Copepods in a warming climate: A pan-regional model of Arctic and Northwest Atlantic systems.

PIs: Cabell Davis, Rubao Ji, Robert Beardsley (WHOI), Changsheng Chen (UMASSD)

Project Summary

The goal of GLOBEC is to understand the underlying biological-physical interactions that determine how climate change affects abundance of marine animals. The GLOBEC approach focuses on individuals and populations dynamics of target species. The proposed study will address major PRS themes by examining the influence of climate on physical and biological processes for a synthetic understanding of how basin- and global-scales changes in climate force physical processes that control local and pan-regional-scale biological communities. We will use the approaches suggested in the RFP, including pan-regional physical-biological modeling, by connecting and comparing NWA and Arctic Ocean regions. As part of the GLOBEC NW Atlantic (NWA) program, we developed a 3D biological-physical model to examine effects of climate forced boundary conditions on plankton and dominant copepod species dynamics in the Georges Bank-Gulf of Maine region. Separately, we have developed a new 3D model of the Arctic Ocean (AO) region and are using it to examine transport of dominant copepod species. As yet, these two models have not been connected to each other. In this pan-regional study, we propose to combine these models to study linkages between these two systems under scenarios of global warming. We will examine a series of hypotheses that address how dominant copepod species populations in these regions may interact under future warming conditions. Specifically we will use the combined model together with existing data on abundances and vital rates to study how a melting Arctic is likely to affect the distribution and abundance of copepod species across the whole of the Arctic-North Atlantic pan-regional domain. The proposed work involves four steps: 1) merge the NWA and AO physical models via a new global model grid, extending our lower food web model (NPZD) across the pan-regional domain, to generate present and future (2050) environmental conditions. 2) use these modeled environmental conditions together with life histories of key species to determine their population growth potential within and across regions, 3) use an individual based model (IBM) parameterized for key species to examine effects of transport and behavior on population growth and resulting pan-regional distribution patterns, 4) develop a new evolutionary IBM for a generic copepod to determine selection of optimal life history traits under existing and future (warm) conditions across the pan-regional domain.

Intellectual Merits: The proposed detailed, process-oriented, pan-regional modeling study will provide new insights into the biological-physical mechanisms that determine how global warming affects populations of key marine zooplankton species, which occupy a central position in marine food webs. The resulting model will provide a powerful new tool for understanding how pan-regional interactions control ecology and biogeography of dominant marine species.

Broader Impacts: Results of the proposed work will be broadly disseminated to the general oceanographic community, K-12 institutions, and to the population at large, through web-based servers using existing infrastructure at the proposers' institutions. Web-based users can access model results and run the model using chosen parameter settings to obtain predictions of currents, hydrography, and plankton abundance patterns given selected climate forcing scenarios. We will sponsor undergraduate students in scientific and public outreach aspects of our project. Collaboration with the NE COSEE, SEA LAB, and Whyville programs for educational outreach with K12 students and the public both nationally and internationally.

1. Background

The GLOBEC approach — Understanding complex marine ecosystems requires use of simplifying assumptions, which historically has involved trophodynamic analysis of energy or mass flow by measurement and modeling (Lindeman, 1942; Teal, 1962; Odum, 1957; Steele, 1974). In regions of high diversity such as the oligotrophic ocean this approach remains the only feasible method of analysis (e.g., Sarmiento et al., 1993, Friedrichs et al., 2007). As an alternative, in low diversity regions, it is possible to study the population dynamics of a few dominant target species to understand processes controlling their abundance and to obtain information about system level functioning (Davis, 1987a, DeYoung et al, 2004).

The goal of GLOBEC is to quantify the effects of climate change on marine animal populations by focusing on target species, and their associated prey and predators, at the organismal and population levels (GLOBEC, 1991a,b), with less emphasis on higher and lower trophic levels (and thus limited or no data collection at these levels; cf, rhomboid method, DeYoung et al, 2004). A key aspect of GLOBEC is the recognition that the principal natural determinants of population size in marine animals are rooted in the survival of early life stages, i.e., in recruitment processes (Peterson and Powell, 1991). Given this planktonic focus, GLOBEC studies the interactions between physical and biological processes, including transport of populations to/from favorable habitats as well as effects of temperature, turbulence, and stratification on vertical distribution, growth, reproduction, and predation (GLOBEC, 1992, Wiebe et al. 2002). Regional US GLOBEC programs have focused on target species, their prey/predators, and interactions with the physical environment as it relates to global climate change (GLOBEC, 1991b, 1992, 1996, 1997, 2000). These programs have produced a wealth of data and new models which reveal strong links between climate forcing and target populations at the regional scale. Zooplankton species are emphasized because of their central position in the food web.

This proposed study will address major PRS themes. Specifically, it will examine the influence of climate on physical and biological processes for a synthetic understanding of how basin- and global-scales changes in climate force physical processes that control local and regional-scale biological communities. We will use the approaches suggested in the RFP, including pan-regional physical-biological modeling, by connecting and comparing NWA and Arctic Ocean regions. We will connect our NWA and AO Finite Volume Community Ocean Model (FVCOM) grids together via the global FVCOM grid to study pan-regional interactions of dominant copepod species populations.

Northwest Atlantic–Arctic Linkage – The NW Atlantic (NWA) GLOBEC program has found strong linkages between low salinity anomalies, phytoplankton blooms, copepod abundances, and larval fish growth and survival. The low salinity water originates from the Labrador Sea (based on oxygen isotope signature, Houghton and Fairbanks, 2003) and has been hypothesized to result from Arctic meltwater (Greene and Pershing, 2007). As part of this program, we are modeling the impact of freshwater intrusions on regional plankton and copepod species dynamics in the Gulf of Maine using upstream boundary forcing in FVCOM. In a separate project, we have adapted the FVCOM to study the 3D circulation (including ice dynamics) in the Arctic Ocean and marginal seas and are incorporating copepod species dynamics into this model. We propose to join these two FVCOM models together, using a global FVCOM grid, for a pan-regional analysis of the biological-physical mechanisms that control how climate change affects the abundance and distribution of these dominant copepod species across the Arctic-NWA regions.

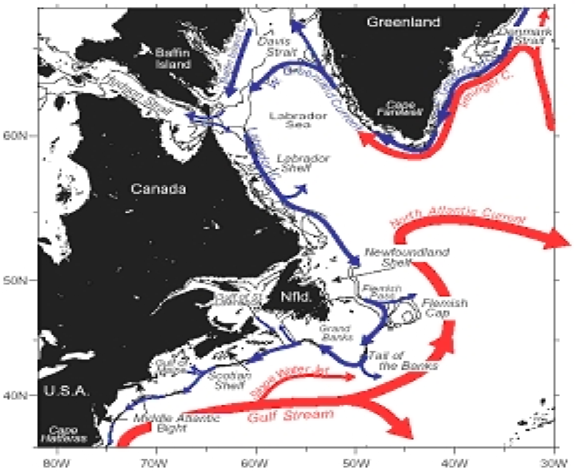


Figure 1. Schematic of the western North Atlantic shelf-break current system in summer.

1.1. The NWA Physical Environment

Georges Bank (GB), the Gulf of Maine (GOM), and Scotian Shelf (SS) are part of a single regional coastal current system, driven in large part by upstream mass and buoyancy forcing (Fig. 1, Fratantoni and Pickart, 2007). The bank itself is a quasi-flow-through system, with water from offshore and upstream sources arriving on the bank, being modified locally by surface forcing and tidal mixing before moving off-bank to the Mid-Atlantic Bight or re-circulated northward along the Great South Channel (Figs. 1, 2).

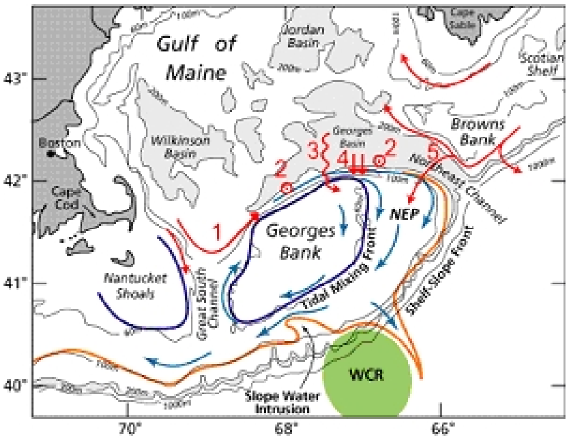


Fig. 2. Circulation: 1 flow across GSC into north flank jet, 2 tidal-pumping of deep water onto GB, 3 wind-driven near-surface flow, 4 small-scale cross-frontal processes, 5 SS cross-over

The strongest currents over the bank are of tidal origin, and turbulent mixing associated with the tidal bottom boundary layer is most intense over the shallow cap of the bank, effectively eliminating local vertical temperature and salinity stratification throughout the year. As seasonal stratification increases on the flanks of the bank, the tidal mixing front forms with associated secondary flow. The clockwise around-bank residual flow increases with seasonal stratification, becoming partially closed from June through September until fall storms and surface cooling destroy the local stratification. Surface heating drives the development of the seasonal thermocline. Salinity on the bank is controlled by advective and mixing processes along the northern and southern flanks. On the southern flank salinity is influenced by on-bank intrusions of saline shelf-break frontal water and very saline warm-core ring water (Fig. 2). Along the northern flank salinity is controlled by advection from the western Gulf across the northern Great South Channel (Fig. 2, 1), tidally-driven near-bottom residual flow (the "tidal pump", Fig. 2, 2), wind-driven near-surface flow (Fig. 2, 3), small-scale cross-frontal processes (Fig. 2, 4), and intermittent cross-over of low salinity SS surface water (Fig. 2, 5). The tidal pump in particular provides a strong mechanism for bringing deep water from Georges Basin up onto the bank (Chen and Beardsley, 1998; Chen et al., 2003).

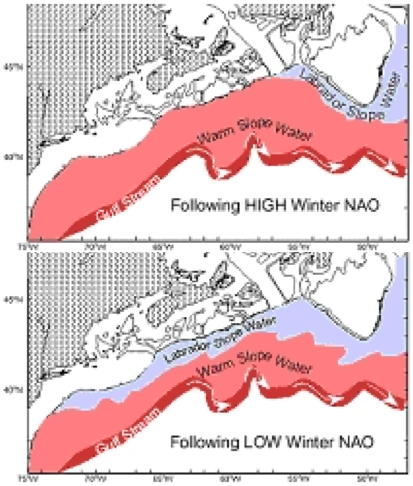


Figure 3. Schematic showing the strong westward penetration of LSW. (Drinkwater et al, 2003)

Water enters the GOM via two primary paths: (1) the flow of relatively fresh water above 100m from the SS and (2) warmer, more saline Slope Water (SW) at depths greater than 100m through the Northeast Channel (NEC). The primary source of SS water is the West Greenland-Labrador Current system, with additional input from the St. Lawrence system (Fig. 1). As the Labrador Current flows around the Grand Banks, the large shoaling in shelf-break depth from ~300m in the north to ~100m to the southwest helps force the deeper Labrador Current water to flow along the upper slope, thus forming Labrador Slope Water (LSW), which flows west into the Laurentian Channel and along the Scotian upper slope. The westward extent of LSW depends on its source strength, thought to depend on basin-scale forcing (NAO) (Fig 3), and degree of mixing with ambient Warm Slope Water (WSW) of Gulf Stream origin. Since WSW is warmer, more saline, and nutrient rich than LSW, the relative mix of these two end members entering the NEC, and its transport relative to the inflow of SS water, strongly influences circulation, water property distributions, and nutrient content in the GOM/GB system.

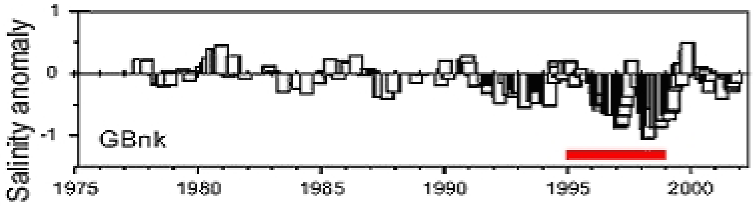


Fig. 4. GB salinity anomaly (Mountain, 2005)

Data from the 1995-1999 GB GLOBEC field study provide an excellent example of the flow-through nature of the GB/GOM system and its linkage to larger basin-scale forcing. The salinity on GB exhibited two

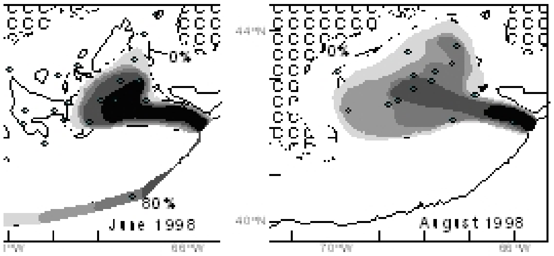


Fig. 5a. Percent LSW in bottom water (150-200 m) in 1998. (Drinkwater et al, 2003)

significant freshening events between early 1996 to early 1997 and between late 1997 through 1998, with a net drop of ~1 psu (Fig. 4). The source of this fresher water was identified from oxygen isotope ratios as the Labrador Sea (Houghton and Fairbanks, 2001).

These two events also were observed in surface (0-30m) GOM waters, suggesting significant increases in freshwater influx from the SS (Smith et al., 2001). In the NEC, WSW was replaced by cooler, fresher LSW in January 1998 as the leading edge of LSW flow extended west due to an increase in the Labrador Current associated with a low NAO. As LSW entered the GOM during 1998, it mixed with resident GOM water (Fig 5a). By early 1999, WSW was again flowing into the GOM through the NEC. Since the tidal pump mechanism can carry deep water up on the northern flank of GB (Fig. 5b), advection of LSW in Georges Basin onto the bank can occur on relative short time scales (>=1 month), suggesting that part of the freshening on GB observed during 1998 was due to the influx of LSW into the GOM. Clearly, variations in the primary upstream sources (the SS Water, the mix of WSW versus LSW) linked to basin-scale forcing strongly control the water properties (including heat, salt and nutrients) through the GOM and onto GB.

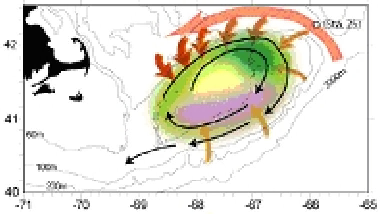
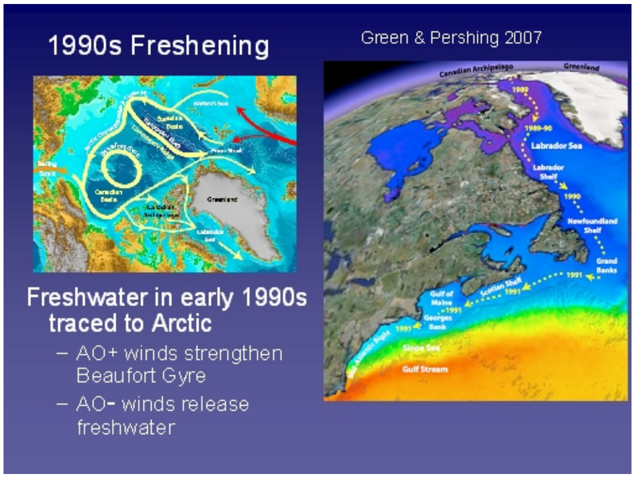


Fig. 5b. Scenario of nutrient input onto GB from the NEC (Townsend et al., 2004).


1990s Freshening

Green & Pershing 2007

Freshwater in early 1990s traced to Arctic

- AO+ winds strengthen Beaufort Gyre
- AO- winds release freshwater

Fig. 5c. NWA freshened by Arctic meltwater

The anomalously fresh SSW is from the Labrador Sea and likely originates from a melting Arctic (Fig. 5c) (Häkkinen, 2002; Greene and Pershing, 2007). Low salinity water is thought to accumulate in the Beaufort Gyre during the anticyclonic phase (AO+) and is released during its cyclonic phase (AO-) (Proshutinsky, et al. 2002), the resulting outflow entering the Labrador Sea via the Canadian archipelago and Fram Strait (Greene and Pershing, 2007).

1.2. *Connection between climate forcing and copepods in the GOM-GB region*

NAO-dependent intrusions of LSW and WSW through the NEC influence the nutrient (N, Si) input into the GOM-GB region. The tidal pumping mechanism along the northern edge of the bank can quickly transport nutrients from Georges Basin up onto the NE peak of GB, impacting the productivity of the bank very rapidly (Fig. 5b). The lower nutrients in the LSW will reduce productivity. The ratio of N and Si in the inflow water can influence the duration of the diatom bloom (Ji et al. 2006a). In general, the NEC inflow can affect the total salt and nutrient budget of the GB/GOM, determining the thermohaline circulation and influencing upwelling along the western GOM and subsequent nutrient transport to western GB.

In addition to the inflow of LSW versus WSW and its impact on nutrients and productivity, the low salinity SSW affects the stratification in the SS and GOM-GB region, which in turn causes an earlier spring phytoplankton bloom and higher copepod abundance (Fig. 5d) (Ji et al, 2007a, Durbin et al. 2003, Buckley and Durbin, 2006, Durbin and Casas, 2006).

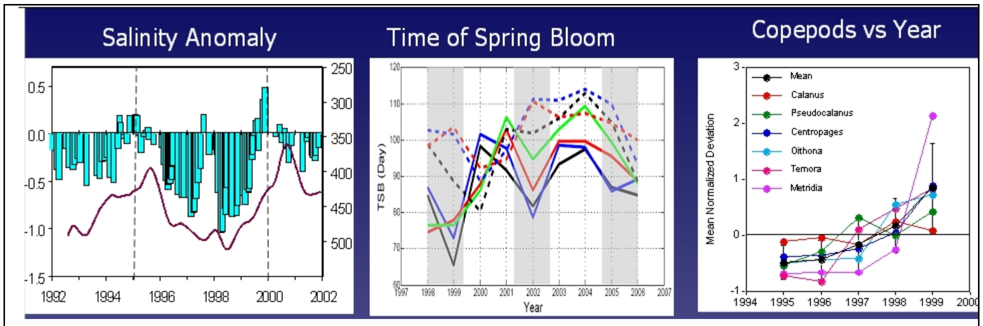


Fig. 5d. Low salinity anomalies cause earlier spring bloom, higher copepod abundance.

While this freshening of the GB-GOM affects stratification and leads to earlier spring phytoplankton blooms and increased concentrations of spring copepod abundance, it reduces overall productivity later in the year due to reduced vertical mixing and limited nutrient exchange (Ji et al., 2007, in press).

1.3. GB-GOM copepods

The GB meso-zooplankton community is dominated by the copepods *Calanus finmarchicus*, *Pseudocalanus* spp., *Oithona similis*, *Centropages* spp., and *Temora longicornis*, and *Paracalanus parvus* (Bigelow, 1926; Davis, 1984, 1987b; Sherman et al, 1987; Durbin et al., 2003; Durbin and Casas, 2006). Each species exhibits a characteristic life cycle and seasonal/spatial pattern in the GB/GOM region. *Calanus finmarchicus* and *Pseudocalanus* spp. are cold-water species that avoid the warm surface layer (>10-12^{o}C) during summer and fall and produce large spring populations. *Centropages* spp, *Temora*, and *Paracalanus* are warm water species and are most abundant during late summer and fall. *Oithona* is plentiful throughout the GB/GOM region year round.

Calanus finmarchicus— This species spends the warmer months in a state of diapause as stage CV in cooler waters (5-7 ^{o}C) at depth in the GOM (Fig. 6). During late December, it emerges from diapause (mechanism unknown), swims to the surface and molts to adult. Subsequent egg production depends on availability of phytoplankton (Durbin et al., 2003), with the first generation born in late December-early January (Durbin et al., 1997). Generation time is ~2 months at the cold winter/spring temperatures (~5 ^{o}C), so G1 adults appear in March, and there is time for a total of 3 generations by the end of its growing season in July. Overwintering females produce eggs for a prolonged period, smearing out cohorts (Durbin and Casas, 2006). This annual cycle in the GB/GOM appears stable, having persisted for many decades (Bigelow, 1926; Clarke et al, 1946; Meise-Munns et al., 1990).

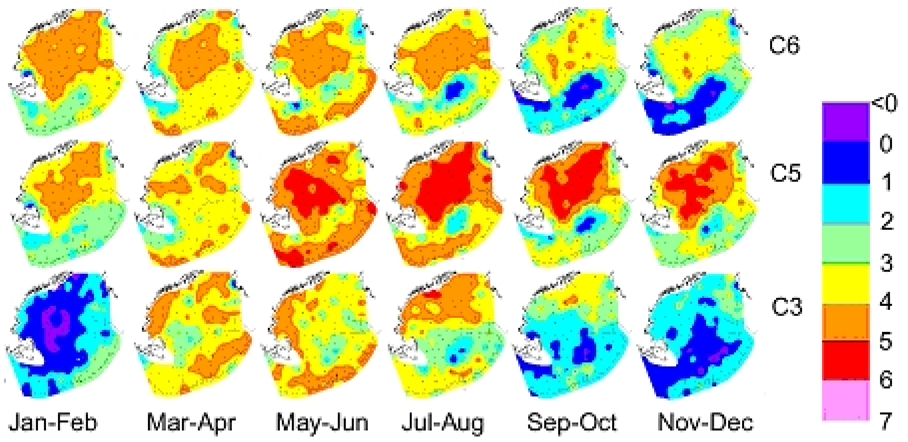


Fig. 6. *Calanus finmarchicus* abundance ($\log_{10}$(#/10m^{2})) in the GB/GOM, mean 1977-1987, (MARMAP data redrawn from Meise and OReilly, 1998).

Calanus finmarchicus is an open ocean species, occurring throughout the northern North Atlantic from the eastern US to the Barents Sea, with centers of population abundance in the Norwegian and Labrador seas (Fig. 7). Immigration into the GB/GOM population from upstream sources may contribute to the apparent stability of the population. *C. finmarchicus* enters the GOM from the SS and possibly from the SW

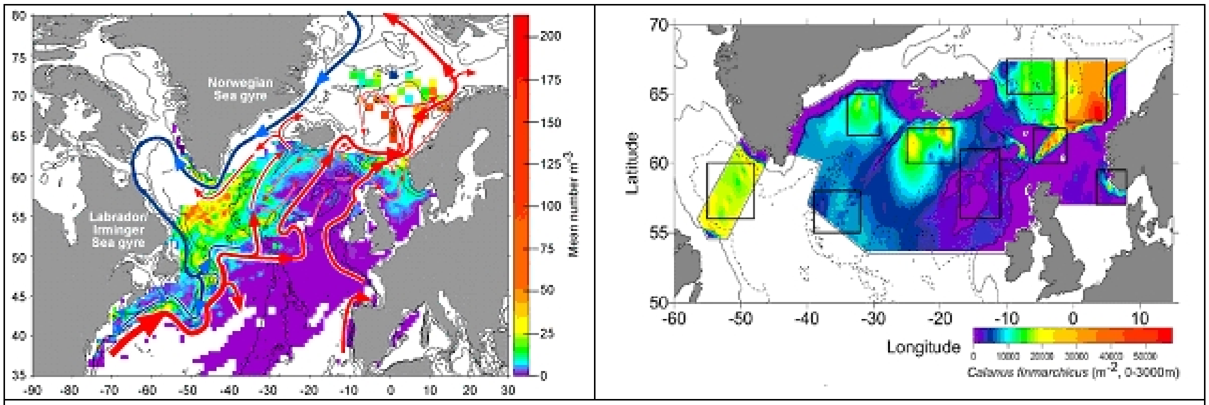


Fig. 7. *Calanus finmarchicus* abundance in the N Atlantic from CPR data (Spears 2005) and nets/OPC (Heath et al. 2004). Note high densities in the Labrador and Norwegian Seas.

through the NEC. *C. finmarchicus* in the SW originate from the Labrador Sea and to an unknown extent from spill-over of the productive shelf populations. Scotian Shelf *C. finmarchicus* originate from Labrador Sea via the SW (Head et al., 1999) and to some degree from the productive Gulf of St. Lawrence population (Zakardjian et al. 2003). It is unlikely that immigration directly determines the large spring abundance peak in *C. finmarchicus* in the GB/GOM, since the water mass turnover time is long relative to the generation time, but a seeding type of immigration during the “off-season” could be important in determining the size of the startup population of CVs in December (Saumweber and Durbin, 2006). Since the diapausing SW population resides at a depth of 500m (below the NEC sill depth), and high concentrations are not observed in the upper water column until April (Miller et al., 1991), well-after initiation of the GB/GOM population growth, it is unlikely that a SW population entering through the NEC contributes significantly to the GB/GOM *C. finmarchicus* population.

It may well be that the resident diapausing GOM population is sufficient to produce the large spring GOM/GB population. At the end of the growing season, downward migrating diapausing CVs cannot reach their normal open ocean depths of 500-2000m, and they become trapped in the GOM basins. A similar effect has been observed on the SS basins (Sameoto and Herman, 1990) and for *C. pacificus* in the Santa Barbara basin (Osgood and Checkley, 1997). Lagrangian modeling studies have found retention of diapausing CVs in the GOM to be high, especially if the animals stay below 150 m (Johnson et al., 2006). Thus it appears possible that the GB/GOM population could be self-sustaining, and we are conducting 3D modeling, using a concentration-based approach, to quantify population dynamics and transport within this region over multiple years.

***Pseudocalanus* spp.**— Like *Calanus*, the growth season for *Pseudocalanus* is winter/spring (Figs. 9-11). Its abundance is higher in shallower areas (<100m) and is highest in the crest region of the bank in June.

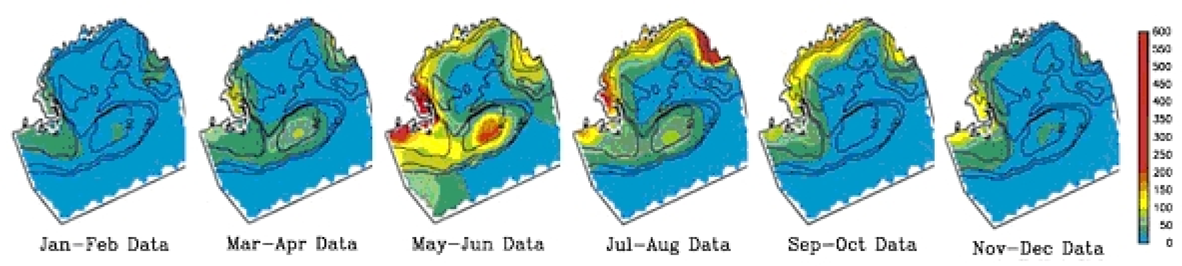


Fig. 9. *Pseudocalanus* abundance in the GB/GOM. MARMAP bi-monthly means 1977-1987 (from McGillicuddy et al., 1998).

Pseudocalanus does not overwinter in the GOM as does *Calanus* and is not normally present in the central Gulf during winter. This genus is an egg carrier and consequently has lower egg production and egg mortality rates (Corkett and McLaren, 1978; Ohman et al., 2002). *Pseudocalanus* in the GB/GOM region

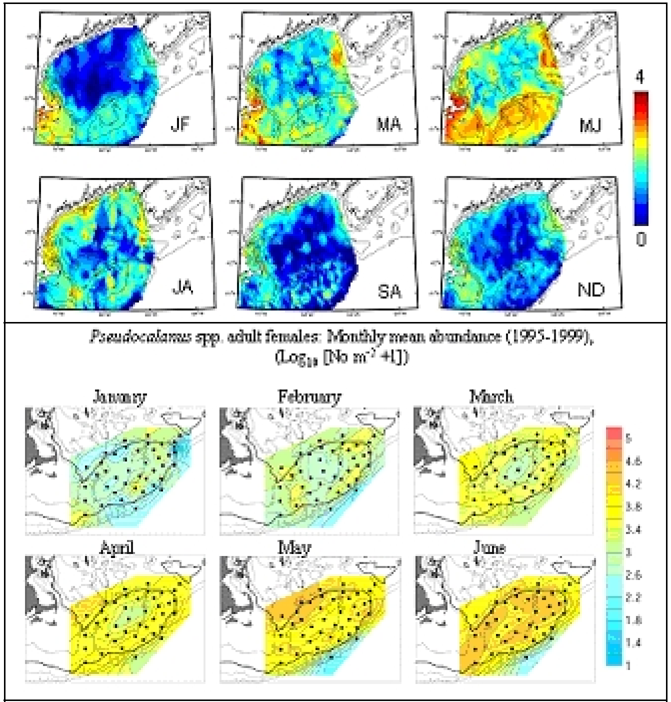


Fig. 10. Ecomon (upper) and GLOBEC (lower) data for *Pseudocalanus* in the GB-GOM region.

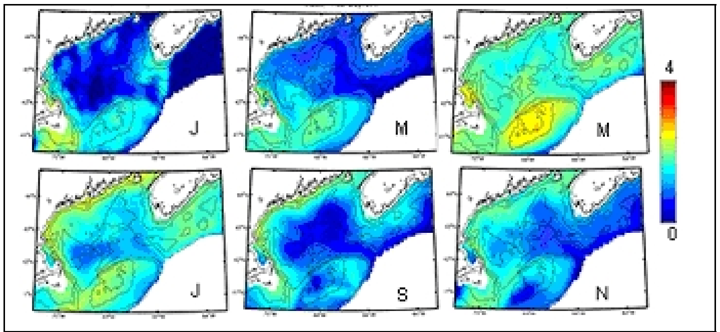


Fig. 11. *Pseudocalanus* 3D FVCOM, surface, 1999 (log#/m^3)

comprises two species: *P. newmani* and *P. moultoni* (Frost, 1989; McLaren et al., 1989a; Bucklin et al., 1998, 2001; McGillicuddy and Bucklin, 2002), although their vital rates appear similar with large variation in laboratory data (McLaren et al., 1989a,b). Davis (1984) modeled *Pseudocalanus* transport around GB using a temperature-dependent molting rate that was an average of these two species. *P. moultoni* appears to be a colder water species and more abundant during winter/spring, while *P. newmani* is more plentiful during spring/summer (McLaren et al., 1989a,b). *P. moultoni* is thought to be a coastal species and *P. newmani* an offshore one (Frost, 1989). Thus *P. moultoni* may be carried onto the bank from western GOM coastal waters (e.g., Cape Cod Bay), while *P. newmani* may have a source from SS water, either crossing over the NEC, or indirectly through the central GOM (McGillicuddy and Bucklin, 2002). Inverse (adjoint) modeling, representing the biology by a single source/sink term, revealed that the two species are likely to have different source locations on the bank but intermingle by June (McGillicuddy and Bucklin, 2002). The use of a simple cost function instead of a population model, however, meant that the independent species-specific life history information could not be included in the model.

We have developed a concentration based copepod model (Hu et al., in press a, b) and incorporated it together with NPZD dynamics into FVCOM to simulate the evolution of 3D spatial distributions of *Pseudocalanus* in the GB-GOM region during the GLOBEC years (Fig. 11). Model parameter values were determined from literature information on development, growth and egg production as a function of food and temperature for *Pseudocalanus* (Corkett and McLaren, 1978; Vidal, 1980; Davis, 1983, 1984a,b; McLaren et al., 1989b; Ban et al., 2000; Lee et al., 2003; Dzierzbicka-Glowacka, 2004). We are modeling the impact of upstream boundary forcing on the distribution of *Pseudocalanus* within the GOM-GB region during 1995-1999.

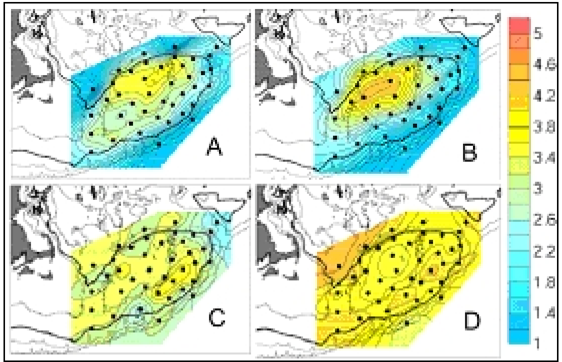


Fig. 12. A) *Temora*, B) *Centropages hamatus* C) *Centropages typicus*, D) *Oithona similis*. Mean monthly GLOBEC data for 1995-1999, A,B,D May; C January; log$_{10}$(#/m^3+1)

Other Dominant Copepod Species — Each dominant copepod species on GB has its own characteristic temporal-spatial patterns and life histories (e.g., Davis, 1987a). Copepods that lay bottom resting eggs, including *Centropages hamatus* and *Temora longicornis*, have well defined populations on the crest of the bank (Fig. 12) (Davis, 1987; Sherman et al., 1987). It has been suggested that these species use resting eggs as a strategy for “gluing” their populations to regions that are favorable for growth (Davis, 1987; Lindley and Hunt, 1989; Lindley, 1990; Marcus, 1996; Marcus and Lutz, 1998), and we are exploring this possibility via modeling. *Centropages typicus* abundance is highest during late summer and fall and decreases markedly during winter and spring. It is most abundant in the warm surface layer above the thermocline and is not restricted to the crest of GB like *C. hamatus*. *Oithona similis* is abundant year round and is not restricted to GB but has a pattern similar to *C. finmarchicus*, with a large off-bank population. The characteristics of each species are being combined with the environmental conditions generated by the 3D FVCOM model to determine the mechanisms controlling their distributions in the GB-GOM region.

1.4. Arctic copepod modeling

We presently are studying the effects of climate warming on distributions of *Calanus* species within the Arctic Ocean and marginal seas by incorporating individual based models of *Calanus hyperboreous*, *Calanus glacialis*, and *Calanus finmarchicus* population dynamics into the 3D FVCOM model of this region. The physical model includes atmosphere, ice, and ocean components of the system and establishes the environmental framework in which the *Calanus* population dynamics operate. About half of the Arctic Ocean comprises shelf regions, and the project focuses on the productive inflow shelves, the Chukchi and Barents Seas (Carmack and Wassman 2006, Grebmeier and Barry 1991, Grebmeier et al. 1995, Sakshaug 2004, Wassman et al., 2006) and their interaction with adjacent basins. The physical model domain (Fig. 13) also includes the main outflow regions, the Canadian Archipelago into the Labrador Sea and Fram Strait into the East Greenland Sea, which impact the NW Atlantic hydrography and circulation.

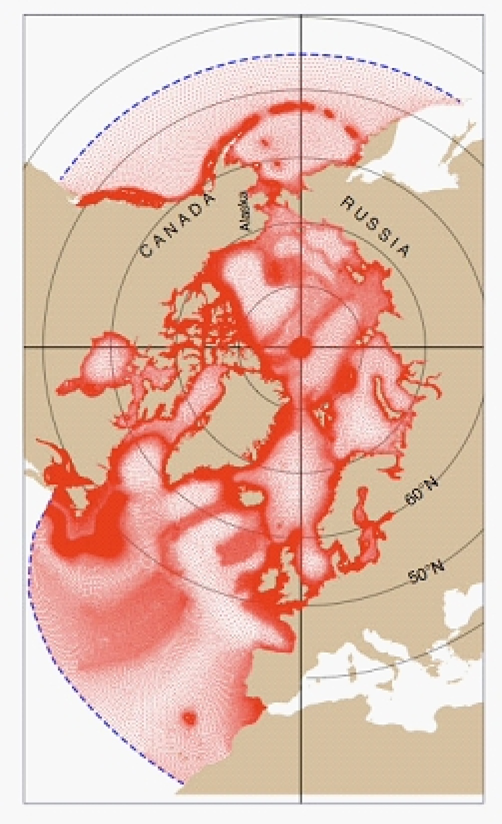


Fig. 13 Unstructured triangular grid of the expanded AO-FVCOM with horizontal resolution varying from less than 0.5 km on the shelves to 15 km in the Arctic Basin.

Arctic copepods – Two species of *Calanus* are endemic to the Arctic Ocean. *Calanus glacialis* occurs primarily in shelf areas, while the large *C. hyperboreus* dominates the central Arctic Basin (Lane et al. in revision, Campbell et al., subm., Tande 1989; Arashkevich et al. 2002; Wassmann et al. 2006, Conover 1988, Smith and Schnack-Schiel 1990). *C. glacialis* requires higher food concentraions and grows faster than *C. hyperboreus* (1-2 yr vs 3-4 yrs; Levinsen et al. 2000, Campbell et al. subm, Smith and Schnack-Schiel 1990, Arashkevich et al. 2002, Ashjian et al. 2003). *C. hyperboreus* accumulates lipids slowly, producing buoyant eggs and nauplii at depth well before the spring surface bloom (Smith and Schnack-Schiel 1990, Hirche and Niehoff 1996, Conover, 1962, Ashjian et al. 2003). *C. glacialis*, depends on high ambient food for reproduction (Kosobokova and Hirche 2001, Hirche and Bohrer 1987; Plourde et al. 2005). C. hyperboreus migrates seasonally to great depths and has even been found next to the bottom at 2500m in the Greenland Sea (Hirshe et al 2006).

Other *Calanus* species in the Arctic are expatriated from adjacent seas, including *C. finmarchicus* from the Barents Sea and *C. marshallae* through the Bering Strait. *C. finmarchicus* does not maintain an Arctic population north of the polar front and is not found regularly on the Pacific side of the Arctic Ocean (Tande 1989, Arashkevich et al. 2002, Smith and Schnack-Schiel 1990, Hirche and Mumm 1992, Ashjian et al.

2003). *C. finmarchicus* may be less adaptable to food shortages than *C. glacialis* (Runge and Plourde 1996). Throughout its range *C. finmarchicus* spends the non-productive season as diapausing CV at depth. Although *C. finmarchicus* has multiple generations annually in the NWA (Davis, 1987a; Durbin et al. 1997), it appears to have one generation the Barents Sea (Arashkevich et al. 2002). *C. marshallae* (Frost 1974) is dominant in the Bering Sea (Smith and Vidal 1986; Baier and Napp 2003) and occurs down to the Oregon coast (Peterson, 1998) and (rarely) up to the Chukchi Sea (Frost 1974). There are 1-2 generations/yr in the Bering Sea (where it overwinters) (Smith and Vidal 1986, Baier and Napp 2003) and several per year off the Oregon coast (Peterson, 1998). Increase warming and production in the Chukchi Sea may allow *C. marshallae* to colonize the Arctic. Our current modeling project is focusing on how climate change in the Arctic will affect the distributions of *Calanus* species within this region. In addition to *Calanus*, other copepod species commonly found in the Arctic include *Metridia longa*, *Microcalanus pygmaeus*, *Oithona similis*, *Pseudocalanus minutus*, and *Pseudocalanus acuspes* (Ashjian, 2003, Hopcroft et al 2005, Lischka and Hagen, 2005). The smaller species dominate numerically, while the larger species are the biomass dominants (Hopcroft et al 2005). *Pseudocalanus* appears to be more common in the Atlantic side. There is a growing literature on the life histories and ecology of these species in the Arctic (Fortier, 2001, Werner and Martinez-Arbizu 1997; Ringuette et al 2002; Ashjian, 2003, Hopcroft et al 2005, Lischka and Hagen, 2005). It is likely that with increased warming the habitat for all endemic Arctic species will shrink and copepod species from adjacent sea will invade and colonize the inflow shelves.

1.5. Interconnections between NWA-Arctic copepods

Global warming is likely to cause a bidirectional interaction between the NWA and Arctic copepod populations through a combination of northward range extensions of lower latitude species and southward transport of Arctic meltwater. It is now well established that climate warming trends are affecting phenology of marine zooplankton species and geographic ranges of subtropical and temperate species are extending northward (e.g. Beaugrand et al. 2002, 2003, 2007, Bonnet et al, 2005, 2007, Edwards et al. 2006, Valdes et al. 2007, ICES 2007). Statistical analyses of field data show clearly that warming trends, together with decadal and multi-decadal climate oscillations, are associated with latitudinal shifts in species-specific temperature optima and food levels (productivity and compositions, e.g., Beaugrand, 2002, 2007, Bonnet et al., 2007), but the underlying mechanisms have not be demonstrated. The temperate species *Centropages typicus* is shifting northward on both sides of the Atlantic (Bonnet et al., 2007, Head and Sameoto, 2007). The increase in abundance of this species in the Newfoundland and Scotian Shelf (Head and Sameoto, 2007) is against the mean along-shelf southwest flow, and the biological/physical mechanisms controlling its northward progression are unknown. The influx of low salinity water from the Arctic and Labrador seas carry Arctic species southward into the NWA, including *Calanus glacialis* and *C. hyperboreus*, and *Metria longa* which are commonly found in the NWA region (Mullin, 1963, Head and Sameoto, 2007). The warming climate is increasing the flow of this low salinity water, enhancing the pathway for transport of Arctic species into the NWA, but the underlying biological-physical mechanisms remain poorly understood. It is likely in the future that *C. finmarchicus* and *C. marshallae* will invade and colonize the Arctic Ocean and there may be a Pacific-Atlantic crossover of these species through the Arctic.

2. Proposed Research

2.1. Hypotheses

General hypothesis: Global warming will cause a retraction of endemic Arctic copepod species range and will extend the range northward of species from lower latitudes. Despite SW transport of low salinity water, the optimal population growth conditions will shift northward for both Arctic and NWA populations resulting in a concomitant northward increase in NWA species and shrinkage of Arctic species range.

$H1_0$: Boreal species in the NWA, *Calanus finmarchicus* and *Pseudocalanus newmani* and *P. moultoni* will expand into Arctic Ocean despite limitations due to the mean southwest advective flow.

H2$_0$: Arctic species, *Calanus glacialis* and *C. hyperboreus*, abundance will decrease in the NWA and their ranges will be contracted within the Arctic Ocean itself. Alternatively, (H2$_a$) abundance of these species will increase in the NWA due to increased Arctic outflow.

H3$_0$: *Calanus marshallae* will expand into the Arctic and be carried through the Canadian archipelago into the NWA

H4$_0$: The warm water NWA species, *Centropages typicus* and *Centropages hamatus* will expand northward increasing abundance the Labrador Sea and Canadian archipelago. The rate of expansion will be slower for *Centropages hamatus* which lays bottom resting eggs.

H5$_0$: The mechanisms controlling biogeographic patterns in copepod species can be understood by modeling the evolution of optimal life history traits for given environmental conditions and climate scenarios.

2.2. Objectives

2.2.1. Environmental model – Join the NWA and Arctic FVCOM high resolution domains together via the global FVCOM to generate environmental conditions for existing and future (warm) climate scenarios across the Arctic-NWA regions. Extend the present NWA NPZD model into the combined model domain to generate copepod food fields

2.2.2. Population growth potential – Given the environmental conditions generated by the pan-regional FVCOM, determine the static population growth "potential" for key copepod species by mapping their life histories onto the FVCOM environmental output.

2.2.3. Population growth with transport – Use an IBM with parameters values for a key copepod species to examine effects of transport and behavior together with population growth.

2.2.4. ***Evolutionary copepod model –*** Use a single generic copepod IBM together with a genetic algorithm to determine, through evolution, the optimal traits for different environments. Run the IBM repeatedly over the generational time-scale using only the fittest "survivors" at the end of each run to start new runs. Compare evolved traits with known traits of Arctic and NWA species to gain insight into how species distributional patterns may change with climatic conditions.

This work will provide insights into how the distributions of dominant copepod species throughout the Arctic-North Atlantic regions are likely to change from existing to future warm conditions

2.3. Methods

2.3.1. *Physical Models*

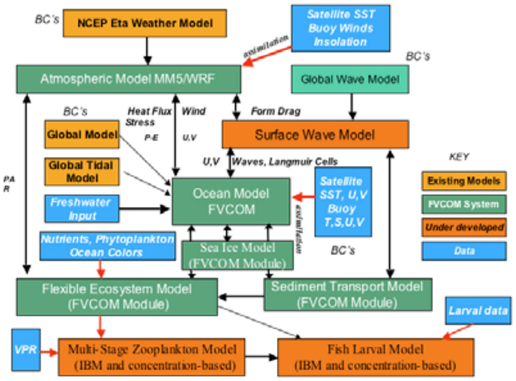


Fig. 14 Schematic of the integrated FVCOM model system. The sea-ice model was added as part of the FVCOM-Arctic development.

As part of NWA GLOBEC, our UMASS-WHOI research team developed an integrated model system (FVCOM-NWA) for the GOM/GB region (Fig. 14). Major components of this system include: (1) nested regional community atmospheric mesoscale models (MM5 and WRF), (2) the unstructured grid Finite-Volume Community Ocean circulation Model (FVCOM), (3) a generalized lower trophic level food web model, and (4) multi-stage zooplankton models. Simple (nudging, 4-D optimal interpolation) and advanced (Kalman filter) data assimilation methods can be used to incorporate remote sensing and in-situ oceanographic data in model simulations conducted with realistic forcing and boundary conditions and observed ocean response for specific periods of time. Recently we developed an integrated model system for the Pan-Arctic region (Fig. 14). Building on

FVCOM-NWA, key advances include (1) extension of FVCOM to spherical coordinates and elimination of the pole singularity and (2) addition of an unstructured-grid sea ice model. We propose here to combine these two regional models into a single pan-regional model (FVCOM-NWA-Arctic) embedded in a coarser resolution global FVCOM. Brief descriptions of the two regional model systems and merged system follow. (See http://fvcom.smast.umassd.edu/ for details about FVCOM and these regional model systems.)

FVCOM-NWA

MM5/WRF— Both regional systems use either the fifth-generation mesoscale regional weather model (MM5) developed by NCAR/Penn State (Dudhia et al., 2003; Grell et al., 1994) or the newer community Weather Research and Forecast (WRF) mesoscale model to construct surface weather hindcast (and forecast) fields that are then used to compute surface forcing fields (with 10-km horizontal resolution) that drive FVCOM. Both MM5 and WRF feature 2-way nesting and are driven by larger-scale NCEP models (e.g., NAM). To improve the model-based surface wind field, wind stress and heat flux estimates over the ocean, we use the COARE 2.6 bulk algorithm (Fairall et al, 2003) for the air-sea fluxes, satellite-based insolation, cloud cover, and SST data (International Satellite Cloud Climatology Project) for the radiative fluxes, and assimilation of coastal and surface weather data available in the local domain.

FVCOM— FVCOM is a prognostic, unstructured grid, finite-volume, free-surface, 3D primitive equation coastal ocean circulation model (Chen et al., 2003; Chen et al. 2004a). In common with other coastal models, FVCOM uses the modified Mellor and Yamada level 2.5 (MY-2.5) and Smagorinsky turbulent closure schemes for vertical and horizontal mixing, respectively (Mellor and Yamada, 1982; Galperin et al., 1988; Smagorinsky, 1963), and a generalized terrain-following vertical coordinate to match bottom topography. The General Ocean Turbulent Model (GOTM) (Burchard, 2002) has been added to FVCOM to provide optional vertical turbulent closure schemes. FVCOM is solved numerically by a second-order accurate discrete flux calculation of the integral form of the governing equations over an unstructured triangular grid. This approach combines the best features of finite-element methods (grid flexibility) and finite-difference methods (numerical efficiency and code simplicity) and provides a much better numerical representation of both local and global momentum, mass, salt, heat, and tracer conservation.

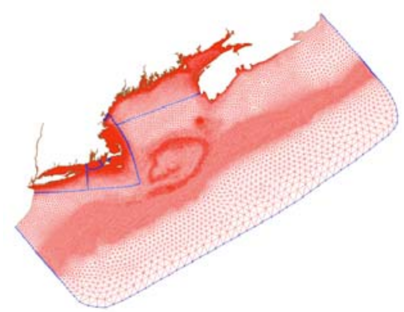


Fig. 15: FVCOM-NWA grid. The blue lines indicate boundaries of nested sub-domains with higher resolution (e.g., FVCOM-MASS).

The FVCOM-NWA domain is centered on GB/GOM (Fig.15). The model grid has been optimized to resolve the circulation on GB, GOM, SS, and the continental slope that acts as a conduit for deep flow into and out of the GOM through the Northeast Channel. The mesh uses variable resolution ranging from 3 km on top of GB to 45 km at the open boundary. The bathymetry is truncated at 1500 m off shelf to reduce time step restrictions, but real bathymetry is retained inside the GOM where maximum depths reach 360 m in Georges Basin. The “upstream” boundary of FVCOM-NVA cuts across the Scotian Shelf and upper slope through Banquereau Bank. This choice simplifies the cross-shelf bathymetry and separation of along-shelf flow into inner-shelf and shelfbreak components (Han et al, 1997). We use a combination of the Hannah et al (2001) seasonal-mean boundary conditions, a statistical method to compute the along-shelf wind-driven time-dependent transport over the inner-shelf (Schwing, 1992), and US and Canadian hydrographic and moored data to construct the best set of upstream boundary conditions for both process and long-term hindcast simulations.

FVCOM-Arctic

The FVCOM-Arctic domain covers the pan-Arctic region including the Bering Sea and south of 45^o N in the North Atlantic (Fig. 13). The horizontal resolution in this extended domain is 1 km or less in the slope, deep ridges and inshore coastal regions and 5-15 km in the deep interior. In the Canadian Archipelago, the horizontal resolution in many regions is less than 0.5 km. In the vertical, the generalized terrain-following coordinate is used, with 20 uniform-thickness layers in the upper 100 m, 4 uniform-thickness layers in the near-bottom 20 m, and 16 non-uniform layers in the interior. The model includes tidal dynamics via prescription of tidal elevations along open boundaries and direct astronomical forcing; atmospheric loading via adding of inverted barometer effects in the model governing equations; daily varying river discharge and Bering Strait inflow; and fast ice prescribed based using an empirical algorithm described below. Conditions along the two Atlantic and Pacific open boundaries are determined using climatologies and/or Mercator OPA or HYCOM global/basin solutions. FVCOM-Arctic has been successfully used to study the ice-free tides in the Arctic Ocean (Chen et al, 2007). (For detailed model description, results, and model-data comparisons, see http://fvcom.smast.umassd.edu/research_projects/ArcticGlobalM/index.html.)

Last year, we converted CICE (the community Los Alamos Sea Ice Model developed by Hunke and Lipscomb 2006) into an unstructured-grid finite-volume version (CICE-UG) and coupled it to FVCOM-Arctic. This new unstructured-grid ice model takes advantage of grid flexibility to resolve detailed ice dynamics in coastal regions and over steep bottom topography. This ice model has passed benchmark tests with direct comparisons with the original structured-grid CICE, and is presently being used to hindcast physical conditions for the last 50 years. We also implemented the multi-ice model developed by Hibler (1979) and Zhang and Hibler (1997).

Proposed FVCOM-NWA/Arctic System

We propose to use one-way nesting to embed the two regional models in a lower-resolution pan-regional version of FVCOM. FVCOM-Global (Fig. 16) has been configured with an initial horizontal resolution of 25-50 km and 46 non-uniform layers in the vertical. This nesting is done by having common meshes around the boundaries of the two regional models within the global model. FVCOM-Global is spin up initially for 50 years with hourly climological forcing fields and eight major tidal constituents. Both hydrographic and current and ice fields after the 50-year spin up run will be used as the initial condition to drive the merged model run for the study years. We will use IPCC projected forcings for the 2050 case. Data assimilation will be used to integrate hydrographic, satellite-derived SST and currents over the global scale to produce more realistic circulation and hydrographic fields. FVCOM-Global output will then be used as boundary conditions to drive FVCOM-NWA and FVCOM-Arctic. This approach has been validated for our Arctic Ocean modeling and it works well.

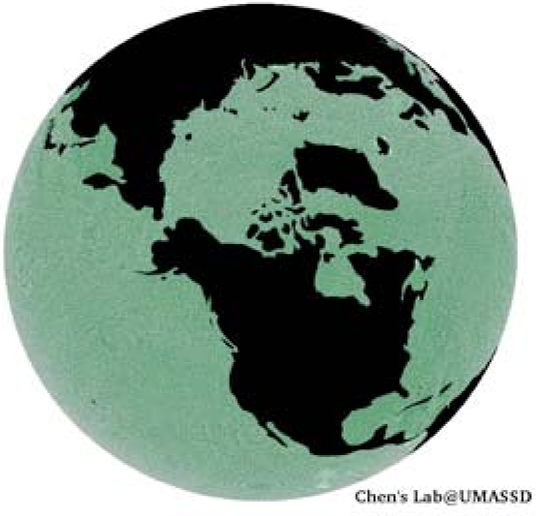


Fig. 16 FVCOM-Global mesh

To improve the computational efficiency of FVCOM, we have upgraded FVCOM into a semi-implicit version in which the free-surface elevation is computed implicitly and not explicitly. By using a parallelized scalable sparse matrix solver library (called PETSc) (Balay et al., 2007) and high performance pre-conditional HYPRE software library, the semi-implicit FVCOM can be run with a much longer time step. An example has been tested using FVCOM-Arctic. The comparison between the original mode-split FVCOM and new semi-implicit FVCOM shows that for a given time step, the semi-implicit FVCOM is twice as fast as the mode-split FVCOM. Since the semi-implicit FVCOM can be run with a time step about 10-20 times larger than the mode-split FVCOM, the effective speed up is quite significant. With a horizontal resolution of 20-50 km, the mode-split FVCOM-Global can run with a time step of 1 min, while the time step for the semi-implicit FVCOM-Global can be up to 20 min. This means that it will take just a few days for the semi-implicit FVCOM-Global to run a 50-year spin up simulation on the UMASSD cluster. This improvement will ensure the success of our merged FVCOM model system to the proposed research effort.

2.3.2. *Biological Models*

We will use an existing copepod IBM, a newly proposed evolutionary IBM, and a simple food web model (NPZD) in FVCOM. We will extend our present modeling work involving *Calanus*, *Pseudocalanus*, and *Centropages* into the new pan-regional domain of FVCOM.

Lower trophic level food web model — As part of our current GLOBEC NWA study, we have implemented a simple NPZD model to provide food for the species-specific copepod models (Fig. 17). This model is robust and captures the 3D seasonal evolution of the phytoplankton and nutrient fields well (Fig. 15) (Ji et al., 2006b, 2007, in press). The AO-FVCOM contains the NPDZ module already and extension to the pan-regional case is straightforward. The resulting model will provide 4D food fields for the copepod species to be modeled using the IBM.

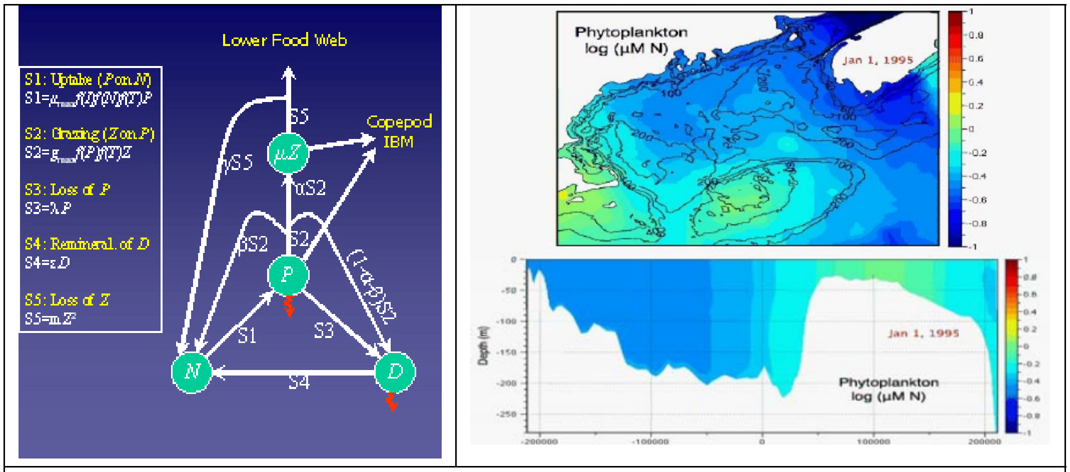


Fig. 17. NPZD model structure (left) and example output (right).

Copepod modeling — As stated in the objectives, copepod modeling will be carried out in three steps: 1) Static population projections, 2) IBM transport, and 3) evolutionary IBM.

<u>Static population projection</u> **–** The output from the two FVCOM cases, recent (1995-present) and future (2050) climate forcing in the North Atlantic and Arctic Oceans, will be used to establish environmental conditions within which the copepod population dynamics will be modeled. In the first step, these environmental conditions will simply be used to determine the potential population growth of each copepod species (i.e., in the absence of transport) at geographic locations selected throughout the pan-regional model domain (see Figs. 13, 15) and at monthly or seasonal intervals. The regions examined will include the NWA and AO as well as inlets (Barents and Bering) and outlets (Fram Strait and Canadian archipelago) to the Arctic. We will use a stage-based matrix population model we recently developed in the NWA Globec program (Hu et al., in press a, b) parameterized for *Calanus finmarchicus, Pseudocalanus newmani and P. moultoni*, *Centropages hamatus*, *Centropages typicus*, *Calanus glacialis*, and *Calanus marshallae*. Model parameterization has been/is being done for these species as part of our two parallel studies in the AO and NWA, based on extensive literature for these species. We will use these models to make population projections assuming static environmental conditions set by FVCOM (Caswell, 2002). This will provide insights into the growth potential of each species population throughout the pan-regional domain if conditions were to remain constant. The model includes temperature dependent development rate (Belehradek's equation) and food-dependent egg production functions for each species. For mortality, in case of sparse data on predator abundances and consumption rates, we will explore bottom-depth and temperature as proxies as well as quadradic loss terms and use empirical stage-size-based functions.

IBM-Transport – The next step will be to use an IBM to determine the combined effect of population growth together with transport and behavior on the species distributions. A spatially explicit Lagrangian tracking IBM will be used to understand the influence of physical and biological (vertical migration, temperature-/food- dependent growth, development, reproduction and mortality) processes on the population development and growth potential of the target copepod species through numerically tracking a large number ($O(10^5)$) of copepod individuals using a Lagrangian trajectory method. Various initial distributions will be used, including random seeding throughout the AO-NWA pan-regional domain (Figs. 13, 15) as well as targeted locations including Arctic basins and shelves, inlet (Barents/Bering) and outlet (Fram Strait/Canadian Archipelago) regions, and the NWA regions. These conditions will allow us to quantify the potential transport and colonization rates for target species under present and future climate conditions. The IBM will incorporate detailed copepod vital rate information, vertical migration, diapause stages (including bottom resting eggs), and dynamics of spatial variability in fully three-dimensional flow fields to track the temporal evolution and spatial trajectories and connectivity of copepod populations. The general model framework is shown in Figure 18. Numerical experiments will start from Lagrangian tracking for passive particles only, driven by temperature, mixing and current fields derived from FVCOM. This will allow a detailed picture of the possible pathways and environmental conditions that zooplankton populations experience at different times and the connectivity of populations among different shelf and basin ecosystems in the AO-NWA pan-regional system. The second group of numerical experiments is to extend the passive particle tracking to IBM, incorporating vital rates vertical migration behavior and diapause characteristics (from Runge et al GLOBEC 4B study). We also will allow production of eggs as new particles (culling randomly as needed), including bottom resting eggs for *C. hamatus*.

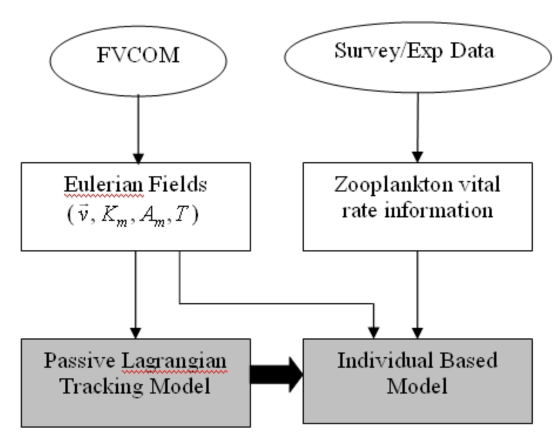


Figure 18 Flow chart for the spatially explicit Lagrangian tracking and individual based model

In the Lagrangian particle tracking model, the movement of each individual copepod through advection (and vertical migration) has been implemented in FVCOM (Chen et al. 2006b, Ji et al 2006a, Huret et al 2007) by solving the equation, $d\vec{x}/dt = \vec{v}(\vec{x}(t),t) + v_b$, where $\vec{x}$ is the particle position at time *t*, and $\vec{v}$ is the velocity from the surrounding model grids provided by FVCOM. The biological behavior term v_b is derived from the literature/field measurements. A random walk model will be used to simulate the movement of individual copepod in response the turbulent diffusion, with a special attention to avoiding the artificial particle aggregations in a spatially non-homogenous diffusivity field (Visser 1997, Ross and Sharples 2004). The model can be run simultaneously together with FVCOM with parallelization (so-called “online” mode) or driven separately by FVCOM model output (“offline” mode).

IBMs have been used to model zooplankton population dynamics for different species in different ecosystems (e.g. Batchelder and Williams, 1995; Carlotti and Wolf, 1998; Miller et al., 1998; Batchelder et al., 2002). The nature of the IBM allows incorporation of detailed biology, especially diapausing mechanisms, that are critical for accurate population assessment and difficult if not impossible to include in concentration based models (either forward or inverse models). In the AO study we are using a model adapted from Miller et al. (1998) that was developed for *C. finmarchicus* in the Gulf of Maine/Georges Bank region. The whole life cycle of target zooplankton species is divided into multiple morphologically distinct stages including egg, nauplii, copepodite and adult stages. An individual copepod is represented as a vector in the model with information such as location (x,y,z), sex, age, stage, ovarian status and other population dynamic variables (referred as *i*-state by Metz and Diekmann, 1986). Each vector is updated at each time step according to development rate and reproductive functions derived from field measurements and lab experiments. The model starts with an initial population structure and distribution, then monitors the change of each individual by recording the *i*-state of individual *j* at any time *t* (Carlotti et al., 2000):

$$X_{i,j}(t) = X_{i,j}(t-dt) + f(x_{1,j}(t-dt),\ldots x_{i,j}(t-dt),\ldots,T,\ food,\ldots),$$

where $X_{i,j}(t)$ is the value of the *i*-state of individual *j* and *f* is the process modifying $X_{i,j}$ as a function of the values of different *i*-states of the organisms, and external parameters such as the temperature *T* and food concentration. To deal with the possible significant variation of individual numbers during the simulation as a result of reproduction and mortality, a special form of IBM called super IBM (SIBM), will be implemented to better represent the variation and dynamics of population without tracking impractically large number of individuals (Scheffer et al. 1995). The SIBM treats each particle as a group of individuals (rather than one individual) that are born almost simultaneously, experience the same environmental conditions and have the same vital rates. This technical treatment has been widely used in many population dynamic studies (Hogeweg and Richter 1982; Woods and Onken 1982, Woods and Barkmann 1995, Carlotti and Wolf 1998).

<u>Evolutionary IBM</u> – In order to determine the optimal life history strategies for copepod species in the AO-NWA pan-regional domain, we propose to use a genetic algorithm. Genetic algorithms (GAs) are a heuristic search tool that have been successfully used to model behavioral decisions in adult fish (Dagorn et al. 1997, Huse & Giske 1998, Giske et al. 2003) and zooplankton migration (Fisken 2000, Eiane 2001), but have not, to our knowledge been used to determine the optimal life history strategies and behaviors of copepods. Given an equation, a GA searches for the best combination of parameters to use in the equation. These parameter sets or “strategies” are coded within the GA, and they compete and reproduce with each other to produce the next generation of strategies. This process results in keeping the best strategies and searching for better ones. Unlike other search and optimization methods, GAs may not find the optimal solution for certain conditions but will perform well across environmental variability.

Instead of examining individually a whole suite of alternate life history traits for multiple species and which possible combinations are best adapted to which environments, we propose to use a GA to determine them simultaneously. The standard IBM is essentially an equation that gives the suitability of a certain habitat as a function of internal states and environmental conditions. We will use an IBM parameterized for a generic copepod, one that has the possibility of going into diapause, laying bottom resting eggs, holding eggs in clutches, broadcast spawning, in addition to having the standard formulations for temperature and food dependent development and reproduction rates. The parameters values of this IBM can range across species and will be determined by the GA so that each individual copepod may end up with a different parameter set. Individual copepods are transported through many environmental conditions and their behaviors may select the best local vertical position or time to enter diapause. A second equation describes an individual’s fitness as a function of its development, reproductive, and survival rate as the individual moves through 3D space. After a generation time period has elapsed the fitness will be evaluated for each individual, and reproduction of the next generation will be proportional to an individual’s fitness. This process is repeated, using release locations of parents, over many generations until the parameter set converges to a stable solution. Multiple forms of both the decision-making and fitness equations will be tested. With the “offline” mode Lagrangian tracking, the physical model need only be run once, making the problem easily tractable on our 256-CPU computer cluster.

<u>Effects of warming climate on selection of copepod life history traits –</u> The evolutionary IBM will be initialized using a large number of individuals spread throughout the AO-NWA pan-regional domain, during both present and future warming conditions. The optimal life histories that evolve from the evolutionary IBM, initiated with a generic copepod, under the present and future conditions will provide insights into which traits are best adapted to which geographic locations and oceanographic habitats. Matching these traits with those of known copepod species will allow inferences to be made regarding optimal environmental conditions and locations for each species.

3. Significance of Proposed Research– Intellectual Merit

The proposed work will provide new insights into the mechanisms through which global warming may affect distributional patterns in marine copepod species locally and biogeographically across the pan-regional domain of the AO-NWA. The proposed models to be developed are an extension of our existing physical/biological models of the AO and NWA, and their linkage will provide a powerful new tool for studying copepod species patterns across broad ocean areas. The development of the Genetic Algorithm, evolutionary IBM, for determining optimal life history traits in copepods is new and its use with the 3D transport model will allow new understanding of how global change affects copepod species distributions. The methods to be developed are generically applicable to any ocean region. The results of the proposed study may provide new unifying principles in ecology and biogeography of marine species and will allow inferences to be made about how ecosystem structure may change in response to climate warming due to shifts in dominant zooplankton species distributions.

4. Broader Impacts

The New England Center for Ocean Science Education Excellence (COSEE) at WHOI will work with us to facilitate development of the education and outreach component of this project. COSEE is a national program, with regional centers, designed to facilitate K-12, college, and public education and outreach. The proposed work will provide a state-of-the art coupled biological/physical models of the Arctic, North Atlantic, and linkages to the global ocean model. We envision a broad user-base for this model, which will be served via the web to our scientific colleagues as well as to fishermen, K-12 educators, and the general public. The main web-page will be located at WHOI with links to the other institutions. We will work with COSEE in the context of WHOI's virtual oceanography presence at Whyville.net (web-based educational site for elementary and middle school students). We will sponsor undergraduate summer students to work on the project. The PIs regularly mentor undergraduate research assistants in their labs. In particular, students will be engaged in scientific and public outreach by maintaining a publicly accessible internet database that summarizes results, assist with peer-reviewed publications, and give presentations in national and international conferences. Chen's group at UMASSD will create a website specifically for this work, extending their already remarkable FVCOM site, which has user-friendly operational modeling capacity. Users will be able to examine 4D model data from the proposed runs. Users will be able to change model parameters and create new model runs, with the level of sophistication depending on skill level. We will to work with the SEA LAB Marine Science Education Center to develop teaching modules about the general oceanography in the N Atlantic and Arctic Oceans. As a part of the New Bedford public school system, SEA LAB is located next to Chen's Lab, facilitating collaboration on the design and content of the proposed UMASSD website and K-12 teaching modules.

5. Results of Prior NSF support

R. Ji, C. S. Davis, R. C. Beardsley, C. Chen, D. W. Townsend: Collaborative Research: Interannual Variability of Coastal Phytoplankton Blooms in the Gulf of Maine and Their Relationships to Local and Remote Forcings (OCE 0727033: $360,324, 10/1/2007-9/30/2010). This project has just been started. We have compiled and analyzed satellite and hydrographic data in the Gulf of Maine region. A model framework has been set up and several numerical experiments were successfully conducted, showing that the change of freshwater influx at the upstream boundary (Nova Scotia Shelf) has significant impact on the phytoplankton dynamics in the Gulf.

C. Chen: GLOBEC-01: Cross-frontal Exchanges on Georges Bank: Controls and Production of Phytoplankton (OCE-0234545: $185,000, 09/01/02-08/31/06). Chen has been a principal investigator in the NSF/NOAA U.S. GLOBEC Georges Bank program since 1992. In this phase IV grant, Chen and coworkers have developed an FVCOM-based integrated coastal ocean model system and applied it to the GoM/GB region. Chen has published 13 papers using previous GLOBEC support. The current GLOBEC funds have produced five manuscripts in press in *Deep-Sea Res. II* special GLOBEC/GB issues, *J. Geophys. Res.*, and *Oceanography.*

References

Arashkevich E, Wassmann P, Pasternak A, Wexels Riser C (2002) Seasonal and spatial changes in biomass, structure, and development progress of the zooplankton community in the Barents Sea. Journal of Marine Systems 38:125-145

Ashjian CJ, Campbell RG, Welch HE, Butler M, Van Keuren D (2003) Annual cycle in abundance, distribution, and size in relation to hydrography of important copepod species in the Western Arctic Ocean. Deep-Sea Research I 50:1235-1261

Baier CT, Napp, J.M. 2003. Climate-induced variability in Calanus marshallae populations. J. Plankt.Res. 25: 771-782.

Ban S, H. Lee, A. Shinada, and T. Toda. 2000. In situ egg production and hatching success of the marine copepod Pseudocalanus newmani in Funka Bay and adjacent waters off southwestern Hokkaido, Japan: associated to diatom bloom. J. Plankton Res. 22, 907-922.

Barlay S, K. Buschelman, V. Eijkhout, W. Group, D. Kaushik, M. Knepley, L. G. McInnes, B. Smiith and H. Zhang (2007), PETSc user manual. ANL-95/11-Revision 2.3.3., Mathematics and Computer Science Division, Argonne National Laboratory, 190pp.

Batchelder HP, and R. Williams, Individual-based modelling of the population dynamics of Metridia lucens in the North Atlantic. ICES Journal of Marine Science 52(3-4): 469-482.

Beaugrand G, Brander KM, Alistair Lindley J, Souissi S, Reid PC (2003) Plankton effect on cod recruitment in the North Sea. Nature 426:661-664

Beaugrand G, Lindley JA, Helaouet P, Bonnet D (2007) Macroecological study of Centropages typicus in the North Atlantic Ocean. Progress In Oceanography, The Biology and Ecology of Centropages typicus 72:259-273

Beaugrand G, Reid PC, Ibanez F, Lindley JA, Edwards M (2002) Reorganization of North Atlantic Marine Copepod Biodiversity and Climate. Science 296:1692-1694

Bigelow HB (1926).Plankton of the offshore waters of the Gulf of Maine. Bull. US Bur. Fish. 40:1-507

Bonnet D, Harris R, Lopez-Urrutia A, Halsband-Lenk C, Greve W, Valdes L, Hirche H-J, Engel M, Alvarez-Ossorio MT, Wiltshire K (2007) Comparative seasonal dynamics of Centropages typicus at seven coastal monitoring stations in the North Sea, English Channel and Bay of Biscay. Progress In Oceanography, The Biology and Ecology of Centropages typicus 72:233-248

Bonnet D, Richardson A, Harris R, Hirst A, Beaugrand G, Edwards M, Ceballos S, Diekman R, Lopez-Urrutia A, Valdes L, Carlotti F, Molinero JC, Weikert H, Greve W, Lucic D, Albaina A, Yahia ND, Umani SF, Miranda A, Santos Ad, Cook K, Robinson S, Fernandez de Puelles ML (2005) An overview of Calanus helgolandicus ecology in European waters. Progress In Oceanography 65:1-53

Buckley LJ, Durbin EG (2006) Seasonal and inter-annual trends in the zooplankton prey and growth rate of Atlantic cod (Gadus morhua) and haddock (Melanogrammus aeglefinus) larvae on Georges Bank. Deep Sea Research Part II: Topical Studies in Oceanography Dynamics of Plankton and Larval Fish Populations on Georges Bank, the North Atlantic U.S. GLOBEC Study Site 53:2758-2770

Bucklin A, A. M. Bentley and S. P. Franzen. 1998. Distribution and relative abundance of the copepods Pseudocalanus moultoni and P. newmani on Georges Bank based on molecular identification of sibling species. Mar. Biol., 132, 97-106.

Burchard H, 2002. Applied turbulence modeling in marine waters. Springer:Berlin-Heidelberg-New York-Barcelona-Hong Kong-London-Milan Paris-Tokyo, 215pp.

Campbell R, Sherr, E., Ashjian, C., Plourde, S., Sherr, B, Hill, V., and Stockwell, D.. Mesozooplankton prey preference and grazing impact in the western Arctic Ocean. Deep Sea Research II submitted

Carlotti F, and Wolf, U., 1998. A Lagrangian ensemble model of Calanus finmarchicus coupled with a 1-D ecosystem model. Fisheries Oceanography, 7: 191-204.

Carmack E, Wassmann, P. 2006. Food webs and physical-biological coupling on pan-Arctif shelves: Unifying concepts and comprehensive perspectives. Progress in Oceanography 71: 466-477.

Caswell H (2002) Matrix Population Models: Construction, Analysis, and Interpretation. Sinauer Associates, Sunderland, Massachusetts

Chen C, Beardsely R (1998) Tidal mixing and cross - frontal particle exchange over a finite amplitude asymmetric bank : A model study with application to Georges Bank. Journal of Marine Research 56:1163

Chen C, G. Gao,, A. Proshutinsky and R. C. Beardsley, 2007. A high-resolution, unstructured grid, finite-volume pan-arctic ocean model (FVCOM-Arctic). Presentation at the Joint AOMIP-ARCMIP-SEARCH for DAMOCLES workshop in Paris, October 28-31, 2007, Paris. Abstract and PPT presentations files are available.

Chen C, Liu H, Beardsley RC (2003) An Unstructured Grid, Finite-Volume, Three-Dimensional, Primitive Equations Ocean Model: Application to Coastal Ocean and Estuaries. Journal of Atmospheric and Oceanic Technology:159-186

Clarke GL, 1946. Dynamics of production in a marine area. Ecol. Monogr. 16, 321-337.

Conover RJ (1988) Comparative life histories in the genera Calanus and Neocalanus in high latitudes of the northern hemisphere. Hydrobiologia 167-168:127-142

Conover RJ, 1962. Metabolism and growth in Calanus hyperboreus in relation to its life cycle. Rapports Process et Verbaux Reunions, Conseil Permanent pour la International Exploration de la Mer 153: 190-197.

Corkett C, and I. A. McLaren. 1978. The biology of Pseudocalanus. Adv. Mar Biol., 15, 1-231.

Dagorn L, Petit, M., Stretta, J.M. 1997. Simulation of large-scale tropical tuna movement in relation with daily remote sensing data: the artificial life approach. BioSystems 44: 167-180.

Davis CS (1984) Interaction of a copepod population with the mean circulation on Georges Bank. J. Mar. Res. 42:573-590

Davis CS (1987a) Components of the zooplankton production cycle in the temperate ocean. J. Mar. Res. 45: 947-983

Davis CS (1987b) Zooplankton life cycles. In: Backus RH, Bourne DW (eds) Georges Bank. MIT Press, p 593

Davis CS, 1983. Laboratory rearing of marine calanoid copepods. J. Exp. Mar. Biol. Ecol., 71, 119-133.

deYoung B, Heath M, Werner F, Chai F, Megrey B, Monfray P (2004) Challenges of Modeling Ocean Basin Ecosystems. Science 304:1463-1466

Dudhia J, D. Gill, K. Manning, W. Wang, C. Bruyere, J. Wilson, and S. Kelly, 2003: PSU/NCAR mesoscale modeling system tutorial class notes and user's guide, MM5 modeling system version 3, Mesoscale and Microscale Meteorology Division, National Center for Atmospheric Research.

Durbin EG, Campbell RG, Casas MC, Ohman MD, Niehoff B, Runge J, Wagner M (2003) Interannual variation in phytoplankton blooms and zooplankton productivity and abundance in the Gulf of Maine during winter. Marine Ecology-Progress Series 254:81-100

Durbin EG, Casas MC (2006) Abundance and spatial distribution of copepods on Georges Bank during the winter/spring period. Deep-Sea Research Part Ii-Topical Studies in Oceanography 53:2537-2569

Durbin EG, Runge JA, Campbell RG, Garrahan PR, Casas MC, Plourde S (1997) Late fall-early winter recruitment of Calanusfinmarchicus on Georges Bank. Marine Ecology Progress Series 151:103-114

Dzierzbicka-Glowacka L, 2004. Growth and development of copepodite stages of Pseudocalanus spp., J. Plankton Res., 26, 49-60.

Edwards M, Johns DG, Licandro P, John AWG, Stevens DP (2006) Ecological Status Report: results from the CPR survey 2004/2005. SAHFOS Technical Report, Plymouth, U.K. ISSN 1744-0750. 3:1-8

Eiane K, Parisi D (2001) Towards a robust concept for modelling zooplankton migration. Sarsia 86:465-475.

Fairall CW, E. F. Bradley, J.E. Hare, A.A. Grachev, and J. B. Edson, 2003. Bulk parameterization of air-sea fluxes: updates and verification for the COARE algorithm. J. Climate, 16, 571-590

Fiksen O (2000) The adaptive timing of diapause - a search for evolutionarily robust strategies in Calanus finmarchicus. ICES J. Mar. Sci. 57:1825-1833

Fortier M, Fortier L, Hattori H, Saito H, Legendre L (2001) Visual predators and the diel vertical migration of copepods under Arctic sea ice during the midnight sun. J. Plankton Res. 23:1263-1278

Fratantoni PS, Pickart RS (2007) The Western North Atlantic Shelfbreak Current System in Summer. Journal of Physical Oceanography:2509-2533

Friedrichs MAM, Dusenberry JA, Anderson LA, Armstrong RA, Chai F, Christian JR, Doney SC, Dunne J, Fujii M, Hood R, McGillicuddy DJ, Moore JK, Schartau M, Spitz YH, Wiggert JD (2007) Assessment of skill and portability in regional marine biogeochemical models: Role of multiple planktonic groups. Journal of Geophysical Research-Oceans 112

Frost B, 1989. A taxonomy of the marine calanoic copepod genus Pseudocalanus. Can J Zool 67: 525-551

Frost BW, 1974. Calanus marshallae, a new species of calanoid copepod closely allied to the sibling species C. finmarchicus and C. glacialis. Marine Biology 26, 77-99.

Galperin B, L. H. Kantha, S. Hassid, and A. Rosati, 1988. A quasi-equilibrium turbulent energy model for geophysical flows. Journal of the Atmospheric Sciences, 45, 55-62.

Giske J, Mangel, M., Jakobsen, P., Huse, G., Wilcox, C., Strand, E. 2003. Explicit trade-off rules in proximate adaptive agents. Evolutionary Ecology and Research 5: 835-865.

GLOBEC (1991) U. S. GLOBEC: Northwest Atlantic Program, GLOBEC Canada/U.S. Meeting on N.W. Atlantic Fisheries and Climate. Report Number 2

GLOBEC. (1991) U. S. GLOBEC: Initial Science Plan. Report Number 1

GLOBEC. (1992) U. S. GLOBEC: Northwest Atlantic Implementation Plan. Report Number 6

GLOBEC. (1996) U. S. GLOBEC: Northeast Pacific Implementation Plan,. Report Number 17

GLOBEC. (1997) U. S. GLOBEC: Workshop on Modeling the Southern Ocean Ecosystem. Report Number 18

Grebmeier JM, Barry, J.P., 1991. The influence of oceanographic processes on benthic-pelagic coupling in polar regions: A benthic perspective. Journal of Marine Systems 2: 495-518.

Greene CH, Pershing AJ (2007) OCEANS: Climate Drives Sea Change. Science 315:1084-1085

Grell GA, J. Dudhia, and D. R. Stauffer, 1994: A description of the Fifth-Generation Penn State/NCAR Mesoscale Model (MM5). NCAR Technical Note, NCAR/TN 398+STR, 117pp.

Hakkinen (2002) Freshening of the Labrador Sea surface waters in the 1990 s - Another great salinity anomaly. Geophysical Research Letters 29:2232

Han G, C. E. Hannah, J. W. Loder, and P. C. Smith, 1997. Seasonal variation of the three-dimensional mean circulation over the Scotian Shelf. J. Geophysical Research, 102(C1), 1011-1025.

Hannah CG, J. A. Shore, J. W. Loder, and C. E. Naimie, 2001. Seasonal circulation on the western and central Scotian Shelf. J. Phys. Oceanography, 31(2), 591-615.

Head EJH, Harris, L.R., Petrie, B., 1999. Distribution of Calanus spp. on and around the Nova Scotia Shelf in April: evidence for an offshore source of Calanus finmarchicus to the central and western regions. Canadian Journal of Aquatic Sciences 56, 2463-2476.

Head EJH, Sameoto DD (2007) Inter-decadal variability in zooplankton and phytoplankton abundance on the Newfoundland and Scotian shelves. Deep Sea Research Part II: Topical Studies in Oceanography, Effects of Climate Variability on Sub-Arctic Marine Ecosystems - A GLOBEC Symposium, GLOBEC-ESSAS Symposium on "Effects of climate variability on sub-arctic marine ecosystems" 54:2686-2701

Hibler III WD, 1979. A dynamic thermodynamic sea ice model. J. Phys. Oceanogr., 9, 815-843.

Hirche H-J, Bohrer, R.N., 1987. Reproduction of the Arctic copepod Calanus glacialis in Fram Strait. Mar. Biol. 94: 11-17.

Hirche HJ, Muyakshin S, Klages M, Auel H (2006) Aggregation of the Arctic copepod Calanus hyperboreus over the ocean floor of the Greenland Sea. Deep Sea Research Part I: Oceanographic Research Papers 53:310-320

Hirche H-J, Niehoff, B. (1996) Reproduction of the Arctic copepod Calanus hyperboreus in the Greenland Sea - field and laboratory observations. Polar Biology 16:209-219

Hogeweg P, and Richter, A.F., 1982. INSTAR, a discrete event model for simulating zooplankton dynamics. Hydrobiologia, 95: 275-285.

Hopcroft RR, Clarke C, Nelson RJ, Raskoff KA (2005) Zooplankton communities of the Arcticâ€™s Canada Basin: the contribution by smaller taxa. Polar Biology 28:198-206

Houghton RW, Fairbanks RG (2001) Water sources for Georges Bank. Deep Sea Research Part II: Topical Studies in Oceanography, Coupled biological and physical studies of plankton populations on Georges Bank and related North Atlantic regions 48:95-114

Hu Q, C. Davis, and C. Petrik. A simplified age-stage model for copepod population dynamics. Mar. Ecol. Prog. Ser. (in press a) doi: 10.3354/meps07314

Hu Q, Petrik C, Davis CS Normal versus Gamma: Stochastic model of copepod molting process. J. Plankton Res. (in press b)

Hunke EC, and W. H. Lipscomb (2006), CICE: The Los Alamos Sea Ice Model, documentation and software, Version 3.14, Los Alamos Natl. Lab., Los Alamos, NM, pp59

Huret M, Runge JA, Chen C, Cowles G, Xu Q, Pringle J (2007) Dispersal modeling of fish early life stages: Sensitivity with application to Atlantic cod in the western Gulf of Maine. Marine Ecology Progress Series 347:261–274

Huse G, Giske J (1998) Ecology in Mare Pentium: an individual-based spatio-temporal model for fish with adapted behaviour. Fisheries Research 37:163-178

ICES (2007) Report of the Working Group on Zooplankton Ecology (WGZE), 26–29 March 2007, Riga, Latvia. ICES CM 2007/OCC:04. 66 pp

Ji R, C Davis, C Chen, R Beardsley (In Press) Influence of local and external processes on the annual nitrogen cycle and primary productivity on Georges Bank: A 3-D biological-physical modeling study. Journal of Marine Systems

Ji R, Chen C, Franks PJS, Townsend DW, Durbin EG, Beardsley RC, Gregory Lough R, Houghton RW (2006a) The impact of Scotian Shelf Water "cross-over" on the plankton dynamics on Georges Bank: A 3-D experiment for the 1999 spring bloom. Deep Sea Research Part II: Topical Studies in Oceanography, Coupled biological and physical studies of plankton populations on Georges Bank and related North Atlantic regions, Dynamics of Plankton and Larval Fish Populations on Georges Bank, the North Atlantic U.S. GLOBEC Study Site 53:2684-2707

Ji R, Chen C, Franks PJS, Townsend DW, Durbin EG, Beardsley RC, Gregory Lough R, Houghton RW (2006b) Spring phytoplankton bloom and associated lower trophic level food web dynamics on Georges Bank: 1-D and 2-D model studies. Deep Sea Research Part II: Topical Studies in Oceanography, Dynamics of Plankton and Larval Fish Populations on Georges Bank, the North Atlantic U.S. GLOBEC Study Site 53:2656-2683

Ji R, Davis C, Chen C, Townsend DW, Mountain DG, Beardsley RC (2007) Influence of ocean freshening on shelf phytoplankton dynamics. Geophys. Res. Let. 34, L24607, doi:10.1029/2007GL032010

Johnson C, Pringle J, Chen C (2006) Transport and retention of dormant copepods in the Gulf of Maine. Deep Sea Research Part II: Topical Studies in Oceanography, Dynamics of Plankton and Larval Fish Populations on Georges Bank, the North Atlantic U.S. GLOBEC Study Site 53:2520-2536

Kosobokova KN, Hirche, H.-J. 2001. Reproduction of Calanus glacialis in the Laptev Sea, Arctic Ocean. Polar Biol. 24: 33-43.

Lane PVZ, Llinas, L., Smith, S.L., Pilz, D., Zooplankton distribution in the western Arctic during summer 2002, hydrographic habitats and implications for food chain dynamics. J. Mar. Res. In revision.

Lee H, S. Ban, T. Ikeda and T. Matsuishi. 2003. Effect of temperature on development, growth and reproduction in the marine copepod Pseudocalanus newmani at satiating food condition. J. Plankton Res. 25, 261-271.

Levinsen H, Turner, J.T., Nielsen, T.G., Hansen, B.W., 2000. On the trophic coupling between protists, and copepods in arctic marine systems. Marine Ecology Progress Series 204 -

Lindeman RL (1942) The trophic-dynamic aspect of ecology. Ecology 23:399-418

Lindley J, and HG Hunt, 1989. The distribution of Labidocera wollastoni and Centropages hamatus in the North Atlantic Ocean and the North Sea in relation to the role of resting eggs in the sediment. In: Ryland JS, Tyler PA (eds) Reproduction, genetics and distributions of marine organisms. Olsen and Olsen, Fredensborg, pp 407-413

Lischka S, Hagen W (2005) Life histories of the copepods Pseudocalanus minutus, P. acuspes (Calanoida) and Oithona similis (Cyclopoida) in the Arctic Kongsfjorden (Svalbard). Polar Biology 28:910-921

Marcus N, 1996. Ecological and evolutionary significance of resting eggs in marine copepods: past, present, and future studies. Hydrobiologia, 320: 141-152.

Marcus NH, and R. V. Lutz., 1998. Longevity of subitaneous and diapause eggs of Centropages hamatus (Copepoda: Calanoida) from the northern Gulf of Mexico, Marine Biology, 131, 249-257.

McGillicuddy D, A. Bucklin., 2002. Intermingling of two Pseudocalanus species on Georges Bank. J. Mar. Res. 60: 583-604.

McGillicuddy DJ, D. R. Lynch, A. M. Moore, W. C. Gentleman, C. S. Davis, and C. J. Meise. 1998. An adjoint data assimilation approach to the diagnosis of physical and biological controls on Pseudocalanus spp. populations in the Gulf of Maine - Georges Bank Region. Fisheries Oceanogr., 7, 205-218.

McLaren IA LE, Corkett CJ, Sevigny J-M 1989a Life cycles of four species of Pseudocalanus in Nova Scotia. Can J Zool 67: 552-558

McLaren IA SJ-M, Corkett CJ 1989b Temperature-dependent development in Pseudocalanus species. Can J Zool 67: 559-564

Meise-Munns C, J. Green, M. Ingham, and D. Mountain, 1990. Interannual variability in the copepod populations of Georges Bank and the western Gulf of Maine, Mar. Ecol. Progr. Ser., 65, 225-232,

Mellor GL, and T. Yamada, 1982. Development of a turbulence closure model for geophysical fluid problem. Reviews of Geophysics and Space. Physics, 20, 851-875.

Metz JAJ, and Diekmann, O., 1986. The dynamics of physiologically structured populations. Springer-Verlag, Berlin, Germany

Miller CB, T. J. Cowles, P. H. Wiebe, N. J. Copley, and H. Grigg, 1991. Phenology in Calanus finmarchicus: Hypotheses about control mechanisms, Mar. Ecol. Progr. Ser., 72, 79-91,.

Mullin M (1963) Some factors affecting the feeding of marine copepods of the genus Calanus. Limnology and Oceanography 8:239-250

Odum HT (1957) Trophic structure and productivity of Silver Springs, Florida. Ecological Monographs 27:55-112

Ohman MD, J. A. Runge, E. G. Durbin, D. B. Field and B. Niehoff. 2002. On birth and death in the sea. Hydrobiol., 480, 55-68.

Osgood KE, D. M. Checkley. 1997. Seasonal variations in a deep aggregation of Calanus pacificus in the Santa Barbara Basin. Mar. Ecol. Prog. Ser., 148, 59 69.

Peterson WT, 1998. Life cycle strategies of copepods in coastal upwelling zones. J. Mar. Systems 15: 313-326.

Plourde S, Campbell, R.G., Ashjian, C.J., Stockwell, D. 2005. Seasonal and regional patterns in egg production of Calanus glacialis/marshallae in the Chukchi and Beaufort Seas during spring and summer, 2002. Deep-Sea Research II 52: 3411-3426.

Proshutinsky A, Bourke RH, McLaughlin FA (2002) The role of the Beaufort Gyre in Arctic climate variability: Seasonal to decadal climate scales. Geophysical Research Letters 29

Ringuette M, Fortier L, Fortier M, Runge JA, Belanger S, Larouche P, Weslawski J-M, Kwasniewski S (2002) Advanced recruitment and accelerated population development in Arctic calanoid copepods of the North Water. Deep Sea Research Part II: Topical Studies in Oceanography, The International North Water Polynya Study 49:5081-5099

Ross ON, and Sharples, J., 2004. Recipe for 1-D Lagrangian particle tracking models in space-varying diffusivity. Limnology and Oceanography-Methods, 2: 289-302.

Runge JA, Plourde, S. 1996. Fecundity characteristics of Calanus finmarchicus in coastal waters of eastern Canada. Ophelia 44: 171-187.

Sakshaug E, 2004. Primary and secondary production in the Arctic Seas. In: Stein, R., Macdonald, R.W. (Eds.), The organic carbon cycle in the arctic Ocean. Springer, Berlin-Heidelberg, pp 57-81.

Sameoto DD, and A. W. Herman. 1990. Life cycle and distribution of Calanus finmarchicus in deep basins on the Nova Scotia shelf and seasonal changes in Calanus spp., Mar. Ecol. Progr. Ser., 66, 225-237,.

Sarmiento JL, Slater RD, Toggweiler JR, Fasham MJR, Ducklow HW, Evans GT (1993) A seasonal three-dimensional ecosystem model of nitrogen cycling in the North Atlantic euphotic zone. Journal: Global Biogeochemical Cycles; : 7:417-450

Saumweber WJ, Durbin EG (2006) Estimating potential diapause duration in Calanus finmarchicus. Deep Sea Research Part II: Topical Studies in Oceanography, Dynamics of Plankton and Larval Fish Populations on Georges Bank, the North Atlantic U.S. GLOBEC Study Site 53:2597-2617

Scheffer M, Baveco, J.M., DeAngelis, D.L., Rose, K.A. and Van Nes, E.H., 1995. Super-individuals a simple solution for modelling large populations on an individual basis. Ecological Modelling, 80(2): 161-170.

Schwing FB (1992) Subtidal Response of Scotian Shelf Circulation to Local and Remote Forcing. Part I: Observations. Journal of Physical Oceanography:523-541

Sherman K, Smith WG, Green JR, Cohen EB, Berman MS, Marti KA, R. GJ (1987) Zooplankton production and the fisheries of the northeastern shelf. In: Backus RH, Bourne DW (eds) Georges Bank. MIT Press, Cambridge, MA, p 268–282

Smagorinsky J, 1963. General circulation experiments with the primitive equations, I. The basic experi-ment. Monthly Weather Review, 91, 99-164.

Smith PC, R.W. Houghton, R.G. Fairbanks, and D.G. Mountain. 2001. Interannual variability of boundary fluxes and water mass properties in the Gulf of Maine and on Georges Bank: 1993-1997. Deep Sea Res. II, 48, 37-70.

Smith SL, Schnack-Schiel, S.B., 1990. Polar Zooplankton. In: Smith, W.O. Jr., (Ed.), Polar, Oceanography Part B C, Biology, and Geology, Academic Press, San Diego, CA, pp. 527-598.

Smith SL, Vidal, J. 1986. Variations in the distribution, abundance, and development of copepods in the southeastern Bering Sea in 1980 and 1981. Cont. Shelf. Res. 5: 215-239.

Steele JH (1974) The Structure of Marine Ecosystems. Harvard Univ. Press, Cambridge, MA

Tande KS, 1989,. Calanus in North Norwegian fjords and in the Barents Sea. Pol. Res 10: 389-407.

Teal JM (1962) Energy Flow in the Salt Marsh Ecosystem of Georgia. Ecology 43:614-624

Valdes L, Lopez-Urrutia A, Cabal J, Alvarez-Ossorio M, Bode A, Miranda A, Cabanas M, Huskin I, Anadon R, Alvarez-Marques F, Llope M, Rodriguez N (2007) A decade of sampling in the Bay of Biscay: What are the zooplankton time series telling us? Progress In Oceanography, Ecological Functioning of the Iberian Seas: A synthesis of GLOBEC Research in Spain and Portugal 74:98-114

Vidal J (1980) Physioecology of zooplankton. I. Effects of phytoplankton concentration, temperature, and body size on the growth rate of Calanus pacificus and Pseudocalanus sp. Marine Biology 56:111-134

Visser AW, 1997. Using random walk models to simulate the vertical distribution of particles in a turbulent water column. Marine Ecology-Progress Series, 158: 275-281.

Wassman P, Reigstad, M., Haug, T., Rudels, B., Carroll, M.L, Hop, H., Gabrielsen, G.W., Falk-Petersen, S., Denisenko, S.G., Arashkevich, E., Slagstad, D., Pavlova, O. 2006. Food web and carbon flux in the Barents Sea. Progress in Oceanography 71: 232-287.

Werner I, Martinez Arbizu P (1999) The sub-ice fauna of the Laptev Sea and the adjacent Arctic Ocean in summer 1995. Polar Biology 21:71-79

Wiebe PH, Beardsely R, Mountain D, Bucklin A (2002) US GLOBEC Northwest Atlantic/Georges Bank Program. Oceanography 15:13-29

Woods J, and Onken, R., 1982. Diurnal variation and primary production in the ocean - primary results of a Lagrangian ensemble model. Journal of Plankton Research, 4: 735-756.

Woods JD, and Barkmann, W., 1995. Modeling oligotrophic zooplankton production: seasonal oligotrophy off the Azores. ICES Journal of Marine Science, 52: 723-734.

Zakardjian BA, J. Sheng, J. A. Runge, I. McLaren, S. Plourde, K. R. Thompson, and Y. Gratton . 2003. Effects of temperature and circulation on the population dynamics of Calanus finmarchicus in the Gulf of St. Lawrence and Scotian Shelf: Study with a coupled, three-dimensional hydrodynamic, stage-based life history model, J. Geophys. Res., 108(C11), 8016, doi:10.1029/2002JC001410.

Zhang J, and W. D. Hibler III, 1997. On an efficient numerical method for modeling sea ice dynamics. J. Geophys. Res., 102, 8691-8702.