Results From Prior NSF Support

McGillicuddy: **EDdy Dynamics, mIxing, Export, and Species composition (EDDIES)** (OCE-0241310) co-PIs Buesseler, Jenkins, Ledwell, Bates, Falkowski, Hansell, Siegel; companion projects led by Steinberg and Carlson: total $3,102,629, WHOI portion $1,837,261; 7/1/2003-6/30/2008. The EDDIES project has documented how mid-ocean eddies, together with wind-forced motions, cause episodic bursts of nutrient supply to the upper ocean, changes in plankton community structure, and export of organic material to the deep sea (McGillicuddy et al., 2007). A special issue of *Deep-Sea Research II* is in preparation jointly with the E-FLUX project, to which 25 manuscripts have been submitted. In a companion study, the Video Plankton Recorder was towed across the North Atlantic to measure the abundance and distribution of the nitrogen-fixing cyanobacteria of the genus *Trichodesmium*. Abundance had a basin-scale trend, a clear association with anticyclonic eddies, and was apparently not affected by hurricane-forced mixing. Subsurface abundance was higher than previously reported, and may have important implications for the global ocean nitrogen cycle (Davis and McGillicuddy, 2006).

Bucklin: **ZooGene, a DNA sequence database for calanoid copepods and euphausiids: an OBIS tool for uniform standards of species identification** (OCE-0003884) P.I.s: Ann Bucklin (UNH), B.W. Frost (UW), P.H. Wiebe (WHOI), and M.J. Fogarty (NEFSC): $500,000; 9/1/2000 - 8/31/2004. An international partnership of four principal investigators and thirteen taxonomic consultants from seven countries was established; a database of DNA type sequences for calanoid copepods and euphausiids was created. Genes analyzed were mitochondrial cytochrome oxidase I (mtCOI), 16S rRNA, and cytochrome b (mtCYB). ZooGene resulted in 150 mtCOI sequences for 81 species of copepods and 44 DNA sequences for 37 species of euphausiids. Multiplexed species-specific PCR (SS-PCR) protocols were designed from mtCOI sequences to discriminate cryptic copepod species, including two species of *Pseudocalanus* and four species of *Calanus* (Bucklin et al., 2001; Bucklin et al., 1999; Hill et al., 2001). Phylogenetic relationships among genera and families of calanoid copepods and euphausiids were reconstructed using 18S rRNA sequences (Bucklin et al., 2003).

Haidvogel: **Nested Interdisciplinary Models for the Gulf of Alaska** (OCE-0113461, 03/15/01-02/28/07, $571,564) and **Effects of Seasonal and Interannual Variability of Zooplankton Populations in the California Current System using Coupled Biophysical Models** (OCE-0002893; 07/01/00-06/30/05, $759,000): We have developed a suite of coupled physical/ecosystem models to explore the mechanisms by which interannual/interdecadal variability of physical fields affect the production of GLOBEC target zooplankton species and the feeding of juvenile salmon in the Coastal Gulf of Alaska (CGOA) and the California Current System (CCS). Nested domains include: a basin-scale model encompassing the North Pacific Basin at 20-40 km resolution (NPac), a regional model at ~10 km resolution spanning the Northeast Pacific (NEP), and finally local models at ~3 km resolution in regions of specific interest to U.S. GLOBEC [CCS and CGOA]. Publications resulting thus far include Hermann *et al.* (2002a; 2002b), Curchitser *et al.* (2005), Powell *et al.* (2006), and Weingartner *et al.* (2002). Data from these simulations has been provided for use in many other regional modeling studies (Gan et al., 2006). Over 70 presentations have been given by the PIs on various aspects of this work. Output is viewable through a Live Access Server: http://ferret.pmel.noaa.gov/FOCI/servlets/dataset.

Wiebe: **WinDSSOck: Winter distribution and success of southern ocean krill** (OPP-9910307) P.I.s: P.H. Wiebe, C.J. Ashjian, C.S. Davis, and S.M. Gallager, WHOI. Amount/period of award: $1,423,505; 10/01/00 - 09/30/03. The U.S. SO GLOBEC Program conducted a study of the shelf circulation on the Western Antarctic continental shelf, sea ice formation, and Antarctic krill (*Euphausia superba*) distribution, survivorship, and availability to higher trophic levels. We determined the broad-scale distribution of krill in the study area relative to the distributions of other zooplankton and to regional circulation and seasonal changes in ice cover. Three instrument platforms were used on four RVIB N.B. Palmer broad-scale cruises in Austral fall and winter of 2001 and 2002: a 1-m^2 MOCNESS, the BIOMAPER-II (acoustic, video, and environmental data), and a ROV with a camera. Findings are reported in four cruise reports, eight published papers, four papers in press, and fourteen talks/posters presented at national and international meetings. Much of the processed MOCNESS and BIOMAPER-II data are available on the U.S. GLOBEC web site and database.

1. Prologue

The study of the dynamics of key zooplankton species in terms of their coupling to the physical and biological environment and their response to climate change has been underway for more than a decade in the North Atlantic. In addition to the U.S. GLOBEC Northwest Atlantic Georges Bank Study, many other national and international GLOBEC programs have been carried out (described in Section 5 below). The NW Atlantic U.S. GLOBEC program began its synthesis phase in 2002, focusing first on results within the region (Phase IV) with subsequent expansion in scope to begin to put the regional-scale studies in context (Phase IVb). However, it has been clear for some time that basin-scale forcing has given rise to a number of the perturbations that were observed in the Gulf of Maine/Georges Bank region (Conversi et al., 2001; Greene et al., 2003; Greene and Pershing, 2000; Greene and Pershing, 2003). The current call for proposals seeks “integrated understanding of the effect of climate on the systems represented in U.S. GLOBEC”, recognizing that this “will require comparison with results of national and international programs in other similar systems.” This pan-regional synthesis proposed herein will use observations together with biological-physical modeling approaches developed during earlier phases of the NWA Georges Bank Program to understand basin-scale population dynamic processes of a target species in a realistic physical setting.

2. Introduction

Calanus finmarchicus is a large boreal copepod that is distributed from the northern reaches of the Norwegian and Barents Sea in the eastern North Atlantic to southwestern portions of the Slope Water off New England. Population centers occur in the Norwegian Sea Basin, the northern North Atlantic (Irminger and Labrador Seas), and in the Western North Atlantic off New England. In many areas throughout its range, it reaches maximum abundance in June. *C. finmarchicus* can dominate the numbers and biomass of the zooplankton throughout much of the northern North Atlantic (Astthorsson and Gislason, 1995; Heath et al., 1999; Planque and Ibanez, 1997). For example, in the spring surveys of plankton and hydrography around Iceland, *C. finmarchicus* normally makes up about 80% of the zooplankton biomass (Astthorsson and Gislason, 1995) and up to 70 % in other parts of the eastern North Atlantic during summer (Heath et al., 1999). In the Northwest Atlantic/Gulf of Maine region, it also can account for > 80% of the spring-time zooplankton biomass (Greene and Pershing, 2003).

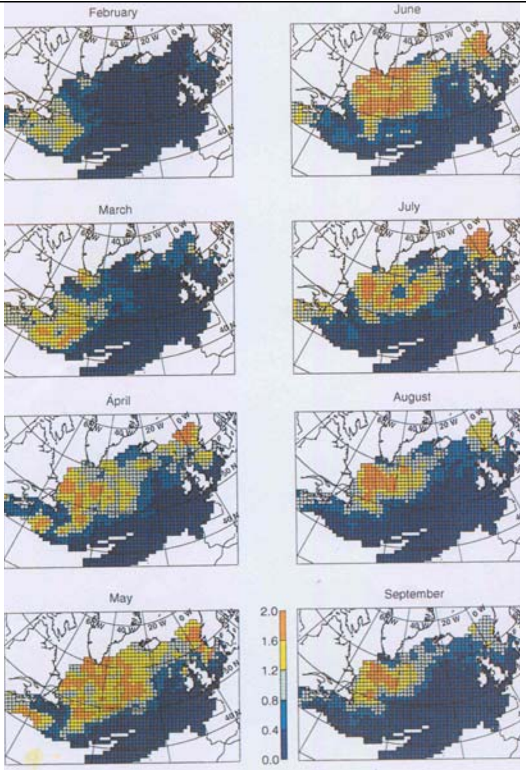

Figure 1. Basin wide distribution of *C. finmarchicus* based on CPR data from Planque et al. (1997).

C. finmarchicus enters diapause as fifth-stage copepodid in mid-summer and spends the warm stratified period or fall and winter months at depths of 50-300 m in the Gulf of Maine (Bigelow, 1926; Clarke, 1933; Clarke, 1934; Mullin, 1963) and around 500 m in Northwest Atlantic Slope Water (Miller et al., 1991). In other parts of the North Atlantic, it overwinters at depths between 500 and 2000 meters (Heath et al., 2004;

Heath et al., 2000b; Hirche, 1996; Kaartvedt, 1996). Its basin-scale distribution has been described by Planque et al. (1997) based on data from the Continuous Plankton Recorder (CPR; Figure 1).

This species plays a central role in ocean-basin wide dynamics of seasonal cycling and year-to-year variability of zooplankton and dependent fish stocks. Year-to-year variation in the standing stock of *C. finmarchicus* may play a major role in determining the success or failure of larval fish development and ultimately recruitment into the adult fish stock. For example, in Icelandic waters the strength of the 0-group cod is associated with the abundance of zooplankton (where, as noted above, *C. finmarchicus* typically accounts for 50 to 80 % of the numbers of zooplankton in the samples (Astthorsson and Gislason, 1995)). In addition, there is close timing between fish reproduction and egg laying, and the start of *C. finmarchicus* production with the emergence from the diapause, which may vary from January on Georges Bank to May/June in the Gulf of Saint Lawrence. The variation does not seem to be related to latitude (or a physical feature related to latitude), but to the timing of the spring bloom in each region. It has been suggested in the Match/Mismatch hypothesis (Cushing, 1990) that particularly successful fish recruitment follows large bursts of *C. finmarchicus* production. The coupling between *C. finmarchicus* and the redfish, North Atlantic salmon, and Norwegian herring recruitment has also been suggested.

Based on an analysis of the CPR data, Planque and Ibanez (1997) showed that *C. finmarchicus* spatial patterns in the North Atlantic are only spatially coherent in regions 400 to 1000 km in radius and that there is no spatial coherence in long-term variations in abundance for the North Atlantic basin as a whole. The eight separate regions they identified in CPR records from 1962 to 1974 showed large differences in their annual changes. A key conclusion was that "...plankton changes at the scale of an oceanic basin cannot be easily extrapolated from regional observations".

The scales of spatial coherence may in part be related to the fact that the seasonal cycle in production of a species may vary across an ocean basin. The annual production cycle of *C. finmarchicus* had three dominant patterns temporally and spatially in the region in the North Atlantic surveyed by the CPR between 1962 and 1974 (Planque et al., 1997). In the sea area south of Newfoundland, production started early and ended early (February to May). In the Labrador Sea south of Greenland, production started later and ended much later (April to October). In the rest of the Atlantic and portions of the Norwegian Sea, production started later and ended in mid-summer (March to July/August).

Recently, there have been large biogeographic shifts of the zooplankton in the mid-latitudes in the eastern portion of the Atlantic. *C. finmarchicus* has retreated from large areas including the North Sea and has been replaced by *C. helgolandicus* (Beaugrand et al., 2002; Bonnet et al., 2005). Because the two congeners have substantially different life cycles with peak abundances of *C. helgolandicus* occurring later in the year, this has likely resulted in diminished food resources for fish species that depend upon *C. finmarchicus* as food for their larval stages (Edwards and Richardson, 2004; Richardson and Schoeman, 2004). These changes have been linked to fluctuations in the physical environment—especially temperature. Such observations support the hypothesis that climate variability will cause significant alteration of the biological structure of the upper ocean and will have a direct bearing on the distribution, abundance, and dynamics of zooplankton and icthyoplankton inhabiting the ecosystem. The research proposed herein will utilize a basin-scale model to examine the factors that control *C. finmarchicus* throughout its range and to provide insight into how changes in climate may further impact this species and the ecosystem in which it lives.

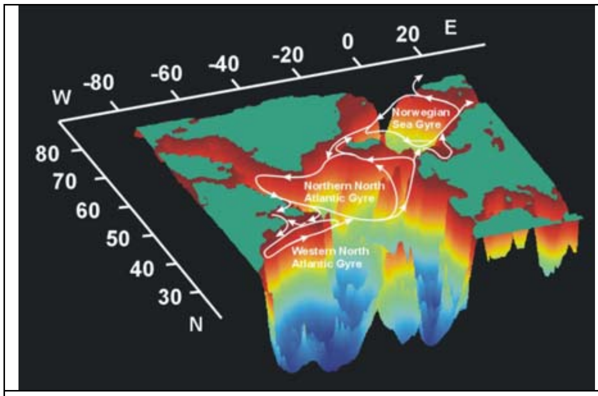

Figure 2. Schematic diagram of the three-gyre conceptual model for *C. finmarchicus* in the North Atlantic.

A conceptual model for the distribution and dynamics of *C. finmarchicus* in the North Atlantic has been suggested (Figure 2) in which the population inhabits three main gyres (Bucklin et al., 2000; Wiebe, 2001). Most southerly is (1) a small gyre in the northwestern Atlantic consisting of the western portion of the Grand Banks, the Gulf of Saint Lawrence, Scotian Shelf, Gulf of Maine, Georges Bank, and Slope Water. The largest gyre consists (2) of the northern North Atlantic ocean basin bounded on the west by Labrador, on the north by Greenland, Iceland, the Faeroes, and the submarine ridges in between, on the east by the UK and on the south by the Gulf Stream extension and the North Atlantic current (this area includes the Labrador Sea and the Irminger Sea). Most northerly is (3) the Norwegian Sea area including the North Sea shelf, the Norwegian shelf and fjords, and the Barents Sea. Our null hypothesis is:

H_0: C. finmarchicus populations in the three gyres are independent and self-sustaining.

We will test this hypothesis by assimilating the CPR and other data sets into a coupled physical biological model, and diagnosing the rate of exchange between the populations from the model solutions. The simulation results will be compared with genetic data, which will provide independent estimates of the degree of reproductive isolation amongst *C. finmarchicus* population in the three gyres. Once we have established the mechanisms underlying the mean seasonal cycle (project years 1 and 2), we will examine interannual fluctuations about that mean (year 3). This will set the stage for realistic coupling of this basin-wide model with shelf seas, a topic that will be the subject of future work.

3. Population Genetic Analysis of *C. finmarchicus*

Patterns of dispersal, reproduction, and mortality of plankton are reflected in the spatial and temporal patterns of genetic variation of the species. Population genetic structure (i.e., genetic differences between geographic populations) may be used as a measure of the transport and mixing (i.e., gene flow) among geographic populations across a species' range. The expectation for high-gene-flow species - such as copepods - is that populations may be discriminated by significant differences in allele or genotype frequencies, not by “unique” or private alleles restricted to a particular population or region. Thus, genetic methods will allow us to quantify population genetic structure and to estimate exchange among geographically distinct populations. By itself, genetic information does not permit identification of source regions or transport pathways of the entrained populations. Therein lies the appeal of using such data together with a coupled physical-biological model, which explicitly resolves the interconnectivity between subpopulations.

C. finmarchicus shows lower levels of molecular genetic diversity than other temperate and subtropical copepod species. The species’ abundance may vary significantly on climatic to evolutionary time scales, generating low levels of molecular genetic diversity. In addition, effective female population size for the species (~10^5 individuals) is much smaller than census female population size (~10^{15} individuals), which may reflect the impact of glaciation during the past 20,000 years (Bucklin and Wiebe, 1998). During the last glacial maximum, *C. finmarchicus* may have experienced 75% range reduction and latitudinal displacement, giving rise to a genetic bottleneck (Bucklin and Wiebe, 1998).

Even though intraspecific genetic diversity is low, *C. finmarchicus* shows significant population genetic structuring at large oceanographic scales (Bucklin and Kocher, 1996; Bucklin et al., 1996; Bucklin et al., 2000). In fact, there may be a number of distinct populations of *C. finmarchicus* inhabiting regions with distinct annual cycles across the N. Atlantic (Planque and Ibanez, 1997). Genetic differentiation of *C. finmarchicus* may have occurred simply due to geographic isolation by distance, and also due to large-scale ocean structure and circulation patterns. A partitioning of the ocean basin by these circulation patterns may also provide geographic boundaries to dispersal of *C. finmarchicus*.

Bucklin et al. (1996, and see Bucklin and Kocher 1996) previously found significant frequency differences in mitochondrial 16S rRNA sequences for *C. finmarchicus* populations inhabiting the NW Atlantic, Norwegian Sea, and Gulf of St. Lawrence. Bucklin et al. (2000) analyzed single nucleotide polymorphisms (SNPs) for a putative COI pseudogene and coding and non-coding regions of the gene for phosphoglucose isomerase (PGI). All traits and both genes revealed significant population genetic differentiation among samples collected from the Northwest Atlantic, Norwegian Sea, North Sea, and Icelandic waters (Bucklin et al., 2000).

Currently, Bucklin's Ph.D. student Ebru Ünal is completing a basin-scale analysis of population genetic structure of *C. finmarchicus* based on ~600 individuals from >60 samples. Sampling was done during 2005 and was designed to allow testing the hypothesis that *C. finmarchicus* populations are genetically differentiated in the different North Atlantic gyres. The genetic characters are allele frequencies at ~25 SNP sites in four nuclear protein-encoding genes (see above). Preliminary data for eight SNPs of a heat shock protein (HSP-70) has revealed significant differentiation (P=0.0000 based on Monte Carlo chi-square) among geographic populations (Figure 3). Allelic variation at all SNP sites was silent (i.e., caused no change in amino acid sequence) and is presumably selectively neutral. As such, these markers do not tie specific genetic traits to any population dynamic character; the genetic characters serve only as indicators of dispersal and inter-population exchange.

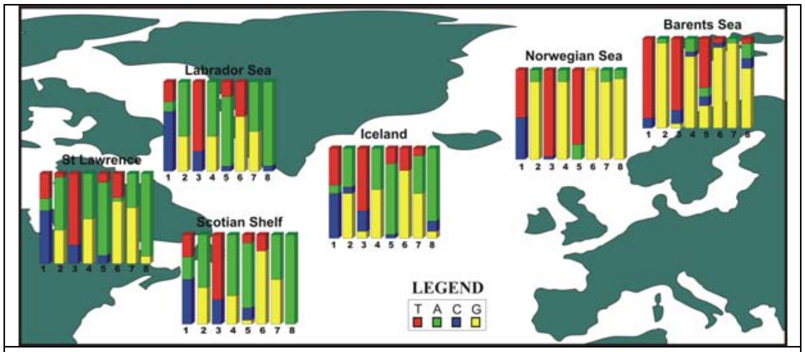

Figure 3. Allele frequencies for eight SNPs in the gene encoding a heat shock protein (HSP-70) for six geographic populations of *C. finmarchicus*. These data demonstrate significant differentiation of populations across the basin.

4. Research Approach: Biological Data Assimilation Using the Adjoint Method

The interaction of planktonic population dynamics with oceanic circulation can create enormously complex patterns in abundance. Even an ocean at rest could accommodate significant spatial and temporal inhomogeneity through geographic variations in environmental parameters, time-dependent forcing mechanisms, and organism behavior. Fluid motions tend to amalgamate these effects in addition to introducing yet another source of variability: space-time variability: fluctuations in the flows themselves that impact biological processes. Understanding the mechanisms responsible for observed variations in population abundance is thus a difficult task. Coupled physical-biological models offer a framework for dissection of these manifold contributions to structure in population distributions. However, their utility is predicated on an ability to construct a simulation that is representative of the natural system. One technique for doing so (the "forward" problem) is to initialize a coupled model with a set of observations, integrate forward in time, and then compare with the next set of observations. A successful outcome results in minor discrepancies between observations and predictions, and the model solutions thus can be used as a basis for diagnosis of the processes controlling the observed patterns. Unfortunately, satisfactory completion of the forward problem is not always achievable, owing to limitations in the models, in the observations, or in both. Adjoint data assimilation methods provide a complementary approach that is particularly useful in such cases. These techniques can be used to determine the model inputs (e.g. parameters, forcing functions) that minimize the misfit between observations and predictions, thereby producing an optimal solution from which the underlying dynamics can be determined.

Based on classical variational principles and optimal control theory, adjoint data assimilation was introduced into the field of dynamic meteorology in the 1980s (Le Dimet and Talagrand, 1986; Lewis and Derber, 1985). Since then, these methods have become increasingly common in oceanographic applications, beginning with 3-D circulation modeling (Bennett, 1992; Gunson and Malanotte-Rizzoli, 1996a; Gunson and Malanotte-Rizzoli, 1996b; Long and Thacker, 1989a; Long and Thacker, 1989b; Moore, 1991; Schroter et al., 1993; Seiler, 1993; Tziperman and Thacker, 1989). More recently, adjoint techniques have been used for biological problems in the context of parameter estimation in zero-dimensional planktonic ecosystem models (Lawson et al., 1996; Lawson et al., 1995). Matear and Holloway (1995) applied the adjoint method to biogeochemical cycling of phosphorus in a 3-D model of the North Pacific.

The general approach begins with the definition of a cost function, which is a measure of the misfit between model predictions and observations. If prior information about parameters or inputs is available, a Bayesian approach can be taken by appending the cost function with a term penalizing deviations from the prior estimate. The goal of the assimilation procedure is to minimize the cost function subject to the constraint that the model equations are obeyed. This is accomplished through adjustment of specified control variables, such as initial conditions, boundary conditions, forcing functions, and/or model parameters. The adjoint method is an efficient iterative technique for solving this minimization problem, which consists of the following steps. Starting with some initial estimate of the control variables, the forward model is integrated to evaluate the cost function. Then the adjoint equations (forced by the model-data misfits) are run backward in time to calculate the gradient of the cost function with respect to the control variables. A descent algorithm is then used to produce a new estimate of the control variables, and the procedure is repeated until convergence is achieved.

The results of this process provide a variety of means for scientific inquiry into the mechanisms controlling the system of interest. First, the final values of the control variables contain information about the characteristics of the model inputs required for consistency with observations. A solution containing unrealistic values of the control variables would indicate deficiency of the forward model; reasonable values and a good fit to observations form the basis of a solution that is amenable to term-by-term analysis of the dynamics underlying the forward problem. Finally, integration of the adjoint equation facilitates explicit diagnosis of the propagation of information within the system.

Example application: C. finmarchicus on Georges Bank

Observations from the GLOBEC (Global Ocean Ecosystem Dynamics) Georges Bank broad-scale surveys (Figure 4) provide an opportunity to investigate the physical and biological mechanisms controlling the population dynamics of *C. finmarchicus* (Li et al., 2006). The approach is to compute a monthly stage-based climatology from these observations, and to assimilate these data into a physical-biological model based on the climatological hydrodynamics of the region (Lynch et al., 1996). The inverse problem is formulated by specification of the velocity and diffusivity fields, observed monthly distributions on Georges Bank, and development rates that depend on temperature and the availability of food (Campbell et al., 2001). The adjoint method is used to infer stage-based mortality fields, off-bank initial conditions, and sources of the youngest stage resolved by the model (N_3). The resulting inverse solutions are then diagnosed to quantify physical and biological controls on the climatological abundance and distribution of *C. finmarchicus* on Georges Bank.

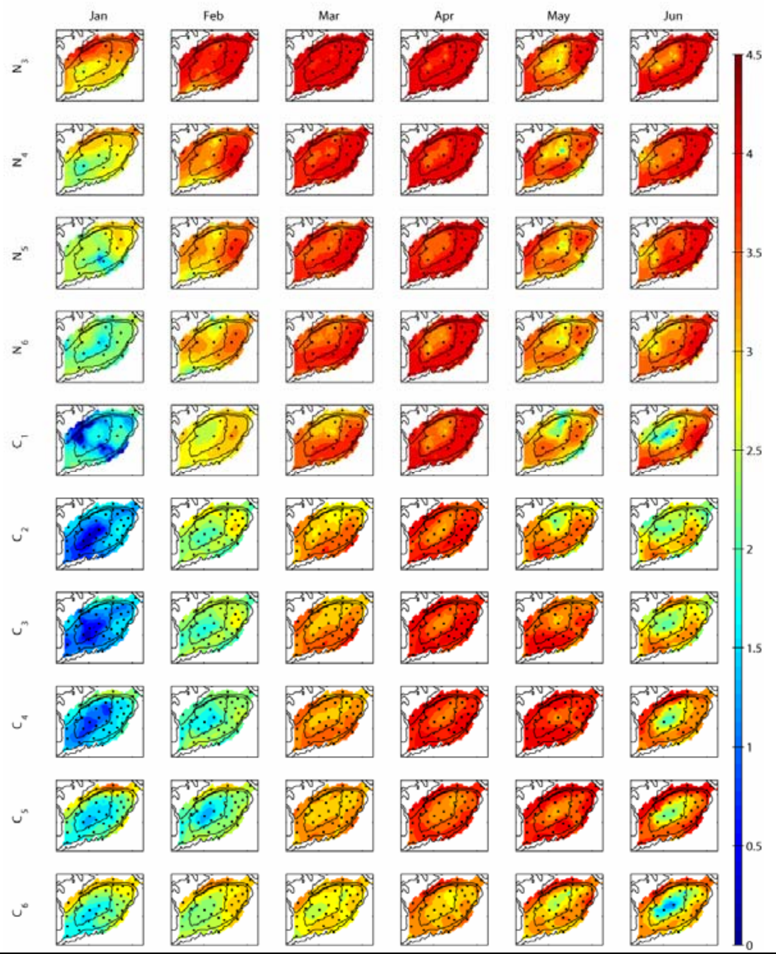

Figure 4. Mean monthly distributions of vertically integrated *C. finmarchicus* N_3-C_6 [$\log_{10}(1 + \#/m^2)$] observed between 1995-1999. Station locations are indicated by black dots. Geographic coverage of the maps is confined to the area in which the expected error computed in the objective analysis is less than approximately 40 percent.

The forward model is an off-line version (“Acadia”) of a finite element hydrodynamic model developed at the Dartmouth Numerical Methods Laboratory (Lynch et al., 1996). The advection-diffusion-reaction equation is written as:

$$\frac{\partial C_i}{\partial t} + \vec{\mathbf{v}} \cdot \nabla C_i - \frac{1}{H} \nabla \cdot (HK \nabla C_i) = \delta_{i-1} R - F_i + (F_{i-1} + \mu_i C_i)(1 - \delta_{i-1}) \tag{1}$$

Here C is the vertically averaged zooplankton concentration, H the bottom depth, **v** the vertically-averaged flow velocity and K the horizontal diffusivity from the bimonthly climatology. Prior to assimilation, the vertically integrated abundance data (Figure 4) were transformed into vertically averaged concentrations by dividing by the bottom depth. The modeled zooplankton concentrations were changed back to the vertically integrated abundances for presentation, so as to be consistent with the data units of the observations. Subscript i is the stage index, with 1 to 10 representing N_3 to C_6, respectively. R includes the input sources and mortality of N_3, with δ_{i-1} a functional that is 1 at i=1 and zero at other stages. F_i and μ_i represent stage-specific molting flux and mortality, respectively. Sign conventions are such that molting flux is positive and mortality is negative (Equation 1).

Molting fluxes at stages N_3-C_5 are computed according to

$$F_i = \frac{C_i}{D_i} \tag{2}$$

where the stage-specific duration D_i depends on both temperature and food availability. In a food abundant condition, the temperature-limited stage duration D_T is described by the Belehradek equation

$$(D_T)_i = a_i (T_m - \alpha)^{\beta} \tag{3}$$

The parameters a_i, α, and β are specified according to Campbell et al. (2001); T_m is the vertically-averaged bimonthly climatological temperature from Lynch et al. (1996).

The effect of food availability on the stage duration was estimated from the Ivlev function (e.g., Campbell et al., 2001). At T=$8^o C$, the food dependent stage duration D_{Chl} is represented as

$$(D_{Chl})_i = \frac{1}{b_i (1 - e^{(-0.0253*(Chl_C + 4.968))})} \tag{4}$$

with Chl_C the food concentration given in terms of carbon (μg C l^{-1}). Values of b_i are based on the data presented in Campbell et al. (2001). The food concentration was obtained from the climatological chlorophyll fields derived from the MARMAP observations (O'Reilly and Zetlin, 1996). The ratio of carbon to chlorophyll was set to 50 mg C (mg Chl a)$^{-1}$, consistent with previous studies (e.g., Hind et al., 2000; Hirche and Kwasniewski, 1997).

If we assume that food concentration has the same proportionate effect at all temperatures, the temperature and food dependent duration D_i is thus

$$D_i = (D_T)_i \,|_{T=T_m} * \frac{(D_{Chl})_i}{(D_T)_i \,|_{T=8}} \tag{5}$$

We regard the estimation of the stage duration described above as a first-order approximation of true food-temperature dependency, ignoring complex details about food-temperature interaction.

We seek to minimize the misfit between simulated and observed concentrations of *C. finmarchicus*, subject to the constraint that the forward model (Equation 1) is strictly obeyed. The model-data misfit, or cost function J, is defined to be

$$J = \frac{1}{N_{mon}} \sum_{k}^{N_{mon}} \frac{1}{N_{stage}} \sum_{j}^{N_{stage}} \frac{1}{N_{obs}} \sum_{i}^{N_{obs}} (C_m - C_{obs})^2 \tag{6}$$

where C_m and C_{obs} are modeled and observed zooplankton concentrations, N_{mon} the number of months in the integration period, N_{stage} the number of modeled stages, and N_{obs} the number of observations at each stage in each month. The control parameters for this problem are the monthly varying source/sink R (input source + mortality) of N_3, mortality μ_i at stages N_4-C_6 over the whole model domain, and the initial off-bank fields on January 15 where observations were not present (model domain is larger than the box in Figure 4). All control variables were allowed to vary independently at corresponding model nodes. The first-guess values of all control variables were set to zero.

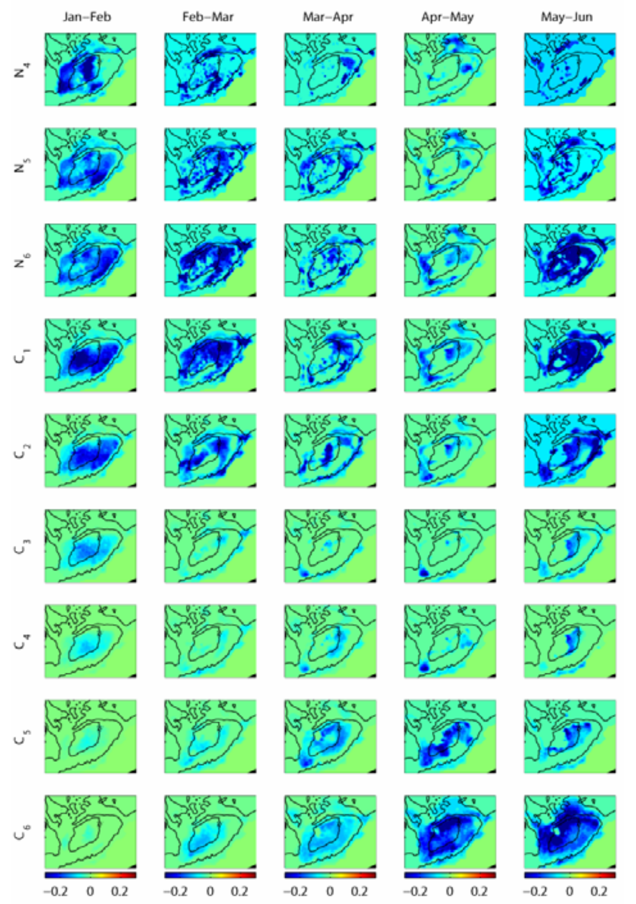

Figure 5: Inferred mortality fields (d^{-1}).

The inversion procedure dramatically improved model performance with optimal estimates of initial fields in January, space-time varying sources/sinks of N_3 and mortality rates at stages N_4 to C_6. After the inversion, mean-square model-data misfit was reduced by about 93%, approximately an order of magnitude less than that resulting from the first-guess values of the control variables. We regard that the first-order inferences have been achieved by the inversion, because the constrained model successfully reproduced the most salient features of the observations both in terms of bank-wide averages and spatial distributions (not shown).

The inferred mortality distributions reveal significant structure in time and space (Figure 5). In general, highest mortalities occur on the bank and in the adjacent areas of the Great South Channel, the Northeast Channel, and southern Georges Basin. Two major episodes of mortality affect the nauplii and early copepodids (C_1 and C_2), the first at the beginning of the growing season (January-February and February-March) and the second during May-June. Mortality of these stages is relatively modest during the intervening period (March-April and April-May). Copepodid stages C_3 and C_4 suffer comparatively little mortality throughout the simulated time period, except for a few hotspots in the southern Great South Channel in April-May, and the eastern side of the Crest during May-June. Mortality of the oldest stages C_5 and C_6 is very low at the beginning of the growing season and generally increased over time.

Spatial coherence in mortality patterns makes it possible to compute meaningful bank-wide averages. In January-February, the naupliar and copepodid stages bear the brunt of the losses: mortality peaks at copepodid C_1, and decreases monotonically to the adult stage. In February-March, mortality of the younger naupliar stages decreases and oldest copepodid stages begins to increase, resulting in a bimodal stage distribution of mortality. This bimodal characteristic persists in March-April, albeit with lower mortality in the naupliar and early copepodid stages. The bimodality is accentuated in the last two bimonthly periods due to increasing mortality in the oldest copepodid stages and the sharply increasing mortality of N_5-C_2 in May-June. Interestingly, this bimodal characteristic is robust in the spatially and temporally averaged mortality (Figure 11 of Li et al., 2006), a finding that is qualitatively consistent with Ohman et al. (2002). Detailed comparisons of these two different approaches to estimating mortality are provided in Li et al. (2006).

The temporally and spatially averaged values of those physical and biological controls on GB provide insight into their relative effect on *C. finmarchicus* population dynamics (Figure 14 of Li et al. 2006). On average, biological reaction terms govern the annual population cycle on GB. The space-time averaged convergences of advective and diffusive fluxes over GB are small relative to molting fluxes and mortality. The standard deviations of physical transports, however, are large and vary with stage and time. Casting the term balances in terms of magnitude (Figure 15 of Li et al. 2006), physical transports are clearly of the same order as the biological sources and sinks. Thus, physical transports are locally important, even though inputs and outputs tend to counterbalance each other when spatially averaged over the bank.

Although their net effect is small, the bank-wide averages of the transport terms do exhibit some clear trends. For example, diffusive transport constitutes a net loss of *C. finmarchicus* for all stages at all times. The term maps (Figure 13 of Li et al. 2006) suggest this results primarily from diffusive flux across the shelf break on the Southern Flank. Generally speaking, advection provides a net source of naupliar stages N_4 and N_5 early in the growing season. In contrast, advection tends to be a net sink for the older copepodids, especially in April-May and May-June. This latter effect tends to be associated with westward transport off the bank from the Southern Flank into the Great South Channel.

5. Specific Objectives

Our scientific objective is to determine the mechanisms that control mean seasonal variations in the abundance and distribution of *C. finmarchicus* in the North Atlantic. It is postulated that the observed distributions result from the interaction of population dynamics with physical transport. A tremendous variety of space and time scales are potentially relevant to this endeavor, ranging from storm-driven advective events to interannual and decadal variations in which the seasonal trends are embedded. Within this broad envelope of scales, a very specific aspect is investigated here: the relationship between seasonal climatologies (long-term means) of both animal abundance and circulation. This is not to say that other scales (or interactions among scales) are not pertinent; rather, in attempting to grapple with an extremely complex coupled problem, it is reasonable to begin by exploring the degree to which the seasonal mean physics and biology are related.

Data on abundance and distribution of *C. finmarchicus* will be obtained primarily from the CPR data (Beaugrand, 2004). The CPR is a small self contained instrument that is towed behind ships of opportunity at an average speed of 20 km hr^{-1} and a depth of 6.5 m (Hays and Warner, 1993). Plankton are collected on a strip of 270 μm silk gauze and in the laboratory sections corresponding to 10 nautical miles (sample volume ca. 3 m^3) are cut and analyzed (Warner and Hays, 1994). Samples in the data series were collected between 1958 and 1999, number over 155,000, and span main portions of the Northern North Atlantic where *C. finmarchicus* occurs.

We will utilize additional data sets generated by other programs to provide information on the vertical distribution of *C. finmarchicus* and their distribution and abundance in regions not covered by the CPR (Figure 6). These include: the U.S. GLOBEC Northwest Atlantic Georges Bank Study (Wiebe and Beardsley, 1996; Wiebe et al., 2001; Wiebe et al., 2006), Canadian GLOBEC that was carried out from the Grand Banks to the Scotian Shelf, including the Gulf of Saint Lawrence (deYoung et al., 1994), the Trans-Atlantic Study of *Calanus* (TASC - Dale et al., 1999; Dale and Kaartvedt, 2000; Heath et al., 2000a; Heath et al., 2000b; Kaartvedt, 1996; Kaartvedt, 2000; Tande and Miller, 1994; Tande and Miller, 1996; Tande et al., 2000; Tande and Miller, 2000) that focused in eastern North Atlantic waters; the investigation of *C. finmarchicus* migrations between oceanic and shelf seas off north-west Europe (ICOS) (Heath et al., 1999), Mare Cognitum which was carried out in the northern boreal Atlantic (Melle and Skjoldal, 1998; Skjoldal et al., 1993; Skjoldal et al., 2004), and the UK-MarProd study of *C. finmarchicus* in the Irminger Sea (Heath et al., 2008). Results from subsequent studies in these same areas will be used as well (Basedow et al., 2006; Halvorsen et al., 2003; Hirche and Kosobokova, 2003; Ohman et al., 2004; Ohman and Hirche, 2004; Torgersen et al., 2002).

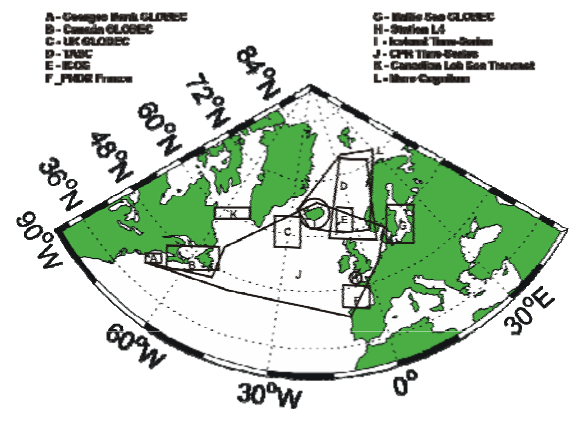

Figure 6. GLOBEC study sites in the North Atlantic (Wiebe *et al.*, 2007).

We will rely on satellite-based ocean color database to provide prey fields for the *C. finmarchicus* population dynamics model. Dramatic changes in surface ocean chlorophyll take place on a seasonal basis, with the spring bloom being one of the most salient features in the North Atlantic. These fluctuations have major implications for *C. finmarchicus* populations, insofar as the timing of emergence from diapause generally coincides with the vernal increase of chlorophyll. As per equations (4) and (5) above, the effect of food availability on stage duration can be parameterized in terms of chlorophyll concentration.

There are of course many caveats to the use of ocean color data as a proxy for food availability. To begin with, *C. finmarchicus* does not graze equally well on all size classes of phytoplankton, many of which are too small for them to process effectively. Moreover, the carbon to chlorophyll ratio can vary considerably in phytoplankton (e.g., Cullen, 1982), thereby influencing food quality. Lastly, *C. finmarchicus* clearly does not rely solely on phytoplankton for its nutrition (Gifford *et al.*, 1996; Harris *et al.*, 2000), with microzooplankton and even detritus being an important component of its diet in many environments. Nevertheless, satellite-based ocean color data provide the only practical means to specify prey fields on the space and time scales necessary for investigations of this scope. We will specify prey fields from monthly climatological mean chlorophyll distributions derived from SeaWiFS data (1998-2007)[1], and we stress that chlorophyll is being used here only as a proxy for food concentration.

5.1 Assimilate monthly climatological mean CPR observations of C. finmarchicus into the North Atlantic ROMS model.

Our general approach will be similar in concept to that described in section 4 above. Monthly climatological mean distributions of *C. finmarchicus* will be provided by Dr. Gregory Beaugrand (see accompanying letter of support). Because these data only resolve copepodid

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[1] Available at http://oceancolor.gsfc.nasa.gov/cgi/climatologies.pl.

stages C_5 and C_6 in surface waters, we will have to rely on other data to provide constraints on the younger stages as well as vertical distribution within the full three-dimensional model. Time-series data at Ocean Weather Station Mike (Irigoien et al., 1998), as well as survey data compiled in Heath et al. (2000a; 2004) will be particularly useful in this regard, although all of the data sets described in the preceding section will be brought to bear in this investigation.

The population dynamics model described in section 4 will be expanded to include all 13 stages of the *C. finmarchicus* life cycle, from egg through adult. Because the underlying physiological and behavioral controls of the animal's diapause state remain enigmatic, we will have to investigate various hypothesized scenarios for entry and exit from diapause. Speirs et al. (2006) describe a set of numerical experiments investigating several controls on entry (food availability, photoperiod) and exit (photoperiod, development rate at depth), concluding that their model of the northeast Atlantic was most consistent with entry cued by food availability and exit cued by photoperiod. We will examine these and possibly other scenarios in our basin-wide inversion of the *C. finmarchicus* data, in which the only free parameter will be spatially-variable, density-dependent, stage-specific mortality rate.

Skill of the biological data assimilation will be assessed using the technique of cross validation (Friedrichs et al., 2007; Friedrichs et al., 2006; Smith et al., submitted) of the predicted fields. A set of twelve experiments will be conducted in which each of the observed monthly *C. finmarchicus* fields (Figure 1) will be removed from the full data set, and the assimilation procedure will be carried out with the remaining eleven months of data. The model will then run forward, and the *C. finmarchicus* field for the missing month is predicted. The difference between this predicted field and the observed field is a proxy for skill of the data assimilative model. This procedure will provide an additional check on how robust the estimated parameters are with respect to assimilation of the full data set.

The circulation model we will use is the Regional Ocean Modeling System (ROMS) http://marine.rutgers.edu/po/index.php?model=roms. ROMS is a free-surface primitive equation ocean model being used by a broad user community (over 800 registered users at last count) for applications from the basin to coastal and estuarine scales (e.g., Dinniman et al., 2003; Haidvogel et al., 2000; Lutjeharms et al., 2003; MacCready and Geyer, 2001; Marchesiello et al., 2003; Peliz et al., 2003; Shchepetkin and McWilliams, 2003; Shchepetkin and McWilliams, 2005; Shchepetkin and McWilliams, 1998; Wilkin et al., 2005). Haidvogel et al. (2008) describes in detail the algorithms that comprise the ROMS computational kernel.

This kernel utilizes consistent temporal averaging of the barotropic mode to guarantee both exact conservation and constancy preservation properties for tracers and therefore more accurately resolves barotropic processes, while preventing aliasing of unresolved barotropic signals into the slow baroclinic motions. Accuracy of the mode-splitting is further enhanced due to redefined barotropic pressure-gradient terms to account for the local variations in the density field (i.e., the pressure-gradient truncation error that has previously plagued terrain-following coordinate models is greatly reduced) without sacrificing the efficiency of the split-explicit formulation. Vertical interpolation is based on conservative parabolic splines. We note that Lagrangian particle tracking in three dimensions is implemented and well tested, offering a powerful tool for characterizing pathways of material transport.

Paramount among these features suited to implementing an advanced data-assimilative physical-biological model are the ROMS tangent linear and adjoint codes, and the variational assimilation schemes they underpin (Moore et al., 2004). These tools are already in place and have been exercised using a simple biological model of the nutrient-phytoplankton-zooplankton type (Fasham et al., 1990). Incorporation of the *C. finmarchicus* population dynamics model will therefore be straightforward. Several other excellent circulation models of the North Atlantic are currently available, including the French Mercator model (www.mercator.com.fr), and the HyCOM GODAE system (hycom.rsmas.miami.edu). ROMS is a particularly appealing choice for the present project as its tangent linear and adjoint systems are ready and available for use as described herein.

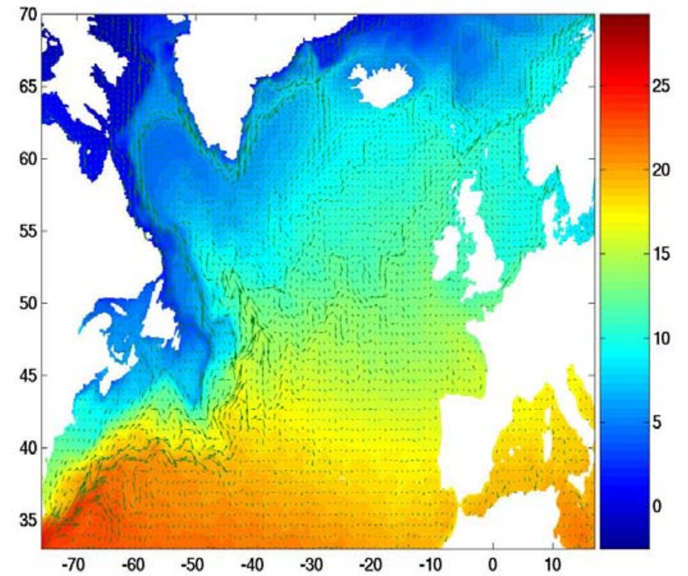

Figure 7: Annual-mean SST and surface circulation in a simulation of the North Atlantic Basin using ROMS at a resolution of 10 km.

Previous evaluations of the ROMS circulation model, as well as its embedded ecosystem components, have shown favorable agreement with observed behavior in both the North Atlantic and North Pacific basins (Curchitser et al., 2005; Fennel et al., 2006; Haidvogel et al., 2000; Hermann et al., 2002a; Powell et al., 2006). In particular, at eddy-permitting horizontal resolution (Figure 7), simulations of the circulation in the North Atlantic show the expected basin-wide, multi-gyre circulation patterns. In the studies proposed here, ROMS will be reconfigured with a northern domain boundary at 80N, and with active sea ice dynamics based upon the newly implemented and tested sea ice module (Budgell, 2005). Additional configuration details of the North Atlantic model are given in Fennel et al. (2006).

The adjoint model, in particular, can be quite costly computationally. Fortunately, both the forward and adjoint ROMS model (including its circulation and ecosystem components) have been efficiently parallelized for high performance on multi-processor computers. Based upon timings obtained for a prototype of the North Atlantic Basin model, we will be able to perform the forward model runs proposed here at eddy-permitting resolution (~10 km, thus capturing both the low-frequency and some of the operative mesoscale processes) and the biological inversions at resolutions appropriate to the CPR data (~0.5 degree).

5.2 Use the genetic data to estimate the rate of population exchange between gyres, and compare with model predictions of same.

Population genetic analysis of *C. finmarchicus* is being carried out in ongoing projects using other funding. Zooplankton collections were made through the Census of Marine Zooplankton (CMarZ), a Census of Marine Life field project funded by the Sloan Foundation (see CMarZ, 2005). The molecular protocols were developed using Prior NSF support (OCE-9911415) and are being carried out by Ebru Ünal, a Ph.D. student of Ann Bucklin's whose graduate studies and dissertation research are being funded by UConn with non-federal funds. No resources are requested in this proposal for the genetic analyses.

An ocean basin-scale view of the population genetic diversity and structure of *C. finmarchicus* will be developed, analyzed, and interpreted using standard statistical and population genetic approaches. Genetic diversity measures will be calculated and tests of neutrality will be performed for each locus, using Tajima and Ewens-Watterson tests (Ewens, 1972; Tajima, 1989; Watterson, 1978), among others. Statistical analysis of allele frequencies will be done by a hierarchical Analysis of MOlecular VAriation (AMOVA) (Excoffier et al., 1992), which evaluates molecular covariance within and among samples, regions, and gyres. Our measure of population genetic structure will be the Φst statistic (Excoffier et al., 1992), which tests the null hypothesis of genetic homogeneity among populations resulting from panmixia (i.e., random interbreeding across the sampled population). The significance of the Φst statistic is evaluated by permutations of the original data set, with all individuals randomly assigned to sub-populations. The proportion and significance of the molecular covariance explained by comparisons among samples and among regions will be used to estimate exchange among geographic populations of *C. finmarchicus* using appropriate statistical techniques at a range of spatial scales. These estimates of exchange will be compared directly to those computed from the model solutions, building upon earlier studies using genetics to estimate plankton exchange in the ocean (Olson and Hood, 1994).

5.3 Interannual to decadal variability: climatic forcing and the North Atlantic Oscillation

Some of the largest amplitude interannual to interdecadal signals in the physics, biology, and chemistry of the North Atlantic are associated with the North Atlantic Oscillation, or NAO (Hurrell et al., 2003; Stenseth et al., 2003). We expect variability in the basin-scale abundance and distribution of *C. finmarchicus* to respond in a complex way to such climatic forcing. Consider the regional example from the Gulf of Maine described by Greene et al. (2004) (Figure 8). During the negative NAO phase of the 1960s and early 1970s, *C. finmarchicus* was generally less abundant on average. In contrast, the predominantly positive NAO phase of the 1980s and 1990s was accompanied by both positive and negative anomalies in the abundance of *C. finmarchicus*. We postulate that our three-dimensional physical-biological model will shed light on the mechanisms underlying the irregular relationships between indices such as these.

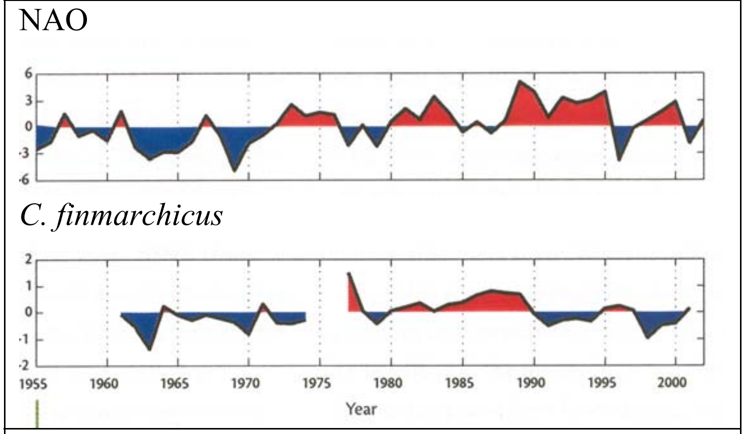

Figure 8. Top: NAO index. Bottom: *C. finmarchicus* mean annual abundance anomaly for late stage copepodids and adults (MERCINA, 2001) computed from CPR data in the Gulf of Maine (Jossi and Goulet, 1993). Adapted from (Greene et al., 2004).

We will begin our investigation of interannual variability by creating hydrodynamic simulations for both positive (1970s and 1980s) and negative (1960s) phases of the NAO. Monthly climatologies of *C. finmarchicus* will likewise be computed for these same periods from the CPR data. Separate inversions for these two time periods will permit quantification of the differences between these two "mean states" of the system. Those results will provide guidance for a sequential hindcast calculation for the entire period using the forward model only. The fidelity of the hindcast simulation will be evaluated using all available data.

6. Responsiveness to Program Solicitation 07-594

The proposed research directly addresses two of the three research themes identified in the announcement of opportunity: (1) The influence of climate on physical and biological processes, and (2) Population dynamics and recruitment of target species. By integrating observations from the U.S. GLOBEC Northwest Atlantic / Georges Bank study with many others throughout the entire Atlantic basin (Figure 6), this project constitutes pan-regional synthesis that forms the basis of this final phase of the U.S. GLOBEC program.

7. Intellectual merit

In order to understand oceanographic phenomena that may unfold on long time scales and large space scales – for which direct observation is not possible – new analytical approaches are needed. This project will entail interdisciplinary collaboration among physical and biological oceanographers, and it will also use a novel analytical approach, including adjoint modeling and molecular population genetics. Both the model and genetic results will be used to evaluate the primary hypothesis, evaluate evidence for and against the three gyre concept, and gain a clearer understanding of biological and physical dynamics at basin scales.

8. Broader Impacts

The broader impacts of this project fall into three main categories as outlined in NSF's Merit Review Broader Impacts Criterion: Representative Activities (July 2007): 1) "enhance infrastructure for research and education by establishing and supporting international collaborations", 2) "advance discovery and understanding while promoting teaching, training and learning", and 3) "broad dissemination to enhance scientific and technological understanding".

This project will utilize a number of international data sets, and as such will require substantial international collaboration for successful completion. To that end, we have initiated contact with a variety of collaborators from around the world. Our lead collaborator, Dr. Gregory Beaugrand, will work closely with us on interpretation of the CPR data (see supporting letter). A number of other international contacts will also be engaged in the synthesis of the data sets described in Section 5 (Figure 6), with Dr. Wiebe taking the lead of that aspect.

In order to promote teaching and training, the approaches and results from the proposed studies will be incorporated into a graduate course in physical/biological interactions being planned by McGillicuddy in the MIT/WHOI Joint Program. This collaborative effort will also provide new opportunities to the graduate and undergraduate students participating in the research at UConn, with one Ph.D. student in the Department of Marine Sciences partially supported by this project. McGillicuddy will attempt to entrain additional undergraduates into the project through the WHOI Summer Student Fellowship / NSF REU program.

We will make use of established education and public outreach networks and their well-developed infrastructure. These networks include the USA project office of the "Census of the Marine Zooplankton" (CMarZ) - a new Census of Marine Life (CoML) field project led by A. Bucklin. The CMarZ Communications Coordinator (Nancy Copley) and CoML Outreach & Education Network will ensure the broad dissemination of results to researchers, students, and educators. In particular, we propose to (1) produce a short (~5 minute) video clip describing the project, (2) contribute to cross-cutting synthesis chapters being planned by CoML, and (3) contribute interviews for the "Who's who" in the "Conversations" section of the CoML web site. A supporting letter from the leader of the CoML Education and Outreach Team (Sara Hickox) provides further details on this partnership.

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