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30 August–1 September 2010

Reykjavik, Iceland



Conseil International pour l'Exploration de la Mer

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H. C. Andersens Boulevard 44–46 DK-1553 Copenhagen V Denmark Telephone (+45) 33 38 67 00 Telefax (+45) 33 93 42 15 www.ices.dk info@ices.dk

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Executive summary

The 2010 ESSAS Annual Science Meeting (ASM) was convened in Reykjavik, Iceland (30/31 August and 1 September 2010), and hosted by the Marine Research Institute (MRI) of Iceland. The main goal of the ESSAS project is to compare, quantify and predict the impact of climate variability on the productivity and sustainability of Sub-Arctic marine ecosystems. The ASM was opened with welcoming remarks from Ken Drinkwater (ESSAS Co-Chair, Norway) and Johann Sigurjonsson (Director MRI, Iceland). Comments on local arrangements and practical information were provided by Ólafur S Astthorsson (Deputy Director MRI and chair of the local organizing committee). Fifty-one scientists from five countries participated. The meeting was divided into five half-day sessions to present ongoing research within the ESSAS areas as well as that conducted by ESSAS working groups (WGs).

Session 1 on the **Iceland Sea and East Greenland Sea Ecosystems** was mainly convened to review the work conducted by MRI as part of their Iceland Sea Ecosystem (ICE) Project to investigate the recent changes in the capelin stock north of Iceland. Presentations covered aspects of the physical oceanography, nutrients and phytoplankton, zooplankton, larval drift and on capelin ecology and the possible causes of recent changes in their distribution. In addition, a talk was given on the exchanges between the Norwegian Sea and the Iceland Sea undertaken as part of a Norwegian IPY project. During 2006–2008 capelin spawning was observed to be earlier and more to the west and north than historic records while adult capelin were distributed more westerly and southerly during summer than previously. The observed decline in recruitment and stock size of capelin appears to be linked to changes in the drift patterns of larval and 0-group capelin since 1995, and in particular since 2003.

Session 2 covered the West Greenland and Labrador Sea Ecosystems. Three presentations were made on research being conducted off West Greenland by Danish scientists in Denmark. A brief talk on the work of the Greenland Climate Institute was followed by details of studies being carried out in Disko Bay and Nuuk Fjord. The importance of the spring phytoplankton bloom was stressed as it determines the extent of the secondary production which feeds the local populations of fish, birds and marine mammals. The time of onset of the spring bloom varies annually depending on the ice duration and meteorological conditions, and there is a strong positive correlation between the open water period and the magnitude of the annual primary production. In addition, 3 Canadian scientists presented results on the physical oceanography and modelling, chemistry and zooplankton. Large phytoplankton in the Labrador have been decreasing in abundance and smaller forms have been becoming more important while the number of bacteria generally have not changed. There has been a downward trend in pH (i.e. increasing acidity) in the Labrador Sea over the last two decades, which might eventually lead to pH levels low enough to dissolve the shells of calcifying organisms before the end of the century.

Session 3 on **Climate Variability and Fish Populations** examined hypothesis of how climate variability affects fish populations. The need for both comparative studies at short (a few years) time scales and empirical observations to resolve cause and affect issues between fish populations and climate was stressed. It was also pointed out that marine ecosystems are dynamically nonlinear with multiple feedback loops and the possibility of continually altering their structure and operation in response to external stresses (climatic variations, fishing, habitat alteration, etc.). This has hampered progress in the understanding of biological responses to climate variability. Examples of

the types of responses of the marine ecosystem to climate variability from the Bering and Barents seas and their possible mechanisms were also provided.

Session 4 on **Modelling Ecosystem Response** showcased some of the work undertaken by the ESSAS Modelling WG. The WG, in cooperation with PICES, has been developing an end-to-end model that will be applied to sardines and anchovies in the Pacific. The results and lessons learned from another type of end-to-end model, AT-LANTIS as applied to the NE US shelf regions were discussed. In addition, several regional modelling studies in the North Atlantic were presented. These included pure physical oceanographic models, larval tracking models, and biophysical models, some of which are being extended to include adult fish some modelling work being carried out in the ESSAS area of the North Atlantic were presented. Two presentations discussed the ecosystems under future climate scenarios.

Session 5 on **Gadoid-Crustacean Interactions in Sub-Arctic Seas** presented the research results by the ESSAS working group on Climate Effects on Upper Trophic Levels, which has been undertaking comparative studies between different sub-Arctic seas to elucidate the processes that lead to shifts between demersal fish, especially gadoids such as cod and pollock, and crustaceans, such as shrimp and crabs. Results from studies on snow crab suggest that colder temperatures generally lead to higher recruitment. On the other hand, both predation and spawner effects showed no consistent relationship with snow crab recruitment between regions and generally weren't statistically significant.

1 Overview

1.1 Introduction

The Ecosystem Studies of Sub-Arctic Seas (ESSAS) is a Regional Program of IMBER (formerly of GLOBEC) and within ICES is under the Steering Group on Regional Seas Programme (SGRSP). The main 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. The geographic foci are the northern regions of the Atlantic and Pacific Oceans. ESSAS holds an annual workshop during which a series of topical session proposed by ESSAS's Working Groups are undertaken. The ICES/ESSAS Workshop in 2010 was held from 30 August to 1 September 2010 in Reykjavik, Iceland and was hosted by the Marine Research Institute of Iceland. The Workshop undertook a review of the ecosystem research being carried out in the Iceland Sea and the Labrador-West Greenland regions, including the Iceland Sea Ecosystem (ICE) Project. The ESSAS WG on gadoid-invertebrate interactions continued their comparisons between different sub-Arctic ecosystems as a means of testing the hypothesis that the disappearance (rise) in gadoids lead to an increase (decrease) in invertebrates. Also, the ESSAS WG on Modelling presented their work on the development of an end-to-end model. Finally, a session on the ecosystem response to climate variability was held as a means to determine what research ESSAS should focus on during the coming years.

There were 51 participants from 6 countries (Canada, Denmark, Iceland, Japan, Norway, and USA). The list of participants appears in Appendix 1.

In total, 35 presentations were given during the workshop (see Appendix 2 for the meeting agenda). Extended abstracts are provided in Appendix 3.

The report was written and compiled by K. Drinkwater, M.M. McBride, E. Head and Ó. Astthorsson.

1.2 Terms of reference

The ICES/ESSAS Workshop on Ecosystem Studies of Sub-Arctic Seas (ICESSAS), chaired by George Hunt, USA, and Ken Drinkwater, Norway, will meet in Reykjavik, Iceland, 30 August – 1 September 2010 to:

- a) Present recently completed ESSAS research carried out in the Barents Sea and the Oyashio System off Japan, as well as comparative studies between Norwegian, US and Canadian ecosystems;
- b) Examine the ecosystem structure and function in, and determine the connectivity between, Icelandic, Greenland and Labrador Sea waters;
- c) Determine the interactions between invertebrate and gadoid populations through comparative analysis between several sub-arctic seas in both the Atlantic and Pacific regions;
- d) Extend modelling efforts to develop an end-to-end ecosystem model with special emphasis on the inclusion of fish populations.

The workshop will complete its Terms of Reference by a series of topical sessions a) to d). ESSAS will provide an oral report to SSGRSP at the 2010 ASC and a written report one month later.

ICESSAS will report by 15 October 2010 (via SSGRSP) for the attention of SCICOM.

1.3 Workshop structure and working procedure

The meeting was actually chaired by Olafur Astthorsson (Iceland) and Ken Drinkwater (Norway) and the agenda (Appendix 2) was divided into five half-day topical sessions to address the terms of reference and to present ongoing research within ESSAS, including those of the ESSAS working groups (WGs). These sessions reflect the goal of ESSAS.

Session 1 on the Iceland Sea and East Greenland Sea Ecosystems was convened to highlight the work conducted by MRI as part of their Iceland Sea Ecosystem (ICE) Project that investigated the recent changes in the capelin stock north of Iceland. In addition, a talk was given on the exchanges between the Norwegian Sea and the Iceland Sea undertaken as part of a Norwegian IPY project. Session 2 on the West Greenland and Labrador Sea Ecosystems presented various research activities by Denmark off West Greenland and by Canadian scientists in the Labrador Sea. These first sessions addressed ToR (b). It was decided to postpone ToR (a) to next year at the ESSAS Open Science Meeting (co-sponsored by ICES) when ESSAS could present their findings to the broader scientific community. Instead, Session 3 was entitled Climate Variability and Fish Populations and examined hypothesis of how climate variability affects fish populations. Session 4 on Modelling Ecosystem Response addressed ToR (d) by showcasing some of the work undertaken by the ESSAS Modelling Working Group. In addition, results from models in the North Atlantic were presented. ToR (c) was undertaken in Session 5 on Gadoid-Crustacean Interactions and was convened by the ESSAS Working Group on Climate Effects on Upper Trophic Levels. They presented comparative studies between different subarctic seas as a means to elucidate the processes that lead to shifts between demersal fish, especially gadoids such as cod and pollock, and crustaceans, such as shrimp and crabs. The last half day of the meeting was dedicated to separate WG discussions on the future research directions of the ESSAS.

2 Session Results

2.1 Iceland Sea and East Greenland

This session provided an overview of progress and status of ecosystem research in the Iceland Sea and adjacent waters, with emphasis on the Iceland Sea Ecosystem Project carried out from 2006–2008. This project was Iceland's contribution to the International Polar Year (IPY). The purpose of the project was to gain insights into the causes of the recent distributional changes and decline in abundance of the capelin stock in the Iceland Sea. The presentations at the Workshop gave a comprehensive coverage of the Iceland Sea Ecosystem, starting with the hydrographic (physical and chemical) regime, followed by talks on the primary and secondary production, with insights into trophic linkages in the pelagic system. Capelin larvae and adults were treated in two final talks, focusing on recent trends in life history in relation to the recent decline in the stock size of capelin. Furthermore, hydrographic properties, including exchange of water masses, on the eastern boundary of the Iceland Sea (Jan Mayen Ridge), were presented based upon data collected on the Norwegian component of the Ecosystem Studies of Subarctic and Arctic Regions (NESSAR), another IPY project. New findings include the following:

- During the ICE project temperatures and salinities were increasing and sea-ice coverage declined.
- A persistent anticyclonic gyre on the east side of the Kolbeinsey Ridge was identified, which appears to act as a retention area for capelin juveniles.
- The first moored current measurements on the Jan Mayen Ridge show (1) a net weak unstable flow of Atlantic Water from the Norwegian Sea to the Iceland Sea over the ridge with no significant seasonal variation, except near the bottom and (2) slightly farther south in a deep channel the currents in the upper 600 m vary seasonally with a net flow from the Norwegian Sea to the Iceland Sea in winter and in the opposite direction during summer while near bottom a net flow of deep water from the Norwegian Sea into the Iceland Sea occurs during both seasons.
- A difference in the nutrient budget was found on the different sides of the Kolbeinsey Ridge with surface layer silicate in summer totally exhausted to the east due to diatom blooms while this was not observed in the waters to the west of the Ridge. During the observation period phytoplankton production and biomass was greater to the east of the Ridge.
- While diatoms dominate the phytoplankton community during the growth season, dinoflagellates were also found to be relatively abundant. The small flagellates are thought to be of great importance in late summer.
- Zooplankton community structure in the Iceland Sea is a mixture of Atlantic and Arctic species and varies longitudinally due to changes in hydrography and phytoplankton production. The dominant Atlantic species is *Calanus finmarchicus* and Arctic species is *C. hyperboreus*. Highest diversity in zooplankton community was found in the frontal areas near the shelf edges.
- There was a relatively high abundance of *C. finmarchicus*, as well as *Oithona* and *Pseudocalanus*, in the Iceland Sea during 2007 compared with 2006 and 2008.
- *Calanus* spp. are important dietary components of most species. Small euphausiids (*T. inermis*) are important in the diet of young capelin while the amphipod *T.libellula* is relatively important in the diet of adult capelin.
- Adults of capelin and blue whiting share the same feeding mode.
- Capelin spawning during 2006–2008 was earlier and more to the west and north than historic records.
- During 2006–2008 the adult capelin were distributed more westerly and southerly than previously while summer 0-group distributions were more northerly since 1995 and mostly north of the Icelandic continental shelf in 2003 and 2006–2008.
- The declining recruitment and stock size of caplin appear to linked to changes in drift patterns of larval and 0-group capelin since 1995, and in particular since 2003.

2.2 West Greenland and the Labrador Sea

In this session six presentations were given covering several different aspects of the West Greenland and Labrador Sea ecosystems. These included a brief description of the Greenland Climate Research Centre (www.natur.gl), whose overall purpose is "to

obtain the scientific basis for a sustainable exploitation of the nature resources in and around Greenland as well as for protecting the environment and the biological diversity". The importance of the close coupling between metrology, oceanography and pelagic ecology was stressed, and it was noted that this needs to be better understood in order to determine the impact of climate change on the marine pelagic ecosystems. The Head of the Climate Research Centre (Dr. Søren Rysgaard) has recently been awarded a Canadian Excellence Research Chair but will, nevertheless, keep his position at the Climate Research Centre, so that his appointment will provide a unique opportunity for future extensive collaborative research between Greenland and Canada.

Some of the main results from research conducted in the waters off West Greenland by DTU Aqua in Denmark include:

- In Disko Bay, a coastal area of West Greenland that is ice-covered during the winter, the time of onset of the spring bloom varies between years depending on the duration of ice cover and the meteorological conditions, and there is a strong positive correlation between the open water period and the magnitude of the annual primary production.
- The spring phytoplankton bloom is the single most important event determining the secondary production capacity of arctic marine food webs, especially the lipid-rich *Calanus* copepods, which in turn attract the large stocks of fish, birds and mammals.
- The Nuuk Fjord, which varies from a warm oceanic environment outside the fjord to ice-covered waters at its head, is being used as a model system to investigate the likely effects of climate change on marine ecology and its processes in arctic fjords.
- The recent warming trend off West Greenland has not led to a return of cod, which had been hoped for since cod stocks were relatively high during previous "warm" decades (1920s and 1930s). This may be because cod recruitment in West Greenland due to larval drift from Iceland has become a rare event.
- Shrimp stocks off West Greenland, which increased greatly during the 1990s, have declined to low levels, even though there has been high female spawning stock biomass, favorable temperature conditions and low predation by cod. The link to possible changes in the timing of the phytoplankton bloom is not clear due to insufficient data or analyses (important processes may act on smaller spatial scales).
- The expectation that warm conditions will lead to a large cod stock and a small shrimp stock have not been fulfilled, thus reliable predictions on possible effects of climate change on cod and shrimp at West Greenland will not be possible until the basic processes are understood.

Main results presented from research by Canadian scientists in the Labrador Sea were:

- Phytoplankton growth in the Labrador Sea is limited by both light and nutrients.
- Large phytoplankton have been decreasing in abundance and smaller forms have been becoming more important, which may be a result of changes in the export flux ratio. Bacterial numbers have not changed, ex-

cept on the Greenland Shelf, where they have increased along with phytoplankton (chlorophyll) concentrations.

- *Calanus finmarchicus* dominates the mesozooplankton biomass in the central Labrador Sea, while *C. glacialis* and *C. hyperboreus* are as important on the Labrador Shelf in spring and summer.
- In the central Labrador Sea local production of *C. finmarchicus* cannot sustain the population from year to year so is probably re-populated each year by transport from the areas of high recruitment. The eastern Labrador Sea is very productive with high abundances of copepodites especially in early summer.
- Recruitment of *Calanus finmarchicus* (the dominant zooplankton species) varies spatially, due to variations in egg mortality, which is probably caused by predation (mostly by *C. finmarchicus* females), and is reduced when an alternative food source (phytoplankton) is abundant.
- Nitrate concentrations have been increasing and silicate concentrations are decreasing, suggesting increased influence of Atlantic versus Arctic water.
- Increasing temperatures in the central Labrador Sea since the late 1990s have led to earlier spring blooms and have advanced the seasonal cycle of *C. finmarchicus,* a trend that is expected to continue under future climate change.
- Mesozooplankton biomass has shown no obvious trend with time.
- During the 1980s and early 1990s, Labrador Sea Water (LSW) became colder and fresher with the deepest convection of over 2000 m in 1994. Since then, LSW has become warmer and more saline and convection depths have been much shallower, except in 2008 (1600 m).
- Convection transports atmospheric gases, including carbon dioxide and transient tracers such as chlorofluorocarbons (CFCs), to intermediate depths and this Labrador Sea Water have been tracked as it spreads throughout the North Atlantic.
- Oxygen isotope studies have identified glacial melt water as a dominant freshwater source in the upper 100 m of the water column in the Greenland Shelf and Slope region.
- Carbon dioxide solubility is higher in cold, fresh water than in warm salty water, so that the Labrador Sea is particularly susceptible to ocean acidification. There has been a downward trend in pH (i.e. increasing acidity) over the last two decades, which is expected to continue and if so will lead to pH levels low enough to dissolve the shells of calcifying organisms before the end of the century.
- The highly advective and seasonal nature of the East and West Greenland Currents makes it very difficult to model accurately even in the mean. The high observed variability is linked to changes in the relative contributions of the Arctic, Greenland, Sub-Polar North Atlantic, and North Atlantic flows.
- The Baffin Island Current that brings cold, low saline Arctic Waters south sometimes extends eastward to affect the hydrographic properties off West Greenland.

2.3 Ecosystem Response to Climate Variability

In a 2010 paper in Journal of Marine Systems, Jim Overland wrote:

"The responses to climate by biological systems are diverse in character because intervening processes introduce a variety of amplifications, time lags, feedbacks, and non-linearities. Decadal ecosystem variability can involve a variety of climate to ecosystem transfer functions. These can be expected to convert red noise of the physical system to redder (lower frequency) noise of the biological response, but can also convert climatic red noise to more abrupt and discontinuous biological shifts, transient climatic disturbance to prolonged ecosystem recovery, and perhaps transient disturbance to sustained ecosystem regimes. All of these ecosystem response characteristics are likely to be active for at least some locations and time periods, leading to a mix of slow fluctuations, prolonged trends, and step-like changes in ecosystems and fish populations in response to climate change."

For investigating relationships between climate and fish populations there are two basic approaches. One is detailed process studies and the other is historical multivariate analysis. The latter can investigate what are the different types of biological responses to different types of forcing shifts. This seems like an important but generally neglected approach. To stimulate discussion and help determine what ESSAS might do in this regard five talks were given. The first 2 invited talks were of a general nature.

- The first presentation stressed the need for relying upon empirical observations to resolve cause and affect issues between fish populations and climate. Testing models with such observations is imperative. It was stressed that one needs to understand the processes. We were also reminded that the egg to larval transformation period is the greatest potential "bottleneck" period for a fish population. High variability is more the norm for most stocks and one must be careful in using percentage change criteria for making statements about fish population trends. The Russian work on cyclic phenomena of fish populations was discussed, including the atmospheric indices and the effects of the earth's rotation.
- In the second talk, many leading hypothesis to account for fish population variability were reviewed. It was also pointed out that marine ecosystems are dynamically nonlinear with multiple feedback loops and the possibility of continually altering their structure and operation in response to external stresses (climatic variations, fishing, habitat alteration, etc.) is high. This has hampered progress in the understanding of biological responses to climate variability. It was suggested that one way to approach this is the comparative method. Further, it was concluded that attempting to resolve these issues by involving complete (complex, nonlinearly-evolving) histories is unlikely to lead to success but one possible fruitful approach might be to focus on fairly short time scales.

The remaining talks provided details and examples from different sub-Arctic seas. Some of the important points made during the talks were as follows.

• An update on the Oscillating Control Hypothesis was provided. This hypothesis predicted that recruitment of pollock year-classes in the Bering Sea should be greatest in years with early ice retreat and late blooms in warm water because more energy would flow into the pelagic vs. benthic

community. It further predicted that, with pollock population growth, there should be a shift from bottom-up to top-down regulation. New data support the predictions that in years with early ice retreat more of the primary production goes to the pelagic realm and that high numbers of age-0 pollock survive to summer. However, in these years, production of large crustacean zooplankton is reduced, depriving age-0 pollock of lipid-rich prey in summer and fall. As a result age-0 pollock have low energy density during warm years and there is enhanced cannibalism.

- Investigations of fish dynamics in the Northeast Pacific showed that the responses to climate by individual species vary. Both recruitment and abundances show long-term (1982–2009) trends with groups of species either positively or negatively associated with these trends. At the same time, it was noted that the long-term temperature trend is a major component of the temperature variability, particularly in Bering Sea. Thus the observed trends in recruitment and abundance may reflect response to this warming trend. However, predictive capability is likely to be low as retrospective patterns frequently change when new data are added. In addition, the Northeast Pacific ecosystem has experienced significant directional (steplike) changes in the biological communities, especially in the eastern Bering Sea over the past 25–30 years.
- In the Barents Sea, boreal cod and herring are impacted by multidecadal climate variations.with high abundance and more northeastward distribution during warm periods. While this may also be true for the arctic capelin, the time series are too short to make a definitive conclusion. Adult cod benefit from times of high capelin abundance by increased growth (and egg production), but cod have alternatives if capelin are scarce.
- Also, in the Barents Sea examples of top-down controls were provided. These included the observation that large capelin populations reduce the abundance of zooplankton prey and high abundance of young herring reduces the abundance of larval capelin, thereby negatively affecting capelin recruitment. From the Norwegian Sea there is emerging evidence of high abundance of pelagic (herring, blue whiting, mackerel) significantly grazing down the population of *C. finmarchicus*.

2.4 Modelling Ecosystem Responses

The ESSAS WG on Modelling Ecosystem Responses led this session in order to present the latest on model developments, especially in the sub-Arctic seas. One of the major activities of this group has been the development of an end-to-end model that covers from climate forcing to fish and fisheries. They joined with PICES scientists in this endeavour and thus the application of this model has been geared towards anchovies and sardines in the North Pacific. However, the model can be generalized and eventually will be applied to the sub-Arctic regions. Three presentations focused on end-to-end models, one of a general nature, one on the progress in developing the WG's model, and one on the application of a different end-to-end model, ATLANTIS, to northeast US waters.

• The general talk on end-to-end models concluded that such models definitely should be developed and that they will be helpful in the future for understanding ecosystem processes and for fisheries manage scenario testing. It remains unclear whether these models can be assembled from existing models or if a new approach is needed. Regardless, great care is required in piecing together end-to-end models. It was suggested that sub-Arctic seas may be a good test bed for such models due to reduced number of major species. However, in the discussion it was noted that the application of such models to demersal fish species is still likely several years away.

- A tightly-coupled model from climate to fish (and fishers) has been developed and is being implemented for sardine and anchovy systems in the North Pacific. This model will be used to examine hypotheses related to the synchrony and alternation in small pelagics in different ecosystems.
- A description and lessons learned from the building and application of the ATLANTIS model to Georges Bank and the Northeastern US indicated that generally the best modelled species were those with the best data, which tended to be the most important (ecologically) to the system.

Results from an ESSAS endorsed workshop on stock production models were also given.

• A stock production modelling workshop held in Woods Hole in May of 2010 that included several ESSAS scientists assembled environmental as well as fish and fisheries data for 11 ecosystems from the United States, Canada and Norway. It then developed several analytical surplus production modelling tools that were used to estimate fishery management biological reference points and explored them across aggregations, drivers, and covariates. Research teams were established to focus on particular comparative aspects from these models and results are to be presented at a follow-up workshop set for the spring of 2011.

Four talks on the application of a variety of regional biophysical models for the Norwegian, Barents and Iceland seas. Some of the important results are listed below.

- A physical oceanographic model of Icelandic waters indicated that the North Icelandic Irminger Current is driven by density gradients in the Denmark Strait area.
- A Norwegian model was described that includes physical oceanography, biogeochemistry and foodwebs, up through to fish with feedbacks between different trophic levels. At present, however, the fish are only included as prey on zooplankton. The model has been applied to the Norwegian Sea pelagic ecosystem and seasonal fish distributions are observationally-based. The model suggests that pelagic stocks in the Norwegian Sea are food limited, but reduced stocks could possibly rebuild within a year.
- Statistical analysis has shown that earlier hatching leads to higher recruitment success of cod spawned along the Norwegian coast. Timing is influenced by the percentage of recruits and wintering temperature. A biophysical model was developed to gain insights as to why earlier hatching leads to higher recruitment. The model showed faster northward transport of larvae if hatching occurs early in the season and the larvae were located near the surface. Rapid northward displacement was often linked to high ambient temperatures, although transport seems to be more important for larval survival than temperature. The transport may reduce the overlap with predators and/or contribute to higher prey densities for the larvae.

• A dynamic energy budget (DEB) model was incorporated into a capelin migration model. Parameters were fit that provide a reasonable match to the observed weight, fat and roe content of capelin.

Finally 2 talks were given on the possible impact of future climate change on components of the marine ecosystem. These indicated the following.

- In the Arctic under projected future warming, primary production is expected to increase 2 or 3-fold but only slightly in the Barents Sea, and decrease in the Norwegian Sea. *Calanus glacialis* production will increase in the Arctic Ocean but disappear from the northern Barents Sea while *C. finmarchicus* production will increase in the Greenland and Iceland seas.
- A model study of larval cod survival in the North Atlantic under future climate change indicated that survival rates will likely increase in the Lofoten area of coastal Norway and off Iceland but decrease in the North Sea and on Georges Bank. Autumn spawning, where it presently occurs, may be reduced because of increased water temperatures. Also, the time window for optimal environmental conditions for larval cod survival, in general, will become narrower.

2.5 Gadoid-Invertebrate Interactions

Representatives from 6 different subarctic ecosystems participated in this session investigating the interactions between gadoid and invertebrate populations. It began with an invited lecture on the physical and biological factors affecting recruitment of Bering Sea snow crab. This was followed by 5 other presentations that included case studies within a specific ecosystem as well as comparative studies between ecosystems. Some of the presentations considered spatial aspects of the distributions and hence interactions, and many incorporated ocean climate data, as had been recommended during the 2009 ESSAS meeting. Several highlights from the presentations follow below.

- A comparative study of variability in snow crab abundance in the eastern Bering Sea, two areas on the Newfoundland/Labrador Shelf, and one in the southern Gulf of St. Lawrence, indicated that in all these systems colder temperatures led to higher recruitment, with 3 out of 4 areas showing statistically significant effects of temperature. On the other hand, both predation and spawner effects showed no consistent relationship with snow crab recruitment between regions and generally weren't statistically significant.
- Modelling drift, growth and settlement of snow crab in the Bering Sea is presently limited by a lack of information on their prey and predators. A statistical model developed for phytoplankton in ice edge blooms, which are preyed upon by crab larvae, was able to match reasonably well chlorophyll biomass variability both temporally and spatially, but not their absolute values.
- A spatially-resolved Bering Sea snow crab recruitment model that included effects of female reproductive output, temperature, prey (chlorophyll-a index), predators (Pacific cod catch per unit effort) was able to capture 75% of the observed recruitment variability.
- On the Newfoundland/Labrador Shelf there is no evidence that predation is controlling snow crab abundance. In the case of shrimp, predation may be a factor, based on increasing importance of shrimp in observed diets of their predators and close predator-prey interactions but the amount of

shrimp consumed is considered more relevant to shrimp mortality rate. Despite increasing importance of shrimp in predator diets shrimp mortality rate is thought to remain low because of high shrimp biomass and low predator biomass.

- The shrimp stock in Ísafjarðardjúp, a fjord in northwestern Iceland, peaked in 1990 and collapsed in 2003. Both cod and haddock prey on shrimp and their abundances increased, after 2000 for cod and after 2003 for haddock. Shrimp and gadoid species inhabited different areas within the fjord in 1990 but the distribution of gadoid species has expanded recently.
- Based on studies of snow crab in several areas on the Newfound-land/Labrador shelves and in the Gulf of St. Lawrence, the size at 50%-maturity significantly increased throughout the available temperature range. Crabs residing at cold (warm) temperatures have relatively high (low) energy balances and undergo their final molt at small (large) sizes.
- Strong year classes in Japan Pacific walleye pollock occur when winds and currents act to retain eggs and larvae in Hidaka Bay, which leads to faster growth and lower mortality rates.

3 Suggestions for future work and recommendations

3.1 WG on Climate Effects on Upper Trophic Levels

The Working Group working on gadoid-invertebrate interactions noted that comprehensive datasets are now available for all systems except West Greenland. A clear picture of the importance of bottom-up (vs. top-down) control of snow crab has recently developed, but the mechanism remains unclear, e.g. temperature vs. chlorophyll. It was therefore recommended that WG should investigate the relationship of bottom temperature at settlement with chlorophyll in affecting snow crab abundance. Also, it was noted that there have been no studies on king crabs. Factors controlling shrimp abundance are poorly understood and need to be addressed. The primary objectives of the WG should be met with the results presented at the OSM in Seattle, 2011 and a special volume of papers on Gadoid-Crustacean interactions published following the meeting. With these the WG ToR will be completed and will terminate.

3.2 WG on Modelling Ecosystem Responses

This WG will continue with the development of the end-to-end model it has been working on. The modelling activities reported upon during the meeting were highly encouraging. Further cooperation and coordination of models and model development is needed. Comparison of ecosystem models of sub-Arctic seas is still a long term goal of the working group in order to increase our understanding the processes linking climate and fisheries to fish population responses. Bern Megrey and Kenny Rose, who have been co-chairs of the WG, announced at the meeting that they would be stepping down. Enrique Curchister will take over in their place.

3.3 Response to Climate Variability

The session on the response to Climate Variability was held in large part to determine where ESSAS should go on this topic. It was organized mainly by Jim Overland, who due to health issues could not attend the meeting. The discussion centred on whether a new ESSAS working group should be formed to focus on the complex topic of ecosystem responses to climate variability. The conversion of red noise of the physical system to redder (lower frequency) noise of the biological response was felt to be of special interest. This would include the abrupt and discontinuous biological (regime) shifts and transient climatic disturbance to prolonged ecosystem recovery. While there was strong support for the formation of a new WG on this topic, a decision on it and the nature it would take was postponed until detailed discussion with Dr. Overland were held.

3.4 Other Issues

The review of completed ESSAS research, which was one of the ToRs for the Workshop, was postponed and delayed until the ESSAS Open Science Meeting to be held in Seattle during May of 2011. This postponement will allow more of the general scientific community to hear and comment of the results of this research.

The contribution from those working in West Greenland waters was greatly appreciated and of interest. ESSAS expressed the desire to see further interaction between West Greenland researchers and those from other sub-Arctic seas in the future. In particular, it is hoped that some of the scientists stationed in Nuuk will join ESSAS. They should be able to benefit from the experience and results of research conducted elsewhere in sub-Arctic regions and ESSAS will gain from comparisons with their studies.

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Name	Country	Institution	E-mail Address
Thor Asgeirsson	Iceland	Marine Research Institute	thoras@hafro.is
Ólafur S. Ástþórsson	Iceland	Marine Research Institute	osa@hafro.is
Kumiko Azetsu-Scott	Canada	Fisheries and Oceans	Azetsu-ScottK@dfo-mpo.gc.ca
Andy Bakun	USA	University of Miami	abakun@rsmas.miami.edu
Stefan Brynjolfsson	Iceland	Marine Research Institute	stefbr@hafro.is
Julian Burgos	Iceland	Marine Research Institute	julian@hafro.is
Enrique Curchitser	USA	Rutgers University	enrique@marine.rutgers.edu
Earl Dawe	Canada	Fisheries and Oceans	earl.dawe@dfo-mpo.gc.ca
Ken Drinkwater (Co- Chair)	Norway	Institute of Marine Research	<u>ken.drinkwater@imr.no</u>
Baldvin Einarsson	Iceland	University of Iceland	baldvine@gmail.com
Haraldur Einarsson	Iceland	Marine Research Institute	<u>haraldur@hafro.is</u>
Hrafnkell Eiriksson	Iceland	Marine Research Institute	<u>keli@hafro.is</u>
Ástþór Gíslason	Iceland	Marine Research Institute	astthor@hafro.is
Hafsteinn Guðfinnsson	Iceland	Marine Research Institute	hafgud@hafro.is
Cecille Hansen	Norway	Institute of Marine Research	cecille.hansen@imr.no
Erica Head	Canada	Fisheries and Oceans	heade@dfo-mpo.gc.ca
Solfrid Sætre Hjøllo	Norway	Institute of Marine Research	Solfrid.hollo@imr.no
George Hunt (Co- Chair)	USA	University of Washington	glhunt@uci.edu
Carsten Hvingel	Norway	Institute of Marine Research	carsten.hvingel@imr.no
Sigrún Jónasdóttir	Denmark	National Institute for Aquatic Resources	<u>sjo@aqua.dtu.dk</u>
Ingibjörg Jónsdóttir	Iceland	Marine Research Institute	ingibj@hafro.is
Steingrímur Jónsson	Iceland	Marine Research Institute	steing@hafro.is
Trond Kristiansen	Norway	Institute of Marine Research	trond.kristiansen@imr.no
Jon Kristjansson	Iceland	Works as consultant	jonkr@mmedia.is
Jason S. Link	USA	National Oceanic and Atmospheric Administration	Jason.link@noaa.gov
Kai Logemann	Iceland	University of Iceland	<u>kai@hi.is</u>
Arni Magnusson	Iceland	Marine Research Institute	arnima@hafro.is
Laurinda Marcello	USA	University of Alaska	laurinda.marcello@alaska.edu
Margaret McBride	Norway	Institute of Marine Research	margaret.mary.mcbride@imr.no
Bernard Megrey	USA	National Oceanic and Atmospheric Administration	
Mikio Moriyasu	Canada	Fisheries and Oceans	Mikio.Moriyasu@dfo-mpo.gc.ca
Kjell Arne Mork	Norway	Institute of Marine Research	kjell.arne.mork@imr.no
Franz Mueter	USA	University of Alaska	fmueter@alaska.edu
Paul Myers	Canada	University of Alberta	Pmyers@ualberta.ca
Torkel Gissel Nielsen	Denmark	National Institute for Aquatic Resources	<u>tgin@aqua.dtu.dk</u>
Sólveig Ólafsdóttir	Iceland	Marine Research Institute	solveig@hafro.is
Jon Olafsson	Iceland	Marine Research Institute	jon@hafro.is

Annex 1: List of participants

Ólafur K. Pálsson	Iceland	Marine Research Institute	okp@hafro.is
Hildur Pétursdóttir	Iceland	Marine Research Institute	hildur@hafro.is
Kenny Rose	USA	Louisiana State University	karose@lsu.edu
Gary Sharp	USA	Center for Climate/Ocean Resources Study	gsharp@redshift.com
Sven Þ. Sigurdsson	Iceland	University of Iceland	sven@hi.is
Thorsteinn Sigurdsson	Iceland	Marine Research Institute	<u>steini@hafro.is</u>
Jóhann Sigurjónsson	Iceland	Marine Research Institute	johann@hafro.is
Dag Slagstad	Norway	SINTEF Fisheries and Aquaculture	Dag.Slagstad@sintef.no
Svein Sundby	Norway	Institute of Marine Research	svein.sundby@imr.no
Konrad Thorisson	Iceland	Marine Research Institute	konrad@hafro.is
Héðinn Valdimarsson	Iceland	Marine Research Institute	hv@hafro.is
Frode Vikebø	Norway	Institute of Marine Research	frode.vikeboe@imr.no
Kai Wieland	Denmark	National Institute for Aquatic	<u>kw@aqua.dtu.dk</u>
Orio Yamamura	Japan	Hokkaido National Fisheries Research Institute	orioy@affrc.go.jp

Annex 2: Agenda

ESSAS Annual Science Meeting 30 August – 1September, 2010 Reykjavik, Iceland

Monday, 30 August

- 08:30-08:00 Registration
- 08:50-09:00 Welcome from Ken Drinkwater (ESSAS Co-Chair, Norway) and Johann Sigurjonsson (Director MRI, Iceland). Local arrangements and practical information Ólafur S Astthorsson (Deputy Director MRI)
- 09:00-12:25 Iceland Sea and East Greenland Sea Ecosystems Chair: Ólafur K. Palsson
- 09:00-09:25 Hedinn Valdimarsson/Steingrimur Jonsson
 The hydrographic conditions of the Iceland Sea and role of the Kolbeinsey Ridge
 09:25-09:50 Kjell Arne Mork/Ken Drinkwater,Steingrimur Jónsson/Tor Villy Kangas,
 - Hédinn Valdimarsson²

Exchanges between Iceland and Norwegian Seas

- 09:50-10:15 Hafsteinn Gudfinnsson/Solveig Olafsdottir Nutrients and phytoplankton changes in the Iceland Sea, 2006-2008
- 10:15-10:45 Break
- 10:45-11:10 Astthor Gislason/Teresa Silva/Hildur Petursdottir/Hafsteinn G. Gudfinnsson Abundance, composition and development of zooplankton in the subarctic Iceland Sea
- 11:10-11:35 Hildur Petursdottir Trophic interactions and energy flow within the pelagic ecosystem in the Iceland Sea, 2007 and 2008
- 11:35-12:00 Konrad Thorisson/Bjorn Gunnarsson Drift, age and origin of capelin larvae
- 12:00-12:25 Ólafur K. Palsson/Sveinn Sveinbjornsson/Hedinn Valdimarsson/Astthor Gislason Capelin life history in the Iceland Sea. Recent stock trends under climate change

12:25-13:30 Lunch

- 13:30-16:55 West Greenland and Labrador Sea Ecosystems Chairs: Kai Wieland/Erica Head
- 13:30-14:15 Torkel Gissel Nielsen/Andy Visser. The Greenland Climate Research Centre and plankton ecology in West Greenland waters with comments on climate effects
- 14:20-14:45
 Sigrun Jonasdottir

 Zooplankton dynamics in a Greenland fjord

14:45-15:15 E	Break
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15:15-15:40	Kai Wieland
	Recruitment failure of shrimp and cod off West Greenland - What went wrong?
15:40-16:05	Erica Head
	Zooplankton and environmental conditions in the Labrador Sea (1995-2008)
16:05-16:30	Kumiko Azetsu-Scott
	A physical-chemical overview of the Labrador Sea: Convection, Circulation,
	Freshwater and Ocean Acidification

- 16:30-16:55 Paul Myers Observations and Modeling of West Greenland and Labrador Currents and their Variability
- 18:00-20.00 Reception

Tuesday, 31 August

09:00-12:15	Climate Variability and Fish Populations
	Chairs: Ken Drinkwater/Jim Overland

09:00-09:40	Gary Sharpe
	Overview of subarctic species and climate
09:40-10:10	Andy Bakun
	Types of biological responses to climate signals
10:10-10:30	Franz Mueter
	PDO, Salmon, and the Bering Sea Revisited

10:10-10:50 Break

10.50-11:10	Svein Sundby
	Cod, Capelin, and Climate in the NE Atlantic/Barents Sea
11:10-11:30	George Hunt
	Update on the OCH Hypothesis- interacting time scales
11:30-12:15	Ken Drinkwater

- Open discussion regarding new ESSAS working group
- 12:15-13:30 Lunch
- 13:30-16:50 WG3 Modeling Ecosystem Response Chairs: Bern Megrey/Kenny Rose
- 13:30-13:50 Enrique Curchitser A Climate-to-fish-to-fishers model for marine ecosystems: Implementation for North Pacific forage fish
 13:50-14:10 Bernard Megrey, et al.
 - CAMEO Stock Production Modeling Workshop: Quantitative tools to compare sub-arctic marine ecosystems
- 14:10-14:30 J.S Link/E.A. Fulton/R.J. Gamble

	Lessons learned from applying an end-to-end full system model in a well- studied fisheries context: The ATLANTIS NEUS experience
14:30-14:50	Kenny Rose
	End-to-End Models: Can we? Should we? What is new?
14:50-15:10	Frode Vikebø
	Modeling of larval herring in the Norwegian Sea- the importance of timing
15:10-15:30	Break
15:30-15:50	Solfrid Hjøllo
	Coupled physical- biological IBM modeling at IMR: from ocean physics to zoo-
	plankton and fish, - and back again
15:50-16:10	Trond Kristiansen/Charles Stock/Ken Drinkwater/Enrique Curchister
	Effects of climate change on the survival of larval cod
16:10-16:30	Kai Logemann/Gudrun Marteinsdottir
	The ocean model CODE and its application to Icelandic waters
16:30-16:50	Baldvin Einarsson/Bjorn Birnir/Svend Þ. Sigurdsson
	Integrating dynamic energy budget model into a capelin migration model
16:50-17:10	Dag Slagstad
	Changes in phytoplankton and zooplankton production in the Nordic Seas un-
	der a warmer climatic regime

Wednesday 1 September

09:00-12:15	WG4 — Gadoid-Invertebrate Interactions
	Co-Chairs: Earl Dawe/Franz Mueter

09:00-09:25	Julian Burgos/Sarah Hinckley/Carolina Parada/Billy Ernst/José María
	(Lobo) Orensanz/ David A. Armstrong/Cody Szuwalski
	Explaining the recruitment of Bering Sea snow crabs based on biological and
	physical factors
09:25-09:50	Laurinda Marcello/Franz Mueter/Earl Dawe/Mikio Moriyasu
	Relative effects of predation and the environment on recruitment in snow crab

09:50-10:15 M. Koen-Alonso/D. Mullowney/D. Stansbury/E. Dawe Predator-prey and spatial interactions between crustaceans (snow crab and northern shrimp) and fishes (Atlantic cod and Greenland halibut) on the Newfoundland-Labrador Shelf

10:15-10:45 Break

10:45-11:10	Ingibjorg Jonsdottir
	Interaction between northern shrimp and cod in Ísafjarðardjúp, northwest Ice-
	land
11:10-11:35	Orio Yamamura/Tetsuichiro Funamoto/Masayuki Chimura/Tomonori
Hamatsu	
	Recruitment control of Japan Pacific walleye pollock in relation to environ-
	mental variability
11:35-12:00	Mikio Moriyasu/Earl Dawe/Darrell Mullowney/Elmer Wade/F. Jacques

Effects of bottom temperature on size at terminal molt in snow crab: Case study off Newfoundland and Labrador and in the southern Gulf of St. Lawrence

- 12:00-12:20 Discussion
- 12:25-13:30 Lunch
- 13:30-16:30 Working Group Closed Sessions Future Directions, Planning Activities, Etc.
- 16:30-18:00 **Open discussion on ESSAS future activities including brief reports from WGs** Chair: Ken Drinkwater
- 18:00 Close of Meeting

Annex 3: Extended abstracts of presentations

Theme Session 1: Iceland Sea and East Greenland Sea Ecosystems

The Hydrographic Conditions of Iceland Sea and Role of Kolbeinsey Ridge

Hedinn Valdimarsson/Steingrimur Jonsson

Marine Research Institute, Iceland

Over the last decades, the Iceland Sea has been influenced increasingly by waters of Atlantic origin via the inflow through the Denmark Strait to the area north of Iceland and the inflow south of Jan Mayen. During this time increasing temperatures and salinities have been observed in the Return Atlantic Water which enters the Iceland Sea from the north. Similarly this period has been one with rather meagre coverage of sea ice in the area. These conditions are reflected in observations taken in the Iceland Sea when the 3-year (2006–2008) ICE Project studying the ecology of the capelin stock was ongoing. In this project, detailed studies were undertaken on the hydrographic and current features on the Kolbeinsey Ridge with a vessel mounted ADCP and a mooring profiler. These revealed an anticyclonic gyre on the east side of the Ridge, which has the potential to act as a retention area for the marine life in this area. This retention area is further supported by the distribution of capelin juveniles.

Exchanges between the Iceland and Norwegian Seas

Kjell Arne Mork¹, Ken Drinkwater¹, Steingrimur Jónsson², Tor-Villy Kangas³, and Hédinn Valdimarsson²

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<sup>1</sup> Institute of Marine Research and Bjerknes Centre for Climate Research, Bergen, Norway
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² Marine Research Institute, Iceland

³ Former Institute of Marine Research, Bergen, Norway

The Jan Mayen Ridge, which runs southwards from Jan Mayen, separates the warmer and saltier Atlantic water in the Norwegian Sea from the colder and fresher Arctic water in the Iceland Sea. The border between these water masses forms the Jan Mayen Front, which is an area of high importance for the ecosystem. Still, little is known in this area regarding the water mass exchanges - in terms of currents and processes, and where the exchanges occur. Two cruises were carried out in this area, in 2007 and 2008, as part of the International Polar Year (IPY) project Norwegian component of the Ecosystem Studies of Arctic and Sub-Arctic Regions (NESSAR). A wide range of field observations were collected, including hydrographic observations. Two moorings were additionally deployed, providing current measurements over 2 years, with the purpose to investigate the flow between the Norwegian and Iceland seas. The 2 moorings were deployed in different areas: on the Ridge at 800 m depth and in a deep canyon within the Ridge at 2000 m depth (Figure 1.). On the Ridge, hydrographic observations show that the depth of modified Atlantic Water ranges from 100 m near Jan Mayen, to 400 m depth in the canyon. In a west-east section across the Ridge, modified Atlantic Water is observed to the west, i.e. in the Iceland Sea. The current measurements show a net weak unstable flow of Atlantic Water from the Norwegian Sea to the Iceland Sea at the Ridge (JM-1), with no significant seasonal variation, except near the bottom. In the channel (JM-2), the current in the upper 600 m varies seasonally; in winter there is a net flow from the Norwegian Sea to the Iceland Sea, in summer the flow is in the opposite direction. Near the bottom in



the channel there is a net flow of deep water from the Norwegian Sea into the Iceland Sea during both seasons.

Figure 1. Upper panel: bottom topography at the Jan Mayen Ridge, and locations of the two moorings (JM-1 and JM-2). Lower panel: time-mean velocities for winter and summer. Positive values are flow from the Iceland Sea to the Norwegian Sea, while negative values are opposite directed flow.

Nutrients and phytoplankton changes in the Iceland Sea 2006–2008

Hafsteinn G. Gudfinnsson, Solveig R. Olafsdottir

Marine Research Institute, Reykjavik, Iceland

The Iceland Sea was sampled during 8 cruises (February–August/ 2006–2008) for hydrography, nutrients, and phytoplankton. Here we present results from a 69°N transect (18°50′W-11°20W) located in the middle of the Iceland Sea, stretching west to east over the Kolbeinsey Ridge. Nutrient concentrations in the surface layer are highest at the end of the winter mixing, which in some years may not finish until March-April. Nutrient concentrations before the spring phytoplankton growth depend on the mixed-layer depth during the winter. Differences in the nutrient budget were found east and west of the Kolbeinsey Ridge with generally lower silicate concentrations on the eastern side of the ridge. This resulted in early silicate depletion on the eastern side of the ridge after the spring diatom bloom; while low silicate concentration were observed on the western side of the ridge. Nitrates and phosphates were found in low concentrations at the surface layer (0–30 m) on the eastern side of the ridge during July 2006 and August 2007; at the same time nitrates and phosphates had been exhausted on the western side. In contrast, both nitrates and phosphates had been totally exhausted in the Iceland Sea during August 2008.

Phytoplankton growth starts in April. Even though stratification is weak, phytoplankton can be found observed down to 100 m depth. Spring bloom maximum is over by the end of May 2006, when phytoplankton growth can only be found within the stratified layer. By this time, diatoms have used up the silicate supplies. Phytoplankton biomass and production decreases during the summer; as the stratified layer becomes stronger and shallower, nutrients are strongly reduced or exhausted. Diatoms seem to be the main producers from early spring to early summer. Small flagellates seem to be important in the ecosystem throughout the growth season, especially during late summer. Dinoflagellates were observed to have similar abundances throughout the growth season.

Daily primary production at a 68°N transect was measured at 0.2 to 2.4 g m-2 day-1 during the phytoplankton growth season; whereas daily production at the 69°N transect was lower and measured 0.2 to 1.1 g m-2 day-1. Primary production during late summer at 69°N is most likely based on regenerated nutrients as stratification is strong and little mixing across the thermocline takes place.

Abundance, composition and development of zooplankton in the subarctic Iceland Sea

Astthor Gislason, Teresa Silva, Hildur Petursdottir, Hafsteinn G. Gudfinnsson

Marine Research Institute, Reykjavik, Iceland

The abundance, composition and development of zooplankton in the subarctic Iceland Sea was studied in relation to hydrographic features and phytoplankton growth during summer in three years (2006–2008), as based on large scale sampling from the upper 50 m of the water column and depth-stratified sampling from the whole water column at selected sites. The region historically serves as the main nursery and feeding grounds of the Icelandic capelin stock. The results show marked differences in abundance and composition of the plankton community both seasonally within the year and between years. Zooplankton was mostly confined to the deeper layers during the winter and had ascended to the surface layers by May. The zooplankton stayed in the surface layers until August, thereafter animals descended to deeper layers. Mesozooplankton diversity in late summer (July/August) was highly variable but tended to be highest near the shelf edges east of Greenland and north of Iceland and during both winter and summer was also generally higher at depth than near the surface. Among the mesozooplankton, six species made up approximately 90% of total numbers and >98% of copepod biomass.

Relations between the zooplankton community and environmental parameters in late summer were established using redundancy analysis (RDA). In total, 27% of meso-zooplankton variability could be explained by five variables (longitude, year, temperature, chlorophyll a, salinity). Two main zooplankton communities could be identified, an Arctic community in the western parts of the study area with *Calanus hyperboreus, C. glacialis* and *Microcalanus* spp. as most abundant, and an Atlantic community in the eastern parts with relatively high numbers of *C. finmarchicus, Oithona* spp. and *Pseudocalanus* spp. It is noteworthy that the Atlantic species were particularly abundant in 2007. The fact that longitude and hydrography (temperature and salinity) had a significant effect on the species composition probably reflects the importance of advection in the system, where cold water species are being advected into the region from the northwest by the East-Greenland Current and warm water species are coming from the east.

The most abundant macroplankton species were the euphausiids Thysanoessa longicaudata, and T. inermis, and the amphipods Themisto abyssorum and T. libellula. As with the mesozooplankton, their distribution seemed to be heavily influenced by advection. Calanus finmarchicus and C. hyperboreus were the biomass-dominant copepods. *C. finmarchicus* overwintered at ~200–600 m depth at low temperatures (~0°C). The animals had ascended to the surface layers by early May where reproduction and growth took place, mainly in the upper 50 m of the water column. After August the animals then returned to deep waters for overwintering. The data on stage structure indicate a one-year life cycle for this species. C. hyperboreus also stayed deep during winter (~200-1000 m). However, in contrast with C. finmarchicus, these animals reproduced at depth during winter and the offspring from the winter reproduction may not have developed beyond stage 3 during the first summer. Thus the seasonal stage structure suggests that this species may have a 2–3 year life cycle. In general, the zooplankton community in the Iceland Sea was characterized by a mixture of Arctic associated and Atlantic associated species, reflecting that the region is a meeting place of Arctic and Atlantic species, with the copepods C. finmarchicus and C. hy*perboreus* as key players.

Trophic relations of zooplankton in the Iceland Sea

Hildur Petursdottir

Marine Research Institute, Reykjavik, Iceland

A trophic study was carried out in August 2007 and 2008 on the pelagic ecosystem in the sub-arctic Iceland Sea, north of Iceland, using carbon and nitrogen stable isotopes and fatty acid biomarkers. The aim was to study trophic linkages and positions of the most important pelagic species in this ecosystem with special emphasis on the trophic ecology of capelin. According to ¹⁵N enrichment it is concluded that there are around 4 trophic levels in this pelagic ecosystem excluding bird and mammals,

where the primarily herbivorous copepod *Calanus finmarchicus* occupies the lowest trophic level of the studied species and adults of capelin (*Mallotus villosus*) and blue whiting (*Micromesistius poutassou*) the highest. *Calanus* spp. proved to be important diet component (high amount of *Calanus* fatty acid trophic markers in the neutral lipid fraction), of most of the studied species. However the euphausiid species *Thy*-*sanoessa inermis* and *T. longicaudata* are exceptions as *Calanus* spp. are of minor importance in their diet. The chaetognath, *Eukrohnia hamata*, is a pure carnivore, feeding almost exclusively on *Calanus* spp., while most of the others zooplankton species studied practice omnivorous-carnivorous feeding mode. Young *T. inermis* is important food component for larvae and juveniles of capelin and large individuals of the amphipod species *Themisto libellula* are important in the diet of adult capelin. The importance of *Calanus* spp. or *Calanus* derived diet increases with the size of capelin. Adults of capelin and blue whiting share the same feeding habits and could therefore be competing for food. This study is a part of an ecological study in the Iceland Sea, with field work lasting from 2006–2008.

Drift, Age, and Origin of Capelin Larvae

Konrad Thorisson and Bjorn Gunnarsson

Marine Research Institute, Reykjavik, Iceland

In 2007 an effort was made to map the spawning and drift of capelin larvae in Icelandic waters. In April and May samples were collected using a 1m² opening Tucker trawl (Figure 1). In August, pelagic 0-group capelin were sampled with a large Tucker (4m² opening) in shelf areas, but larger 0-group capelin found deep off the north coast were sampled with a pelagic juvenile trawl. In subsamples, daily rings in otoliths were read to back-calculate hatch date distributions. Hatch date distributions from the pelagic trawl catches were used to trace the most likely origin of the 0group.



Figure 1. Distribution of capelin larvae in April, May and August. Area of green circles: numbers in Tucker trawl/1000 m³). In August, larvae were also sampled with pelagic juvenile trawl (yellow squares: numbers per nautical mile towed).

Historically, the 0-group capelin found north and east of the country in the fall are believed to originate from the main spawning grounds at the south and west coasts. The capelin drifts with clockwise currents around Iceland, with average speed of about 3 nm/d (Brickman *et al.* 2007). The reconstructed hatch date distribution (Figure 2) shows that the surviving juvenile capelin in August cannot originate from the spawning grounds in the southeast (red X in Figure 2). Capelin drifting against currents from the northeast area is also unlikely. Most of the 0-group capelin thus originate from the southwest and west of Iceland, but at least 10 % originate from spawning areas north off Iceland.

When the present data are compared to earlier findings, all the observed changes are towards earlier and/or more to the north. More (or earlier) spawning west of Iceland than 100 years ago (Petersen 1920), more (or earlier) spawning north of Iceland than 30 years ago (Fridgeirsson 1979) and more 0-group capelin found farther north than earlier (at $\geq 68^{\circ}$ N, MRI reports 1970–2003).



Figure 2. Capelin larvae caught in August using pelagic juvenile trawl (top panel). Backcalculated hatching days (bottom panel) ajusted by assumed mortality. Mortality of early larvae was calculated (as 7%) from a patch in area 1, sampled in April and again in May. Mortality of older larvae (2.5%) is set according to Pedersen *et al.* 2009. The surviving larvae in August (squares in right panel) cannot be from area 1 (red X). Arrows (about 90 nm long) show average drift during one month.

Trends in capelin life-history traits in the Iceland Sea

Ólafur K. Pálsson, Sveinn Sveinbjörnsson, Héðinn Valdimarsson, Ástþór Gíslason, Hjálmar Vilhjálmsson

Marine Research Institute, Reykjavík, Iceland

Capelin (Mallotus villosus) life history was investigated in three extensive surveys in July 2006 and August 2007 and 2008 in the Iceland Sea Project 2006–2008. This paper presents some of the main results of these surveys, incorporating also some data from previous research efforts in the area for comparison. Analyses of life history traits, i.e., growth (length, weight), feeding and fat content, indicate that these traits have generally been without a trend during the last three decades. Distribution of capelin, on the other hand, has changed substantially in recent years. Distribution of 0-group capelin was more westerly and northerly in 2006–2008 than observed before, while distribution of older capelin (ages 1–3), on the other hand, was more southerly and westerly than previously. Further, all age groups were less abundant than in previous years. Capelin ambient temperature on 4 selected stations was in the range -1.5 to 4°C. The geographic distribution of 0-group capelin by mean length in August 2008 indicates that the fish drift into the southern part of the Iceland Sea and from there onto East Greenland continental shelf waters, to new, eventually less favourable, nursery areas. Extreme, northerly distribution pattern of 0-group capelin, outside the Icelandic continental shelf, was first observed in August 2003 and seems to have prevailed since. This coincides with the onset of greatly reduced recruitment in the capelin stock. The hypothesis is tempting that these events may be traced to the same cause, which is likely to originate earlier in capelin life history.

Theme Session 2: West Greenland and Labrador Sea Ecosystems

The Greenland Climate Research Centre: Its oceanography and marine ecology components

Torkel G. Nielsen¹, Andre W. Visser¹, John Mortensen² and Colin Stedmon³ ¹National Institute of Aquatic Resources, Denmark ²Greenland Climate Research Centre ³National Environmental Research Institute, Denmark

The arctic marine ecosystem is under substantial environmental stress. Climate changes will directly or indirectly impact the marine ecosystem, through changes in sea-ice coverage, solar radiation, availability of nutrients and carbon dioxide, and the mixed-layer depth. The seasonality in these factors drives the characteristic annual patterns observed in the plankton succession in the sea. The talk presents our work undertaken at the Greenland Climate Research Centre (www.natur.gl) and stresses the importance of the close coupling between metrology, oceanography and pelagic ecology which if we have to understand to determine the impact of climate change on the marine pelagic ecosystems.

When the sea ice breaks, the establishment of a stratification of the water column triggers the primary production by keeping the phytoplankton in the nutrient rich, illuminated part of the water column and the spring phytoplankton bloom develops. The onset of the spring bloom varies between years depending on the duration of ice cover and the meteorological conditions, and there is a strong positive correlation between the open water period and the magnitude of the annual primary production. The spring phytoplankton bloom is the single most important event determining the secondary production capacity of arctic marine food webs.

A key group in the arctic marine ecosystem is copepods of the genus *Calanus*. Through the food chain, the lipid level increases from 10–20% of dry mass in phytoplankton to 50-70 % in Calanus. This lipid-based energy flux is one of the primary reasons for the large stocks of fish, birds and mammals in Arctic waters. This talk summarizes our work on the pelagic food web in the Disko Bay region with emphasis on how climate changes influence the *Calanus* spp. directly and indirectly and how this may propagate through the food web to higher trophic levels.

Zooplankton dynamics in a Greenland fjord

Sigrún H. Jónasdóttir¹, Kristine Arendt², Eva Friis Møller³, Torkel Gissel Nielsen¹

¹ DTU Aqua, Charlottenlund Denmark

² GNI, Nuuk, Greenland

³ NERI, Roskilde, Denmark The Godthåbsfjord (Nuuk fjord) Western Greenland is an ideal system to study the possible effect of climate change on arctic marine ecosystems. The system offers a gradient from warm oceanic environment outside the fjord (Fylla Bank) to an ice covered water in the head of the fjord where the inland ice flows into the fjord (Figure 1). We can expect that with warmer climate, the physical changes that will impact the arctic ecosystem will be higher atmospheric- and ocean temperatures, less sea-ice coverage, thinner sea-ice, increased glacial melt, increased precipitation and stronger stratification. DTU Aqua, Greenland Climate Research Centre and the National Environmental Research Institute conducted 2 cruises (June 2010 and August 2008) following this gradient. The physical, chemical and biological environment was studied intensively to investigate the varied processes acting along this gradient. Data on copepod species distribution in the fjord show a clear species separation along the 200 km transect. For example, C. finmarchicus was mainly found outside and in the opening of the fjord in waters with coastal water characteristics, while C. glacialis and *Metridia longa* were inside the fjord in cooler fresher waters of a more arctic character. With focus on two of the contrasting copepod species, the boreal C. finmarchicus and the subarctic *M. longa*, we made intensive study on their production rates and faecal pellet production to understand what controls their population growth and biology in the fjord system. Preliminary results from the 2008 cruise were presented.



Figure 1. Density distribution in Godthåbfjord where the warm high density water from the Labrador Sea spills over the sill into the fjord and the cold fresh water from the glacial melt dominates the upper 100 m water in the fjord.

Recruitment Failure of Atlantic Cod and Northern Shrimp off West Greenland – What went wrong?

Kai Wieland

Technical University of Denmark, Institute of Aquatic Resources (DTU Aqua)

Relative warm conditions prevailed at Greenland from the beginning to the mid of the 20th century and in this period a self-sustaining and very abundant cod stock existed in West Greenland offshore waters. A prolonged period of decline in stock biomass was observed from 1950 to 1975 when fishing mortality was far above an appropriate level considering a low productivity of the stock due to unfavourable temperature condition for growth and recruitment. The offshore cod stock collapsed completely in the beginning of the 1990s and fishing on this resource came to an end. First again in 2003, a year classes of considerable size emerged, which have originated through larval drift from spawning off Iceland as there was virtually no spawning stock left off East and West Greenland at that time. Furthermore, this year class had a pronounced southerly distribution, emigrated from West Greenland waters when becoming mature and did thus not contribute to a rebuilding of the spawning stock.

In the mid-1990s, increasing recruitment of Northern shrimp was observed when warmer temperatures returned. The strong year classes resulted in a threefold increase in stock biomass until 2003 following a couple of years with of above average recruitment. In the most recent years, however, shrimp disappeared from Southwest Greenland. Recruitment and subsequently stock biomass decreased although no further increase in temperature occurred and predation by cod remained low due low cod abundances and spatial overlap in the distribution of the two species.

Average air and ocean temperatures in the past 15 years have been the highest on record, but so far the cod stock off West Greenland has not recovered. Hence, expectations based on historical experience that the return of warm conditions would result in a return of cod to West Greenland offshore waters and that predation by an increasing cod stock would cause a drastic decline in biomass of Northern shrimp failed. The ultimate reasons for the recruitment failure of the two species in the recent years are poorly understood and this makes reliable predictions of the effects of climate change on the future development of these two commercially important fishing resources difficult.

Zooplankton and environmental conditions in the Labrador Sea

Erica Head

Fisheries and Oceans, Canada

Distributions of zooplankton species in the Labrador Sea region reflect differences in water sources (Arctic versus N. Atlantic) and in the timing of sampling versus individual species' annual production cycles, which also vary regionally. During spring and summer the N. Atlantic copepod *Calanus finmarchicus* dominates the zooplankton biomass in the central basin, whereas two arctic *Calanus* species (*C. glacialis* and *C. hyperboreus*) are as important on the Labrador/Newfoundland Shelf (Lab/Newf Sh). Year-round sampling on the Newfoundland Shelf, however, shows that the arctic *Calanus* species are absent from July to February. On the Lab/Newf Sh the arctic *Calanus* species reproduce before the spring bloom, so that their offspring are found as young copepodites during the bloom, whereas *C. finmarchicus* reproduces during the bloom with its young stages appearing after the bloom. In the central basin *C. fin*-

marchicus reproduces before and/or during the spring bloom, but large numbers of young stages are found during the bloom only in eastern regions, while in the central region mortality rates seem to be very high. The small ubiquitous copepod *Oithona* spp. is very abundant on the Newfoundland Shelf year-round, with highest numbers occurring in winter. *Oithona* spp. is less abundant on the Labrador Shelf in spring and summer, and reaches high abundances in the central basin only in summer. *Pseudocalanus* spp., another small copepod species, is restricted to the Lab/Newf Sh and is most abundant in fall. Over 12 years of satellite observations, sea-surface temperatures have been increasing in the central basin, spring blooms have been starting earlier and annual average sea-surface chlorophyll concentrations have been increasing. These changes seem to be advancing the seasonal cycle of *C. finmarchicus*. Further temperature increases in the future could lead to a greater degree of synchrony between the timing of the spring bloom and the seasonal cycle of *C. finmarchicus* production in the central Labrador Sea, which might promote higher survival rates and higher overall production.

A physical-chemical overview of the Labrador Sea

Kumiko Azetsu-Scott

Department of Fisheries and Oceans Bedford Institute of Oceanography Canada

Deep convection in the Labrador Sea in late winter varies from 500m to over 2000m depending on atmospheric conditions and stratification in the water column. This produces a relatively homogeneous water mass, Labrador Sea Water (LSW). This well-ventilated water mass, characterized by low salinity and temperature, provides an important vehicle for the transport of atmospheric gases, including carbon dioxide and transient tracers such as chlorofluorocarbons (CFCs), and feeds the intermediate depths of the North Atlantic. At depth in the Labrador Sea, North East Atlantic Deep Water (NEADW) and Denmark Strait Overflow Water (DSOW) that were formed in the Nordic seas flow into the region. Consequently, all of the water masses in the Labrador Sea are relatively young (<20 years). The rate of formation of these water masses influences the global ocean circulation, therefore the modulation of the long-term global climate.

During the 1980s to early 1990s, the record volume of cold and dense LSW was produced and the deep convection reached to 2400m depth. Since the mid-1990s, the LSW has become warmer and saltier and mild winters lead to the relatively shallow convection (500–1100m) during this period. However, the deep convection reached 1600m depth in 2008 and produced a new class of cold and fresh LSW. This disruption of warming trend in the LSW is due to the atmospheric cooling during the winter of 2007/2008.

Freshwater input to the Labrador Sea influences convection regimes, ocean circulation as well as surface chemistry. An estimate using oxygen isotope composition indicated meteoric water (glacial meltwater) was a dominant freshwater source (~4m) in the surface water (<100m) at Greenland Shelf and Slope in 2009. Time series observations of total alkalinity in the newly ventilated LSW showed freshwater incorporated in this water mass had a high alkalinity/salinity ratio, namely Arctic rivers, during the low salinity phase of 1990s to early 2000s.

Arctic outflow and the local uptake of anthropogenic CO₂ (CO₂ released by human activities, mainly by fossil fuel combustion) are major controlling mechanisms of the

ocean acidification state in the Labrador Sea. The Arctic outflow makes regions with highly productive ecosystems and the important commercial fisheries, more susceptible to future ocean acidification. The Labrador Sea is the site of a strong solubility pump, by which anthropogenic CO₂ is sequestered from the atmosphere to the depths by chemical and physical processes. Ocean acidification influences the capacity of the ocean uptake of CO₂ from the atmosphere. In newly ventilated LSW, the steady increase of total CO₂ due to the uptake of anthropogenic CO₂ from the atmosphere, the decreases of pH and the saturation state were observed. In the late-century, the newly ventilated LSW becomes corrosive to the organisms with calcium carbonate shells and skeletons.

Observations and Modeling of West Greenland and Labrador Currents and their Variability

Paul Myers

University of Alberta, Edmonton, Alberta, Canada

Historical data is used to analyze hydrographic properties as well as transports (volume and freshwater) in the boundary currents of the Labrador Sea. Both mean fields as well as long term variability is analyzed. Questions of the influence of Arctic outflows as well as discharge from the Greenland Ice Sheet will be considered. Influence of changes in the ocean circulation in recent years on tidewaters glaciers in West Greenland will also be discussed. The historical observations will be used to help understand and improve eddy-permitting numerical model simulations of the sub-polar gyre. Specific questions of model drift, boundary current dynamics and sea ice representation will be covered.

Theme Session 3: Climate Variability and Fish Populations

Projecting Climate Changes and Ecological Responses: Coping With Changes

Gary D. Sharp¹, Leonid Klyashtorin², and Douglas McLain^{1,3}

¹Center for Climate/Ocean Resources Study, Salinas, CA. ²Russian Federal Research Institute of Fishery and Oceanography (VNIRO), Moscow ³CoML/TOPP, Pacific Grove, CA

Climate change has long been known and documented in many locations as being responsible for major ecological responses in regional ocean ecosystems. In the 1960–1980s I was introduced to some of the 'olde fishing culture' topics by several colleagues, including the Director of FAO Fisheries Department, Armin Lindquist, who we asked to open our discussion on the subject in the 1983 Expert Consultation to Examine the Changes in Abundance and Species Composition of Neritic Fish Resources, San Jose, Costa Rica (Lindquist, 1984). Research programs that were designed to understand these complex interactions on relevant scales have been rare, although a goal for many scientists since the late 1800s, recently reviewed by Julia Lajus – a Russian Social Scientist – at the July 2004 convergence by the International Commission on History of Meteorology under the title "From Beaufort to Bjerknes and Beyond: Critical Perspectives on the History of Meteorology". Lajus' abstract - "Influence of weather and climate on fisheries: overview of emergence, approval and perception of the idea, 1850–1950s".

The Lajus article begins with this: "Fishermen have long known that fisheries appear and disappear in time. Such events were attributed to changes in fish migration routes, harmful growth in numbers of natural predators of fish, and to the human impact: overfishing and water pollution (Smith, 1994, pp. 21-34). To note that weather, especially the changes in wind direction, could influence fisheries, was easier than to suppose that large periods of fish abundance could be connected with the fluctuation of climate. For example, Karl Ernst von Baer, famous German zoologist, who worked in Russia and in addition to many diverse activities was a head of several expeditions which surveyed the state of fisheries in 1850s, explained the severe decline of herring fisheries during several years in the eastern part of the Baltic Sea by very cold and windy springs occurred these years. He supposed that the winds pushed out the spawning herring from their usual spawning grounds (Baer, 1860). But at the same time he did not apply this kind of argumentation when he discussed the possible causes for the cessation of the very prosperous herring fisheries in Bohuslan region on the western coast of Sweden in the early 1800s. He supposed instead that it was the human-induces pollution due to fish oil production. For the first time the climatic explanation for the periodicity of these fisheries was suggested by Axel Ljungman in Sweden (Ljungman, 1882). He noted that the herring catches varied cyclically with a period of the fifty-year sunspot cycle and assumed that this relationship might be explained with changes in the weather. However, he was not able to propose the mechanism for that connection." And finishes with this statement: "After summarizing book by D. H. Cushing (1982) the notion that climate change could influence the fish resources and therefore fisheries became commonplace, but the question is still very important and new facts and correlations are discussed by fishery scientists in cooperation with climatologists and many others... The real issue is whether there is a direct causal link, or these are merely correlated consequences of larger scale processes." (All discussed and reviewed variously in Sharp, 1988, 1991, 1992a, 1992b, 1993a, 1993b, 1995, 1997, 1998, 2000a, 2003).

It has been my goal for decades, to bring local knowledge, expertise based on empirical observations into the resolution of the cause and effect issues – and I was fortunate to have begun my queries while these issues were being actively investigated in the laboratory and at sea by the Reuben Lasker, John Hunter, Elbert Ahlstrom and Paul Smith team at the La Jolla BCF/NOAA-NMFS Fisheries Research Laboratory, where the root stock of these basic approaches had been imported by Lasker *et al.* from the Fisheries Research Services Marine Laboratory - situated in Aberdeen, Scotland.

As Jorge Csirke and I concluded after our (Csirke and Sharp, 1984) review and report (Sharp and Csirke, 1984) of the Changes in Abundance and Species' Composition of Neritic Fish Resources, fisheries, stock assessment would be in a very different state if the North Sea were subject to El Niño events. Recent decades have been the hey-day for the near-miss regression/correlation approach to modeling environmental effects on resources populations.

At the 2000 IFFET gathering in Portland, Oregon, Sharp provided a "Brief Review of the History of Fisheries Science and its Relation to Fish Culture". That presentation outlines the important role of "studies done in the mid-1800s by Norwegian fisheries biologists and laboratory scientists (that) created the first controlled scientific environments for studying the early life history stages, rearing, and release programs in support of ocean fisheries enhancement. By the end of the 19th Century methods and concepts were transferred to Canada and the USA, to become the basis of North American fisheries science." My chapter (Sharp 2000b) entitled "Tuna Oceanography - An Applied Science" was published in "Tuna: Physiology, Ecology & Evolution", edited by Barbara Block and Don Stevens – links all of these developments in time.
Meanwhile, back in 1987 I wrote an essay – on request from John Hunter, editor of the AFS (American Fisheries Society) Monthly - "Averaging the Way to Inadequate Information in a Varying World" in response to the Benguela 86 Symposium where one of the participants decided to make a very strange recantation of the scientific method. There was sufficient evidence, in his view, to suggest that there was no reason to do the causal research in fisheries-related marine ecology, once the conventional average fishery information or parameter estimates were available. This statement came as a surprise - and disappointment - as it came from an exceptionally talented mathematical analyst. Perhaps doubly so, since among the several dozen other presentations at this symposium there were also very memorable contributions that evidenced the value of understanding the causal sequences of climatic to, oceanographic, to ecological events and patterns, that characterize the dynamic Benguela Current Ecosystem, in particular its periodic reversion from one quasi-stable state to another (e.g. Sharp 1987). Once stated, such a position will make it more difficult to induce such "enlightened" folk to recognize the logical errors that lead to these wrong conclusions. Shannon et al. (1992) summarized nicely what had taken place over the previous decade – and expanded the region's approach to System Science, as fisheries science should eventually evolve to become. After a few more years of intensive in situ sampling - Verheye (2000) provided a reasonable historical review for the Benguela Current System that warranted more attention than it received – that confirmed the value of empirically-based science.

While Ocean Fisheries Ecosystem Modeling has become an academic field of general interest, the empirical observations necessary to build and implement effective models are rarely available, creating many examples of unreliable and unverified model results that too often simply do not represent anything of real utility. EG, Models that don't reflect environmental contextual changes, directly, such as changes in thermal habitats, as well as wind and cloud cover related production patterns, and direct species responses to well described known forces, other than simplistic Top-Downdriven trophic energy transfers, cannot reliably provide the needed insights necessary to either explain past changes, or project potential future changes.

There is a subtle philosophical twist attendant to the failure of these partial models to forecast *ad infinitum* the patterns of any populations' responses to regimes outside the models' basis, or too often too short reference period. There is no reason to expect that the low-level population dynamics modeling that we have accomplished could forecast any but past responses. That is 'if' the signals were strong enough to make projections from. Yet, these generic models assume average responses without querying the potential for any other dominant variables to emerge.

In fisheries science, the most important relevant realization that needs to be made is the following: "The average fish dies within its first week of life!"

Where does this leave our 'average' population modelers? With myriad surviving not-so-average fish. In fact the 'average conditions' of the ocean will not support most fish life at all. Therefore, there must be some alternative way to organize the science if we are ever to reach the objective of forecasting even the less subtle aspects of marine populations such as changes in relative abundance or their distributions. I think that the solution is for fisheries researchers to go back to the basic questions of elementary biology. What mechanisms do the various populations have, and at what developmental stages, that allow them to survive local environmental perturbations? What are the conditions to which these individuals are adapted, and finally, what perturbs these conditions in time and space, and what 'options' are available for the generations involved? Unfortunately, due to reluctance by many agency policy makers to fund the necessary monitoring of both physical and ecological components, and the dominant presumption that underlying all ecology there are fundamental equilibrium processes that determine the System State – 'surprises' keep occurring.

Emanating from this cascade of physical and biological signals are the unique experiences of surviving individuals, not the deadly averages. All long known, as per Sharp's Chapter in the 1981 ICES Report, "Colonization in fishes - some inferences concerning requirements and opportunism in the sea" in which I/he brought together the basic concept that was a result of a decade or so of research by the fisheries laboratory staff in La Jolla, that showed that "the egg to larval transformation period" is the greatest potential "bottleneck" period for a fish population, then one can also conclude that the complexities of the following life stages represent an evolutionarily successful egg's way of getting itself reproduced and deposited in an appropriate environment.

Also included were insights from a review of FAO Annual Catch Statistics provided the trajectories of catch trends from 1970 and 1977 (Table 1). The examples in Table 1 provide the relative catch variations in 25 local or regional pelagic fisheries from the years 1970 to 1977. All these examples varied by more than plus or minus 5X during this eight year period. - This is why we need to be careful when 'modern' computer-based studies use *percentage change* criteria as their basis for doom and gloom scenarios – (e.g. Worm *et al.* 2006). As if no oceanic fisheries exhibited this level of apparent abundance variation within short periods, apart from a few cases where political or economic factors other than basic resource abundance, rather than changing markets or environmentally determined vulnerability (or availability) have affected the total landings.

		(A)	(B)	
Species	Area	Peak catch	Low Catch	Ratio A/B
Caranx hippos	West Africa	28 221	1 036	27.0 +
Orcynopsis unicolor	West Africa	2 600	100	26.0
Trachurus capensis	Southwest Africa	690 164	62 300	11.0 +
Trichiurus lepturus	Southwest Africa	28 545	3 800	7.5 +
Trachurus trecae	Southwest Africa	273 700	31 298	8.7
Sardinella spp.	Southwest Africa	142 200	20 986	6.8+
Scomber japonicus	Peru	65 000	8 700	7.5 +
Scomber japonicus	Northeast Atlantic	39 000	6 262	6.2
Rastrelliger spp.	Eastern Indian Ocean	16 300	2 000	9.2 +
Rastrelliger kanagurta	Eastern Indian Ocean	203 100	35 403	5.7
Anchovies	Western Indian Ocean	118 062	16 900	7.0 +
Psenopsis anomala	Northwest Pacific Ocean	n 13 000	1 994	7.0
Sardinops melanosticta	NW Pacific Ocean	1 420 512	16 900	84.0 ++
Engraulis mordax	Eastern Pacific Ocean	289 002	44 600	6.4 +
Cetengraulis mysticete	East Tropical Pacific	168 081	15 551	10.8 +
Trachurus symmetricus	Eastern Pacific Ocean	50 149	9 400	5.3 +
Sarda chiliensis	Southeast Pacific Ocean	74 700	4 341	17.2
Scomberomorus	Peru	2 279	400	5.7 +
Engraulis ringens	Peru	13 059 900	907 175	16.0
Sardinops sagax	Peru-Chile	$1\ 467\ 555$	68 600	21.0 +
Trachurus trachurus	Peru-Chile	839 805	111 300	7.6 +
Thyrsitops lapidopodes	Chile	7 200	630	11.6
Cetengraulis edentulous	Venezuela	4 965	850	5.8+
Decapterus russelli	Malaysia-Thailand	109 337	9 800	11.2 +
St Scomberoides spp.	Indonesia-Philippines	5 186	500	10.0 +

Table 1. Trajectories of catch trends between 1970 and 1977.

Plus and minus signs in Table 1 represent directions of trends during the reference period. Changes in both directions in the order indicated. The indication – + implies sharp changes in both directions, in the order indicated.

Twenty years later I encountered the works of Leonid Klyashtorin (1997, 1998), and introduced him to colleagues at FAO Fisheries Department in Rome. Klyashtorin was invited to come and present his work, and then asked to write a Technical Report – for which I was asked to do the final English editing for publication, Klyashtorin L.B. 2001. "Climate change and long-term fluctuations of commercial catches: the possibility of forecasting." FAO Fisheries Technical Report No.410, 98pp. FAO of the United Nations, Rome. Available online via this link: http://www.fao.org/DOCREP/005/Y2787E/y2787e01.htm#TopOfPage>.

Sharp followed up on this work, and with contributions in collaboration with Joseph Fletcher and Douglas Hoyt (both strong proponents for Solar influences on the ongoing climate changes,) and others, generating another technical report - "Future climate change and regional fisheries: a collaborative analysis" – in which you can read my views on the consequences of future climate change on regional fisheries around the globe - available from FAO Library via this link:

ftp://ftp.fao.org/docrep/fao/006/y5028e/y5028e00.pdf

Given these insights and the long-term insights from olde cultures about Atmospheric Cycles, and consequent species dynamics, it is now possible to focus on when and where to monitor various properties that will enhance the benefits of both System Monitoring and Resource Management. We provide examples for future reference.

In 2001, Klyashtorin was invited as Visiting Scientist at NOAA NMFS Pacific Fisheries Environmental Laboratory in Monterey Bay, and we began sharing ideas and had discussions of how to get the Olde Russian climate science brought into western scientist's attention, to help bring western science forward. On his return to Russia, Klyashtorin has written many new papers with several of his mathematically gifted colleagues - and given presentations at several meetings. In 2005, Leonid Klyashtorin and Alexey Lyubushin's 234 page book on "Cyclic Climate Changes and Fish Productivity" was published – In Russian – providing a long overdue re-introduction to the means for coping with the comings and goings of major fisheries populations. In 2007 the English translation was published, for which I was, again, asked to do the final editing. Among some hundred graphics, the following three provide useful hints about where we should all be heading – by looking forward – based on Historical Information. Their work shows that year-to-year forecasts are not rigorous, only longer time spans and cycle-related trends.

Types of biological responses to climate signals: How are we ever going to finally figure this out?

Andrew Bakun

Rosenstiel School of Marine and Atmospheric Science, University of Miami, USA

It is clear that climatic variability can have major effects on the population dynamics of exploited fish stocks. The resulting unexplained variability in resource abundance and distribution tends even to obscure the key linkages and dynamical thresholds that determine the consequences of human impacts, notably fishing, on marine populations and ecosystems. In particular, we seem to be continually surprised by the population responses even of the primary exploited population itself. And if surprise remains the rule, i.e., if we cannot predict the outcomes of actions taken, how can we hope to manage the heavy impacts we impose on the systems so as to yield the results that we consider most preferable (or least deplorable)? Nevertheless, after decades of effort, an adequate understanding of the linkages of climate to fish population dynamics continues to largely elude us. We have various assumptions as to the nature of those linkages, and lots of ostensibly predictive models based on those assumptions, but little real predictability and little clear understanding (other than the obvious asymptotic limit to all possible dynamical trajectories, i.e., that if we catch all the fish today, there will be none to catch tomorrow).

Certainly, the conventional paradigm that has dominated fisheries science over the past half-century has clung to some rather arbitrary assumptions that seem to have been largely based on terrestrial, rather than marine, experiences and insights (i.e., perhaps better reflecting the dynamics of one's garden pond than those of an ocean ecosystem). On the contrary, analysis of measured data has shown marine ecosystems to be dynamically nonlinear (Hsieh *et al.*, 2005). There appear to be abundant possibilities for self-amplifying nonlinear feedback loops (Bakun & Weeks, 2006). To the extent that such feedbacks are realized, system trajectories may not converge toward unique solutions. Moreover, as the record of available experience lengthens, it is becoming apparent that marine ecosystems in many ways operate as **complex**

adaptive systems (Levin, 1998, 1999), meaning that the systems may be continually altering their structure and operation as they react to a suite of external stresses (climatic variations, fishing, habitat alteration, etc.), which calls into question assumptions of stationarity needed for empirical analysis, parameterization of models, etc.

So how can we hope to obtain the multiple realizations (empirical degrees of freedom) needed to develop sufficient understanding of mechanisms to guide actions toward preferred outcomes? It is clear that setting up totally separate autonomous local models, each tuned to separate available local data sets and based on postulated terrestrial-like conceptual, has not worked, and most likely will not work. Rather, it would appear necessary to find ways to generalize the problem, so as to bring all available pertinent information together in some universal context to first solve (or to at least gather insight on) basic issues. Ernst Mayr (1982) identifies "the experimental method and the comparative method" as "the two great methods of science". On the scale on which large, mobile marine populations operate, experimental controls are generally impractical. The comparative method is the available alternative. But effectively utilizing experiences in multiple different systems requires a consistent comparative framework on which to array the information in a way that may reveal informative patterns. Attempting to do this in terms of complete (complex, nonlinearly-evolving) histories seems pretty futile. One fruitful approach might be to focus on fairly short time scales (one to several years) when a particular "response template" (Bakun 2010) may stand out in a recognizable way.

Prominent among such templates that have been proposed and elaborated in the scientific literature are the following:

- 1. Response in direct phase with climatic forcing
- 2. Multiple stable states (Scheffer et al. 2001)
- 3. "Regime shifts" (as usually conceived, a simple combination of items '1' and '2')
- 4. Match-mismatch hypothesis (Cushing 1971, 1975, 1990)
- 5. Connectivity ("member-vagrant") (Sinclair1988, Cowen et al. 2006)
- 6. School trap (Bakun and Cury 1999)
- 7. Loopholes (Bakun and Broad 2003)
- 8. Ocean triads (Bakun 1996)
- 9. Stable ocean hypothesis (Lasker 1975, 1978)
- 10. Optimal environmental window (Cury and Roy 1989)
- 11. Basin model (MacCall 1990)
- 12. Dynamic pattern (MacCall 2002)

Nonlinear feedback mechanisms

- 13. "P2P" loop (Walters and Kitchell 2001), Bakun and Weeks 2006).
- 14. "School-mix feedback" loop (Bakun 2001, 2005)
- 15. "Predator pit" loop (Bakun 2006)

As an illustrative example of the proposed approach, the famous mid-1970s Pacific Ocean-wide "regime shift" (Lluch Belda *et al.* 1989, Beamish 1995), most often attributed as a combination of item '2' (multiple stable states) and item '1' (response in direct phase with climatic forcing), is shown to perhaps better correspond to an interpretation in terms of a "loopholes" template (Bakun and Broad 2003).

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Linking climate and fish in the Northeast Pacific

Franz Mueter¹ and Mike Litzow²

¹ School of Fisheries and Ocean Sciences, University of Alaska, USA ² Blue World Research, Anchorage, Alaska, USA

We re-examined decadal-scale and longer-term trends in physical and biological indicators of Northeast Pacific climate variability and how they may affect fish populations, with particular emphasis on the eastern Bering Sea. The Pacific Decadal Oscillation continues to dominate sea-surface temperature (SST) variability in the Northeast Pacific, accounting for 22% of the variability in 1900–2009 gridded SST data (NOAA extended reconstructed dataset ERSST v.3), while the second mode of variability (Victoria Pattern) accounted for 12% of the variability. If global means are not removed prior to the analysis, the first mode remains associated with the PDO-type pattern and the long-term (linear) trend accounts for approximately 10% of the overall variability in 1900-2009 SST data. The long-term linear trend is most pronounced in the summer and has a spatial pattern which suggests warming throughout the North Pacific with the most pronounced warming trends in the eastern Bering Sea and around Japan (Figure 1). While the long-term trend accounts for less than 5% of the overall variability over much of the North Pacific, it accounts for 20–25% of the 1900–2009 variability in the Bering Sea. Based on climate projections, the long-term trend will be the dominant mode of variability in the 21st century (Overland and Wang 2007), accounting for 56% of North Pacific SST variability in (for example) GFDL climate model projections (ESM2.1 model, R. Rykaczewski, pers. comm.). In the eastern Bering Sea, the SST trend has been associated with an increase of over 50% in "growing degree days", defined as degree days above the overall mean SST (~ 4° C). This is likely to have profound impacts on the physiology of many marine organisms.



Figure 1. Long-term trends in summer (June-September) sea-surface temperature in the northern North Pacific from 1900–2009 (°C/decade) based on NOAA extended reconstructed data (ERSST v.3).

A directional trend in the overall physical and biological variability in the Northeast Pacific, which may reflect a response to the long-term warming trend, is evident in an update and re-analysis of the physical and biological data series compiled by Hare and Mantua (2000). We updated 98 of the original 100 time series and summarized variability in these series using a Principal Components Analysis. The first two principal components (PCs) accounted for 33% of the overall variability and suggested a directional change in Northeast Pacific variability characterized by three successive "states" (Figure 2). The transition from the first to the second state corresponds to the well-documented regime shift of 1976/1977 and represents the largest change in the space of the first two principal components observed in any given year. The second transition occurred more gradually and corresponds to the 1988/1989 shift that was also previously documented by Hare and Mantua (2000). The largest single-year shift after the 1976/1977 transition occurred in 1999, but was short-lived with conditions quickly returning to those characteristic of the 1990s. A separate analysis of physical (31) and biological (67) time series showed that the 1976/1977 transition is evident in both the physical and biological series, while later changes are only evident in the biological series. Principal components based on physical time series of variability displayed high interannual variability, while PCs based on biological series showed much more gradual, but also more pronounced directional changes.



Figure 2. First two modes of variability from a Principal Components Analysis of 98 time series representing physical and biological variability in the Northeast Pacific Ocean from 1965-2006. Three sequential clusters were identified by a cluster analysis. The two largest changes in the time series are indicated by arrows.



Figure 3. Sockeye survival rate index against eastern Bering Sea sea-surface temperature during summer of outmigration with linear regression fit and survival index over time with linear time trend for 1977–2006.

The response of individual species to climate variability in the Northeast Pacific is variable and is poorly understood for most species. We briefly discuss several examples of observed responses of fish to climate variability in the eastern Bering Sea for which mechanisms have been proposed. Pacific salmon in the northern part of their range respond directly to changes in coastal sea-surface temperatures during their early marine life stage (Mueter et al. 2002) with higher temperatures leading to faster growth and higher survival, as exemplified by sockeye salmon (Oncorhynchus nerka) in Bristol Bay (Figure 3). However, temperature accounts for a small proportion of the variability in sockeye salmon survival and there has been a steady and significant decrease in average survival since the 1976/1977 shift (Figure 3). Walleye pollock and other groundfish species responded to the 1976/1977 transition to generally warmer temperatures with an increase in average recruitment and many species had several strong year classes in the late 1970s and early 1980s (Mueter et al. 2007). However, recruitment of walleye pollock during recent warm years has been much lower than expected. A mechanism related to variability in temperature and ice conditions and its impact on zooplankton prey has been proposed to explain an observed domeshaped relationship between pollock survival and summer SST (see Hunt, this report). Finally, several flatfish species showed reduced recruitment in the 1990s due to unfavourable winds that failed to transport newly hatched larvae to suitable nursery areas (Wilderbuer et al. 2002).

Simultaneous changes across a range of species in the eastern Bering Sea suggests strong directional changes in relative recruitment success and relative species composition (Figure 4).



Figure 4. Principal Component scores representing major modes of variability in 18 time series of fish and seabird productivity in the eastern Bering Sea (top) and in 46 time series of catch-perunit effort of fish and shellfish taxa from annual eastern Bering Sea bottom trawl survey.

We explored changes across multiple species in the eastern Bering Sea through multivariate ordinations of 18 time series of productivity of fish and seabird populations from 1977–2005 and of 46 time series of trawl survey abundances of selected fish and shellfish taxa from 1982–2008. The first mode of variability accounted for 23% of the variability in productivity series and 21% of the variability in (fourth-root transformed) catch-per-unit-effort series (Figure 4). In both cases, results suggest a strong and significant directional trend over time.

We conclude that the long-term trend in SST over the last century represents a major component of SST variability in the North Pacific, particularly in the Bering Sea, and is likely to represent the dominant mode of variability in the 21st century. Simultaneously, the Northeast Pacific ecosystem has experienced directional changes since the mid-1960s that can be represented by three successive ecosystem states with a short-term "reversal" in 1999 towards conditions resembling those of the pre-1977 period. This perturbation was short-lived, possibly indicating inherent resilience of the system. Strong directional shifts in biological communities in the eastern Bering Sea over the past 25–30 years appear to exceed decadal scales of variability and may reflect a response to the long-term temperature trend rather than a response to decadal-scale variability. While these long-term trends were evident across multiple species, the responses of individual species to climate variability are highly variable and the mechanisms driving these responses are poorly understood. Extrapolating multivariate trends into the future is not advised without a better mechanistic understanding for predicting future productivity or abundance of individual species of interest.

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Cod, capelin, and climate in the NE Atlantic/Barents Sea

Svein Sundby, Geir Odd Johansen and Jan Erik Stiansen

Institute of Marine Research, Bergen, Norway

Cod, capelin, herring and other key fish species in the Barents Sea have changed their areas of distribution towards the north and east during the recent warming since the mid-1980s of the North Atlantic. The distributions of the fish stocks developed similarly during the previous warming from the 1920s to the 1940s, and during the cooling (1960s–1970s) between these two periods the opposite change occurred with a southward and westward shift in habitat distributions. Boral species like cod and herring also increased in abundance during the warmings and decreased in abundance during the coolings. The Arcto-Norwegian cod has also changed their spawning areas on a multidecadal time scale, moving northwards along the Norwegian coast when warming occurred and moving southwards along the coast when cooling occurred. The changes in abundance of arctic species like capelin due to climate changes are not similarly clear. However, capelin is probably affected indirectly through the responses from their predators with an inverse development of the abundance.

Since the 1970s capelin biomass has been strongly fluctuating with a decadal periodicity. During the high capelin biomass events adult cod are benefitting from predation and increase their individual weight, while the prey of the capelin, the arctoboreal and arctic amphipodes, are deceasing in abundance. Moreover, high abundance of young herring (0–3 years) in the Barents Sea feed heavily on capelin larvae and represses recruitment of capelin.

Past multidecadal climate variability during the 20th century has revealed that ocean climate has impacted zooplankton and fish species in a linear and reversible manner with respect to both changes in distribution and abundance. Future climate change in the Barents Sea might cause ecosystem changes that are more abrupt because of more fundamental responses from both zooplankton and fish. Such responses could be changes in overwintering areas and spawning areas.

Climate impacts on eastern Bering Sea food webs: A synthesis of new data and an assessment of the Oscillating Control Hypothesis

George L. Hunt, Jr.¹, Kenneth O. Coyle³, Lisa Eisner⁴, Edward V. Farley⁴, Ron Heintz⁴, Franz Mueter⁵, Jeffery M. Napp², James E. Overland⁶, Patrick H. Ressler², Sigrid Salo⁶ Phyllis J. Stabeno⁶

¹School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA, USA
 ² NOAA-National Marine Fisheries Service, Alaska Fisheries Science Centre, Seattle, WA, USA
 ³Institute of Marine Science, University of Alaska, Fairbanks, AK, USA
 ⁴NOAA-National Marine Fisheries Service, Alaska Fisheries Science Centre, Juneau, AK, USA
 ⁵Juneau Centre, School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Juneau, AK, USA

⁶NOAA/OAR Pacific Marine Environmental Laboratory, Seattle, WA, USA

Walleye pollock (Theragra chalcogramma) is an important component of the eastern Bering Sea ecosystem and the subject of major fisheries. The Oscillating Control Hypothesis (OCH) predicted that recruitment of pollock year-classes should be greatest in years with early ice retreat and late blooms in warm water because more energy would flow into the pelagic (vs. benthic) community. The OCH further predicted that, with pollock population growth, there should be a shift from bottom-up to topdown regulation. New data support the predictions that, in years with early ice retreat, more primary production accrues to the pelagic compartment, and that high numbers of age-0 pollock survive to summer. However, in these years, production of large crustacean zooplankton is reduced, depriving age-0 pollock of lipid-rich prey in summer and fall. Consequently, age-0 pollock energy reserves (depot lipids) are low and predation on them is increased. A disconnect between the number of age-0 pollock in their first summer and the number of age-1 recruits the following year results. A revised OCH indicates bottom-up constraints on pollock recruitment in very warm periods (Figure 1), as limitations in the availability of large crustacean zooplankton in fall result in age-0 pollock with insufficient lipid reserves for over-winter survival, and prey switching by larger fish, which results in increased predation on age-0 pollock (Figure 2). Prolonged warm periods with decreased ice cover will likely cause diminished pollock recruitment, and as a result fishery catches of pollock in the Bering Sea are likely to be severely reduced relative to recent values.



Figure 1. Revised OCH cartoon emphasizing that in warm years with an early ice retreat and a late bloom, mostly small, neritic copepods will be produced, whereas in cold years with late ice retreat and an early, ice-associated bloom, large Calanus marshallae will be favoured. Additionally, late ice retreat appears to favour the production of the shelf euphausiid, Thysanoessa raschii.

Warm year with late bloom and few large copepods or euphausiids





Cold year with early bloom and abundant large copepods and euphausiids

Figure 2. Cartoon emphasizing the shift in energy flow that results from the shift between a preponderance of small copepods and a preponderance of large copepods. When only small copepods are available, then age-0 walleye pollock are low in energy and may not have sufficient lipid reserves to survive their first winter. Additionally, larger fish, including walleye pollock and salmon may shift from a diet of mostly large copepods and euphausiids to one in which age-0 pollock play an important role.

Theme Session 4: Modelling Ecosystem Response

A Climate-to-fish-to-fishers model for marine ecosystems: Implementation for North Pacific forage fish

Enrique Curchitser

No Abstract available.

CAMEO Surplus Production Modelling Workshop: Quantitative tools to compare subarctic marine ecosystems

Bernard A. Megrey, Jason S. Link, Thomas J. Miller, Tim Essington, R. Ian Perry, Alida Bundy, Ken F. Drinkwater, and Erlend Moksness

Given the inherent complexity and large scale of marine ecosystems, progress toward understanding how marine ecosystems influence and regulate patterns of fisheries production requires a comparative approach. We present the results of an international workshop focused on applying various surplus production model configurations as a tool for ecosystem comparison with the goal to answer the question - how does ecosystem structure and function interact to support fisheries production, and what processes amplify, dampen or obstruct the production that ecosystems provide? Our workshop goal was to understand how multiple drivers of productivity in fishery ecosystems simultaneously interact to determine overall production levels. These drivers reflect the triad of factors influencing fisheries production including fisheries, the environment, and trophodynamics. In this presentation, we describe a common methodological framework (i.e., surplus production models) that span several levels of taxonomic aggregation for several species and communities from several marine ecosystems and examine model outputs from multiple production modelling packages. The methodology was applied to 11 northern hemisphere ecosystems (Figure 1). We estimate management-relevant metrics and ecosystem attributes and compare them across populations and ecosystems. We also describe the utility of applying surplus production models in single-species, multi-species, and aggregate species group frameworks. We conclude by elucidating challenges of fitting such modelling approaches to similar species or functional guilds in contrasting arrangements (different species within ecosystems and similar species between ecosystems) to better delineate what controls ecosystem fisheries production. Implications of our results for future work relevant to operational oceanography, population and community modelling, and ecosystem-based fisheries management are discussed.



Figure 1. The various Northern Hemisphere marine ecosystems examined.

Lessons learned from applying an end-to-end full system model in a well-studied fisheries context: The ATLANTIS NEUS experience

Jason S. Link¹, Elizabeth A. Fulton², Robert J. Gamble¹

¹NOAA, National Marine Fisheries Service, Northeast Fisheries Science Center, Woods Hole, MA, USA ²CSIRO Wealth from Oceans Flagship, Division of Marine and Atmospheric Research, Hobart, Tasmania, Australia

Increasingly, a broad range of considerations have come to the fore in the context of living marine resource and ocean-use management. These processes include a suite of various drivers, including bottom-up forcing, top-down caps, and middle-out tro-phodynamics. Furthermore, the management of living marine resources will increasingly require operating models that consider this wide range of processes that affect the function, structure and dynamics of a wide range of living marine resources and their supporting marine ecosystems. One way to elucidate this broad range of considerations is to use full ecosystem, or end-to-end, models. ATLANTIS is one such model which is not only capable of exploring the effects of fishing and ecological interactions among its modelled functional groups, but also incorporates such factors as hydrodynamics, nutrients, phytoplankton and zooplankton processes, fleet dynamics, and fishery markets. We present one application of ATLANTIS, as applied to the Northeast U.S. large marine ecosystem.

This work presents a brief view of the structure of this "virtual ecosystem" including the dynamics of water mass flow, nutrient, lower trophic level, upper trophic level, and fleet behaviour. We then highlight the main features of the calibration and validation process of this virtual system, executed at three levels of dynamism. Our results indicate that we can reasonably capture many of the main features of this ecosystem, particularly the dynamics of ecologically and commercially important biota. We also note instances where disconnects in our model validation exercise led to improved understanding of the ecosystem.

Additionally, in addition to the system dynamics, proposed management actions can also be modelled within ATLANTIS. Management actions can be applied at various reference levels, ranging from typical single species reference points to ecosystembased indicators. The management options which can be simulated by ATLANTIS are quite varied and include: catch and effort controls, spatial management, seasonal closures, technical controls, and discard rates. The goal of an operating model such as ATLANTIS is to provide strategic information regarding the potential effects of different management scenarios on an ecosystem.

We present example scenarios and how their results could be used to inform living marine resource management in a strategic manner, particularly in the assessment of large marine ecosystems. These scenarios not only show the potential efficacy of various management actions to achieve the goals set for the targeted functional groups, but also the indirect effects of such actions on other portions of the ecosystem and how they might be further modified under different environmental conditions caused by climate change. We conclude by discussing how one might utilize this modelling approach as an operating model for the implementation of Integrated Ecosystem Assessments in particular and Ecosystem Approaches to Management in general. We assert that the value of such an approach is to "test-drive" management decisions on a marine ecosystem before they are actually implemented, and in so doing identify those management strategies that are apt to be the most robust.

End-to-End Models: Should We? Can We? What is New?

Kenneth A. Rose¹, Enrique N. Curchitser², Kate Hedstrom³, Jerome Fiechter⁴, Sean Creekmore¹, Kate Shepard¹, Miguel Bernal²*, Shin-ichi Ito⁵, Salvador Lluch-Cota⁶, Alan Haynie⁷, Bernard A. Megrey⁷, Chris Edwards⁴

¹Department of Oceanography and Coastal Sciences, Louisiana State University, Baton Rouge, LA, USA
 ²Institute of Marine and Coastal Sciences, Rutgers University, New Brunswick, NJ, USA
 ³Arctic Region Supercomputing Center, Fairbanks AK, USA
 ⁴Ocean Sciences Department, University of California, Santa Cruz, CA, USA
 ⁵Tohoku National Fisheries Research Institute, Fisheries Research Agency, Shiogama-city Miyagi, Japan
 ⁶CIBNOR (The Northwestern Center of Biological Research), La Paz, Mexico
 ⁷NOAA Alaska Fisheries Science Center-NOAA, Seattle WA, USA

An ecosystem approach to understanding large-scale patterns in exploited fisheries systems caused by both climate change and human activity increasingly relies on the use of numerical models. In the past, physical, lower, and higher trophic level models were developed, tested, and implemented independently of each other. Recently, the advances in physics and biology have created the needed pieces for end-to-end (climate-to-physics-to-fish-to-fisheries) ecosystem models, including representing humans as a dynamical component. We discuss the current state-of-the-art of the end-to-end modelling in order to answer three questions: Should we? Can we? What is new?

Should we? Answer: yes. There is accelerating interest in end-to-end models. Fisheries management has been criticized for relying too heavily on a single-species approach. End-to-end models are conceptually and politically attractive because they address the demands for ecosystem-based fisheries management, and are well-suited for simulating climate change effects on fish and fisheries.

Can we? Answer: We think so. There is growing recognition of the need for integrative research from climate to physics to fish. There have also been advances in data collection, computing power, and physical and biological modelling that suggest the needed ingredients for end-to-end models are available. The issue of how to combine processes and models on different spatial and temporal scales remains a challenge. Two recent review papers (Plagnayi 2007; Fulton 2010) also suggest that end-to-end models can be developed. What is new? Answer: Caution is needed so we do not simply repackage poorlyperforming sub-models into poorly-performing "mega" (end-to-end) models. Rose et al. (2010) recently summarized the conclusions of a workshop and listed issues related to developing end-to-end models. These issues were: (1) the new goal of zooplankton modelling in nutrient-phytoplankton-zooplankton models of providing prey to fish rather than simulating biogeochemical cycling, (2) the need to include traditionally over-simplified or ignored organisms (e.g., jellyfish, fishers' behavior), (3) possibility of organisms acclimating and adapting to new conditions within model simulations, (4) how to combine sub-models that operate on different spatial and temporal scales; typical end-to-end models will include hydrodynamics on minutes and fish that live decades and organisms ranging in body weight from 10^{-8} to 10^{6} grams, (5) realistically representing behavioural movement of juvenile and adult fish, (6) software aspects of developing end-to-end models so that information can be easily shared among developers, (7) how to efficiently solve end-to-end models using uncoupled (off-line) and fully coupled solutions, and avoid artificial results with techniques such as super-individuals (e.g., Parry and Edwards 2008).

We present examples of our progress in three of these issues. In terms of issue (2), we describe how we are simulating fishing boats using a bioeconomic location choice submodel in an ongoing effort to develop an end-to-end model of sardine and anchovy in the California Current. We also present some results of our evaluation of using artificial neural networks with genetic algorithms to simulate behavioural movement of fish (Issue 5), and use a 2-dimensional model of Atlantic croaker in the Gulf of Mexico to illustrate a numerical artifact introduced by using superindividuals with density-dependent mortality (Issue 7).

We conclude by stating that end-to-end models should and can be developed. Some emphasize taking small steps first and incorporating climate into traditional population dynamics models for more immediate use for management decision-making (Stock *et al.* in press). In agreement with Stock *et al.* (in press), we encourage both the modification of existing models for near-term benefits and the development of new end-to-end models as a longer-term investment. We recommend that end-to-end models be carefully constructed to avoid creating a Frankenstein model (ugly piecing together of model parts) and avoid "just putting lipstick on a pig."

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Modelling of larval herring in the Norwegian Sea - the importance of timing

Vikebø, F.B., Husebø,Å., Slotte, A., Stenevik, E. K., and Lien, V. S.

Institute of Marine Research, Bergen, Norway.



Figure 1. Norwegian spring-spawning herring: (a) top - observed annual larval survival and mean hatch day, 1987–2004 (from Husebø et al., 2009); and (b) bottom - mean hatch day, simulated annual average latitude after 60 days of drift and average ambient temperature encountered, 1989–2008. Years for which enhanced survival was observed are shaded (from Vikebø *et al.*, 2010; Hinrichsen *et al.* 2010).

In building IBMs for larval Northeast Arctic cod and larval Norwegian springspawning herring, the physical environment of the Barents Sea ecosystem has been characterized using an ROMS model with an ice-module component (Budgell, 2005). The horizontal resolution is 4 × 4 km and daily averages are calculated and archived. Vertical forcing is effected using six-hourly information on ocean-atmosphere heat exchange and windstress. This approach appears to capture the main physical features of the larval habitats of both cod and herring (Vikebø et al., 2010). With respect to herring, a time-series analysis of observation and biophysical modeling results suggest that early hatching dates result in better survival (Figure 1a), although the initial temperatures experienced by larvae are lower than later in the season (Husebø et al., 2009; Vikebø et al., 2010, Hinrichsen et al., 2010). The greater survival of earlyhatched larvae might be partly caused by smaller spatio-temporal overlap with potential predators, along the drift route from the spawning areas to the nursery grounds. Northward displacement of the larvae after 2 months was generally higher when hatching happened early in the season, and this effect appears to be more important for larval survival than the ambient temperature (Figure 1b). The model also revealed that transport was faster at shallow depths than at greater depths. Identifying the temporal and spatial distributions of relevant prey and predators of larval cod and herring is essential for the existing models to be improved and recruitment predictions enhanced.

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Coupled physical- biological IBM modeling at IMR: from ocean physics to zooplankton and fish, - and back again

Solfrid Sætre Hjøllo, Geir Huse, Kjell Utne, and Morten D. Skogen

Institute of Marine Research, Bergen, Norway

Energy flow and bottom-up or top-down regulations are often well understood in closed freshwater communities. These regulations are harder to understand in large marine ecosystems, as the ecosystems extend over large areas and are influenced by surrounding marine areas. Fully coupled models have increased in popularity the last years, but these models are still in their infancy. Here we present NORWE-COM.E2E; a two-way coupled model system of the Norwegian Sea, including an ocean model, a phytoplankton model and individual based models of *Calanus finmarchicus* and planktivorous fish. We use ROMS fields of temperature, turbulence and current from the Regional Ocean Modelling System (ROMS) as an input to the other model component, and primary production from the NORWegian ECOlogical Model system (NORWECOM) (Skogen *et al.* 2007) to a *Calanus finmarchicus* IBM (Huse et al, submitted). The copepod *Calanus finmarchicus* is the dominant species of the mesozooplankton in the Norwegian Sea, and constitutes an important link between the phytoplankton and the higher trophic levels in the Norwegian Sea food chain. The *C. finmarchicus* IBM is based on super individuals and evolving traits for

behaviour, stages etc, and are two-way coupled to primary production model and IBM models for fish migration. The fish migration model is mainly driven by survey observations, but also *Calanus finmarchicus* densities. This leads to a predation pressure on zooplankton by fish in time and space that mimics what is observed in nature. The predation pressure by fish on the zooplankton stock is calculated by modeling individual fish growth using bioenergetics models.

First, we tested the model system by applying a uniform mortality rate for the Calanus, i.e. C. finmarchicus mortality from fish is parameterized as prey size and daylight dependent only (Hjøllo et al., subm). One year of modelled C. finmarchicus spatial distribution, production and biomass are compared to pointwise and areaintegrated observations, and are found to represent these reasonably well for the higher copepodite stages, while the abundance and biomass are above the observations for lower copopodite stages. Secondary production reaching 60gCm⁻² are found along the Norwegian shelf break and at the rim of the basins, and total annual Norwegian Sea production amounts to 34 mill tonnes Carbon (Figure 1). Monthly biomass estimates reveal an emergent PB-ratio; ranging from 5.4 to 7.4 for the summer months, which is comparable to previous estimates for the Norwegian Sea. Sensitivity tests show that the modelling system is robust to initial values of behavioural traits and with regards to the number of super individuals simulated given that this is above about 50 000 individuals. Experiments with the model system indicates that it provides a valuable tool for studies of ecosystem responses to causative forces such as prey density, fish predation or climate change; for example to introduce food limitations reduces the stock dramatically, while on the other hand, a reduced stock may rebuild in one year under normal conditions.

Thereafter, we applied the full two-way coupled model system to the same year; i.e. *C. finmarchicus* mortality from pelagic fish is year specific and geographically varying (Utne *et al.*, subm). We estimated that the major pelagic fish stocks in the Norwegian Sea, herring, mackerel and blue whiting, consumed a total of 82 million tons of zoo-plankton, including 35 million tons *C. finmarchicus*, in 1997. Furthermore, the interspecific competition has the greatest effect on blue whiting consumption, while herring consumption is unaffected by other fish species. We also analyzed the spatial distribution of *C. finmarchicus* in June and August and found the highest densities in the northern Norwegian Sea and around Iceland (Figure 2). The results give us a better understanding of the effect from fish predation on the Norwegian Sea ecosystem, and how this affects the *C. finmarchicus* stock.

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Figure 1. Geographical distribution of a) annual production and b) mean of daily top to bottom biomass within the Norwegian Sea. Units are in gC m⁻².



Upper 400m, C4-C6 C.Finmarchicus abundance [1000 individuals/m²] a) Mid-June with dynamic fish distribution b) Mid-Aug with dynamic fish distribution

Figure 2. The spatial distribution of *C. finmarchicus* in mid-June and mid-August from the model system when the predation from fish is uniform over the entire domain (a and c) and when the predation from fish is spatially explicit from the fish model (b and d).

Effects of climate change on the survival of larval cod

Trond Kristiansen¹, Charles Stock², Ken Drinkwater¹, and Enrique N. Curchitser³

¹Insititute of Marine Research, Nordnes, Norway ²Geophysical Fluid Dynamics Laboratory, Princeton University, USA ³Institute of Marine and Coastal Sciences, Rutgers University, New Jersey, USA

Understanding how climate change may impact important commercial fisheries is critical for developing sustainable fisheries management strategies. In this study, we used simulations from an Earth System Model (NOAA GFDL ESM2.1) to assess how future temperature and primary production will control the metabolic needs and growth potential of larval Atlantic cod. The physical and environmental data were incorporated into a mechanistic individual-based model used to simulate the critical early phases in the life of larval fish (e.g. cod) in a changing environment. A mechanistic approach allowed us to disentangle the key processes that regulate growth and survival of larval fish, and to identify how these processes operate in a nonlinear fashion. We also determined if future potential recruitment of Atlantic cod will differ strongly among populations in the North Atlantic because of differences in temperature and productivity. Local cod populations will be regulated by their physiological temperature limits and the predicted levels of prey abundance. We also analyze how climate change may affect the timing and production of phytoplankton, which we use to develop indices of timing of zooplankton, the main prey item for larval fish. Model simulations allow us to generate scenarios of survival for Atlantic cod across the North Atlantic to the year 2100. Together, these analyses will provide detailed predictions on the survival of larval cod in the North Atlantic under climate change.

The ocean model CODE and its application to Icelandic waters

Kai Logemann and Gudrun Marteinsdottir

University of Iceland, Department of Biology, Reykjavik, Iceland

In order to gain deeper insights into the role of physical processes in determining the variability of the Icelandic marine eco-system the workgroup MARICE, University of Iceland, is running a numerical model of the hydrodynamics of Icelandic waters and adjacent seas. The ocean model CODE (Cartesian coordinates Ocean model with three-Dimensional adaptive mesh refinement and primitive Equations) is used to create a dataset which contains the three-dimensional fields of temperature, salinity and flow around Iceland covering the years 1948 to 2008 with a spatial and temporal resolution of 1 km and 3 hours respectively. The model, its numerics and layout are described. The simulation and new insights into the circulation of Icelandic waters are presented.

Integrating a dynamic energy budget model into a capelin migration model

Baldvin Einarsson, Björn Birnir, and Sven Sigurðsson

University of Iceland, Reykjavik, Iceland University of California, Santa Barbara, CA, USA

We discuss previous results from an interacting particle model, which was used to model the spawning migration of the Icelandic capelin (*Mallotus villosus*). We describe a Dynamic Energy Budget (DEB) model on the inner dynamics of the capelin. We introduce to the DEB model a new state variable to describe the roe production. The parameters of the DEB model are then fitted to data on the capelin from the Marine Research Institute of Iceland and Matís, an Icelandic Food and Biotech R&D. We describe how measurable quantities are obtained from the DEB state variables. Plausible parameter values are found which result in good fits between theory and observations. The DEB theory successfully reproduces weight, length, fat percentage, and roe percentage of the Icelandic capelin. We then discuss how we intend to use these results with the interacting particle model, mentioned above, by letting the speed and temperature preference of particles be determined by their roe percentage.

Changes in phytoplankton and zooplankton production in the Nordic Seas under a warmer climatic regime

Dag Slagstad

SINTEF Fisheries and Aquaculture (Norwegian: Stiftelsen for industriell og teknisk forskning), Trondheim, Norway

The production regime in the Nordic Seas is to a large degree controlled by different water masses. In Atlantic regions, deep winter mixing ensures that nutrients are brought towards the surface. Thermal stratification initiates the spring bloom, but does also limits the nutrient supply during the summer. In Arctic and Coastal region stratification is first initiated by melting ice or fresh water supply from land. These processes are likely to change with the predicted increase in air temperature, especially at high latitudes. One way to assess the effect of such changes on the biological processes is to use numerical models. We present here results from a coupled hydrodynamic, ice, chemical and biological models system (SINMOD) of the Arctic ocean and the Nordic Seas using atmospheric forcing from 1979 to 2009 (ECMWF). Results from sensitivity tests using output from a global atmospheric model (ECHAM5/MPI-

OM ensemble runs for the IPCC A2) and scenarios using artificial increase in Arctic air temperature will also be shown. Preliminary results indicate that there will be a shift in distribution of *Calanus finmarchicus* and *C. glacialis* in the Barents Sea around 2060 (A2 scenario). *C. finmarchicus* will still not be able to develop a population in Arctic Ocean even in a strong warming scenario. Primary production in the Norwe-gian and Southern Barents Sea appears to be more constrained by nutrient limitation when stratification increases as a result of reduced heat flux to the atmosphere.

Theme Session 5: Gadoid-Invertebrate Interactions

Relative effects of predation and the environment on recruitment in snow crab

Laurinda Marcello¹, Franz Mueter¹, Earl Dawe², and Mikio Moriyasu³

¹School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Juneau, AK 99801 ²Fisheries and Oceans Canada, Northwest Atlantic Fisheries Centre, St John's, NL ³Fisheries and Oceans Canada, Gulf Fisheries Centre, Moncton, Canada

Variability in the abundance or biomass of snow crab is thought to be driven largely by changes in recruitment (Zheng & Kruse 2006). Recruitment to a certain size class, which reflects production and early survival, is highly variable (Example: Figure 1). However, it is poorly known what drives recruitment variability.



Bering Sea Snow Crab Recruitment



We investigated the effects of the environment, predation and spawners on snow crab. We hypothesized that 1) colder temperatures or higher ice/cold area coverage would be associated with increased recruitment, 2) increased biomass/abundance of potential predators would be associated with decreased recruitment, and 3) spawners would have an effect (possible density-dependence). We used a regression approach to model the relationship between these explanatory variables and snow crab recruitment (or, where not available, CPUE) in four areas representing three large marine ecosystems: the Eastern Bering Sea, NAFO (Northwest Atlantic Fisheries Organization) Division 3K and Division 3L on the Newfoundland/Labrador Shelf, and Division 4T in the Gulf of St. Lawrence. Results were compared across systems to determine if estimated effects were consistent among regions.

In exploratory analyses, several different time lags and rolling averages of explanatory variables were used to examine potential relationships occurring at appropriate snow crab life stages. Several lags were tested to bracket biologically reasonable time frames for the hypothesized effects of predation and environmental influences (Hérbert *et al.* 2002, Chabot *et al.* 2008, Dawe *et al.* 2010). After determining the appropriate lags, generalized additive models were used to check for any obvious non-linear effects. If non-linear effects were identified, we substituted polynomial terms with the equivalent degrees of freedom for ease of model comparison and interpretation. Also, the response variable (snow crab recruitment or catch-per-unit-effort) was examined to see whether a transformation was required to achieve approximate normality of the residuals.

For each system, the full model(s) included one environmental variable, one or more predators, and a spawning biomass time series (or proxy). Non-significant variables were eliminated from the model and residuals were tested for autocorrelation (Durbin-Watson test). If autocorrelation was present, we included a first-order autoregressive error term in the model and re-estimated the model using generalized least squares. The small-sample Akaike Information Criterion was used to determine the best model. For some ecosystems the predator and/or spawner series were much shorter than other data series, so for these systems both "short" and "long" models were tested. Results from analyses using the short and long series were then compared for consistency.

In all cases, significant autocorrelation was present in the residuals and generalized least squares models with a first-order autoregressive structure were selected as the best model. Temperature was significantly negatively related to CPUE or to the log of snow crab recruitment in three of the four ecosystems, meaning that colder temperatures were linked with increased recruitment (Table 1). Higher ice cover was linked with increased recruitment in two ecosystems. Neither predators nor spawners showed a consistent effect across systems. Each of these variables was significantly negatively related to CPUE or log recruitment in only one system (predators in Division 3L and spawners in the eastern Bering Sea).

Table 1. Summary of model results for four areas. For the Bering Sea and Gulf of St. Lawrence the response variable was the log of the estimated number of recruits at a small size. In the two Newfoundland/Labrador systems the response variable was snow crab catch-per-unit-effort. Variables which were significant to the best model are shown in bold red. Variables marked "NS" were not significant. The sign of the non-significant effect is show in parentheses. "n=" indicates the number of years modelled for each system. In cases where the time series for predator and/or spawner variables were shorter than others, the shorter number of years modelled for each variable is also listed. In two cases the short models yielded results that were not consistent (marked "NC") with longer models because the sign of other significant variables changed.

	Bering Sea	New./Lab. 3K	New. /Lab. 3L	Gulf of St. Law-
	(n=24)	(n=32)	(n=35)	rence
				(n=21)
Temperature	Negative	NS (negative)	Negative	Negative
Ice or Cold	Not tested	Positive	Positive	NS (negative)
Area				
Gadoid	Pacific cod	Atlantic cod (n=18)	Atlantic cod (n=16)	Atlantic cod
Predators	NS (positive)	NC (positive)	Negative	NS (negative)
				Greenland hali-
				but(n=16)
				NC
Spawners	Negative	(n=21)	(n=24)	NS (positive)
		NS (positive)	NS (negative)	

The environmental effects found supported the hypothesis that colder temperatures during the early juvenile stages improve snow crab recruitment. However, for both gadoid predators and spawners, results were generally not as hypothesized and were inconsistent among regions. If the population distributions of or surveys for gadoid predators and snow crab recruits have little spatial or temporal overlap, then these variables may show no statistical relationship. Also, because Atlantic cod populations have recently been at low levels compared to historic trends, these populations may be too small to exert a top-down control on young snow crab.

In conclusion, our results suggest that while gadoid predators or spawners may be important in some systems, the environment has a larger and more consistent influence on snow crab recruitment. In all of the systems examined, colder conditions during the early juvenile stages appear to be associated with increased survival and therefore increased recruitment. However, we found residual patterns in recruitment and abundance in each system that were not explained by environmental variability, suggesting that other factors are important. These patterns were often cyclical at a decadal period and may result from internal community dynamics such as cannibalism of older/larger cohorts on younger cohorts.

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Predator-prey and spatial interactions between crustaceans (Snow Crab and Northern Shrimp) and fishes (Atlantic Cod and Greenland Halibut) on the Newfoundland-Labrador Shelf

M. Koen-Alonso/D. Mullowney/D. Stansbury/E. Dawe

E. Dawe, M. Koen-Alonso, D. Stansbury and D. Mullowney

Population Trends

A sharp 'regime shift' in the fishery on the Newfoundland-Labrador (NL) shelf occurred in the mid-1990s, as reflected by a sharp decline in landings of Atlantic Cod (*Gadus morhua*) and other groundfish and a sharp increase in landings of crustaceans; snow crab and northern shrimp (Figure 1). While the collapse of groundfish stocks has been widely attributed to heavy exploitation, the entire fish community collapsed, including most functional groups and non-commercial species. Only populations of arctic species, such as Greenland Halibut, did not collapse. Capelin, the most important forage species in this ecosystem, showed a dramatic decline in the early 1990s which was accompanied by significant changes in its biology.



Figure 1. Trends in annual landings of Atlantic Cod, Greenland Halibut, Northern Shrimp and Snow Crab on the NL shelf.

The concurrent increase in landings of crustaceans has been attributed primarily to release from predation by fishes. However, this increase is largely due to redirection of commercial fishing effort from collapsed groundfish stocks to crustacean resources. Survey time series of biomass indices are too short, especially for the crustaceans, to adequately address relationships between predator and prey population trajectories. Fishery abundance indices (CPUE) are slightly longer but are still inadequate to determine abundance relationships, especially for shrimp and its predators. However it appears that snow crab CPUE oscillated without change in level throughout the period of fish collapse to the present time.

Predator Diets

The issue of top-down control of crustacean populations was also addressed by examining the diet of potentially most important predators, Atlantic Cod and Greenland Halibut, from fall surveys conducted throughout the NL shelf. Trends in diets since the late 1970s show that benthic invertebrates (including snow crab) has not been an important component of the diet of either predator throughout the time series. However, the contribution of shrimp to the diet of both predators has increased since the early 1990s, concurrent with the decline in capelin abundance.



Capelin Shrimp Snow Crab Other

Figure 2. Spatial trends in contribution (percent by weight) of capelin, shrimp, snow crab, and other prey to the diet of Turbot during 2004–2008 and to that of cod in 2008.

In recent years (2004–2008, Figure 2) the contribution of snow crab to the diets of turbot (Greenland Halibut) and cod appears to be minimal for both fish predators considered. Presence of snow crab in the diet of turbot is truly sporadic. The shrimp contribution to the diet of turbot does not show any obvious trend in this period. On average, this prey constitutes 17% of turbot's diet (in biomass) in the northern region (Div. 2J3KL).

Shrimp was a very important prey for cod in 2008, but only in the northern area (Div. 2J3KL). In this region it represented 57% of the diet (in biomass). This represents a marked change from the more capelin-dominated diet observed in the period (1986–1996). The available data for the Grand Bank area suggest that shrimp is not a significant prey there for either of these predators. A recent decline in shrimp biomass has been observed in the entire region, but this is only clearly evident in 2009. Stomach contents for 2009 are currently being processed.

An increasing trend in fish biomass was observed between 2003–2007 but overall biomass levels are still well below pre-collapse levels. In terms of mortality on shrimp, these results suggest that predation mortality should have increased since the mid-1990s, given the increasing shrimp contribution to diets and the positive trend in overall fish biomass. This effect is expected to be distributed across many predators, and not necessarily linked to a single predator species (e.g. cod).



Figure 3. Annual trends in the Global Index of Colocation (GIC) for each predator-prey population component interaction, from fall NAFO Div. 2J3KL trawl survey data.

Predator-Prey Spatial Interactions

Spatial interaction between populations of predators and prey was investigated by calculating the Global Index of Colocation (GIC) between each predator-prey pair, as recently applied by Wieland et al. (2007). The GIC is based on differences in centers of gravity (CG) or 'mean location' between populations and Inertia (horizontal dispersion) of each population. The GIC may range from 0 (distinctly different GC) to 1 (two GCs are coincident). Initial comparison of CGs for total populations indicated that CGs were most similar between cod and crab and between Greenland Halibut and shrimp. Annual trends in GIC were compared based on those size groups of prey that were most important to each predator and those size groups of predators that preved most intensely on each prey species, according to the literature (Dwyer et al. 2010, Lilly 1984, 1991, Chabot et al. 2008). All predator-prey comparisons indicated a high degree of spatial interaction, with GIC usually exceeding 0.8 (Figure 3). Greenland halibut and shrimp spatial interaction was especially close, with GIC near 1.0 throughout the 1997–2009 time series (Figure 3), indicating that the CGs of predatory Greenland Halibut and shrimp prey population components have been virtually coincident.

Summary and Conclusions

There is no evidence that predation is controlling snow crab. In the case of shrimp, predation may be a factor, based on importance of shrimp in diets and close predator-prey interactions. but the amount of shrimp consumed is more relevant to shrimp mortality rate. Despite increasing importance of shrimp in predator diets shrimp mortality rate may remain low, relative to the pre-collapse period, due to recent high shrimp biomass and low predator biomass.

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Interactions between northern shrimp and cod in Ísafjarðardjúp, northwest Iceland

Ingibjörg G. Jónsdóttir

Marine Research Institute, Reykjavik, Iceland

Inshore shrimp fishery started in Ísafjarðardjúp in 1935 but later in five other inshore shrimp fishing areas northwest and north of Iceland. In the time period between 1998 and 2004 all of the shrimp stocks collapsed and the fishing grounds were closed for shrimp fishing. The catch was highest around 1995/1996 in the four areas north of Iceland and there was a rapid decline in biomass in the years before 2000. The shrimp stock in Ísafjarðardjúp collapsed in 2003 and shrimp fishing in this area has been closed since 2003.

Abundance of gadoid species has increased in the past years and increase in the number of cod was at a similar time as when the shrimp stock collapsed. Since the shrimp stock collapsed the haddock abundance has increased greatly. Ísafjarðardjúp is a nursery ground for gadoid species and the individuals are mainly young fish at age between 1 and 4 years.

The proportion of fish that consumed shrimp ranged yearly between 13 and 50%, 3 and 33% and 10 and 33% for cod, haddock and whiting, respectively. In general, shrimp was the main prey of the individuals that did consume shrimp. For cod and haddock the importance of shrimp was less with increasing fish length. Shrimp may therefore be a more important food source for smaller cod. However, shrimp may not be an important prey for 1 year old fish.

In 1990, when the abundance of shrimp was high, shrimp and gadoid species inhabited different areas within Ísafjarðardjúp. In 2000, the distribution of shrimp and gadoid fish species had changed and all species were found within the same area. In the first years after the collapse of the shrimp stock, shrimp was not found in its earlier habitats but in 2009 shrimp was found in low biomass but had inhabited former areas.

Recruitment control of Japan Pacific walleye pollock in relation to environmental variability

Orio Yamamura/Tetsuichiro Funamoto/Masayuki Chimura/Tomonori Hamatsu

Hokkaido National Fisheries Research Institute, FRA Japan

The Japan Pacific population of walleye pollock (JPP) is one of the most important fisheries in Japanese EEZ. The spawning of JPP occurs during winter (January-March) in the area of Funka Bay. A substantial part of age-0 pollock settles during late summer and early autumn into the Doto area, where they winter and reside for years. Its recruitment level has been variable ranging from 0.6 to 5.4 billion in the last 30 years with no clear relationship with spawner biomass. Strong year class occurring every 5–10 years has sustained the population. We clarified factors determining recruitment of JPP pollock, and then proposed a hypothesis on the occurrence of strong year classes.

Larval transport. The spawning ground is influenced by both clockwise current produced by NW seasonal wind and counter-clockwise current produced by Coastal Oyashio Current (COC). We reproduced the flow fields around the spawning ground during winter of 1993–2003 using the JCOPE (Japan Coastal Ocean Predictability Experiment) reanalysis data, and then performed the particle tracking experiments to evaluate the fate of eggs and larvae as a result of passive transport. In the years when both currents balanced well, eggs and larvae tended to persist in and adjacent to Funka Bay. The duration positively correlated with reproductive success index (RPS) of JPP.

Hatch dates. Of the 3-mo duration of spawning, the majority of spawning occurs during early half of the period. When hatch dates of early and late juveniles sampled during same years compared, no difference was found in the strong year class whereas average or below-average year class showed earlier hatch dates in early juvenile. This difference indicates that average strong year classes occur when early hatchers survived.

Body size of juvenile. The body length of early juveniles (ca. 100-d age) showed no correlation between survival rates, whereas those of late juveniles (>6-mo age) were crucial to survival. Better survival was observed when juvenile pollock settled with larger BLs. This relationship represents the size-dependent nature of predation mortality mentioned below.

Juvenile predation. Post-settlement juveniles are exposed to cannibalism and predation by demersal fishes including Kamchatka flounder *Atheretes evermanni* and Pacific cod. Both species increased in the last decade making the predation pressure severer. Monthly comparison of body lengths (BLs) of juvenile pollock between ingested fish and sampled by the net revealed that the predation is size-dependent. Although BLs of ingested and sampled fish were identical during August, the difference between both groups became wider as the season progressed.

An hypothesis on occurrence of strong year classes. Strong year classes occur when the early hatchers representing the majority of the spawning survived. In the years of average or below-average recruitment, they are washed out due to strong southward flow. When the clockwise flow, because of NW seasonal wind, and counterclockwise flow because of COC, are well balanced, the early hatchers survive. They settle with larger body size, and the predation mortality they suffer is eased substantially due to the size-dependent nature of the mortality.



Figure 1. A schematic diagram representing the hypothesis on the occurrence of strong year class in JPP pollock.

Relationship of bottom temperature versus molting probability and average size at terminal molt: Case study off Newfoundland and Labrador and in the southern Gulf of St. Lawrence

E. Dawe¹, D. Mullowney¹, M. Moriyasu², E. Wade² and F. Jacques²

¹Department of Fisheries and Oceans, Newfoundland and Labrador Region, Northwest Atlantic Fisheries Centre, St. John's, Newfoundland and Labrador, Canada ²Department of Fisheries and Oceans, Gulf Region, Gulf Fisheries Centre, Moncton, New Brunswick, Canada

The snow crab (*Chionoecetes opilio*) is a circumpolar species that supports fisheries in the north Pacific and north Atlantic Oceans. Fisheries in the northwest Atlantic are prosecuted on the Newfoundland and southern Labrador Shelf, in the Gulf of St. Lawrence, and on the eastern Nova Scotian Shelf. All snow crab fisheries prosecute only males. Females cease molting when they attain sexual maturity at sizes smaller than the minimum legal size, set at 95 mm carapace width (CW) for Canadian fisheries. The size of mature females ranges about 30-70 mm CW at Newfoundland and Labrador (NL) as well as in the southern Gulf of St. Lawrence (sGSL). However, while males also become sexually mature at small sizes (adolescents) they continue to molt until they develop enlarged chelae, and are then considered to be fully functional adults. The male final molt to adulthood may occur across a very broad size range; adult males range about 40-140 mm CW in Canadian waters. Normally males and females larger than 30mm CW molt once a year during the late winter-early spring, but some individuals skip a regular molting schedule (called skip molters). Therefore, the size at which males molt to adulthood has important implications for such fishery issues as recruitment and yield-per-recruit.

The broad size range, of adult males in particular, implies that some biotic or abiotic factors affect the size at which snow crabs commit to terminally molting to maturity (females) or adulthood (males). Studies in the Eastern Bering Sea have shown a latitudinal cline in the size of mature females that has been attributed to either genetic variation (Somerton, 1981; Otto and Pengilly, 2002) or environmental control (Zheng

et al., 2001; Ernst *et al.* 2005). Most recently, Orensanz *et al.* (2007) showed that this cline is associated with spatial variation in bottom temperature, with mature females being larger in the warm low latitudes than in the cold high latitudes. They hypothesized that female size-at-maturity was triggered by some life history trait such as age and that temperature affected size-at-maturity through a direct effect of temperature on molting frequency and growth in early life. Burmeister and Sainte-Marie (2009) showed that size at terminal molt was positively correlated with temperature in both sexes and crabs were larger at instar in a colder than in a warmer site resulting in a change in the number of instars before terminal molt.

Materials and Methods

Data on bottom water temperature and snow crab biological characteristics were acquired from 1996-2009 spring multispecies stratified random bottom trawl surveys (with a Campelen 1800 net) and 1997–2009 fall snow crab trawl survey (with a Nephrops net) with a depth rage of 50–730 m and 35–380 m in NL and sGSL regions, respectively. Individuals of both sexes were measured in carapace width and their shell conditions were noted. Males were also sampled for chela height and maturity status was assigned to females as either immature or mature. Males were partitioned between two molt-related categories (adult and juvenile/adolescent). Carapace width, for each sex, was summarized into 3-mm (for NL) and 1-mm (for sGSL) groupings for subsequent analysis. Only new-shelled crabs were selected to compare size at maturity or adulthood with temperature based on the assumption that size-at-terminal molt is conditioned by the thermal regime experienced during the intermolt period leading up to the most recent molt, and that the temperature at the capture site reflects that recent thermal history. The percentage of juvenile/adolescent males with older carapaces (skip molters) was also investigated in relation to temperature. For the study of size-at-terminal molt bottom temperature data were selected, for each sex-specific comparison, only from those sets that caught new-shelled crabs of that sex. For the study of skip molting bottom temperature data were selected from those sets that caught any adolescents or new-shelled adults. Temperatures were grouped into one-degree bins, which ranged from -1 to 4°C (for NL) or 5°C (for sGSL).

The effect of temperature on size-at-terminal molt / skip molting was investigated by comparing the size-at-maturity/terminal molt (size at 50% maturity and mean size of mature crabs) of recently terminally-molted females and males as well as male skip molters with the bottom temperature at which they were caught in bottom trawl surveys. Difference in size distributions between warmer and colder fishing grounds is also shown to highlight the temperature effects on the commercial fishery (i.e. size of male snow crabs).

Results & Discussion

This study was conducted based on the assumption that the size at which crabs commit to their final molt is conditioned by the thermal regime experienced during their most recent inter-molt period and is related to temperature-dependent energy budgets. The preliminary results obtained from NL (Figures 1–2) and sGSL (Figures 3–4) corroborate the temperature effects on the growth pattern in snow crab. In both regions, the size at 50%-maturity significantly increased throughout the available temperature range. The size frequency distributions of trap sampled male crabs in warmer and colder fishing grounds showed a conspicuous difference. Crabs residing at favourable (cold) temperatures have relatively high energy balances and undergo their final molt early at small sizes. Males residing at unfavourable (warm) temperatures delay their final molt and ultimately undergo their molt to adulthood at large

size and with low energy balance. In addition, there was an obvious difference in the male size at 50% maturity at different temperature between two regions. In NL the size at 50% terminal molt was much smaller compared to that observed in the sGSL. Although the comparison between NL and sGSL is difficult to interpret due to the difference on sampling method and season, the sizes at 50% maturity in females at different temperature were comparable between the regions. This may lead to a hypothesis that males show more ontogenetic and seasonal migration than females, and so males may be less well conditioned by temperature than females.

The implications of temperature change to natural mortality and recruitment to fisheries as well as reproductive potential are important. Higher temperature regimes may result in a relatively large portion of a male cohort undergoing the final molt achieving larger than the minimum legal size limit. The fishing induced mortality by discarding newly molted crab may increase. In addition, the spawning cycle of females may speed up to 1 year compared to 2-year cycle in colder water temperature, which requires more mating partners (sperms). The delay in achieving terminal molt in males together with a requirement of higher amount of sperm/mating partners makes snow crab stocks more vulnerable to fishing pressure. Although extreme temperatures would promote recruitment through positive effects on both size at recruitment, delaying the final molt to ultimately molt at 'energetically unfavourable' temperatures with low energy balance implies a high mortality that would negatively affect recruitment level. Also the higher temperatures would negatively impact on the post-larval settlement, survival of early benthic stages and finally the level of recruitment to the fishery.



Newfoundland and Labrador

Figure 1. Percentage of terminal molt at a given size class (carapace width) at different bottom temperature for female (lower) and male (upper) snow crab off Newfoundland and Labrador (3LNOPs).



Figure 2. Mean size of terminally molted female (upper) and male (lower) snow crab in relation to bottom temperature off Newfoundland and Labrador (3LNOPs).





Figure 3. Percentage of terminal molt at a given size class at different bottom temperature for female (upper) and male (lower) snow crab in the southern Gulf of St. Lawrence (4T).


Figure 4. Mean size (blue) and size at 50% (red) maturity of terminally molted female (top) and male (bottom) snow crab in relation to bottom temperature in the southern Gulf of St. Lawrence (4T).

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