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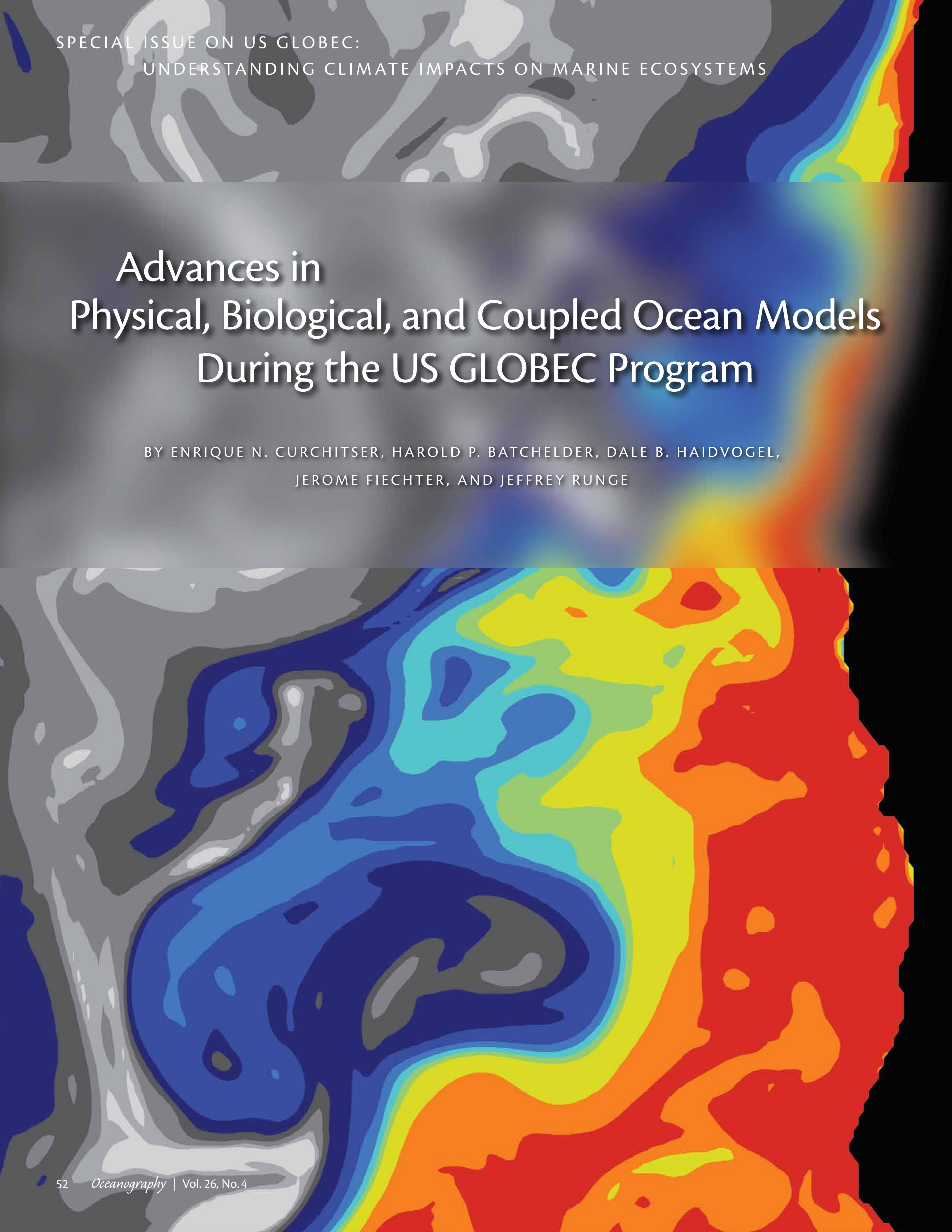
SPECIAL ISSUE ON US GLOBEC:
UNDERSTANDING CLIMATE IMPACTS ON MARINE ECOSYSTEMS



Advances in Physical, Biological, and Coupled Ocean Models During the US GLOBEC Program

BY ENRIQUE N. CURCHITSER, HAROLD P. BATCHELDER, DALE B. HAIDVOGEL, JEROME FIECHTER, AND JEFFREY RUNGE

ABSTRACT. From the planning days preceding the establishment of the US Global Ocean Ecosystem Dynamics (GLOBEC) program, modeling was recognized as one of the program's pillars. In particular, predictions of future ecosystem states in an evolving climate system required new interdisciplinary approaches that brought together physicists, biologists, modelers, and observational scientists. The GLOBEC program coincided with, took advantage of, and contributed to significant advances in ocean modeling capabilities. During the GLOBEC years, computer power increased substantially to the point where coupled physical-biological models, at resolutions where important interactions are resolved, became feasible. Ocean models were maturing so that complex coastal processes were explicitly represented, and advances in different ways of modeling the biosphere, from Lagrangian individuals to Eulerian community-based, multitrophic models, were emerging. The US GLOBEC program addressed the question: How can we use all these developments to help us understand how ecosystems will respond to climate change? This paper includes a review of state-of-the-science modeling at the onset of the GLOBEC program and highlights the evolution of physical and biological models used for the program's target regions and species throughout the GLOBEC years, 1992–2012.

INTRODUCTION

The US Global Ocean Ecosystem Dynamics (GLOBEC) program emerged from the recognition that variability in ocean ecosystems is intricately connected to a changing climate (e.g., Steele, 1998). Furthermore, because the early life stages of many organisms are planktonic, there is a strong coupling between the biology and the physics in the ocean and, by extension, Earth's climate. The program recognized that physical oceanographers and marine biologists needed to work together to evaluate how population and ecosystem dynamics are linked to physical phenomena across a wide range of temporal and spatial scales. From the beginning, the GLOBEC program highlighted numerical modeling and, in particular, coupled bio-physical models, as central to its ability to both test current understanding of ecosystem dynamics and to anticipate potential future states under a changing climate (Barange et al., 2010).

Modeling (or, for that matter, observing) the global ocean down to turbulence scales and all the species in a food web is, to date, an impossible task. Thus, the GLOBEC program focused its efforts on four coastal systems (Northwest Atlantic, California Current, Coastal Gulf of Alaska, and the western Antarctic Peninsula; see Turner et al., 2013, in this issue) that represent a range of environmental and ecosystem conditions. For the biology, the emphasis—though not exclusively—was on the early life stages of selected key species (deYoung et al., 2004) and the connection to the underlying dominant physics of the particular system (e.g., upwelling, buoyancy-driven flows, sea ice).

With a stated goal of developing predictive models based on mechanistic approaches that can be applied in a range of environments, the GLOBEC program first focused on developing both modeling and observational capabilities that could explore the dynamics of currents in the four target coastal regions. The models that emerged from this approach were necessarily complex, if not comprehensive. As a result of GLOBEC science, regional, time-evolving, spatially explicit circulation models were developed in each of the target regions. The science requirements stimulated the development and then improvement of regional circulation models now used by thousands of researchers worldwide (e.g., Regional Ocean Modeling System [ROMS], Haidvogel et al., 2008, and unstructured grid Finite Volume Coastal Ocean Model [FVCOM], Chen et al., 2007; see Box 1). The challenge was, and remains, to develop physical models that encompass the spatio-temporal scales of processes significant to the biology. For coastal ecosystems, this requires an accurate representation of the bathymetry and coastline geometry as well as such dynamical characteristics as vertical stratification, mixed-layer depth, and mesoscale features (e.g., fronts and eddies) over climate time scales.

Field observations collected by GLOBEC were designed to improve our knowledge of the systems directly, provide data for evaluating model output (skill assessment; e.g., Stow et al., 2009), and enable improved model performance through data assimilation. The assimilation of observations into models was recognized as a means of improving model fidelity for both physics and biology.

For both logistical and scientific

BOX 1. DEFINITIONS OF MODEL TYPES: IMPORTANT TERMS AND CONCEPTS

ADJOINT TECHNIQUE: A technique used in some types of data assimilation to speed up the computations used in the minimization of model-data misfits.

BIOENERGETIC MODEL: A model of the energy flow in a living system. Typically, this includes modeling processes affecting the growth (caloric ingestion), reproduction, respiration (movement), and excretion of an organism.

DATA ASSIMILATION: A technique by which observational data are used to improve model simulations.

DIAPAUSE: A state of dormancy in an organism used to survive predictable adverse conditions.

ENSO: El Niño-Southern Oscillation index, used to categorize climate states in the tropical Pacific ocean.

FINITE ELEMENT METHOD: A numerical technique based on the calculus of variations used to solve differential equations on a computer.

FINITE VOLUME METHOD: A numerical technique for solving differential equations based on fluxes between adjacent grid cells; one example is FVCOM (http://fvcom.smast.umassd.edu).

FVCOM: Finite Volume Coastal Ocean Model (http://fvcom.smast.umassd.edu).

HYDRODYNAMIC MODEL: A numerical (computer) model used to solve the equations of fluid flow.

INDIVIDUAL BASED MODEL: A biological model based on simulating the behavior of individual organisms.

NAO: The North Atlantic Oscillation, a leading climate mode of variability in the North Atlantic.

NPGO: The North Pacific Gyre Oscillation, a climate mode of variability in the North Pacific.

NPZD: Nutrient-Phytoplankton-Zooplankton-Detritus model, typically a concentration-based approach used to model primary and secondary production in the ocean.

OSSE: Observational System Simulation Experiments, use of synthetic data to help design observational networks.

OPEN BOUNDARY CONDITIONS: Used to supply boundary conditions to regional models, typically from global models or observational data.

ROMS: Regional Ocean Modeling System (http://www.myroms.org).

UNSTRUCTURED GRID: An irregular way of discretizing a space with simple shapes, such as triangles or quadrilaterals.

QUODDY: A finite element coastal ocean model (http://www-nml.dartmouth.edu/Software/quoddy).

reasons, the scope of the biological modeling focused on ecology, specifically, population dynamics of selected key species, rather than on biogeochemical cycles (e.g., deYoung et al., 2010). The logistical rationale was to minimize overlap of the US GLOBEC program with US JGOFS (Joint Global Ocean Flux Study), which were two of the large, multiregional programs within the US Global Change Research Program portfolio (Haidvogel et al., 2013, in this issue). JGOFS, initiated before GLOBEC, focused on nutrient cycling and the fate of carbon, especially the vertical flux of carbon, mostly in open ocean regions. In contrast, GLOBEC focused on the dynamics of marine animal populations, specifically zooplankton and fish populations in coastal marine systems, where the bulk of capture fisheries occur worldwide (Steele, 1998). Scientifically, the problem of fish recruitment and oceanographic factors, including climate variability, that controlled recruitment (e.g., fisheries oceanography) demanded more thorough multidisciplinary examination of the mechanisms responsible for the large interannual variation in population abundances of fish in coastal systems at multiple spatial and temporal scales. Mechanistic understanding was essential if the objective of forecasting population responses to future climate variation and change were to be met.

It is estimated that approximately 15–20% of all US GLOBEC funding over 20 years was devoted to research that could be labeled “modeling.” While not all of that was bio-physical modeling, it is the coupled models that ultimately led to new understanding and were most responsive to the goals of the program. It is also important to emphasize that the modeling activity in GLOBEC was dependent on the physical and ecological observations and experiments done by GLOBEC and other programs.

In the sections below, we review and illustrate with examples some of the advances in both disciplinary and coupled bio-physical modeling that emerged during the US GLOBEC program. The specific model results described below are a small subset of GLOBEC modeling results; we attempt to cite other similar results without detailed description, but could not cite all of the relevant and applicable literature.

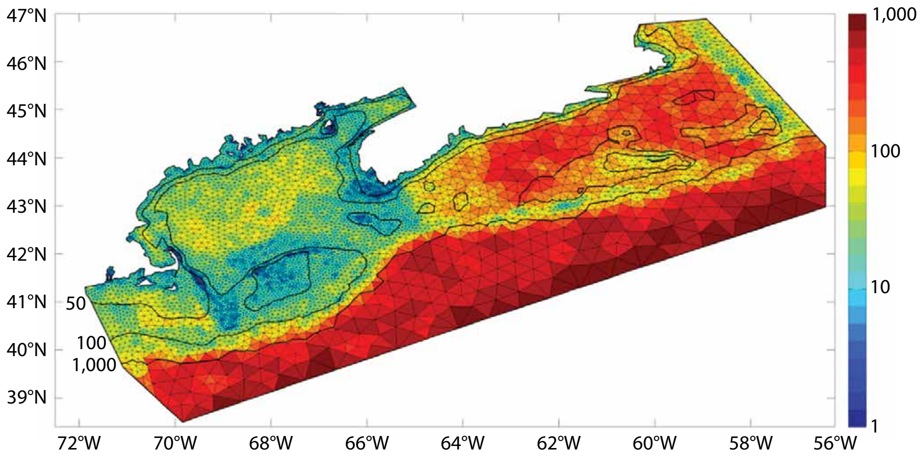


Figure 1. Unstructured grid for the Northwest Atlantic Gulf of Maine region representative of those used with the QUODDY model to study transport and trophodynamics of fish and invertebrate larvae (e.g., Tremblay et al., 1994). The model was based on triangular finite elements. The technique allows for selective mesh refinement over coastal or topographic features. The color bar describes element size in km^2.

MODELS OF THE OCEAN PHYSICS

The desire to make the connection between climate drivers and local ecosystem dynamics led to development and implementation of numerical models with a range of techniques addressing the multiscale nature of the problem. One of the earlier models implemented in the Northwest Atlantic region was based on unstructured finite elements capable of intelligently refined resolution. This model, QUODDY (Lynch et al., 1996; Figure 1), was used to study the drift of scallop larvae on Georges Bank (Tremblay et al., 1994), as well as to study the transport of cod and haddock on Georges Bank (see below). Unstructured grid models remained a mainstay for GLOBEC, particularly in the Northwest Atlantic. A more recent model, FVCOM (Chen et al., 2011), based on the unstructured finite volume technique, was used, among other applications, to study tidal dynamics in the Gulf of Maine; particular care was taken to resolve prominent bathymetric and coastal features of the region. The advent of unstructured models for regional applications in oceanography allowed improved representation of circulation features to be included in research with coupled bio-physical models.

A different approach to the multiscale challenge implemented by GLOBEC scientists is use of nested structured models (Figure 2). In this technique, a high-resolution model is nested inside a coarser model of a more extensive region. Examples of this approach are the ROMS implementations of Curchitser et al. (2005) and Hermann et al. (2009a), where high-resolution models of the Northeast Pacific are nested within a basin-scale implementation of ROMS. The basin-scale simulations are used to simulate the region's large-scale climate, which is then used to force a higher-resolution limited-area model that resolves the scales more appropriate for studying biological and coastal processes. In these papers, the authors show that nesting allows large-scale remotely generated signals, such as the El Niño-Southern Oscillation (ENSO), to be represented in the higher-resolution regional nests. The challenge with nesting techniques has been to develop a robust implementation of the open boundary conditions used to communicate between the nested domains.

Significant advances were made in the development and implementation of data assimilation techniques for both physics and biology. McGillicuddy et al. (1998) used an adjoint approach for investigating physical and biological controls on the population dynamics of the planktonic copepod *Pseudocalanus* spp. on Georges Bank in the Northwest Atlantic. Data assimilation contributed to analysis and assessment of the research cruise

Enrique N. Curchitser *(enrique@marine.rutgers.edu) is Associate Professor, Department of Environmental Sciences and Institute of Marine and Coastal Sciences, Rutgers University, New Brunswick, NJ, USA.* **Harold P. Batchelder** *is Professor, College of Earth, Ocean, and Atmospheric Sciences, Oregon State University, Corvallis, OR, USA.* **Dale B. Haidvogel** *is Professor, Institute of Marine and Coastal Sciences, Rutgers University, New Brunswick, NJ, USA.* **Jerome Fiechter** *is Assistant Researcher, Institute of Marine Sciences, University of California, Santa Cruz, CA, USA.* **Jeffrey Runge** *is Professor, School of Marine Sciences, University of Maine, Gulf of Maine Research Institute, Portland, ME, USA.*

sampling strategy employed in the Northwest Atlantic using observational system simulation experiments (OSSEs; McGillicuddy et al., 2001) in real time as part of the US GLOBEC Georges Bank program (Lynch et al., 2001), and assimilation of altimetry data in an eddy-resolving model improved the skill of the coupled ecosystem model in the coastal Gulf of Alaska (CGOA; Fiechter et al., 2011).

In the Northeast Pacific, assimilation of physical observations (satellite altimetry, in situ temperature, and salinity) substantially increased the accuracy with which the ROMS model reproduced the frequency, duration, and intensity of eddy events along the CGOA shelf break (Fiechter et al., 2011). Improving the representation of oceanic mesoscale variability also enhanced realism in the biological response predicted by the lower trophic level ecosystem model coupled to ROMS (Figure 3). Overall, the results from the data assimilative simulations confirmed observed evidence that ecosystem dynamics along the northwestern CGOA shelf break is closely tied to eddy activity. Successful assimilation of physical observations into circulation models also opened the door for future assimilation of biological observations to further increase the realism of coupled bio-physical model solutions.

COUPLED BIO-PHYSICAL MODELS

In reviewing recent advances in coupled bio-physical modeling in GLOBEC, it is appropriate to recognize that the earliest bio-physical models in oceanography were those of Gordon Riley (1942, 1946, 1947), who was studying phytoplankton production and zooplankton populations on Georges Bank (one of the four regions studied by US GLOBEC). In the two decades that encompass the GLOBEC years (1992–2012), coupled bio-physical modeling advanced greatly. These advancements were achieved because of the confluence of (1) improved and more accessible computing capabilities; (2) orders of magnitude increases in ocean observations and experiments; (3) higher education opportunities for specialization and training in bio-physical modeling leading to highly capable, multidisciplinary modelers; and (4) a need by society, in the face of unprecedented changes (e.g., eutrophication, acidification, climate change), for prediction of future states of ocean ecosystem environments, including productivity, distribution, and species composition.

GLOBEC developed an approach for coupling models of varying resolution across trophic levels in order to simulate unobservable complex processes; previously, these processes were often inferred from observed correlations between environmental variability and ecological variables (including productivity and fish recruitment) that influence the distribution, abundances, life cycles, and dynamics of marine animal populations. Figure 4 shows a schematic of the GLOBEC vision for a framework that can be used for examining hypotheses and linking observations, experiments, and process studies. It consists of multiscale physical (atmosphere-ocean) models coupled with both lower trophic level nutrient and prey models that, in turn, are used to link to upper trophic levels that can be modeled as individuals.

In the next sections, various approaches to ecological modeling that formed part of the GLOBEC program are described. These include models that were specifically designed to address questions pertaining to the

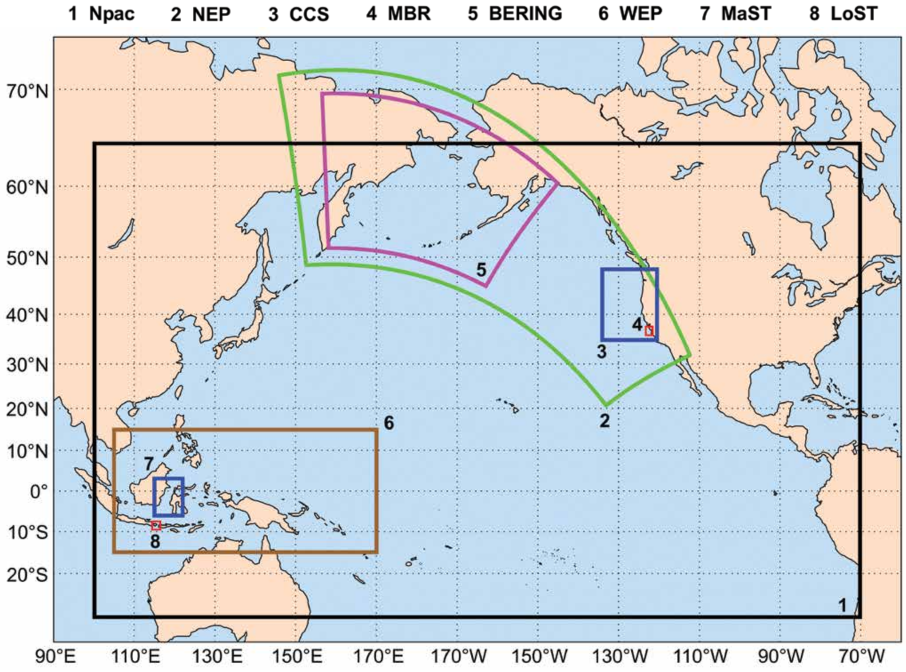


Figure 2. North Pacific nested domain configuration. The approximate resolutions of the component grids are: NPac, 0.4°; NEP, 10 km; California Current System (CCS) and coastal Gulf of Alaska (CGOA), 2–3 km; and Monterey Bay Region (MBR), 250 m (Curchitser et al., 2005). Boundary conditions for the outermost grids were extracted from either global models or data sets. For subsequent refinements, boundary conditions were extracted from the next-up coarser model.

role of physical transport in retention and connectivity; coupled models of physics, nutrients, and lower trophic levels; models of the energy flow through organisms (bioenergetics); population dynamics models that allow a dynamic description of the interactions between life history strategies and the physical environment; and, finally, models that attempt to integrate the various aspects of the ecosystem (end-to-end).

MODELS FOR TRANSPORT, RETENTION, AND CONNECTIVITY

Transport and retention, and in recent years connectivity, have been examined with numerical modeling using both Eulerian and Lagrangian techniques. Eulerian models provide three-dimensional, time-dependent estimates of properties at specific fixed locations on a spatial grid, while the Lagrangian approach follows moving points (or particles) through space and time. In a combined Eulerian-Lagrangian approach, Lagrangian particles (representing, say, fish) are given appropriate behavioral responses as they move through the ocean. As they do so, they obtain environmental information from Eulerian models, which may provide physical variables, such as velocity and temperature, or bio-physical variables, such as fields of prey for the organisms (e.g., mesozooplankton). Combined Eulerian-Lagrangian models (ELMs) were used to examine many processes in GLOBEC regional studies. When temperature and food fields are included in ELMs to explicitly simulate the ingestion, respiration, reproduction, and mortality of individuals, they are usually referred to as bioenergetics models, which are described in a subsequent section.

The development of more sophisticated and higher spatial resolution ocean hydrodynamic models over the past two decades (e.g., ROMS, FVCOM) improved the representation of temporal and spatial variations of temperature and currents, and it also improved their reliability when coupled with ecological models (Powell et al., 2006; Fiechter et al., 2011) or with transport models (Werner et al., 1993; Johnson et al., 2006; Piñones et al., 2011, 2013) to examine retention, dispersion, and connectivity. Circulation and organism vertical behavior influence residence time

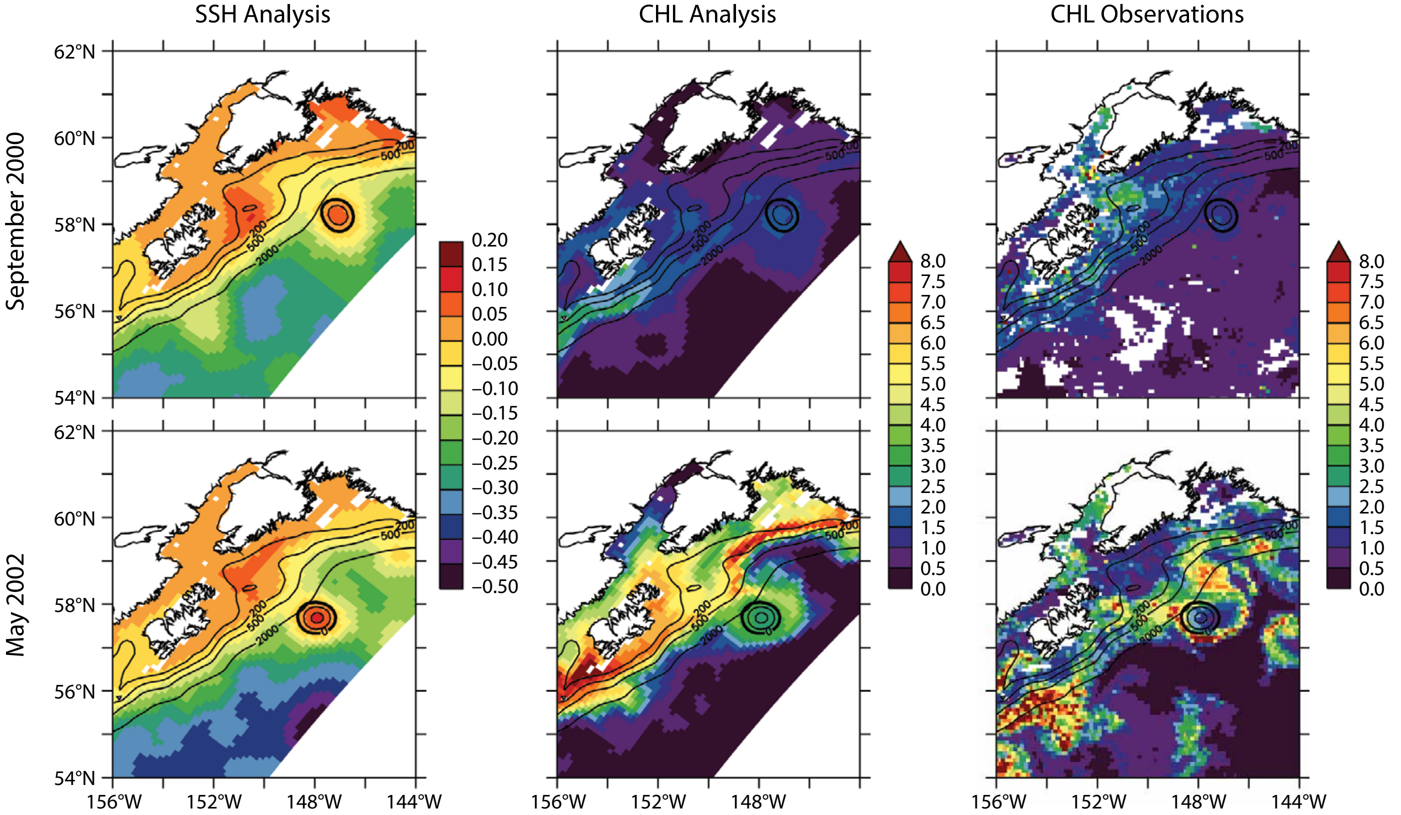


Figure 3. Impact of mesoscale eddies on biological activity in the northwestern CGOA during the weeks of September 1, 2000 (top), and May 21, 2002 (bottom). (left and center) Sea surface height (SSH; m) and surface chlorophyll concentrations (mg m^{-3}) from data assimilative solution. (right) Corresponding observed chlorophyll concentrations (mg m^{-3}) from SeaWiFS satellite data. Contour lines represent simulated SSH anomalies and identify eddy locations. *Figure reproduced from Fiechter et al. (2011)*

and retention of diapausing *Calanus finmarchicus* in Gulf of Maine deep waters (Johnson et al., 2006; Figure 5). Modeling of larval cod and haddock on Georges Bank (Werner et al., 1993), copepods on the shelf in the Northern California Current (Batchelder et al., 2002a), and Antarctic krill along the western Antarctic Peninsula (Piñones et al., 2011; Figure 6) showed similar results, highlighting the importance of vertical position or behaviors on retention. Similar model approaches examined potential range expansions of copepods from the North Atlantic into Arctic regions with anticipated global warming (Ji et al., 2012b). Some studies included temperature-dependent development or stage durations. Others included the influence of both temperature and food, depending on the hypothesized relations and the data sets available to support the modeling.

Survival of cod early life stages to recruitment is also dependent upon successful transport to nursery areas where juvenile survival and membership in local populations are enhanced. Application of a coupled Individual-Based Model (IBM) to a circulation model showed that transport of Gulf of Maine cod eggs and larvae to local nursery areas was influenced by interaction of wind-driven transport with the larger-scale Gulf of Maine circulation, providing a mechanistic explanation for the observed relationship between downwelling wind speed during the spawning period and an index of recruitment for the Gulf of Maine cod stock (Huret et al., 2007; Churchill et al., 2011). A system of linked coupled models integrating influences of physical forcing on transport and planktonic production on larval growth was put forward as a tool to forecast environmental influences on Gulf of Maine cod recruitment (Runge et al., 2010).

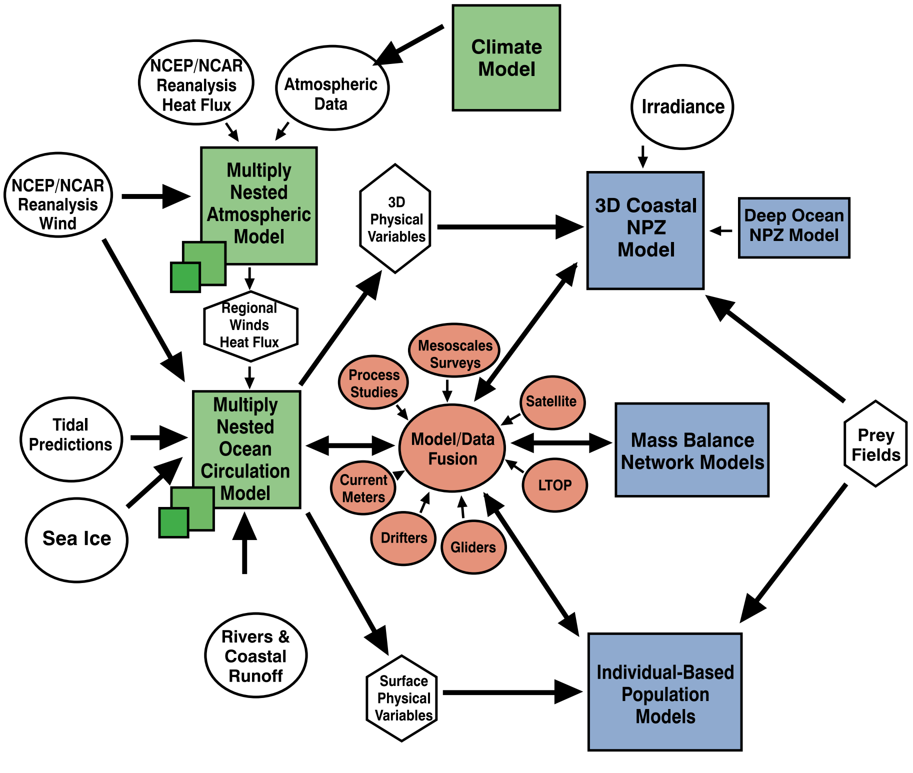


Figure 4. Schematic diagram of one possible configuration for a multiscale model based on the nesting concept. The primary elements of the modeling system include (1) a climate forcing model, (2) a nested hierarchy of (global/basin/regional/local) physical circulation models for the ocean and the atmosphere, (3) one or more food web models including mass balance network models and NPZD models, (4) one or more individual-based models for relevant higher trophic level species, and, finally, (5) appropriate mechanisms (possibly utilizing advanced data assimilation) for comparison and/or fusion of these forward models with available retrospective and contemporary data sets (GLOBEC, 2007).

Connectivity between source and destination has applications beyond understanding recruitment; it is critical for implementing coastal and marine spatial planning, which is currently being implemented in several states along the California Current region and elsewhere. Knowing which sites are well connected to many potential sites of recruitment aids the identification of high-priority sites for protection from adverse environmental effects such as eutrophication, habitat modification, or fishing extraction. GLOBEC research on ocean retention and dispersal connectivity (Werner et al., 2007) contributed to the assessment and design of marine reserves in Oregon (Heppell et al., 2008); similar research done elsewhere along the West Coast made like contributions (Mitarai et al., 2009; Petersen et al., 2010; Drake et al., 2011).

LOWER TROPHICS AND NUTRIENT DYNAMIC MODELS

Coupled physical-ecosystem models in a Eulerian framework are important for understanding spatial and temporal patterns of primary and secondary productivity (phytoplankton and smaller zooplankton) and for quantifying mechanisms that link climate forcing (wind, freshwater runoff, and ice in high latitudes) with ecosystem responses. Powell et al. (2006) coupled a high-resolution three-dimensional circulation model of the California Current System (CCS) with a relatively simple (one component in each category) lower trophic level ecosystem model for Nutrient-Phytoplankton-Zooplankton-Detritus (NPZD) and compared the model-deduced temporal patterns to satellite observations (Figure 7). For the upwelling CCS, Powell et al. showed significant skill of the coupled bio-physical model. Di Lorenzo et al. (2008) and Macias et al. (2012) evaluated the effects of low-frequency climate fluctuations such as ENSO or the North Pacific Gyre Oscillation (NPGO) on ecosystems of the California Current. Such models also serve as the link between the physics and upper trophic level individual-based models by providing time/space varying prey fields.

A further example from a GLOBEC-specific study region is the model developed for the CGOA (Hermann et al., 2009b; Coyle et al., 2012) for examining primary production, nutrient limitation, and pathways of nutrient supply to the photic zone. In the generally downwelling CGOA, the physical processes that supply nutrients to the photic zone to sustain primary production leading to the high fish biomass produced on the shelf of the Gulf of Alaska were unknown; models allowed the various hypothesized processes to be isolated and examined to assess their relative importance to nutrient supply (see also Fiechter and Moore, 2009). The addition of an iron limitation component to NPZD models was critical to reproducing primary and secondary production in the CGOA (e.g., Fiechter and Moore, 2009; Hinckley et al., 2009) and ecosystem response to eddy activity (Fiechter and Moore, 2012).

A coupled FVCOM-NPZD model of Georges Bank and the Gulf of Maine was used to identify the times and sources of nitrate to Georges Bank (the entire bank as well as the well-mixed central region) and to examine the seasonal nitrate and production processes (Ji et al., 2008a,b). The results suggest that physical transport onto the bank provided only about 20% of nitrate used by phytoplankton, with internal nitrogen regeneration being by far the dominant process from April through November, which allows for high primary productivity on the central bank during summer when nitrate is low. North Atlantic Oscillation (NAO)-related changes in deep nutrient concentrations had relatively little impact on nutrient and phytoplankton dynamics in the well-mixed central bank, slightly larger effects in the stratified flank regions, and much greater effects in the deeper basins of the Gulf of Maine.

BIOENERGETICS MODELS

Because recruitment and year class strength are presumed to be controlled by processes that occur early in the life history of organisms (following Hjort, 1914; Leggett and Deblois, 1994), emphasis has been placed on modeling that enables integration of processes that affect growth rates of larvae at local scales (food and temperature) with processes that affect populations at regional scales (advective losses). Two early US GLOBEC models focused on the circulation on Georges Bank and its effect on the transport of larvae spawned on the bank (regional scale). The results showed the importance of the larvae's vertical depth and directional swimming behavior (Werner et al., 1993) and interannual variability in wind conditions on retention of larvae on Georges Bank (Lough and Potter, 1993). Werner et al. (1996) modeled larval cod growth as a result of deterministic space-time trajectories through a spatially heterogeneous prey field (prescribed from field surveys), modified by a stochastic contribution to prey encounter and a turbulence influence on prey encounter rates. Individuals whose weight declined below a stage-specific critical threshold, due to lack of success in encountering or consuming appropriate prey, were assumed not to survive (representing

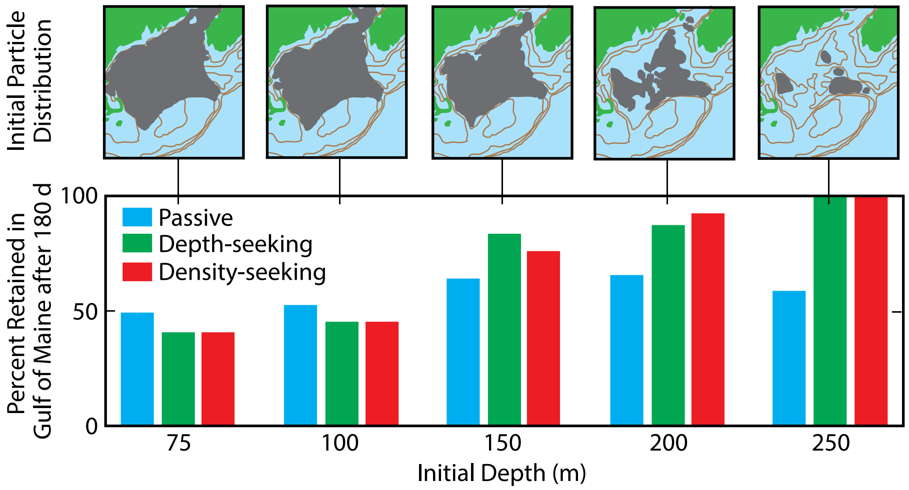


Figure 5. The retention of diapausing copepods in the Gulf of Maine after six months (July 1–January 1) is influenced by both initial depth (75–250 m) and active depth control (passive transport, or depth- or density-seeking behaviors). Upper panels show the initial regions of diapausing copepods for each depth range (gray regions). Land is green and ocean is blue. *Figure modified from Johnson et al. (2006)*

mortality by starvation). Starvation was most important in first-feeding larvae. Turbulence enhanced contact rates by factors of two to five, and was most effective in enhancing growth in the same regions where on-bank retention was highest. Werner et al. (2001) modified the model and observed that the ability of the larvae to swim and aggregate in the vertical to take advantage of local regions of higher prey availability is critical to their survival and for reproducing their distributions as observed in the field.

Lough et al. (2005) used a one-dimensional numerical model that included the effects of light intensity on feeding and the effects of temperature on larval metabolic costs and ingestion rates to explore larval cod growth and its seasonal and interannual variability. They showed that maximum growth occurred at 20–60 m depth, while in shallower waters, warmer temperatures and reduced prey densities combined to yield reduced net growth. At deeper depths, reduced feeding due to light limitation led to reduced growth, despite generally high prey densities. Finally, Kristiansen et al. (2007, 2009) hypothesized that perception-based differential encounter of prey due to their abundance and visibility (size), combined with the larvae's ability to capture a species, influenced the diet, so they incorporated visual abilities, prey abundance, and prey size into their model of feeding.

Similar bioenergetics-based modeling has been done for other pelagic species, ranging from juvenile salmon to copepods (Miller et al., 1998; Batchelder et al., 2002b; Neuheimer et al., 2009; Ji et al., 2009; Stegert et al., 2012), euphausiids (Dorman et al., 2011; Lowe et al., 2012; Lindsey, 2014), and larval cod and/or haddock (references above; Leising and Franks, 1999). Many other particular cases from the GLOBEC program could be described. Here, we focus on the example of the Antarctic krill *Euphausia superba* found in the slope and shelf regions of the Southern Ocean. How larvae cope with the harsh conditions of Southern Ocean winters, when much of the shelf is covered by ice and phytoplankton primary production is extremely low (mostly due to light limitation), was not known, but it was evident that some did survive the winter (Daly, 1990).

Early modeling of the bioenergetics of Antarctic krill and their environmental conditions favored certain hypotheses about feeding behaviors and physiological responses that larval krill might use to allow successful overwintering, but they also indicated that lack of wintertime observations prevented narrowing the list of possible mechanisms (starvation, body shrinkage, reduced metabolism, diversified diet) to one, or a few, probable mechanisms (Hofmann and Lascara, 2000). US GLOBEC research cruises in the Southern Ocean focused on austral winter of 2001 and 2002, and complemented NSF-funded Palmer Long-Term Ecological Research (LTER) that has run continuously since 1991 (http://pal.lternet.edu). Lowe et al. (2012) suggested that larval krill survival and recruitment to adults was linked to fall and winter variability in the timing and duration of phytoplankton availability to larval krill. Early sea ice formation enhances the dynamics and abundances of the sea ice algae and microbial communities that represent a late fall-winter food source for larval krill after ice formation (Fritsen et al., 2008). In the Southern Ocean GLOBEC program, the bioenergetics approach was also used to track the flow of energy through the ecosystem, from primary to upper trophic level productivity, and its response to varying environmental conditions

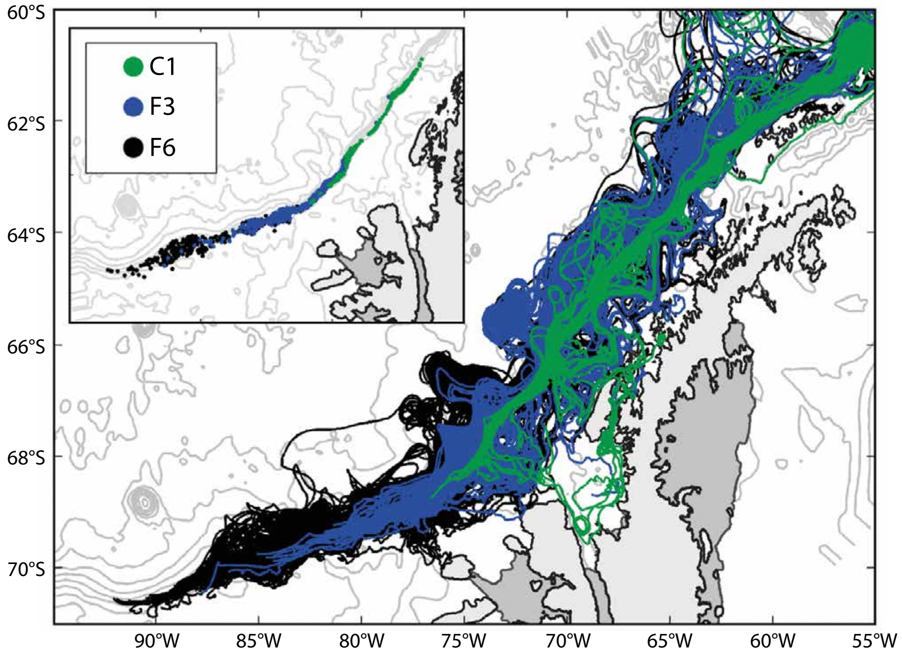


Figure 6. Source regions (inset plot) and simulated trajectories for particles released along the shelf break of the western Antarctic Peninsula. The source regions represent particles that entered the Marguerite Bay shelf region as euphasiid larval stages calyptopis 1, furcilia 3, and furcilia 6 (green-, blue-, and black-dot trajectories, respectively). *Figure from Piñones et al. (2013)*

(Ballerini et al., in press; Figure 8).

Generally, most of these studies were directed at understanding how a species coped with environmental hardships, whether it was avoiding transport to unfavorable environments (or the converse, retention in favored regions), or periods of sustained adverse temperatures or low food availability. The progressive inclusion of new physiological and behavioral details and the environmental conditions that influence these processes have led to increased understanding of the mechanisms that contribute to larval survival and the potential for large year classes.

POPULATION DYNAMICS/ LIFE HISTORY MODELS

One of the early goals of the GLOBEC program was "a modeling effort to determine how well we are able to put together our present knowledge of physical oceanography with the known population biology of marine organisms that have numerous, distinct, planktonic life stages" (GLOBEC, 1991, p. 4). If a model is capable of successfully reproducing the basic spatio-temporal pattern of variability of a particular species by incorporating our existing understanding of life history traits and vital rates of zooplankton species, then it can

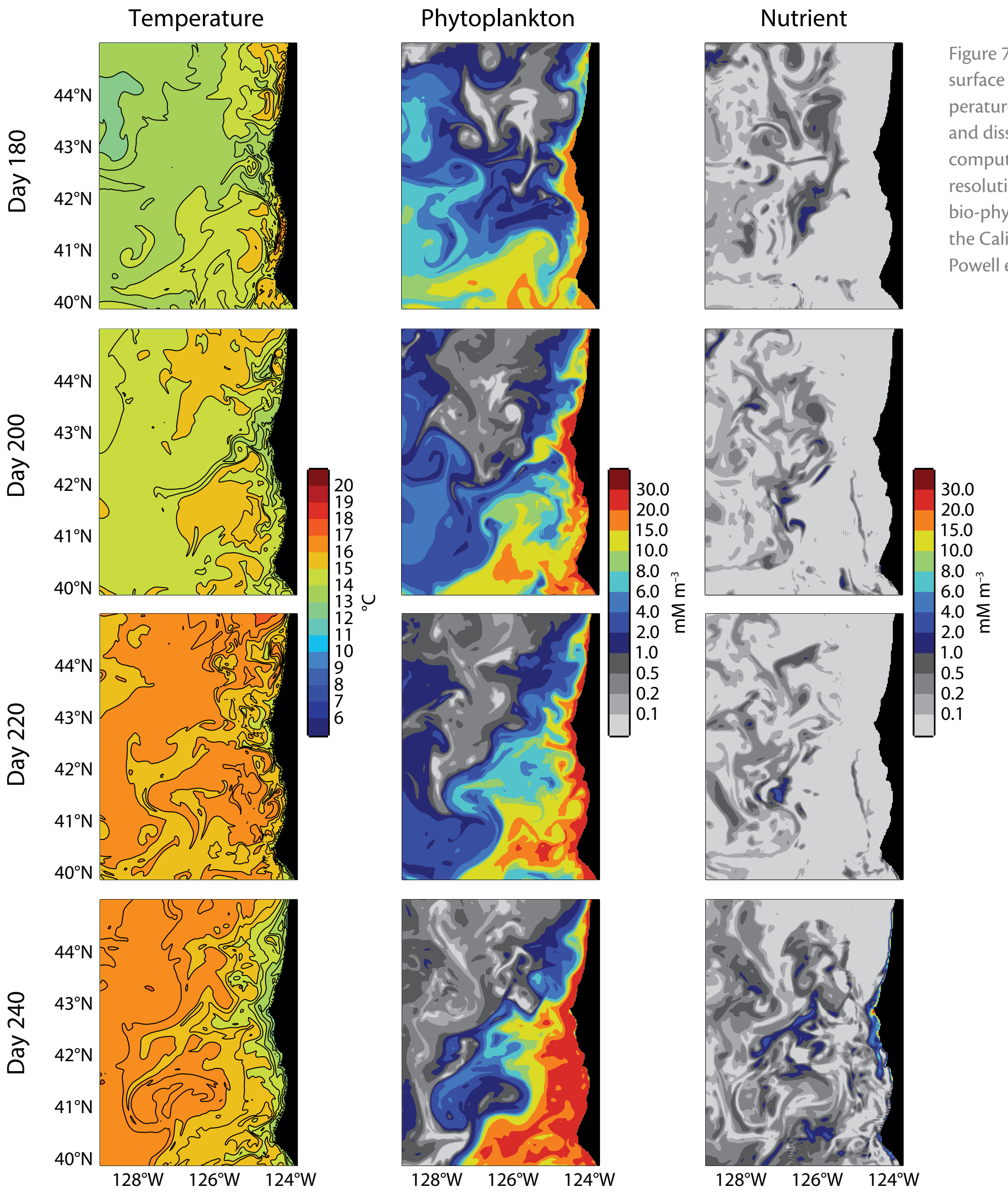


Figure 7. Evolution of the surface expression of temperature, phytoplankton, and dissolved nitrogen as computed with a high-resolution (3 km) coupled bio-physical model of the California Current by Powell et al. (2006).

help us to (1) assess the contribution of different factors that determine local abundance and patterns of distribution (i.e., diagnose), and (2) test the sensitivity of abundance and distribution patterns to changes in life history traits and the physical environment (i.e., forecasting or scenario projection, also a GLOBEC objective). If a model fails to match observations, the mismatch between model and observation may provide valuable insights and direction on possible missing components and/or key biological processes that require further investigation.

Coupled bio-physical population models were developed by GLOBEC to understand the spatio-temporal distribution pattern of zooplankton species in the North Atlantic (e.g., Ji et al., 2009; Stegert et al., 2012), Northeast Pacific (Dorman et al., 2011), and Southern Ocean (Piñones et al., 2013). In the North Atlantic, Ji et al. (2012a) used a coupled hydrodynamics/food-web/population-dynamics model to assess the sensitivity of the small copepods *Pseudocalanus* spp. and *Centropages typicus* to changes in phytoplankton biomass and bloom timing, as well as to changes in mortality regime. The results showed that the population size in these copepods is more sensitive to changing (predation) mortality than to changes in food availability and peak timing. However, top-down control is difficult to observe and quantify (Davis, 1984; Ji et al., 2012a).

While the impacts of physical changes on dynamics of the local abundance of the planktonic copepod *C. finmarchicus* are not yet fully understood, the life history knowledge and bio-physical modeling capacity acquired during the GLOBEC program provide the foundation for understanding mechanisms that regionally sustain the population. *C. finmarchicus* is a key functional component of the Northwest Atlantic food web that is locally very productive in the Gulf of Maine/Georges Bank region (e.g., Runge et al., 2006), which lies at the southern edge of the copepod's subarctic range. How anticipated future surface and deep warming will influence its population abundance remains an open question.

A key to understanding climate forcing on local *Calanus* abundance is the effect of temperature on the species' life cycle, which involves a lipid-rich dormancy stage from late summer through early winter. Modeling of *C. finmarchicus* population dynamics has been impeded until recently by a lack of understanding of the mechanisms of dormancy control, which affect the timing of population recruitment and growth in relation to environmental events such as the spring phytoplankton bloom. GLOBEC studies identified lipid accumulation and metabolism as the mechanisms controlling the timing of entry and exit into dormancy (Johnson et al., 2008). This understanding of dormancy control has been incorporated into a one-dimensional life history model of *C. finmarchicus* in the deep western Gulf of Maine basin (Maps et al., 2012). The model results indicate that the present warm overwintering temperatures in deeper layers of the Gulf of Maine force early exit from dormancy, inducing a biphasic dormancy pattern (i.e., exit of summer dormant copepods in early fall and reentry into dormancy in late fall; Figure 9). A full understanding of the influence of climate forcing on *C. finmarchicus* awaits investigation of the interaction between the species' life history and local and regional advective processes.

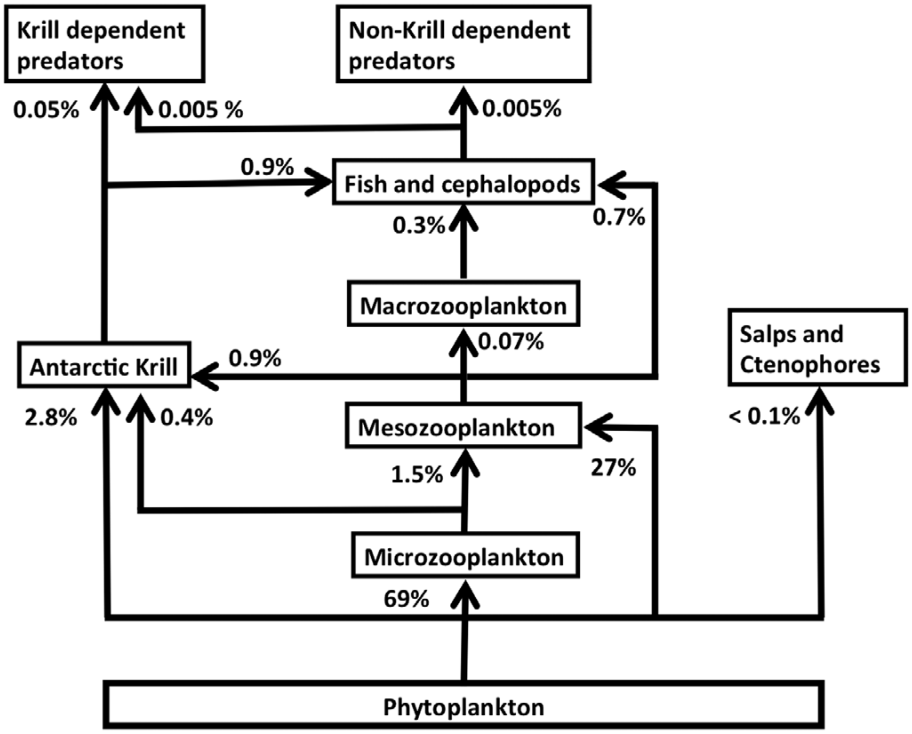


Figure 8. Summary of the percent transfer of primary production between the pelagic components of the food web model developed for the southern region of the West Antarctic Peninsula continental shelf (Ballerini et al., in press).

In a different approach, Batchelder (2006) implemented backtracking of particles (i.e., running the model backward in time) to estimate probability distributions of their locations at earlier times, or, for meroplankton (organisms that are planktonic only for part of their life cycles), to identify possible source locations of the benthic adults that produced the egg and larval meroplankton being tracked. The rationale for backtracking was driven primarily by computational efficiency for questions that focus on where individuals came from and the conditions they encountered that led to their present state. Other authors have examined more rigorously the assumptions required of backtracking (Christensen et al., 2007). While the assumptions about the irreversibility of some biological process (mortality) and diffusion may restrict some applications of backtracking, it has become a common approach for identifying subregions for forward simulations, while greatly reducing the number of particles that must be modeled. Backtracking of larval fish from the location of capture has enabled better understanding of spawning sites and environmental conditions leading to variability in growth estimated for several fish species (Itoh et al., 2011; Payne et al., 2013).

A new approach to estimating stage-dependent mortality rates of zooplankton is to model the dynamics of a plankton population through time. The data requirements for this are extensive, usually including repeated observations of the abundance and distribution of a species over a significant portion of its life history. Abundance observations need to be complemented by using population dynamic variables (egg production rates, stage durations, and development rates) estimated independently, often from ship-based incubations. Because individual water parcels are dynamic in the ocean, such population-model-based mortality estimations, in all but the simplest scenarios, need to be coupled to a model of physical circulation to account for advective and dispersive losses of individuals. Such complete data are rarely available.

GLOBEC sampled zooplankton during five consecutive years on Georges Bank. The five years were averaged to produce monthly climatological distributions of the feeding stages of *Calanus finmarchicus.* Li et al. (2006) used a tidal-, wind-, and density-driven seasonal climatology of circulation in the Northwest Atlantic (Naimie et al., 1994) to transport and disperse *C. finmarchicus* during the vernal bloom period (January to June). Data assimilation was used to minimize the mismatch between the monthly climatologically modeled

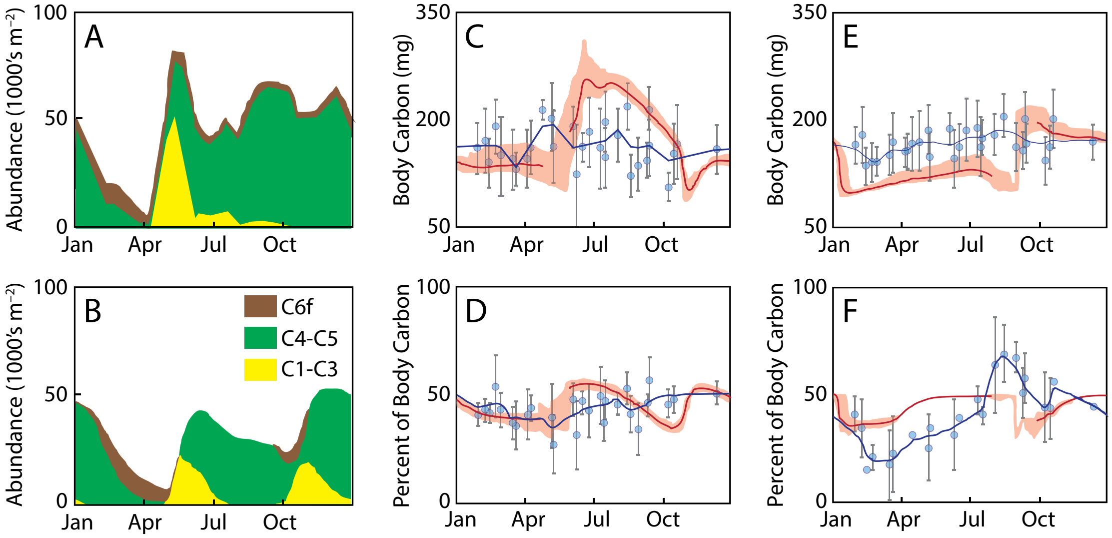


Figure 9. Comparison of observations with *Calanus finmarchicus* Individual-Based Model (IBM) simulation results in the Gulf of Maine. (A) Observed abundances of young copepodid stages (C1–C3), advanced copepodid stages (C4–C5), and adult females (C6f). (B) Average of the simulated abundances of C1–C3, C4–C5, and C6f. (C) Observed and simulated body mass in carbon of stage C5. (D) Observed and simulated lipid content as percent of body carbon of C5. (E) Observed and simulated body mass in carbon of C6f. (F) Observed and simulated lipid content as percent of body carbon of C6f. For (C) to (F), blue dots and bars = observations + standard error. Thin blue line = lowest fit to observations. Thick red line = model ensemble average (missing in regions where variability among individuals in ensemble was very high). Pale red areas = range of individual model results of members constituting the ensemble. *Modified from a figure in Maps et al. (2012)*

abundances and monthly objectively analyzed maps of *C. finmarchicus* stage abundance. The assimilation results suggested significant abundances of the youngest life stage were present initially in (unsampled) off-bank regions in the deep basins of the Gulf of Maine, north of the bank, that were advected onto the bank by seasonal flows from January through February. This is expected, as *C. finmarchicus* descend to deep waters off the bank to spend the late summer to early winter in diapause.

END-TO-END FOOD WEB MODELS

During the synthesis phase of GLOBEC, substantial effort was directed toward developing more holistic descriptions (models) of the regional ecosystems—so called "end-to-end (E2E) food web models" (Ruzicka et al., 2013, in this issue). This was a new activity for GLOBEC, which previously had focused on population dynamics of individual target species of interest. E2E models were developed for Georges Bank/Northwest Atlantic (Steele et al., 2007), Northern California Current (Ruzicka et al. 2012), and Southern Ocean (Murphy et al., 2012, 2013). Food web structures within an ecosystem can shift significantly due to climate forcing (Francis et al., 2012; Ruzicka et al., 2012). Steele and Gifford (2010) compare E2E and population dynamics approaches, concluding that they are complementary, and noncontradictory. Steele et al. (2013) describe how such models could be used in resource management and decision making. End-to-end models hold promise for an eventual link between GLOBEC research and managers, whose mandates include ecosystem approaches to resource management (Barange et al., 2011; Fogarty et al., 2013, in this issue).

US GLOBEC MODELING ACCOMPLISHMENTS AND EMERGING APPLICATIONS

US GLOBEC advanced multiscale approaches to physical modeling of the ocean, explored connections between basin-scale and regional-to-local scale models, linked global climate scenario modeling and coastal region modeling, and provided new approaches to and implementations of coupled bio-physical modeling. These accomplishments not only significantly advanced hydrodynamic and coupled bio-physical modeling but also provided new scientific understanding of regional variability and the mechanisms contributing to (1) cod recruitment in the North Atlantic (Kristiansen et al., 2011), (2) salmon survival in the North Pacific (Burke et al., 2013), (3) climate forcing of krill population dynamics and ecosystem functioning in the Southern Ocean (Piñones et al., 2011, 2013; Murphy et al., 2012, 2013), and (4) the influence of dominant modes of North Pacific climate variability (the Pacific Decadal Oscillation and North Pacific Gyre Oscillation) on California Current and Gulf of Alaska ecosystems (Di Lorenzo et al., 2008; Keister et al., 2011; see also Di Lorenzo et al., 2013, in this issue).

The challenge of understanding the functioning of ecosystems in the context of climate change remains at the forefront of oceanographic research (e.g., Stock et al., 2011). Using the concepts and foundations that emerged during programs such as GLOBEC, modelers continue to develop frameworks for studying the ocean in a more integrated way. The goal, as described in the final report from the Steering Committee of the US GLOBEC program (see Figure 4 in GLOBEC, 2007), is multiscale ocean and atmospheric physics coupled to both community- and individual-based ecosystem models, where the ecosystem includes the influence of human activity. Progress toward this goal and future directions for coupled bio-physical research are further described in Haidvogel et al. (2013, in this issue).

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