Supply-Side Ecology Response of Climate-Driven Changes in North Atlantic Ocean

BY THE MERCINA WORKING GROUP

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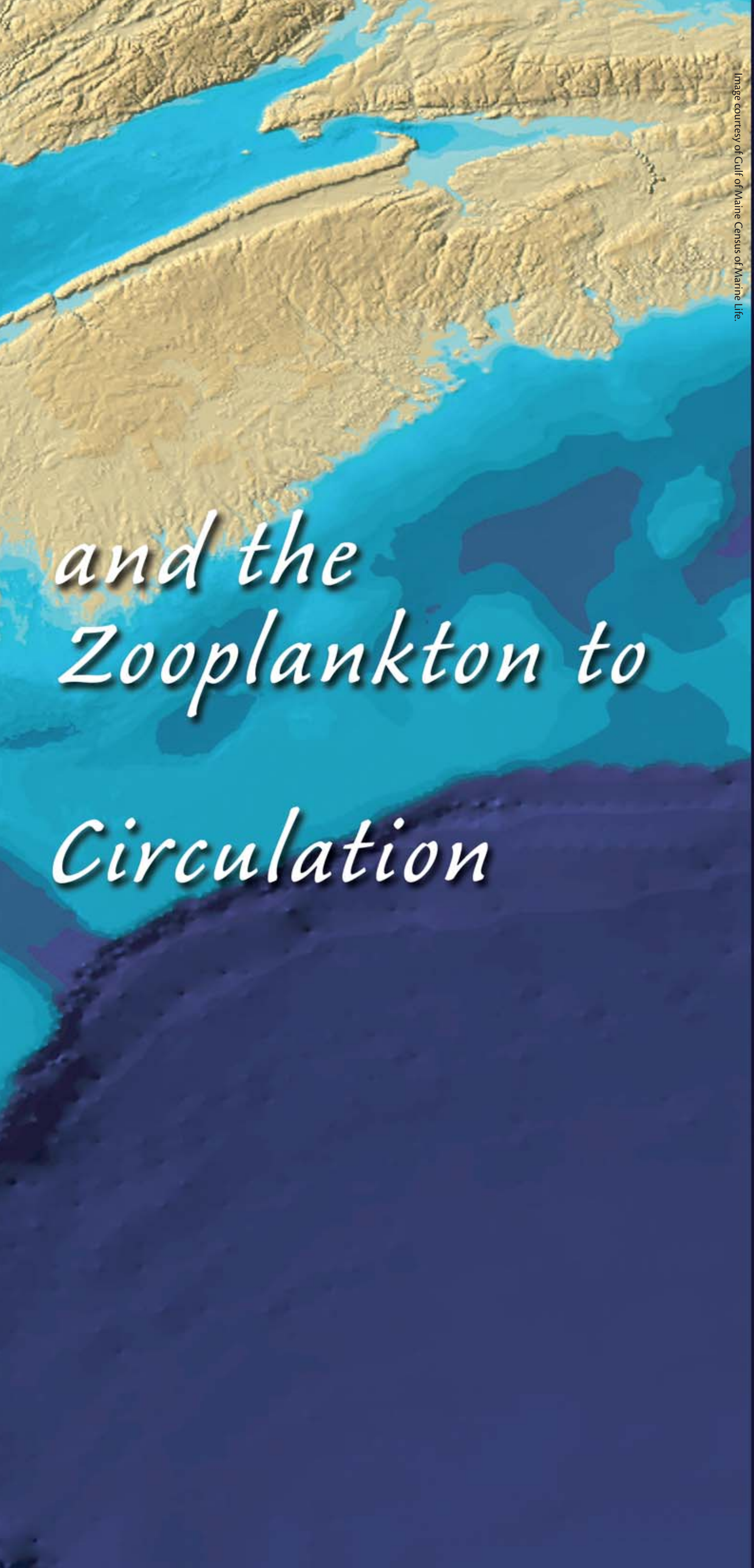

and the Zooplankton to Circulation

Image courtesy of Gulf of Maine Census of Marine Life.

Recent findings from oceanographic field studies conducted on both sides of the North Atlantic have dramatically altered our view of how zooplankton populations respond to climate-driven changes in ocean circulation. Shelf populations of the copepod species *Calanus finmarchicus* dominate springtime secondary production in many shelf ecosystems throughout the North Atlantic. Despite their seasonal dominance, these shelf populations must be supplied by advection from oceanic sources or else they would be driven to local extinction. It now appears that the supply of external recruits is not only important to the long-term persistence of these shelf populations, but also central to their dynamics on seasonal to interdecadal time scales. Here, we present a synthesis of findings from the U.S. Global Ocean Ecosystem Dynamics (GLOBEC) Northwest Atlantic Field Study. This synthesis reveals that climate-driven changes in the circulation of the Northwest Atlantic can account for a large amount of the variability in *C. finmarchicus* abundance observed in the Gulf of Maine/Georges Bank region during recent years and over the past half century.

Calanus finmarchicus dominates the springtime zooplankton biomass and secondary production in many shelf ecosystems throughout the North Atlantic Ocean (Mauchline, 1998). Despite its seasonal dominance, *C. finmarchicus* is an expatriate species in these shelf ecosystems whose populations must be replenished every year or every few years by advection from external oceanic sources (Greene and Pershing, 2000; MERCINA, 2003). This dependence on advective supply makes *C. finmarchicus* a good indicator of climate-driven changes in ocean circulation patterns (Greene and Pershing, 2000; MERCINA, 2001, 2003; Pershing et al., 2004) and therefore a suitable target species for climate change research (Wiebe et al., 2002).

The U.S. GLOBEC Northwest Atlantic Field Study, part of a large international effort to study the effects of climate change on marine ecosystems, was conducted in the Gulf of Maine/Georges Bank region from 1995 through 1999. *Calanus finmarchicus* was chosen as one of the principal target species for investigation during this field study. While it has long been recognized that populations of *C. finmarchicus* in the Gulf of Maine and on Georges Bank are tightly coupled (Bigelow, 1926; Davis, 1987a; Sherman et al., 1987), recent findings suggest that there is considerable variability in the physical-biological coupling between these two ecosystems. In the sections that follow, we review hypotheses suggesting how these physical and biological processes interact seasonally in the two ecosystems. Initially, we focus on the typical or climatological seasonal cycles in the Gulf of Maine and on Georges Bank. Then, we describe anomalies from these seasonal cycles observed from 1995 to 1999. After providing this background information, we develop a synthesis that integrates findings from recent U.S. GLOBEC field studies with retrospective time-series analyses of hydrographic and continuous plankton recorder data. Our goals are (1) to identify key processes regulating the population dynamics of *C. finmarchicus* in the region from 1995 to 1999, (2) to understand how climate-driven changes in the circulation patterns of the Northwest Atlantic affect these processes on interannual to interdecadal time scales, and (3) to present a conceptual framework for studying the trans-Atlantic population responses of *C. finmarchicus* to climate variability and change.

CLIMATOLOGICAL SEASONAL CYCLES

When reviewing the climatological seasonal cycles of *C. finmarchicus*, it is important to point out that the species exhibits considerable variability in its phenology throughout the North Atlantic (Conover, 1988; Miller et al., 1991). In the more northerly regions of its distribution, *C. finmarchicus* spends most of the year in a resting or diapause state (Hirche, 1996), with populations typically passing through only a single generation during the few months of active growth (Conover, 1988). In contrast, populations in the Gulf of Maine/Georges Bank region spend approximately half of the year in diapause before passing through two or three generations during the other half of the year (Conover, 1988). Typically, *C. finmarchicus* enters diapause during summer to early autumn when environmental conditions in the upper water column become less favorable for population growth. Diapause is initiated as the late copepodid stages, typically the fifth copepodites, undergo an ontogenetic vertical migration into deeper waters. The duration of the diapause period is regionally dependent, and the cues for emergence from diapause are not well understood at present (Hirche, 1996). Once the cues for emergence are triggered, the population of newly matured adults vertically migrates back to the upper water column where they reproduce to form the next year's first generation.

In the Gulf of Maine/Georges Bank region, the climatological seasonal cycles of *C. finmarchicus* (Figure 1) can be pieced together based partly on results from the U.S. GLOBEC Northwest Atlantic Field Study and partly on hypotheses generated prior to it (GLOBEC, 1991). These climatological, seasonal cycles are best viewed as working hypotheses consistent with existing field data.

During a typical winter period (late December to early March), most of the Gulf of Maine *C. finmarchicus* popula-

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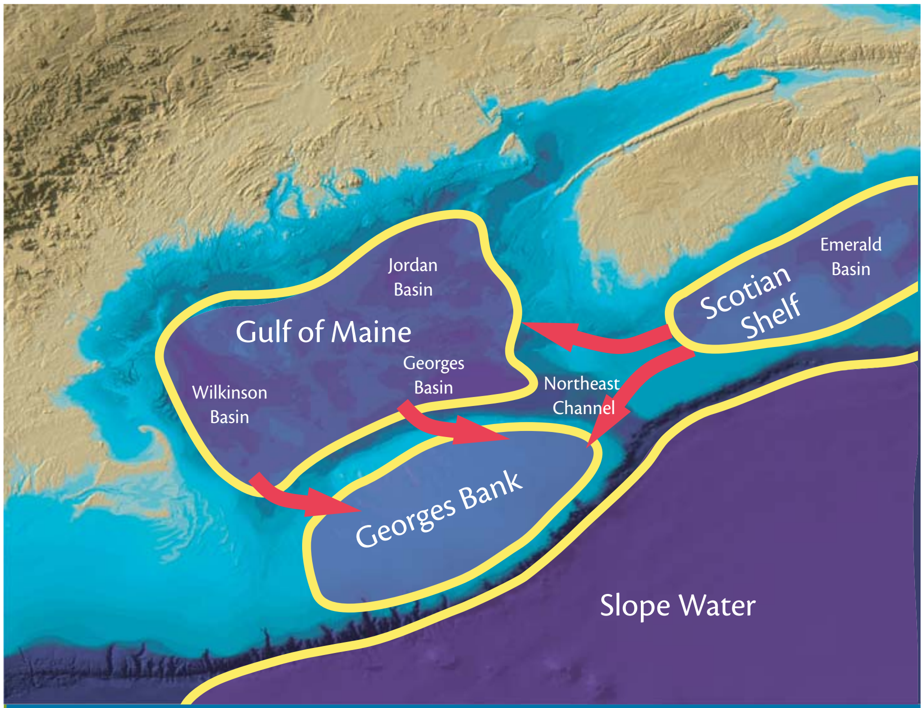
tion emerges from diapause, and egg production by its females is food limited (Lynch et al., 1998; Durbin et al., 2000). The Georges Bank population is dependent on the supply of "zero generation" (G_0) adults advected onto the Bank from the deep basins of the Gulf of Maine (Hannah et al., 1998; Lynch et al., 1998; Miller et al., 1998), with first generation (G_1) nauplii also supplied from the southern Gulf waters adjacent to the Bank (Durbin et al., 2000). Once on Georges Bank or in adjacent shallow waters, the G_0 females are no longer food limited and egg production begins (Durbin et al., 1997). The G_1 animals on Georges Bank grow at rates determined primarily by temperature, with no evidence for food limitation (Durbin et al., 2000).

During a typical early spring period (mid-March to late April), the vernal phytoplankton bloom occurs in the Gulf of Maine, and the *C. finmarchicus* population is no longer food limited for either egg production or growth (Durbin et al., 1995a; 2000). The G_1 animals in the Gulf of Maine now grow at rates determined primarily by temperature (Durbin et al., 2000). Since residence times on Georges Bank are estimated to be on the order of 30-60 days, roughly comparable to the generation time of *C. finmarchicus* (Lynch et al., 1998), the Bank population can only be sustained by continuous inputs from upstream. Primarily G_1 animals, with some remnants from G_0 adults, continue to recruit from the Gulf of Maine to Georges Bank (Durbin et al., 2000). Given the increased shallow inflows into the Gulf of Maine/Georges Bank region from the Scotian Shelf during spring (Smith et al., 2001; Zakardjian et al., 2003), we hypothesize that such inflows are another important source of



Winter	
Gulf of Maine	1. G_0 generation emerges from diapause.
	2. Growth and reproduction are food limited.
Georges Bank	1. Population supply-limited from Gulf of Maine.
	2. Growth and reproduction are not food limited.
Early Spring	
Gulf of Maine	1. Spring bloom, population no longer food limited.
	2. Population supplied from Scotian Shelf/Slope Water.
Georges Bank	1. Population supply-limited from Gulf of Maine/Scotian Shelf.
	2. Population becomes food limited in April.
Late Spring-Early Summer	
Gulf of Maine	1. Growth and reproduction are food limited.
	2. Population supplied from Scotian Shelf/Slope Water.
	3. Diapause stocks build.
Georges Bank	1. Growth and reproduction are no longer food limited.
Late Summer-Autumn	
Gulf of Maine	1. Most of population is in diapause.
	2. Small active population.
Georges Bank	1. *Calanus finmarchicus* disappears from Georges Bank due to predation and advective losses.

Figure 1. Characterizing the climatological seasonal cycles for *C. finmarchicus* in the Gulf of Maine and on Georges Bank. These characterizations are based in part on early results from the U.S. GLOBEC NW Atlantic/Georges Bank Field Program and in part on hypotheses generated prior to it. Gulf of Maine bathymetry provided by Martin Jakobsson, Stockholm University, and Lewis Incze, University of Southern Maine and available from the Gulf of Maine Census of Marine Life (www.usm.maine.edu/gulfofmaine-census).

C. finmarchicus to the Bank. These Scotian Shelf recruits to Georges Bank may arrive through direct crossover events or by transiting through the Northeast Channel and Georges Basin before entering the Bank's circulation (Bisagni et al., 1996; Smith et al., 2001). During late March, G_1 females first appear on Georges Bank, and, by early April, they have largely replaced the G_0 females (Durbin et al., 2000). Food limitation (Campbell et al., 2001) and predation (Sullivan and Meise, 1996; Madin et al., 1996; Sell et al., 2001) increase significantly on Georges Bank during this period, reducing *C. finmarchicus* abundance as well as the population's egg production and growth rates.

During a typical late spring/early summer period (early May to early July), we hypothesize that animals continue to recruit to the Gulf of Maine/Georges Bank region from the Scotian Shelf. The *C. finmarchicus* population in the Gulf of Maine becomes food limited, nauplii become scarce, and many late copepodites begin to descend into the diapause stock (Durbin et al., 1995b, 2000; Miller et al., 2000). On Georges Bank, nauplii also become scarce in early May, only to reappear in greater abundance during June (Durbin et al., 2000). Miller et al. (1998) hypothesize that this decline in the abundance of nauplii corresponds to a gap in naupliar production associated with the development time to maturation of the G_1 females while egg production by the G_0 females diminishes. However, as Miller et al. (1998) note, the gap in production of G_2 nauplii occurs approximately one month later than expected if development were not food limited. Durbin et al. (2000) suggest that food limitation and predation may explain this discrepancy, although the relative importance of each is presently unknown. Whether food limitation or predation is the major factor limiting naupliar abundance during early May, feeding conditions improve on Georges Bank during late May/early June, and *C. finmarchicus*' abundance as well as egg production and growth rates increase (Durbin et al., 2000). Mortality rates, presumably associated with increased predation, are high during this period, however, and few copepodites survive to mature and reproduce (Durbin et al., 2000).

During a typical late summer/autumn period (late July to mid-December), the active *C. finmarchicus* population in the Gulf of Maine declines rapidly, and most of the late copepodites surviving from the G_1 and G_2 generations have entered the diapause stock. We hypothesize that the decline in the active population is the result of reduced advective supply from the Scotian Shelf (Zakardjian et al., 2003) combined with increased losses due to advection, predation, and vertical migration into the diapause stock. Despite these net losses, a small population remains active in the Gulf of Maine throughout the period (Durbin et al., 1997). The population on Georges Bank largely disappears during this period due to advective losses and predation.

The abundance and survivorship of the Gulf of Maine diapause stock subsequently determine the abundance of G_0 animals recruiting to Georges Bank the following winter. While G_1 and G_2 late copepodites are both known to enter diapause, prosome length analyses indicate that only the smaller G_2 copepodites appear to survive until the following winter (Durbin et al., 2000). The larger G_1 copepodites, which developed during the colder spring conditions, apparently fail to make it through the seven to eight months of diapause. The timing and duration of this apparent mass mortality of the G_1 portion of the diapause stock is unknown at present, as is the mortality rate of the diapause stock as a whole.

ANOMALIES FROM THE CLIMATOLOGICAL SEASONAL CYCLE DURING 1995–1999

In this section, we describe anomalies from the climatological seasonal cycle observed during 1995-1999. As in the previous section, the description that follows is best viewed as containing working hypotheses that are consistent with existing field data.

Relative to the previous quarter century, the period from 1995–1999 was a very unusual time in the Gulf of Maine/Georges Bank region. From the early 1970s until 1995, the North Atlantic Oscillation (NAO) Index exhibited an unusually persistent, positive trend (Hurrell et al., 2003). In particular, the decade of the Marine Monitoring, Assessment, and Prediction (MARMAP) Program during the late 1970s and early 1980s (Meise and O'Reilly, 1996; Sherman, 1980), was a time of strongly positive NAO conditions. During winter 1996, however, the NAO Index underwent its largest single-year drop of the twentieth century, attaining a negative value not seen since the 1960s. It has been hypothesized that this large drop in the NAO Index led to a large-scale reorganization of circulation patterns in the Northwest Atlantic (MERCINA, 2001; Greene and Pershing, 2003). To comprehend the magnitude of these changes, one must first understand conditions prior to this event.

The Northwest Atlantic's slope waters have been shown to respond as a coupled system to major changes in climate (Pickart et al., 1999; Keigwin and Pickart, 2000; Loder et al., 2001; MERCINA, 2001; Greene and Pershing, 2003). During the positive NAO conditions of the past quarter century, this coupled slope water system (CSWS) has operated predominantly in its maximum modal state, with relatively warm and saline Atlantic Temperate Slope Water (ATSW) advancing northeastward along the shelf break and converging with relatively cold and fresh Labrador Subarctic Slope Water (LSSW) at a front near the Gulf of St. Lawrence (see Figure 1d in MERCINA, 2001). This advance of ATSW typically coincides with reduced transport in the Labrador Current and an enhanced hydrographic signature of Labrador Sea Water in the Deep Western Boundary Current (Pickart et al., 1999).

After the NAO Index's large drop during 1996, the CSWS shifted to its minimum modal state over the next two years, with LSSW advancing along the shelf break, displacing ATSW offshore, and extending to the southwest as far as the Middle Atlantic Bight (see Figure 1c in MERCINA, 2001). In addition to this advance along the shelf break, the LSSW also entered the deep basins of the Gulf of Maine and Western Scotian Shelf (see Figure 2 in MERCINA, 2001). By early winter 1998, LSSW had replaced the deep waters of Emerald Basin on the Western Scotian Shelf and began entering the Gulf of Maine through the Northeast Channel. By early autumn 1998, the hydrographic properties of the Gulf of Maine deep basins reflected the advective replacement and mixing that had occurred between the newly arrived LSSW and the resident deep waters derived largely from ATSW.

The observed hydrographic changes did not last long, however. The NAO Index's large drop during winter 1996 persisted only a year, and the Index returned to positive values from 1997 to 2001 (Greene and Pershing, 2003). During 1999, the CSWS shifted back to its maximum modal state, with the Labrador Current weakening and the frontal boundary of the LSSW retreating northeastward along the Scotian Shelf (MERCINA, 2001). As the supply of LSSW to the region decreased, ATSW returned to its previous position adjacent to the shelf break and began resupplying the deep basins of the Gulf of Maine and Western Scotian Shelf. By the end of 1999, the Gulf of Maine and Western Scotian Shelf deep basins exhibited hydrographic conditions similar to those observed prior to the apparent NAO-forced modal shift in the CSWS.

The changes in ocean circulation patterns attributed to NAO forcing during the late 1990s appear to have had dramatic impacts on the population dynamics of *C. finmarchicus* in the Gulf of Maine/Georges Bank region (MERCINA, 2001, 2003; Pershing et al., 2004). Although the drop in the NAO Index occurred during winter 1996, the seasonal cycles of *C. finmarchicus* in the region did not exhibit obvious anomalies until 1998. In general, the diapause stock observed in the Gulf of Maine deep basins during autumn 1997 was not remarkable, although the abundance of diapausing copepodites in Jordan Basin was high (See Figure 5 in MERCINA, 2003). The spring bloom was delayed in the northern Gulf of Maine and on the Western Scotian Shelf during early 1998 (Figure 2), but *C. finmarchicus* population growth on Georges Bank appeared strong and was not delayed by food limitation, with the population reaching high numbers of copepodites throughout the spring (Figure 3). In contrast, as 1998 progressed, currently unresolved regional processes led to the formation of a very small autumn diapause stock in the Gulf of Maine deep basins (see Figure 5 in MERCINA, 2003). It is possible that the poor early-season growth conditions for phytoplankton on the Western Scotian Shelf may have impacted *C. finmarchicus*' population growth rates in this important source region. It is also possible that the extension of LSSW down the continental margin effectively blocked the advective supply of *C. finmarchicus* from the Slope Waters to the upstream population on the Scotian Shelf and/or to the Gulf of Maine directly through the Northeast Channel. In either case, we hypothesize that poor recruitment from upstream sources led to a late-season decline in the Gulf of Maine *C. finmarchicus* population. Without a good supply source, this population produced an autumn diapause stock an order of magnitude lower in abundance than the climatological mean (See Figure 5 in MERCINA, 2003).

In contrast to 1998, the phytoplankton bloomed early in the Gulf of Maine during winter 1999 (Figure 2). Hence, the conditions for growth and egg production by *C. finmarchicus* were unusually good in the Gulf of Maine during that winter (Durbin et al., 2003). As a consequence, even though the supply of G_0 animals recruiting to Georges Bank during winter 1999 was the lowest observed during the U.S. GLOBEC Northwest Atlantic Field Study, the spring and early summer abundances of G_1 copepodites were at levels consistent with the typical or climatological seasonal cycle (Figure 3). This return to more typical conditions was also reflected in the diapause stock observed during autumn 1999 (See Figure 5 in MERCINA, 2003).

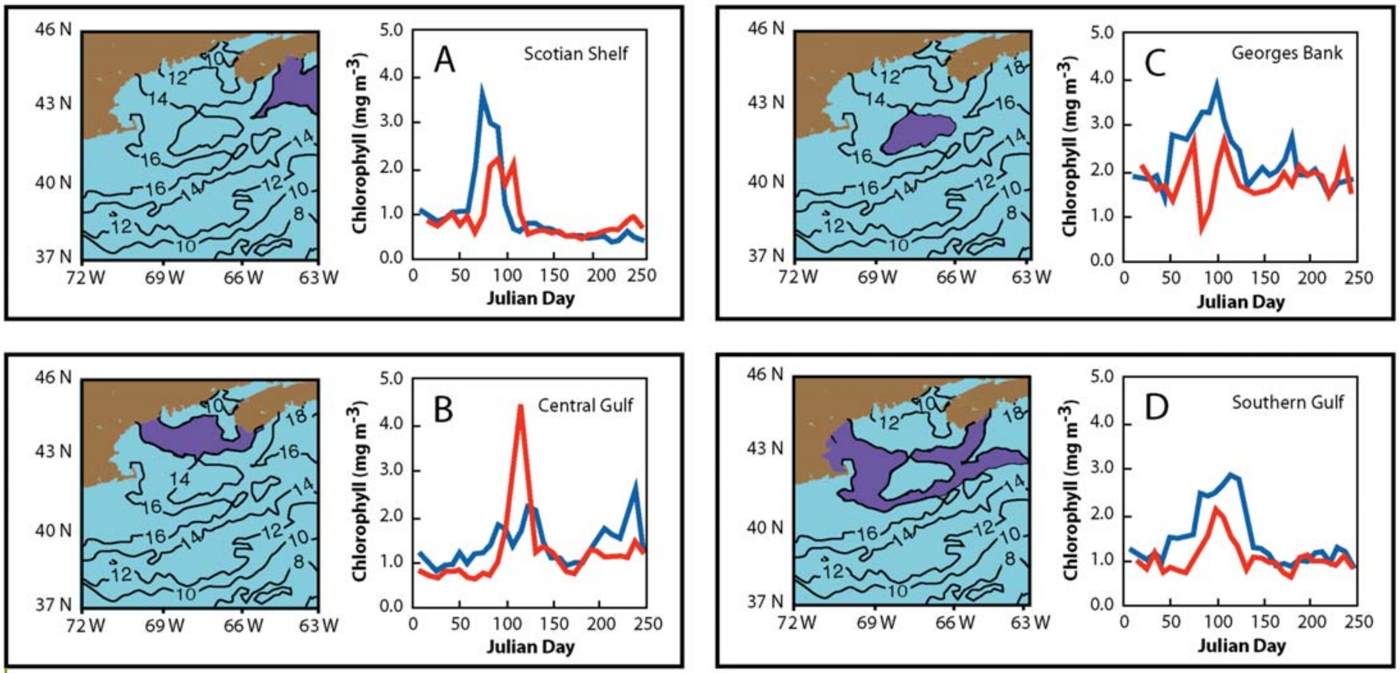


Figure 2. Large interannual differences in the seasonal cycles of chlorophyll concentration were observed during 1998 (red lines) and 1999 (blue lines) in four subregions of the Northwest Atlantic: (A) the southwestern Scotian Shelf, (B) the central Gulf of Maine, (C) Georges Bank, and (D) the southern Gulf of Maine and deep waters adjacent to Georges Bank. For each subregion (shaded on each map in purple), the chlorophyll time series are derived from spatial averages of Sea-viewing Wide Field-of-View Sensor data (SeaWIFS 4th reprocessing data set distributed by NASA's Goddard Space Flight Center Earth Sciences Distributed Active Archive Center). Subregions are based on similarity in the amplitude of seasonal change in sea-surface temperature (SST) as determined from analysis of Advanced Very High-Resolution Radiometer climatology data (AVHRR Pathfinder data set distributed by the NASA Jet Propulsion Laboratory's Physical Oceanography Distributed Active Archive Center). The analysis involves computing the amplitude of seasonal change in SST at each pixel location and then contouring the result at 2-degree intervals. Individual subregions are bound by the 2-degree contour intervals shown on each map.

RETROSPECTIVE ANALYSIS: PROVIDING A CLIMATOLOGICAL CONTEXT FOR OBSERVATIONS FROM THE U.S. GLOBEC NW ATLANTIC FIELD STUDY

The oceanographic events observed in the Gulf of Maine/Georges Bank region during the late 1990s provide circumstantial evidence linking interannual variability in *C. finmarchicus* abundance to NAO-associated modal shifts in the CSWS. To generalize from these observations, we now place them in the context of time-series data collected over the past half century. Analyses of time series for three indices, the NAO Index (Hurrell, 1995), the Regional Slope Water Temperature (RSWT) Index (MERCINA, 2001), and the *C. finmarchicus* Abundance Index (MERCINA, 2001, 2003), provide valuable insights into the physical-biological coupling regulating the regional abundance of *C. finmarchicus* on interannual to interdecadal time scales (Figure 4).

From 1950 to 2000, the NAO Index and RSWT Index exhibited considerable interannual variability (Figure 4a, b). Against this background of interannual variability in the time series, two long-term patterns are apparent. During the decade of the 1960s, the NAO Index was in a predominantly negative phase, and the RSWT Index exhibited conditions characteristic of the CSWS's minimum modal state (Loder et al., 2001; MERCINA, 2001). From the early 1970s to the present, the NAO Index has been predominantly positive (Hurrell et al., 2003), and the RSWT Index typically has exhibited conditions characteristic of the CSWS's maximum modal state (Loder et al., 2001; MERCINA, 2001). Five times during these last three decades (1977, 1979, 1985, 1987, 1996), the NAO Index has dropped to negative values for a single year. In each case, the CSWS appears to have responded to a drop in the NAO Index by shifting toward its minimum modal state after a one- to two-year time lag (1978, 1981, 1987, 1989, 1998). While the first two apparent responses of the CSWS, in 1978 and 1981, were relatively small, the latter responses were more substantial. The apparent response to the 1985 and 1987 drops in the NAO Index involved a multi-year modal shift lasting from 1987 to 1990. The apparent response to the 1996 drop in the NAO Index was the largest since the 1960s and the best-documented modal shift to date (MERCINA, 2001; Greene and Pershing, 2003).

The above time-series observations support the view that phase reversals in the NAO are capable of forcing modal shifts in the CSWS on interannual to interdecadal time scales. If this is indeed the case, then it is reasonable to ask whether or not the *C. finmarchicus* population in the Gulf of Maine/Georges Bank region responds as expected to these modal shifts on comparable time scales (Figure 4c). During the 1960s, when the NAO Index was predominantly negative and the CSWS was in its minimum modal state, slope water temperatures and *C. finmarchicus* abundance were relatively low (Greene and Pershing, 2000; Conversi et al., 2001; MERCINA, 2001, 2003; Pershing et al., 2004). Dur-

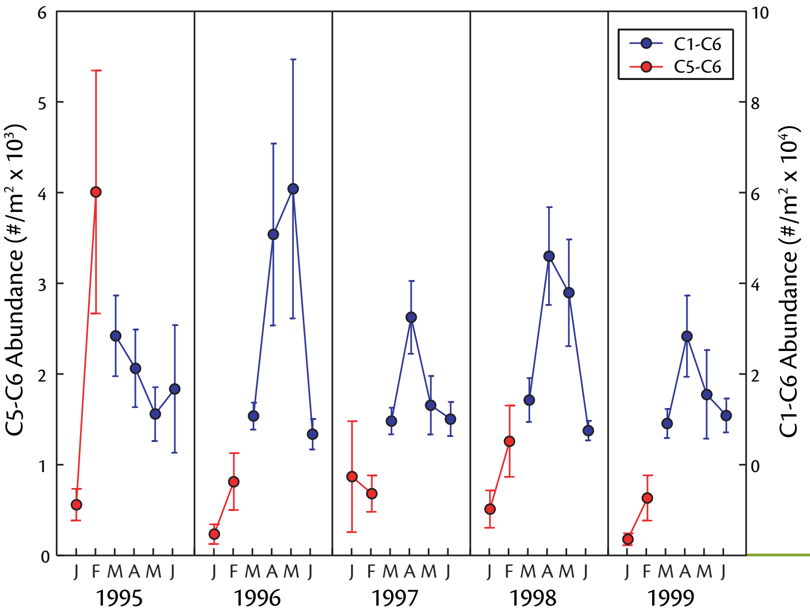


Figure 3. Interannual differences in the mean abundances of *C. finmarchicus* copepodites observed on Georges Bank from 1995-1999 as determined from the U.S. GLOBEC Northwest Atlantic/Georges Bank Broad-Scale Sampling Program. This broad-scale sampling program included Multiple-Opening Closing Net and Environmental Sensing System tows from approximately 40 stations spread relatively uniformly over Georges Bank and its surrounding waters (McGillicuddy et al., 2001). Copepodite five and six (C5-C6) abundances are shown for January and February in red. These are principally G_0 animals that grew up the previous year and subsequently emerged from diapause. Copepodite one through six (C1-C6) abundances are shown for March through June in blue. These are principally G_1 and G_2 animals that grew up in the specified year. Bars through circles correspond to 95 percent confidence intervals.

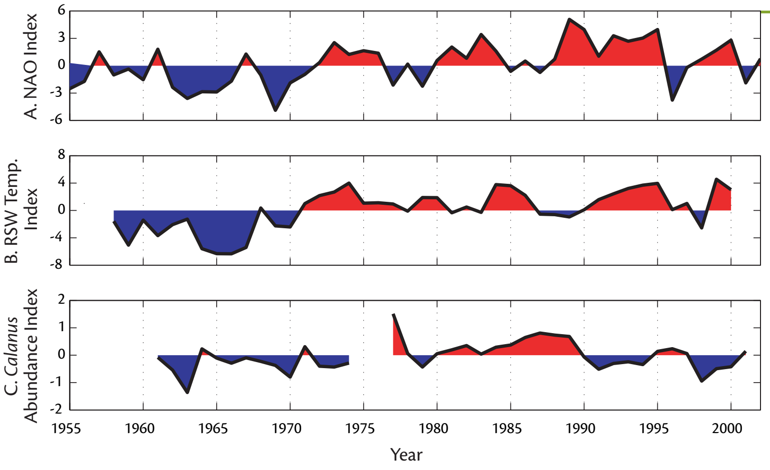


Figure 4. Considerable interannual variability was observed in the time series of A.) the NAO Index, B.) the RSWT Index, and C.) the *C. finmarchicus* Abundance Index. The NAO Index is the mean difference, expressed as an anomaly from the long-term mean, in atmospheric pressure during winter between the North Atlantic's subtropical high-pressure system, measured in Lisbon, Portugal, and the subpolar low pressure system, measured in Stykkisholmur, Iceland (Hurrell, 1995). The RSWT Index is the dominant mode derived from a principal components analysis of eight slope-water temperature-anomaly time series from the Gulf of Maine and Western Scotian Shelf (MERCINA, 2001). It was introduced as an indicator of the modal state of the CSWS, with positive values of the index corresponding to maximum modal state conditions and negative values corresponding to minimum modal state conditions. The *C. finmarchicus* Abundance Index is the mean annual abundance anomaly for late copepodites and adults of this species calculated each year as the mean difference between log-transformed observed abundances and log-transformed expected abundances (MERCINA, 2001). It is derived from Continuous Plankton Recorder survey data that have been collected from the Gulf of Maine since 1961 (Jossi and Goulet, 1993).

ing the 1980s, when the NAO Index was predominantly positive and the CSWS was predominantly in its maximum modal state, slope water temperatures and *C. finmarchicus* abundance were relatively high (Greene and Pershing, 2000; Conversi et al., 2001; MERCINA, 2001, 2003; Pershing et al., 2004). During each of the maximum to minimum modal shifts in the CSWS after 1980, *C. finmarchicus* abundance declined in subsequent years. The modal shift during 1981-1983 preceded a large, single-year decline in abundance during 1983. The modal shift during 1988-1991 preceded a large decline in abundance that persisted throughout the early 1990s. Then, after *C. finmarchicus* abundance began building up again during the mid-1990s, the NAO Index underwent its drop of the century during 1996. This event triggered the intense modal shift of the CSWS over the next two years, which, in turn, led to the very low abundance of *C. finmarchicus* observed during 1998 and early 1999 (MERCINA, 2001, 2003; Pershing et al., 2004).

Once consistent patterns were identified qualitatively, cross-correlation analyses were conducted to look for statistical relationships among the three time series. The cross correlation between the NAO Index and *C. finmarchicus* Abundance Index time series was found to be statistically significant from 1961-1989, but became non-significant when data from the 1990s were included (MERCINA, 2003). Even if we exclude data from the latter part of the 1990s, when the NAO exhibited particularly unusual behavior (Hurrell and Dickson, 2004), any simple statistical relationship between the two time series is weak at best. The lack of a simple statistical relationship, however, should not be interpreted as evidence for little or no relationship between the NAO and *C. finmarchicus* abundance in the Gulf of Maine/Georges Bank region. Rather, it reflects the complex dynamics linking NAO forcing to the regional abundance of *C. finmarchicus*. The effects of the NAO on this species' population dynamics are mediated by the CSWS, a complex circulation system involving several shallow-, intermediate-, and deep-water masses (Pickart et al., 1999). The RSWT Index is a proxy for the state of the CSWS, and its time series exhibits a significant positive cross correlation with the NAO Index time series (MERCINA, 2001). The cross correlation between the two time series is strongest with a lag of one year ($r^2 = 0.31$); however, this lag has been interpreted as variable and ranging from one to two years (Box 2 in MERCINA, 2001). The RSWT Index time series also exhibits a significant positive cross correlation with the *C. finmarchicus* Abundance Index time series (MERCINA, 2001). The cross correlation between these two time series is strongest with a lag of three years ($r^2 = 0.25$); however, this lag has been interpreted as centered on three years, but variable and ranging from two to four years (Box 2 in MERCINA, 2001). We suggest that the failure to detect a simple statistical relationship between the NAO Index and *C. finmarchicus* Abundance Index time series is due in large part to the variable time lags found in the chain of events linking *C. finmarchicus* abundance in the Gulf of Maine/Georges Bank region to NAO forcing. Furthermore, the simple correlation-based analyses we have conducted cannot capture the nonlinearities associated with the Northwest Atlantic's physical and biological responses to phase reversals in the NAO (MERCINA, 2001, 2003). While each of these factors contributes to the overall complexity underlying *C. finmarchicus*' regional population responses to NAO forcing, the mechanisms linking this species' population dynamics to climate-driven changes in ocean and atmospheric circulation patterns are beginning to emerge (MERCINA, 2001, 2003; Pershing et al., 2004). Due to the time lags involved, an improved understanding of these mechanisms should lead to the development of predictive models capable of forecasting climate-driven changes in *C. finmarchicus* abundance one to several years in advance.

SUPPLY-SIDE ECOLOGY AND TRANS-ATLANTIC STUDIES OF *CALANUS FINMARCHICUS*

Supply-side ecology is a phrase introduced over 15 years ago (Lewin, 1986) to characterize an emerging concept in the marine ecological literature—that the external supply of recruits can be at least as important as local processes in regulating the dynamics of a metapopulation (Hanski, 1998). Although this concept emerged from studies of marine benthic populations, it is equally applicable to marine holoplanktonic populations. The dynamics of planktonic metapopulations are determined by local processes affecting birth, growth, and mortality rates and by external processes affecting rates of advective supply and loss. Determining the relative importance of local versus external processes is central to establishing the relevance of the supply-side concept to a particular species' population ecology.

The population ecology of *C. finmarchicus* has been studied extensively in shelf ecosystems on both sides of the North Atlantic, with a rich history of modeling studies focused on Georges

Bank and North Sea populations dating back to the late 1940s (e.g., Riley, 1947; Steele, 1974; Steele and Frost, 1977; Davis, 1987b; Carlotti, 1996). Emphasizing local biological processes linking birth, growth, and mortality rates of *C. finmarchicus* to the abundances of its prey and predators, the increasingly sophisticated models used in these studies have captured many of the essential features observed in both phytoplankton and zooplankton seasonal cycles. As satisfying as the results from these modeling studies have been in simulating the seasonal cycles of plankton, they have been of limited value in revealing the sources of interannual to interdecadal variability observed in shelf populations of *C. finmarchicus*.

Using data from the North Sea, Colebrook (1986) was the first to provide evidence that interannual variability in shelf populations of *C. finmarchicus* can be linked to the supply of animals recruiting each spring from winter diapause stocks. The main source of recruits to the North Sea shelf population is the stock of diapausing late copepodites found in the oceanic waters of the Faroe-Shetland Channel (Heath et al., 1999). Analyses of time-series data have shown that year-to-year fluctuations in the abundance of *C. finmarchicus* in the North Sea are negatively correlated with the NAO Index (Planque and Reid, 1998; MERCINA, 2003). The current interpretation of this negative correlation is as follows. During positive NAO years, an increased inflow of warm oceanic upper-layer water from the North Atlantic tends to transport fewer *C. finmarchicus* into the North Sea, thereby reducing the species' on-shelf recruitment (Reid et al., 2001, 2003). In addition, the warmer conditions during such years are hypothesized to provide a less favorable environment for growth and reproduction of this cold-water boreal species (Fromentin and Planque, 1996). In contrast, during negative NAO years, an increased inflow of cooler deepwater from the Norwegian Sea into the North Sea tends to transport more *C. finmarchicus* onto the shelf (Reid et al., 2001, 2003), and the cooler conditions are hypothesized to be more favorable for growth and reproduction (Fromentin and Planque, 1996).

The negative correlation between the NAO Index and abundance of *C. finmarchicus* in the North Sea is the result of diverging trends in the two time series since the 1960s as well as negatively correlated, year-to-year fluctuations in the detrended time series of both variables (MERCINA, 2003). For over three decades, as the NAO Index time series has exhibited a trend towards persistently positive conditions, the North Sea *C. finmarchicus* population has steeply declined in abundance (Planque and Reid, 1998). Two NAO-associated physical mechanisms, each operating on different time scales, have been hypothesized to account for this steep negative trend in *C. finmarchicus* abundance (MERCINA, 2003). The first of these mechanisms involves the year-to-year fluctuations in advective transport of *C. finmarchicus* into the North Sea as described above. With the increasing frequency of positive NAO years, one would expect a corresponding reduction in the number of good recruitment years for *C. finmarchicus* as its advective supply into the North Sea is inhibited (MERCINA, 2003). This interpretation, however, does not appear sufficient to fully explain the overall decline observed in *C. finmarchicus* abundance. Heath et al. (1999) have hypothesized that physical processes operating on a longer, interdecadal time scale also play an important role. Since the middle of the 20th century, the production and transport of Norwegian Sea Deep Water has steadily declined, leading to a reduced flux of this water mass across the Iceland-Scotland Ridge and through the Faroe-Shetland Channel (Hansen et al., 2001). This multi-decadal change in deep-water circulation has been hypothesized to reduce the supply of diapausing late copepodites in the Faroe-Shetland Channel available for subsequent recruitment into the North Sea (Heath et al., 1999). Both of these supply-side hypotheses provide reasonable explanations for the strong negative correlation between *C. finmarchicus*' abundance in the North Sea and the NAO Index as well as the species' general decline in abundance observed there since the early 1970s.

When comparing these findings from the North Sea with those reported earlier in this paper from the Gulf of Maine/Georges Bank region, striking differences as well as similarities become apparent in the population ecology of *C. finmarchicus* on both sides of the North Atlantic. The most obvious difference can be found in the regional dependence of this species' population responses to basin-scale NAO forcing. Whereas the *C. finmarchicus* population in the North Sea exhibits a negative correlation with the NAO Index, populations in the Gulf of Maine and on Georges Bank exhibit a more complex, positive association with the index (Greene and Pershing, 2000; MERCINA, 2003). Since ocean-circulation responses to the NAO vary in different regions of the North Atlantic, it is not too surprising that the population responses of *C. finmarchicus* vary by region as well. Perhaps more surprising, however, are the similarities in processes that underlie these regional differences in population responses. In the North Sea as well as the Gulf of Maine/Georges Bank region, shelf populations of *C. finmarchicus* are dependent on the advective supply of recruits from external oceanic sources. This supply of external recruits is not only important to the long-term persistence of these shelf populations, but also central to their dynamics on seasonal to interdecadal time scales. While recruitment details such as the mode of supply (e.g., pulsed versus continuous recruitment) and number of sources (e.g., single versus multiple sources of recruits) may vary among ecosystems, supply-side ecology clearly provides a unifying conceptual framework for studying the trans-Atlantic population dynamics of *C. finmarchicus*, especially the species' responses to changes in climate.

One obvious consequence of adopting this new conceptual framework is that future field and modeling studies must do a better job of accounting for advective exchanges between neighboring metapopulations of *C. finmarchicus*. For example, any follow-up to the U.S. GLOBEC Northwest Atlantic Field Study must, at a minimum, attempt to quantify the fluxes of *C. finmarchicus* not only between the Gulf of Maine and Georges Bank, but also among these ecosystems and the Scotian Shelf and adjacent slope waters. In both conceptual and mathematical models, we must gradually begin to build a basin-wide view of this species' North Atlantic distribution as a network of metapopulations, each with its own unique internal dynamics and unique interactions with neighboring metapopulations (e.g., see Zakardjian et al., 2003). Until these more sophisticated models become more common, simple models of the type introduced by Aksnes and Blindheim (1996) can be used to scale the key physical and biological processes, thereby enabling one to quantitatively assess the relative importance of local versus advective exchange processes. For example, while advective exchange processes appear to play a central role in the dynamics of metapopulations inhabiting relatively small shelf ecosystems, such as those discussed in this paper, local processes begin to dominate the dynamics of metapopulations as ecosystem size increases in oceanic regions (Aksnes and Blindheim, 1996). Our ultimate goal should be to understand how each metapopulation in the network functions and how each contributes to the basin-wide population ecology of *C. finmarchicus*.

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REFERENCES

Aksnes, D.L., and J. Blinheim. 1996. Circulation patterns in the North Atlantic and possible impact on population dynamics of *Calanus finmarchicus*. *Ophelia* 44:7-28.

Bigelow, H.B. 1926. Plankton of the offshore waters of the Gulf of Maine. *Bull. US Bur. Fish.* 40:127-142.

Bisagni, J.J., R.C. Beardsley, C.M. Ruhsam, J.P. Manning and W. Williams. 1996. Historical and recent evidence of Scotian Shelf Water on southern Georges Bank. *Deep-Sea Res. II* 43:1439-1471.

Campbell, R.G., J.A. Runge, and E.G. Durbin. 2001. Evidence of food limitation of *Calanus finmarchicus* production rates on the southern flank of Georges Bank during April 1997. *Deep-Sea Res. II* 48:531-549.

Carlotti, F. 1996. A realistic physical-biological model for *Calanus finmarchicus* in the North Atlantic. A conceptual approach. *Ophelia* 44:47-58.

Colebrook, J.M. 1986. Environmental influences on long-term variability in marine plankton. *Hydrobiologia* 142:309-325.

Conover. R.J. 1988. Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the northern hemisphere. *Hydrobiologia* 167/168: 127-142.

Conversi, A., S. Piontkovski, and S. Hameed. 2001. Seasonal and interannual dynamics of *Calanus finmarchicus* in the Gulf of Maine (Northeastern U.S. shelf) with reference to the North Atlantic Oscillation. *Deep-Sea Res. II* 48:519-530.

Davis, C.B. 1987a. Zooplankton life cycles. In: *Georges Bank*. R.H. Backus and D.W. Bourne, eds. Massachusetts Institute of Technology Press, Cambridge, MA, pp. 256-267.

Davis, C.B. 1987b. Components of the zooplankton production cycle in the temperate ocean. *J. Marine Res.* 45:947-983.

Durbin, E.G., A.G. Durbin, and R.C. Beardsley. 1995a. Springtime nutrient and chlorophyll concentrations in the southwestern Gulf of Maine. *Cont. Shelf Res.* 15:433-450.

Durbin, E.G., R.G. Campbell, S.L. Gilman, and A.G. Durbin. 1995b. Diel feeding behavior and ingestion rate in the copepod *Calanus finmarchicus* in the southern Gulf of Maine during late spring. *Cont. Shelf Res.* 15:539-570.

Durbin, E.G., J.A. Runge, J.A., R.G. Campbell, P.R. Garrahan, M.C. Casas, and S. Plourde. 1997. Late fall-early winter recruitment of *Calanus finmarchicus* on Georges Bank. *Mar. Ecol. Prog. Ser.* 151:103-114.

Durbin, E.G, P.R. Garrahan, and M.C. Casas. 2000. Abundance and distribution of *Calanus finmarchicus* on the Georges Bank during 1995 and 1996. *ICES J. Mar. Sci.* 57:1664-1685.

Durbin, E.G., R.G. Campbell, M.C. Casas, M.O. Ohman, B. Niehoff, J. Runge, and M. Wagner. 2003. Interannual variation in phytoplankton blooms and zooplankton productivity and abundance in the Gulf of Maine during winter. *Mar. Ecol. Prog. Ser.* 254: 81-100.

Fromentin, J.-M., and B. Planque. 1996. *Calanus* and environment in the eastern North Atlantic. II. Influence of the North Atlantic Oscillation on *C.*

finmarchicus and *C. helgolandicus*. *Mar. Ecol. Prog. Ser.* 134:111-118.

Global Ocean Ecosystem Dynamics (GLOBEC). 1991. *GLOBEC: Northwest Atlantic Program*. No. 2. Joint Oceanographic Institutions, Inc, Washington, DC.

Greene, C.H., and A.J. Pershing. 2000. The response of *Calanus finmarchicus* populations to climate variability in the Northwest Atlantic: Basin-scale forcing associated with the North Atlantic Oscillation. *ICES J. Mar. Sci.* 57:1536-1544.

Greene, C.H., and A.J. Pershing. 2003. The flip-side of the North Atlantic Oscillation and modal shifts in slope-water circulation patterns. *Limnol. Oceanogr.* 48:319-322.

Hannah, C.G., C.E. Naime, J.W. Loder, and F.E. Werner. 1998. Upper-ocean transport mechanisms from the Gulf of Maine to Georges Bank, with implications for *Calanus* supply. *Cont. Shelf Res.* 17:1887-1911.

Hansen, B., W.R Turrell, and S. Osterhus. 2001. Decreasing overflow from the Nordic seas into the Atlantic Ocean through the Faeroe Bank channel since 1950. *Nature* 411:927-930.

Hanski, I. 1998. Metapopulation dynamics. *Nature* 396:41-49.

Heath, M.R., J.O. Backhaus, K. Richardson, E. McKenzie, D. Slagstad, D. Beare, J. Dunni, J.G. Fraser, A. Gellego, D. Hainbucher, and S. Hay. 1999. Climate fluctuations and the spring invasion of the North Sea by *Calanus finmarchicus. Fish. Oceanogr*. 8:163-176.

Hirche, H.-J. 1996. Diapause in the marine copepod, *Calanus finmarchicus*: A review. *Ophelia* 44:129-143.

Hurrell, J.W. 1995. Decadal trends in the North Atlantic Oscillation: Regional temperatures and precipitation. *Science* 269:676-679.

Hurrell, J.W., Y. Kushnir, G. Ottersen, and M. Visbeck. 2003. An overview of the North Atlantic Oscillation. In: *The North Atlantic Oscillation: Climatic Significance and Environmental Impact.* J.W. Hurrell, Y. Kushnir, G. Ottersen, and M. Visbeck, eds. American Geophysical Union, Washington, DC, pp. 1-35.

Hurrell, J.W., and R.R. Dickson. 2004. Climate variability over the North Atlantic. In: *Ecological Effects of Climate Variations in the North Atlantic*. Stenseth, N.C., G. Ottersen, J.W. Hurrell, and A. Belgrano, eds. Oxford University Press, Oxford, UK, pp. 15-31.

Jossi, J.W., and J.R. Goulet, Jr. 1993. Zooplankton trends: U.S. north-east shelf ecosystem and adjacent regions differ from north-east Atlantic and North Sea. *ICES J. Mar. Sci.* 50:303-313.

Keigwin, L.D., and R.S. Pickart. 2000. Slope water current over the Laurentian Fan on interannual to millennial time scales. *Science* 286:520-523.

Lewin, R. 1986. Supply-side ecology. *Science* 234:25-27.

Loder, J.W, J.A. Shore, C.G. Hannah, and B.D. Petrie. 2001. Decadal-scale hydrographic and circulation variability in the Scotia-Maine region. *Deep-Sea Res. II* 48:3-35.

Lynch, D.R., W.C. Gentleman, D.G. McGillicuddy, Jr., and C.S. Davis. 1998. Biophysical simulations of *Calanus finmarchicus* population dynamics in the Gulf of Maine. *Mar. Ecol. Prog. Ser.* 169:189-210.

Madin, L.P., S.M. Bollens, E. Horigan, M. Butler, J. Runge, B.K. Sullivan, G. Klein-MacPhee, E. Durbin, A. Durbin, D. Van Keuren, S. Plourde, A. Bucklin, and M. Clark. 1996. Voracious planktonic hydroids: unexpected predatory impact on a coastal marine ecosystem. *Deep-Sea Res. II* 43:1823-1829.

Marine Ecosystem Responses to Climate in the North Atlantic (MERCINA). 2001. Oceanographic responses to climate in the Northwest Atlantic. *Oceanogr*. 14 (3):76-82.

Marine Ecosystem Responses to Climate in the North Atlantic (MERCINA). 2003. Trans-Atlantic responses of *Calanus finmarchicus* populations to basin-scale forcing associated with the North Atlantic Oscillation. *Progr. Oceanogr*. 58:301-312.

Mauchline, J. 1998. *The Biology of Calanoid Copepods.* Academic Press, San Diego, CA.

McGillicuddy, D.J., D.R. Lynch, P. Wiebe, J. Runge, E.G. Durbin, W.C. Gentleman, and C.S. Davis. 2001. Evaluating the synopticity of the U.S. GLOBEC Georges Bank broad-scale sampling pattern with observational system simulation experiments. *Deep-Sea Res. II* 48:483-499.

Meise, C.J., and J.E. O'Reilly. 1996. Spatial and seasonal patterns in abundance and age composition of *Calanus finmarchicus* in the Gulf of Maine and on Georges Bank 1977-1987. *Deep Sea Res. II* 43:1473-1501.

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

Miller, C.B., D.R. Lynch, F. Carlotti, W.C. Gentleman, and C.V.W. Lewis. 1998. Coupling of an individual-based population dynamic model of *Calanus finmarchicus* to a circulation model for the Georges Bank region. *Fish. Oceanogr*. 7:219-234.

Miller, C.B., J.A. Crain, and C.A. Morgan. 2000. Oil storage variability in *Calanus finmarchicus*. *ICES J. Mar. Sci.* 57:1786-1800.

Pershing, A.J., C.H. Greene, B. Planque, and J.-M. Fromentin, 2004. The influence of climate variability on North Atlantic zooplankton populations. In: *Ecological Effects of Climatic Variations in the North Atlantic.* N.C. Stenseth, G. Ottersen, J.W. Hurrell, and A. Belgrano, eds. Oxford University Press, Oxford, pp. 59-69.

Pickart, R.S., T.K. McKee, D.J. Torres, and S.A. Harrington. 1999. Mean structure and interannual variability of the slopewater system south of Newfoundland. *J. Phys. Oceanogr*. 29:2541-2558.

Planque, B., and P.C. Reid. 1998. Predicting *Calanus finmarchicus* abundance from a climatic signal. *J. Mar. Biol. Assoc*. (UK) 78:1015-1018.

Reid, P.C., M.D. Borges, and E. Svedsen. 2001. A regime shift in the North Sea circa 1988 linked to changes in the North Sea fishery. *Fish. Res.* 50:163-171.

Reid, P.C., M. Edwards, G. Beauregard, M. Skogen, and D. Stevens. 2003. Periodic changes in the zooplankton of the North Sea during the twentieth century linked to oceanic inflow. *Fish. Oceanogr*. 12:260-269.

Riley, G.A. 1947. A theoretical analysis of the zooplankton population on Georges Bank. *J. Mar. Res.* 6:104-113.

Sell, A.F., D. Van Keuren, and L.P. Madin. 2001. Predation by omnivorous copepods on early developmental stages of *Calanus finmarchicus* and *Pseudocalanus* sp. *Limnol. Oceanogr.* 46:953-959.

Sherman, K. 1980. MARMAP, a fisheries ecosystem study of the Northwest Atlantic fluctuations in icthyoplankton-zooplankton components and their potential for impact on the system. In: *Advanced Concepts for Ocean Measurements for Marine Biology.* F.P. Diemer, F.J. Vernberg, and D.Z. Mirkes, eds. University of South Carolina Press. Charleston, SC, pp. 3-37.

Sherman, K., W.G. Smith, J.R. Green, E. Cohen, M.S. Berman, K.A. Marti, and J.R. Goulet. 1987. Zooplankton production and fisheries of the northeastern shelf. In: *Georges Bank.* R.H. Backus, and D.W. Bourne, eds. Massachusetts Institute of Technology Press, Cambridge, MA, pp. 268-282.

Smith, P.C, 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.

Steele, J.H. 1974. *Structure of Marine Ecosystems*. Harvard University Press, Cambridge, MA.

Steele. J.H., and B.W. Frost. 1977. The structure of plankton communities. *Phil. Trans. Roy. Soc*. London 280 (Series B):485-534.

Sullivan, B.K., and C.J. Meise. 1996. Invertebrate predators of zooplankton on Georges Bank, 1977-1987. *Deep-Sea Res. II* 43:1503-1519.

Wiebe, P., R. Beardsley, D. Mountain, and A. Bucklin. 2002. U.S. GLOBEC Northwest Atlantic/Georges Bank Program. *Oceanogr*. 15:13-29.

Zakardjian, B.A., 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.* 180(C11):8016, doi:10. 1029/2002JC001410.