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Collaborative Research: Life Histories of Species in the Genus Calanus in the North Atlantic and North Pacific Oceans and Responses to Climate Forcing

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Project Participants

Senior Personnel

Name: Runge, Jeffrey
Worked for more than 160 Hours: Yes
Contribution to Project:

Name: Pershing, Andrew
Worked for more than 160 Hours: Yes
Contribution to Project:

Post-doc

Graduate Student

Undergraduate Student

Technician, Programmer

Other Participant

Research Experience for Undergraduates

Organizational Partners

University of Maryland Center for Environmental Sciences
Dr. James Pierson is a collaborator in the research. He is actively involved in the data synthesis phase of the project and will be a coauthor on publications arising from this project.

East Carolina University
Dr. David Kimmel is an active collaborator in the project. He is responsible for developing ocean climatologies for use in our models of Calanus life histories in the North Atlantic and North Pacific Oceans.

Plymouth Marine Laboratory
Dr. Roger Harris is one of our international collaborators, supplying data and knowledge about Calanus life histories in the Northeast Atlantic.

Bedford Institute of Oceanography
Dr. Catherine Johnson is one of our international collaborators actively participating in project workshops and data analysis. She is a coauthor on presentations and manuscripts in preparation arising from the project.

Institut Maurice Lamontagne

Dr.Stephane Plourde is one of our international collaborators actively participating in project workshops and data analysis.

Institute of Oceanographic Sciences

Dr. David Mackas is one of our international collaborators supplying data and knowledge of Calanus life histories in the North Pacific Ocean.

Institute of Marine Research

Dr. Webjorn Melle, IMR, Norway, is one of our international collaborators supplying data and knowledge of Calanus finmarchicus life histories in the Norwegian Sea.

Universit? Montpellier II

Dr. Delphine Bonnet is an international collaborator from France supplying data and knowledge about Calanus heloglandicus life histories in the North Atlantic.

NOAA/Southwest Fisheries Science Center

Dr. Andrew Leising is a principal collaborator actively participating in project workshops and Calanus life history model development. He is a coauthor on presentations and manuscripts in preparation arising from the project.

Marine Research Institute, Iceland

Dr. Astthor Gislason is one of our international collaborators supplying data and knowledge about Calanus finmarchicus life histories in Icelandic waters.

Other Collaborators or Contacts

Activities and Findings

Research and Education Activities: (See PDF version submitted by PI at the end of the report)

Species in the genus Calanus are predominant in the mesozooplankton of the North Atlantic and North Pacific Oceans. Their key role in marine food web interactions has been recognized in GLOBEC programs, both in the U.S. and internationally. Considerable knowledge of life history characteristics, including growth, reproduction, mortality, diapause behavior and demography has been acquired from both laboratory experiments and measurements at sea. This project reviews and synthesizes this knowledge and uses it to develop an Individual Based Life Cycle model for sibling species in two sympatric species pairs, C. marshallae and C. pacificus in the North Pacific Ocean and C. finmarchicus and C. helgolandicus in the North Atlantic. Species in the genus Calanus have been the particular focus of GLOBEC programs and other recent research projects in the U.S., Canada and Europe.

The life cycle model employs a conceptual understanding of Calanus dormancy that is consistent with demographic data from the northwest Atlantic and northeast Pacific Oceans. It embodies the hypothesis that timing of entry and exit from dormancy, as modulated by species-specific physiology and effects of climate-forced variability of food and ambient temperature on lipid accumulation, exerts an important control on population dynamics. The model is parameterized for the particular life history traits of each species, tested and refined across species and regions. It is then applied to make predictions about the life history response of each species to forcing under reasonable climate change scenarios for ambient food and temperature. Life history theory is explored as a way to estimate 'climatological' natural mortality rates from the observed life history characteristics (adult body weight and functional relationships of development, growth and egg production) and predictions are compared with mortality rates from empirical data and modeled results. The study includes compilation and analysis of data on life history characteristics of each species across its range, allowing investigation of the potential for phenotypic differences in physiology associated with genotypic differences across species' ranges and for adaptive change in physiological responses due to climate forcing.

Our research activities have advanced along several fronts:

1) Dr. Andrew Leising, project collaborator from the NOAA Southwest Fisheries Science Center, has led the development of a Calanus life

history model that produces a standard run with a base parameter set for C. finmarchicus conforming to climatological observations in the Gulf of St. Lawrence. The model captures not only the annual demographic cycle including timing of appearance of the first generation but also the annual cycle in body weight. Mortality is set as a function of temperature to yield a relatively constant mortality across stages when taking into account development time. The model and base parameter set will be published as a methods paper, showing how it also compares using same parameter values at the other 3 AZMP stations. An important part of the paper is also the sensitivity analysis to climate sensitive variables.

2) We have held three project workshops:
- Life history model development. (NOAA Pacific Fisheries Environmental Laboratory, 2008)
- Results, planning and Pan Regional Synthesis collaboration (Gulf of Maine Research Institute, 2009).
- Coordination and planning (University of Maryland, 2010)

These workshops have facilitated to collaboration required to achieve proposal objectives, leading directly to preparation of a number of manuscripts.

3) In March, 2010, we held an international workshop on the life histories of Calanus finmarchicus and C. helgolandicus in the North Atlantic Ocean. Participants included researchers from the U.S, Canada and Europe. J. Runge, R. Jones, F. Maps, A. Leising and J. Pierson gave a presentation, entitled 'The life history of Calanus finmarchicus in the Gulf of Maine. Life histories of the planktonic copepods, Calanus finmarchicus and Calanus helgolandicus: Advances in understanding in the Gulf of Maine and across the North Atlantic'. The workshop established connections for compilation and collaboration about Calanus data among North American and European investigators. This workshop served to meet one of the project objectives to engage international collaboration to predict Calanus responses to climate forcing. The outcome of this collaboration is a manuscript reviewing trans-Atlantic C. finmarchicus life history characteristics that was recently submitted to Prog. Oceanogr. (Melle et al. submitted).

4) Dr. Jeffrey Runge presented results from the project at the ICES Working Group in Zooplankton Ecology (WGZE) annual meeting held in Torshavn, Faroe Islands, in March, 2009 and results of the 2010 workshop at the Working Group annual meeting held in Portland, ME in March, 2010. In March, 2012, he presented the results of the international collaboration (Melle et al. submitted) to the WGZE meeting in Malaga, Spain.

5). Dr. David Kimmel has produced environmental climatologies for the North Atlantic Ocean for use in the model analysis of Calanus life history sensitivity to climate forcing. The climatologies identify several dominant models in temperature, wind velocity and chlorophyll a concentration at a gridded basin scale. Regional areas for more fine scale gridded climatologies have been identified for regional application of model sensitivity analysis.

6) Two oral presentations were given at the GLOBEC Open Science Meeting in Victoria in 2009:

- 'Why doesn't C.marshallae live in the Atlantic; a comparison across the copepod genus Calanus' physiological rates with implications for mortality rates under climate variability', (Leising lead author);

- 'Population responses to environmentally forced shifts in timing of diapause in Calanus finmarchicus in the Gulf of Maine' (F. Maps, project postdoctoral researcher, lead author).

7) Three oral presentation were given at the Gulf of Maine Science Symposium held in St. Andrews, N.B. in October, 2009:

- Johnson, C., J. Runge, A. Bucklin, K. A. Curtis, E. Durbin, J. A. Hare, L. S. Incze, J. Link, G. Melvin, T. O'Brien and L. Van Guelpen. Biodiversity and ecosystem function in the Gulf of Maine: pattern and role of zooplankton and pelagic nekton. Technical Workshop on Biodiversity in the Gulf of Maine. Gulf of Maine Symposium-Advancing Ecosystem Research for the Future of the Gulf. St. Andrews, NB. October, 2009.

- Jones, R.J. and J.A. Runge. Results of a collaborative monitoring program of coastal zooplankton and ichthyoplankton in the western Gulf of Maine: 2003-2008. Gulf of Maine Symposium-Advancing Ecosystem Research for the Future of the Gulf. St. Andrews, NB. October, 2009.

- Maps, F., A. Leising, J. Runge and A. Pershing. Population response of the planktonic copepod, Calanus finmarchicus, to environmental change in the Gulf of Maine: the role of diapause. Gulf of Maine Symposium-Advancing Ecosystem Research for the Future of the Gulf. St. Andrews, NB. October, 2009.

8) J. Runge, A. Leising, J. Pierson and F. Maps attended the GLOBEC Pan Regional Synthesis National Workshop III in Boulder, CO. April, 2010, where they gave a presentation entitled 'Life histories of Calanus species in the North Atlantic and North Pacific Ocean and responses to

climate forcing'.

9) Three talks were presented at the 5th International Zooplankton Production Symposium held in Pucon, Chile in March, 2011:

- Johnson, C., J. Runge and K. A. Curtis. Interannual variability in the Scotian Shelf (Northeast Atlantic) zooplankton community and influence on the Gulf of Maine..

- Kimmel, D., S. Plourde, A. Leising, J. Pierson, J. Runge and F. Maps. Regional scale climatological forcing of Calanus finmarchicus dynamics in the Gulf of Maine and Gulf of St. Lawrence.

- Runge, J, F. Maps, A. Leising, A. Pershing, J. Pierson and D. Kimmel. Scenarios of climate change impacts on local production of the subarctic copepod, Calanus finmarchicus, in the Gulf of Maine.

10) Two outreach presentations were given at the Maine Fishermen's Forum in March, 2011:

- Runge, J., A. Pershing, N. Record and R. Jones. Abundance & distribution of Calanus finmarchicus, prey of the northern right whale, in Maine's coastal waters.

- Jones, R. and J. Runge. Interannual, Seasonal and Spatial Variability of Calanus finmarchicus in the Gulf of Maine

11) Four presentations were given at a ESSAS (Ecosystem Studies of Sub-Arctic Seas) Open Science meeting in Seattle in May, 2011:

- Thompson, C. and J. Runge. Mortality estimation of the copepod Calanus finmarchicus.

- Leising, A. and J. Pierson. Is Calanus pacificus just a warmer-adapted Calanus finmarchicus?

- Pierson, J, J. Runge, E. Head, S. Plourde, C. Johnson, A. Leising, F. Maps, D. Kimmel and A. Pershing. Predicting copepod dormancy timing in response to climate change.

- Plourde, S, J. Runge, J. Pierson, E. Head, P.Pepin, C. Johnson, A.Gislason, X. Irigoien, D. Kimmel, A.Leising, A. Pershing, F. Maps and W. Melle. A pan-regional comparison of the seasonal climatology in mortality and population dynamics of Calanus finmarchicus across the North Atlantic.

12) J. Runge gave a keynote presentation, entitled: 'GLOBEC: Population dynamics in an ecosystem context' at the GLOBEC Final Symposium in Washington, D.C. in October, 2011. Findings of the PRS project were also provided in two posters that were presented at the Final Symposium.

13) J. Runge presented the PRS research in a poster, entitiled 'Phenology and persistence of Calanus finmarchicus under climate forcing in the Gulf of Maine' at the Ocean Sciences Meeting. Salt Lake City. Feb. 2012.

14) Data synthesis of Calanus finmarchicus life history characteristics, including egg production, mortality rates and dormancy patterns in the North Atlantic were achieved as part of the recent international synthesis effort (Melle et al. submitted). Synthetic data products that are not already submitted to accessible databases will be submitted to the Pangea Database (http://www.pangaea.de/) along with publication of the paper.

15) Activities to observe change in C. finmarchicus in the NW Atlantic, including maintaining a time series of C. finmarchicus demographic characteristics in coastal Gulf of Maine waters, were also partially supported under this award. The data for this time series are archived at BCO-DMO Data Management Office (http://osprey.bcodmo.org/project.cfm?flag=viewd&id=10&sortby=project).

A complete list of presentations at scientific meetings, workshops and seminar series supported by this award is as follows:

Morrison, J.R., N.R. Pettigrew, J. O'Donnell and J. A. Runge. Rapid detection of climate scale variability in the Gulf of Maine. Oceans'12 Meeting of the Marine Technology Society (MTS) and the Oceanic Engineering Society of IEEE (IEEE/OES). Hampton Roads, Va. October, 2012.

Runge, J.A. What controls the abundance of Calanus finmarchicus in the Gulf of Maine? The Gulf of Maine in a Changing Climate. Bowdoin College. June, 2012.

Runge, J.A., W. Melle, E. Head, S. Plourde, P. Licandro, C. Castellani, S. Jonasdottir and J. Pierson. Calanus finmarchicus life histories in the North Atlantic Ocean: A transatlantic synthesis. ICES Working Group in Zooplankton Ecology. Malaga, Spain, March, 2012.

Runge, J. A., Maps, F., Pershing, A., Leising, A., Kimmel, D. and J. Pierson. Phenology and persistence of Calanus finmarchicus under climate forcing in the Gulf of Maine. Ocean Sciences Meeting. Salt Lake City. Feb. 2012.

Runge, J. A. GLOBEC: Population dynamics in an ecosystem context. GLOBEC Final Symposium. Washington, D.C. Oct. 2011.

Thompson, C. and J. Runge. Mortality estimation of the copepod Calanus finmarchicus. ESSAS Open Science Meeting. Seattle, Wa. May, 2011.

Runge, J, F. Maps, A. Leising, A. Pershing, J. Pierson and D. Kimmel. Scenarios of climate change impacts on local production of the subarctic copepod, Calanus finmarchicus, in the Gulf of Maine. 5th International Zooplankton Production Symposium, Pucon, Chile. March, 2011.

Johnson, C., J. Runge and K. A. Curtis. Interannual variability in the Scotian Shelf (Northeast Atlantic) zooplankton community and influence on the Gulf of Maine. 5th International Zooplankton Production Symposium, Pucon, Chile. March, 2011.

Kimmel, D., S. Plourde, A. Leising, J. Pierson, J. Runge and F. Maps. Regional scale climatological forcing of Calanus finmarchicus dynamics in the Gulf of Maine and Gulf of St. Lawrence. 5th International Zooplankton Production Symposium, Pucon, Chile. March, 2011.

Runge, J., A. Pershing, N. Record and R. Jones. Abundance & distribution of Calanus finmarchicus, prey of the northern right whale, in Maine's coastal waters. Maine Fishermen's Forum. March, 2011.

Runge, J. A. Climate change and the coastal ocean ecosystem in the Gulf of Maine: linking observations with integrative models. Gulf of Maine Council Working Group Meeting, Portland, Me., Dec. 2010.

Runge, J.A., F. Maps, A. Leising, A. Pershing, J. Pierson and D. Kimmel. Impacts of climate change on the subarctic copepod, Calanus finmarchicus, in the Gulf of Maine: is it in hot water? RARGOM Annual Science Meeting: Climate change in the Gulf of Maine. Portsmouth, NH. October, 2010.

Runge, J., Leising, A,, Pierson, J., Kimmel, D., Pershing, A., Maps, F. and Johnson, C. Life histories of Calanus species in the North Atlantic and North Pacific Ocean and responses to climate forcing. GLOBEC Pan Regional Synthesis National Workshop III. Boulder, CO. April, 2010.

Runge, J.A., R. Jones, F. Maps and A. Leising. The life history of Calanus finmarchicus in the Gulf of Maine. Life histories of the planktonic copepods, Calanus finmarchicus and Calanus helgolandicus: Advances in understanding in the Gulf of Maine and across the North Atlantic. RARGOM Theme Session, Portland, ME. March, 2010.

Pierson, J.J., Leising, A.W., Runge, J., Maps, R., Johnson, C., Plourde, S., Pershing, A., Kimmel, D. Predicting the response of copepod dormancy to climate change: Implications for lipid accumulation. Invited talk. Ocean Sciences Meeting 2010, Portland, OR.

Johnson, C., J. Runge, A. Bucklin, K. A. Curtis, E. Durbin, J. A. Hare, L. S. Incze, J. Link, G. Melvin, T. O'Brien and L. Van Guelpen. Biodiversity and ecosystem function in the Gulf of Maine: pattern and role of zooplankton and pelagic nekton. Technical Workshop on Biodiversity in the Gulf of Maine. Gulf of Maine Symposium-Advancing Ecosystem Research for the Future of the Gulf. St. Andrews, NB. October, 2009.

Jones, R.J. and J.A. Runge. Results of a collaborative monitoring program of coastal zooplankton and ichthyoplankton in the western Gulf of Maine: 2003-2008. Gulf of Maine Symposium-Advancing Ecosystem Research for the Future of the Gulf. St. Andrews, NB. October, 2009.
Maps, F., A. Leising, J. Runge and A. Pershing. Population response of the planktonic copepod, Calanus finmarchicus, to environmental change in the Gulf of Maine: the role of diapause. Gulf of Maine Symposium-Advancing Ecosystem Research for the Future of the Gulf. St. Andrews, NB. October, 2009.

Runge, J.A., A. Kovach, R. Jones, S. Tallack, J. Churchill, C. Chen, G. Sherwood, H. Howell, J. Grabowski and D. Berlinsky. Understanding climate impacts on the spatial dynamics of Atlantic cod in coastal waters of the Gulf of Maine. GLOBEC Open Sciences Meeting. Victoria BC. June, 2009.

Runge, Jeffrey, Leising, Andrew, Catherine Johnson and Frederic Maps. Population responses to environmentally forced shifts in timing of diapause in Calanus finmarchicus in the Gulf of Maine. GLOBEC Open Sciences Meeting. Victoria BC. June, 2009.

Leising,A., J. Pierson, J.Runge, and C.Johnson. Why doesn't C.marshallae live in the Atlantic; a comparison across the copepod genus Calanus' physiological rates with implications for mortality rates under climate variability. GLOBEC Open Sciences Meeting. Victoria BC. June, 2009.

Runge, J., Leising, A,, Pierson, J., Kimmel, D., Pershing, A., Maps, F. and Johnson, C. Life histories of Calanus species in the North Atlantic and North Pacific Ocean and responses to climate forcing. ICES Working Group on Zooplankton Ecology. Torshavn, Faroe Islands. March, 2009.

Runge, J., Leising, A,, Pierson, J., Kimmel, D., Pershing, A., Maps, F. and Johnson, C. Life histories of Calanus species in the North Atlantic and North Pacific Ocean and responses to climate forcing. GLOBEC Pan Regional Synthesis National Workshop II. Boulder, CO. February, 2009.

Findings: (See PDF version submitted by PI at the end of the report)

1. A 1-D individual-based Calanus life cycle model that incorporates the Lipid Accumulation Window hypothesis was developed to explain observed life cycle patterns of Calanus species. The model captures not only the annual demographic cycle including timing of appearance of the first generation but also the annual cycle in body weight. The sensitivity of model outputs was evaluated against changes in 23 parameter values. In all cases the model was most sensitive to change in the lipid threshold value for initiating dormancy processes and the rate at which lipids can be produced in stage CIV, the stage preceding dormancy.

2. Record et al. (2010) developed an approach by using a genetic algorithm to parameterize biological?physical coupled copepod population dynamics computation. The model was applied to forecast Calanus and other copepod species abundance in Cape Cod Bay, Massachusetts, for the purpose of understanding distribution of northern right whales. While a good fit to data does not necessarily imply a valid parameterization, an ensemble of good fits provides information on the accuracy of parameter values, on the functional importance of parameters, and on the ability to forecast accurately with an incorrect set of parameters. The findings demonstrate that the technique is a useful tool for operational forecasting

3. Maps et al. (2012) applied the IBM Calanus life cycle model to the Calanus finmarchicus population dynamics in the coastal Gulf of Maine. They use the model to examine how local climate-forced variability in seasonal primary productivity and ambient overwintering temperature influence lipid reserves and diapause and whether this population, which exists at the limit of its biogeographical range, would be threatened by a small increase in the mean overwintering temperature. The modeling approach implements the Lipid Accumulation Window hypothesis and employs a genetic algorithm for parameter estimation in order to reproduce the observed phenology and demography of C. finmarchicus populations from contrasting Gulf of St. Lawrence (GSL) and Gulf of Maine (GoM) locations on the northwest Atlantic shelf. In the GSL, the model reproduced the timing of dormancy, the abundance and individual condition of late copepodid stages. In the GoM, the model produced a semi-annual dormancy pattern, as no locally-produced individual could last the six to eight months of dormancy inferred from the available observations. The findings provide a foundation for a 3-D modeling approach that explicitly addresses the complex interactions between circulation and local production in sustaining high concentration of Calanus in the GoM.

4. Runge and Jones (2012) report on seasonal and interannual variability of Calanus finmarchicus in the coastal Gulf of Maine. In this region, C. finmarchicus resides at the southern edge of its subarctic range. The species is nevertheless a prominent component of the zooplankton in the GoM system. In spring and summer in coastal regions of the GoM, C. finmarchicus can dominate not only biomass but abundance of zooplankton in the catch of plankton nets with > 200 um mesh size. The abundance of lipid-rich late developmental stages varied by a factor of five or more on the coastal shelf where they are primary prey for herring and other forage fish supporting higher trophic levels in the GoM marine food web. Runge and Jones hypothesize that a negative correlation of coastal abundance with salinity is the consequence of interannual variation in local freshwater discharge into the Gulf of Maine. This local forcing would be under the influence of climate change, affecting coastal fisheries.

5. Pierson et al (submitted) used an existing model for dormancy duration in Calanus (Saumweber and Durbin 2006) to explore potential changes in dormancy duration with warming waters. To make the calculations, they also applied size changes associated with animals growing at higher temperatures, as determined from the work of Campbell et al. (2001). Their findings suggest with temperature changes up to 2 deg. C, dormancy duration could be shortened by up to 45 days in some instances, and the effect is most pronounced when the shift occurs in colder water. In other words, a change in temperature from 2-4 deg. C induced a greater decrease in dormancy duration than a shift in temperature from 8-10 deg. C. This has implications for dormancy entry and emergency, and the close links between the timing of Calanus life history events and fish recruitment (e.g. the Match-Mismatch hypothesis of Cushing 1990 and references therein). Included in this manuscript are some

corrections and simplifications to the original model by Saumweber.

6. Thompson et al. (in prep) investigated the demography and mortality rates of Calanus finmarchicus in Gulf of Maine coastal waters, hypothesized to be a critical source of production sustaining the species in this region. Mortality was estimated from the vertical life table method (VLT) as well as a new method that employs at-sea observations to estimate molting rates and consequently mortality in copepodid stages. The results are consistent with the hypothesis mortality rates of older and larger copepodid stages are higher on the nearshore shelf than further offshore, where the water column is deeper.

7. As part of a broader overview of biodiversity of marine life in the Gulf of Maine, Johnson et al. (2011) synthesize current data on species diversity of zooplankton and pelagic nekton, including compilation of observed species and descriptions of seasonal, regional and cross-shelf diversity patterns. Zooplankton diversity in the GoM is characterized by spatial differences in community composition among the neritic environment, the coastal shelf, and deep offshore waters. Copepod diversity increases in late summer, and interdecadal diversity shifts occur, including a period of higher diversity in the 1990s. Changes in species diversity were greatest on interannual scales, intermediate on seasonal scales, and smallest across regions, in contrast to abundance patterns, suggesting that zooplankton diversity may be a more sensitive indicator of ecosystem response to interannual climate variation than zooplankton abundance. Calanus finmarchicus was acknowledged as a key structural species for which there is no functional redundancy in the GoM ecosystem. Ultimately, sustained observations and modeling analysis of biodiversity must be effectively communicated to managers and incorporated into ecosystem approaches for management of GoM living marine resources.

8. Leising et al, (ESSAS workshop presentation, 2011) compare development and growth rates among the two sympatric Calanus species pairs. Although all four species share many similarities, each has distinct responses to temperature in their growth and development rates, which may control their success within the different habitats. Publication of this work is in preparation.

9. Ji et al. (2010) review understanding of phenology and life history of Calanus and other plankton in relation to climate change. They indicate directions to better quantify and monitor future plankton phenology shifts, including (i) examining the main mode of expected future changes (ecological shifts in timing and spatial distribution to accommodate fixed environmental niches vs. evolutionary adaptation of timing controls to maintain fixed biogeography and seasonality), (ii) broader understanding of phenology at the species and community level, (iii) improving and diversifying statistical metrics for indexing timing and trophic synchrony and (iv) improved consideration of spatio-temporal scales and the Lagrangian nature of plankton assemblages to separate time from space changes.

10. Runge et al. (2010) showed how life history modeling of copepod populations, including C. finmarchicus in the Gulf of Maine, can be integrated into an observing and modeling strategy for evaluating effects of environmental forcing on the dynamics of spatially structured fish populations. Coupled physical - biological modeling has advanced to the point where within-decade forecasting of environmental conditions for recruitment into fish populations is feasible. However, the modeling needs to be supported by hydrographic, primary production and zooplankton life history data collected both remotely and by nets at fixed stations. Forecasts of environmentally driven dispersal and growth of planktonic early life stages, combined with an understanding of possible population-specific predator fields, usage of coastal habitat by juveniles and adult resident and migratory patterns, can be used to develop scenarios for spatially explicit population responses to multiple forcings.

11. Melle et al. (submitted) compiled demographic and life history data for Calanus finmarchicus across the North Atlantic, covering its entire biogeographic range. Abundance, dormancy, egg production and mortality in relation to temperature and phytoplankton biomass, using chlorophyll a as a proxy, were analyzed in the context of understanding factors involved in determining the distribution and abundance of C. finmarchicus across its range. Several findings emerged: (1) transport of C. finmarchicus is from the south to the north in the northeast Atlantic, but from the north to the south in the western North Atlantic, which has implications for understanding population responses to climate forcing on coastal shelves, (2) recruitment to the youngest copepodite stages occurs during or just after the phytoplankton bloom in the east while it occurs after the bloom in many western sites, (3) while the deep basins in the Labrador Sea and Norwegian Sea are primary sources of C. finmarchicus production, the western North Atlantic marginal seas have an important role in sustaining high C. finmarchicus abundance on the western North Atlantic shelves, (4) differences in mean temperature and chlorophyll concentration between the western and eastern North Atlantic are reflected in regional differences in female body size and egg production responses, (5) differences in functional responses in egg production rate may reflect genetic differences between western and eastern populations, (6) dormancy duration is generally shorter in the deep waters adjacent to the lower latitude western North Atlantic shelves than in the east, and (7) differences in stage-specific mortality rates are related to bathymetry, temperature and potential predators, notably the abundance of congeners Calanus hyperboreus and C. glacialis, which likely feed on early life stages of C. finmarchicus. This collaboration involving researchers from the U.S, Canada and Europe fulfills one of the major objectives of this NSF award.

12. Morrison et al. (2012) report data from the Northeast Regional Association of Coastal Ocean Observing Systems (NERACOOS) showing an increase in water column temperatures in the Gulf of Maine of 2 deg.C over the past 8 years, from 2004, when the last NERACOOS buoy

was installed in the deep Northeast Channel, until 2011. This temperature increase represents a 20-fold increase over the century-long upward trend in sea surface temperature in the Gulf of Maine and along the east coast. The implications of this temperature rise to the Gulf of Maine ecosystem, including the potential for disappearance of lipid rich Calanus finmarchicus as it shifts its biogeographic range northward, are discussed.

Training and Development:

Dr. Frederic Maps was engaged as a postdoctoral research fellow. He gained experience in the application of IBM life history models, writing of research papers and working in a collaborative team project, with the opportunity to make connections to a wide network of collaborators. The results of his research have been published in the Journal of Plankton Research. He is presently a research associate at the Institut Maurice Lamontagne in Quebec, Canada.

Cameron Thompson has completed requirements for an M.Sc. degree at the School of Marine Sciences, University of Maine. His thesis research investigates the hypothesis of cross shelf variation in Calanus mortality rates related to water column depth. He was trained in biological oceanography, IBM population dynamics modelling and zooplankton ecology. He is supported by this award.

Phoebe Jekielek completed the requirements for an M.Sc. degree in the graduate program at the School of Marine Sciences, University of Maine. Her thesis research investigates lipid accumulation rates of Calanus copepodid stages in the Gulf of Maine and the role of Calanus lipids in the energy budget of the Gulf of Maine pelagic food web. Her graduate studies are partially supported by this award.

Outreach Activities:

Jeffrey Runge was interviewed by the Maine Lobsterman's Association (MLA)about marine ecological impacts of deep sea drilling in the Gulf of Mexico and Northwest Atlantic shelf off Canada. The interview was published in the monthly newsletter of the MLA published in July, 2010 (Vol. 18, No. 7).

Two outreach presentations were given at the Maine Fishermen's Forum held in Rockport, Maine, in March, 2011:

- Runge, J., A. Pershing, N. Record and R. Jones. Abundance & distribution of Calanus finmarchicus, prey of the northern right whale, in Maine's coastal waters.

- Jones, R. and J. Runge. Interannual, Seasonal and Spatial Variability of Calanus finmarchicus in the Gulf of Maine.

The Maine Fishermen's Forum is a major annual event, gathering fishermen and the fishing support industries for four days of seminars and presentations related to Gulf of Maine fishing and its ecosystem.

Jeffrey Runge was interviewed in 2012 by the Associated Press about recent warming in the Gulf of Maine. An article, entitled, 'Gulf of Maine ocean temperatures above normal' was published in the Boston Globe on Mar. 29, 2012.

Jeffrey Runge was interviewed by SeaFood Business Magazine twice in 2012. Two articles were published: 'Researchers delve into impacts of ocean acidification on key finfish species' (March 5, 2012) and 'Gulf of Maine productivity plunges amid record rainfall, climate change' (Sept. 1, 2012).

The University of Maine magazine, UMaine Today, published an article about the project's research in the summer, 2011 issue. The article is entitled 'Fueling the ocean: Calanus finmarchicus research is leading to better understanding of how the copepods power the Gulf of Maine ecosystem.'

Jeffrey Runge participated in a COSEE (Centers for Ocean Science Education Excellence) Curriculum Development Workshop, in which researchers work with high school and junior high school teachers to develop maps of marine science concepts for incorporation into the school-based science curriculum.

Journal Publications

Johnson, C., J. Runge, A. Bucklin, K. A. Curtis, E. Durbin, J. A. Hare, L. S. Incze, J. Link, G. Melvin, T. O'Brien and L. Van Guelpen., "Biodiversity and ecosystem function in the Gulf of Maine: pattern and role of zooplankton and pelagic nekton.", PLoS One, p. 1, vol. 6, (2011). Published,

Ji, R., M. Edwards, D. Mackas, J. Runge and A. Thomas., "Marine plankton phenology and life history in a changing climate: Current research and future directions", J. Plankton Res., p. 13, vol. 32, (2010). Published,

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Bibliography: Report for the Oceans?12 Meeting of the Marine Technology Society (MTS) and the Oceanic Engineering Society of IEEE (IEEE/OES). Hampton Roads, Va

Web/Internet Site

URL(s):

http://www.pangaea.de/

http://osprey.bcodmo.org/project.cfm?flag=viewd&id=10&sortby=project

Description:

Data synthesis of Calanus finmarchicus life history characteristics, including egg production, mortality rates and dormancy patterns in the North Atlantic were achieved as part of the recent international synthesis effort (Melle et al. submitted). Synthetic data products that are not already submitted to accessible databases will be submitted to the Pangea Database (http://www.pangaea.de/) along with publication of the paper.

Activities to observe change in C. finmarchicus in the NW Atlantic, including maintaining a time series of C. finmarchicus demographic characteristics in coastal Gulf of Maine waters, were also partially supported under this award. The data for this time series are archived at BCO-DMO Data Management Office.

Other Specific Products

Product Type:

Community White Paper

Product Description:

A gap assessment of the present northeast U.S. marine ecosystem was conducted and published as a Community White Paper submitted to the Interagency Ocean Observation Committee as part of the 2012 Integrated Ocean Observing System (IOOS) summit. The reference is:

Runge, J.A., M. Cot?, B. Thompson, J.R. Morrison, D. Anderson, I. Cetinic, B.Cowie Haskell, S. Gallager, J. Hare, C. Johnson, J. Salisbury, R. Steneck and R. Young Morse. 2012. Integrated Sentinel Monitoring for the Northeast Region: Gap Assessment. Community White Paper. Interagency Ocean Observation Committee.

Sharing Information:

The community white paper is available at:

http://www.iooc.us/summit/white-paper-guidelines/community-white-paper-submissions/

Contributions

Contributions within Discipline:

Our synthesis of data and IBM life history model integrate current understanding of physiological and ecological processes controlling the life histories of species of Calanus in the North Atlantic and North Pacific Oceans. In particular, the IBM model of Calanus spp. growth and development captures the dynamics of lipid accumulation and diapause. The project results contribute to understanding of environmental forcing on Calanus species abundance and distribution. These models can be linked to other ecosystem processes to provide a general understanding of how coastal and oceanic marine ecosystems will respond to climate change. We actively collaborated with other groups in the U.S. GLOBEC Pan-Regional Synthesis program towards this end, as well as with European and Canadian colleagues. This collaboration resulted in the preparation of a major synthesis of C. finmarchicus life history data across the North Atlantic (Melle et al. submitted).

Contributions to Other Disciplines:

Our findings contribute to the capability for coupling population dynamics models of marine populations to physical circulation models. These coupled physical-biological models have potential applications in fisheries science and ecosystem approaches to management in general. They

provide quantitative predictive tools for how environmental forcing and climate change can impact resource populations, especially in their early life stages.

Contributions to Human Resource Development:

Our project has resulted in the training of one postdoctoral research associate and two graduate students who have obtained dual degrees in marine sciences and marine policy.

Contributions to Resources for Research and Education:

Dr. Jeffrey Runge participated in a COSEE (Centers for Ocean Science Education Excellence) Curriculum Development Workshop, in which researchers work with high school and junior high school teachers to develop maps of marine science concepts for incorporation into the school-based science curriculum. He has contributing a concept map for the COSEE resource library that can be developed into a teaching tool for secondary schools pending additional funding.

Contributions Beyond Science and Engineering:

Since the two Calanus species pairs are predominant mesozooplankton in their respective ecosystems, understanding of climate influences on their population dynamics informs management policy for regional populations of harvested fish, marine mammals and seabirds. Climate-forced changes to life-cycle timing are known to occur, with subsequent impacts on recruitment in higher trophic levels. Our synthesis will promote and identify data needs for development of zooplankton production indices for use in recruitment prediction. We are also developing collaborative projects at the Gulf of Maine Research Institute and with NOAA and fishing industry partners to evaluate climate change effects on lipid budgets in temperate and subarctic coastal fisheries. Our research on climate change impacts on lipid accumulation in Calanus, a major producer of zooplankton lipids, a key source of energy in subarctic systems, will contribute to the development and understanding of energy transfer in temperate and subarctic coastal fisheries, including the Gulf of Maine Calanus- herring-tuna interactions.

Diapausing C. finmarchicus are an important resource not only for both commercially important species such as herring but also for protected species such as the North Atlantic right whale. With funding from NOAA and NASA, Dr. A. Pershing is using a stage-resolved C. finmarchicus model to estimate right whale feeding areas in the Gulf of Maine, with applications in the management of this endangered population. By incorporating a more accurate representation of C. finmarchicus diapause dynamics into this system, it will be possible to extend forecasts throughout the year and into important feeding areas such as the Bay of Fundy. These models are used by regulatory agencies, such as the Maine Department of Marine Resources, to guide establishment of risk management policy for the northern right whale.

Conference Proceedings

Categories for which nothing is reported:

Any Conference

1. Leising et al. have developed a 1-D individual-based *Calanus* life cycle model that incorporates the Lipid Accumulation Window hypothesis to explain observed life cycle patterns of *Calanus* species. The model captures not only the annual demographic cycle including timing of appearance of the first generation but also the annual cycle in body weight. Leising et al. examined sensitivity of model outputs to changes in 23 parameter values. In all cases the model was most sensitive to change in the lipid threshold value for initiating dormancy processes and the rate at which lipids can be produced in stage CIV, the stage preceding dormancy.

2. Leising et al. (submitted) investigated the relationship between environmental conditions and the onset and duration of dormancy in populations of *Calanus pacificus* and *Calanus marshallae* from several locations throughout their geographical range.. For *C. marshallae* off coastal Oregon, day of year of entrance to dormancy could be predicted using the sum integration of daily average sea-surface temperature (SST). Entrance to dormancy also typically coincided with declining upwelling strength, which may indicate loss from the station due to advection rather than an entrance to dormancy. Both species show considerable variability in their dormancy timing, both interannually and among locations. Leising et al. propose that both species require a favorable set of environmental conditions (temperature and food) to acquire an adequate lipid supply for lasting through the dormancy period and molting to adult.

3. Runge and Jones (in press) report on seasonal and interannual variability of *Calanus finmarchicus* in the coastal Gulf of Maine. In this region, *C. finmarchicus* resides at the southern edge of its subarctic range. The species is nevertheless a prominent component of the zooplankton in the GoM system. In spring and summer in coastal regions of the GoM, *C. finmarchicus* can dominate not only biomass but abundance of zooplankton in the catch of plankton nets with > 200 μm mesh size. The abundance of lipid-rich late developmental stages varied by a factor of five or more on the coastal shelf where they are primary prey for herring and other forage fish supporting higher trophic levels in the GoM marine food web. Runge and Jones hypothesize that a negative correlation of coastal abundance with salinity is the consequence of interannual variation in local freshwater discharge into the Gulf of Maine. This local forcing would be under the influence of climate change, affecting coastal fisheries.

4. Record et al. (2010) developed an approach by using a genetic algorithm to parameterize biological–physical coupled copepod population dynamics computation. The model was applied to forecast *Calanus* and other copepod species abundance in Cape Cod Bay, Massachusetts, for the purpose of understanding distribution of northern right whales. While a good fit to data does not necessarily imply a valid parameterization, an ensemble of good fits provides information on the accuracy of parameter values, on the functional importance of parameters, and on the ability to forecast accurately with an incorrect set of parameters. The findings demonstrate that the technique is a useful tool for operational forecasting.

5. Maps et al. (submitted) have applied the IBM *Calanus* life cycle model to the *Calanus finmarchicus* population dynamics in the coastal Gulf of Maine. They use the model to examine how local climate-forced variability in seasonal primary productivity and ambient overwintering temperature influence lipid reserves and diapause and whether this population, which exists at the limit of its biogeographical range, would be threatened by a small increase in the mean overwintering temperature. The modeling approach implements the Lipid Accumulation Window hypothesis and employs a genetic algorithm for parameter estimation in order to reproduce the observed phenology and demography of *C. finmarchicus* populations from contrasting Gulf of St. Lawrence (GSL) and Gulf of Maine (GoM) locations on the northwest Atlantic shelf. In the GSL, the model reproduced the timing of dormancy, the abundance and individual condition of late copepodid stages. In the GoM, the model produced a semi-annual dormancy pattern, as no locally-produced individual could last the six to eight months of dormancy inferred from the available observations. The findings provide a foundation for a 3-D modeling approach that explicitly addresses the complex interactions between circulation and local production in sustaining high concentration of *Calanus* in the GoM.

6. As part of a broader overview of biodiversity of marine life in the Gulf of Maine, Johnson et al. (2011) synthesize current data on species diversity of zooplankton and pelagic nekton, including compilation of observed species and descriptions of seasonal, regional and cross-shelf diversity patterns. Zooplankton diversity in the GoM is characterized by spatial differences in community composition among the neritic environment, the coastal shelf, and deep offshore waters. Copepod diversity increases in late summer, and interdecadal diversity shifts occur, including a period of higher diversity in the 1990s. Changes in species diversity were greatest on interannual scales, intermediate on seasonal scales, and smallest across regions, in contrast to abundance patterns, suggesting that zooplankton diversity may be a more sensitive indicator of ecosystem response to interannual climate variation than zooplankton abundance. *Calanus finmarchicus* was acknowledged as a key structural species for which there is no functional redundancy in the GoM ecosystem. Ultimately, sustained observations and modeling analysis of biodiversity must be effectively communicated to managers and incorporated into ecosystem approaches for management of GoM living marine resources.

7. Leising et al, (ESSAS workshop presentation, 2011) compare development and growth rates among the two sympatric *Calanus* species pairs. Although all four species share many similarities, each has distinct responses to temperature in their growth and development rates, which may control their success within the different habitats.

8. Pierson et al. (ESSAS workshop presentation, 2011) have compiled data from studies of *Calanus finmarchicus* egg production rate in the northwest Atlantic Ocean. The results reveal a hyperbolic relationship between egg production rate and chlorophyll a concentration, used as a proxy for food availability. The critical concentration at which egg production rate is maximal is approx. 1µg Chl. a/ liter. These results will

be compared with data from studies in the northeast Atlantic, where the relationship with chlorophyll a is expected to be different.

9. Ji et al. (2010) review understanding of phenology and life history of *Calanus* and other plankton in relation to climate change. They indicate directions to better quantify and monitor future plankton phenology shifts, including (i) examining the main mode of expected future changes (ecological shifts in timing and spatial distribution to accommodate fixed environmental niches vs. evolutionary adaptation of timing controls to maintain fixed biogeography and seasonality), (ii) broader understanding of phenology at the species and community level, (iii) improving and diversifying statistical metrics for indexing timing and trophic synchrony and (iv) improved consideration of spatio-temporal scales and the Lagrangian nature of plankton assemblages to separate time from space changes.

Species in the genus *Calanus* are predominant in the mesozooplankton of the North Atlantic and North Pacific Oceans. Their key role in marine food web interactions has been recognized in GLOBEC programs, both in the U.S. and internationally. Considerable knowledge of life history characteristics, including growth, reproduction, mortality, diapause behavior and demography has been acquired from both laboratory experiments and measurements at sea. This project reviews and synthesizes this knowledge and uses it to develop an Individual Based Life Cycle model for sibling species in two sympatric species pairs, *C. marshallae* and *C. pacificus* in the North Pacific Ocean and *C. finmarchicus* and *C. helgolandicus* in the North Atlantic. Species in the genus *Calanus* have been the particular focus of GLOBEC programs and other recent research projects in the U.S., Canada and Europe.

The life cycle model employs a conceptual understanding of *Calanus* dormancy that is consistent with demographic data from the northwest Atlantic and northeast Pacific Oceans. It embodies the hypothesis that timing of entry and exit from dormancy, as modulated by species-specific physiology and effects of climate-forced variability of food and ambient temperature on lipid accumulation, exerts an important control on population dynamics. The model is parameterized for the particular life history traits of each species, tested and refined across species and regions. It is then applied to make predictions about the life history response of each species to forcing under reasonable climate change scenarios for ambient food and temperature. Life history theory is explored as a way to estimate 'climatological' natural mortality rates from the observed life history characteristics (adult body weight and functional relationships of development, growth and egg production) and predictions are compared with mortality rates from empirical data and modeled results. The study includes compilation and analysis of data on life history characteristics of each species across its range, allowing investigation of the potential for phenotypic differences in physiology associated with genotypic differences across species' ranges and for adaptive change in physiological responses due to climate forcing.

Our research activities in the first three years of this project have advanced along several fronts:

1) Dr. Andrew Leising, project collaborator from the NOAA Southwest Fisheries Science Center, has led the development of a Calanus life history model that produces a standard run with a base parameter set for C. finmarchicus conforming to climatological observations in the Gulf of St. Lawrence. The model captures not only the annual demographic cycle including timing of appearance of the first generation but also the annual cycle in body weight. Mortality is set as a function of temperature to yield a relatively constant mortality across stages when taking into account development time. The model and base parameter set will be published as a methods paper, showing how it also compares using same parameter values at the other 3 AZMP stations. An important part of the paper is also the sensitivity analysis to climate sensitive variables.

2) We have held three project workshops:

- Life history model development. (NOAA Pacific Fisheries Environmental Laboratory, 2008)
- Results, planning and Pan Regional Synthesis collaboration (Gulf of Maine Research Institute, 2009).
- Coordination and planning (University of Maryland, 2010)

3) In March, 2010, we held an international workshop on the life histories of *Calanus finmarchicus* and *C. helgolandicus* in the North Atlantic Ocean. Participants included researchers from the U.S, Canada and Europe. J. Runge, R. Jones, F. Maps, A. Leising and J. Pierson gave a presentation, entitled 'The life history of *Calanus finmarchicus* in the Gulf of Maine. Life histories of the planktonic copepods, *Calanus finmarchicus* and *Calanus helgolandicus*: Advances in understanding in the Gulf of Maine and across the North Atlantic'. The workshop established connections for compilation and collaboration about *Calanus* data among North American and European investigators. This workshop served to meet one of the project objectives to engage international collaboration to predict *Calanus* responses to climate forcing.

4) Dr. Jeffrey Runge presented results from the project at the ICES Working Group in Zooplankton Ecology annual meeting held in Torshavn, Faroe Islands, in March, 2009 and results of the 2010 workshop at the Working Group annual meeting held in Portland, ME in March, 2010.

5) We have continuing data synthesis activities with a compilation of *Calanus finmarchicus* egg production rates in the Northwest Atlantic. Dr. James Pierson from the University of Maryland CES is leading this research activity.

6. Dr. David Kimmel has produced environmental climatologies for the North Atlantic Ocean for use in the model analysis of *Calanus* life history sensitivity to climate forcing. The climatologies identify several dominant models in temperature, wind velocity and chlorophyll a concentration at a gridded basin scale. Regional areas for more fine scale gridded climatologies have been identified for regional application of model sensitivity analysis.

7) Two oral presentations were given at the GLOBEC Open Science Meeting in Victoria in 2009:

- 'Why doesn't *C.marshallae* live in the Atlantic; a comparison across the copepod genus *Calanus*' physiological rates with implications for mortality rates under climate variability', (Leising lead author);

- 'Population responses to environmentally forced shifts in timing of diapause in *Calanus finmarchicus* in the Gulf of Maine' (F. Maps, project postdoctoral researcher, lead author).

8) Three oral presentation were given at the Gulf of Maine Science Symposium held in St. Andrews, N.B. in October, 2009:

- Johnson, C., J. Runge, A. Bucklin, K. A. Curtis, E. Durbin, J. A. Hare, L. S. Incze, J. Link, G. Melvin, T. O'Brien and L. Van Guelpen. Biodiversity and ecosystem function in the Gulf of Maine: pattern and role of zooplankton and pelagic nekton. Technical Workshop on Biodiversity in the Gulf of Maine. Gulf of Maine Symposium-Advancing Ecosystem Research for the Future of the Gulf. St. Andrews, NB. October, 2009.

- Jones, R.J. and J.A. Runge. Results of a collaborative monitoring program of coastal zooplankton and ichthyoplankton in the western Gulf of Maine: 2003-2008. Gulf of Maine Symposium-Advancing Ecosystem Research for the Future of the Gulf. St. Andrews, NB. October, 2009.

- Maps, F., A. Leising, J. Runge and A. Pershing. Population response of the planktonic copepod, Calanus finmarchicus, to environmental change in the Gulf of Maine: the role of diapause. Gulf of Maine Symposium-Advancing Ecosystem Research for the Future of the Gulf. St. Andrews, NB. October, 2009.

9) J. Runge, A. Leising, J. Pierson and F. Maps attended the GLOBEC Pan Regional Synthesis National Workshop III in Boulder, CO. April, 2010, where they gave a presentation entitled 'Life histories of *Calanus* species in the North Atlantic and North Pacific Ocean and responses to climate forcing'.

10) Three talks were presented at the 5th International Zooplankton Production Symposium held in Pucon, Chile in March, 2011:

- Johnson, C., J. Runge and K. A. Curtis. Interannual variability in the Scotian Shelf (Northeast Atlantic) zooplankton community and influence on the Gulf of Maine..

- Kimmel, D., S. Plourde, A. Leising, J. Pierson, J. Runge and F. Maps. Regional scale climatological forcing of *Calanus finmarchicus* dynamics in the Gulf of Maine and Gulf of St. Lawrence.

- Runge, J, F. Maps, A. Leising, A. Pershing, J. Pierson and D. Kimmel. Scenarios of climate change impacts on local production of the subarctic copepod, *Calanus finmarchicus*, in the Gulf of Maine.

11) Two outreach presentations were given at the Maine Fishermen's Forum in March, 2011:

- Runge, J., A. Pershing, N. Record and R. Jones. Abundance & distribution of *Calanus finmarchicus*, prey of the northern right whale, in Maine's coastal waters.

- Jones, R. and J. Runge. Interannual, Seasonal and Spatial Variability of *Calanus finmarchicus* in the Gulf of Maine

12) Four presentations were given at a ESSAS (Ecosystem Studies of Sub-Arctic Seas) Open Science meeting in Seattle in May, 2011:

- Thompson, C. and J. Runge. Mortality estimation of the copepod *Calanus finmarchicus*.

- Leising, A. and J. Pierson. Is *Calanus pacificus* just a warmer-adapted *Calanus finmarchicus*?

- Pierson, J, J. Runge, E. Head, S. Plourde, C. Johnson, A. Leising, F. Maps, D. Kimmel and A. Pershing. Predicting copepod dormancy timing in response to climate change.

- Plourde, S, J. Runge, J. Pierson, E. Head, P.Pepin, C. Johnson, A.Gislason, X. Irigoien, D. Kimmel, A.Leising, A. Pershing, F. Maps and W. Melle. A pan-regional comparison of the seasonal climatology in mortality and population dynamics of *Calanus finmarchicus* across the North Atlantic.