last 50 years. Little to no ice is observed in the southwestern Barents Sea over deep water, which receives direct input of Atlantic water, or in the southeastern region of the Bering Sea.

During the winter season, ice generally begins to form first in the north, and spreads by a combination of ice transport and local formation. The maximum ice coverage usually occurs in March or April. Once the ice cover is established, polynyas can form in the lee of the islands and coastal promontories. Their formation, location and size depend on strong, frigid winds, usually out of the north (Smith *et al*., 1990). Polynyas can be a major source of heat to the atmosphere, brine to the water column, and regions of high productivity and biological activity throughout the winter (Stirling, 1980; Dunbar, 1981).

The rate of formation and break-up of sea ice, as well as its duration, depends upon many factors including winds, air and water temperatures, surface salinities, waves and currents. Lower temperatures and salinities and calm winds speed up the formation of ice, although under some circumstances strong winds can enhance sea ice formation by increasing the flux of heat from the ocean. Waves and currents that disperse the newly forming ice can lead to greater ice formation.

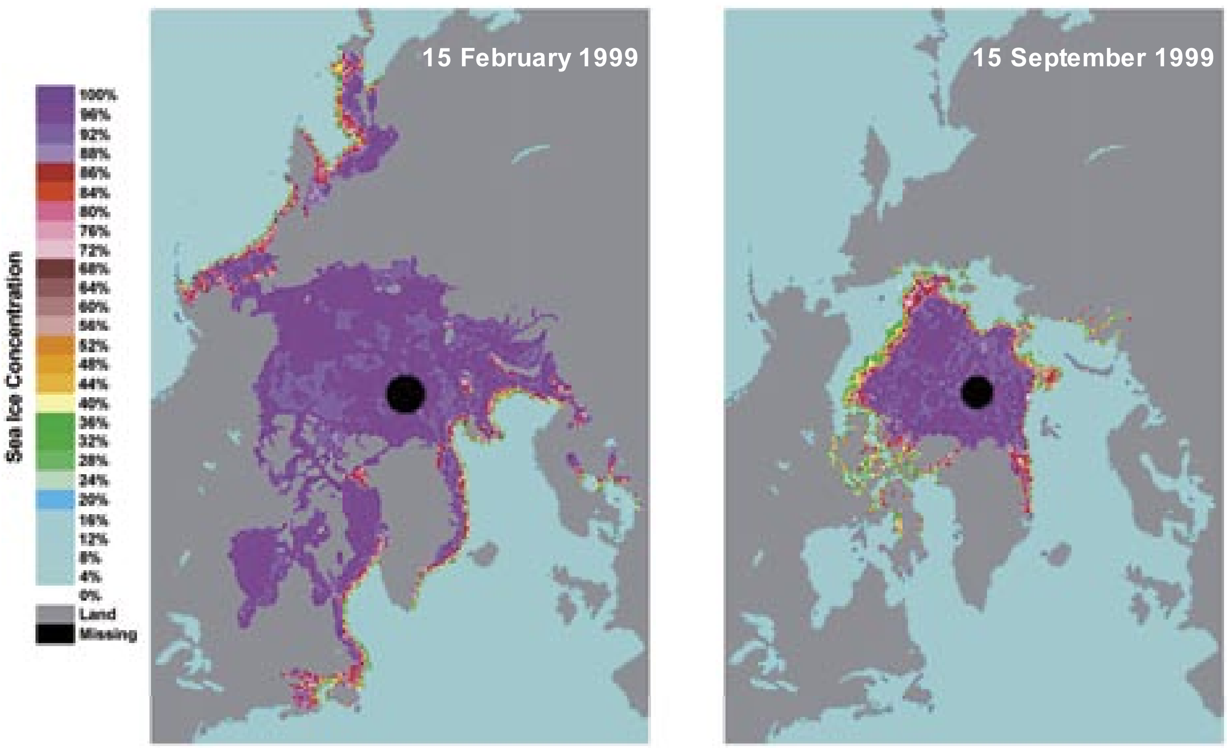


Figure 7. Maximum and minimum sea-ice extent in 1999. This was a year with low ice cover in the Atlantic sector, but quite heavy ice in the Bering Sea. From http://nsidc.org/sotc/sea_ice.html

It is generally predicted by climate models that, in the future, Sub-Arctic Seas will have reduced ice coverage (including later formation, shorter duration and earlier disappearance) or no ice at all (IPCC, 2001; ACIA, 2004). However, the exact response of the Sub-Arctic Seas to climate changes is unclear. **Since the presence of sea ice strongly influences the timing, duration and fate of production on the shelf, mechanisms linking climate to ecosystem response cannot be fully understood without understanding the effects of climate on sea ice.**

Sea-ice effects the salinity distribution in Sub-Arctic Seas. This occurs during sea ice formation through brine rejection and during melting when freshwater is released. The salt released during ice formation increases the density of the water that then sinks and so contributes to convection. This is an important process in the Barents Sea, since the higher density water tends to sink and then flow horizontally across the shelf into the deep reaches of the Arctic Ocean (Rudels *et al*., 1994; Schauer *et al*., 1997, 2002). The ice-edge is where there is a balance between ice formation (or transport) and melting. The melt-water increases the stratification of the water column and therefore increases the energy required to mix the water vertically. Impacts of sea ice on the ecosystems of the Bering Sea shelf are discussed in **Section III**.

2.4 Tides

Tidal forcing is also important in Sub-Arctic Seas. Tides tend to dominate the overall current variability and play an important role in vertical mixing on shelves. Over the shelf in the eastern Bering Sea, tides contribute to the formation of hydrographic domains in summer (Coachman, 1986; Schumacher and Stabeno, 1998). The coastal domain is weakly stratified because of the overlapping of mixing due to winds and tides, while the two-layer middle shelf domain forms by the abutment of the upper mixed layer (wind-mixed upper layer) and tidally-mixed lower layer (Schumacher and Stabeno, 1998). On the northern Labrador Shelf, tidally well-mixed waters emanating from Hudson Strait result in weak stratification and high near-surface nutrient concentrations throughout the summer and autumn that in turn lead to high "new" primary production (Drinkwater and Harding, 2001). In the Barents Sea, well-mixed waters on top of Svalbard Bank south of Spitzbergen are thought to be due to tidal mixing. **The relative importance of tides in determining the extent of vertical mixing in Sub-Arctic Seas and their role in vertical nutrient fluxes are poorly known.**

In addition to vertical mixing, tides also contribute to horizontal transport. For example, tides are rectified within the Aleutian Passes, thus adding to the net northward transport of Pacific Water into the Bering Sea (Reed and Stabeno, 1993, Stabeno *et al*., in press). Tidal rectification in regions of strong tides can also lead to anticyclonic circulation around banks and small islands (Loder, 1980; Stabeno *et al*., 1999a; Kowalik and Stabeno, 1999), which may be important in some Sub-Arctic Seas. Such currents tend to lengthen the residence times of the water on these banks and around these islands, and these regions of retention are often the sites of spawning or nursery grounds. Models are needed to investigate the strength of residual tidal currents in the areas of strong tides within Sub-Arctic Seas and their influence on circulation and nutrient dynamics.

Since they are not strongly modified by climatic variability, tides can provide a stabilizing influence on the physical forcing of Sub-Arctic Seas.

2.5 Freshwater Discharges

All Sub-Arctic Seas receive some direct freshwater input along their coastlines. River flows are typically highly seasonal with a maximum discharge in the late spring or early summer and minimum in the winter. In the Bering Sea, the Yukon River in particular provides a critical seasonal buoyancy flux to the coastal regions that enhances the baroclinic flow of the Alaska Coastal Current on its way towards the Chukchi and Beaufort Seas. On the Labrador coast, low salinity waters emanating from Hudson Strait and the freshwater outflows from Hamilton Inlet contribute to the near-shore buoyancy-driven flow along the Labrador and northeast Newfoundland shelves. Similarly, the south coast of the Barents Sea receives a large flux of low-salinity waters transported northward along the Norwegian coast, which is enhanced by local river runoff, particularly from the Pechora and Severnaya Dvina rivers.

Freshwater also influences the vertical stratification of the water column that in turn determines the extent of the vertical mixing by the winds or the tides. Salinity is the dominant factor affecting density in the cool waters typical of many Sub-Arctic Seas (-2º to 5ºC). In spite of these important effects, little is known of the relative importance of local freshwater runoff on the physical oceanography of Sub-Arctic Seas. While in most Sub-Arctic Seas the local freshwater runoff is probably of minor importance (the Bering Sea, Hudson Bay and the Gulf of St. Lawence being exceptions), the possibility of increased runoff under climate change scenarios requires answers determining the potential effect of such an increase on stratification and currents. A combination of modeling and observational studies should be used to address these questions.

2.6 Fronts

Fronts, which consist of relatively sharp horizontal gradients between water properties, are found in most Sub-Arctic Seas. They are frequently the site of high primary production and therefore may play an important role in the total biological production. Strong along-front currents and weak across-front flows are usually present.

Fronts form for several reasons. They can separate major water masses such as in the Barents Sea where the Polar Front separates the cold Arctic waters to the north from the warm Atlantic waters to the south. Fronts also form between fresher, colder coastal waters and warmer offshore waters as observed in the Bering and Barents seas, or off Newfoundland/Labrador and West Greenland. Fronts can be seasonal as in the case of the summer front that separates the Spitzbergen water, formed by atmospherically heated sea-ice melt, from Arctic Water in the Barents Sea. Fronts also form between vertically well-mixed waters and more stratified waters. The mixing may be tidally induced, or in the case of the Bering Sea, the result of a combination of wind and tidal mixing.

Baroclinic instabilities, which can result in the formation of eddies, can develop along fronts. This phenomenon is often found in transition areas between Arctic and temperate waters in the Sub-Arctic Seas, but their quantitative importance has not been estimated. Recent developments of 3D sampling platforms have provided new understanding of the importance of such eddies in enhancing biological production. Although mesoscale meandering and eddy formation may be less important than upwelling phenomena in the vertical transport of nutrients into the upper layers, their role may increase in a future ecosystem of the Sub-Artic Seas.

2.7 Questions Related to Physical Features and Forcing Mechanism

The following are some of the questions ESSAS will address in regards to the physical environment. Questions related to the effects of the physical oceanography on the marine ecosystem will appear in subsequent sections. It is clear that these questions can only be addressed using a combination of retrospective analyses, observations and modelling.

a) ***What is the relative importance of atmospheric forcing, advection, tides and freshwater discharge in the heat, salt and nutrient budgets of Sub-Arctic Seas?***

   Each of these processes contributes to the amount and distribution of heat, salt and nutrients within Sub-Arctic regions but their relative contribution is usually unknown. Knowing the relative contributions will allow determination of which Sub-Arctic sea might be most susceptible to climate change.

b) ***What are the physical processes influencing the internal nutrient dynamics within Sub-Arctic Seas?***

   New production within the ocean depends upon replenishment of nutrients. This occurs in winter through wind-induced mixing that brings high nutrient concentrations from the deep waters into the surface layers. During the late spring to autumn, however, processes such as storms, tidal mixing, eddies, and upwelling could pump nutrients from the deep layers towards the surface. What is the relative importance of these processes and how do they vary between Sub-Arctic Seas?

c) ***How will changes in the ocean circulation patterns associated with climate change impact Sub-Arctic Seas? What impact will this have on the Arctic, Atlantic and Pacific oceans?***

   The flows through Sub-Arctic Seas on their way to or from the Arctic are predicted to change under future climate scenarios, although how and to what extent is still highly uncertain (ACIA, in press). To determine how any change will impact the Sub-Arctic and beyond, we need to understand the physical processes associated with these currents. This would include transport, mixing and modification of hydrographic properties as well as the transport of planktonic organisms.

d) ***What is the relative importance of atmospheric and oceanic processes on seasonal and interannual variability in the sea ice formation, thickness, distribution, and retreat?***

   There have been significant interannual variations in the amount of ice in Sub-Arctic Seas in both the Atlantic and Pacific. Changes in winds and air temperatures associated with large-scale atmospheric pressure patterns affect the timing of ice formation and retreat, and the amount of ice (thickness and coverage), as do oceanic heat fluxes and advection of ice by ocean currents. The relative importance of the atmospheric and oceanic processes in controlling ice processes will be studied.

e) ***What effect will reduced ice coverage have on the hydrographic characteristics and mixing within Sub-Arctic Seas?***

   Reduced ice coverage potentially will mean a larger area exposed to winter mixing and cooling. There will be reduced brine rejection during sea-ice formation and reduced sea-ice melt, thereby decreasing the seasonality in salinity. The reduction, or even absence, of sea-ice melt will lead to weaker stratification and hence the potential for increased vertical mixing. Changes in salinity could also modify density-driven currents.

f) Why does large-scale climate variability introduce temporal and spatial fluctuations in the Sub-Arctic ecosystems that are out of phase in opposite (east-west) sides of major oceanic basins?

In the North Atlantic there are out of phase responses to atmospheric forcing associated with the NAO, i.e. during high NAO periods, temperature change in the Barents Sea is positively correlated with the NAO index but negatively correlated in the Labrador Sea. However, in some years this has not held, e.g. in the late 1990s the temperatures in both regions were high in spite of a high NAO. This is believed to be due to the eastward shift in the centers of the Icelandic Low and Azores High. This is important for understanding the observed relationships between ecosystem traits (phytoplankton, zooplankton, fish) and the NAO (e.g. Drinkwater *et al*., 2003). Less clear is the relationship between opposite sides of the Pacific, but because of the greater width of the Pacific relative to the width of the Aleutian Low, it will likely depend upon the intensity and geographical position of the Low.

g) Why are there temporal changes in the relationship between the large-scale and local atmospheric patterns and the physical responses in Sub-Arctic Seas, including both hydrographic conditions and circulation?

During the past 40 years there has been a general increase in the NAO/AO in addition to strong decadal fluctuations. During this time there have been strong correlations between the NAO/AO and hydrographic properties, convective processes and the circulation. However, prior to that time the correlations of the NAO/AO with many of the ocean properties were non-significant. This suggests that other atmospheric modes may have been more important than the NAO/AO or that the large-scale oceanic circulation played a greater role in determining changes in ocean temperatures. Studies should focus on why the NAO/AO in some periods is the dominant atmospheric mode linked to the ocean circulation and properties and in other periods it is not.

h) Are there significant teleconnections between atmospheric pressure patterns and hence the ecosystem responses of the Sub-Arctic Seas?

Due to the existing large-scale atmospheric teleconnection patterns, e.g. PNA (Pacific/North American), AO, etc., it might be expected that the physical and biological responses in Sub-Arctic Seas to these atmospheric modes will be related. Statistical studies to explore such relationships will be undertaken. If such relations exist, there is a need to explain their underlying mechanisms. In addition, other teleconnections have been suggested but not well established, i.e. links with ENSO events.

(i) What controls the position and strength of oceanic fronts in the Sub-Arctic Seas?

Fronts in the ocean act as barriers for many marine organisms. Their edges are important feeding areas for many higher-trophic-level organisms. Many oceanic fronts are linked to bottom topography and will therefore respond to climate change by maintaining their present positions or by relocating to a nearby and similar topographical feature. It is, however, extremely difficult to provide good estimates of what will happen to fronts that are not controlled by topography, since few models provide such information.

SECTION III: HOW DO PHYSICAL PROCESSES AND BIOLOGICAL INTERACTIONS INFLUENCE MARINE ECOSYSTEMS IN SUB-ARCTIC SEAS?

Marine ecosystem structure in Sub-Arctic Seas is influenced by a variety of physical factors, which are here grouped under the headings: light, temperature, sea-ice, and stratification. These divisions are somewhat arbitrary and artificial, since all of these factors are related at some level. Thus, for example, temperatures in the Sub-Arctic Seas are influenced by the extent and duration of seasonal sea-ice cover and by water movements (horizontal and/or vertical), but these water movements themselves affect the extent of seasonal ice-cover. The onset of insolation during spring causes surface water temperatures in open waters to rise, but it also causes ice to melt. Both of these processes lead to increased stratification, which can be broken down by vertical mixing. Clearly, a series of complex interactions combine to define a local physical environment for a given region within a Sub-Arctic Sea. Temperature has a fundamental forcing function in biology, with direct influences on rate processes in poikilothermic (cold-blooded) organisms and on the distribution of mobile species that have preferred temperature ranges. Sea-ice, light, stratification and water movements also affect the physiology and distribution of marine organisms, and the organisms themselves interact so as to create distinct ecosystems.

The size, ambit (geographic area covered during a lifetime), and life span of an organism greatly affect its role in an ecosystem and the rate at which its population responds to change (Fig. 8). The size of individuals range from a few µm for phytoplankton to 25-30 m for large cetaceans and life spans are measured in hours to a day for phytoplankton, months to years for zooplankton, years for fish and seabirds, and decades for marine mammals such as cetaceans. As conditions in the Sub-Arctic Seas change, some species populations will respond more quickly than others, thereby resulting in significant changes in the species composition and food web structure of the Sub-Arctic Seas.

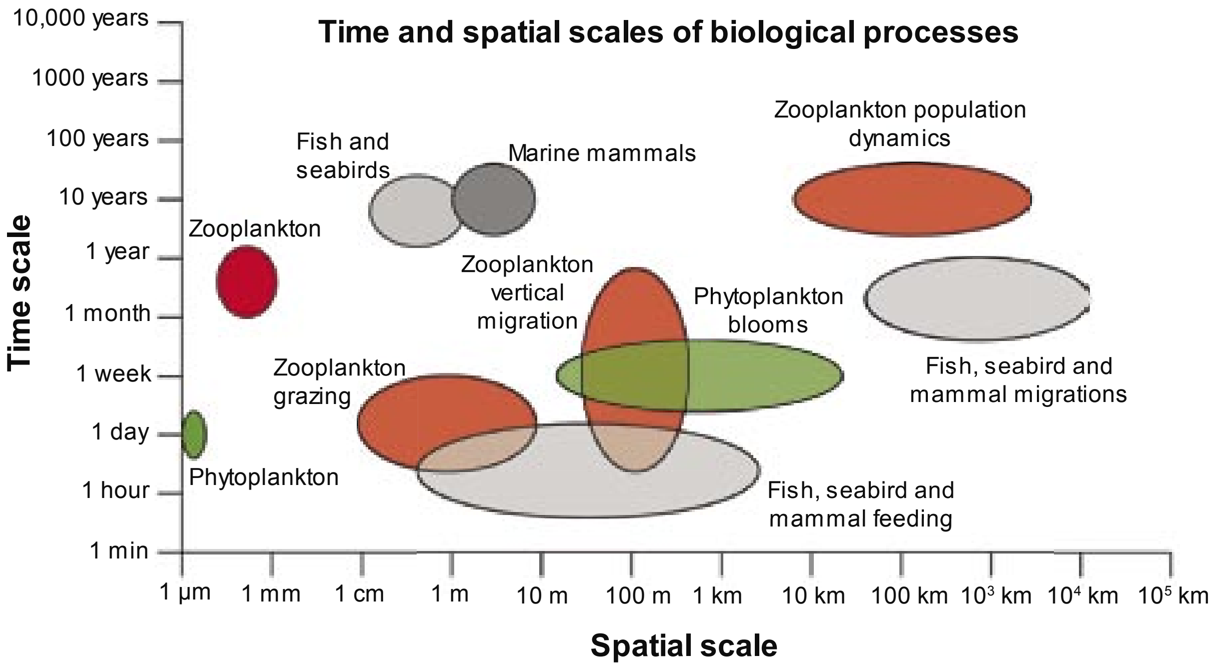


Figure 8. The biological time and space scales (modified by E. Head, Bedford Institute of Oceanography, Dartmouth, NS, after a version by S. Strom, Western Washington University, Bellingham, WA, USA).

3.1 Physical Processes

3.1.1 Light

Two determinants of the properties of the light environment in the ocean are the nature of the incident light flux on the ocean surface from above, and the optical properties of the water itself. The incident solar irradiation is a function of both the time of the day and the time of the year. In accordance with the solar elevation at noon, the maximum solar irradiation will decrease with increasing latitude (Fig. 9). During summer, however, this effect is counteracted by the increase in day length in high-latitude regions. Several of the Sub-Arctic Seas are located north of the Arctic Circle at 66°30'N. The high irradiance at 80°N shown in the figure illustrates the effect of the day length on the daily surface irradiance. During summer, high-latitude regions can experience a slightly higher daily surface irradiance than tropical regions. During winter, the daily surface irradiance will obviously be much less in high-latitude regions than in low-latitude regions (Kirk, 1994). **How the seasonal distribution of solar irradiance affects annual productivity in the Sub-Arctic Seas as compared to productivity at lower latitudes has yet to be investigated.** In this regard, the large latitudinal range in the Sub-Arctic Seas from 45°N to almost 80°N offers great potential to explore the effects of light in a comparative approach.

The irradiance curves in Figure 9 are modeled assuming cloudless days. Northern and southern ocean waters are often cloud covered (Bishop and Rossow, 1991). A few scattered clouds may increase the diffuse light flux and thereby slightly increase the daily surface irradiance (5-10%). As well, light penetration into the water column is influenced by a number of factors including phytoplankton concentration and resuspension of sedimentary material in shallow turbulent areas. Overcast sky and/or fog may reduce the daily surface irradiance to 10-20% of the maximum value (Kirk, 1994; Luccini *et al*., 2003). For a two-month period during the summer of 2000 at Paradise Bay (65°S in the Antarctic Peninsula), the mean surface irradiation was 43% of the maximum value (Luccini *et al*., 2003). It is reasonable to assume that daily surface irradiance in the Sub-Arctic Seas will be at a similar, or lower, level.

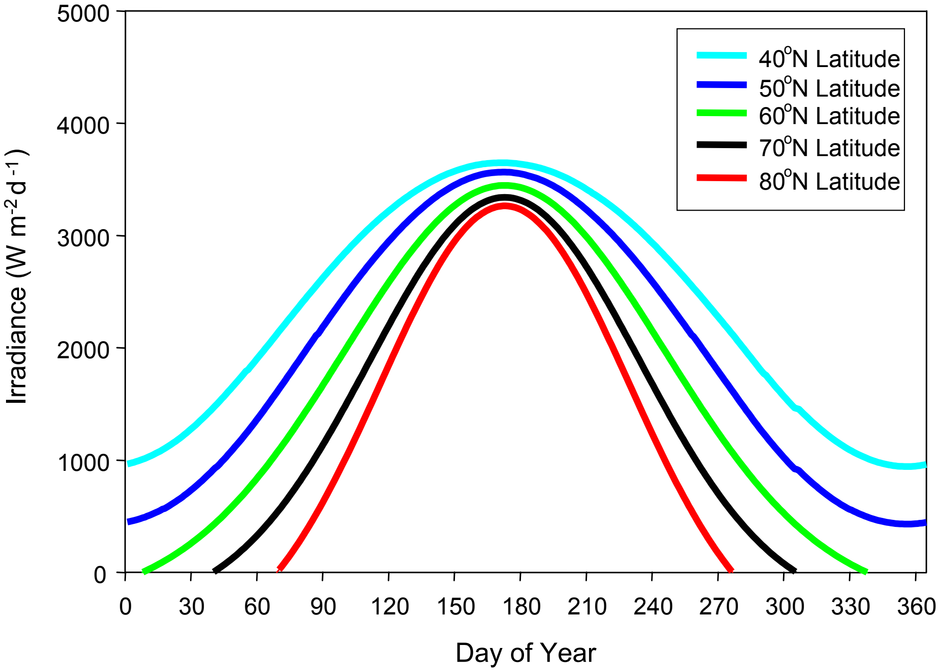


Figure 9. Irradiance as a function of latitude, as estimated by the model of Sathyendranath and Platt (1988).

Ice and snow cover may reduce irradiance to less than 1% of the surface irradiance, and the organisms living under the ice are often well adapted to this low light environment. Some of the ice algae, especially those living in land-fast ice regions, have shown some of the most extreme low-light adaptations recorded (Horner, 1985; Arrigo, 2003).

That increased Ultra-Violet Radiation (UVR) in polar regions results from ozone depletion has been known for several years (Santee *et al*., 1995). Ozone depletion was first reported from Antarctica in the mid-1980s, and it is often referred to as “the Antarctic ozone hole” (Farman *et al*., 1985). In the last 10-15 years, ozone depletion and increased UVR have also become evident in the Arctic (Rodriguez, 1993). Although a considerable amount is known about the effects of increased UVR on the Antarctic marine environment (e.g. de Mora *et al*., 2000), considerably less information is available from the Arctic (AMAP, 1998; de Mora *et al*., 2000; ACIA, in press). Thus, **investigation of how climate change may affect the amount and effects of UVR on Sub-Arctic marine ecosystems is needed.**

3.1.2 Temperature

Changes in rate processes, as well as behavioral responses to temperature, can alter the species composition and energy flow in both pelagic and benthic ecosystems. Interannual and longer-term variability in water column temperatures in the Sub-Arctic Seas may result from several mechanisms, including the formation and melting of sea ice, advection of warm water from the south or cold water from the north, and anomalous summer heating or winter cooling. Because the rates of physiological processes of organisms are sensitive to temperature, reproduction, growth and trophic transfer of material will be affected by changes in temperature. Thus, **there is a need to learn how species present in the Sub-Arctic Seas will respond to changing water temperatures.**

In the Sub-Arctic Seas, growth rates of ice-algae and phytoplankton are more strongly influenced by the availability of light and nutrients than by temperature. Blooms of ice-algae typically occur at zero or sub-zero temperatures, and phytoplankton blooms are generally over well before temperatures approach their seasonal maxima. On the other hand, the warmer waters of the North Atlantic and North Pacific, which flow into the Sub-Arctic Seas from the south, have higher levels of nutrients than the colder Arctic waters that flow in from the north. Thus, higher temperatures will generally be associated with overall higher water column productivity.

In contrast, water temperature exerts a strong influence on the growth rates of zooplankton and may often be more important than food availability for limiting the growth rates of short-lived small-bodied copepods (McLaren, 1963; Corkett and McLaren, 1978; Huntley and Lopez, 1992). **Growth and development rates of the dominant large-bodied zooplankton are influenced by both temperature and food availability.** In the laboratory, the combination of low temperature and high food concentration will yield large sizes-at-stage, but long stage durations, and the combination of high temperature and low food will give small sizes-at-stage and short stage durations (Campbell *et al*., 2001). In nature, temperature/food interactions are not necessarily clear. Generation times are generally longer at low temperatures, but this may sometimes give adaptive advantages. For example, the temperate species *Calanus finmarchicus* has a one-year life cycle, whereas the Arctic congeners *C. glacialis* and *C. hyperboreus* have 2 year and 2-4 year life cycles, respectively (Mauchline, 1998; Tande, 1991). The Arctic species are, however, larger (size-at-stage), have a higher energy storage capacity, and, unlike *C. finmarchicus*, the adults are able to reproduce without feeding in advance of the spring bloom. For *C. hyperboreus*, the offspring can develop into early copepodite stages before blooms occur, which allows them to take full advantage of blooms that in more northern regions are often intense and of short duration (Slagstad and Tande, 1996).

Changes in temperature can affect the productivity and biomass of zooplankton. Modeling studies in the Labrador Sea suggest that temperature changes of only 0.5°C can change the abundance of *C. finmarchicus* by as much as 20% and a 1°C change will cause abundance changes of 40-60% (Tittensor *et al*., 2003). Higher (lower) temperatures result in higher (lower) abundances, primarily through increased (decreased) growth rates. In the southeast Bering Sea, *C. marshallae* produced two cohorts in a warm year (1981) and only one in a cool year (1980) (Smith and Vidal, 1986), and in a cold year (1999) springtime abundance of small, neritic copepod species was reduced by up to 90% when compared to their abundance in warm years (1997, 1998) (Coyle and Pinchuk, 2002a). Changes in temperature may also influence the timing of reproduction of euphausiids. In the Bering Sea in cold years, adult euphausiids may still be present in summer, whereas in warm years they may reproduce earlier and die. Changes in the timing of the availability of adult euphausiids may affect the growth and survival of their predators, such as sockeye salmon (*Onchorhynchus nerka*) and short-tail shearwaters (*Puffinus tenuirostris*), which are present in summer (Nishiyama, 1974; Baduini *et al*., 2001a; Hunt *et al*., 2002b). Temperature change can also influence the timing of life cycle events in marine copepods. For example, Mackas *et al*. (1998) document interdecadal variations in developmental timing of *Neocalanus* at a monitoring site (Ocean Station P) in the northeastern Pacific, which have been linked to differences in feeding success of Cassin's auklets (*Phytoramphus aleuticus*) (Bertram *et al*., 2001).

Water temperature affects not only the productivity of zooplankton, but also the match or mismatch between phytoplankton and its grazers (micro- and meso-zooplankton) (Napp *et al*., 2000). In the southeastern Bering Sea when water temperatures during the spring bloom are cold (< 2ºC), as occurs when there is an ice-edge bloom, zooplankton reproduction and population growth will be retarded and the spring phytoplankton bloom will be less vulnerable to control by zooplankton grazing (Napp *et al*., 2000; Coyle and Pinchuk, 2002a,b). Under these circumstances, most of the primary production is predicted to go to the benthos (Walsh and McRoy, 1986; Alexander *et al*., 1996). Thus, Walsh and McRoy (1986) interpreted the presence of a sub-surface chlorophyll maximum in the middle domain of the southeastern Bering Sea as evidence of transfer of phytoplankton to the benthos, and a lack of tight coupling between primary production and copepod grazing (Fig. 10).

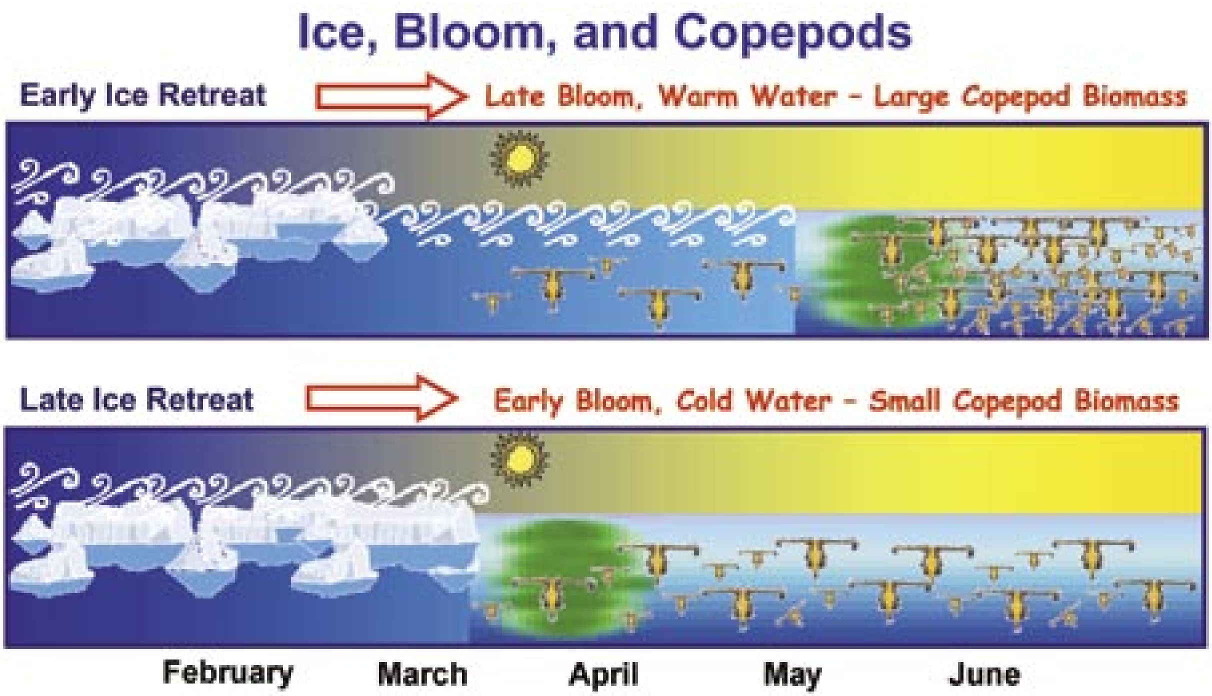


Figure 10. Relationships among the timing of sea-ice retreat, water temperature, the timing of the spring bloom and the production of small neritic copepods in the southeastern Bering Sea. If the ice retreats early in the spring, the spring phytoplankton bloom is delayed until the water column is stratified by insolation, presumably because there is insufficient light to support an ice-edge bloom. In contrast, late ice retreat is accompanied by ice edge blooms that occur in cold melt water (After Hunt *et al.*, 2002a).

In contrast, high zooplankton production is associated with late blooms in warm water, and most of the energy is hypothesized to remain in the water column (Walsh and McRoy, 1986; Niebauer *et al*., 1990; Hunt *et al*., 2002a; Hunt and Stabeno, 2002). These hypothesized, temperature-mediated differences in the fate of production need to be tested.

The phytoplankton dynamics in this scenario have some similarities to the pattern that is seen in the Labrador Sea region. In the warm, ice-free central region the bloom is later and less intense than in slope water regions influenced by ice-melt from the adjacent shelves. In contrast to the Bering Sea, however, *C. finmarchicus* abundance is much higher in the cold slope water regions than the warm central region (E. Head, unpublished data). Yet a third pattern is seen in the Barents Sea, where the more southerly ice-free region has higher levels of *C. finmarchicus* than northerly areas closer to the ice. Here, however, a large proportion of the biomass is thought to be produced elsewhere and advected into the region (Skjoldal *et al*., 1992).

To predict the effect of climate change on higher trophic levels, we need to develop conceptual models, based on appropriate observations, and numerical models, verified by the data, relating the effects of increased temperature and reduced sea-ice on the annual cycle and productivity of the lower trophic levels.

Changes in temperature conditions may also have contributed to the outbreaks and subsequent collapse of jellyfish (*Chrysaora melanaster*) that have occurred in the Bering Sea since the early the 1990s (Brodeur *et al*., 1999; Hare and Mantua, 2000) or to changes in their distribution (Brodeur *et al*., 2002) (Fig. 11). Other possible causes for the surge in jellyfish abundance include decreasing competition for food because of reduced consumption by planktivorous forage fish. No such jellyfish outbreaks have been reported in the North Atlantic Sub-Arctic Seas, perhaps because sampling for gelatinous zooplankton has been rare, but such outbreaks have been reported in temperate waters of the North Atlantic (Mills, 2001). Predation by jellyfish has significant impacts on mesozooplankton and larval fish (Brodeur *et al*., 2002). **We need to document the abundance levels of gelatinous zooplankton throughout the Sub-Arctic Seas, to understand what controls their variability and their role in Sub-Arctic marine ecosystems.**

Growth rates of fish also vary with temperature. For example, a comparison amongst Atlantic cod stocks from the North Atlantic showed that the log transformed weights of age-4 fish varied linearly with average bottom temperature. The maximum weight was 7.32 kg (Celtic Sea stock, average bottom temperature *ca*. 11°C) and the minimum, 0.61 kg (Labrador/Grand Bank stock, average bottom temperature *ca*. 2°C) (Brander, 1994). In addition, the interannual variability in growth rates within a stock was also temperature dependent (Brander, 1995, 2001; Campana, 1995; Shelton *et al*., 1996). **As water temperatures rise, how will the increased growth rates of the principal species of predatory fish (e.g. cod and pollock) affect ecosystem structure and function?**

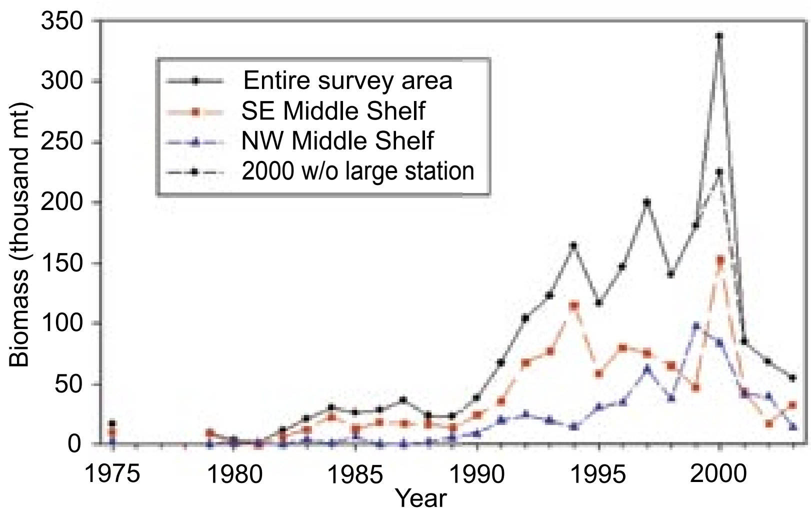


Figure 11. Biomass in thousands of metric tonnes of large medusae in the eastern Bering Sea (Courtesy of G. Walters, NOAA, AFSC, Seattle WA, USA)

Despite their ability to swim away from waters with unfavorable temperature conditions, **some fish show evidence of adaptation to cold temperatures**. For example, cod from the cold waters of the Newfoundland/Labrador Shelf are able to manufacture a protein that prevents their tissues from freezing at temperatures that cod from other stocks could not tolerate (Goddard *et al*., 1992, 1999). Also, there is a stock of pollock in the Sea of Okhotsk that spawns under the ice-covered Kunashiri Strait (A. Krovnin, pers. comm.). Generally pollock is thought of as a warm water species in the Sub-Arctic Seas. Perhaps this stock has some genetic adaptation that allows it to tolerate low temperature. **There is a need to learn whether these adaptations to water temperature are facultative or genetically fixed, and how these fish would respond to changing water temperatures.**

Although most poikilothermic animals show temperature-dependent changes in metabolic rates, growth and reproduction, organisms from different environments may respond differently to a given change in temperature because of adaptation to local conditions. Long-term genetic adaptations within a species, or leading to species differentiation, mean that cold-adapted strains or species perform at higher rates at low temperatures than their warm-adapted equivalents (Hochachka and Somero, 1973; Heinle, 1981; Clarke, 2003). Within the range of adaptation of a species or local population, warmer temperatures may result in accelerated rates, but temperatures above the preferred range may result in a decrease in function or death. This phenomenon has been little studied in the Sub-Arctic Seas, and **there is a need to examine the temperature responses of representative organisms from the Sub-Arctic to derive realistic estimates of their potential response to changes in water temperature.**

Temperature also has a large effect on distribution and community structure. **Most of the zooplankton in each of the Sub-Arctic Seas can be divided into two distinct communities: those derived from the warmer temperate waters originating to the south and those associated with colder Arctic waters.** In the North Atlantic, *C. finmarchicus* is the dominant member of the warm water copepod community (Planque *et al*., 1997). In contrast, in the areas of the North Atlantic influenced by Arctic waters (the northern Barents Sea, the East and West Greenland Shelves, northeast of Iceland and on the Newfoundland/Labrador Shelf), the Arctic species, *C. hyperboreus* and *C. glacialis*, are dominant (Conover, 1988), with *C. hyperboreus* more dominant in the deep waters and *C. glacialis*, restricted to the colder shelves and regions north of the Polar Front.

In the North Pacific, *Neocalanus cristatus*, *N. plumchrus* and/or *N. flemingeri* are generally the dominant copepods of the warm water community. Although Arctic copepods are not found in the Bering Sea, *C. glacialis* is broadly distributed in the cold regions of the Sea of Okhotsk (V. Shuntov, pers. comm.). In the Bering Sea, *C. marshallae* is the dominant large copepod of the cool shelf waters of the southeastern Bering Sea. Amongst the small copepods, *Pseudocalanus* spp. are abundant in the shelf waters of all the Sub-Arctic Seas, as are *Oithona* spp., which are often the most abundant copepods in cool shelf and warm deep water regions. Neither of these taxa are ever a large proportion of the zooplankton biomass.

Decadal-scale changes in temperature on the Newfoundland Shelf have been accompanied by changes in the biota. Temperatures (and salinities) during the 1960s were higher than those of the 1990s. Over the intervening period there have been substantial changes in the abundance and distribution of many fish species, with cold water species seen much farther south later in the period, and dramatic shifts from groundfish to invertebrates (Rose *et al*., 2000; Drinkwater, 2002; deYoung *et al*., 2003). Some of these effects are probably anthropogenic, but there are clearly substantial environmental effects both on productivity and distribution of organisms. Also, the 1990s showed large increases in dinoflagellate abundance during the fall and winter months and of Arctic copepod species (*C. glacialis*, *C. hyperboreus* and *Pseudocalanus* spp.) in spring. **It is unclear whether the changes in the plankton have affected higher trophic levels (Rice, 2002; deYoung *et al*., 2003).**

Water temperature has an important influence on the distribution of fish. Fish tend to prefer specific temperature ranges, so that changes in temperature can lead to changes in their distribution, which are generally most evident near the northern or southern boundary of a species' range (Myers, 1998). For example, on the West Greenland Shelf, the distribution of the warm water species, cod, herring and halibut, extended farther north during the warm 1920s and 1930s (Jensen and Hansen, 1931; Hansen, 1949), while since 1970, their abundance there has been low (Buch *et al*., 1994). Similarly, on the Newfoundland/Labrador Shelf, decreasing temperatures through the 1990s may have driven the Atlantic cod south, while also allowing capelin to extend their range eastward to Flemish Cap and southward onto the northeastern Scotian Shelf off Nova Scotia (Frank *et al*., 1996). These conditions may also have resulted in the southward extension of Arctic cod, *Boreogadus saida* (Lilly *et al*., 1994). Following years of high inflow of Atlantic water into the Barents Sea (warm), the abundance of young herring increases, leading to an increased predation pressure on recruiting capelin (Hamre, 2003). In addition, cod are located farther eastward during high inflow years and more restricted towards the western sections of the Sea during low inflow (cold) years (Nakken and Raknes, 1987; Ottersen *et al*., 1998). **Shifts in the distribution of these species are important, since they may govern the recruitment of capelin and thus the feeding conditions for other species higher in the food web.**

Changes in water temperature may affect predator-prey interactions with significant consequences for existing food webs. For example, the disappearance of cod from the Newfoundland/Labrador Shelves has been followed by a proliferation of northern shrimp (*Pandulus borealis*), which may have resulted from a release of predation pressure (Worm and Myers, 2003). In the northern Bering Sea, the Chirikov Basin is a major feeding ground for the California gray whale, the only cetacean known to feed primarily on benthic infaunal invertebrates (Rice and Wolman, 1971). The benthic community in the Chirikov Basin can sustain intense whale predation because of its high productivity (Highsmith and Coyle, 1990), and because many groundfish predators, which consume benthic amphipods, are excluded from the northern Bering Sea by cold bottom water temperatures. The disappearance of cold bottom water from the northern Bering Sea could permit groundfish from the southeastern Bering Sea to extend their range northward, altering energy pathways and threatening marine mammal food resources. In recent surveys during warm years, both juvenile and adult pollock were caught in the northern Bering and Chukchi Seas (Wyllie-Echeverria, 1995), much as had been predicted by Strickland and Sibley (1984). Thus, warming sea temperatures could severely impact whale populations by permitting a greater percentage of the overall benthic production to flow through a fish-dominated food web. Such competition would, in turn, force the gray whales to forage farther north, something that is already beginning to occur as the amphipod beds decline (Moore *et al*., 2003). **There is a need to assess the probable impacts on ecosystem structure and function as predators-prey interactions change in response to variations in the community structure.**

Understanding the potential impact of climate-related shifts in the distribution of fish on the structure of the shelf ecosystems requires additional fieldwork and modeling.

3.1.3 Sea ice

Sea ice is an important characteristic of most Sub-Arctic regions. The under-side of sea-ice provides a substrate for an epontic flora and fauna, while the surface is used as a platform by marine mammals and birds. The formation, melt and retreat of sea-ice provide physical conditions that also influence the structure and function of pelagic and benthic communities.

Reductions in seasonal ice cover in the Sub-Arctic Seas predicted by climate models are expected to lead to decreases in ice-algal production, and thus perhaps reduced fluxes of organic material to the benthos. Micro-algae start to grow in the bottom surface of sea ice when light reaches a sufficiently high level. Ice thickness and snow cover modify light penetration to the under-ice surface. In the Sub-Arctic Seas, ice is generally relatively thin first-year ice and ice algae can be found by the end of February as far north as the northern Barents Sea (Hegseth, 1992).

Amphipods (e.g. *Apherusa glacialis*, *Onisimus* spp.) graze the ice algae directly from the under side of the ice and, in turn, are consumed by Arctic cod. The copepods *Pseudocalanus* spp. and *C. glacialis* also feed on ice-algae, although apparently only when the algae are sloughed off into the water column (Runge and Ingram, 1991). **It is not known if other copepods (e.g. *C. hyperboreus*, *C. finmarchicus* or any of the North Pacific Sub-Arctic copepods) or euphausiids consume ice-algae.**

With the onset of melting, ice algae are mostly washed out of the ice to aggregate and sink to the benthos. However, in some Sub-Arctic Seas (e.g. the Labrador/ Newfoundland Shelf) where ice blooms are accompanied by an influx of Arctic copepods that may be adapted to episodic, intense blooms, a large proportion of the ice-bloom production may be consumed before sinking to the bottom. **There is a need for direct measurements that provide an estimate of annual ice-algal production, the amount grazed, and the contribution of pelagic and ice-associated algae and fecal pellets to the total annual sedimentary flux.**

Ice-edge blooms tend to follow the seasonal retreat of the ice, so that, for example, the bloom on the Newfoundland Shelf peaks in April, whereas in the vicinity of Hudson Strait, the peak is in July (Fig. 12). The timing of water column blooms is sometimes less straightforward. For example, while in general in the southern Barents Sea blooms occur following stratification (May/June), in some localized areas north of 70ºN blooms can occur as early as April (Kristiansen *et al*., 1994).

Because estimates of ice-algal production in seasonal ice are generally minute compared to those for open ocean production (Andersen, 1989; Gradinger, 1996; Juterzenka and Knickmeier, 1999), the largest effect of possible reduced sea ice on primary production will be in the longer duration and larger area of open ocean. This is expected to lead to higher overall production in the Sub-Arctic Seas under global climate change (ACIA, in press). Since the overall production for a water

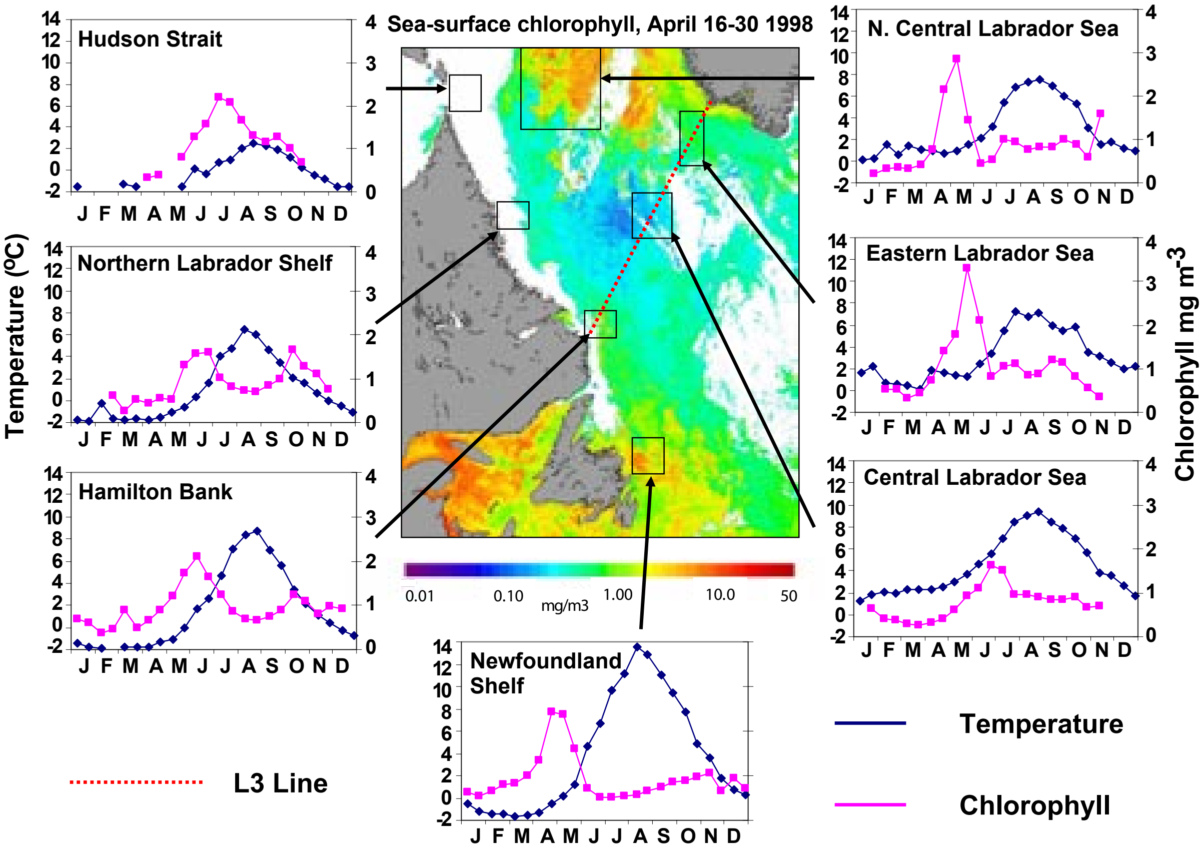


Figure 12. Estimates of average seasonal cycles of sea surface temperature and chlorophyll for regions of the Labrador Sea, 1998-2002, (1998-2000 for NCLS and ELS) from SeaWiFS and NOAA AVHR satellite imagery. Courtesy of E. Head, Bedford Institute of Oceanography).

column bloom is higher than for the ice-associated blooms, greater open-water production might result in a flux of material to the benthos that was not very different from that resulting from ice-associated blooms. **Reliable quantitative budgets of carbon flux (primary production/grazing/sedimentation) have not been produced for most of the Sub-Arctic Seas.**

In the midst of the ice-cover, there are areas of open water (leads and polynyas). In the Bering Sea, the St. Lawrence Island Polynya is an area of high organic flux to the benthos and consequently high benthic productivity occurs below it (Grebmeier and Cooper, 1995; Cooper *et al*., 2002). Benthic productivity here is directly linked to higher trophic levels, since the abundant benthic amphipods and mollusks of the region are important food sources for seabirds and marine mammals, for which the open water provides access to the water column and the benthos during the winter (Fig. 13).

Sea ice also serves as a platform on which some animals spend part of their lives. For example, walrus (*Odobenus rosmarus*), as well as ringed (*Phoca hispeda*), ribbon (*P. fasciata*) and bearded seals (*Erignathus barbatus*) all use the ice as part of their habitat. In the Bering Sea, spotted seals (*P. largha*) pup within 25 km of the ice-edge in cold years when it extends to the shelf-break (Braham *et al*., 1984). The richest feeding grounds are over the shelf-edge and in warm light-ice years the seals may have to haul out and pup several hundred kilometers away (Lowry *et al*., 2000). In this case, ice conditions may well affect the ability of spotted seals to forage effectively. Several species of mammals follow the ice edge as it retreats north in summer, and advances in winter. For example, between 2 and 4 million harp seals (*P. groenlandica*) follow the expanding ice pack from Baffin Island 1600 km south to the Newfoundland Shelf and Gulf of St. Lawrence. The seals pup on the pack ice in February or early March, when the ice is at its maximum extent, returning north with the retreating ice-edge through the summer months.

Baleen whales are found associated with the ice edge (e.g. minke *Balaenoptera acutorostrat*a; bowhead, *Balaena mysticetus*), where they feed on plankton and small fish. Toothed whales associated with ice include belugas (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*), which feed on fish, squid and crustaceans. Killer whales (*Orcinus orca*) are also common in the Sub-Arctic Seas, where they feed on fish and mammals, including baleen whales, seals and walruses.

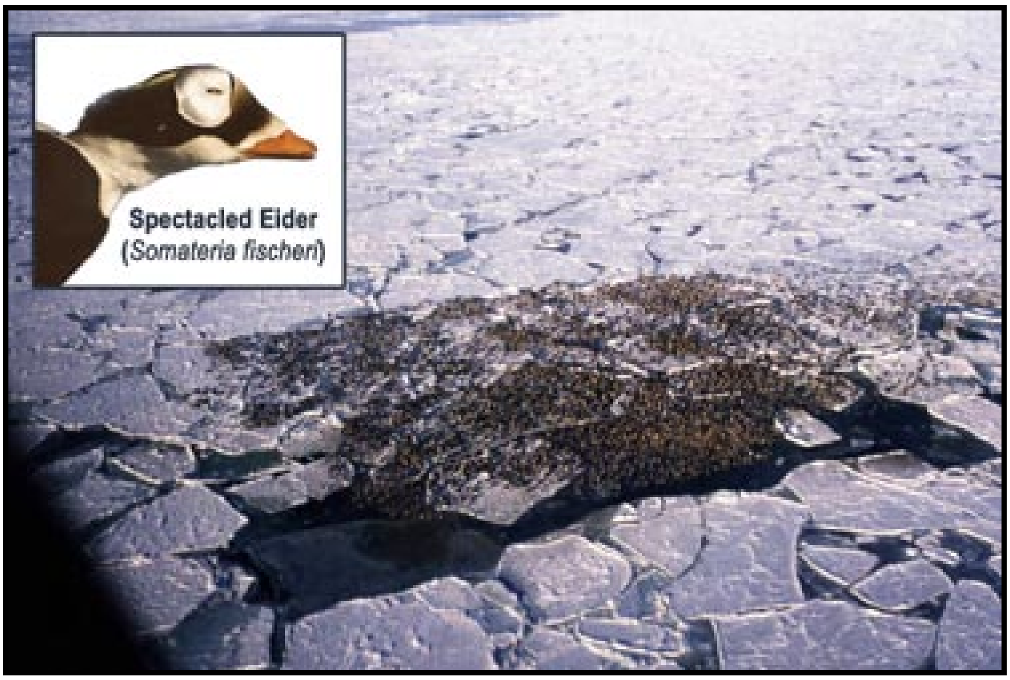


Figure 13. Spectacled Eiders (inset, adult male) in pack ice south of St. Lawrence Island, Bering Sea, March 2001. Photos by James Lovvorn.

Changes in the extent and distribution of sea ice will influence the distribution and abundance of animals that use the sea ice as a habitat. One consequence of reduced ice coverage in the Bering Sea could be that haul-out areas for walruses and seals will generally be farther from their preferred feeding areas. On the Newfoundland Shelf, it has been suggested that reduced ice-cover in the last few years may have reduced reproductive success in harp and hooded seals (*Cystophora cristata*) (ACIA, 2004). Changes in the extent or occurrence of polynyas, such as the St. Lawrence Island Polynya in the northern Bering Sea, could lead to alterations in the distribution or size of "cold pools" of water on the shelf. These are thought to exclude fish from the highly productive benthos, leaving it available for foraging by walruses, bearded seals and seabirds. **Since many of the species that use sea ice as habitat occur throughout the Sub-Arctic Seas, it may be possible to employ comparative studies to assess the probable impacts of changing sea-ice cover on marine mammals.**

3.1.4 Stratification

In ice-free areas of the Sub-Arctic Seas, increasing solar irradiance and air temperatures in the spring lead to increasing stratification. How rapidly the surface warming occurs and how deep the layer is depend on the level of irradiance, which is influenced by latitude and cloud cover, and the rate at which the water column is being mixed. In the open waters of the Sub-Arctic Seas, stratification does not usually occur until May/June, and is a pre-condition for the initiation of most open-water phytoplankton blooms. Stratification also forms a barrier to the supply of nutrients (notably nitrate, silicate and/or phosphate) that become depleted in the surface mixed layer during the course of the bloom. Thereafter, recycling of nutrients within the mixed layer must fuel phytoplankton growth, unless more nutrients are supplied from depth by processes that lead to vertical mixing (e.g. storms, eddies, tides, upwelling) (e.g. Sambrotto *et al*., 1986). The ability of summer storms to mix nutrients into the upper mixed layer depends not only on the strength and duration of the storms, but also on winter conditions that set the strength of the pycnocline.

Phytoplankton blooms generally occur at the ice edge, as it retreats during the spring/summer. This is because the melting ice forms a layer of relatively fresh water, thus promoting water column stability. Low salinity water originating from ice melt can also be advected into regions that do not themselves have ice cover (e.g. Labrador/Newfoundland slope water regions, southern regions of the Barents and Bering Seas and the Oyashio Current). The density-induced stratification of melt waters tends to be stronger and shallower than the thermal stratification that develops in the southern, permanently ice-free waters of the Sub-Arctic Seas. As a result, ice-edge blooms tend to be intense because the phytoplankton are maintained at depths where light intensity is high, but of short duration because nutrient concentrations are relatively low and rapidly depleted (Kristiansen *et al*., 1994). Nutrient concentrations are relatively low partly because the ice-covered waters are often of Arctic origin, and partly because they are diluted with ice-melt. **Ice-edge blooms may be prolonged when physical dynamical processes (storms, upwelling, downwelling, advection, eddies) bring nutrients into the surface layers, but these processes have not been well studied.**

Over the next few decades, the expected increase of freshwater in the Sub-Arctic Seas due to freshwater ice melt and possibly a slight increase in freshwater runoff (ACIA, 2004) will likely be unfavorable to the current endemic to Arctic lower trophic-level biota. Our current understanding emphasizes a change in the onset of the spring bloom and a shift in the coupling to the components further up in the food chain. Still we have few data on how the effect of freshwater run-off may operate as a major signal in the Sub-Arctic Seas. One good example is from Iceland, where detailed studies have shown interactions between freshwater run-off and the wind regime influence interannual variations in the timing of the onset of the spring bloom of phytoplankton (Thordardottir, 1986). When primary production is averaged for the years 1958-1982, there are several distinct seasonal patterns. At the station farthest from the shore, there is little primary production in March and April, a single major bloom in May, and relatively low production for the rest of the season. However, close to shore, production begins in March and remains at a relatively constant level through the summer. This study ruled out light and nutrients as factors determining the timing of the bloom along different parts of the Icelandic coast. Instead, the beginning of the bloom was associated with reduced salinity caused by freshwater run off. Breakdown of stratification was associated with strong winds.

Although stratification is generally thought a requirement for the onset of primary production, there are instances where a bloom appears to occur without evidence of stratification (Townsend *et al*., 1992). In the southwestern Barents Sea, small, localized phytoplankton blooms can occur in late March or April before thermal stratification has developed (Eilertsen, 1993; Hegseth *et al*., 1995). Blooms also occur in unstratified waters in the slope regions beyond the Newfoundland/Labrador and West Greenland Shelves in May (Stuart *et al*., 2000, E. Head, unpublished data). **There is a need to learn how blooms in apparently unstratified waters are initiated.**

3.2 Biological Processes and Interactions

Blooms of algae occur when rates of primary production exceed those of grazing and sedimentation. In general, growth rates of nanophytoplankton (e.g. flagellates) are closely matched to those of their microzooplankton grazers, so that these phytoplankton do not often form blooms (Kiørboe, 1993, Verity *et al*., 2002). Instead, it is the larger phytoplankton (e.g. diatoms) that accumulate in the water column because their mesozooplankton grazers have much lower growth rates than the phytoplankton. Blooms in the Sub-Arctic Seas are normally dominated by diatoms, which are readily grazed by the abundant large-bodied copepods and euphausiids, which in turn provide the food source for higher trophic levels (e.g. pelagic fish, baleen whales and seabirds).

Figure 14. *Emiliania huxleyi*. Photo from: http://www.soes.soton.ac.uk/staff/tt/eh/.

There are, however, two phytoplankton species that frequently form blooms in Sub-Arctic Seas that are not diatoms. The first is the coccolithophore, *Emiliania huxleyi* (Fig. 14).

This is a unicellular prymesiophyte *ca*. 8 microns in diameter that carries highly refractile “coccoliths” or plates composed of calcium carbonate (Fig. 14). For this reason, blooms are clearly visible in satellite images and they have been seen in the Bering Sea, the Barents Sea and on the Newfoundland Shelf (Brown and Yoder, 1994) (Fig. 15). Conditions for their proliferation seem to include a shallow mixed layer depth, and may involve a competitive advantage at high light levels and low phosphate concentrations (Tyrrell and Taylor, 1995). Most organisms of similar size do not form blooms, because they are grazed by rapidly growing microzooplankton. Grazing on *E. huxleyi* may be less efficient, however, because when grazed it produces chemicals (acrylate and dimethyl sulphide, DMS) that deter grazers (Wolfe *et al*., 1997). Mesozooplankton do consume *E. huxleyi*, but only when it reaches high concentrations (Nejstgaard *et al*., 1997).

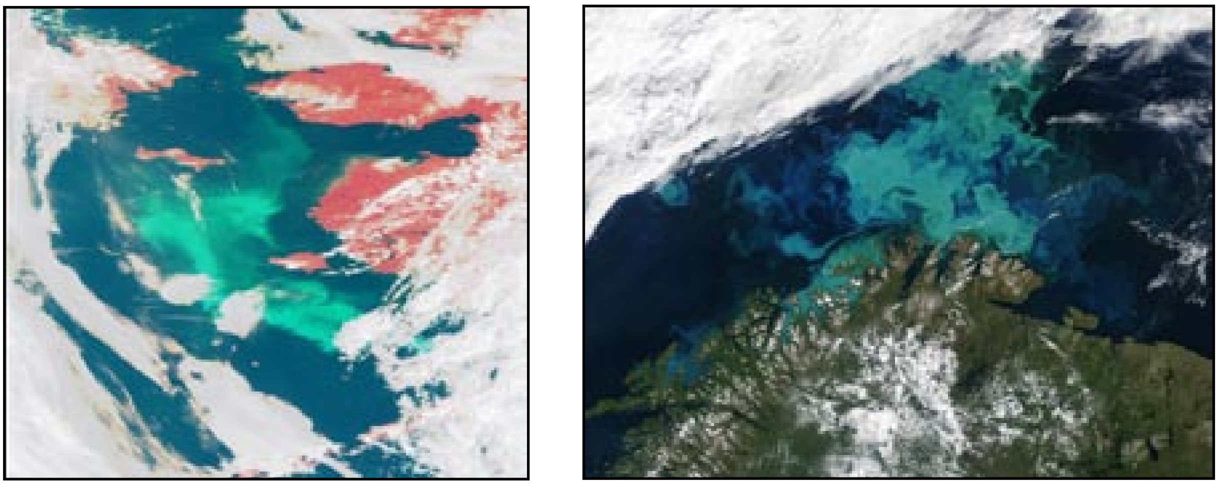


Figure 15. SeaWiFS false color images of coccolithophore blooms; left, in the Bering Sea on 20 July 1998 (from Napp and Hunt, 2001, processed by S. Zeeman, University of New England) and right, in the Barents Sea on 27 July 2004 (from http://www.redtailcanyon.com/items/310071.aspx).

The second non-diatom bloom-species is *Phaeocystis pouchetii*. This species can exist in a unicellular flagellated form (*ca*. 3 μm in diameter), but when in blooms, it is in its colonial form, with groups of cells embedded in a gel-like matrix. *Phaeocystis* blooms are frequently seen in the Bering Sea (Sukhanova *et al*., 1999), the Barents Sea (Hansen *et al*., 1996) and on the West Greenland (Stuart *et al*., 2000; Munk *et al*., 2003) and Newfoundland shelves (E. Head, pers. comm.). Conditions that favor the proliferation of *Phaeocystis* are thought to include low silicate: nitrate ratios and low light levels; *Phaeocystis* blooms sometimes occur in areas with deep mixed layers or in unstratified waters. *Phaeocystis* colonies may also accumulate because they are not readily grazed by meso- or microzooplankton.

It is unclear how *E. huxleyi* and *Phaeocystis* blooms influence the flow of carbon to higher trophic levels, although both can contribute directly to sedimentary carbon flux, *E. huxleyi* by producing and shedding coccoliths, and *Phaeocystis* by forming rapidly-sinking aggregates (DiTullio *et al*., 2000). Both species are sources of the greenhouse gas DMS. **There is a need to know more about the ecological roles of *E. huxleyi* and *Phaeocystis* in the Sub-Arctic Seas.**

Timing of development affects the ability of zooplankton to crop ice algae and the spring bloom. For example, in *C. glacialis*, grazing by females on ice algae may increase egg production rates or extend the period over which eggs are produced, and early spawning may allow the offspring to feed on ice-algal blooms sloughing off into the water column, thus extending their growth season (Werner and Hirche, 2001). *C. hyperboreus* offspring can develop into early copepodite stages before the water column bloom occurs, which allows them to take full advantage of blooms, which in more northern regions are often intense and of short duration. *C. finmarchicus*, by contrast, produce eggs soon after the phytoplankton bloom occurs in a given area, often at relatively low temperatures. Thus, in the northern Labrador Sea (*ca*. 60°N), the phytoplankton bloom occurs in April, co-incident with the main reproductive period of the *C. finmarchicus* population, at surface temperatures close to 1°C (Fig. 12) (Head *et al*., 2000), while in the Lower St Lawrence Estuary, ice-melt, the spring bloom, and *C. finmarchicus* reproduction all occur in June (Pluorde and Runge, 1993). **There is a need to evaluate the relative importance of ice-algae and open water blooms for transfer of energy to zooplankton in the spring.**

Over the southeastern Bering Sea shelf, *Neocalanus plumchrus* (plus *N. flemingeri*, Miller and Clemons, 1988) reproduction and development appear to be linked to spring bloom development (Vidal and Smith, 1986). However, at lower latitudes in the Sub-Arctic northeastern Pacific, the timing of reproduction in *N. plumchrus* is earlier and may be temperature-related (Batten *et al*., 2003). In the western Sub-Arctic Pacific, *N. flemingeri* from the low temperature/high food environment of the Sea of Okhotsk have larger sizes-at-stage than do those from the warmer/lower food environment of the Oyashio Current region. **In the Oyashio Current region individuals can have either a 1 or 2-year life cycle** (Kobari and Ikeda, 2001), **although how this is regulated is not known.**

On the southeastern Bering Sea shelf, ecological models of carbon flow predict that roughly 40% of the annual carbon production in the outer (warm) domain is consumed by zooplankton, while only 20% is consumed in the middle (cool) domain (Walsh and McRoy, 1986). Primary production is more-or-less the same in both areas (160 g C m^{-2} y^{-1}) and the difference in consumption is driven mainly by differences in zooplankton biomass and composition: the middle domain has lower biomass and lower grazing potential. Annual primary production rates are also similar for the (cool) Labrador Shelf (Hamilton Bank) and (warm) central Labrador Sea (130 vs.100 g C m^{-2} y^{-1}). Here, however, *Calanus* spp. biomass is similar in both areas during the phytoplankton growth season (spring, 3.7 *vs*. 5.2 g dry wgt. m^{-2}; summer 4.5 *vs*. 4.7 g dry wgt. m^{-2}) (Fig. 16), due to the influx of the large Arctic *Calanus* spp. from the north on the shelf. Preliminary calculations suggest that in both areas *Calanus* spp. may graze a large proportion of the primary production. ESSAS will investigate how the input of sedimentary material to the benthos is influenced by zooplankton abundance and grazing.

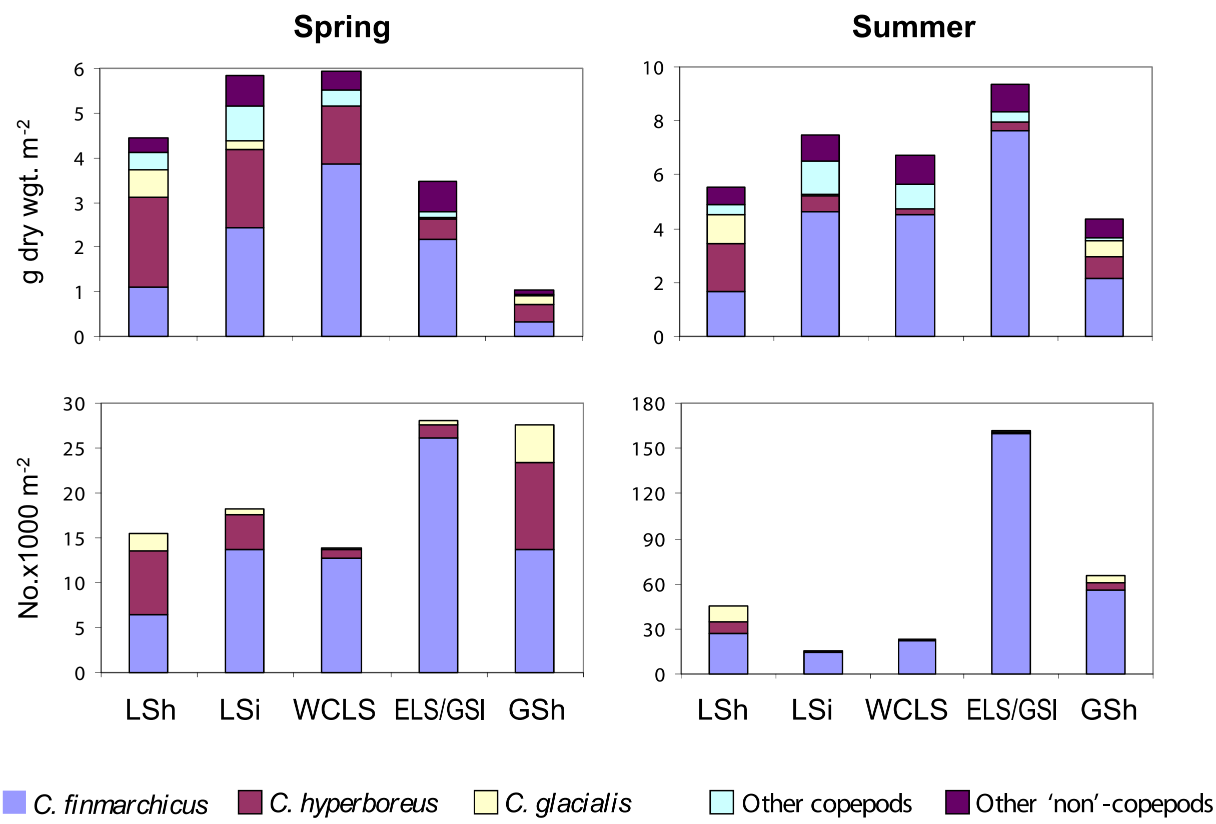


Figure 16. Biomass of mesozooplankton and the abundance of Calanus spp. For regions of the L3 section (see Figure 15) across the Labrador Sea. LSh- Labrador Shelf; LSI- Labrador Slope; WCLS- Western Central Labrador Sea; ELS/GSI- Eastern Labrador Sea/Greenland Slope; GSh- Greenland Shelf. Courtesy of E. Head, Bedford Institute of Oceanography.

In the Barents Sea the vertical flux of carbon in spring was found to be more-or-less the same in Arctic (cold) and Atlantic (warm) waters (*ca*. 200 mg C m^{-2} d^{-1}) (Olli *et al*., 2002). Ungrazed phytoplankton accounted for up to 50% of the flux and zooplankton fecal pellets, a variable but sometimes large proportion. In summer, the flux was reduced by a factor of 1.7, probably due in part to increased recycling within the near-surface layers: microzooplankton grazing accounted for a up to 97% of phytoplankton production (Verity *et al*., 2002). Despite the apparent similarity of vertical fluxes of organic material in Arctic and Atlantic waters, it appears that benthic biomass in warm areas of the Barents Sea is higher than that found in cold areas (see Hunt and Drinkwater, 2005).

Our current knowledge of the pathways of carbon flux through the lower trophic levels in the Sub-Arctic Seas is generally limited, as is our understanding of how changes in the plankton impact higher trophic levels. For example, there have been few investigations of the role of microzooplankton (e.g. Olson and Strom, 2002; Verity *et al*., 2002), or measurements of sedimentary flux. Without a better understanding of the 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 highly uncertain. Modeling and observational programs are required to address question concerning carbon flux through the lower trophic levels and to the benthos and the effects of climate on the processes involved.

3.2.1 Bottom-Up and Top-Down Control

Bottom-up control is a description of an ecosystem in which the size of a population is limited by the availability of prey, and may occur when a population is stable or in decline because of insufficient food for maximum growth or reproduction. Top-down control occurs when a population is limited by predation. Although a large portion of variability in fish year-class strength is attributed to environmental factors influencing early life history survival, predator populations can provide a dampening effect on prey population abundance at juvenile and later stages. For example, cannibalism by walleye pollock in the eastern Bering Sea explains at least part of the density-dependent patterns of recruitment seen at large adult pollock spawning stock sizes (Livingston and Methot, 1998). Multi-species modeling of predation on walleye pollock indicates that predation mortality on juvenile pollock varies across time, depending on the population levels of predators on juvenile pollock (Livingston and Jurado-Molina, 2000). Hunt *et al*. (2002a) hypothesized that, in the Bering Sea, top-down control of pollock recruitment may occur periodically when the biomass of adults is sufficiently large that cannibalism of juveniles limits recruitment (Fig. 17). Cannibalism is also observed in Atlantic cod stocks under high abundance levels and can be important as a controlling factor on recruitment (Uzars and Plikshs, 2000; Neuenfeldt and Koester, 2000).

There is a strong possibility that the degree of top-down versus bottom-up control in marine ecosystems is situational; that is, in times of increasing food supply (warm conditions), top-down control may dominate, but in times of decreasing food supply (cold conditions) bottom-up control may dominate (Fig. 17) (Hunt *et al*. 2002a). Seen on the time scale of regimes, the presence of predators may control the peaks and troughs of this alternating cycle even if, at any given moment, control may be primarily “top-down” or “bottom-up”. Predators are often long-lived species, so that in the context of climate change/ecosystem response, they introduce an internal time lag or memory in the system with a corresponding filtering effect for several years.

There are conflicting opinions about the importance of top-down control in food webs. Polis and Strong (1996) conclude that trophic cascades and top-down community regulation are relatively uncommon in nature, but that top-down effects are more likely when consumers in a particular food chain are subsidized with energy from outside that food chain. This subsidy allows consumer population and biomass to increase and potentially depress the resources available to them inside the central food chain. This effect might be an important consideration in marine food webs that have migratory species or on-shelf transport of alternative prey species. Density-dependence in the functional

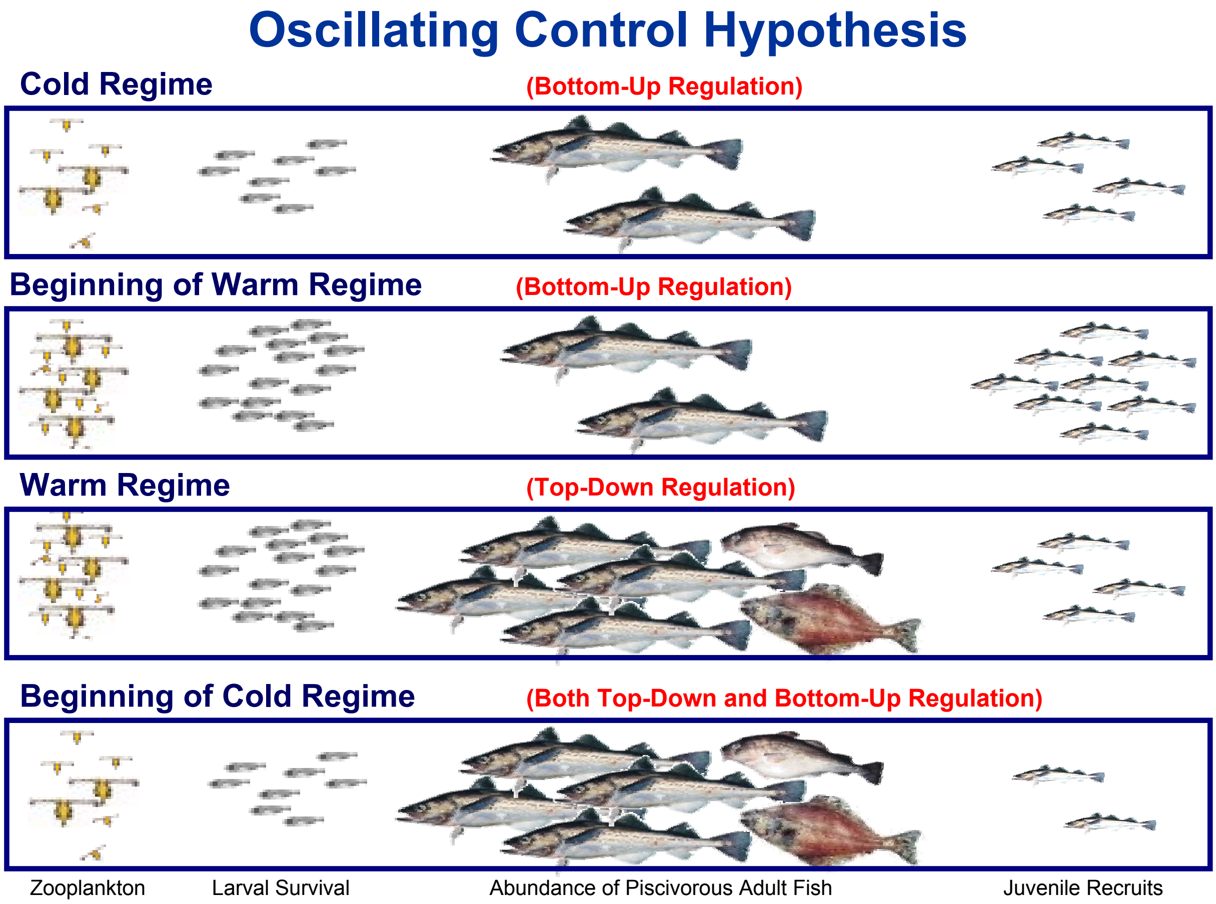


Figure 17. Hypothesized relationship between climate regimes and the production potential for Bering Sea. After a prolonged period of cold years with low production of copepods, recruitment should be limited from the bottom-up (top panel). When warm conditions occur, there are expected to be an abundance of zooplankton for larval and juvenile fish, and recruitment should be strong (second panel). However after a period of strong recruitment the number of cannibalistic adults should build up and recruitment should be top-down limited (third panel). Upon return to cold conditions after a prolonged period of warm years, pollock recruitment should be particularly weak, as there will be both bottom-up and top-down limitation (bottom panel). (After Hunt *et al.*, 2002a)

response of predators may be a stabilizing force in food webs (Murdoch and Oaten, 1975), and competition between predators may play the same role. A relatively constant amount of piscivory, but alternation in the dominant predators in the system, has been noted in the northeast Atlantic (Link and Garrison, 2002). Changes in the piscivore populations in the eastern Bering Sea may be occurring, but without synoptic diet data and understanding of predator functional responses, it is difficult to assess the degree of predator control in the system. **The potential for alternation between top-down and bottom-up control has also been explored for the Barents Sea and is being studied for West Greenland, but elsewhere in the Sub-Arctic Seas, the potential for climate variability to affect control mechanisms has yet to be explored.**

Removal of top predators by fisheries may cause trophic cascades that could mask the potential effects of climate change on marine ecosystems. In particular, severe fishing pressure on stocks could decouple those fish stocks from their prey. This decoupling might apply only to the adult biomass, or it might also include a decoupling of pre-recruits and their prey. To assess the impacts of fishing on components of marine ecosystems, ESSAS could take advantage of time series that include abrupt beginnings or ends to fishing. However, for the most part, **ESSAS will have to depend on modeling to assess how unfished ecosystems might have appeared, and how fisheries removals may have altered the way that ecosystems respond to climate change.**

The economies of coastal communities of the Sub-Arctic Seas are generally highly dependent on marine resources, and are thus very sensitive to changes in the productivity and structure of their marine ecosystems. For example, the collapse of the cod fishery on the Newfoundland/Labrador Shelf led to devastating socio-economic effects in the region: large-scale unemployment and emigration of a significant proportion of the younger members of the population. The subsequent development of the lucrative shrimp and snow crab fisheries has benefited far fewer people. Ecosystem models developed in ESSAS will be used to predict climate and human (fishing) induced changes of the marine ecosystems. One of the goals of ESSAS will be to facilitate communication between those making such predictions and social scientists trying to anticipate the likely effects on local communities and their economies.

The Sub-Arctic Seas are also likely to come under increased use by groups other than the harvesters of their living resources. Examples that are already known include oil and gas development in the Sea of Okhotsk and increased shipping along the Newfoundland/Labrador Shelf due to nickel mining in Labrador. Other activities that might be anticipated to increase include ecotourism and commercial cargo traffic as northern transportation routes become ice-free for longer periods of the year. These human activities are likely to bring increased prosperity to some local communities, and may lead to a lessening dependence of their economies on their living marine resources, but they also bring risks to the marine ecosystems, e.g. of chemical pollution and of marine mammal/ship encounters.

3.3 Questions Related to Biophysical Coupling and its Effects

a) ***What is the relative importance of advection of nutrients and biological material as compared to local processes in determining ecosystem structure and function?***

Warm, nutrient rich waters are advected northward into the Sub-Arctic Seas on the eastern sides of the Atlantic and Pacific while cold relatively nutrient poor waters are advected southward on the western sides of these oceans. Variability in advective fluxes might thus be expected to influence overall primary production rates, although in some areas benthic regeneration and seasonal mixing of the water column may provide the main source of nutrients. We need to understand the balance between these nutrient supply processes, since they will respond differently to different physical forcing. The mesozooplankton grazers that transfer organic material to higher trophic levels are also advected into the Sub-Arctic Seas. Their presence probably requires annual replenishment, but the roles of *in situ* growth versus production advected from elsewhere and the impact of variable advective fluxes are not generally well known and may vary between Sub-Arctic Seas. This problem will be approached principally through modeling studies.

b) ***How does variability in physical forcing mechanisms (temperature, sea-ice, wind, light, water movements) influence the timing, location, intensity and duration of algal blooms and the fate of primary production?***

The location and timing of ice-algal, ice-edge and water-column blooms are influenced by the extent of ice-cover, water column stability and stratification caused by ice-melt or surface warming. Mixed-layer depth, nutrient levels/supply, sedimentation and zooplankton grazing influence bloom intensity and duration. It has been hypothesized that, in the Bering Sea, cold conditions, including extensive ice-cover, favor sedimentation over pelagic grazing, and may lead to bottom-up control of fish recruitment. This hypothesis should be tested through field programs, retrospective analyses and observations.

c) How does the frequency and intensity of storm events influence primary and secondary production and the transfer of energy to higher trophic levels?

The frequency, intensity and duration of storm events influence primary production by causing vertical mixing, which can either increase rates, by introducing nutrients into the mixed-layer, or decrease rates, by deepening the mixed layer to beyond the critical depth. Storms can also disrupt the vertical distribution of zooplankton and their ability to feed and may break up aggregations that are fed upon by higher trophic levels (e.g. mammals and seabirds). In addition they may disrupt the circulation patterns (gyres) that serve to retain fish eggs and larvae in spawning and nursery areas. There has been little study of the effects of storms on Sub-Arctic marine ecosystems. We need a better understanding if we are to attempt to predict the effects of changes in the intensities and tracks of storms that are expected to occur in future. Through a combination of fieldwork and modeling, estimates of the increase in primary and secondary production and biomass accumulation, as a function of the number and intensity of storms will be sought. Through time series of storm tracks, size and intensity, estimates of the effects of such storms on the overall productivity of Sub-Arctic Seas will be estimated.

d) How is energy flow at lower trophic levels controlled and directed?

Phytoplankton species composition may impact the direction of energy flow. Diatom blooms are grazed readily by mesozooplankton, *Phaeocystis* and *E. huxleyi*, less readily. Do blooms of these latter organisms result in enhanced fluxes of organic matter to the benthos? Also, microzooplankton may consume a large proportion of primary production, especially after the spring bloom. At this time, when phytoplankton levels are low, mesozooplankton populations are still growing. To what extent does their growth depend on their grazing on microzooplankton?

e) Does a smaller proportion of primary productivity sediment to the benthos in northern regions of the North Atlantic Sub-Arctic Seas as compared with the North Pacific Sub-Arctic Seas?

There is a large biomass of Arctic copepods in the northern regions of the North Atlantic Sub-Arctic Seas that is apparently absent from the Northern Bering Sea. In the North Atlantic Sub-Arctic Seas, do these grazers, which may be adapted to utilize ice-algae and to graze on intense, short-lived blooms, prevent the development of a highly productive benthic biomass, such is found on the northern Bering Sea Shelf?

f) How does variability in the timing, location, intensity and duration of algal blooms influence production in the mesozooplankton?

The ecologically significant copepods of the Sub-Arctic Seas have annual life cycles, with a dormant over wintering period. In the deep waters of the Labrador Sea, early intense blooms stimulate early reproduction and high survival success. Later blooms that are of low intensity are accompanied by high reproductive rates, but low survival success. To what extent is this pattern true for other deep-water regions of the Sub-Arctic Seas (e.g. southern Bering Sea, Icelandic waters, Oyashio Current region, etc.)? Does this pattern also apply on the shelves? Is it related to differences in predation rates on copepod eggs and nauplii (including cannibalism)?

g) What regulates recruitment of key species of fish and the structure of fish communities?

The springtime supply of over-wintered large-bodied copepods and the timing of their reproduction affect the recruitment of key fish species. The springtime supply of copepods depends on the over-wintering biomass and advection. The timing of reproduction is influenced by spring bloom dynamics, and may be influenced by temperature. Predation by invertebrates (e.g. jellyfish) and cannibalism (e.g. pollock) may also affect recruitment, and physical processes that could transport larval fish to an unfavorable environment, or affect the integrity of a breeding stock may also be important. Within ESSAS, we will focus upon environmental conditions affecting recruitment, in particular identifying those that lead to good recruitment. This will be done through a combination of statistical analyses and modeling.

SECTION IV. ECOSYSTEM RESPONSE TO CLIMATE VARIABILITY: INTEGRATION AND FORECASTING ACROSS SPACE AND TIME SCALES

It is clear that retrospective analyses and data collection alone will never be sufficient to provide the answers to questions about the long term impacts of global change, or any predictive capacity. Instead, they will be employed in combination with numerical models. The comparative approach will highlight model features and processes that are common or different between the Sub-Arctic Seas and greatly enhance our understanding of these valuable marine ecosystems and their likely responses to climate change.

4.1 Integration Across Space and Time Scales

Scientific disciplines work at a variety of temporal and spatial scales, from that of global climate change at geological time scales or longer, to physiological processes or activities of plankton, or even viruses and bacteria, that occur in milliseconds over millimeters in distance. Concepts of scale are particularly important for developing model frameworks. They define the context for local, regional and large-scale interactions, integration of single species processes into multiple species models, and up-scaling and downscaling of climate effects. At the ecosystem level, the space and time scales associated with physical and biological oceanographic processes in Sub-Arctic marine ecosystems encompass many orders of magnitude (Figures 2 and 8).

Attempts to understand how marine ecosystems react to climate and human influences pose huge sampling problems for analysis at the scale of whole ecosystems. Current understanding suggests that the impacts of large-scale climate shifts are not uniform, but seem to be temporally and spatially distributed in ways that are not fully understood. Two aspects may be important contributors to this uncertainty: (1) variability in the timing, location, and duration of primary productivity each year as influenced by weather—a kind of “timing is everything” issue; and (2) spatial patchiness on a variety of length scales in forage stocks responding locally to changing temperature, salinity, currents, and other ocean characteristics. This is a key rational as to why ESSAS needs to study a number of different environments at different times to fully understand the ecological ramifications of climate-driven change, and that care must be taken in generalizing about cause and effect within the region.

Understanding the consequences of different life-history patterns of organisms is important for integration across time and space scales. Concepts of scale are particularly important for developing model frameworks. The challenge is to be able to scale down from the climate events to the impact of physical aspects of the environment on the lives of single organisms, and to scale up from organism-level processes, including life-history characteristics, to the responses of populations and ecosystems.

With the models developed within and during ESSAS, it should be possible to separate the impact of climate from those of more direct anthropogenic forcing (fisheries, pollution etc.). The types of models and specific modeling approaches that might be useful to deal with these types of problems are difficult to identify at this early stage, since there are no standard accepted ways to model top-down *vs*. bottom-up ecosystem effects. However, it is safe to say that a complete suit of modeling approaches will be utilized, similar to a model taxonomy exercise depicted in Figure 18. Added to these approaches would be mechanistic, process-oriented lower trophic level (LTL) models (i.e., nutrient-phytoplankton-zooplankton, NPZ, models), LTL models embedded in general circulation models (GCM), and hierarchically nested LTL-GCM models coupled with fisheries individual-based models (IBM). The appropriate modeling approach will depend on the question or hypothesis posed, skill of the modeling team, and data availability. Ideally the same modeling approach would be applied to each ESSAS region so that differences in model output arise from the suit of physics and biology unique to each region and not to model architecture.

SECTION I: RATIONALE FOR THE ESSAS PROGRAM

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

1.1 Introduction

A comprehensive scientific study of Sub-Arctic Seas is needed to provide the basis for understanding how global change may impact their ecosystem structure and productivity. The Sub-Arctic Seas, including the Sea of Okhotsk, the Oyashio Shelf, the Bering Sea, the Barents and Nordic seas, the waters of Iceland and Greenland, the Newfoundland/Labrador Shelf, the Gulf of St. Lawrence and Hudson Bay (Fig. 1), support some of the world's most productive fisheries, most of which are based on cod or pollock, as well as immense populations of marine birds and mammals and subsistence activities. All but the Sea of Okhotsk exchange water with the Arctic.

Figure 1. Location of the regions (in red) referred to as the Sub-Arctic Seas in this document. Included are regions that are influenced by Arctic waters, that are seasonally ice-covered or impacted by the seasonal advection of sea ice, and that have important stocks of gadoid fish. The presence of capelin could also be a marker. Not all regions have all of these characteristic components, but most share most of them.

When water flows through the Sub-Arctic Seas between the Arctic Ocean and the temperate seas, its heat, salt and freshwater content are modified. These changes influence the strength of the permanent halocline in the Arctic Ocean and the amount of freshwater and heat in its upper layers (e.g. Aagaard and Carmack, 1994; McLaughlin *et al*., 1996; Kristmannsson, 1998; Valdimarsson and Malmberg, 1999; Hansen and Østerhus, 2000; Orvik and Niiler, 2002; Jónsson and Briem, 2003; Reverdin *et al*., 2003; Jónsson and Valdimarsson, 2004). The Sub-Arctic Seas also modify Arctic water as it flows south towards the North Atlantic and North Pacific Oceans. These changes provide a feedback to global climate change.

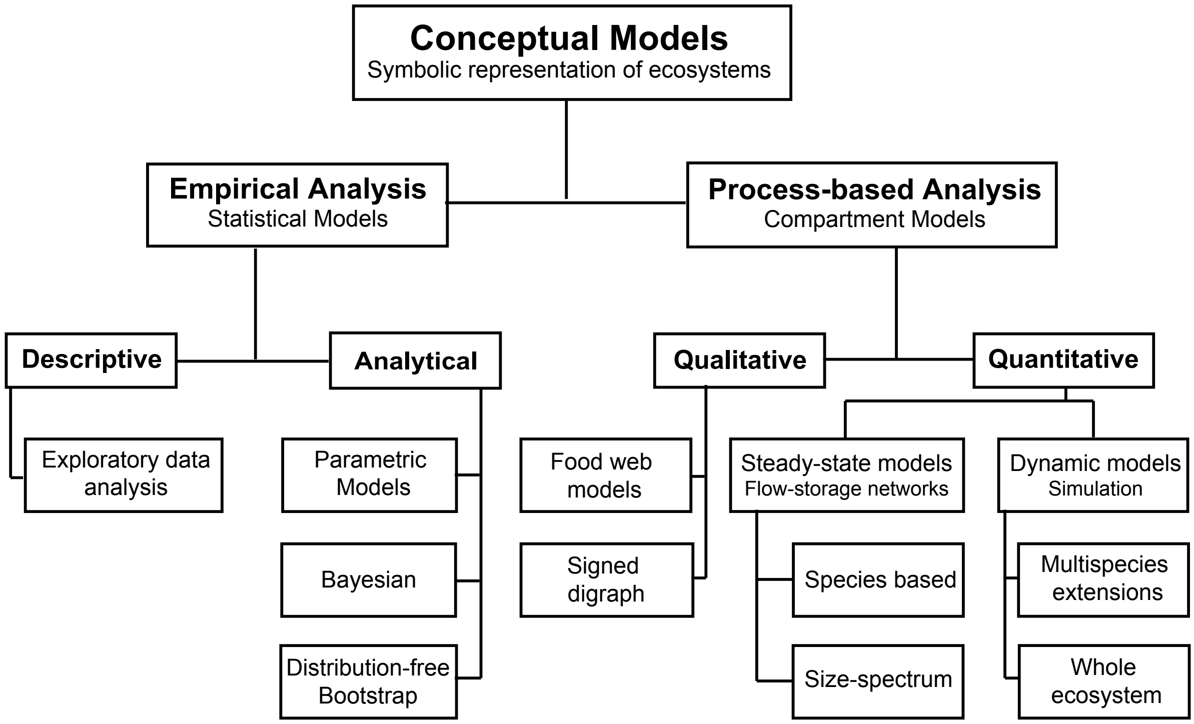


Figure 18. Taxonomy and model classification used to describe of model types that address top-down ecosystem effects (i.e., fishing and predation). From Whipple *et al.* (2000).

4.2 Modeling Approaches

One of the ultimate goals of the ESSAS Program will be a coupled modeling system that can be used to understand, predict and forecast Sub-Arctic marine ecosystems. Such a modeling system would include components for realistically simulating the ocean circulation, sea-ice conditions, water optical properties, and water mass properties. This model in turn would be coupled to models that provide predictive simulations of the lower trophic levels, including primary and secondary productivity, and the linkages of these to the upper trophic levels. Large-scale ocean general circulation models (OGCMs) provide an approach for specifying boundary conditions for regional and local ecosystem models that are configured at finer resolutions. These regional models would then allow inclusion of local processes as well as feedbacks with the larger-scale regional to climate change. Properly nested models within larger-scale OGCMs allow downscaling of large-scale information to local ecosystem models, which in turn upscale local information to the larger-scale OGCM. Coupled physical (e.g. sea ice-ocean) models exist and can be further improved with more realistic physical forcing functions, including sea ice, tides, advection, shelf-basin exchanges, and freshwater runoff. Likewise, ecosystem models exist which, if provided with realistic and high-resolution initial conditions and physical forcing coupled with better process formulations and parameterizations, should yield realistic simulations of food web dynamics and variability.

Developing the ability to predict how climate change will affect Sub-Arctic marine ecosystems will not be easy, but neither was the development of long-range weather forecasting. Recent advances in synoptic observational and numerical modeling capability make ecosystem prediction a realistic goal. Marine organisms are influenced by a variety of currents, frontal regions, eddies, water temperatures, and salinities. These conditions define the ocean state and reflect the influence of weather and climate. However, one of the largest challenges hampering our ability to develop predictive tools useful for forecasting is the current lack of knowledge about which biological interactions (predation, competition, top down vs. bottom up control, match-mismatch, etc.) structure Sub-Arctic ecosystems. Thus it is critical that the ESSAS Program develop a hierarchical modeling strategy to ensure that smaller time and space scales of biological interactions are adequately integrated with larger-scale physical processes. Thus, to construct successful ecosystem models, we must understand existing biological and physical models, identify critical space and time scales, identify missing data of importance, and provide data assimilation and analysis strategies. It is also essential that we understand how changes in adjacent ecosystems affect the system of interest.

Models provide a framework for testing hypotheses that are not immediately amenable to experimental testing or observation. They can also highlight the parameters and processes to which a system is most sensitive, thereby pointing to the ecosystem elements that must be the focus of experimental or observational studies. The efficacy of the models can be tested through a variety of approaches and the ESSAS program will strive to provide the measurements and data types that will be needed to calibrate and verify the modeling system developed for the regional polar marine ecosystems.

An often-overlooked benefit of models is that they can facilitate communication among researchers, managers, and the public.

4.3 Impacts of fishing: linking bottom-up with top-down dynamics

Another important goal of the ESSAS modeling will be to differentiate the effects of fishing from natural variability, thus allowing investigation of how fishing and other anthropogenic effects might interact with those of natural variability. The relative importance of top-down and bottom-up forcing may depend on what aspects of a marine ecosystem we focus upon. In issues of recruitment, especially where the relationship between spawner biomass and recruits may be weak, climate, advection and other bottom-up forcing may play a more important role in determining fish recruitment than fishing. However, when examining stocks where there is a tight spawner-recruit relationship, or where the focus is on the role of adult fish in the ecosystem, then fisheries takes will likely play a more dominant role than climate. Alternatively, in modeling the effects of climate on marine ecosystems, we can start with the systems that we have, many of which have greatly depleted stocks. Given that starting point, we can then ask, "How will climate change affect the productivity of this system?" Thus, in modeling the relative importance of climate and fishing on marine ecosystems, it will be essential to identify which aspects of the system we are trying to understand.

Although the coasts of the Sub-Arctic Seas are sparsely populated, human impacts, e.g. fishing and whaling, have major effects on their ecosystems (e.g. OSPAR Commission, 2000). Because of the magnitude of these anthropogenic impacts, there is a continued need to separate the effects of fishing and hunting from climate-driven variability in the development of science-based input to management. For example, there is a considerable tradition in modeling impacts of fishing in an ecosystem context in the Barents Sea (e.g. Bogstad *et al*., 1995, 1997; Tjelmeland and Bogstad, 1998 a,b), including links to economic models (Eide and Flaaten, 1998). Eide and Heen (2002) also discussed the possible effects of global warming in the Barents Sea on the Barents Sea fisheries, using a multispecies, multi-fleet model and economic input-output modeling. They concluded: "Even though global warming may have a great potential for altering catches, profitability, employment and income generation from the cod fisheries (for better or for worse), changes in management may even have a bigger potential in influencing the results."

In Icelandic waters, several fish stocks have recently been below precautionary reference points (OSPAR Commission, 2000). Possible causal factors include: an excessively high fishing capacity; historically, a fishing mortality that has been too high; and a one-sided emphasis on input- or output-based fisheries management (Stefánsson, 2003). It is hypothesized that the "carrying capacity of Icelandic waters is probably about 2-3 times greater than needed to sustain the biomass of commercial species in the area at the present time" (ACIA, in press). Spatially explicit, dynamic models of commercially exploited marine populations and their interactions that allow estimation of the impact of fisheries on these stocks are available (Stefánsson and Pálsson, 1997; Stefánsson, 2004). In principle, these models can, be linked to models of lower trophic level dynamics such as those being used or developed within GLOBEC and ESSAS.

In Greenland, multispecies models of intermediate and higher trophic levels of the “Ecopath with EcoSim” type are available (Bundy *et al*., 2000, Pedersen and Zeller, 2001, Jarre, 2002). For West Greenland, spatial considerations are presently being built into these models (Jarre *et al*., in prep.). These models cannot at present be linked to models of lower trophic level dynamics. However, as an initial step, and while more complex models are being developed, environmental forcing can be linked to EcoSim model dynamics as forcing functions.

Livingston and Jurado-Molina (2000) constructed a Multi-Species Virtual Population Analysis (MSVPA) model for the eastern Bering Sea for the period 1979–1995. The main conclusion from this analysis was that predation is an important process influencing pollock recruitment (see also Fig. 17), but improved understanding will require (i) the development of spatially-explicit models of predation, and (ii) the establishment of linkages to climate-related models allowing examination of the factors influencing larval survival.

Annual migrations are without doubt an important characteristic of Sub-Arctic ecosystems. In comparing two spatial models (Multspec and Bormicon) with an aggregated model (MSVPA), the ICES Multispecies Assessment Working Group discussed that, for many applications, it might not be necessary to include spatial structure in a multispecies model if some way could be identified to reduce prey vulnerability to predation for at least a part of the year (ICES, 1996). Nevertheless, recent results indicate the need to include spatial interactions into ecosystem models (Livingston and Jurado-Molina, 2000; Hinckley *et al*., 2001; ICES, 2003). In addition, and with respect to fisheries management, model results are likely to be best acceptable to stakeholders if they reflect properties of the natural system (Degnbol, 2003). The possibility of illustrating changes in spatial distribution and species/groups overlap imposed through altered transport and/or migration routes, e.g. due to climate change, may therefore counterbalance the additional difficulties in development and testing posed by more complex models.

Top-down issues are tackled by several (predominantly fisheries sector) research institutes and multispecies models of the intermediate and higher trophic levels are available, as mentioned above. In line with the approach suggested by deYoung *et al*. (2004), **ESSAS will establish working links to these institutes and their scientists in order to work towards improved coupling of models of hydrodynamics and lower trophic level dynamics (notably plankton) on the one hand to models of intermediate and upper trophic level dynamics, including those of marine birds and mammals, on the other.**

4.4 Comparative Analyses

Ecosystem comparison is an integrating activity common to all GLOBEC regional programs (see GLOBEC, 1999). Comparative studies of the Sub-Arctic marine ecosystems may provide key insights into how they will respond to climate change. All of these areas are undergoing rapid change, an important component of which is caused by climate forcing (IPCC, 2001; ACIA, in press). The synthesis work needed to achieve these comparisons should start as soon as the beginning of each regional program in order to track progress, compare experiences among projects, and recognize and act upon surprise events as they occur rather than decades later (for example, shifts between “regimes” or “ecosystem states”).

The overall objectives of comparison studies between the Sub-Arctic Seas and with other regional GLOBEC ecosystem studies will be to:

- Define if similar marine ecosystem typologies (structure and functioning) occur in the different regions; and
- Synthesize the responses of these ecosystems to large-scale global changes down to regional/local changes.

Modeling is a central approach for comparative analyses of ecosystems, i.e., concerning the structures, functioning and impact responses of marine ecosystems. It is important for process and modeling studies to identify if interrelationships amongst physical and biological variables are the same in different locations, or whether certain relationships vary geographically. This will permit an opportunity to evaluate to which point the understanding of each system could be beneficial for the understanding of the other Sub-Arctic systems.

Sub-Arctic ecosystem dynamics will be modelled using biophysical models integrating marine food web and population processes at different scales. It will be important to apply similar modelling approaches for the different regions using:

- A suite of circulation models (Shelf circulation, Open ocean – shelf exchanges);
- A suite of coupled demographic – circulation models relating circulation to demographic structure in space and time;
- Coupled circulation - plankton models at various scales (meso-scale forcing, seasonal forcing, physical dynamics from meso- to regional scale).

The comparisons of ecosystem structures should be made by identifying the main internal and external variables of the system to be modeled. This step should permit identification of:

- Potential gaps in knowledge in one system compared to others;
- Comparable key species or species assemblages;
- Comparable food-web structure and trophodynamics.

The comparison of ecosystem functioning will also include different time and space scales. Process-specific model development should be accompanied by studies on parameterisation of these processes at the larger scales where their effects are emergent. Comparisons of both process-specific models and parameterisations should be realised within and among marine ecosystems. Identification of mechanisms underlying trophic transfer efficiency among trophic levels, understanding of the major differences in the spatial structure of food web, population timing (e.g. life history events of key species) and community dynamics are possible through comparative studies across ecosystem types.

Understanding and prediction of the different responses by these “ecosystem-types” from large-scale to regional and to local forcing (both natural, such as climate variability, and anthropogenic, such as fishing) is a core objective of ESSAS and GLOBEC. This objective includes:

Identifying and characterizing components of the major marine ecosystems which are likely to be affected at an early stage by global changes (i.e., early-warning indicators);

- Quantifying the historic ecosystem states and variability over the Sub-Arctic regions;
- Understanding the responses to global change of each component of the ecosystem, focusing on both zooplankton and fish;
- Integrating multidisciplinary process knowledge towards overall quantitative understanding of the ecosystem functioning;
- Using 3-D models as advanced interpolation tools (in space and time) based on sporadic observations of the ecosystems (data assimilation);
- Quantifying the future ecosystem states and variability based on future climate and fisheries scenarios;
- Using ecosystem models to identify and compare predicted and observed responses of polar marine ecosystem to global changes.

A key outcome of these comparisons is expected to be the identification of "early-warning" indicators of large-scale ecosystem changes under corresponding exploitation regimes, and the extent to which there may be similar indices among a variety of ecosystem types. Identification of potential indicators early in the ESSAS program would provide for their monitoring and assessment throughout the duration of ESSAS field and modelling activities.

Further key outputs of these syntheses should include evaluation of what the effects of changes in marine ecosystems may be to global biogeochemical processes and to human social systems.

4.5 Prediction

Numerical models are quantitative representations of our understanding of ocean ecosystem dynamics. The development of successful models of physical structure and circulation has enabled the integration of biological and physical models in the ocean (Hofmann and Lascarra, 1998). To date, our ability to forecast future states of the ecosystem has been fairly limited. Nonetheless, it now appears that the marine science community is poised to make a breakthrough in the development and application of ecosystem models, both at the regional (e.g. Stefansson, 2004; Ribergaard *et al*., 2004) and at the basin-scale (deYoung *et al*., 2004). There are many societal questions, for example the possible impact of anthropogenic climate change on marine ecosystems that require numerical modeling.

Changes in marine ecosystem can have great social and economic impact. Commercial fisheries, and fishing communities, depend on a long-term supply of marine resources. Effective management of human exploitation must be based upon sound scientific advice on possible changes in the quantity or quality of these resources. Likewise, changes in the ability of these regional seas to support the populations of seabirds and marine mammals that migrate there to forage in summer may impact other marine ecosystems where they spend the remainder of the year. Developing an ability to predict how climate change will affect these exports will allow adjustments in resource management to take advantage of improvements in resource availability and to minimize the impacts of decreases in resource availability.

It should be possible to determine the large-scale effects of climate change in Sub-Arctic Seas where it is expected that there will be substantial changes in the seasonal cycle and in the mean annual state of the physical forcing factors. Models developed through ESSAS will be useful to explore possible future states of the ecosystems in different climate warming scenarios, providing us with guidance about the potential for impacts on much longer time-scales, decadal and longer, than it is possible to infer from the measurements alone.

The first step on the path to reliable predictions is an ability to model the changes in the physical ocean features, the hydrography and stratification, which will require the development of regional models that can be coupled with the global climate models that integrate the features that regulate the large-scale climate patterns. These physical models must then be integrated with biological models that must be tested against observations to determine their capabilities and weaknesses. We must learn the limits of the models, seek to develop understanding of the potential uncertainty of the model simulations, and strive for the methodology to reduce them.

It is important that we estimate the uncertainty associated with model predictions so that we can develop appropriate responses. Different approaches to estimating uncertainty are now being considered, including applications of model ensembles to allow prediction of a range of possibilities. This approach has been used with some success by the Inter-governmental Panel on Climate Change (Houghton *et al*., 2001) and has been suggested for application to ecosystem modeling, in particular for application to issues of societal concern. While it may be difficult to predict the detailed future state of Sub-Arctic marine ecosystems, it may be possible to predict trends and changes in overall structure of marine food webs, e.g. changes from dominance by groundfish or invertebrates, in response to changes in environmental conditions.

4.6 Questions Appropriate for Modeling and Comparative Studies

Some of questions relevant to models and modeling not previously addressed are the following.

a) ***How do different models of Sub-Arctic Seas compare?***

Regional physical and ecosystem models are being produced for many of the Sub-Arctic Seas to explore the effects of climate variability and change on the ecosystem. These usually differ not only in the region they are trying to model but in terms of model resolution, formulation and parameterization. In an attempt to improve the models, comparisons will be preformed between models by applying different models to the same Sub-Arctic Sea with similar forcing. The results will be tested with observational data, where available, to assess the predictive capabilities of the models. Through such comparisons, improvement to the models will be made.

b) ***What are the effects of future climate change on the physical oceanography of the Sub-Arctic Seas?***

General Circulation Models (GCMs), and in some cases regional atmospheric models, are available that provide future climate scenarios for the Sub-Arctic Seas for the next 100 years or so. Different GCMs usually produce different results. The range of values between models provides an estimate of the uncertainties in the different variables. Using these estimates and their uncertainties, and the knowledge gained on the physical oceanographic processes and their causes, predictions will be made on the impact of climate change to the physical oceanography of the Sub-Arctic Seas.

c) ***What are the effects of future climate change on the marine ecosystems of the Sub-Arctic Seas?***

One of the ultimate goals of ESSAS is to be able to predict the effects of climate variability and change on the marine ecosystem of the Sub-Arctic Seas. Using the results from processes studies within ESSAS and predicted changes to the physical oceanography, predictions will be made on the effects of climate variability and change on phytoplankton and zooplankton and their interactions, including changes in the timing of their production cycles. In addition, the effects of climate change on fish stocks will be assessed, including possible influences on migration patterns, distribution, growth rates, larval drift and recruitment success.

d) ***How does climate variability and change coupled with fishing effort affect fish stocks in Sub-Arctic Seas?***

The changes in fish communities are a result of both fishing and climate variability. Most fisheries assessments or fisheries studies only consider the effects of one factor or the other. However, we know from experience that they act and interact together to produce the changes we observe. ESSAS will assess the combined effects of climate and fishing, by coupling predictions of climate-induced changes to fish stocks with various levels of fishing effort to model the combined effect.

In addition to the above modeling efforts, there is also the possibility of examining the socio-economic impacts of the predicted changes to the fish community. While ESSAS will undertake some research along these lines, and seek to strengthen the links between natural and social sciences, most of the social science research is expected to be carried out in other programs, e.g. UNESCO's MOST Programme, Canada's "Coast under Stress", etc.

SECTION V. PRELIMINARY ESSAS IMPLEMENTATION PLAN

5.1 Initial Symposium

As a kick-off to the ESSAS program, a multi-national Symposium on the Effects of Climate Variability on the Ecosystems of Sub-Arctic Seas is planned for May of 2005 in Victoria, British Columbia, Canada. It will be co-convened by Drs. George Hunt (USA) and Ken Drinkwater (Norway) with a Scientific Steering Committee (SSC) consisting of 18 scientists covering most Sub-Arctic Sea regions and cutting across most disciplines. It will include a combination of keynote speakers, oral presentations, posters and discussions. One of the purposes of the Symposium is to review what is known about the ecosystems of Sub-Arctic Seas and it will begin with brief summaries of different Sub-Arctic Seas. These summaries will cover similar subtopics (important physical forcing mechanisms, primary and secondary productivity, role of forage fishes, demersal to pelagic ratio of fishes, etc.) in order to help begin the comparative process. The symposium will also present recent research results and identify the knowledge gaps in ecosystem studies. It will provide a forum for presentation of results from national programs focusing on Sub-Arctic Seas and the opportunity for exchange of ideas between researchers from different Sub-Arctic Seas. Finally, it will provide a benchmark with which to gauge future progress within the program. Arrangements have been made to publish the proceedings of the meeting in a primary scientific journal. The symposium will be the major undertaking for the summary component of the ESSAS implementation plan. A 1-day ESSAS workshop will follow the Symposium to further develop and refine the implementation plan, and to develop the ways and means to begin to carry it forward.

5.2 ESSAS Program

At present, we see the implementation plan of ESSAS consisting of five main activities. These include:

5.2.1 Ecosystem Summaries

As a first step ESSAS will assemble information on each of the major Sub-Arctic Seas to facilitate comparisons between the regions. This will be achieved primarily through literature surveys. A large part of this has already taken place through the planning process for ESSAS (see Hunt and Drinkwater, 2005) or is available as results from other programs (AMAP, 1998; ACIA, in press). Completion of this task will coincide with the 2005 ESSAS Symposium, when ecosystem summaries containing similar types of information will be produced for many of the Sub-Arctic Seas. ESSAS will publish these regional summaries in a reviewed scientific journal as part of the Symposium volume. In addition, relevant time series from each of the regions will be assembled and made available on an ESSAS website.

5.2.2 Regional Studies

The purpose of the regional program is to carry out the goals of ESSAS in each of the Sub-Arctic Seas. Emphasis will be on addressing the first of the two major areas of inquiry for ESSAS, i.e. (1) determining the external forcing functions linking climate processes to the physical oceanography of the Sub-Arctic Seas and (2) the response of the ecosystem to the variability in climate. These will be achieved through a combination of integrated field studies, retrospective analyses (including time series analysis) and modeling. Although climate will be the primary focus, it is recognized that major impacts to the ecosystem are also imposed directly by humans through harvesting and hence an important aspect of the work will be to determine the relative importance of climate forcing compared to fisheries or internal ecosystem dynamics. There will also be an attempt to fill in the gaps of knowledge identified during the review process.

The regional work will be mainly undertaken within national programs. Important within this context are the large-scale projects, some of which are completed (MARE COGNITUM on the Norwegian Sea), some that are presently underway (ECOBE in the Barents Sea), and others that have not started but are well along in the planning stages (BEST in the Bering Sea, ECOGREEN off West Greenland, BaySYS and MERICA in Hudson Bay and Japanese studies focusing upon pollock in the Oyashio Region). Other national studies that are equally important within ESSAS but not yet part of any large-scale integrated project include the research by Russia on the Barents and Bering Seas and the Sea of Okhotsk, by Japan and Korea in the Sea of Okhotsk, by Canada in the Labrador Sea, the Labrador and Newfoundland shelves and the Gulf of St. Lawrence, by Iceland in its waters and off East Greenland, by France and Germany in the Nordic and Barents Sea, by Greenland/Denmark and Germany off West Greenland, by the UK in the Nordic Seas, by Poland in the Barents Sea, and many others. It is hoped that, coordinated through ESSAS, some of these nations might develop their own research projects on their specific Sub-Arctic Sea. The research to illuminate the important ecosystem processes in Sub-Arctic Seas will proceed through a combination of retrospective analysis, field programs and modeling. Satellite imagery will be used to examine both physical and biological properties and where possible, new technologies will be used to obtain data in those areas not presently sampled or at times when it has been difficult to sample. In addition, data archaeology to save time series and to put older time series into electronic format will be carried out. ESSAS will actively work to encourage and carry out such research. Data collected under ESSAS will be made available through distributed databases.

Research on the human dimension aspects of the changes will be encouraged. For example, as part of a comprehensive study of the Bering Sea, the investigations of the marine ecosystems (BEST) will be complemented by a closely associated social science program on the human dimension of ecosystem change. Work is presently underway in Norway, and will be expanded within ESSAS, to determine the economic and social impacts of climate-change-driven fisheries responses in the Barents Sea. Opportunities for similar examination of the societal impacts of changing marine ecosystems will be found in many of the Sub-arctic Seas. Also, one of the theme sessions during the inaugural Symposium is dedicated to research on the human dimension aspects.

5.2.3 Comparative Studies

This component will actively undertake comparative analyses of the Sub-Arctic Seas through a combination of statistical analyses and modeling studies. It will represent a major emphasis and undertaking of ESSAS since much of the regional work will be carried out as part of national programs. Comparisons between Sub-Arctic Seas will provide the opportunity to gather insights that could not be achieved within the regional studies. For example, the latitudinal range for the Sub-Arctic Seas extends from 45°N to 80°N and thus a comparative study offers the potential of gaining improved insights into the effects of maximum light intensity, day length and seasonality on phytoplankton production and its fate.

The comparative component of ESSAS will occur concurrently with the regional studies and will influence them. As well, the regional studies will influence what comparative studies might be worthwhile pursuing. Inter-comparison of models used in different Sub-Arctic Sea regions will be carried out including applying models developed for one region to investigate a different Sub-Arctic Sea. This component of ESSAS will also undertake the analysis of the linkages between the Sub-Arctic regions including the role played by the large-scale climate forcing such as the NAO, AO or PDO. Much of this work will be undertaken by ESSAS Working Groups that will focus on specific objectives (e.g. inter-comparison of models, or effects of large-scale forcing, or the variations in primary production between areas within individual Sub-Arctic Seas and between different Sub-Arctic Seas, etc.) and would be composed of interested participants from each of the regional studies. In addition to the natural sciences, ESSAS will encourage international meetings between natural and social scientists to discuss and address economic and social issues associated with climate effects on fisheries.

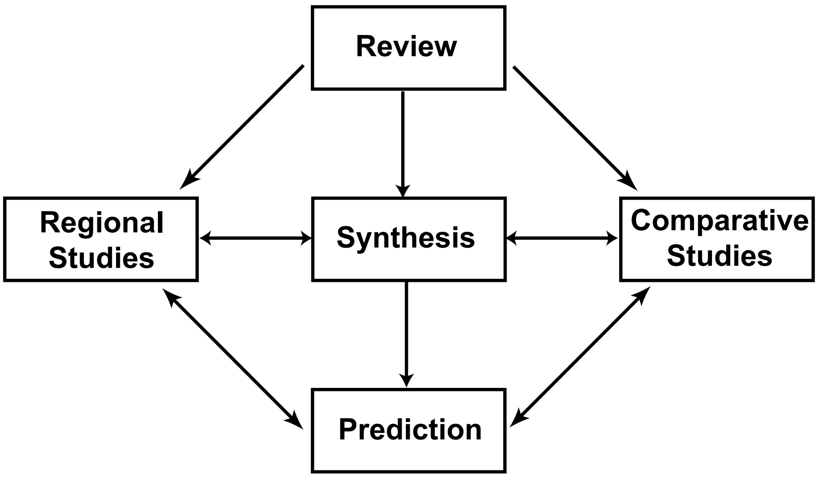
5.2.4 Prediction

A major goal of ESSAS will be predictions of ecosystem response both to climate variability in the short-term and to climate change in the longer-term. The results from components 2 and 3 will be combined with information or models of future climate variability and climate change to forecast the effects of climate on the ecosystem for the regional Sub-Arctic Seas. While these predictions will be an ultimate product from the program, the predictive modeling will be ongoing at the same time as the regional and comparative studies. The results from the predictive modeling will feed back to the regional and comparative studies. The latter will carry out the necessary research needed to improve the predictive models. The bulk of the work in this component would be directed and carried out by national programs or researchers. However, comparative studies between models will help to improve their predictive capabilities.

5.2.5 Synthesis

Synthesis will be at forefront of ESSAS even from the beginning of the program. One part of the synthesis will be the regional predictions of changes to the ecosystem under climate change. In addition, the results of the comparative studies will be used to determine what, if any, generalizations can be made regarding the structure and function of marine ecosystems in Sub-Arctic Seas and the response to climate variability and change.

The five components will be linked in the following manner.



5.3 ESSAS Structure

The organization of the ESSAS program will include a Scientific Steering Committee (SSC) and a number of Working Groups. **Initially it is anticipated that ESSAS will not have an International Project Office (IPO) and that such meetings as are deemed necessary will be organized with the help of the GLOBEC IPO. As ESSAS matures, it may well be necessary to develop an ESSAS IPO to alleviate an undue burden on the GLOBEC IPO.**

The SSC will oversee the program and ensure steady progress towards developing the ability to predict the impact of climate change on the productivity and sustainability of Sub-Arctic marine ecosystems. At the outset, it will develop synthesis goals. As the program progresses, it will ensure that the program remains focused on achieving the long-term goals of ESSAS, and to provide advice and guidance concerning methods and approaches for achieving these goals. It will form working groups (WGs) to undertake the research and work of ESSAS. The SSC will facilitate cross-disciplinary communication and coordination of the national programs through and between the WGS. The SSC will also be responsible for facilitating and coordinating interactions with other programs such as other regional GLOBEC programs (CCC, CCCC, SO, SPACC) and with other relevant programs such as ASOF, CLIVAR, etc. The ESSAS SSC will also interact with and report to the GLOBEC SSC and its International IPO and SSC. The ESSAS SSC should meet annually to assess progress toward the synthesis goals and review reports on progress and plans from the various Working Groups.

Membership of the ESSAS SSC would include scientists from each of the countries participating in ESSAS (~ 70%) and scientists who are unaffiliated with an ESSAS project (~ 30%). Countries whose scientists have been involved in the planning of ESSAS and are expected to participate include Japan, Russia, USA, Canada, Greenland, Iceland, Norway, Britain, France and Germany. We would expect the SSC to number about 12 to 15 people, and to include, ex-officio, the chairs of the Working Groups. Co-chairs would be elected from the SSC members, one each from the Pacific and Atlantic regions. Membership on the SSC would be expected to rotate, including the Co-chairs, most likely on a three or four year cycle.

The primary objectives of the Working Groups will be to develop and conduct comparative studies among the national programs and/or independent researchers, and to ensure that the data and information generated by the various programs flows freely among them. Initially, we envisage that the SSC will form WGs on Modeling, Time-Series Analysis, Atmospheric/Physical Oceanographic Processes, and Biophysical/ Trophic Coupling Processes. Other subject areas or combinations of disciplines may be identified at the initial Implementation Workshop planned for May 2005 in Victoria. Once formed, the Working Groups will be encouraged to develop long-term plans for contributing to the achievement of the ESSAS goals, to prioritize these tasks, and set goals for the timing of their completion. These Task Plans will be subject to review by the SSC, primarily to insure that they contribute to the overall goal of ESSAS. The membership of the Working Groups would include interested scientists who were willing to participate and carry out the work required. National programs would be encouraged to have representatives on each of the ESSAS Working Groups. Where no large national program exists, interested individual researchers will be sought. Chairs or Co-Chairs will be selected by the Working Groups or appointed by the SSC and will automatically become ex-officio members of the SSC. While the ESSAS SSC will ensure that the overall aims of the program will be carried through, ESSAS will be primarily a bottom-up driven science program through the Working Groups.

The Working Groups will determine how best to carry out their tasks. We anticipate that these will be through meetings or workshops. The SSC will encourage joint meetings or workshops, to facilitate communication and interaction across disciplines and working groups (e.g. the Modeling and Time-Series Analysis Working Groups could meet together). Working Groups would be expected to meet at least once every two years, and to have inter-sessional activities as appropriate.

The work of components 3 and 4 in particular will be undertaken through a variety of means. This could include a dedicated individual or group of individuals chosen by the Working Groups to conduct a particular analysis, modeling exercise, or series of measurements. It may also include Workshops to concentrate on a particular question or issue, or perhaps address questions via theme sessions in meetings such as PICES or ICES or at annual meetings of large scientific organizations.

Science meetings focused on ESSAS results will be held every three to five years, either as stand-alone Open Science Meetings, or in conjunction with other meetings of the GLOBEC community. These meetings will provide an essential opportunity for exchange of information among disciplines, national programs and working groups. In addition it is hoped that this will encourage scientists not already associated with ESSAS to share their views and knowledge with those in the ESSAS community.

5.4 Data Issues

It is anticipated that the national programs and researchers within ESSAS will collect extensive data. To help in the comparative studies, ESSAS will encourage access to these data through distributed databases, with links on an ESSAS website. In addition, the time series assembled early in the program also will be made accessible on the ESSAS website. In addition to observational data, model data will also be considered for web distribution, where thought useful. The Working Groups and the SSC will work towards ensuring that the data collected in different regions are comparable, through comparable methods and techniques, intercalibration, and similar formats.

5.5 Communications

An ESSAS website will be established as a means of communication between the participants of the ESSAS and also to inform the outside community of the ongoing activities and results of the work.

SECTION VI. LITERATURE CITED

ACIA (Arctic Climate Impact Assessment). 2004. Impacts of a warming Arctic. Arctic climate impact assessment. Cambridge University Press, Cambridge, 139pp.

ACIA (Arctic Climate Impact Assessment). In press. Arctic Climate Impact Assessment Report.

Aagaard, K. and E.C. Carmack. 1994. The Arctic Ocean and climate. p.33-46. In: O.M. Johannessen, R.D. Muench and J.E. Overland (Eds.). The Polar Oceans and their Role in Shaping the Global Environment. Geophysical Monographs Series 85, AGU, Washington, DC, USA.

Aagaard, K. and R.A. Woodgate. 2001. Some thoughts on the freezing and melting of sea ice and their effects on the ocean. Joint Institute for the study of the Atmosphere and Ocean (JISAO), Contribution 679, 15pp.

Alexander, V., S.M. Henrichs and H.J. Niebauer. 1996. Bering Sea ice dynamics and primary production. Proceedings of the NIPR Symposium. Polar Biology 9: 13-25.

AMAP (Arctic Monitoring and Assessment Programme). 1998. AMAP Assessment Report: Arctic Pollution Issues. Arctic Monitoring and Assessment Programme, Oslo, 859pp.

Andersen O.G.N. 1989. Primary production, chlorophyll, light, and nutrients beneath the Arctic sea ice. p.147-191. In: Y. Herman (Ed.), The Arctic Seas. Climatology, Oceanography, and Biology. van Nostrand Reinhold, New York, USA.

Arrigo, K.R. 2003. Primary production in sea ice. p.143-183. In: D.N. Thomas and G.S. Dieckmann (Eds.). Sea Ice - An Introduction to its Physics, Chemistry, Biology and Geology. Blackwell Science Ltd., Oxford, UK.

Arzhanova, N.V. and V.L. Zubarevich. 1997a. Chemical fundamentals of biological productivity of the Sea of Okhotsk. p.86-92. In: Complex Investigations of the Sea of Okhotsk Ecosystem. Moscow, VNIRO. [in Russian]

Arzhanova, N.V. and V.L.Zubarevich. 1997b. The seasonal variations in the nutrient stocks in the Sea of Okhotsk as a basis for the estimation of phytoplankton production. p.92-98. In: V.V. Sapozhnikov (Ed.). Complex studies of ecosystem of the Sea of Okhotsk, VNIRO, Moscow. [in Russian]

Batten, S.D., D.W. Welch and T. Jonas. 2003. Latitudinal differences in the duration of development of *Neocalanus plumchrus* copepodites. Fisheries Oceanography 12: 201-208.

Battisti, D.S., U.S. Bhatt and M.A. Alexander. 1995. A modeling study of the interannual variability in the wintertime North Atlantic Ocean. Journal of Climatology 8: 3067-3083.

Beamish, R.J., D.J. Noakes, G.A. McFarlane, L. Klyashtorin, V.V. Ivanov and V. Kurashov. 1999. The regime concept and natural trends in the production of Pacific salmon. Canadian Journal of Fisheries and Aquatic Sciences 56: 516-526.

Belkin, I.M. 2004. Propagation of the “Great Salinity Anomaly” of the 1990s around the Northern North Atlantic. Geophysical Research Letters 31, L08306, 10.1029/2003GL019334.

Belkin, I.M., S. Levitus, J.I. Antonov and S.-A. Malmberg. 1998. ”Great Salinity Anomalies” in the North Atlantic. Progress in Oceanography 41: 1-68.

Bertram, D.F., D.L. Mackas and S.M. McKinnell. 2001. The seasonal cycle revisited: interannual variation and ecosystem consequences. Progress in Oceanography 49(1-4): 283-307.

Bishop, J.K.B. and W.B. Rossow. 1991. Spatial and temporal variability of global surface solar irradiance. Journal of Geophysical Research 96 (C9): 16839-16858.

Bogstad, B., K.H. Hauge and Ø. Ulltang. 1995. Results of simulation studies using a multispecies model for the Barents Sea (MULTSPEC). International Whaling Commission SC/47/NA1. 33pp.

Bogstad, B., K.H. Hauge and Ø. Ulltang. 1997. MULTSPEC – A multi-species model for fish and marine mammals in the Barents Sea. Journal of Northwest Atlantic Fishery Science 22: 317-341.

Bond, N.A., J.E. Overland, M. Spillane and P.Stabeno. 2003. Recent shifts in the state of the North Pacific. Geophysical Research Letters 30: 2183, doi:10.1029/2003GL018597.

Braham, H.W., J.J. Burns, G.A. Fedoseev and B.D. Krogman. 1984. Habitat partitioning by ice-associated pinnipeds: Distribution and density of seals and walruses in the Bering Sea, April 1976. p.25-47. In: F.H. Fay and G.A. Fedoseev (Eds.) Soviet-American cooperative research on marine mammals. Vol. 1, Pinnipeds. U.S. Department of Commerce, NOAA Technical Report NMFS 12.

Brander, K.M. 1994. Patterns of distribution, spawning, and growth in North Atlantic cod: the utility of inter-regional comparisons. ICES Marine Science Symposia 198: 406-413.

Brander, K.M. 1995. The effect of temperature on growth of Atlantic cod (*Gadus morhua*). ICES Journal of Marine Science 52: 1-10.

Brodeur, R.D., C.E. Mills, J.E. Overland and J.D. Shumacher. 1999. Evidence for a substantial increase in gelatinous zooplankton in the Bering Sea, with possible links to climate change. Fisheries Oceanography 8: 296-306.

Brodeur, R.D., H. Sugisaki and G.L. Hunt, Jr. 2002. Increases in jellyfish biomass in the Bering Sea: implications for the ecosystem. Marine Ecology Progress Series 233: 89-103.

Brown, C. W. and J.A. Yoder. 1994. Coccolithophorid blooms in the global ocean. Journal of Geophysical Research 99: 7467-7482.

Buch, E. 2000. Air-sea-ice conditions off southwest Greenland, 1981-97. Journal of Northwest Atlantic Fishery Science 26: 1-14.

Buch, E., S.-Å. Horsted and H. Hovgård. 1994. Fluctuations in the occurrence of cod in Greenland waters and their possible causes. ICES Marine Science Symposia 198: 158-174.

Buch, E., S.A. Pedersen and M.H. Ribergaad. 2004. Ecosystem variability in West Greenland waters. Journal of Northwest Atlantic Fishery Science 34: 13-28.

Bundy, A., G. Lilly and P.A. Shelton. 2000. A mass-balance model of the Newfoundland -Labrador shelf. Canadian Technical Report of Fisheries and Aquatic Sciences 2310: xiv + 157pp.

Campbell, R.G., M.M. Wagner, G.J. Teegarden, C.A. Boudreau and E.G. Durbin. 2001. Growth and development rates of the copepod *Calanus finmarchicus* reared in the laboratory. Marine Ecology Progress Series 221: 161-183.

Campana, S.E., R.K. Mohn, S.J. Smith and G. Chouinard. 1995. Spatial visualization of a temperature-based growth model for Atlantic cod (*Gadus morhua*) off the eastern coast of Canada. Canadian Journal of Fisheries and Aquatic Sciences 52: 2445-2456.

Clarke, A. 2003. Costs and consequences of evolutionary temperature adaptation. Trends in Ecology and Evolution 18: 573-581.

Coachman, L.K. 1986. Circulation, water masses and fluxes on the southeastern Bering Sea shelf. Continental Shelf Research 5: 23-108.

Colbourne, E.B. and J.T. Anderson. 2003. Biological response in a changing ocean environment in Newfoundland waters during the latter decades of the 1900s. ICES Marine Science Symposia 219: 169-181.

Colbourne, E.B., S. Narayanan and S. Prinsenberg. 1994. Climatic changes and environmental conditions in the Northwest Atlantic, 1970-1993. ICES Marine Science Symposia 198: 311-322.

Conover, R.J. 1988. Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the northern hemisphere. Hydrobiologia 167/168: 127-142.

Cooper, L.W., J.M. Grebmeier, I.L. Larsen, V.G. Egorov, C. Theodorakis, H.P. Kelly and J.R. Lovvorn. 2002. Seasonal variation in sedimentation of organic materials in the St. Lawrence Island polynya region, Bering Sea. Marine Ecology Progress Series 226: 13-26.

Corkett, C.J. and I.A. McLaren. 1978. The biology of *Pseudocalanus*. Advances in Marine Biology 15: 1-231.

Coyle, K.O. and R.C. Highsmith. 1994. Benthic amphipod community in the northern Bering Sea: analysis of potential structuring mechanisms. Marine Ecology Progress Series 107: 233-244.

Coyle, K.O. and P.I. Pinchuk. 2002a. The abundance and distribution of euphausiids and zero-age pollock on the inner shelf of the southeast Bering Sea near the Inner Front in 1997-1999. Deep-Sea Research II 49: 6009-6030.

Coyle, K.O. and P.I. Pinchuk. 2002b. Climate-related differences in zooplankton density and growth on the inner shelf of the southeastern Bering Sea. Progress in Oceanography 55: 77-194.

Dagg, M., T.C. Royer and S.A. Macklin (Eds.). 2002. Ecology of the southeastern Bering Sea. Deep-Sea Research II 49(26), 5809-6168.

Degnbol, P. 2003. Science and the user perspective: the scale gap and the need for co-management. In: D.C. Wilson, J.R. Nielsen and P. Degnbol (Eds.). The Fisheries Co-Management Experience: Accomplishments, Challenges and Prospects. Kluwer, Amsterdam.

de Mora, S., S. Demers and M. Vernet. 2000. The effects of UV radiation in the marine environment. Cambridge University Press, Cambridge, 334pp.

deYoung, B., R. Harris, J. Alheit, G. Beaugrand, N. Mantua and L. Shannon. 2003. Detecting regime shifts in the ocean: data considerations. Progress in Oceanography 60: 143-164.

deYoung, B., M. Heath, F. Werner, F. Chai, B. Megrey and P. Monfray. 2004. Modelling ocean basin ecosystems. Science 304: 1463-1466.

Dickson, R.R., J. Meincke, S.-A. Malmberg and A. Lee. 1988. The “Great Salinity Anomaly” in the Northern North Atlantic 1968-1982. Progress in Oceanography 20: 103-151.

DiTullio, G.R., J.M. Grebmeier, K.R. Arrigo, M.P. Lizotte, D.H. Robinson, A. Leventor, J.P. Barry, M.L. VanWort and R.B. Dunbar. 2000. Rapid and early export of *Phaeocystis* antarctica blooms in the Ross Sea, Antarctica. Nature 404: 595-598.

Drinkwater, K.F. 1996. Atmospheric and oceanographic variability in the Northwest Atlantic during the 1980s and early 1990s. Journal of Northwest Atlantic Fishery Science 18: 77-97.

Drinkwater, K.F. 2000. Changes in ocean climate and its general effect on fisheries: examples from the North-West Atlantic. p.116-136. In: D. Mills (Ed.), The Ocean Life of Atlantic Salmon-Environmental and Biological Factors Influencing Survival. Fishing News Books, Oxford, UK.

Drinkwater, K.F. 2002. A review of the role of climate variability in the decline of northern cod. American Fisheries Society Symposia 32: 113-130.

Drinkwater, K.F., A. Belgrano, A. Borja, A. Conversi, M. Edwards, C.H. Greene, G. Ottersen, A.J. Pershing and H. Walker. 2003. The response of marine ecosystems to climate variability associated with the North Atlantic Oscillation. p.211-234. In: J. Hurrell, Y. Kushnir, G. Ottersen, and M. Visbeck (Eds.). The North Atlantic Oscillation, Climatic Significance and Environmental Impact, Geophysical Monograph Series 134, AGU Press, Washington, DC, USA.

Drinkwater, K.F. and G.C. Harding. 2001. Effects of the Hudson Strait outflow on the biology of the Labrador Shelf. Canadian Journal of Fisheries and Aquatic Sciences 58: 171-184.

Dunbar, M.J. 1981. Physical causes and biological significance of polynyas and other open water in sea ice. p.29-43. In: I. Stirling and H. Cleator (Eds.), Polynyas in the Canadian Arctic. Canadian Wildlife Service Service Occasional Paper 45.

Ebbesmeyer, C.C., D.R. Cayan, D.R. Milan, F.H. Nichols, D.H. Peterson and K.T. Redmond. 1991. 1976 step in the Pacific climate: forty environmental changes between 1968-1975 and 1977-1984. p.115-126. In: J.L. Betancourt and V.L. Tharp (Eds.), Proceedings of the Seventh Annual Climate (PACLIM) Workshop, April 1990. California Department of Water Resources, Interagency Ecological Studies Program Technical Report 26.

Eide, A. and O. Flaaten. 1998. Biological modelling. p.141-172. In: T. Rødseth (Ed.). Bioeconomic Multispecies Models of the Barents Sea Fisheries–New Developments. Physica-Verlag, Heidelberg, Germany.

Eide, A. and K. Heen. 2002. Economic impacts of global warming: a study of the fishing industry in North Norway. Fisheries Research 56: 261-274.

Eilertsen, H.C. 1993. Spring blooms and stratification. Nature 363: p.24.

Farman, J.C., B.G. Gardiner and J.D. Shanklin. 1985. Large losses of total ozone in Antarctica reveal seasonal ClOx/NOx interaction. Nature 315: 207-210.

Francis, R.C., S.R. Hare, A.B. Hollowed and W.S. Wooster. 1998. Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. Fisheries Oceanography 7: 1-21.

Frank, K.T., J.E. Carscadden and J.E. Simon. 1996. Recent excursions of capelin (*Mallotus villosus*) to the Scotian Shelf and Flemish Cap during anomalous hydrographic conditions. Canadian Journal of Fisheries and Aquatic Sciences 53: 1473-1486.

GLOBEC. 1999. Global Ocean Ecosystem Dynamics (GLOBEC) implementation plan. GLOBEC Report 13: 194pp.

Goddard, S.V., M.M. Kao and G.L. Fletcher. 1992. Antifreeze production, freeze resistance, and overwintering of juvenile northern Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 49: 516-522.

Goddard, S.V., M.H. Kao and G.L. Fletcher. 1999. Population differences in antifreeze production cycles of juvenile Atlantic cod (*Gadus morhua)* reflect adaptations to overwintering environment. Canadian Journal of Fisheries and Aquatic Sciences 56: 1991–99.

Gradinger, R. 1996. Occurrence of an algal bloom under Arctic pack ice. Marine Ecology Progress Series 131: 301-305.

Grebmeier, J.M. and L.W. Cooper. 1995. Influence of the St. Lawrence Island polynya on the Bering Sea benthos. Journal of Geophysical Research 100: 4439-4460.

Grebmeier, J.M. and K.H. Dunton. 2000. Benthic processes in the Northern Bering/Chukchi Seas: status and global change. p.80-93. In: H.P. Huntington (Ed.), Impacts of Changes in Sea Ice and Other Environmental Parameters in the Arctic, Marine Mammal Commission Workshop, Girdwood, Alaska, 15-17 February 2000. Marine Mammal Commission, Bethesda, Maryland.

Halvorsen, E., K.S. Tande, A. Edvardsen, D. Slagstad and O.P. Pedersen. 2003. Habitat selection of overwintering *Calanus finmarchicus* in the NE Norwegian Sea and shelf waters off Northern Norway in 2000-02. Fisheries Oceanography 12: 339-351.

Hamre, J. 2003. Capelin and herring as key species for the yield of north-east Arctic cod. Results from multispecies model runs. Scientia Marina 67: 315-323.

Hansen, B., S. Christiansen and G. Pedersen. 1996. Plankton dynamics in the marginal ice zone of the central Barents Sea during spring: carbon flow and structure of the grazer food chain. Polar Biology 16: 115-128.

Hansen, B. and S. Østerhus. 2000. North Atlantic Nordic Seas exchanges. Progress in Oceanography 45: 109-208.

Hansen, P.M. 1949. Studies on the biology of the cod in Greenland waters. Rapports et Proces-verbaux des Reunions. Conseil International pour l'Exploration de la Mer 123: 1-83.

Hare, S.R. and R.C. Francis. 1995. Climate change and salmon production in the northeast Pacific Ocean. In: R.J. Beamish (Ed.), Climate Change and Northern Fish Populations. Canadian Special Publication of Fisheries and Aquatic Sciences 121: 357-372.

Hare, S.R. and N.J. Mantua. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Progress in Oceanography 47: 103-146.

Head, E.J.H., L.R. Harris and R.W. Campbell. 2000. Investigations on the ecology of *Calanus* spp. in the Labrador Sea. I. Relationship between the phytoplankton bloom and reproduction and development of *Calanus finmarchicus* in spring. Marine Ecology Progress Series 193: 53-73.

Hegseth, E.N. 1992. Sub-ice algal assemblages of the Barents Sea: species composition, chemical composition, and growth rates. Polar Biology 17: 235-241.

Hegseth, E.N. 1998. Primary production of the northern Barents Sea. Polar Research 17: 113-123.

Hegseth, E., H. Svensen and C. von Quillfeldt. 1995. Phytoplankton in fjords and coastal waters of northern Norway: environmental conditions and dynamics of the spring bloom. p.45-72. In: H.R. Skjoldal, C. Hopkins, K.E. Erikstad and H.P. Leinaas (Eds.), Ecology of fjords and coastal waters, Elsevier, Amsterdam.

Heinle, D.R. 1981. Chapter 4: Zooplankton. In: F.J. Vernberg and W.B. Vernberg (Eds.). Functional Adaptations of Marine Organisms. Academic Press, New York, NY, USA.

Highsmith, R.C. and K.O. Coyle. 1990. High productivity of northern Bering Sea benthic amphipods. Nature 344: 862-864.

Hinckley, S., A.J. Hermann, K.L. Mier and B.A. Megrey. 2001. Importance of spawning locations and timing to successful transport to nursery areas: a simulation study of the Gulf of Alaska walleye pollock. ICES Journal of Marine Science 58: 1042-1052.

Hochachka, P.W. and G.N. Somero. 1973. Strategies of Biochemical Adaptation. W.B. Saunders, Philadelphia, USA.

Hoffman, E.E. and C.M. Lascarra. 1998. Overview of interdisciplinary modeling for marine ecosystems. p.507-540. In: K.H. Brink and A.R. Robinson (Eds.), The Sea, Volume 10. Wiley and Sons.

Hollowed, A.B., S.R. Hare and W.W. Wooster. 2001. Pacific Basin climate variability and patterns of northeast Pacific marine fish production. Progress in Oceanography 49: 257-282.

Horner, R.A. 1985. Sea Ice Biota. CRC Press, Boca Raton, 214pp.

Houghton, J.T., Y. Ding, D.J. Griggs, M. Noguer, P.J. van der Linden and D. Xiaosu (Eds.). 2001. Climate Change 2001: The Scientific Basis, Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK 944pp.

Hunt, G.L., Jr., C. Baduini and J. Jahncke. 2002b. Diets of short-tailed shearwaters in the southeastern Bering Sea. Deep-Sea Research II 49: 6147-6156.

Hunt, G.L., Jr and Drinkwater, K.F. 2005. Background on the climatology, physical oceanography and ecosystems of the Sub-Arctic Seas. Appendix to the Science Plan. GLOBEC Report 20, viii, 96pp.

Hunt, G.L., Jr. and P.J. Stabeno. 2002. Climate change and control of energy flow in the southeastern Bering Sea. Progress in Oceanography 55: 5-22.

Hunt, G.L., Jr., P. Stabeno, G. Walters, E. Sinclair, R.D. Brodeur, J.M. Napp and N.A. Bond. 2002a. Climate change and control of the southeastern Bering Sea pelagic ecosystem. Deep-Sea Research II 49: 5821-5853.

Huntley, M.E. and M.D.G. Lopez. 1992. Temperature-dependent production of marine copepods: a global analysis. American Naturalist 140: 201-242.

ICES (International Council for the Exploration of the Sea). 1996. Report of the Multispecies Assessment Working Group. ICES Council Meeting Papers, CM 1996/Assess:3. 183pp.

ICES (International Council for the Exploration of the Sea). 2003. Report for the Study Group on Multispecies Assessments in the North Sea. ICES Council Meeting Papers, CM 2003/D:09, 99pp.

IPCC (International Panel on Climate Change). 2001. Climate Change 2001: The Scientific Basis. Cambridge University Press, Cambridge, UK. 882pp.

Jarre, A. 2002. Quantitative ecosystem indicators for fisheries management. p.47-48. In: A. Jarre. (Ed.) Workshop “Ecosystem West Greenland”, Greenland Institute of Natural Resources, 29 November–3 December 2001: A stepping stone towards an integrated marine research programme. Inussuk, Arctic Research Journal 2002-1, p.99. (Abstract)

Jarre, A., K. Wieland, R.P. Frandsen and M. Storr-Paulsen. In prep. Trophic models of the marine ecosystem off West Greenland, 1995-2000.

Jensen, Ad.S. 1939. Concerning a change of climate during recent decades in the Arctic and subarctic regions, from Greenland in the west to Eurasia in the east, and contemporary biological and geophysical changes. Det Kongelige Danske Videnskabernes Selskab. Biologiske Meddelser 14(8). 75pp.

Jensen, Ad.S. and P.M. Hansen. 1931. Investigations on the Greenland cod (*Gadus callarias* L.). Rapports et Proces-verbaux des Reunions. Conseil Permanent International pour l'Exploration de la Mer 72: 1-41.

Jónsson, S. and J. Briem. 2003. The transport of water and fresh water with the East Icelandic Current. ICES Council Meeting Papers CM 2003/T:05, 12pp.

Jónsson, S. and H. Valdimarsson. 2004. A new path for the Denmark Strait overflow water from the Iceland Sea to Denmark Strait. Geophysical Research Letters: 31, L03305, doi:10.1029/2003GL019214.

Juterzenka, K.V. and K. Knickmeier. 1999. Chlorophyll a in water column and sea ice during the Laptev Sea freeze-up study in autumn 1995. p.153-160. In: H. Kassens *et al.* (Eds.). Land-Ocean Systems in the Siberian Arctic: Dynamics and History. Springer, Berlin, Germany.

Kirk, J.T.O. 1994. Light and Photosynthesis in Aquatic Ecosystems. Cambridge University Press, Cambridge. 509pp.

Kiørboe, T. 1993. Turbulence, phytoplankton cell size, and the structure of pelagic food webs. Advances in Marine Biology 29: 1–72.

Kobari, T. and T. Ikeda. 2001. Life cycle of *Neocalanus flemingeri* (Crustacea: Copepoda) in the Oyashio region, western subarctic Pacific, with notes on its regional variations. Marine Ecology Progress Series 209: 243-255.

Kowalik, Z. and P. Stabeno. 1999. Trapped motion around the Pribilof Islands in the Bering Sea. Journal of Geophysical Research 104: 25667-25684.

Kristiansen, S., T. Farbrot and P. A. Wheeler. 1994. Nitrogen cycling in the Barents Sea-seasonal dynamics of new and regenerated production in the marginal ice zone. Limnology and Oceanography 39: 1630-1642.

Kristmannsson, S.S. 1998. Flow of Atlantic Water into the northern Icelandic shelf area, 1985-1989. ICES Cooperative Research Report 225: 124-135.

Lilly, G.R., H. Hop, D.E. Stansbury and C.A. Bishop. 1994. Distribution and abundance of polar cod (*Boreogadus saida*) off southern Labrador and eastern Newfoundland. ICES Council Meeting Papers CM 1994/O:6. 21pp.

Link, J.S. and L.P. Garrison. 2002. Changes in piscivory associated with fishing induced changes to the finfish community on Georges Bank. Fisheries Research 55: 71-86.

Livingston, P.A. and J. Jurado-Molina. 2000. A multispecies virtual population analysis of the eastern Bering Sea. ICES Journal of Marine Science 57: 294-299.

Livingston, P.A. and R.D. Methot. 1998. Incorporation of predation into a population assessment model of eastern Bering Sea pollock. p.663-678. In: Fishery Stock Assessment Models. Alaska Sea Grant College Program Publication AK-SG-98-01. 1037pp.

Loder, J.W. 1980. Topographic rectification of tidal currents on the sides of Georges Bank. Journal of Physical Oceanography. 10: 1399-1416.

Loder, J.W., C.K. Ross and P.C. Smith. 1988. A space- and time-scale characterization of circulation and mixing over submarine banks, with application to the Northwestern Atlantic Continental Shelf. Canadian Journal of Fisheries and Aquatic Sciences 45: 1860-1885.

Lowry, L.F., V.N. Burkanov, K.J. Frost, M.A. Simpkins, R. Davis, D.P. DeMaster, R.S. Suydam and A. Springer. 2000. Habitat use and habitat selection by spotted seals (*Phoca largha*) in the Bering Sea. Canadian Journal of Zoology 78: 1959-1971.

Luccini, E., A. Cede and R.D. Piacentini. 2003. Effect of clouds on UV and total irradiance at Paradise Bay, Antarctic Peninsula, from a summer 2000 campaign. Theoretical and Applied Climatology 75: 105-116.

Mackas, D.L., R. Goldblatt and A.G. Lewis. 1998. Interdecadal variation in developmental timing of *Neocalanus plumchrus* populations at Ocean Station P in the subarctic North Pacific. Canadian Journal of Fisheries and Aquatic Sciences 55: 1–16.

Macklin, S.A., G.L. Hunt, Jr. and J.E. Overland. 2002. Collaborative research on the pelagic ecosystem of the southeastern Bering Sea shelf. Deep-Sea Research II 49(26): 5813–5819.

Macklin, S.A., S.I. Saito, V.I. Radchenko, J.M. Napp, P.J. Stabeno and S.M. McKinnell (Eds.). 2002. Variability in the Bering Sea ecosystem. Progress in Oceanography 55 (1-2).

Mann, K.H. and J.R.N. Lazier. 1996. Dynamics of Marine Ecosystems: Biological-Physical Interactions in the Oceans. 2nd Edition. Blackwell Science. 394pp.

Mantua, N.J., S.R. Hare, Y. Zhang, J.M. Wallace and R.C. Francis. 1997. A Pacific interdecadal oscillation with impacts on salmon production. Bulletin of the American Meteorological Society 78: 1069-1079.

Martin, J.E., R.D. Grauman and N. Marsili. 2001. Surface cyclolysis in the North Pacific Ocean. Part I: A synoptic climatology. Monthly Weather Review 129: 748-765.

Mauchline, J. 1998. The Biology of Calanoid Copepods. Academic Press, New York, 710pp.

McFarlane, G.A., J.R. King and R.J. Beamish. 2000. Have there been recent changes in climate? Ask the fish. Progress in Oceanography 47: 147-169.

McLaren, I.A. 1963. Effects of temperature on growth of zooplankton and the adaptive significance of vertical migration. Journal of the Fisheries Research Board of Canada 20: 685-727.

McLaughlin, F.A., E.C. Carmack, R.W. MacDonald and J.K.B. Bishop. 1996. Physical and geochemical properties across the Atlantic/Pacific water mass boundary in the southern Canadian Basin. Journal of Geophysical Research 101(C1): 1183-1197.

Miller, C.B. and M.J. Clemons. 1988. Revised life history analysis for large grazing copepods in the subarctic Pacific Ocean. Progress in Oceanography 20: 293-313.

Mills, C.E. 2001. Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? Hydrobiologia 451: 55-68.

Moore, S.E., J.M. Grebmeier and J.R. Davies. 2003. Gray whale distribution relative to forage habitat in the northern Bering Sea: current conditions and retrospective summary. Canadian Journal of Zoology 81: 734-742.

Moseidjord, H., H. Svendsen and D. Slagstad. 1999. Sensitivity studies of circulation and ocean-shelf exchange off northern Norway. Sarsia 84: 191-198.

Munk, P., B.W. Hansen, T.G. Nielsen and H.A. Thomsen. 2003. Changes in plankton and fish larvae communities across hydrographic fronts off West Greenland. Journal of Plankton Research 25: 815-830.

Murdoch, W.W. and A. Oaten. 1975. Predation and population stability. Advances in Ecological Research 9: 1-131.

Myers, R.A. 1998. When do environment-recruit correlations work? Reviews in Fish Biology and Fisheries 8: 285-305.

Nakken, O. and A. Raknes. 1987. The distribution and growth of Northeast Arctic cod in relation to bottom temperatures in the Barents Sea, 1978-1984. Fisheries Research 5: 243-252.

Naletova, I.A., V.V. Sapozhnikov and M.P. Metreveli. 1997. Features of primary production distribution in summer period and estimation of total production in the Sea of Okhotsk. p.98-103. In: Complex investigations of the Sea of Okhotsk Ecosystem. Moscow, VNIRO. [in Russian]

Napp, J.M. and G.L. Hunt, Jr. 2001. Anomalous conditions in the south-eastern Bering Sea, 1997: Linkages among climate, weather, ocean, and biology. Fisheries Oceanography 10: 61-68.

Napp, J.M., A.W. Kendall, Jr. and J.D. Schumacher. 2000. A synthesis of biological and physical processes affecting the feeding environment of larval walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea. Fisheries Oceanography 9: 147-162.

Nejstgaard, J.C., I. Gismervik and P.T. Solberg. 1997. Feeding and reproduction by *Calanus finmarchicus*, and microzooplankton grazing during mesocosm blooms of diatoms and the coccolithophore *Emiliania huxleyi.* Marine Ecology Progress Series 147: 197-217.

Neuenfeldt, S. and F.W. Koester. 2000. Trophodynamic control on recruitment success in Baltic cod: the influence of cannibalism. ICES Journal of Marine Science 57: 300-309.

Niebauer, H.J., V. Alexander and S. Henrichs. 1990. Physical and biological oceanographic interaction in the spring bloom at the Bering Sea marginal ice edge zone. Journal of Geophysical Research 95: 22,229-22,242.

Nishiyama, T. 1974. Energy requirements of sockeye salmon in Bristol Bay and the eastern Bering Sea. p.321-343. In: D.W. Hood and E.J. Kelly (Eds.), Oceanography of the Bering Sea with emphasis on renewable resources. Institute of Marine Sciences, University of Alaska, Fairbanks, Alaska. Occasional Publication No. 2.

NPFMC (North Pacific Fishery Management Council). 2003. Stock Assessment and Fishery Evaluation Document.

Olli, K, C.W. Riser, P. Wassmann, T. Ratkova, E. Arashkevich and A. Pasternak. 2002. Seasonal variation in vertical flux of biogenic matter in the marginal ice zone and the central Barents Sea. Journal of Marine Systems 38: 189-204.

Olson, M.B. and S.L. Strom. 2002. Phytoplankton growth, microzooplankton herbivory and community structure in the southeast Bering Sea: insight into the formation and temporal persistence of an *Emiliania huxleyi* bloom. Deep-Sea Research II 49: 5969-5990.

Orvik, K. A. and P. Niiler. 2002. Major pathways of Atlantic water in the northern North Atlantic and Nordic Seas toward Arctic. Geophysical Research Letters 29: 19, 1896, doi: 10.1029/2002GL015002.

OSPAR Commission. 2000. Quality Status Report 2000, Region I-Arctic Waters. OSPAR Commission, London. 102pp.

Ottersen, G., J. Alheit, K. Drinkwater, K. Friedland, E. Hagen and N.C. Stenseth. 2004. The response of fish to ocean climate variability. p.71-94. In: N.C. Stenseth, G. Ottersen, J. Hurrell and A. Belgrano (Eds.) Marine Ecosystems and Climate Variation: the North Atlantic. Oxford University Press, Oxford, UK.

Ottersen, G., K. Michalsen and O. Nakken. 1998. Ambient temperature and distribution of north-east Arctic cod. ICES Journal of Marine Science 55: 67-85.

Ottersen, G., B. Planque, A. Belgrano, E. Post, P.C. Reid and N.C. Stenseth. 2001. Ecological effects of the North Atlantic Oscillation. Oecologia 128: 1-14.

Ottersen, G. and S. Sundby. 1995. Effects of temperature, wind and spawning stock biomass on recruitment of Arcto-Norwegian cod. Fisheries Oceanography 4: 278-292.

Overland, J.E., N.A. Bond and J.M. Adams. 2001. North Pacific atmospheric and SST anomalies in 1997: Links to ENSO? Fisheries Oceanography 10: 69-80.

Overland, J.E., N.A. Bond and J.M. Adams. 2002. The relation of surface forcing of the Bering Sea to large-scale climate patterns. Deep-Sea Research II 49: 5855-5868.

Ozhigin, V.K., A.G. Trofimov and V.A. Ivshin. 2000. The Eastern Basin Water and currents in the Barents Sea. ICES Council Meeting Papers CM 2000/L:14. 19pp.

Pedersen, S.A. and D. Zeller. 2001 A mass-balance model for the West Greenland marine ecosystem. In: S. Guénette, V. Christensen and D. Pauly (Eds.). Fisheries impacts on North Atlantic ecosystems: models and analyses. Fisheries Centre Research Report 9(4): 111-127.

Peterson, W.T., J.E. Kister and L.R. Feinberg. 2002. The effects of the 1997-1999 El Niño- La Niña events on the hydrography and zooplankton off the Central Oregon coast. Progress in Oceanography 54: 381-398.

Petrie, B., S. Akenhead, J. Lazier and J. Loder. 1988. The cold intermediate layer on the Labrador and northeast Newfoundland Shelves, 1978-1986. NAFO Scientific Council Studies, 12: 57-69.

Petrie, B., J.W. Loder, S. Akenhead and J. Lazier. 1991. Temperature and salinity variability on the eastern Newfoundland Shelf: the annual harmonic. Atmosphere - Ocean 29: 14-36.

Planque, B., G.C. Hays, F. Ibanez and J.C. Gamble. 1997. Large scale spatial variations in the seasonal abundance of *Calanus finmarchicus*. Deep-Sea Research I 44: 315-326.

Plourde, S. and J.A. Runge. 1993. Reproduction of the planktonic copepod *Calanus finmarchicus* in the Lower St. Lawrence Esturary-relation to the cycle of phytoplankton production and evidence for a *Calanus* pump. Marine Ecology Progress Series 102: 217-227.

Polis, G.A. and D.R. Strong. 1996. Food web complexity and community dynamics. American Naturalist 147: 83-846.

Reed, R.K. and P.J. Stabeno. 1993. The recent return of the Alaskan Stream to Near Strait. Journal of Marine Research 51: 515–527.

Reverdin G., P.P. Niiler and H. Valdimarsson. 2003. North Atlantic Ocean surface currents. Journal of Geophysical Research 108: C1, 3002, doi:10.1029/2001JC001020.

Rey, F. and H. Loeng. 1985. The influence of ice and hydrographic conditions on the development of phytoplankton in the Barents Sea. p.49-63. In: J.S. Gray and M.E. Christiansen (Eds.). Marine Biology of Polar Regions and Effects of Stress on Marine Organisms, Proceedings of the 18th European Marine Biology Symposium, University of Oslo, Norway, 14-20 August 1983. European Marine Biology Symposia, 18. Wiley-Interscience, Chichester, UK.

Ribergaard, M.H., S.A. Pedersen, B. Aadlandsvik and N. Kliem. 2004. Modelling the ocean currents on the West Greenland shelf with special emphasis on northern shrimp recruitment. Continental Shelf Research 24: 1505-1519.

Rice, D.W. and A.A. Wolman. 1971. The life history and ecology of the gray whale (*Eschrichtius robustus*). American Society of Mammalology Special Publication 3, 142pp.

Rice, J. 2002. Changes to the Large Marine Ecosystem of the Newfoundland-Labrador Shelf. p.51-104. In: K. Sherman and H.R. Skjoldal (Eds.). Large Marine Ecosystems of the North Atlantic-Changing States and Sustainability. Elsevier, Amsterdam.

Rodriguez, J.M. 1993. Probing stratospheric ozone. Science 261: 1128-1129.

Rose, G.A., B. de Young, D.W. Kulka, S.V. Goddard and G.L. Fletcher. 2000. Distribution shifts and overfishing the northern cod (*Gadus morhua*): a view from the ocean. Canadian Journal of Fisheries and Aquatic Sciences 57: 644-663.

Rudels, B., E.P. Jones, L.G. Anderson and G. Kattner. 1994. On the intermediate depth waters of the Arctic Ocean. p.33-46. In: O.M. Johannessen, R.D. Muench and J.E. Overland (Eds.). The Polar Oceans and their Role in Shaping the Global Environment. Geophysical Monographs Series 85, AGU, Washington, DC, USA.

Runge, J.A. and R.G. Ingram. 1991. Under-ice feeding and diel migration by the planktonic copepods *Calanus glacialis* and *Pseudocalanus minutus* in relation to the ice algal production cycle in southeastern Hudson Bay, Canada. Marine Biology 108: 217-225.

Sakshaug, E., A. Bjørge, B. Gulliksen, H. Loeng and F. Mehlum (Eds.). 1992. Økosystem Barentshavet (Barents Sea Ecosystem). Norges almenvitenskapelige forskningsråd, Norges fiskeriforskningsråd, Miljøverndepartementet. Lillehammer, Norway. 304pp. [in Norwegian]

Sakshaug, E. and D. Slagstad. 1991. Light and productivity of phytoplankton in polar marine ecosystems: a physiological view. Polar Research 10: 69-85.

Sambroto, R.N., H.J. Niebauer, J.J. Goering and R.L. Iverson. 1986. Relationships among vertical mixing, nitrate uptake and phytoplankton growth during the spring bloom in the southeast Bering Sea middle shelf. Continental Shelf Research 5: 161-198.

Santee, M.L., W.G. Read, J.W. Waters, L. Froidevaux, G.L. Manney, D.A. Flower, R.F. Jarnot, R.S. Harwood and G.E. Peckham. 1995. Interhemispheric differences in Polar stratospheric HNO_3, H_2O, ClO, and O_3. Science 267: 849-852.

Sathyendranath, S. and T. Platt. 1988. The spectral irradiance field at the surface and in the interior of the ocean: a model for applications in oceanography and remote sensing. Journal of Geophysical Research 93: 9270–9280.

Schauer, U., H. Loeng, B. Rudels, V.K. Ozhigin and W. Dieck. 2002. Atlantic water flow through the Barents and Kara Seas. Deep-Sea Research I 49: 2281-2298.

Schauer, U., R.D. Muench, B. Rudels and L. Timokhov. 1997. The impact of eastern Arctic Shelf Waters on the Nansen Basin intermediate layers. Journal of Geophysical Research 102: 3371-3382.

Schumacher, J.D. and P.J. Stabeno. 1998. The continental shelf of the Bering Sea. p.789-823. In: The Sea, Vol. 11, The Global Coastal Ocean: Regional Studies, Synthesis, J. Wiley, New York, USA.

Schwing, F.B. and C.S. Moore. 2000. A year without summer for California: or a harbinger of a climate shift. Transactions of the American Geophysical Union 81: 301.

Shelton, P.A., G.R. Lilly and E. Colbourne. 1996. Patterns in the annual weight increment for 2J3KL cod and possible prediction for stock projection. NAFO SCR Document 96/47, Serial Number N2722, 19pp.

Skjoldal, H.R. 2004. The Norwegian Sea Ecosystem. Tapir Academic Press, Trondheim, Norway. 559pp.

Skjoldal, H.R., H. Gjøsæter and H. Loeng. 1992. The Barents Sea ecosystem in the 1980: ocean climate, plankton and capelin growth. ICES Marine Science Symposia 195: 278–290.

Skjoldal, H.R. and F. Rey. 1989. Pelagic production and variability of the Barents Sea ecosystem. p.241-286. In: K. Sherman and L.M. Alexander (Eds.). Biomass Yields and Geography of Large Marine Ecosystems, AAAS Selected Symposium 111.

Slagstad, D. and K.S. Tande. 1996. The importance of seasonal vertical migration in across shelf transport of *Calanus finmarchicus*. Ophelia 44: 189-205.

Smith, S.D., R.D. Muench and C.H. Pease. 1990. Polynyas and leads: an overview of physical processes and environment. Journal of Geophysical Research 95: 9461-9479.

Smith, S.L. and J. Vidal. 1986. Variations in the distribution, abundance and development of copepods in the southeast Bering Sea in 1980 and 1981. Continental Shelf Research 5: 215-239.

Springer, A.M., C.P. McRoy and M.V. Flint. 1996. The Bering Sea green belt: shelf-edge processes and ecosystem production. Fisheries Oceanography 5: 205-223.

Stabeno, P.J., N.A. Bond, N.B. Kachel, S.A. Salo and J.D. Schumacher. 2001. On the temporal variability of the physical environment of the south-eastern Being Sea. Fisheries Oceanography 10: 81-98.

Stabeno, P.J., D. Kachel and M. Sullivan. In press. Transport through the Aleutian Passes. Fisheries Oceanography.

Stabeno, P.J., N.B. Kachel, M. Sullivan and T.E. Whitledge. 2002a. Variability of physical and chemical characteristics along the 70m isobath of the southeast Bering Sea. Deep-Sea Research II 49(26): 5931–5943.

Stabeno, P.J. and J.E. Overland. 2001. Bering Sea shifts toward an earlier spring transition. EOS, Transactions of the American Geophysical Union 82: 317, 321.

Stabeno, P.J., J.D. Schumacher and K. Ohtani. 1999a. The physical oceanography of the Bering Sea. p.1-28. In: T.R. Loughlin and K. Ohtani (Eds.). Dynamics of the Bering Sea: Physical, Chemical and Biological Characteristics and a synopsis of research on the Bering Sea. University of Alaska Sea Grant, AK-SG-99-03, Fairbanks.

Stefánsson, G. 2003. Multipecies and ecosystem models. p.171-188. In: M. Sinclair and G. Valdimarsson (Eds.). Responsible Fisheries in the Marine Ecosystem. Rome; Food and Agriculture Organization of the United Nations, and CABI Publishing, UK. 426pp.

Stefánsson, G. (Ed.) 2004. Development of structurally detailed, statistically testable models of marine populations. QLK5-CT1999-01609. Progress Report for 1 January 2003 to 31 December 2003. Marine Research Institute (Reykjavík, Iceland) Technical Report 98, 346pp.

Stefánsson, G. and O. Pálsson. (Eds.) 1997. BORMICONT. A boreal migration and consumption model. Marine Research Institute (Reyjkavík, Iceland) Report 58, 223pp.

Stern, H.L. and M.P. Heide-Joergensen. 2003. Variability of sea ice in Baffin Bay and Davis Strait. Polar Research 22: 11-18.

Stirling, I. 1980. The biological significance of polynyas in the Canadian Arctic. Arctic 33: 303-315.

Stone, R.S. 1997. Variations in the western Arctic temperatures in response to cloud radiative and synoptic-scale influences, Journal of Geophysical Research 102: 21,769-21,776.

Strickland, R.M. and T. Sibley. 1984. Projected effects of CO_2-induced climate change on the Alaska walleye pollock fishery in the eastern Bering Sea and Gulf of Alaska. University of Washington, Seattle, Washington, FRI-UW-8411. 112pp.

Stuart, V., S. Sathyendranath, E.J.H. Head, T. Platt, B. Irwin and H. Maass. 2000. Bio-optical characteristics of diatom and prymnesiophyte populations in the Labrador Sea. Marine Ecology Progress Series 201: 91-106.

Sugimoto, T. and K. Tadokoro. 1998. Interdecadal variations of plankton biomass and physical environment in the North Pacific. Fisheries Oceanography 7: 289-299.

Sukhanova, I.N., H.J. Semina and M.V. Venttsel. 1999. Spatial distribution and temporal variability of phytoplankton in the Bering Sea. p.193-215. In: T.R. Loughlin and K. Ohtani (Eds.). Dynamics of the Bering Sea. University of Alaska Sea Grant, AK-SG-99-03, Fairbanks, Alaska.

Tamura, T. and H. Kato. 2003. Long-term changes in food and feeding habits of the common minke whales in western North Pacific region. PICES XI (W2-MBM-AP), Seoul, October 2003, p.192.

Tande, K.S. 1991. *Calanus* in north Norwegian fjords and in the Barents Sea. Polar Research 10: 389-407.

Tande, K.S. 2001. Norwegian multidisciplinary marine research programmes during the last 20 years: lessons learnt. p.54-55. In: A. Jarre (Ed.), Workshop “Ecosystem West Greenland”: A stepping stone towards an integrate marine research programme. Inussuk, Arctic Research Journal 2002-1, p.99. (Abstract)

Thompson, D.W.J. and J.M. Wallace. 1998. The Arctic Oscillation signature in the wintertime geopotential height and temperature fields. Geophysical Research Letters 25: 1297-1300.

Thordardottir, T. 1986. Timing and duration of spring blooming south and southwest of Iceland. p.345-360. In: S. Skreslet (Ed.), The Role of Freshwater Outflow in Coastal Marine Ecosystems, Proceedings of a NATO advanced research workshop, Bodo, Norway, May 21 25, 1985. Springler Verlag, Berlin.

Titov O.V. 1994. Primary production in the Barents Sea (reference material). Murmansk, PINRO. 73pp. [in Russian]

Tittensor, D.P., B. de Young and C.L. Tang. 2003. Modelling the distribution, sustainability and diapause emergence timing of the copepod *Calanus finmarchicus* in the Labrador Sea. Fisheries Oceanography 12: 299-316.

Tjelmeland, S. and B. Bogstad. 1998a MULTSPEC–a review of a multispecies modelling project for the Barents Sea. Fisheries Research 37: 127-142.

Tjelmeland, S. and B. Bogstad. 1998b. Biological modelling. p.69-97. In: T. Rødseth (Ed.). Models for Multispecies Management. Physica-Verlag, Heidelberg, Germany.

Townsend, D.W., M.D. Keller, M.E. Sieracki and S.G. Ackleson. 1992. Spring phytoplankton blooms in the absence of vertical water column stratification. Nature 360: 59–62.

Trenberth, K.E. and J.W. Hurrell. 1995. Decadal coupled atmospheric-ocean variations in the North Pacific Ocean. In: R.J. Beamish (Ed.). Climate Change and Northern Fish Populations. Canadian Special Publication of Fisheries and Aquatic Sciences 121: 15-24.

Tyrrell, T and A.H. Taylor. 1995. A modelling study of *Emiliania huxleyi* in the NE Atlantic. Journal of Marine Systems 9: 195-203.

Uzars, D. and M. Plikshs. 2000. Cod (*Gadus morhua* L.) cannibalism in the Central Baltic: interannual variability and influence of recruit abundance and distribution. ICES Journal of Marine Science 57: 324-329.

Valdimarsson, H. and S.-A. Malmberg. 1999. Near-surface circulation in Icelandic waters derived from satellite tracked drifters. Rit Fiskideildar 16: 23-39.

Verity, P.G., P. Wassmann, M.E. Frischer, M.H. Howard-Jones and A.E. Allen. 2002. Grazing of primary production by microzooplankton in the Barents Sea during early summer. Journal of Marine Systems 38: 109-123.

Vidal, J. and S.L. Smith. 1986. Biomass, growth, and development of populations of herbivorous zooplankton in the southeastern Bering Sea during spring. Deep-Sea Research 33: 523-556.

Vilhjálmsson, H. 2002. Capelin (*Mallotus villosus*) in the Iceland-East Greenland Jan Mayen. ICES Journal of Marine Science 59: 870-883.

Walsh, J.J. and C.P. McRoy. 1986. Ecosystem analysis in the southeastern Bering Sea. Continental Shelf Research 5: 259-288.

Werner, I. and H.-J. Hirche. 2001. Observations on *Calanus glacialis* eggs under the spring sea ice in the Barents Sea. Polar Biology 24: 296-298.

Whipple, S.J., J.S. Link, L.P. Garrison and M.J. Fogarty. 2000. Models of predation and fishing mortality in aquatic ecosystems. Fish and Fisheries 1: 22-40.

Wolfe, G.V., M. Steinke and G.O. Kirst. 1997. Grazing-activated chemical defence in a unicellular marine alga. Nature 387: 894-897.

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

Wyllie-Echeverria, T. 1995. Sea-ice conditions and the distribution of walleye pollock (*Theragra chalcogramma*) on the Bering and Chukchi shelf. In: R.J. Beamish (Ed.). Climate Change and Northern Fish Populations. Canadian Special Publication of Fisheries and Aquatic Sciences 121: 131-136.

Yndestad, H. 1999. Earth nutation influence on the temperature regime of the Barents Sea. ICES Department of Commerce, NOAA Technical Memorandum NMFS-AFSC-113.

Zelikman, E.A. 1977. Communities of the Arctic pelagial. Biology of the ocean. Biological production in the ocean. Moscow, No. 2: 43-55. [in Russian]

Zenkevich, L.A. 1963. The Sea of Okhotsk. p.783-817. In: Biology of the Seas of USSR. Interscience, New York, 955pp.

APPENDIX I

Members of the ESSAS International Planning Workshop held in Laguna Beach, California, USA, 4 -6 September 2002

Richard Beamish
Fisheries and Oceans Canada
Nanaimo, BC, Canada
E-mail: BeamishR@pac.dfo-mpo.gc.ca

Ken Drinkwater
Fisheries and Oceans Canada
Dartmouth, NS, Canada
E-mail: DrinkwaterK@mar.dfo-mpo.gc.ca

Present Address:
Institute of Marine Research
Bergen, Norway
ken.drinkwater@imr.no

Mikhail Vladimirovich Flint
P.P. Shirshov Institute of Oceanology
Moscow, Russia
E-mail: m_flint@orc.ru

Jackie Grebmeier
University of Tennessee
Knoxville, TN, USA
E-mail: jgrebmei@utk.edu

Roger Harris
Plymouth Marine Laboratory
Plymouth, UK
E-mail: rph@pml.ac.uk

George L. Hunt, Jr.
University of California
Irvine, CA, USA
E-mail: glhunt@uci.edu

Present Address:
School of Aquatic and Fishery Sciences
University of Washington
Seattle, WA 98195-5020, USA

Nina Karnovsky
University of California
Irvine, CA, USA
E-mail: nkarnovs@uci.edu

Harald Loeng
Havforskningsinstituttet / Institute of Marine Res.
Bergen, Norway
E-mail: harald.loeng@imr.no

James Morison
University of Washington
Seattle, WA, USA
E-mail: morison@apl.washington.edu

Jeff Napp
Alaska Fisheries Science Center
Seattle, WA, USA
E-mail: Jeff.Napp@noaa.gov

Brenda L Norcross
University of Alaska, Fairbanks
Fairbanks, Alaska, USA
Email: norcross@ims.uaf.edu

Geir Ottersen
University of Oslo
Oslo, Norway
E-mail: geir.ottersen@bio.uio.no

Clarence Pautzke
North Pacific Research Board
Anchorage, AK, USA
E-mail: cpautzke@nprb.org

Neil Swanberg
National Science Foundation
Washington, DC, USA
E-mail: nswanber@nsf.gov

APPENDIX II

Members of the ESSAS International Planning Workshop held in Bergen, Norway, 26-28 May 2003

Olafur S. Astthorsson
Marine Institute of Iceland
Reykjavik, Iceland
E-mail: osa@hafro.is

Manuel Barange
Director GLOBEC IPO
Plymouth Marine Laboratory
Plymouth, UK
E-mail: m.barange@pml.ac.uk

Francois Carlotti
C.N.R.S. / Université Bordeaux 1
Arcachon, France
E-mail: carlotti carlotti@epoc.u-bordeaux.fr

Brad deYoung
Memorial University
St. John's, NF
Canada
E-mail: bdeyoung@physics.mun.ca

Ken Drinkwater
Fisheries and Oceans Canada
Dartmouth, NS, Canada
E-mail: DrinkwaterK@mar.dfo-mpo.gc.ca
Present Address:
Institute of Marine Research
Bergen, Norway
ken.drinkwater@imr.no

Hans-Jürgen Hirche
Alfred-Wegener-Institut für Polar- und Meeresforschung (AWI)
Bremerhaven, Germany
E-mail: hhirche@awi-bremerhaven.de

George L. Hunt, Jr.
University of California
Irvine, CA , USA
E-mail: glhunt@uci.edu
Present Address:
School of Aquatic and Fishery Sciences
University of Washington
Seattle, WA 98195-5020, USA

Makoto Kashiwai
Hokkaido National Fisheries Research Institute
Kushiro, Hokkaido, Japan
E-mail: kashiwai@mua.biglobe.ne.jp

Michio J. Kishi
Hokkaido University/ FRSGC
Hakodate, Hokkaido, Japan
E-mail: kishi@salmon.fish.hokudai.ac.jp

Svein Kristiansen
University of Tromsø
Tromsø, Norway
E-mail: sveinkr@nfh.uit.no

Andrei S. Krovnin
Russian Federal Research Institute of Fisheries and Oceanography (VNIRO)
Moscow, Russia
E-mail: akrovnin@vniro.ru

Harald Loeng
Havforskningsinstituttet / Institute of Marine Res.
Bergen, Norway
E-mail: harald.loeng@imr.no

Bernard A. Megrey
Alaska Fisheries Science Center
National Marine Fisheries Service, NOAA
Seattle, WA, USA
E-mail: Bern.Megrey@noaa.gov

Sue Moore
National Marine Mammal Laboratory
Seattle, USA
E-mail: sue.moore@noaa.gov

Geir Ottersen
Institute of Marine Research
Bergen, Norway
Present Address:
Department of Biology
University of Oslo, Norway
E-mail: geir.ottersen@bio.uio.no

Vladimir Ozhigin
Knipovich Polar Research Institute of Marine Fisheries and Oceanography (PINRO)
Murmansk, Russia
E-mail: ozhigin@pinro.murmansk.ru

Vladimir I. Radchenko
Sakhalin Research Institute of Fisheries and Oceanography (SakhNIRO)
Yuzhno-Sakhalinsk, Russia
E-mail: vlrad@sakhniro.ru

Katherine Richardson
University of Aarhus
Århus, Denmark
E-mail: richardson@biology.au.dk

Yasunori Sakurai
Hokkaido University
Hakodate, Hokkaido, Japan
E-mail: sakurai@pop.fish.hokudai.ac.jp

Kurt Tande
University of Tromsø
Norway
E-mail: kurtt@draugen.nfh.uit.no

APPENDIX III

Members of the ESSAS International Planning Workshop held in Seattle, Washington, USA, 30 October - 1 November 2003

Olafur S. Astthorsson
Marine Institute of Iceland
Reykjavik, Iceland
E-mail: osa@hafro.is

Manuel Barange
Director GLOBEC IPO
Plymouth Marine Laboratory
Plymouth, UK
E-mail: m.barange@pml.ac.uk

Francois Carlotti
C.N.R.S. / Université Bordeaux 1
Arcachon, France
E-mail: carlotti carlotti@epoc.u-bordeaux.fr

Brad deYoung
Memorial University
St. John's, NF, Canada
E-mail: bdeyoung@physics.mun.ca

Ken Drinkwater
Fisheries and Oceans Canada
Dartmouth, NS, Canada
E-mail: DrinkwaterK@mar.dfo-mpo.gc.ca
Present Address:
Institute of Marine Research
Bergen, Norway
E-mail: ken.drinkwater@imr.no

Mads Peter Heide-Jorgensen
ECOGREEN
Nuk, Greenland
Present Address:
National Marine Mammal Laboratory
Seattle, WA, USA
E-mail: madspeter.heide-joergensen@noaa.gov

Hans-Jürgen Hirche
Alfred-Wegener-Institut für Polar- und Meeresforschung (AWI)
Bremerhaven, Germany
E-mail: hhirche@awi-bremerhaven.de

George L. Hunt, Jr.
University of California
Irvine, CA, USA
E-mail: glhunt@uci.edu
Present Address:
School of Aquatic and Fishery Sciences
University of Washington
Seattle, WA 98195-5020, USA

Michio J. Kishi
Hokkaido University/ FRSGC
Hakodate, Hokkaido, Japan
E-mail: kishi@salmon.fish.hokudai.ac.jp

Svein Kristiansen
University of Tromsø
Tromsø, Norway
E-mail: sveinkr@nfh.uit.no

Andrei S. Krovnin
Russian Federal Research Institute of Fisheries and Oceanography (VNIRO)
Moscow, Russia
E-mail: akrovnin@vniro.ru

Harald Loeng
Havforskningsinstituttet / Institute of Marine Res.
Bergen, Norway
E-mail: harald.loeng@imr.no

Bernard A. Megrey
Alaska Fisheries Science Center
National Marine Fisheries Service, NOAA
Seattle, WA, USA
E-mail: Bern.Megrey@noaa.gov

Sue Moore
National Marine Mammal Laboratory
Seattle, USA
E-mail: sue.moore@noaa.gov

Jeffery Napp
Alaska fisheries Science Center
Seattle, WA, USA
E-mail: Jeff.Napp@noaa.gov

Geir Ottersen
Institute of Marine Research
Bergen, Norway
Present Address:
Department of Biology
University of Oslo, Norway
E-mail: geir.ottersen@bio.uio.no

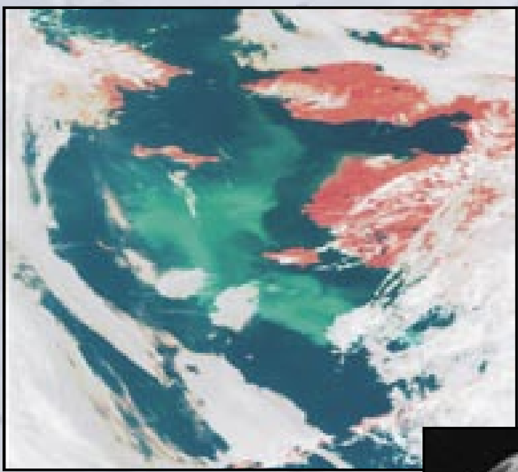
Vladimir Ozhigin
Knipovich Polar Research Institute of Marine Fisheries and Oceanography (PINRO)
Murmansk, Russia
E-mail: ozhigin@pinro.murmansk.ru

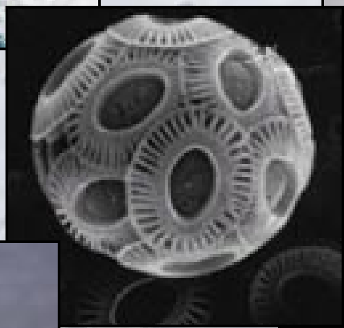
Vladimir I. Radchenko
Sakhalin Research Institute of Fisheries and Oceanography (SakhNIRO)
Yuzhno-Sakhalinsk, Russia
E-mail: vlrad@sakhniro.ru

Katherine Richardson
University of Århus
Århus, Denmark
E-mail: richardson@biology.au.dk

Yasunori Sakurai
Hokkaido University
Hakodate, Hokkaido, Japan
E-mail: sakurai@pop.fish.hokudai.ac.jp

Kurt Tande
University of Tromsø
Norway
E-mail: kurtt@draugen.nfh.uit.no





International Council for Science
Scientific Committee on Oceanic Research

NSF

The Research Council of Norway